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

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66 **1. Introduction**

67 A growing human population has resulted in growing levels of urban development, significantly modifying natural
68 landscapes. Urbanization is associated with a deep restructuring of abiotic parameters, such as temperature or
69 light/noise/chemical pollution, as well as the modification of biotic parameters, such as low vegetation cover or
70 changes in fauna/flora, species interactions, or human density (Gil and Brumm, 2013). These rapid environmental
71 changes have direct consequences on the demography of many species, particularly birds, due to the impact of the
72 environment on the reproductive success of individuals (Chamberlain et al., 2009; Shochat et al., 2015b).
73 Numerous factors can influence the reproductive success of urban birds. Urban habitats are considered to be of
74 lower quality compared to rural habitats (Bailly et al., 2016; Kempnaers et al., 2010; Meillère et al., 2015a;
75 Schroeder et al., 2012). Modifications of photoperiod and local increase of temperatures due to anthropogenic
76 structures often lead to advance the phenology of urban birds which can result to mismatch between prey
77 phenology and young rearing (Chamberlain et al. 2009). Moreover, urban habitat also offer a lower prey
78 availability due to the poorer invertebrate density associated with a reduced vegetal cover (Fenoglio et al., 2020).
79 Some studies have pointed out that urban food is also of lower nutritional quality, such as lower antioxidant
80 contents (Isaksson and Andersson, 2007), which can lead to nutritional deficiencies (Bailly et al., 2017). A lower
81 quality and quantity of prey leads to a reduction of clutch size (Wawrzyniak et al., 2015) but also to a poorer
82 physical condition of nestlings (Bailly et al., 2017; Meillère et al., 2015a) and lower fledging rates. Poor
83 reproductive success and low rates of nestling survival are also correlated with increasing chemical component
84 exposure as a result of increasingly intense anthropogenic activities. Numerous studies have found that pollutants,
85 such as polycyclic aromatic hydrocarbons (PAHs, whose emissions are associated with road traffic) or
86 polychlorinated biphenyl (PCB), can affect egg production and egg quality, leading to higher rates of hatching
87 failure (higher embryonic mortality and development abnormalities, Albers, 2006; Kimberly J. Fernie, 2000; Vos,
88 1972) Similarly, some metals, such as cadmium (Cd) and lead (Pb), whose emissions may be linked to industrial
89 activities, can interfere with calcium metabolism, leading to thinner eggshells (Eeva and Lehikoinen, 1995;
90 Scheuhammer, 1996) but also to osteogenesis abnormalities (Eeva and Lehikoinen, 1996b; Goyer, 1997) or
91 oxidative stress responses during the growth of nestlings which can jeopardize fledging success (Berglund et al.
92 2007; Chatelain et al. 2021b).

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

106 One hypothesis for this inter-annual variability is the variation in weather parameters. In fact, the reproductive
107 success of birds is dependent on weather conditions and, nestling survival and fledging rate in passerine birds are
108 often negatively correlated with rainfall and cold temperatures (Cox et al., 2019; Öberg et al., 2015). Low
109 temperatures impose thermal challenge for nestlings which must allocate more energy in thermoregulation at the
110 expense of growth and self-maintenance leading to physiological cost as growth delay (Yahav 2002; Krijgsveld et
111 al. 2003; Dawson et al. 2005) or altered immune functions (Ardia et al. 2010). Harsh condition also increase
112 reproductive cost for parents notably to maintain the brood to optimal temperature reducing the time for self-
113 maintenance and foraging (Amininasab et al. 2016). Moreover, low temperatures lead to a decline in invertebrates
114 due to emergence delay (Buse et al., 1999), while rain spells increase the difficulty of catching them (Avery and
115 Krebs, 2008; Dawson and Bortolotti, 2000) and increase the foraging energy expenditure under harsh weather
116 conditions (Cox et al., 2019; Dawson et al., 2005). Similarly high temperatures can also have detrimental effect
117 on nestling growth and survival (Cunningham et al. 2013; Salaberria et al. 2014). Moreover, the presence of
118 mineral surfaces as concrete or asphalt lead to an increase of local temperatures in cities also called urban heat
119 island, which could represent a thermal challenge for urban birds compared to forest birds, especially during heat
120 waves (but see Pipoly et al. 2022). Weather conditions can also amplify or limit the exposure to chemical
121 pollutants. For example, a lack of wind can lead to the stagnation of aerial chemical pollutants (Liu et al., 2015),
122 while heavy precipitation can lead to pollutants being washed off inert urban surfaces (e.g. roads and roofs) and
123 being more easily mobilized in ecosystems (review by Gosset et al. 2016, Shinya et al. 2003). Similarly, weather
124 conditions can also enhance the negative effects of chemical compounds. For example, in tree swallows, unusually
125 high seasonal temperatures have been found to lead to lower reproductive success at mercury-polluted nesting
126 sites, while the number of nestlings at the control sites increased with increasing seasonal temperatures (Hallinger
127 and Cristol, 2011). Similarly, a reduction in the surface tension of feathers due to contamination with organic
128 pollutants can increase the permeability of feathers to water while decreasing their insulating properties, which
129 induces additional physiological requirements for thermoregulation during cold weather events (Stephenson,
130 1997). Since invertebrate communities and food availability are already poor in cities (Fenioglio et al. 2020), in
131 addition to having higher levels of pollutant, unfavorable weather conditions could potentially increase urban
132 stress, leading to a more deleterious effect on the reproductive success in cities than in rural or forest habitats.
133 However, it is also possible that environmental constraints in urban areas are so strong that weather parameters
134 only have a moderate effect on reproductive parameters compared to other factors, such as in house sparrows,
135 where reproductive success was found to be consistently lower in cities, even between years with contrasting
136 weather conditions (Seress et al., 2012).

137 The first aim of this study was to measure the reproductive success (measured as hatching date, clutch size,
138 hatching rate, nestling number before fledge and fledging rate) of great tits in urban and forest habitats and to
139 characterize each site in terms of pollution and food availability. Secondly, this study aimed to determine weather
140 variations during the breeding period between years and to test if it affects the reproductive success depending on
141 breeding sites. For this purpose, we followed two different populations of great tits over four years in a city
142 (Strasbourg, France) and a forest (La Wantzenau forest, 20km away of Strasbourg city center). The great tit is
143 considered an urban adapter and has been the subject of numerous studies concerning the impact of urban
144 environmental factors on population dynamics (Wawrzyniak et al., 2020, Biard et al. 2017, Caizergues et al. 2021).
145 To characterize the habitat at each site, we evaluated vegetal cover, prey availability, and pollution. For this last

146 parameter, we measured different polychlorinated biphenyls, polycyclic aromatic hydrocarbons, and pesticides in
147 the air, and trace metal elements in leaves, prey, and the feathers of birds. We expected a lower level of pollution
148 and a higher vegetal cover and prey availability in the forest site compared to the urban site, and a higher
149 reproductive success in the forest site. For the second aim of this study, concerning the relationship between
150 weather parameters, reproductive success, and site, we evaluated the relationship between rainfall and temperature
151 data and reproductive success. We expected greater differences between sites in years with unfavorable weather
152 conditions (i.e. high precipitation rate and cold temperatures) due to the higher sensitivity of urban birds.

153 2. Material and methods

154 1. Study sites, animal model, and reproduction monitoring

155 This study was realized on the first broods of two populations of great tit in the Eurometropole of Strasbourg
156 (region Alsace, France) for four years (2015, 2016, 2018, and 2019). The great tit is a relevant biological model
157 because it can easily breed in artificial nest boxes, facilitating the biomonitoring of its reproduction. The studied
158 populations were housed in artificial nest boxes (124 and 60 nest boxes installed within the urban site and the
159 forest site, respectively); however, it is worth noting that the occupancy rate of the nest boxes in urban sites was
160 lower than in forest site (see Appendix A1). The occupancy rate was comprised between 31 % and 43% in the
161 urban site whereas it was comprised between 53% and 68% in the forest site. Nest boxes in the urban site (Urban)
162 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
163 $N_{2018-2019}=12$) in the city center of Strasbourg and in a residential area (called “La Robertsau”, $N_{2015}=20$, $N_{2016}=39$,
164 $N_{2018}=0$ and $N_{2019}=39$; mean DD coordinates: 48.5793°, 7.7677°). See location details in Appendix A2. The forest
165 site (Forest) was located 20 km north of Strasbourg’s city center (mean DD coordinates: 48.6480°; 7.8337°; see
166 location details in Appendix A2) in La Wantzenau.

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

180 2. Environmental parameters

181 a) Vegetation cover and vegetation sampling

182 The GPS coordinates of each nest box were used to estimate the vegetation cover over a 50 m radius around each
183 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
184 tit (Demeyrier et al. 2016). Several categories of land usage were determined: no-vegetation surfaces (roads, bare

185 rock, soil, and building), arable lands, high vegetation (forest, isolated trees, groves, and hedges), low vegetation
186 (herbaceous), and water surfaces. For each nest, the percentage of each category was determined using QGIS from
187 land use maps (50 cm resolution) created by the LIVE (Laboratoire Image, Ville, Environnement, UMR 7362
188 Strasbourg France). In addition, leaf samples were collected several times during the breeding season at each site
189 in 2016. For urban site, leaf samples were collected three times in the city center and two times in the suburban
190 zone of La Robertsau. For forest site three leaf samples were collected during breeding season. Each sample was
191 composed of 10 leaves of different trees among the major tree species observed in both sites. Some of the tree
192 species sampled were the same at both sites, although the choice was more limited in urban areas, where many
193 exotic and ornamental tree species were found. Tree species common on each sites were *Carpinus betulus*, *Acer*
194 *pseudoplatanus*, *Fagus sylvaticus*. Tree species sampled only in forest site were *Quercus sp.*, *Fraxinus excelsior*
195 and *Corylus avellana* and tree species sampled only in urban site were *Robinia pseudoacacia*, *Aesculus*
196 *hippocastanum* and *Ulmus minor*. Samples were frozen at -80°C until the measurement of pollutants.

197 *b) Prey availability*

198 Great tits feed primarily on arthropods during the breeding period, while adults essentially feed their nestlings with
199 caterpillars or spiders (Michalski et al., 2011). To estimate prey availability, invertebrates were sampled at each
200 site three times during the breeding period in 2015 and six times in 2016 using a method modified from (Colas G.
201 1948). Invertebrates were collected by vigorously shaking a branch over a large umbrella (91.5 cm radius, that is,
202 an area of 2.63 m^2). The operation was repeated under 10 trees of different species (the same tree species used for
203 leaves sampling), randomly chosen on each site for an overall representation of the invertebrate composition of
204 the site. Tree species composition varied slightly between years and between different invertebrate sampling on
205 the same site. Collected invertebrates were classified into three categories: “caterpillars,” “spiders,” and “others,”
206 and counted. Caterpillars and spiders were stored at -80°C until the measurement of pollutants. Mean prey
207 availability at each site was estimated by taking into account the average high vegetation area within the home
208 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
209 umbrella area, $2.63 \times 10 = 26.3 \text{ m}^2$). Calculations were performed for each spider and caterpillar sampling. More
210 precisely, the following equation was used:

$$211 \quad \text{prey availability}_{(\text{count})} = \text{harvested preys}_{(\text{count})} \times \frac{A_{HV\text{mean}}}{A_{U\text{tot}}}$$

212 *c) Measurement of contaminants in biological samples*

213 The concentrations of 15 trace metal elements and metalloids (TME) were analyzed in bird feathers ($N_{\text{urban}} = 13$
214 individuals representing 12 nests and $N_{\text{forest}} = 20$ in 18 different nests), leaves ($N_{\text{urban}} = 5$ samples and $N_{\text{forest}} = 3$),
215 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
216 sites in 2015 (invertebrates) and 2016 (feathers, leaves, invertebrates).

217 Before TME analysis, biological samples were prepared and mineralized. Between 5 and 10 mg of feathers
218 samples were washed three times with NaOH concentrated at 0.25 mol L^{-1} (3 mL) for 1 minute. The feathers were
219 then rinsed three times with ultrapure water (3 mL) for 1 min. The final wash was performed with water (3 mL)
220 for 1 h. Digestion was performed by heating the samples at 60°C with 65% HNO_3 (1 mL) for 15 h in capped tubes.
221 Ultrapure water was used to obtain a final volume of 5 mL. For vegetation, 200 mg of samples were subjected to
222 the same digestion protocol without the washing step, and with 2 mL of 65% HNO_3 with a final volume adjusted

223 to 10 mL. Prey (spiders and caterpillars) were dried overnight at 80°C. The samples were then ground in a mortar,
224 and 200 mg of dried samples were digested with 65% HNO₃ (2 mL) for 15 h at 60°C. The final volume was
225 adjusted to 10 mL using ultrapure water. For all samples, blanks were prepared and measured in the same manner
226 to control for contamination from reagents and laboratory environment.

227 The concentrations of the following elements were determined using inductively coupled plasma mass
228 spectrometry (ICP-MS, Agilent 7700): aluminum (Al), arsenic (As), barium (Ba), cadmium (Cd), cerium (Ce),
229 chromium (Cr), cobalt (Co), copper (Cu), lead (Pb), molybdenum (Mo), nickel (Ni), rubidium (Rb), strontium (Sr),
230 vanadium (V), and zinc (Zn). The corresponding concentrations were determined using a calibration curve
231 prepared by the dilution of a multi-element certified standard (10 µg mL⁻¹, CPI International). Indium 10 ppb
232 (1000 µg mL⁻¹, CPI International) was used as an internal standard (see Appendix B for the operational conditions
233 and instrumental limits of detection of the ICP-MS analysis). The specificity of the analytical methods was
234 evaluated by recovery measurements of the spiked samples. The recovery values were 90–110% for all the
235 elements. Results are expressed in mg kg⁻¹ of total weight for feathers and vegetation samples and in mg kg⁻¹ of
236 dry weight for prey.

237 *d) Air pollution*

238 The air contaminants were trapped in each site with an XAD-2[®] passive air sampler and renewed every two weeks
239 during the reproduction of birds (end of March to end of May) in 2015 and 2016. Due to the heterogeneity of the
240 urban matrix, two samplers were placed simultaneously: one in the city center and one in the residential area of
241 La Robertsau. For the forest site, only one sampler was placed at a time. It represents three samplings per year in
242 2015 and 2016 for the forest site and six (2015) or seven (2016) sampling for the urban site. Contaminants were
243 extracted using the methodology developed by Al Dine et al. (2015) and Lévy et al. (2018, 2020). This type of
244 sampler allowed for the detection of four types of pollutants classified into eight categories according to their
245 characteristics and toxicity: polychlorinated biphenyl (PCB) separated in dioxin-like PCBs (DL-PCBs) and non-
246 dioxin-like PCBs (NDL-PCBs), polycyclic aromatic hydrocarbons (PAHs), organochlorine pesticides (OCCs), and
247 non-organochlorine pesticide components split into insecticides, herbicides, and fungicides (see Appendix C1 for
248 a list of the pollutants in each category). For each sampling, the concentrations of pollutants in the same category
249 were summed. Among the 169 air pollutants (measured in ng m⁻³) we aimed to identify, 89 had concentrations
250 above their quantification limits (Lévy et al., 2018).

251 *e) Weather conditions and temperature*

252 A temperature logger (Thermochron iButton; Embedded Data Systems[®]) was placed under one nest box at the
253 forest site, while two nest boxes were used at the urban site (one in the city center and one in the residential area
254 of La Robertsau), protected from the sun, to measure ambient temperature (1 measure/h) between April and May
255 in 2015 and 2016, but not in 2018 and 2019. Temperatures showed no significant differences between sites during
256 the total reproductive period (LM: F = 0.946, p = 0.39). Temperature data from each site obtained with loggers
257 were similar to those recorded by the logger of the weather station of Météo-France (station N°67482001,
258 48.5819444 °, 8.2688889°DD) in the city (Mann-Whitney-Wilcoxon test: Urban (center), W = 4019 and p = 0.21;
259 Urban (residential), W = 3417 and p = 0.93; Forest, W = 3571 and p = 0.65). Therefore, hourly temperature and
260 hourly precipitation data provided by Météo-France in 2015, 2016, 2018, and 2019 were used for the following
261 analyses. To transform hourly data in daily data, we calculated the mean daily temperature and the daily range of

262 temperature and, for precipitations; we sum up the total daily precipitations. For each occupied nest box, two
263 periods were defined: the incubation period (14 days before hatching) and the rearing period (14 days after
264 hatching, hatching date included). For nest failing before hatching and for which laying date was determined with
265 certitude, the incubation period was calculated as 14 days after the date of laying of the last egg (laying date of 1st
266 egg + clutch size). For each period and for each nest, the average temperature (T_{mean} , in °C) and average daily
267 temperature range (T_{range} , in °C) were calculated. The average daily rainfall rate (RR, in mm) and the number of
268 rainy days (NbRD with a rainy day considered as a day with $RR > 0$) during each period were also calculated.
269 More details on value of each weather parameter and comparison of loggers and weather station parameters are
270 provided in appendix C.5.

271 3. Statistical analyses

272 Statistical analyses were performed using R (version 3.6.2) in RStudio (R Development Core Team, 2021). The
273 hatching date was converted in relative days from March 1st and scaled for the analyses including this parameter
274 as an explanatory variable. The significance level alpha was set at 0.05. Predated nests or nests with dead adults
275 inside were excluded from the analyses ($N_{\text{urban}} = 2$ and $N_{\text{forest}} = 8$; see Appendix 1 for more details).

276 a) Differences in environmental parameters between sites

277 Aerial pollutants, the TME concentrations in the biological tissues (bird feathers leaves and invertebrates), and
278 vegetation cover between urban and forest sites were examined using principal component analyses (PCA)
279 (“FactoMineR” package, Lê et al. 2008). The values were scaled before the analyses. Missing values for feathers
280 (26 %), leaves (14%) and prey (9% for spiders and 10% for caterpillars) due to concentrations below the limit of
281 detection (LOD) were imputed by the value of $LOD/\sqrt{2}$ (Helsel 2011). Four separate PCAs were performed: (i)
282 air pollution, (ii) feather pollutants, (iii) leaves and invertebrates (caterpillars and spiders) pollutants, and (iv)
283 vegetation cover (see Appendix C for more details). The percentages of variation explained by the first two axes,
284 PC1 and PC2, of the different PCAs were 71.1% for the air pollution PCA (Fig. 1A); 52.7% for the TME
285 concentration in bird feathers PCA (Fig. 1C), 65.3% for the TME concentration in leaves and invertebrates PCA
286 (Fig. 1B), and 64.3% for the vegetation cover PCA (Fig. 2A). Differences between sites along the PCA axes were
287 tested using the Wilcoxon test for aerial pollutants and vegetal cover, and the Kruskal-Wallis rank sum test with
288 Holm correction (function “dunn.test (method = “holm”)” in R) for biological tissues. Differences in prey
289 availability were tested using linear mixed models with the interaction between the type of prey (i.e. caterpillars
290 or spiders) and the site as an explanatory variable, and the sampling ID as a random variable to take into account
291 tree species variation during invertebrate collection. The normality of the residuals was verified using the
292 Kolmogorov-Smirnov test and heteroscedasticity with a Bartlett test. *Post-hoc* differences between sites and
293 between types of preys were tested using Tukey’s test.

294 b) Differences in reproductive outputs between sites

295 Generalized linear models (GLMs) with the Poisson family (link function: “log”) followed by type III Wald tests
296 were used for clutch size, nestling number before fledge, and hatching date. GLM with the binomial family was
297 used for the hatching and fledging rates (see reproduction monitoring for definition, link function: “logit”). The
298 models included the site, the year and the interaction between site and year as the explanatory variables. Non-
299 significant interactions were excluded from the models if $p > 0.10$. The overdispersion of all models was verified
300 (ratio model deviance on model df residual). If data were over-dispersed (ratio > 1), we used quasi-binomial or

301 quasi-Poisson families. Some nests were excluded from the models due to missing or imprecise data (two nests
302 excluded for clutch size and six for hatching and fledging rate, nestling number, and hatching date). The hatching
303 date and fledging rate were calculated, excluding nests in which no eggs hatched (N = 26). The normality of the
304 residuals was verified using the Kolmogorov-Smirnov test and heteroscedasticity with a Bartlett test. *Post-hoc*
305 differences between sites per year and between years per site were tested using Tukey's test.

306 *c) Effect of weather on reproduction*

307 Weather parameters calculated for the incubation and rearing period of each nest were probed using PCA
308 ("FactoMineR" package). The values were scaled before the analyses. The first two axes, PC1 and PC2, of weather
309 PCA explained 75.5% of the inter-annual variation. These two components were used as composite variables to
310 describe the weather conditions during reproduction for each nest. Differences between years in PC1 and PC2
311 were tested using the Kruskal-Wallis rank sum test with Holm correction (function "dunn.test (method = "holm")"
312 in R). These components were further used in generalized linear mixed models (Poisson or binomial depending on
313 parameters; see above for more details) followed by type III Wald tests, with reproduction parameters (nestling
314 number, hatching, and fledging rate). For some nests included in the reproduction parameter analysis (N = 8), the
315 weather parameters could not be calculated because of the unknown hatching date. These nests were therefore
316 excluded from the analyses. The analyses included PC1 and PC2 in interaction with site as explanatory variables,
317 the hatching date as a covariable, and the year as a random effect. For hatching models, only PC1 was included in
318 the models because PC2 was mainly related to temperature during rearing (see Results for more details). Non-
319 significant interactions were removed sequentially from the models if $p > 0.10$ to show marginal significance if it
320 exist.

321 **3. Results**

322 1. Environmental parameters in urban and forest sites

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

326 For the TME concentrations in the leaves and invertebrates, Cd, Al, Ce and Ba were identified as the major
327 contributors to PC1, whereas Cr was the major contributor to PC2 (Fig. 1B, see also Appendix C2). No significant
328 differences were observed between sites (Wilcoxon for PC1: $W = 183$, $p = 0.91$ and PC2: $W = 192$, $p = 0.91$).
329 However, significant differences were observed between leaves, spiders and caterpillars metal concentrations (Fig.
330 1B PC1: Kruskal-Wallis, $\chi^2 = 22.08$, $p < 0.001$ and PC2: Kruskal-Wallis, $\chi^2 = 14.37$, $p < 0.001$). PC1 separated
331 spiders from caterpillars and leaves which contained higher concentration of Cd, Al, Ce and Ba ($p_{\text{caterpillars-}}$
332 $\text{spiders} < 0.001$ and $p_{\text{spider-leaves}} = 0.01$ and $p_{\text{leaves-caterpillars}} = 0.30$). The PC2 separated spiders from caterpillars.
333 Concentrations of Cr are higher in spiders than in caterpillars ($p < 0.01$). No difference was observed between
334 spiders and leaves concentrations nor leaves and caterpillars concentrations ($p_{\text{leaves-spiders}} = 0.41$ and $p_{\text{caterpillars-leaves}}$
335 $= 0.06$).

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

339 The vegetation cover differed significantly between sites on both PC1 ($W = 4240.5$, $p < 0.01$) and PC2 ($W =$
340 2949.5 , $p = 0.047$). PC1 was negatively related to the high vegetation surfaces and positively related to the non-
341 vegetal surfaces (Fig. 2A, see Appendix C4). The major contributors of PC2 were arable and low vegetation
342 surfaces (Fig. 2A, see Appendix C4). The urban site was mainly characterized by a high proportion of non-vegetal
343 surfaces on PC1 and, to a lesser extent, by a higher proportion of low vegetation and arable surface on PC2. The
344 forest site was mainly characterized by high vegetation.

345 Regarding prey availability, the number of prey was significantly different between the sites (LMM, $F_{\text{site}} = 73.02$,
346 $p < 0.001$, Fig. 2B), and between the type of prey (LMM, $F_{\text{type}} = 35.10$, $p < 0.001$, Fig. 2B). The interaction between
347 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
348 lower at the urban site than at the forest site (Tukey, $p = 0.02$, Fig. 2B), and the average number of spiders was
349 higher than the average number of caterpillars (Tukey, $p < 0.001$, Fig. 2B).

350 2. Differences in reproductive outputs between sites and years

351 The interaction between site and year was significant for the hatching date (Table 1 and Fig. 3A). For a given year,
352 no difference was observed between sites (Tukey, all $p > 0.14$) but inter-annual differences varied between sites.
353 Earlier hatching dates were observed in 2019 compared to all other years in urban site (Table 1, Tukey, $p_{2019\text{-other}}$
354 $\text{years} < 0.001$ and all other $p > 0.62$). For forest site, similar differences were observed, except for 2015 (Tukey,
355 $p_{2019\text{-other years}} < 0.005$ and $p_{2019\text{-2015}} > 0.07$, Fig. 3A). The clutch size was significantly different between the sites
356 but not between the years (Table 1), with a smaller clutch for urban breeders (Tukey, $p < 0.001$, Fig. 3B for clutch
357 size).

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

365 3. Relationship between weather and reproduction parameters

366 First, the weather parameters during the incubation and rearing periods according to years were analyzed using the
367 two axes of the PCA. PC1 was found to be negatively correlated with temperature (T_{mean} and T_{range}) during
368 incubation and RR during rearing and positively related to rain (RR during incubation, NbrD during incubation,
369 and NbrD during rearing, Fig. 4A, see Appendix C.5). PC2 was positively correlated with temperature (T_{mean} and
370 T_{range}) during rearing. Significant differences between years were revealed for both PC1 and PC2 (Fig. 4B,
371 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
372 were significantly different on PC1, except in 2015 and 2019, which were not different ($p_{2015\text{-2019}} = 0.11$ and all
373 others $p < 0.001$). All years were different for PC2 (all $p \leq 0.0053$). These results indicate that the year 2015 was
374 characterized by high temperatures during rearing, 2016 by low temperature during incubation and high
375 precipitation during the reproduction period (incubation and rearing). Year 2018, in opposition to the year 2016 is
376 characterized by high temperatures during reproduction period, low precipitation during the incubation and some

377 occasional rainfall during rearing. Year 2019 is characterized by mild temperatures and rainfall during incubation,
378 and low temperatures during the rearing period.

379 Next, we analyzed the link between breeding parameters and weather principal components. There was a
380 significant interaction between the site and PC1 for the hatching rate. However, for both sites, correlations between
381 hatching rate and PC1 were not significant ($p_{\text{urban}} = 0.95$, $p_{\text{forest}} = 0.11$). The fledging rate and the nestling number
382 before fledge were not significantly correlated with PC1 (Table 2, see also Appendix E); however, these parameters
383 were significantly correlated with the interaction between PC2 and site (Table 2 and Fig. 5). The fledging rate and
384 the nestling number increased with increasing PC2 (positively correlated to temperature during rearing) in the
385 urban site (Tukey, $p = 0.02$ for fledging rate, $p = 0.01$ for nestling number) but not in the forest site (Tukey, $p >$
386 0.05).

387 **4. Discussion**

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

392 *a) Reproductive differences between urban and forest populations: role of environmental parameters*

393 For a given year, our study revealed that the hatching date did not differ between urban and forest site, contrary to
394 previous studies (Bailly et al., 2016; Charmantier et al., 2017; Wawrzyniak et al., 2015b). Some studies have
395 shown that advanced hatching dates in cities are related to the heat halo associated with concrete surfaces
396 (Chmielewski et al., 2013). However, in the present study, no variation in temperature was observed between the
397 urban and forest sites during reproduction, which could explain the similar hatching date found between sites. The
398 urban heat halo is mitigated by the presence of greenery (Onishi et al. 2010; Price et al. 2015) and most of the nest
399 boxes in our study were placed in urban parks maybe explaining the lack of temperatures differences. Moreover,
400 we only measured temperature during the reproduction. It is possible that the temperature differences between our
401 two sites are more pronounced later in the season in summer or even in winter. The clutch size and hatching rate
402 of urban birds in our study were lower than those of forest birds, regardless of the year and weather parameters, as
403 observed in several other studies on great tits. Some studies have reported on the impact of pollutant exposure on
404 these breeding parameters (Scheuhammer 1987; Koivula and Eeva 2010; Hellou et al. 2013). No differences in
405 pollutant concentration was observed between the urban and forest sites, neither for air pollutants nor for TME
406 pollution in leaves, prey, and feathers, contrary to studies that showed a higher concentration of TME in the
407 feathers of urban blackbird (*Turdus merula*) (Scheifler et al. 2006; Meillère et al. 2016) and house sparrow (Bichet
408 et al. 2013) in other cities. However, no pollutant difference between urban site and forest is in line with the result
409 of Chatelain et al (2021a) that has shown little differences in metal concentrations between urban parks and
410 adjacent forests.

411 Moreover, the concentrations measured in Strasbourg were much lower than those reported in other cities. For
412 example, the Pb feather concentration obtained in Strasbourg (on average 2.53 mg/kg) was much lower than that
413 found in sparrows in other French cities, such as Paris (19.54 mg/kg), Gennevilliers (18.70 mg/kg), or Berk (6.7
414 mg/kg) (Bichet et al. 2013), suggesting that the city of Strasbourg could be a low metal-polluted site. Exposure to

415 pollutants, therefore, does not appear to be a reason for the reproductive differences observed between urban and
416 forest sites. However, the sample size of this study was small, and further research is required to validate this
417 hypothesis (e.g. by increasing the number of replicates and distinguishing between urban and suburban areas, for
418 example). Moreover, contaminants are concentrated in new feathers formed during the molting of individuals,
419 which generally occur at the end of the breeding period, which was outside of our study interval, as first brood
420 interval was examined in this study. Therefore, metal concentrations measured in this study reflect pollution levels
421 at adult's previous breeding ground. The possibility that adults may disperse between the two breeding seasons
422 cannot be dismissed even though we have not yet found any individuals banded in the forest and found in town or
423 vice versa. Other environmental constraints, such as noise or light pollution, can cause chronic stress in individuals,
424 leading to the production of reactive oxygen species (Isaksson 2015) and oxidative stress. Chronic exposure to a
425 stressful environment can alter the fertility of individuals, and thus the number of laid eggs for females (Isaksson
426 et al. 2008; Bize et al. 2008; Wawrzyniak et al. 2020) or egg fertilization for males (Vallverdú-Coll et al. 2016;
427 Mora et al. 2017; Bisht et al. 2017). The smaller clutch size and the lower hatching rate could be therefore related
428 to a lower egg quality in the city, as observed in other studies on urbanization (Isaksson et al. 2008; Toledo et al.
429 2016). Stress constraints could also increase the corticosterone concentration (Meillère et al. 2016; Marasco et al.
430 2017), reduce parental care (Angelier and Chastel 2009), potentially leading to nest desertion, in favor of parental
431 survival. A lower fecundity due to physiological stress can also be proposed (Bize et al. 2008).

432 In this study we also highlighted lower prey availability in the city. The urban environment in Strasbourg was
433 mainly characterized by low vegetal and non-vegetal surfaces. Surprisingly, there was also a notable part of arable
434 surfaces, probably due to the presence of fields in the suburban part of Strasbourg (*La Robertsau*). Reduced
435 vegetation cover in cities has a direct impact on invertebrate populations (Thomas et al. 2001, Jones and Leather
436 2012). The number of preys available for each nest on the urban site in our study was, on average, two times less
437 than that for the forest site. This lack of prey is likely to impose an increased effort on urban adult birds to search
438 for prey. Urban birds have to search over a greater distance (Bonier et al., 2007a; Stauss et al., 2005), which
439 increases the time spent searching for preys (Jarrett et al., 2020; Naef-Daenzer and Keller, 1999) and increases the
440 energy expenditure associated with foraging (Hinsley et al., 2008). The association between the amount of food
441 during egg laying and clutch size in cities has already been demonstrated in great tits (Wawrzyniak et al., 2020,
442 2015) and blue tits (Marciniak et al., 2007). Some studies point to the fact that low food availability leads to a
443 reduction in clutch size due to a suboptimal diet (Wawrzyniak et al., 2015) or to increased competition for resources
444 in the city (Chamberlain et al., 2009). A study testing reproductive selection in the city showed that birds with
445 larger clutches in city have better fitness which tends to confirm that smaller clutches in city result from food
446 limitations in urban areas (Caizergues et al. 2018). Yet, a smaller clutch size requires less food after hatching, this
447 would allow parents to invest enough to ensure the survival of their young (Martin et al., 2000). Our results showed
448 that while the nestling number before fledge was generally lower at the urban site than at the forest site, the fledging
449 rate did not differ between the two environments (except in 2019). This suggests that the reduced clutch size in
450 urban sites could be an adaptation to environmental constraints (Boyce and Perrins 1987) and that different
451 reproductive strategies exist between urban and forest areas and, more generally, a difference in the pace of life
452 (Charmantier et al., 2017; Sepp et al., 2017). Urban individuals tend to have a slower pace of life and invest more
453 in their own survival than in reproduction, thus laying smaller clutches and rearing fewer chicks than their
454 counterparts in the forest. This hypothesis on the pace of life should be tested by simultaneously measuring several

455 life history traits. This hypothesis could also explain that clutch size is the only reproductive parameter that did
456 not vary between years. Similar results were also observed in a long-term study of the same species (Wawrzyniak
457 et al., 2020, 2015).

458 b) Reproductive differences between urban and forest populations: inter-annual variations and role of
459 weather parameters

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

477 For the fledging rate, our study revealed differences between years and within sites for the same year as in 2019.
478 This result could be directly related to inadequate food availability, as found in several other studies (Seress et al.
479 2012, Caizergues et al. 2021). Interestingly, contrary to our initial hypothesis that proposed a greater inter-annual
480 variation in the reproductive success of urban birds due to the strongest effect of weather, low inter-annual
481 variations in nestling number before fledge were observed for each site. Nestling number remained constantly
482 lower in urban site whatever the year. Moreover, the mean nestling number before fledge in cities was never above
483 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
484 nestlings in the forest site. Considering that the clutch size is lower in the urban site, this result could suggest that
485 urban birds would invest more in their own survival than parental care, as described in the slow pace of life theory.
486 However, both nestling number before fledge and fledging rate were positively correlated with PC2 weather only
487 in urban areas and not in the forest site. The nestling number calculated here represents the reproductive success
488 of breeders, including all failed nests (incubation or rearing), whereas the annual mean fledging rate is
489 representative of nestling mortality during rearing (excluding the deserted nests during incubation). In the present
490 study, high temperatures during the rearing period increased fledging in the city, but also increased their survival.
491 A lower urban fledging rate was observed in 2019, the coldest of the four years (during rearing). However, no
492 difference was observed at the forest site for this parameter. Previous studies have already shown a positive
493 correlation between nestling survival with temperature, and a negative correlation with heavy rains (Dawson et al.,

494 2005; Dawson and Bortolotti, 2000; Eeva et al., 2002; Kosicki, 2012; Krijgsveld et al., 2003). Low temperatures,
495 especially when chicks are thermo-dependent (Dawson et al., 2005), and the negative impact of heavy rain on prey
496 availability and catching (Avery and Krebs, 2008; Dawson and Bortolotti, 2000), led to nestlings suffering from
497 hypothermia and/or starvation, increasing the risk of death. Adults may also have more difficulties meeting their
498 own needs (Öberg et al., 2015). Unfavorable climatic conditions can also increase corticosterone concentrations
499 in parents (Cīrule et al., 2017; Wingfield, 1988) which enhances the probability of desertion (Love et al., 2004;
500 Thierry et al., 2013). The food limitation observed in urban sites and others environmental constraints (e. g. noise
501 and light pollution) in urban areas may contribute to exacerbate effect of unfavorable weather during reproduction,
502 leading to a decrease in urban productivity and higher nestling mortality. To really understand the link between
503 weather parameters, food availability and reproduction it could be interesting to follow the annual variations of
504 prey abundance in both sites.

505 To conclude, in a medium-sized city, such as Strasbourg, the constraints linked to urbanization seem to be mainly
506 related to the reduction of the vegetation cover, which limits the availability of food for insectivorous passerines,
507 compared to other cities where birds also have to deal with higher levels of chemical pollution. Our results
508 therefore highlight that lower food availability could considerably limit the nestling number, especially during
509 harsh years. The lower nestling numbers and poor inter annual variation in urban environments for this parameter,
510 suggests a threshold of breeding performance that parents cannot exceed. However the lower productivity would
511 lead to a decline in the population of great tits in cities, particularly if one tough year followed another. It is worth
512 noting that a lower nestling number may be compensated by a higher survival, especially in winter. To determine
513 whether urban populations are sustainable or whether they are maintained due to continuous immigration from
514 rural areas, there is a need to measure the rates of survival, recruitment, and immigration. In addition, our results
515 showed negative impact of cold weather on reproductive success of birds but it also known that warm temperatures
516 and heat wave can have negative consequences on birds reproduction impacting both birds fertility and nestling
517 development (Pipoly et al. 2013; Salaberria et al. 2014; McCowan and Griffith 2021). Long-term studies are
518 therefore necessary to understand all the aspects of the additive effects of weather conditions and the urban
519 environment, especially during the rearing of offspring.

520 **5. References**

- 521 Al Dine EJ, Mokbel H, Elmoll A, et al (2015) Concomitant evaluation of atmospheric levels of polychlorinated
522 biphenyls, organochlorine pesticides, and polycyclic aromatic hydrocarbons in Strasbourg (France) using
523 pine needle passive samplers. *Environ Sci Pollut Res* 22:17850–17859. doi: 10.1007/s11356-015-5030-5
- 524 Albers PH (2006) Birds and polycyclic aromatic hydrocarbons. *Avian Poult Biol Rev* 17:125–140
- 525 Amininasab SM, Kingma SA, Birker M, et al (2016) The effect of ambient temperature, habitat quality and
526 individual age on incubation behaviour and incubation feeding in a socially monogamous songbird. *Behav*
527 *Ecol Sociobiol* 70:1591–1600. doi: 10.1007/s00265-016-2167-2
- 528 Angelier F, Chastel O (2009) Stress, prolactin and parental investment in birds: A review. *Gen Comp Endocrinol*
529 163:142–148. doi: 10.1016/j.ygcen.2009.03.028
- 530 Ardia DR, Pérez JH, Clotfelter ED (2010) Experimental cooling during incubation leads to reduced innate
531 immunity and body condition in nestling tree swallows. *Proc R Soc B Biol Sci* 277:1881–1888. doi:
532 10.1098/RSPB.2009.2138

533 Ardia DR, Pérez JH, Clotfelter ED (2010) Experimental cooling during incubation leads to reduced innate
534 immunity and body condition in nestling tree swallows. *Proc R Soc B Biol Sci* 277:1881–1888. doi:
535 10.1098/RSPB.2009.2138

536 Arnold KE, Ramsay SL, Henderson L, Larcombe SD (2010) Seasonal variation in diet quality: antioxidants,
537 invertebrates and blue tits *Cyanistes caeruleus*. *Biol J Linn Soc* 99:708–717. doi: 10.1111/j.1095-
538 8312.2010.01377.x

539 Avery MI, Krebs JR (2008) Temperature and foraging success of Great Tits *Parus major* hunting for spiders. *Ibis*
540 (Lond 1859) 126:33–38. doi: 10.1111/j.1474-919X.1984.tb03661.x

541 Bailly J, Faivre B, Bernard N, et al (2017) Multi-Element Analysis of Blood Samples in a Passerine Species:
542 Excesses and Deficiencies of Trace Elements in an Urbanization Study. *Front Ecol Evol* 5:6. doi:
543 10.3389/fevo.2017.00006

544 Bailly J, Scheifler R, Berthe S, et al (2016) From eggs to fledging: Negative impact of urban habitat on
545 reproduction in two tit species. *J Ornithol* 157:377–392. doi: 10.1007/s10336-015-1293-3

546 Berglund ÅMM, Sturve J, Förlin L, Nyholm NEI (2007) Oxidative stress in pied flycatcher (*Ficedula hypoleuca*)
547 nestlings from metal contaminated environments in northern Sweden. *Environ Res* 105:330–339. doi:
548 10.1016/j.envres.2007.06.002

549 Biard C, Brischoux F, Meillère A, et al (2017) Growing in cities: an urban penalty for wild birds? A study of
550 phenotypic differences between urban and rural great tit chicks (*Parus major*). *Front Ecol Evol* 5:1–14. doi:
551 10.3389/fevo.2017.00079

552 Bichet C, Scheifler R, Cœurduassier M, et al (2013) Urbanization, trace metal pollution, and malaria prevalence in
553 the house sparrow. *PLoS One* 8:e53866. doi: 10.1371/journal.pone.0053866

554 Bisht S, Faiq M, Tolahunase M, Dada R (2017) Oxidative stress and male infertility. *Nat Rev Urol* 14:470–485.
555 doi: 10.1038/nrurol.2017.69

556 Bize P, Devevey G, Monaghan P, et al (2008) Fecundity and survival in relation to resistance to oxidative stress
557 in a free-living bird. *Ecology* 89:2584–2593. doi: 10.1890/07-1135.1

558 Bonier F, Martin PR, Wingfield JC (2007) Urban birds have broader environmental tolerance. *Biol Lett* 3:670–
559 673. doi: 10.1098/rsbl.2007.0349

560 Boyce MS, Perrins CM (1987) Optimizing great tit clutch size in a fluctuating environment. *Ecology* 68:142–153.
561 doi: 10.2307/1938814

562 Bryan SM, Bryant DM (1999) Heating nest-boxes reveals an energetic constraint on incubation behaviour in great
563 tits, *Parus major*. *Proc R Soc B Biol Sci* 266:157–162. doi: 10.1098/rspb.1999.0616

564 Buse A, Dury SJ, Woodburn RJW, et al (1999) Effects of elevated temperature on multi-species interactions: the
565 case of Pedunculate Oak, Winter Moth and Tits. *Funct Ecol* 13:74–82. doi: 10.1046/j.1365-
566 2435.1999.00010.x

567 Caizergues AE, Grégoire A, Charmantier A (2018) Urban versus forest ecotypes are not explained by divergent
568 reproductive selection. *Proc R Soc B Biol Sci* 285:. doi: 10.1098/rspb.2018.0261

569 Caizergues AE, Charmantier A, Lambrechts MM, et al (2021) An avian urban morphotype: how the city
570 environment shapes great tit morphology at different life stages. *Urban Ecosyst* 24:929–941. doi:
571 10.1007/s11252-020-01077-0

572 Chamberlain DE, Cannon AR, Toms MP, et al (2009) Avian productivity in urban landscapes: A review and meta-

573 analysis. *Ibis* (Lond 1859) 151:1–18. doi: 10.1111/j.1474-919X.2008.00899.x

574 Charmantier A, Demeyrier V, Lambrechts M, et al (2017) Urbanization is associated with divergence in pace-of-
575 life in great tits. *Front Ecol Evol* 5:40–47. doi: 10.3389/fevo.2017.00053

576 Charmantier A, McCleery RH, Cole LR, et al (2008) Adaptive Phenotypic Plasticity in Response to Climate
577 Change in a Wild Bird Population. *Science* (80-) 320:800–803. doi: 10.1126/science.1157174

578 Chatelain M, Da Silva A, Celej M, et al (2021a) Replicated, urban-driven exposure to metallic trace elements in
579 two passerines. *Sci Reports* 2021 11:1–10. doi: 10.1038/s41598-021-99329-2

580 Chatelain M, Massemin S, Zahn S, et al (2021b) Urban metal pollution explains variation in reproductive outputs
581 in great tits and blue tits. *Sci Total Environ* 776:145966. doi: 10.1016/j.scitotenv.2021.145966

582 Chmielewski F-M, Blümel K, Scherbaum-Heberer C, et al (2013) A model approach to project the start of egg
583 laying of Great Tit (*Parus major* L.) in response to climate change. *Int J Biometeorol* 57:287–297. doi:
584 10.1007/s00484-012-0553-7

585 Cīrule D, Krama T, Krams R, et al (2017) Habitat quality affects stress responses and survival in a bird wintering
586 under extremely low ambient temperatures. *Sci Nat* 104:99. doi: 10.1007/s00114-017-1519-8

587 Colas G. (1948) *Guide de l'Entomologiste*, Editions N. Persée - Portail des revues scientifiques en SHS

588 Cormont A, Vos C, van Turnhout C, et al (2011) Using life-history traits to explain bird population responses to
589 changing weather variability. *Clim Res* 49:59–71. doi: 10.3354/cr01007

590 Cox AR, Robertson RJ, Lendvai AZ, et al (2019) Rainy springs linked to poor nestling growth in a declining avian
591 aerial insectivore (*Tachycineta bicolor*). *Proc R Soc B Biol Sci* 286:20190018. doi: 10.1098/rspb.2019.0018

592 Cunningham SJ, Martin RO, Hojem CL, Hockey PAR (2013) Temperatures in Excess of Critical Thresholds
593 Threaten Nestling Growth and Survival in A Rapidly-Warming Arid Savanna: A Study of Common Fiscals.
594 *PLoS One* 8:e74613. doi: 10.1371/JOURNAL.PONE.0074613

595 Dawson RD, Bortolotti GR (2000) Reproductive success of American Kestrels: the role of prey abundance and
596 weather. *Condor* 102:814–822. doi: 10.1093/condor/102.4.814

597 Dawson RD, Lawrie CC, O'Brien EL (2005) The importance of microclimate variation in determining size, growth
598 and survival of avian offspring: Experimental evidence from a cavity nesting passerine. *Oecologia* 144:499–
599 507. doi: 10.1007/s00442-005-0075-7

600 Demeyrier V, Lambrechts MM, Perret P, Grégoire A (2016) Experimental demonstration of an ecological trap for
601 a wild bird in a human-transformed environment. *Anim Behav* 118:181–190. doi:
602 10.1016/j.anbehav.2016.06.007

603 Durant SE, Hopkins WA, Hepp GR, Walters JR (2013) Ecological, evolutionary, and conservation implications
604 of incubation temperature-dependent phenotypes in birds. *Biol Rev* 88:499–509. doi: 10.1111/brv.12015

605 Eeva T, Lehikoinen E (1995) Egg shell quality, clutch size and hatching success of the great tit (*Parus major*) and
606 the pied flycatcher (*Ficedula hypoleuca*) in an air pollution gradient. *Oecologia* 102:312–323. doi:
607 10.1007/BF00329798

608 Eeva T, Lehikoinen E (1996) Growth and mortality of nestling great tits (*Parus major*) and pied flycatchers
609 (*Ficedula hypoleuca*) in a heavy metal pollution gradient. *Oecologia* 108:631–639. doi:
610 10.1007/BF00329036

611 Eeva T, Lehikoinen E, Rönkä M, et al (2002) Different responses to cold weather in two pied flycatcher
612 populations. *Ecography* (Cop) 25:705–713. doi: 10.1034/j.1600-0587.2002.250606.x

613 Gil D, Brumm H (2013) Avian Urban Ecology. Oxford University Press
614 Goyer RA (1997) Toxic and essential metal interactions. Annu Rev Nutr 17:37–50. doi:
615 10.1146/annurev.nutr.17.1.37
616 Hallinger KK, Cristol DA (2011) The role of weather in mediating the effect of mercury exposure on reproductive
617 success in tree swallows. Ecotoxicology 20:1368–1377. doi: 10.1007/s10646-011-0694-1
618 Hellou J, Lebeuf M, Rudi M (2013) Review on DDT and metabolites in birds and mammals of aquatic ecosystems.
619 Environ. Rev. 21:53–69
620 Helsel DR (2011) Statistics for censored environmental data using Minitab® and R. John Wiley & Sons, Inc.,
621 Hoboken, NJ, USA
622 Hinsley SA, Hill RA, Bellamy PE, et al (2008) Effects of structural and functional habitat gaps on breeding
623 woodland birds: Working harder for less. Landsc Ecol 23:615–626. doi: 10.1007/s10980-008-9225-8
624 Isaksson C (2015) Urbanization, oxidative stress and inflammation: A question of evolving, acclimatizing or
625 coping with urban environmental stress. Funct Ecol 29:913–923. doi: 10.1111/1365-2435.12477
626 Isaksson C, Andersson S (2007) Carotenoid diet and nestling provisioning in urban and rural great tits *Parus major*.
627 J Avian Biol 38:564–572. doi: 10.1111/j.2007.0908-8857.04030.x
628 Isaksson C, Johansson A, Andersson S (2008) Egg yolk carotenoids in relation to habitat and reproductive
629 investment in the great tit *Parus major*. Physiol Biochem Zool 81:112–118. doi: 10.1086/522650
630 Jarrett C, Powell LL, McDevitt H, et al (2020) Bitter fruits of hard labour: diet metabarcoding and telemetry reveal
631 that urban songbirds travel further for lower-quality food. Oecologia 193:377–388. doi: 10.1007/s00442-
632 020-04678-w
633 Jones EL, Leather SR (2012) Invertebrates in urban areas: A review. Eur J Entomol 109:463–478. doi:
634 10.14411/eje.2012.060
635 Josse J, Husson F (2016) missMDA: A package for handling missing values in multivariate data analysis. J Stat
636 Softw 70:1–31. doi: 10.18637/jss.v070.i01
637 Kempenaers B, Borgström P, Loës P, et al (2010) Artificial night lighting affects dawn song, extra-pair siring
638 success, and lay date in songbirds. Curr Biol 20:1735–1739. doi: 10.1016/j.cub.2010.08.028
639 Kimberly J. Fernie GRB (2000) Changes in Egg Composition of American Kestrels Exposed to Dietary
640 Polychlorinated Biphenyls. J Toxicol Environ Heal Part A 60:291–303. doi: 10.1080/00984100050027833
641 Koivula MJ, Eeva T (2010) Metal-related oxidative stress in birds. Environ Pollut 158:2359–2370. doi:
642 10.1016/j.envpol.2010.03.013
643 Kosicki JZ (2012) Effect of weather conditions on nestling survival in the White Stork *Ciconia ciconia* population.
644 Ethol Ecol Evol 24:140–148. doi: 10.1080/03949370.2011.616228
645 Krijgsveld KL, Visser GH, Daan S (2003) Foraging behavior and physiological changes in precocial quail chicks
646 in response to low temperatures. Physiol Behav 79:311–319. doi: 10.1016/S0031-9384(03)00117-3
647 Lê S, Josse J, Husson F (2008) FactoMineR: An R package for multivariate analysis. J Stat Softw 25:1–18. doi:
648 10.18637/jss.v025.i01
649 Lévy M, Al-Alam J, Delhomme O, Millet M (2020) An integrated extraction method coupling pressurized solvent
650 extraction, solid phase extraction and solid-phase micro extraction for the quantification of selected organic
651 pollutants in air by gas and liquid chromatography coupled to tandem mass spectrometry. Microchem J
652 157:104889. doi: 10.1016/j.microc.2020.104889

653 Lévy M, Al-Alam J, Ridacker C, et al (2018) Use of XAD®-2 passive air samplers for monitoring environmental
654 trends of PAHs, PCBs and pesticides in three different sites in Strasbourg and its vicinity (east of France).
655 Atmos Environ 195:12–23. doi: 10.1016/j.atmosenv.2018.09.052

656 Liu H, Ma W, Qian J, et al (2015) Effect of urbanization on the urban meteorology and air pollution in Hangzhou.
657 J Meteorol Res 29:950–965. doi: 10.1007/s13351-015-5013-y

658 Love OP, Breuner CW, Vézina F, Williams TD (2004) Mediation of a corticosterone-induced reproductive
659 conflict. Horm Behav 46:59–65. doi: 10.1016/j.yhbeh.2004.02.001

660 Marasco V, Stier A, Boner W, et al (2017) Environmental conditions can modulate the links among oxidative
661 stress, age, and longevity. Mech Ageing Dev 164:100–107. doi: 10.1016/j.mad.2017.04.012

662 Marciniak B, Nadolski J, Nowakowska M, et al (2007) Habitat and Annual Variation in Arthropod Abundance
663 Affects Blue Tit *Cyanistes caeruleus* Reproduction. Acta Ornithol 42:53–62. doi: 10.3161/068.042.0113

664 Martin TE, Martin PR, Olson CR, et al (2000) Parental care and clutch sizes in north and south american birds.
665 Science (80-) 287:1482–1485. doi: 10.1126/science.287.5457.1482

666 McCowan LSC, Griffith SC (2021) Baked eggs: catastrophic heatwave-induced reproductive failure in the desert-
667 adapted Zebra Finch (*Taeniopygia guttata*). Ibis (Lond 1859) 163:1207–1216. doi: 10.1111/IBI.12958

668 Meillère A, Brischoux F, Bustamante P, et al (2016) Corticosterone levels in relation to trace element
669 contamination along an urbanization gradient in the common blackbird (*Turdus merula*). Sci Total Environ
670 566–567:93–101. doi: 10.1016/j.scitotenv.2016.05.014

671 Meillère A, Brischoux F, Parenteau C, Angelier F (2015) Influence of urbanization on body size, condition, and
672 physiology in an urban exploiter: A multi-component approach. PLoS One 10:1–19. doi:
673 10.1371/journal.pone.0135685

674 Michalski M, Nadolski J, Marciniak B, et al (2011) Faecal analysis as a method of nestling diet determination in
675 insectivorous birds: A case study in Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major*. Acta Ornithol
676 46:164–172. doi: 10.3161/000164511X625937

677 Mora AR, Firth A, Blareau S, et al (2017) Oxidative stress affects sperm performance and ejaculate redox status
678 in subordinate house sparrows. J Exp Biol 220:2577–2588. doi: 10.1242/jeb.154799

679 Naef-Daenzer B, Keller LF (1999) The foraging performance of great and blue tits (*Parus major* and *P. caeruleus*)
680 in relation to caterpillar development, and its consequences for nestling growth and fledging weight. J Anim
681 Ecol 68:708–718. doi: 10.1046/j.1365-2656.1999.00318.x

682 Naef-Daenzer L, Naef-Daenzer B, Nager RG (2000) Prey selection and foraging performance of breeding Great
683 Tits *Parus major* in relation to food availability. J Avian Biol 31:206–214. doi: 10.1034/j.1600-
684 048X.2000.310212.x

685 Öberg M, Arlt D, Pärt T, et al (2015) Rainfall during parental care reduces reproductive and survival components
686 of fitness in a passerine bird. Ecol Evol 5:345–356. doi: 10.1002/ece3.1345

687 Onishi A, Cao X, Ito T, et al (2010) Evaluating the potential for urban heat-island mitigation by greening parking
688 lots. Urban For Urban Green 9:323–332. doi: 10.1016/J.UFUG.2010.06.002

689 Pipoly I, Bókony V, Seress G, et al (2013) Effects of Extreme Weather on Reproductive Success in a Temperate-
690 Breeding Songbird. PLoS One 8:e80033. doi: 10.1371/JOURNAL.PONE.0080033

691 Pipoly I, Preiszner B, Sándor K, et al (2022) Extreme Hot Weather Has Stronger Impacts on Avian Reproduction
692 in Forests Than in Cities. Front Ecol Evol 10:218. doi: 10.3389/FEVO.2022.825410/BIBTEX

693 Price A, Jones EC, Jefferson F (2015) Vertical Greenery Systems as a Strategy in Urban Heat Island Mitigation.
694 Water Air Soil Pollut 226:. doi: 10.1007/S11270-015-2464-9

695 R Development Core Team (2021) R: A language and environment for statistical computing. Vienna, Austria

696 Salaberria C, Celis P, López-Rull I, Gil D (2014) Effects of temperature and nest heat exposure on nestling growth,
697 dehydration and survival in a Mediterranean hole-nesting passerine. Ibis (Lond 1859) 156:265–275. doi:
698 10.1111/IBI.12121

699 Schaper S V., Dawson A, Sharp PJ, et al (2012) Increasing temperature, not mean temperature, is a cue for avian
700 timing of reproduction. Am Nat 179:. doi: 10.1086/663675

701 Scheifler R, Cœurassier M, Morilhat C, et al (2006) Lead concentrations in feathers and blood of common
702 blackbirds (*Turdus merula*) and in earthworms inhabiting unpolluted and moderately polluted urban areas.
703 Sci Total Environ 371:197–205. doi: 10.1016/j.scitotenv.2006.09.011

704 Scheuhammer AM (1996) Influence of reduced dietary calcium on the accumulation and effects of lead, cadmium,
705 and aluminum in birds. Environ Pollut 94:337–343. doi: 10.1016/S0269-7491(96)00084-X

706 Scheuhammer AM (1987) The chronic toxicity of aluminium, cadmium, mercury, and lead in birds: A review.
707 Environ Pollut 46:263–295. doi: 10.1016/0269-7491(87)90173-4

708 Schroeder J, Nakagawa S, Cleasby IR, Burke T (2012) Passerine birds breeding under chronic noise experience
709 reduced fitness. PLoS One 7:e39200. doi: 10.1371/journal.pone.0039200

710 Sepp T, McGraw KJ, Kaasik A, Giraudeau M (2017) A review of urban impacts on avian life-history evolution:
711 Does city living lead to slower pace of life? Glob Chang Biol 24:1452–1469. doi: 10.1111/gcb.13969

712 Seress G, Bókony V, Pipoly I, et al (2012) Urbanization, nestling growth and reproductive success in a moderately
713 declining house sparrow population. J Avian Biol 43:403–414. doi: 10.1111/j.1600-048X.2012.05527.x

714 Shochat E, Lerman S, Fernández-Juricic E (2015) Birds in urban ecosystems: Population dynamics, community
715 structure, biodiversity, and conservation. In: Urban Ecosystem Ecology, Agronomy Monograph. American
716 Society of Agronomy, Crop Science Society of America, Soil Science Society of America, pp 75–86

717 Stauss MJ, Burkhardt JF, Tomiuk J (2005) Foraging flight distances as a measure of parental effort in blue tits
718 *Parus caeruleus* differ with environmental conditions. J Avian Biol 36:47–56. doi: 10.1111/j.0908-
719 8857.2005.02855.x

720 Stephenson R (1997) Effects of oil and other surface-active organic pollutants on aquatic birds. Environ Conserv
721 24:121–129. doi: 10.1017/S0376892997000180

722 Thierry A-MM, Massemin S, Handrich Y, Raclot T (2013) Elevated corticosterone levels and severe weather
723 conditions decrease parental investment of incubating Adélie penguins. Horm Behav 63:475–483. doi:
724 10.1016/j.yhbeh.2012.12.011

725 Thomas DW, Blondel J, Perret P, et al (2001) Energetic and fitness costs of mismatching resource supply and
726 demand in seasonally breeding birds. Science (80-) 291:2598–2600. doi: 10.1126/science.1057487

727 Toledo A, Andersson MN, Wang HL, et al (2016) Fatty acid profiles of great tit (*Parus major*) eggs differ between
728 urban and rural habitats, but not between coniferous and deciduous forests. Sci Nat 103:1–11. doi:
729 10.1007/s00114-016-1381-0

730 Vallverdú-Coll N, Mougeot F, Ortiz-Santaliestra ME, et al (2016) Effects of lead exposure on sperm quality and
731 reproductive success in an avian model. Environ Sci Technol 50:12484–12492. doi:
732 10.1021/acs.est.6b04231

733 Vos JG (1972) Toxicology of PCBs for Mammals and for Birds. *Environ Health Perspect* 1:105–117. doi:
734 10.1289/ehp.7201105

735 Wawrzyniak J, Gładalski M, Kaliński A, et al (2020) Differences in the breeding performance of great tits *Parus*
736 *major* between a forest and an urban area: a long term study on first clutches. *Eur Zool J* 87:294–309. doi:
737 10.1080/24750263.2020.1766125

738 Wawrzyniak J, Kaliński A, Gładalski M, et al (2015) Long-Term Variation in Laying Date and Clutch Size of the
739 Great Tit *Parus major* in Central Poland: A Comparison between Urban Parkland and Deciduous Forest.
740 *Ardeola* 62:311–322. doi: 10.13157/arla.62.2.2015.311

741 Wawrzyniak J, Kaliński A, Gładalski M, et al Long-Term Variation in Laying Date and Clutch Size of the Great
742 Tit *Parus major* in Central Poland: A Comparison between Urban Parkland and Deciduous Forest. doi:
743 10.13157/arla.62.2.2015.311

744 Webb DR (1987) Thermal tolerance of avian embryos: A review. *Condor* 89:874–898

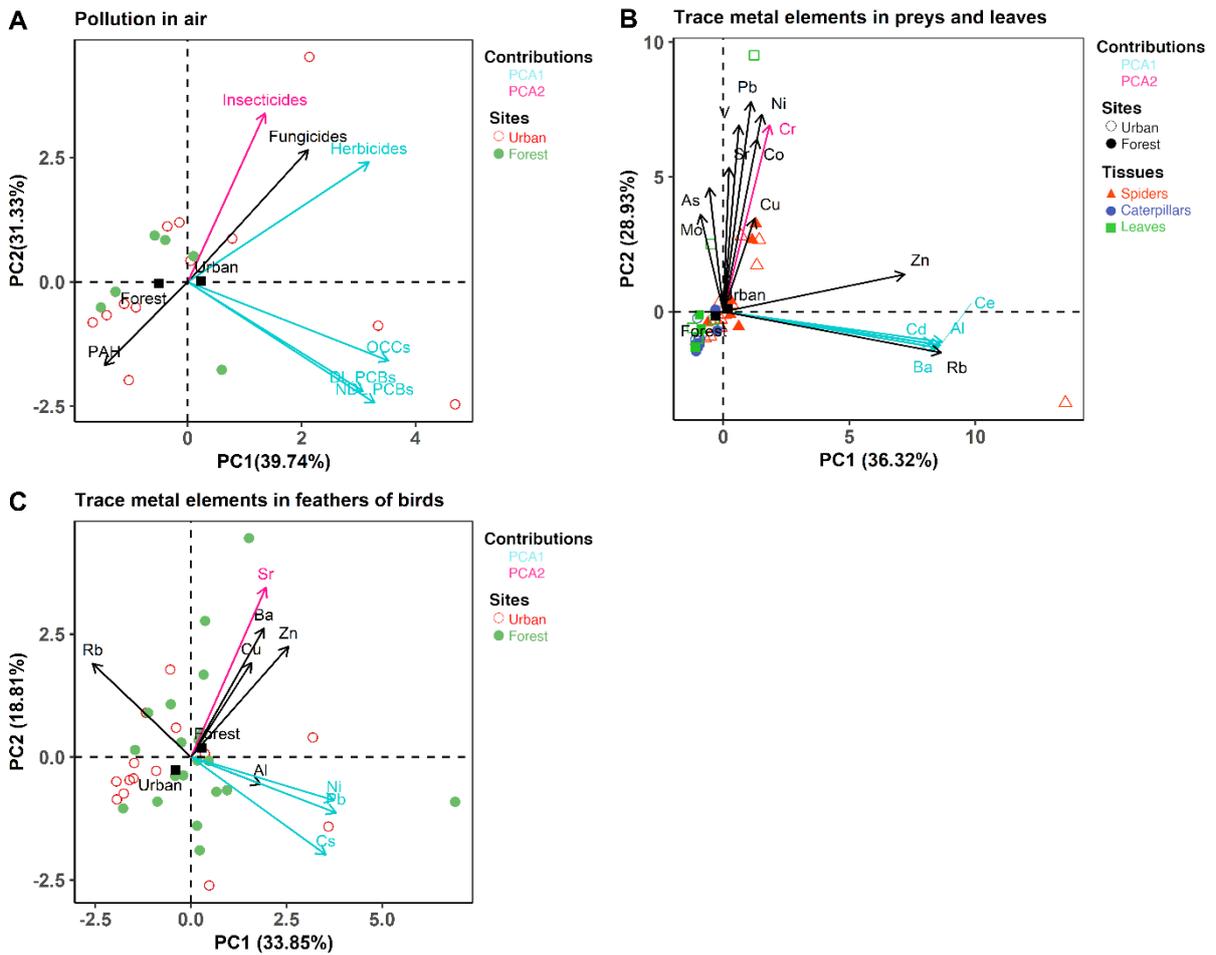
745 Wingfield JC (1988) Changes in reproductive function of free-living birds in direct response to environmental
746 perturbations. Springer, New York, NY, pp 121–148

747 Yahav S (2002) Limitations in energy intake affect the ability of young turkeys to cope with low ambient
748 temperatures. *J Therm Biol* 27:103–108. doi: 10.1016/S0306-4565(01)00021-3

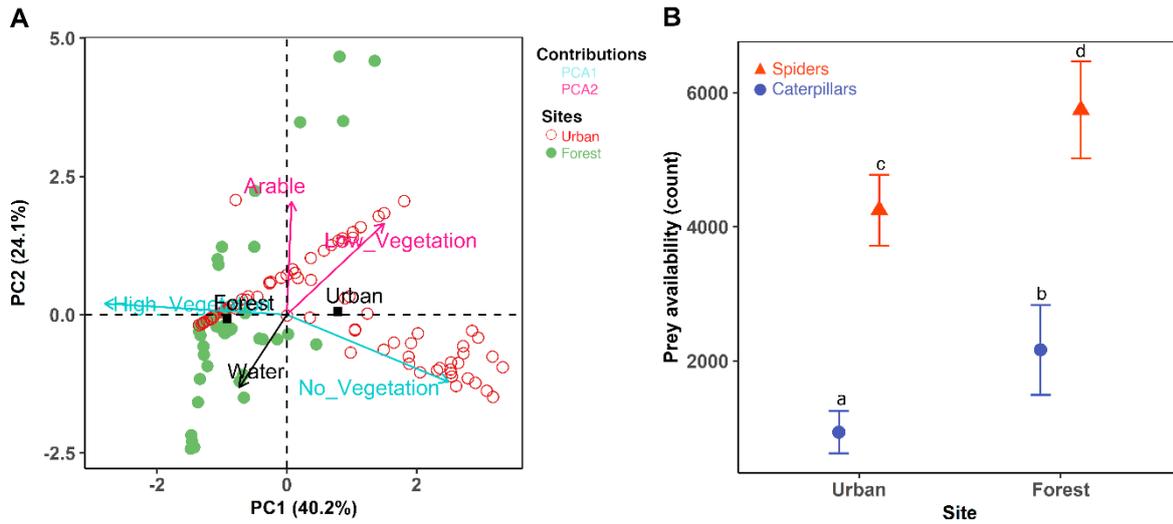
749 Zuur AF, Ieno EN, Walker NJ, et al (2009) *Mixed effects models and extension in ecology with R*, First Edit.
750 Springer

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



762

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

767

768 **Tables**

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

	Site			Year		Site*Year	
	N	F (df)	p	F (df)	p	F (df)	p
Hatching date (From March 1st)	N=204	4.98 (1,197)	0.03	37.84(3,197)	<0.001	3.86 (3,193)	0.01
Clutch size	N=230	45.08 (1, 227)	<0.001	0.56 (3, 227)	0.64		
Hatching rate	N=226	6.34 (1, 212)	0.012	12.87 (3, 212)	<0.001		
Fledging rate	N=198	2.26 (1, 191)	0.13	6.47 (3, 191)	<0.001	5.06 (3, 191)	<0.001
Nestling number (before fledge)	N=224	6.45 (1, 217)	0.01	2.08 (3, 217)	0.10	2.53 (3, 217)	0.06

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

773

774 **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 X ² (df)	p	N=198 X ² (df)	p	N=217 X ² (df)	p
Site	11.31 (1, 210)	0.03	6.14 (1,189)	0.04	29.86 (1,199)	<0.001
PC1	0.06 (1, 210)	0.80	0.04 (1,189)	0.82	0.22 (1,199)	0.64
PC2			6.25 (1,189)	0.01	8.01 (1,199)	0.004
Hatching date	4.02 (1, 210)	0.05	0.32 (1,189)	0.57	0.054 (1,199)	0.81
Site*PC1	6.25 (1,210)	0.01				
Site*PC2			5.57 (1,189)	0.03	7.37 (1,199)	0.007

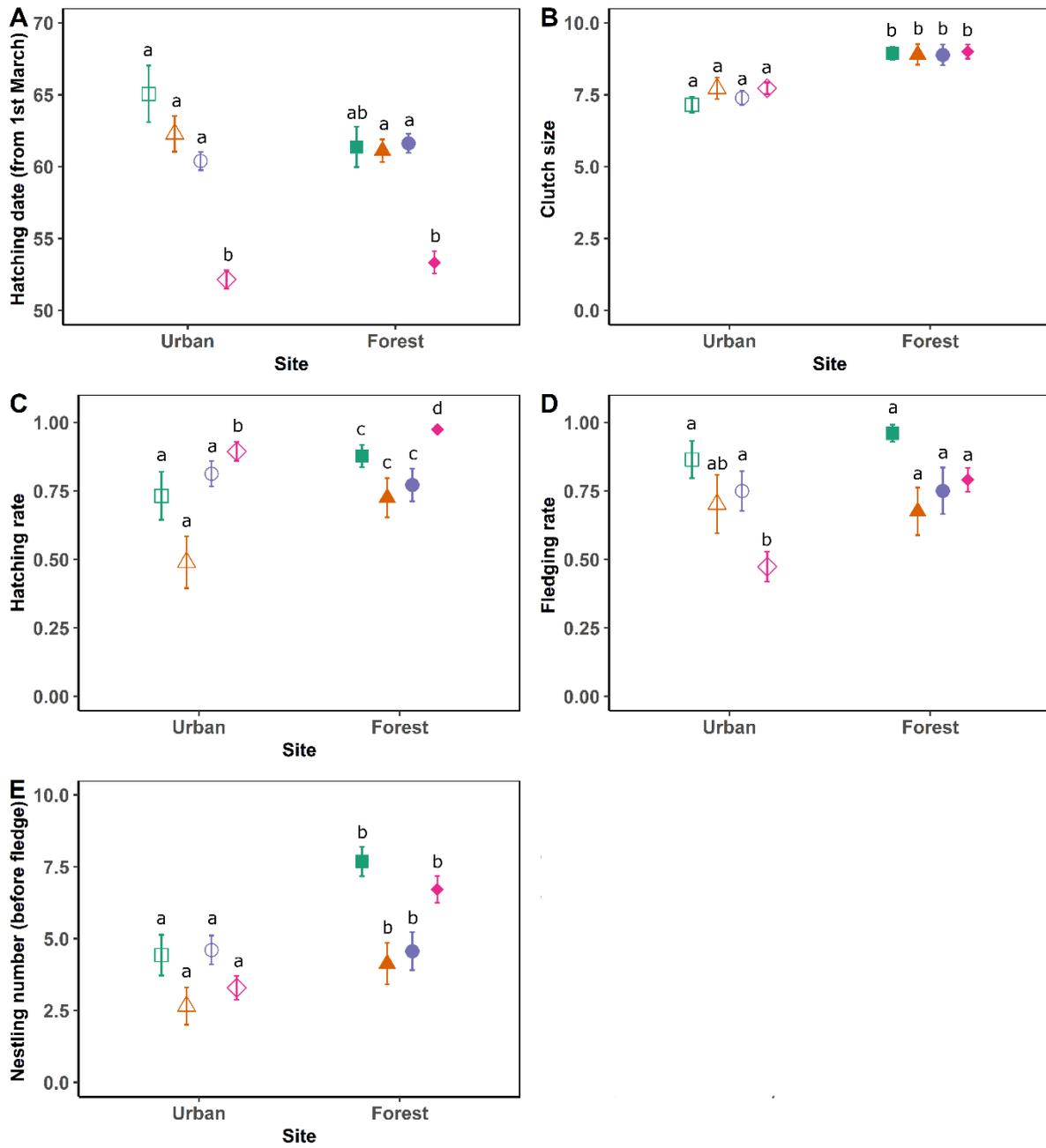
775 df = degree of freedom. These results were obtained using generalized linear models followed by the type III Wald
 776 test. See the Methods section for further details.

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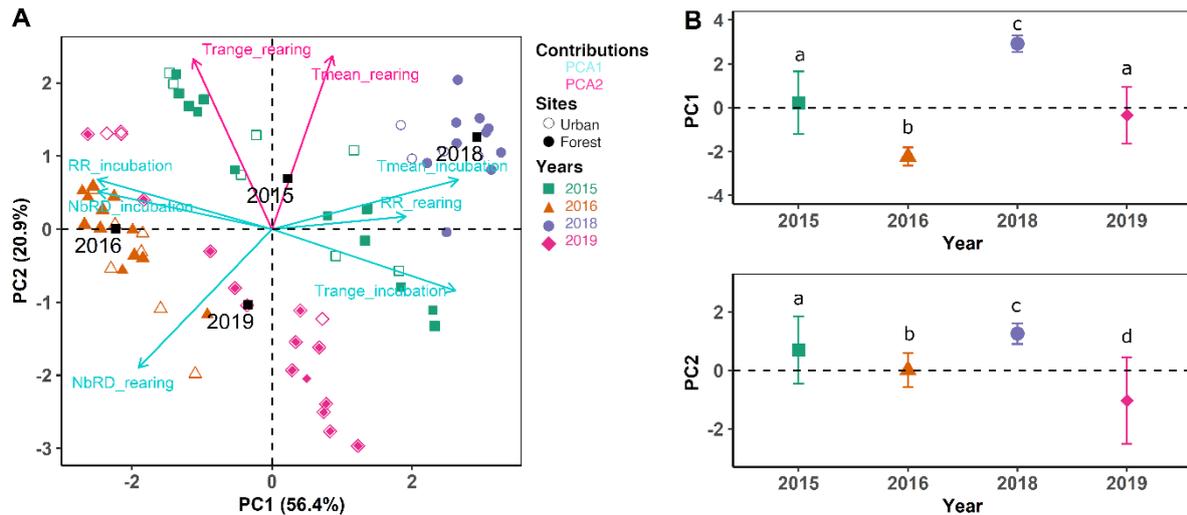
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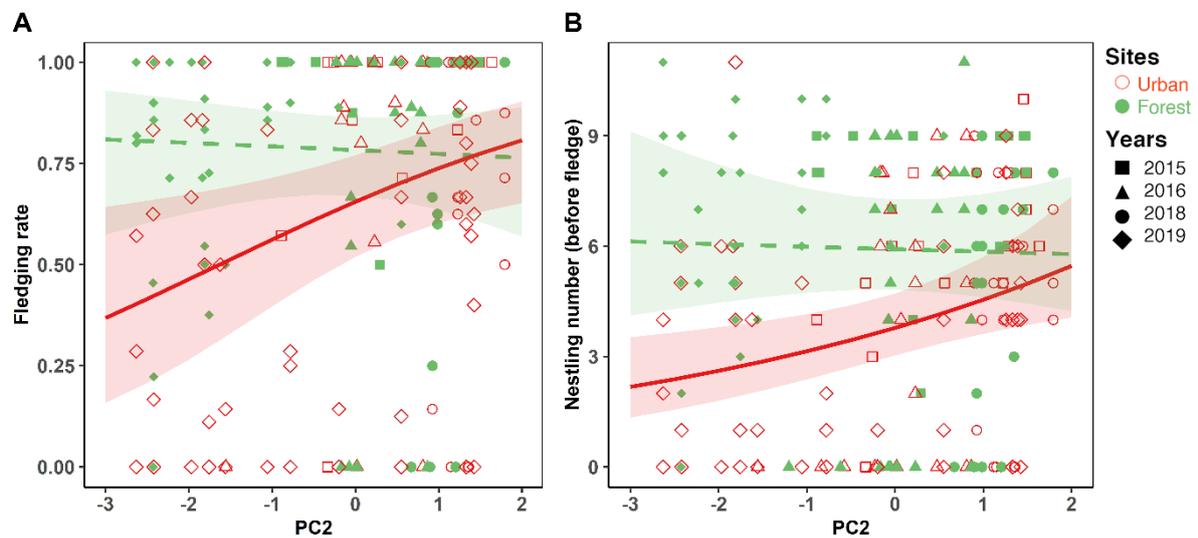
Fig. 3 Reproductive parameters for birds at urban and forest sites across the years. For post-hoc tests, we tested differences between years for a given site and also differences between sites for a given year. Different letters illustrate significant differences. Results are shown as means and standard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



787

788 **Fig. 4** Representation of (A) PCA of weather parameters during the reproduction of birds and (B) inter-annual
 789 differences on PC1 and PC2. See Appendix E for details of each variable contribution for A. Mean coordinates of
 790 each site are represented by black squares. T_{mean} corresponds to average temperatures ($^{\circ}C$), T_{range} corresponds to
 791 average daily temperature range ($^{\circ}C$), RR corresponds to the average daily rainfall rate (in mm) and NbRD the
 792 number of rainy days ($RR > 0$) during rearing or incubation. In B, different letters represent significant differences
 793 in post-hoc tests. Results are shown as means and standard deviations.

794



795

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

799