

1 **Silver spoon effect: Natal noise is associated with telomere dynamics in**  
2 **adult birds**

3

4 **Authors:** (^shared correspondence; \*equal/joint last-authorship)

5 1. Yuheng Sun^

6 Groningen Institute for Evolutionary Life Sciences, University of Groningen, Linnaeusborg,  
7 Groningen, the Netherlands

8 School of Natural Sciences, Faculty of Science and Engineering, Macquarie University,  
9 Sydney, New South Wales, Australia

10 yuhengsun0@gmail.com

11 2. Terry Burke

12 Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield, Sheffield,  
13 United Kingdom

14 t.a.burke@sheffield.ac.uk

15 3. Julia Schroeder\*

16 Department of Life Sciences, Imperial College London, Silwood Park, Ascot, Berkshire, UK

17 julia.schroeder@imperial.ac.uk

18 4. Hannah L Dugdale\*^

19 Groningen Institute for Evolutionary Life Sciences, University of Groningen, Linnaeusborg,  
20 Groningen, the Netherlands

21 h.l.dugdale@rug.nl

22

23 **Running title: Natal noise effects on fitness**

24

25 **Keywords:** house sparrows, anthropogenic noise, life history plasticity, adaptation, incubation  
26 environment, prenatal environment, pre-hatching environment, early-life environment stress, cross-  
27 fostering, intergenerational effects

28

29 **Corresponding authors:**

30 Yuheng Sun: School of Natural Sciences, Faculty of Science and Engineering, Macquarie University,  
31 205a Culloden Rd, 2113 Sydney, New South Wales, Australia. TEL: +61 (0)490 503 836. E-mail:  
32 yuhengsun0@gmail.com

33 Hannah L. Dugdale: Groningen Institute of Evolutionary Life Sciences (GELIFES), University of  
34 Groningen, Nijenborgh 7, 9747 AG Groningen, Netherlands. TEL: +31 (0)50 363 9683. E-mail:  
35 h.l.dugdale@rug.nl

36

37 **Abstract**

38 Anthropogenic noise disturbance on wildlife is of growing concern. Environmental noise during  
39 incubation can negatively impact fitness in wild animal populations. Here, we hypothesised that  
40 chronic noise introduces stress through oxidative damage to wild bird embryos, resulting in short-term  
41 fitness reductions and long-term physiological changes. To test this hypothesis, we investigated the  
42 effects of chronic noise on chick body condition, fledging success, and adult telomere shortening in  
43 wild house sparrows *Passer domesticus*, using 13 years of data. We disentangled the effects of noise  
44 in the natal and rearing environments using cross-fostering. We found no evidence of an association  
45 between natal noise and chick mass, body condition at fledging, and fledging success. However,  
46 adults with shorter telomeres were underrepresented at older ages when they were incubated in  
47 chronic noise conditions. Such a silver spoon effect of early-life noise pollution has implications for  
48 the management of wild populations.

49

## 50 **Introduction**

51 Anthropogenic noise has profound impacts on wildlife, ranging from alterations in individual  
52 behaviours to changes in the structure of ecological communities (for an overview see Shannon et al.,  
53 2016). Importantly, chronic noise pollution experienced in early life can introduce a silver spoon  
54 effect to individuals, referring to lasting deficits due to an adverse developmental environment  
55 (Grafen, 1988). Long-term consequences associated with early-life noise include impaired body  
56 development (de Soto et al., 2013; Nedelec et al., 2015), accelerated reproductive schedules (Sun et  
57 al., 2025), and reduced lifetime reproductive output (Meillère et al., 2024; Sun et al., 2025). These  
58 lifetime fitness impacts could be introduced directly by stress effects through noise, even without any  
59 change of parental behaviour due to noise (Meillère et al., 2024).

60 The effects of noise during development can stem not only from the environment where the animal  
61 was reared but also from the maternal environment during pregnancy or *in ovo*. In mammals, such as  
62 humans (Vincens & Persson Waye, 2023), mice (Jafari et al., 2017) and rats (Kim et al., 2006),  
63 studies mainly focus on the consequences of prenatal environmental noise on auditory development,  
64 cognition or psychology, with a few studies finding associations with increased risks of congenital  
65 anomalies (e.g. Dzhambov et al., 2014; Ward et al., 1970). Yet, whether noise exposure during  
66 pregnancy is associated with perinatal mortality in mammals is unresolved (reviewed in Vincens &  
67 Persson Waye, 2023). In oviparous animals, noise in the pre-hatching environment can impair  
68 physiology (Meillère et al., 2024) and somatic development (Kesar, 2014; Meillère et al., 2024;  
69 Nedelec et al., 2014), and even lead to increased embryo mortality. The negative effect of noise in the  
70 pre-hatching environment on reproductive output can even be stronger than the effect of post-hatching  
71 noise (Meillère et al., 2024). These effects of natal noise can indirectly affect embryos through altered  
72 incubation behaviours of the parents induced by noise (Viigipuu et al., 2023) or directly affect the  
73 embryos (Kesar, 2014; Meillère et al., 2024).

74 Noise could introduce negative consequences by mediating the oxidative stress pathways (Manukyan,  
75 2022; Münzel & Daiber, 2018). Telomere length is a biomarker that can reflect oxidative stress,

76 although there are mixed results on the association between oxidative stress and telomere dynamics  
77 (Armstrong & Boonekamp, 2023; Reichert & Stier, 2017). Telomeres are repeating DNA sequences  
78 (TTAGGG) capping the ends of linear chromosomes (Blackburn, 1991). They protect the linear  
79 chromosomes from shortening due to the end-replication problem during cell divisions or due to  
80 oxidative stress (Houben et al., 2008; Levy et al., 1992), with short telomeres associated with high  
81 mortality (Wilbourn et al., 2018). In some bird species, early-life anthropogenic noise is associated  
82 with accelerated telomere shortening (e.g. Dorado-Correa et al., 2018; Grunst et al., 2020; Injaian et  
83 al., 2019). However, previous studies have not disentangled the effects of noise exposure during  
84 incubation from those arising in the rearing environment, on telomere shortening (except that Meillère  
85 et al., 2024 tested for telomere length). Stages before and just after hatching could play a key role in  
86 telomere dynamics (Xiong et al., 2025).

87 Lifetime fitness consequences of natal noise exposure can be sex-specific. For example, female but  
88 not male house sparrows (*Passer domesticus*) hatched in a noisy environment had reduced lifetime  
89 reproductive output, controlling for the noise in their rearing environment (Sun et al. 2025). We  
90 hypothesise that noise in their natal environment leads to stress that negatively impacts the embryos.  
91 The stress has sex-specific long-term outcomes on reproduction, possibly because oocytes form at the  
92 embryo stage while sperm form after sexual maturity (Aire, 2014; Johnson, 2014). Additionally,  
93 although noise in the rearing environment reduced overall chick mass and fledging success due to  
94 reduced provisioning rates, whether noise in the natal environment affects chick mass and fledging  
95 success remains unexplored (Schroeder et al., 2012).

96 We investigated the short- and long-term effects of natal environmental noise in a wild bird  
97 population. We disentangled the effects of natal and rearing environments using a multi-year cross-  
98 fostering experiment. We tested short-term effects of natal noise on chick mass, body condition at  
99 fledging, and fledging success, predicting that these would be lower in noisy compared to quiet natal  
100 environments. We then tested long-term effects of natal noise on adult telomere shortening, predicting  
101 that noise would lead to faster telomere shortening in adulthood. We also tested whether the effect on  
102 telomere shortening differed between females and males.

103

## 104 **Material and methods**

### 105 *Study population*

106 We used data from wild house sparrows hatched between 2000-2012 on Lundy Island (51°10'N,  
107 4°40'W). This population has been systematically monitored for breeding activities and survival since  
108 2000. Nest boxes were placed in and near the village. During breeding seasons (April—August), all  
109 nest boxes and known natural nests have been checked routinely for nest-building activities. Once a  
110 nest was complete, it was checked every second day for eggs, and after the 12<sup>th</sup> day after laying, it  
111 was checked every day for hatchlings, and therefore precise hatching dates are known (Cleasby et al.,  
112 2010). Birds were typically ringed on the 12<sup>th</sup> day after hatching, each with a unique combination of  
113 three colour rings and a numbered metal ring from the British Trust for Ornithology, allowing  
114 individual identification upon sighting and recapture. The few birds that were not caught this way  
115 were ringed as first-year juveniles, captured with walk-in traps or mist nets during the breeding  
116 seasons and one or two weeks in the winter. More than 99% of birds were ringed within their first  
117 year and are therefore of known age (Schroeder et al., 2015). Sightings and recaptures were carried  
118 out throughout the breeding seasons and for the one or two weeks each winter, with an annual re-  
119 sighting rate of 0.96 (95% CI: 0.95-0.97, Simons et al., 2019).

120 Cross-fostering experiments were carried out routinely between same-aged broods during 2000–2012,  
121 except in 2008 and 2010, due to a low population size (Winney et al., 2015). Chicks were typically  
122 swapped when they were two days old, except that in 2000-2003, cross-fostering occurred at three  
123 days old (Cleasby et al., 2010). Broods were swapped entirely, or partially if that was required to  
124 maintain the original brood size. Depending on the location of the same-aged brood(s), cross-fostering  
125 occurred within or between noisy and quiet areas. Chicks remained in their foster broods until they  
126 fledged. There was no evidence for kin recognition, and parent birds did not alter their parental care  
127 behaviour to cross-fostered broods (Lattore et al., 2019).

128

129 ***Noise impact***

130 Around a quarter of the nest boxes (29 in 2008, 28 in 2023) were impacted by chronic background  
131 noise from a set of power generators. These generators ran each day between 06:00-24:00 (Schroeder  
132 et al., 2012). The low-frequency noise produced by these generators reverberates in the surrounding  
133 area, a semi-open workshop with corrugated roofing and stone walls, with a permanently open gate  
134 and a louvered window allowing the birds access (Sun et al., 2025). The noise level in this area was at  
135 68dB, and significantly higher than at other breeding sites (Schroeder, et al. 2012), and they are  
136 hereby defined as “noisy” and “quiet” areas, respectively (Fig. 1). Territory and parent quality did not  
137 significantly differ between noisy and quiet areas (Schroeder, et al. 2012). Sound insulation was  
138 added in 2013 to reduce the noise level in the workshop because provisioning behaviour of the house  
139 sparrow females was disturbed by the noise (Schroeder et al. 2012; Sun et al., 2025). Therefore, we  
140 only included birds hatched before 2013 to keep the natal noise at a constant level. All birds in this  
141 dataset died by the end of 2022.

142

143 ***Data collection***

144 We weighed chicks at the ages of 2, 6 and 12 days with an electronic scale, but occasionally we  
145 weighed chicks one day earlier or later or on day 14, depending on their growth. We measured tarsus  
146 length at the last nest visit. Chicks that survived to the last nest visit were considered fledged. We  
147 measured relative telomere length (RTL) from blood samples collected from the birds upon  
148 subsequent captures. Sampling frequency for RTL per bird per year ranged between one to five (Chik  
149 et al., 2024). Detailed methods for quantifying RTL and the resulting dataset are provided in Chik et  
150 al. 2024. In summary, we used a monochrome multiplex quantitative polymerase chain reaction  
151 (MMqPCR) and RTL was expressed in a ratio of telomeric signals to that of a single-copy reference  
152 gene (GAPDH; Chik et al., 2024). The intra-plate, between-duplicate repeatability of RTL was 95.7%  
153 (s.e. = 0.2%); and the inter-plate repeatability was 97.7% (s.e. = 0.9%; Chik et al., 2024). In this

154 population, RTL declines linearly with age within an individual and its individual repeatability was  
155 14.0% (95% CI: 9.1%-19.9%; Chik et al., 2025).

156

### 157 *Statistical analyses*

158 We used Bayesian generalised linear mixed models (GLMMs) to test the effect of natal noise on chick  
159 body mass, body condition at fledging, fledging success, and adult RTL, with *RStan* 2.32.7 (Stan  
160 Development Team, 2025) and *brms* 2.21.0 (Bürkner, 2021) in R 4.4.3 (R Core Team, 2025). For  
161 chick body mass and fledging success, we used a dataset that only contained cross-fostered chicks to  
162 reduce collinearity between natal and rearing environments, which contained 4,143 mass measures  
163 from 1,810 chicks. Body condition at fledging was a subset of this dataset, which only contained  
164 individuals that survived to the last nest visit and had 1,170 measures from 1,170 individuals. Adult  
165 RTL had a much smaller dataset, so we used all 1,236 adult RTL measures from 652 individuals,  
166 including both cross-fostered and non-cross-fostered individuals, to ensure a sufficient sample size.

167

### 168 *Chick mass*

169 We fitted a GLMM with standardised chick mass as the response variable with a Gaussian residual  
170 distribution, and the following variables as fixed effects: presence of noise in the natal environment (1  
171 = present, 0 = absent), presence of noise in the rearing environment (1 = present, 0 = absent), age  
172 (days), brood size (continuous). Brood size was included to control for the effect that chicks from  
173 larger broods were lighter (Cleasby et al., 2011). Sex was not included because the sexes of chicks  
174 that died before we blood sampled them were unknown. The model included the following random  
175 effects: bird ID, to account for the nonindependence of the mass measured for the same chick at  
176 different ages; natal brood ID, to account for the genetic factors that individuals hatched in the same  
177 brood might share (Schroeder et al., 2012); cohort, to account for annual stochasticity. Rearing brood  
178 ID was not included because only cross-fostered individuals were included in this dataset, and thus  
179 rearing brood ID was perfectly correlated with natal brood ID and would explain the same variance.

180

181 *Body condition at fledging*

182 To ensure that the effect of noise was assessed on chick body condition rather than raw body mass,  
183 which could be confounded by skeletal size (Labocha & Hayes, 2012), we fitted a GLMM using a  
184 reduced dataset that included only the measurement taken right before fledging—prior to which tarsus  
185 length was not measured. This model used the same response variable, fixed and random structures as  
186 the chick mass model, except that tarsus length and sex (0 = female, 1 = male) were included as fixed  
187 effects to control for the effects of skeletal size and sex (Cleasby et al., 2011). The random effect bird  
188 ID was removed because each bird was measured only once.

189

190 *Fledging success*

191 We fitted fledging success as the response variable (1 = fledged, 0 = failed to fledge) with a Bernoulli  
192 distribution, and the same fixed and random structure as for the chick mass model. Brood size was  
193 kept in the model to account for the effect that chicks were less likely to fledge as brood size  
194 increased (Cleasby et al., 2010). Bird ID was not modelled as a random effect because there was one  
195 observation per bird.

196

197 *Adult telomere shortening and sex-specific effect*

198 Adult RTL was z-standardised (zRTL) for comparability with other studies (Verhulst, 2020). We  
199 modeled zRTL as the response variable, with a skew-normal distribution to account for the skewness  
200 of the data (Bürkner, 2021). We fitted the presence of noise in the natal environment (1 = present, 0 =  
201 absent) and age (in years) as fixed effects, and their interaction (natal environment \* age) was fitted to  
202 test whether the change in zRTL with age was dependent on the noise presence in the natal  
203 environment. We included age<sup>2</sup> and natal environment \* age<sup>2</sup> to allow the age effect to be non-linear.  
204 We also included the interaction between the natal environment and sex (0 = female, 1 = male) to test

205 whether the natal noise affected males and females differently. The GLMM also included the fixed  
206 effects of blood storage time (blood age, years) and its squared term (blood age<sup>2</sup>), to control for the  
207 effect of the duration for which the samples were stored as whole blood (Chik et al., 2025; Sibma,  
208 2021); DNA storage time (DNA age, years) and its squared term (DNA age<sup>2</sup>), to control the effect of  
209 duration for which the samples were stored as extracted DNA (Chik et al., 2025; Sibma, 2021);  
210 technician identity ( $A = 0, B = 1$ ), to control for the effect of technician performing the laboratory  
211 experiments; age of the genetic father (paternal age at conception, PAC), to control for the potential  
212 effect of PAC on RTL, which was previously found in other species (Eisenberg & Kuzawa, 2018;  
213 Sparks et al., 2022); the interaction between PAC and offspring sex, to account for sex-specific PAC  
214 effect (Bennett et al., 2022). Random effects included bird ID, to account for the nonindependence of  
215 the RTL measures from the same individual; plate, to account for the plate effect in the qPCR (Chik et  
216 al., 2024); year of sampling, to account for the variance introduced by year-dependent environmental  
217 factors (Simons et al., 2019); natal brood ID, to control for the effect that chicks hatched in the same  
218 brood had similar genetic backgrounds; and rearing brood ID, to control for the effect of the quality of  
219 parental care. We removed non-significant interactions from the zRTL model, least significant first  
220 based on the probability of direction, to facilitate interpretation of first-order effects. To account for  
221 the effect of maternal age at conception (MAC) on zRTL (Marasco et al., 2019), we built a separate  
222 model with PAC substituted with MAC, to avoid collinearity from age-assortative mating, and  
223 followed the same procedure to remove non-significant interactions. To account for the impacts of  
224 outliers on the model result, we carried out leave-one-out cross-validation (LOO) using *loo* 2.9.0  
225 (Vehtari et al., 2015).

226 To examine whether the significant interaction of natal environment \* age detected by the previous  
227 model was due to a between-individual effect or a within-individual effect, we decomposed age in the  
228 final zRTL model into two components: mean age (mean of the ages that each individual appeared in  
229 the dataset) and  $\Delta$ age (age – mean age) (van de Pol & Wright, 2009). This decomposition allowed  
230 mean age to capture between-individual differences—i.e., whether individuals that tend to live longer  
231 also differ in average RTL—while  $\Delta$ age captures the within-individual change in RTL with age. We

232 included both natal environment \* mean age and natal environment \*  $\Delta$ age in the model to identify  
233 which effect natal environment interacted with. We then removed natal environment \*  $\Delta$ age because  
234 it was not significant, to facilitate interpretation of first-order effects.

235 We z-standardised all continuous predictors to facilitate model convergence and to ensure that  
236 predictions remained within a biologically interpretable range. We checked collinearity and ensured  
237 that the VIF for all continuous predictors was  $<3$  (Zuur et al., 2009). We used weakly informative  
238 priors in all models (Table S1). We ran all models for four chains, each with 2,000 iterations after a  
239 warm-up of 2,000 iterations. For modelling body condition at fledging, we increased the drift rate  
240 parameter 'delta' to 0.95 to reduce divergent transitions after warm-up, which is within the  
241 recommended range of 0.8 to 1 (Bürkner, 2021). The R hat parameters for all predictors were 1.00,  
242 and the Monte Carlo standard errors (MCSE) for posterior means were  $<0.01$ , indicating stable  
243 estimates. The model fit was then checked by visually inspecting the density and trace plots generated  
244 by the plot function and the posterior predictive plot generated by the pp\_check function in *brms*. All  
245 models showed satisfactory convergence and fit, except for the zRTL model, where the posterior  
246 predictive plot indicated a poor match to the skewed observed data (Fig. S1). Table S2 presents a  
247 summary of the posterior distribution of this model.

248

## 249 **Results**

250 Natal noise did not significantly affect chick mass, body condition at fledging, or fledging success  
251 (Table 1, Fig. 2). Noise in the rearing environment significantly reduced chick mass and body  
252 condition at fledging, and marginally reduced fledging success (Table 1, Fig. 2). The larger the brood  
253 was, the lighter the chicks were, but brood size did not predict body condition at fledging or fledging  
254 success (Table 1, Fig. 2). Chick mass increased with age (Table 1, Fig. 2a). Male chicks were heavier  
255 at fledging, when controlling for tarsus length (Table 1, Fig. 2b).

256 The age effect on adult RTL at old ages was significantly more positive for birds from a noisy natal  
257 environment than it was for birds from a quiet natal environment (Table 2, Fig. 3a). Although the

258 posterior predictive plot showed a suboptimal match to the observed data distribution (Fig. S1), the R  
259 hat parameters and MCSEs indicated stable posterior estimates, suggesting that the model captured  
260 the trend of the data, and parameter estimates and credible intervals can be interpreted with  
261 confidence regarding their direction and relative strength. The model using MAC instead of PAC led  
262 to the same conclusion (Table S4-5), confirming an environmental effect. The LOO identified two  
263 data points with the shape parameter  $k > 1$ , indicating outsized influence of these observations on the  
264 posterior distribution of the model (Vehtari et al., 2017). Removing these two observations let the  
265 credible interval (CrI) of the interaction natal environment \* age border zero (CrI: [-0.00, 0.17]), but  
266 the trend persisted that the age effect was more positive for old birds from a noisy natal environment  
267 than it was for those from a quiet natal environment. We retained these data points in the model  
268 because they were real observations (Fig. S2).

269 The model decomposing age into mean age and  $\Delta$ age indicated that this effect was a between-  
270 individual age effect in response to natal noise: in birds from a noisy natal environment, telomere  
271 length was longer in long-lived birds than it was in short-lived birds, yet this was not the case for  
272 birds from a quiet natal environment (Table 3, Fig. 3b). The interaction between  $\Delta$ age and natal  
273 environment was not significant, indicating that natal noise did not affect the within-individual  
274 telomere shortening rate with age (Table 3). Adult zRTL changed quadratically as  $\Delta$ age increased  
275 (Table 3, Fig. S3).

276

## 277 **Discussion**

278 Natal noise exposure did not predict short-term fitness components, including chick mass, body  
279 condition at fledging, and fledging success. However, we observed a positive effect of the interaction  
280 between natal noise exposure and age on adult telomere length, which was accounted for by between-  
281 individual differences. This indicates selected disappearance—among individuals exposed to natal  
282 noise, those who lived longer tended to also have longer telomeres. We did not observe sex-specific  
283 effects of natal noise on adult telomere shortening.

284 Natal noise exposure did not affect chicks' short-term fitness in our study. Studies specifically testing  
285 the effect of pre-hatching noise on chicks are lacking (except for Kesar, 2014 and Meillère et al.,  
286 2024). Post-hatching or combined pre- and post-hatching environmental noise can affect  
287 corticosterone levels, growth, and body conditions in nestlings in some studies (Injaian et al., 2019;  
288 Injaian, Taff, & Patricelli, 2018; Injaian, Taff, Pearson, et al., 2018), but other studies also found no  
289 support for such effects (Angelier et al., 2016) or even effects contrary to expectations (Crino et al.,  
290 2013). In particular, a previous study in house sparrows measuring corticosterone stress response  
291 found no evidence that chicks exposed to noise during the breeding season (including pre- and post-  
292 hatching stages) suffered from chronic stress (Angelier et al., 2016). It was speculated that this  
293 resistance to noise disturbance might be a characteristic of house sparrows as urban exploiters  
294 (Angelier et al., 2016). Selective disappearance in embryos could also mask the negative effect of  
295 natal noise—i.e., low-quality embryos that died in the noisy environment before they could hatch. The  
296 deleteriousness of noise on embryonic development and survival has been reported in many species,  
297 including birds (Meillère et al., 2024; Potvin & MacDougall-Shackleton, 2015; Williams et al., 2021)  
298 and invertebrates (Nedelec et al., 2014). In our population, however, we do not have sufficient data on  
299 hatching success to test this hypothesis. There was no significant difference in the number of  
300 hatchlings per brood in quiet and noisy environments (t-test,  $p = 0.44$ ), implying no effect of  
301 environmental noise on embryonic survival. However, further studies on whether natal noise is  
302 detrimental to embryonic development are needed to confirm this implication and to help us  
303 understand the mechanisms underlying the natal noise effect in this population.

304 Noise in the rearing environment, on the other hand, had a negative effect on chick mass and body  
305 condition at fledging, and a marginal negative effect on fledging success in our study. Together with  
306 the findings in the same population that noise in the rearing environment was associated with reduced  
307 fledging success, body mass at day 12, and recruitment rate (Schroeder et al., 2012), our study  
308 confirmed the negative short-term fitness consequences of rearing environmental noise in this  
309 population. This is because noise acoustically masked the parent-offspring communications, leading  
310 to reduced provisioning (Schroeder et al., 2012). In summary, the short-term fitness consequences

311 were attributed to the noise exposure in the rearing, rather than the natal environment, in our  
312 population.

313 Brood size was negatively associated with chick mass, in line with a previous study (Cleasby et al.,  
314 2011). However, brood size did not predict fledging success or body condition among fledglings. It is  
315 possible that chicks from larger broods were smaller in skeletal size, which has been observed in  
316 studies using brood size manipulation or food supplements (Cleasby et al., 2011; Hōrak, 2003; Smith  
317 et al., 1989), but not in a study using natural brood size variation (Howard, 1980). Alternatively,  
318 although fledging success did not differ by brood sizes, only chicks with good body condition might  
319 have survived in large broods. Future studies investigating the selective disappearance resulting from  
320 within-brood competition will help tackle this question.

321 We observed a positive interaction between the effects of natal noise and age on adult telomere  
322 length. We revealed that this was due to selective disappearance—i.e., birds that experienced natal  
323 noise and that had longer telomeres lived longer, rather than that telomeres lengthened as an  
324 individual aged (Fig. 3b & S3). As such, birds with shorter telomeres were more likely to disappear  
325 from the population if incubated in the noisy environment. Previous work in the study population  
326 showed that adults with shorter telomeres died earlier, leading to a bias for longer telomeres in older  
327 individuals (Sibma, 2021). Given that telomere length is a biomarker of oxidative stress (Reichert &  
328 Stier, 2017), our finding suggests that individuals from a noisy natal environment might be more  
329 likely to die under oxidative stress of the same intensity than those from a quiet natal environment.  
330 Together with the finding that natal noise was associated with reduced annual reproductive output  
331 (Sun et al. 2025), this suggests that natal exposure to noise is a cause of lifetime physiological  
332 consequences, aligning with the prediction of the silver spoon hypothesis. Our cross-fostering  
333 experiments were not conducted until the second day after hatching. It is possible that the disturbance  
334 of the parents' provisioning behaviour in the first two days played a critical role, as human studies  
335 have shown that provision of nutrition in a very early stage of life could be associated with growth  
336 and neurodevelopmental outcome on some occasions (Poindexter et al., 2006).

337 Adult telomere length first decreased and then slightly increased as an individual aged, and this  
338 within-individual age effect was not affected by the presence of natal environmental noise. Although a  
339 previous study in the same population found a linear relationship between adult RTL and within-  
340 individual-centred age (Chik et al., 2025), the quadratic term in our study was of small effect size  
341 (0.01, with the 95% CrI bordering 0), thus confirming the previous study (Fig. S3 in this study vs. Fig.  
342 1 in Chik et al., 2025). As for whether pre-hatching environmental noise affects telomere dynamics, a  
343 study in Australian zebra finches *Taeniopygia guttata castanotis* found that adult telomeres were  
344 shorter in birds incubated in a noisy environment than in those incubated in a quiet environment, but  
345 the age effect and its interaction with noise were not investigated (Meillère et al., 2024). Although not  
346 on the effect of noise, another study in *Taeniopygia guttata* highlighted a determinant effect of  
347 telomere shortening rate before and just after hatching on post-hatching telomere length (Xiong et al.,  
348 2025). Other studies found negative effects of noise on telomere length, but they focused on nestling  
349 instead of adult telomere lengths and did not separate natal and rearing effects (Grunst et al., 2020;  
350 Injaian et al., 2019; Meillère et al., 2015). We propose two explanations regarding the absence of an  
351 effect of natal noise on within-individual telomere shortening in adulthood in our study. First, because  
352 telomere lengths are considered to reflect cumulative oxidative damage (Boonekamp et al., 2013;  
353 Houben et al., 2008), the effects of natal factors might be diluted as the birds get older. This could be  
354 resolved by measuring nestling telomere lengths. Second, unlike zebra finches, which inhabit  
355 grasslands and open or grassy woodlands with some proportion of inhabitation in cultivated areas  
356 (Payne, 2020), house sparrows are a successful human-commensal species (Ravinet et al., 2018) and  
357 may be more resistant to anthropogenic disturbance such as noise.

358 We did not detect a sex-specific effect of natal noise exposure on body condition at fledging or adult  
359 telomere length, even though natal noise exposure was associated with a significant reduction  
360 specifically in female lifetime reproductive output in this population (Sun et al., 2025). Our results  
361 suggest that the decline in female reproductive performance might not be mediated by a deterioration  
362 in somatic condition. A plausible explanation is that individuals allocated more resources to somatic  
363 maintenance at the cost of future reproductive success under noise stress during embryonic

364 development to maximise lifetime fitness (Kirkwood, 2002). A meta-analysis showed that the  
365 adverse effects of developmental environments were reflected by a faster decline in late-life  
366 reproduction instead of survival, presumably due to the same reason (Cooper & Kruuk, 2018). Male  
367 reproduction is less energetically demanding than female reproduction, which may explain why it was  
368 not detectably affected by natal noise exposure. This life history plasticity to maintain body condition  
369 and survival in response to noise stress during development at the expense of adult reproductive  
370 output might again be one of the manifestations of the superiority of house sparrows to adapt to  
371 human-commensal niches. This might be a direction for future studies to explore.

372 In conclusion, we found that natal noise altered the age-telomere relationship in adulthood, indicating  
373 its potential long-lasting physiological effects. Future studies on the direct effect of noise disturbance  
374 on development, as well as studies on long-term consequences of other natal stressors, will be  
375 valuable for understanding the nature of these long-lasting effects and the mechanisms underlying  
376 them. We also note that the absence of a detectable effect of natal noise on somatic condition in house  
377 sparrows may be attributable to their characteristics as a successful human-commensal.

378

## 379 **Acknowledgements**

380 We sincerely thank Dr Maaïke A Versteegh, Dr Euan Young, and Xia Zhan for their helpful feedback  
381 on the first draft of this manuscript. We thank Prof Ido Pen for his thorough feedback on the statistics  
382 and code. We thank members of the Dugdale Research Group for insightful discussion on this study.

383

## 384 **References**

385 Aire, T. A. (2014). Spermiogenesis in birds. *Spermatogenesis*, 4(3), e959392.  
386 <https://doi.org/10.4161/21565554.2014.959392>

387 Angelier, F., Meillère, A., Grace, J. K., Trouvé, C., & Brischoux, F. (2016). No evidence for an effect of  
388 traffic noise on the development of the corticosterone stress response in an urban exploiter. *General  
389 and Comparative Endocrinology*, 232, 43–50. <https://doi.org/10.1016/j.ygcen.2015.12.007>

390 Armstrong, E., & Boonekamp, J. (2023). Does oxidative stress shorten telomeres in vivo? A meta-  
391 analysis. *Ageing Research Reviews*, 85, 101854. <https://doi.org/10.1016/j.arr.2023.101854>

392 Belmaker, A., Hallinger, K. K., Glynn, R. A., Winkler, D. W., & Hausmann, M. F. (2019). The  
393 environmental and genetic determinants of chick telomere length in Tree Swallows (*Tachycineta*  
394 *bicolor*). *Ecology and Evolution*, 9(14), 8175–8186. <https://doi.org/10.1002/ece3.5386>

395 Bennett, S., Girndt, A., Sánchez-Tójar, A., Burke, T., Simons, M., & Schroeder, J. (2022). Evidence of  
396 paternal effects on telomere length increases in early life. *Frontiers in Genetics*, 13.  
397 <https://doi.org/10.3389/fgene.2022.880455>

398 Blackburn, E. H. (1991). Structure and function of telomeres. *Nature*, 350(6319), 569–573.  
399 <https://doi.org/10.1038/350569a0>

400 Boonekamp, J. J., Simons, M. J. P., Hemerik, L., & Verhulst, S. (2013). Telomere length behaves as  
401 biomarker of somatic redundancy rather than biological age. *Aging Cell*, 12(2), 330–332.  
402 <https://doi.org/10.1111/accel.12050>

403 Bürkner, P.-C. (2021). Bayesian Item Response Modeling in R with **brms** and *Stan*. *Journal of*  
404 *Statistical Software*, 100(5). <https://doi.org/10.18637/jss.v100.i05>

405 Chik, H. Y. J., Mannarelli, M., Dos Remedios, N., Simons, M. J. P., Burke, T., Schroeder, J., & Dugdale,  
406 H. L. (2024). Adult telomere length is positively correlated with survival and lifetime reproductive  
407 success in a wild passerine. *Molecular Ecology*, 33(15), e17455. <https://doi.org/10.1111/mec.17455>

408 Chik, H. Y. J., Sibma, A., Mannarelli, M.-E., Dos Remedios, N., Simons, M. J. P., Burke, T., Dugdale, H.  
409 L., & Schroeder, J. (2025). Heritability and age-dependent changes in genetic variation of telomere  
410 length in a wild house sparrow population. *Evolution Letters*, 9(2), 209–220.  
411 <https://doi.org/10.1093/evlett/qrae055>

412 Cleasby, I. R., Burke, T., Schroeder, J., & Nakagawa, S. (2011). Food supplements increase adult  
413 tarsus length, but not growth rate, in an island population of house sparrows (*Passer domesticus*).  
414 *BMC Research Notes*, 4(1), 431. <https://doi.org/10.1186/1756-0500-4-431>

415 Cleasby, I. R., Nakagawa, S., Gillespie, D. O. S., & Burke, T. (2010). The influence of sex and body size  
416 on nestling survival and recruitment in the house sparrow. *Biological Journal of the Linnean Society*,  
417 101(3), 680–688. <https://doi.org/10.1111/j.1095-8312.2010.01515.x>

418 Cooper, E. B., & Kruuk, L. E. B. (2018). Ageing with a silver-spoon: A meta-analysis of the effect of  
419 developmental environment on senescence. *Evolution Letters*, 2(5), 460–471.  
420 <https://doi.org/10.1002/evl3.79>

421 Crino, O. L., Johnson, E. E., Blickley, J. L., Patricelli, G. L., & Breuner, C. W. (2013). The effects of  
422 experimentally elevated traffic noise on nestling white-crowned sparrow stress physiology, immune  
423 function, and life-history. *Journal of Experimental Biology*, jeb.081109.  
424 <https://doi.org/10.1242/jeb.081109>

425 De Soto, N. A., Delorme, N., Atkins, J., Howard, S., Williams, J., & Johnson, M. (2013). Anthropogenic  
426 noise causes body malformations and delays development in marine larvae. *Scientific Reports*, 3(1),  
427 2831. <https://doi.org/10.1038/srep02831>

428 Dorado-Correa, A. M., Zollinger, S. A., Heidinger, B., & Brumm, H. (2018). Timing matters: Traffic  
429 noise accelerates telomere loss rate differently across developmental stages. *Frontiers in Zoology*,  
430 15(1), 29. <https://doi.org/10.1186/s12983-018-0275-8>

431 Dzhambov, A. M., Dimitrova, D. D., & Dimitrakova, E. D. (2014). Noise Exposure During Pregnancy,  
432 Birth Outcomes And Fetal Development: Meta-Analyses Using Quality Effects Model. *Folia Medica*,  
433 56(3), 204–214. <https://doi.org/10.2478/folmed-2014-0030>

434 Eisenberg, D. T. A., & Kuzawa, C. W. (2018). The paternal age at conception effect on offspring  
435 telomere length: Mechanistic, comparative and adaptive perspectives. *Philosophical Transactions of*  
436 *the Royal Society B: Biological Sciences*, 373(1741), 20160442.  
437 <https://doi.org/10.1098/rstb.2016.0442>

438 Grafen, A. (1988). On the Uses of Data on Lifetime Reproductive Success. *Philosophical Transactions*  
439 *of the Royal Society B: Biological Sciences*, 363, 1635–1645.

440 Grunst, M. L., Grunst, A. S., Pinxten, R., & Eens, M. (2020). Anthropogenic noise is associated with  
441 telomere length and carotenoid-based coloration in free-living nestling songbirds. *Environmental*  
442 *Pollution*, 260, 114032. <https://doi.org/10.1016/j.envpol.2020.114032>

443 Hřrak, P. (2003). When to pay the cost of reproduction? A brood size manipulation experiment in  
444 great tits (*Parus major*). *Behavioral Ecology and Sociobiology*, 54(2), 105–112.  
445 <https://doi.org/10.1007/s00265-003-0608-1>

446 Houben, J. M. J., Moonen, H. J. J., Van Schooten, F. J., & Hageman, G. J. (2008). Telomere length  
447 assessment: Biomarker of chronic oxidative stress? *Free Radical Biology and Medicine*, 44(3), 235–  
448 246. <https://doi.org/10.1016/j.freeradbiomed.2007.10.001>

449 Howard, A. R. (1980). *Growth of Nestling Ipswich Sparrows in Relation to Season, Habitat, Brood Size,*  
450 *and Parental Age.*

451 Injaian, A. S., Gonzalez-Gomez, P. L., Taff, C. C., Bird, A. K., Ziur, A. D., Patricelli, G. L., Hausmann, M.  
452 F., & Wingfield, J. C. (2019). Traffic noise exposure alters nestling physiology and telomere attrition  
453 through direct, but not maternal, effects in a free-living bird. *General and Comparative*  
454 *Endocrinology*, 276, 14–21. <https://doi.org/10.1016/j.ygcen.2019.02.017>

455 Injaian, A. S., Taff, C. C., & Patricelli, G. L. (2018). Experimental anthropogenic noise impacts avian  
456 parental behaviour, nestling growth and nestling oxidative stress. *Animal Behaviour*, 136, 31–39.  
457 <https://doi.org/10.1016/j.anbehav.2017.12.003>

458 Injaian, A. S., Taff, C. C., Pearson, K. L., Gin, M. M. Y., Patricelli, G. L., & Vitousek, M. N. (2018). Effects  
459 of experimental chronic traffic noise exposure on adult and nestling corticosterone levels, and  
460 nestling body condition in a free-living bird. *Hormones and Behavior*, 106, 19–27.  
461 <https://doi.org/10.1016/j.yhbeh.2018.07.012>

462 Jafari, Z., Mehla, J., Kolb, B. E., & Mohajerani, M. H. (2017). Prenatal noise stress impairs HPA axis  
463 and cognitive performance in mice. *Scientific Reports*, 7(1), 10560. [https://doi.org/10.1038/s41598-](https://doi.org/10.1038/s41598-017-09799-6)  
464 [017-09799-6](https://doi.org/10.1038/s41598-017-09799-6)

465 Johnson, A. L. (2014). The avian ovary and follicle development: Some comparative and practical  
466 insights. *Turkish Journal of Veterinary and Animal Sciences*, 38, 660–669.  
467 <https://doi.org/10.3906/vet-1405-6>

468 Kesar, A. (2014). Effect of prenatal chronic noise exposure on the growth and development of body  
469 and brain of chick embryo. *International Journal of Applied and Basic Medical Research*, 4(1), 3.  
470 <https://doi.org/10.4103/2229-516X.125666>

471 Kight, C. R., Saha, M. S., & Swaddle, J. P. (2012). Anthropogenic noise is associated with reductions in  
472 the productivity of breeding Eastern Bluebirds (*Sialia sialis*). *Ecological Applications*, 22(7), 1989–  
473 1996. <https://doi.org/10.1890/12-0133.1>

474 Kim, H., Lee, M.-H., Chang, H.-K., Lee, T.-H., Lee, H.-H., Shin, M.-C., Shin, M.-S., Won, R., Shin, H.-S., &  
475 Kim, C.-J. (2006). Influence of prenatal noise and music on the spatial memory and neurogenesis in  
476 the hippocampus of developing rats. *Brain and Development*, 28(2), 109–114.  
477 <https://doi.org/10.1016/j.braindev.2005.05.008>

478 Kirkwood, T. B. L. (2002). Evolution of ageing. *Mechanisms of Ageing and Development*, 123(7), 737–  
479 745. [https://doi.org/10.1016/S0047-6374\(01\)00419-5](https://doi.org/10.1016/S0047-6374(01)00419-5)

480 Labocha, M. K., & Hayes, J. P. (2012). Morphometric indices of body condition in birds: A review.  
481 *Journal of Ornithology*, 153(1), 1–22. <https://doi.org/10.1007/s10336-011-0706-1>

482 Lattore, M., Nakagawa, S., Burke, T., Plaza, M., & Schroeder, J. (2019). No evidence for kin  
483 recognition in a passerine bird. *PLOS ONE*, 14(10), e0213486.  
484 <https://doi.org/10.1371/journal.pone.0213486>

485 Levy, M. Z., Allsopp, R. C., Futcher, A. B., Greider, C. W., & Harley, C. B. (1992). Telomere end-  
486 replication problem and cell aging. *Journal of Molecular Biology*, 225(4), 951–960.  
487 [https://doi.org/10.1016/0022-2836\(92\)90096-3](https://doi.org/10.1016/0022-2836(92)90096-3)

488 Manukyan, A. L. (2022). Noise as a cause of neurodegenerative disorders: Molecular and cellular  
489 mechanisms. *Neurological Sciences*, 43(5), 2983–2993. <https://doi.org/10.1007/s10072-022-05948-6>

490 Marasco, V., Boner, W., Griffiths, K., Heidinger, B., & Monaghan, P. (2019). Intergenerational effects  
491 on offspring telomere length: Interactions among maternal age, stress exposure and offspring sex.  
492 *Proceedings of the Royal Society B: Biological Sciences*, 286(1912), 20191845.  
493 <https://doi.org/10.1098/rspb.2019.1845>

494 Meillère, A., Brischoux, F., Ribout, C., & Angelier, F. (2015). Traffic noise exposure affects telomere  
495 length in nestling house sparrows. *Biology Letters*, 11(9), 20150559.  
496 <https://doi.org/10.1098/rsbl.2015.0559>

497 Meillère, A., Buchanan, K. L., Eastwood, J. R., & Mariette, M. M. (2024). Pre- and postnatal noise  
498 directly impairs avian development, with fitness consequences. *Science*, 384(6694), 475–480.  
499 <https://doi.org/10.1126/science.ade5868>

500 Münzel, T., & Daiber, A. (2018). Environmental Stressors and Their Impact on Health and Disease  
501 with Focus on Oxidative Stress. *Antioxidants & Redox Signaling*, 28(9), 735–740.  
502 <https://doi.org/10.1089/ars.2017.7488>

503 Nedelec, S. L., Radford, A. N., Simpson, S. D., Nedelec, B., Lecchini, D., & Mills, S. C. (2014).  
504 Anthropogenic noise playback impairs embryonic development and increases mortality in a marine  
505 invertebrate. *Scientific Reports*, 4(1), 5891. <https://doi.org/10.1038/srep05891>

506 Nedelec, S. L., Simpson, S. D., Morley, E. L., Nedelec, B., & Radford, A. N. (2015). Impacts of regular  
507 and random noise on the behaviour, growth and development of larval Atlantic cod (*Gadus morhua*).  
508 *Proceedings of the Royal Society B: Biological Sciences*, 282(1817), 20151943.  
509 <https://doi.org/10.1098/rspb.2015.1943>

510 Payne, R. B. (2020). Zebra Finch (*Taeniopygia guttata*). In S. M. Billerman, B. K. Keeney, P. G.  
511 Rodewald, & T. S. Schulenberg (Eds.), *Birds of the World*. Cornell Lab of Ornithology.  
512 <https://doi.org/10.2173/bow.zebfin2.01>

513 Poindexter, B. B., Langer, J. C., Dusick, A. M., & Ehrenkranz, R. A. (2006). Early provision of parenteral  
514 amino acids in extremely low birth weight infants: Relation to growth and neurodevelopmental  
515 outcome. *The Journal of Pediatrics*, *148*(3), 300-305.e1. <https://doi.org/10.1016/j.jpeds.2005.10.038>

516 Potvin, D. A., & MacDougall-Shackleton, S. A. (2015). Traffic noise affects embryo mortality and  
517 nestling growth rates in captive zebra finches. *Journal of Experimental Zoology Part A: Ecological*  
518 *Genetics and Physiology*, *323*(10), 722–730. <https://doi.org/10.1002/jez.1965>

519 R Core Team. (2025). *R: A Language and Environment for Statistical Computing*. [https://www.R-](https://www.R-project.org/)  
520 [project.org/](https://www.R-project.org/)

521 Ravinet, M., Elgvin, T. O., Trier, C., Aliabadian, M., Gavrillov, A., & Sætre, G.-P. (2018). Signatures of  
522 human-commensalism in the house sparrow genome. *Proceedings of the Royal Society B: Biological*  
523 *Sciences*, *285*(1884), 20181246. <https://doi.org/10.1098/rspb.2018.1246>

524 Reichert, S., & Stier, A. (2017). Does oxidative stress shorten telomeres *in vivo*? A review. *Biology*  
525 *Letters*, *13*(12), 20170463. <https://doi.org/10.1098/rsbl.2017.0463>

526 Schroeder, J., Nakagawa, S., Cleasby, I. R., & Burke, T. (2012). Passerine birds breeding under chronic  
527 noise experience reduced fitness. *PLoS ONE*, *7*(7), e39200.  
528 <https://doi.org/10.1371/journal.pone.0039200>

529 Schroeder, J., Nakagawa, S., Rees, M., Mannarelli, M.-E., & Burke, T. (2015). Reduced fitness in  
530 progeny from old parents in a natural population. *Proceedings of the National Academy of Sciences*,  
531 *112*(13), 4021–4025. <https://doi.org/10.1073/pnas.1422715112>

532 Sibma, A. (2021). *A longitudinal analysis of telomeres in an insular house sparrow population* [PhD  
533 Thesis]. University of Sheffield.

534 Simons, M. J. P., Winney, I., Girndt, A., Rees, M., Nakagawa, S., Schroeder, J., & Burke, T. (2019).  
535 *Ageing in house sparrows is insensitive to environmental effects*. Preprint.  
536 <https://doi.org/10.1101/598284>

537 Smith, H. G., Kallander, H., & Nilsson, J.-A. (1989). The Trade-Off Between Offspring Number and  
538 Quality in the Great Tit *Parus major*. *The Journal of Animal Ecology*, *58*(2), 383.  
539 <https://doi.org/10.2307/4837>

540 Sparks, A. M., Spurgin, L. G., Van Der Velde, M., Fairfield, E. A., Komdeur, J., Burke, T., Richardson, D.  
541 S., & Dugdale, H. L. (2022). Telomere heritability and parental age at conception effects in a wild  
542 avian population. *Molecular Ecology*, *31*(23), 6324–6338. <https://doi.org/10.1111/mec.15804>

543 Stan Development Team. (2025). *RStan: The R interface to Stan. R package version 2.32.7* [Computer  
544 software]. <https://mc-stan.org/>

545 Sun, Y., Burke, T., Dugdale, H., & Schroeder, J. (2025). Long-term fitness effects of the early-life  
546 environment in a wild bird population. *Behavioral Ecology*, *36*(5).  
547 <https://doi.org/10.1093/beheco/araf097>

548 Sun, Y., Burke, T., Dugdale, H., & Schroeder, J. (2026). Data from: Data on natal noise exposure,  
549 nestling fitness measures and adult telomere length in house sparrows.  
550 <https://doi.org/10.5061/dryad.66t1g1kd2>

551 van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within- versus between-  
552 subject effects using mixed models. *Animal Behaviour*, 77(3), 753–758.  
553 <https://doi.org/10.1016/j.anbehav.2008.11.006>

554 Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P.-C., Paananen, T., & Gelman, A. (2015). *loo*:  
555 *Efficient Leave-One-Out Cross-Validation and WAIC for Bayesian Models* (p. 2.9.0) [Dataset].  
556 <https://doi.org/10.32614/CRAN.package.loo>

557 Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out  
558 cross-validation and WAIC. *Statistics and Computing*, 27(5), 1413–1432.  
559 <https://doi.org/10.1007/s11222-016-9696-4>

560 Verhulst, S. (2020). Improving comparability between qPCR-based telomere studies. *Molecular*  
561 *Ecology Resources*, 20(1), 11–13. <https://doi.org/10.1111/1755-0998.13114>

562 Viigipuu, R., Mägi, M., & Tilgar, V. (2023). Great tits alter incubation behaviour in noisy  
563 environments. *Journal of Ethology*, 41(1), 39–46. <https://doi.org/10.1007/s10164-022-00765-y>

564 Vincens, N., & Persson Waye, K. (2023). Occupational and environmental noise exposure during  
565 pregnancy and rare health outcomes of offspring: A scoping review focusing on congenital anomalies  
566 and perinatal mortality. *Reviews on Environmental Health*, 38(3), 423–438.  
567 <https://doi.org/10.1515/reveh-2021-0166>

568 Ward, C. O., Barletta, M. A., & Kaye, T. (1970). Teratogenic Effects of Audiogenic Stress in Albino  
569 Mice. *Journal of Pharmaceutical Sciences*, 59(11), 1661–1662.  
570 <https://doi.org/10.1002/jps.2600591128>

571 Wilbourn, R. V., Moatt, J. P., Froy, H., Walling, C. A., Nussey, D. H., & Boonekamp, J. J. (2018). The  
572 relationship between telomere length and mortality risk in non-model vertebrate systems: A meta-  
573 analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1741), 20160447.  
574 <https://doi.org/10.1098/rstb.2016.0447>

575 Williams, D. P., Avery, J. D., Gabrielson, T. B., & Brittingham, M. C. (2021). Experimental playback of  
576 natural gas compressor noise reduces incubation time and hatching success in two secondary cavity-  
577 nesting bird species. *Ornithological Applications*, 123(1), duaa066.  
578 <https://doi.org/10.1093/ornithapp/duaa066>

579 Winney, I., Nakagawa, S., Hsu, Y., Burke, T., & Schroeder, J. (2015). Troubleshooting the potential  
580 pitfalls of cross-fostering. *Methods in Ecology and Evolution*, 6(5), 584–592.  
581 <https://doi.org/10.1111/2041-210X.12341>

582 Xiong, Y., Melgar, J., Tobler, M., & Hasselquist, D. (2025). Assortative breeding experiment in a  
583 songbird suggests telomere length is determined during early life rather than at conception.  
584 *Scientific Reports*, 15(1), 36510. <https://doi.org/10.1038/s41598-025-23517-7>

585 Zuur, A., Ieno, E., Walker, N., Saveliev, A., & Smith, G. (2009). *Mixed effects models and extensions in*  
586 *ecology with R*. Springer.

587

588 **Tables**

589 Table 1. Fixed and random effect estimates with [95% CrI] from the GLMMs testing the effect of the natal environmental noise on z-standardised chick mass,  
 590 body condition at fledging, and fledging success in Lundy house sparrows. Significant fixed effects are in bold; fixed effects whose 95% CrI borders zero are  
 591 in italics. Number of levels for random effects is in brackets. CrI: credible intervals.

Response variable:		Chick mass	Body condition at fledging	Fledging success
Fixed effects	(Intercept)	0.05	0.03	-1.12
		[-0.03, 0.13]	[-0.14, 0.21]	[-1.63, -0.63]
	Natal environment	-0.03	0.00	0.11
		[-0.06, 0.01]	[-0.11, 0.12]	[-0.24, 0.44]
	Rearing environment	<b>-0.04</b>	<b>-0.11</b>	<i>-0.32</i>
		<b>[-0.08, -0.00]</b>	<b>[-0.22, -0.01]</b>	<i>[-0.65, 0.00]</i>
	Age	<b>0.92</b>	-0.02	

			<b>[0.91, 0.93]</b>	[-0.05, 0.01]	
	Brood size		<b>-0.03</b>	-0.01	-0.09
			<b>[-0.05, -0.02]</b>	[-0.05, 0.04]	[-0.24, 0.05]
	Tarsus length			<b>0.80</b>	
				<b>[0.77, 0.84]</b>	
	Sex	Male		<b>0.10</b>	
				<b>[0.04, 0.16]</b>	
Random effects	Bird ID		0.13		
(number of			[0.12, 0.15]		
levels)			(1810)		
	Cohort		0.13	0.27	0.744
			[0.07, 0.22]	[0.15, 0.46]	[0.36, 1.31]
			(11)	(11)	(11)

Rearing brood
Natal brood

0.15	0.42	0.97
[0.13, 0.16]	[0.38, 0.46]	[0.72, 1.22]
(608)	(462)	(613)

593 Table 2. Fixed and random effect estimates with [95% CrI] from the GLMM testing the effect of the  
 594 natal environmental noise on adult z-standardised relative telomere length (zRTL) in Lundy house  
 595 sparrows. Significant fixed effects are in bold. Number of levels for random effects is in brackets. CrI:  
 596 credible intervals. PAC: paternal age at conception. For results of the full model, see Table S3.

Fixed effects	Level	Estimates
(Intercept)		-0.13 [-0.42, 0.15]
Natal environment	Noisy	0.01 [-0.10, 0.11]
Rearing environment	Noisy	-0.00 [-0.10, 0.09]
Age		-0.02 [-0.07, 0.03]
Age <sup>2</sup>		0.01 [-0.02, 0.03]
<b>DNA age</b>		<b>-0.24 [-0.46, -0.01]</b>
DNA age <sup>2</sup>		0.01 [-0.08, 0.10]
<b>Blood age</b>		<b>-0.27 [-0.48, -0.02]</b>
Blood age <sup>2</sup>		-0.01 [-0.13, 0.12]
PAC		0.01 [-0.02, 0.05]
Sex	Male	0.04 [-0.03, 0.10]
Technician	B	-0.03 [-0.20, 0.14]
<b>Natal environment * age</b>	Noisy	<b>0.09 [0.00, 0.18]</b>
<b>Random effects</b>		<b>Estimates</b>
		<b>(number of levels)</b>
Bird ID		0.07 [0.00, 0.17]

		(652)
Rearing brood		0.09 [0.00, 0.17]
		(446)
Natal brood		0.09 [0.00, 0.18]
		(444)
Capture Year		0.30 [0.17, 0.54]
		(13)
Plate		0.22 [0.16, 0.28]
		(82)

597

598

599 Table 3. Fixed and random effect estimates with [95% CrI] from the GLMM testing the effect of the  
600 natal environmental noise on adult z-standardised relative telomere length (zRTL), with age  
601 decomposed into mean age and within-individual-centred age ( $\Delta$ age). Significant fixed effects are in  
602 bold; fixed effects whose credible interval (CrI) borders zero are in italics. PAC: paternal age at  
603 conception. For output of the reduced model where the non-significant interaction natal environment  
604 \*  $\Delta$ age was removed, see Table S6.

Fixed effects	Level	Estimates
(Intercept)		-0.14 [-0.43, 0.16]
Natal environment	Noisy	0.02 [-0.09, 0.12]
Rearing environment	Noisy	-0.01 [-0.11, 0.09]
$\Delta$ age		-0.01 [-0.05, 0.02]

$\Delta age^2$		0.01 [-0.00, 0.03]
Mean age		-0.01 [-0.06, 0.03]
<b>DNA age</b>		<b>-0.24 [-0.46, -0.01]</b>
DNA age <sup>2</sup>		0.01 [-0.08, 0.10]
<b>Blood age</b>		<b>-0.26 [-0.47, -0.02]</b>
Blood age <sup>2</sup>		-0.01 [-0.14, 0.11]
PAC		0.01 [-0.02, 0.05]
Sex	Male	0.04 [-0.03, 0.10]
Technician	B	-0.03 [-0.19, 0.13]
Natal environment * $\Delta age$	Noisy	0.02 [-0.06, 0.10]
<b>Natal environment * mean age</b>	Noisy	<b>0.10 [0.01, 0.19]</b>
<b>Random effects</b>		<b>Estimates</b>
		<b>(number of levels)</b>
Bird ID		0.08 [0.00, 0.17]
		(652)
Rearing brood		0.09 [0.00, 0.18]
		(446)
Natal brood		0.09 [0.01, 0.18]
		(444)
Capture Year		0.30 [0.17, 0.53]

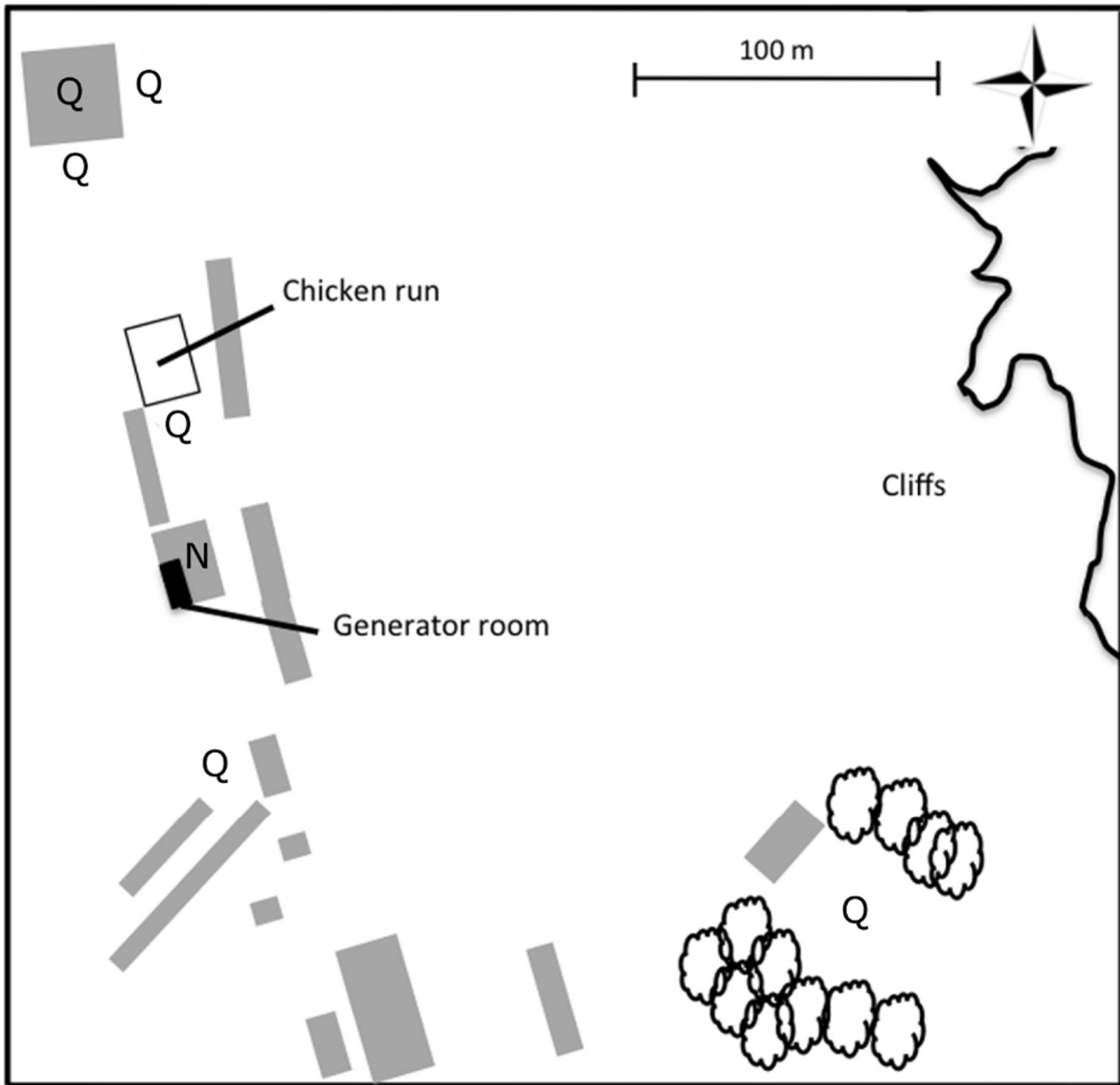
Plate

(13)

0.21 [0.16, 0.28]

(82)

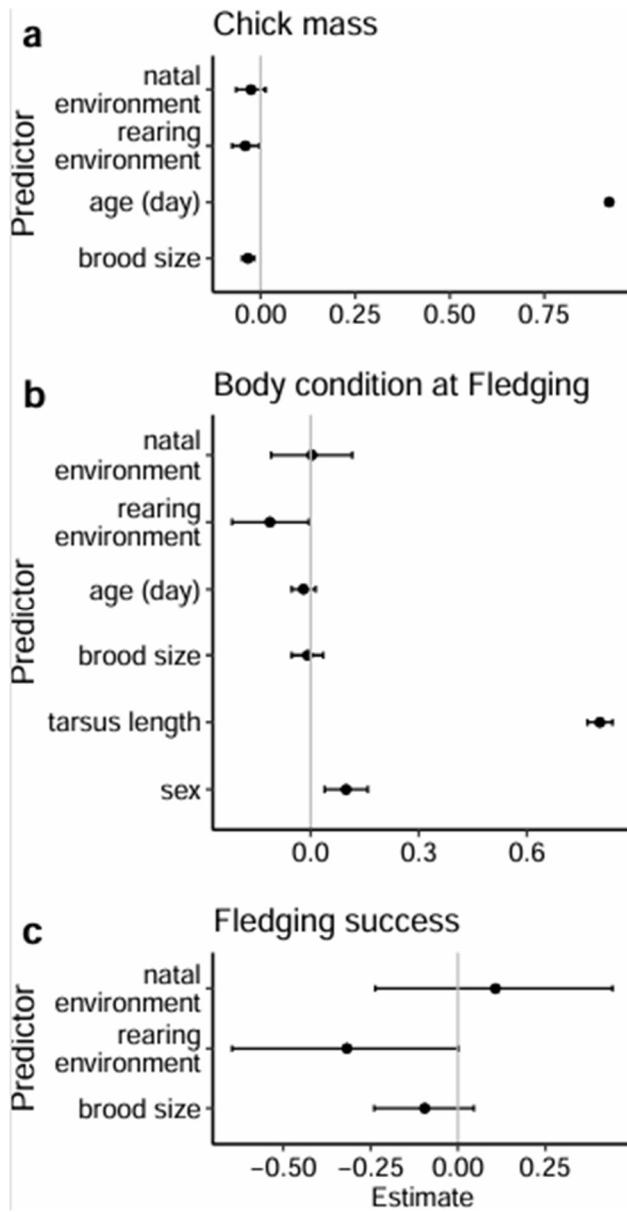
605



607

608 Figure 1. Locations of quiet (Q) and noisy (N) house sparrow breeding sites on Lundy Island. The  
609 chicken run was the main feeding site of the house sparrows. Adopted from Sun et al. (2025).

610

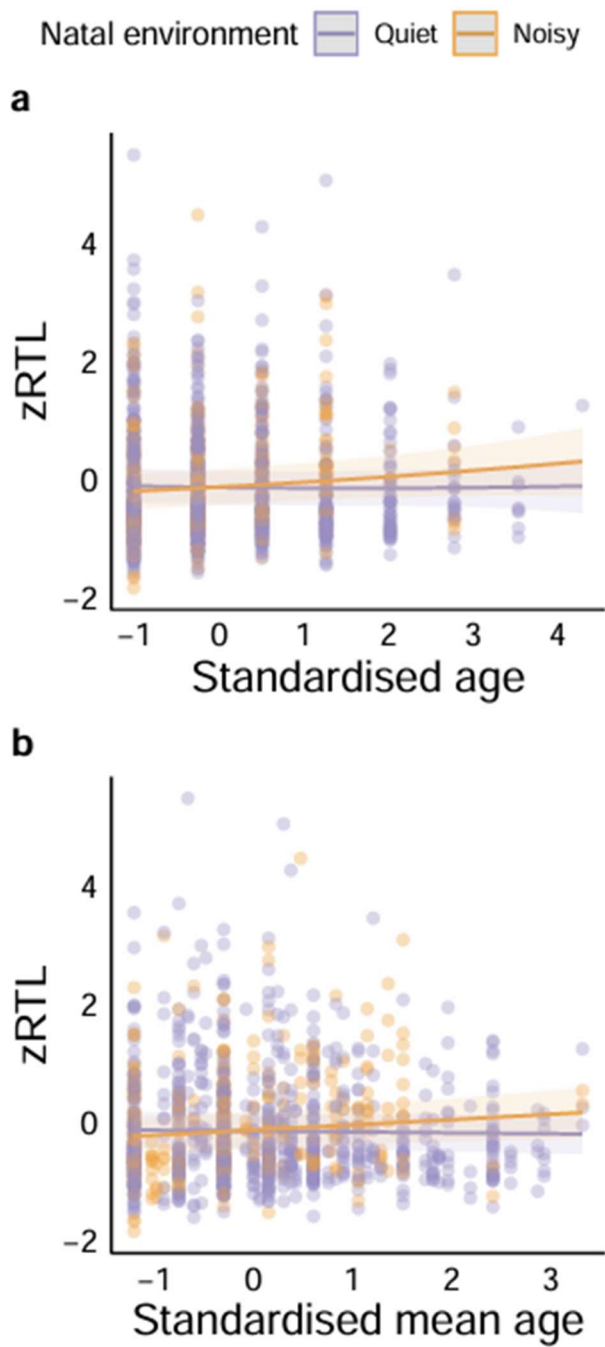


611

612 Figure 2. Effect sizes with 95% credible intervals of the fixed effects predicting (a) chick mass, (b)

613 body condition at fledging and (c) fledging success.

614



615

616 Figure 3. Adult zRTL (z-standardised relative telomere length) in relationship to (a) z-standardised  
 617 age and (b) z-standardised mean age (mean of the ages that each individual appeared in the dataset) in  
 618 Lundy house sparrows. Each dot represents an observation; lines are predicted zRTL; shaded areas  
 619 represent 95% credible intervals.

620

621