

1 **Long-term fitness effects of the early-life environment in a wild bird population**

2 Yuheng Sun^{1,2^}, Terry A. Burke³, Hannah L. Dugdale^{1*^}, Julia Schroeder^{4*}

3 ***Equal/joint last-authorship**

4 1. Groningen Institute for Evolutionary Life Sciences, University of Groningen, Linnaeusborg,
5 Groningen, the Netherlands

6 2. School of Natural Sciences, Faculty of Science and Engineering, Macquarie University, Sydney,
7 New South Wales, Australia

8 3. Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK

9 4. Department of Life Sciences, Imperial College London, Silwood Park, Ascot, Berkshire, UK

10 ^corresponding authors:

11 Yuheng Sun: Groningen Institute of Evolutionary Life Sciences (GELIFES), University of Groningen,
12 Nijenborgh 7, 9747 AG Groningen, Netherlands. TEL: +31 (0)63 097 9752. E-mail: y.sun@rug.nl

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

16

17 **Abstract**

18 Environmental conditions and experiences during development can have long-term fitness
19 consequences, including a reduction of adulthood survival and reproduction. These long-term fitness
20 consequences may play an important role in shaping the evolution of life history. We tested two
21 hypotheses on the long-term fitness effects of the developmental environment – the silver spoon
22 hypothesis and the internal Predictive Adaptive Response (PAR) hypothesis. We compared the

23 change in annual survival and annual reproductive output with age for adult birds hatched and reared
24 in poor (impacted by anthropogenic noise, and/or high sibling competition) and good (not impacted
25 by anthropogenic noise, and/or low sibling competition) environments. We used a 23-year
26 longitudinal fitness dataset from a wild house sparrow (*Passer domesticus*) population that was
27 unusually precise due to the isolation of the population. We used a cross-fostering setup to disentangle
28 postnatal environmental effects from prenatal effects. We found that adults that experienced more
29 within-brood competition had a stronger increase in early-life annual survival, but also a stronger
30 decrease in late-life annual survival. Females that hatched in a noisy environment produced fewer
31 genetic recruits annually, supporting a sex-specific silver spoon effect. Males reared in a noisy
32 environment had accelerated reproductive schedules, presenting a sex-specific internal PAR. Our
33 results highlight that anthropogenic noise can have long-term fitness consequences in wild animals,
34 altering their life-history strategies, and that there may be sex-specific effects.

35

36 Keywords: silver spoon, predictive adaptive response, aging, senescence, noise, competition

37

38 **Introduction**

39 Early-life environments can have profound impacts on individual fitness (Lindström 1999), including
40 rates of senescence (the decline in survival and reproduction in later life; Kirkwood and Austad 2000;
41 Cooper and Kruuk 2018). The silver spoon hypothesis proposes that organisms developing in a
42 superior environment have lifetime fitness benefits because the environmental circumstances
43 constrain the development of the optimum phenotype (Grafen 1988; Monaghan 2008). The predictive
44 adaptive response (PAR) hypothesis proposes that organisms can respond to environmental cues
45 acting at the developmental stage and thus maximize their lifetime fitness for the given circumstances
46 (Gluckman and Hanson 2004; Gluckman et al. 2005; Nettle et al. 2013). Both the silver spoon and the
47 PAR hypotheses recognize the detriment of early-life adversity, but they make different predictions
48 about how individuals respond to early-life adversity.

49 The silver spoon hypothesis predicts that individuals that experience a better early-life environment
50 have higher fitness than those from a worse early-life environment (Grafen 1988). Support for the
51 silver spoon hypothesis is widely found across taxa, including humans (Wu et al. 2010; Hales and
52 Barker) and other animals (Lindström 1999). However, fitness components can respond to early-life
53 environmental conditions in a sex-specific (Sanghvi et al. 2021) or age-specific (Spagopoulou et al.
54 2020; Crosland et al. 2022) manner. A meta-analysis focusing on the effects of early-life
55 environmental conditions on senescence in the wild found no evidence that the early-life environment
56 affected survival senescence, but there was a silver spoon effect of the early-life environment on
57 reproductive senescence, however, the effect was small (Cooper and Kruuk 2018).

58 An alternative hypothesis is the PAR. The internal PAR (also known as the Future Lifespan
59 Expectation) hypothesis proposes that early-life adversity results in a soma that has reduced survival
60 probability at any age; thus it is advantageous for the individual to adjust their reproductive schedule,
61 according to their reduced expected lifespan, to maximise their fitness (Wells 2012; Nettle et al.
62 2013). Therefore, the internal PAR predicts that individuals from adverse early-life environments will
63 exhibit accelerated reproductive schedules. Empirical studies testing the internal PAR are less

64 abundant than for the silver spoon hypothesis and have found mixed results, with some supporting it
65 (Berghänel et al. 2016) but others not (Weibel et al. 2020; van de Crommenacker et al. 2022).

66 Testing the silver spoon and PAR hypotheses on the long-term effects of the early-life environment,
67 especially under wild conditions is important for understanding the evolution of life history and
68 senescence. This is because in captivity environmental conditions are usually controlled and therefore
69 the fitness measures do not reflect the real fitness consequences in the wild (Monaghan 2008) and
70 these fitness consequences play important roles in life-history evolution and population dynamics
71 (Lindström 1999). However, testing these hypotheses in the wild is difficult. First, both hypotheses
72 concern lifetime fitness consequences, which requires complete life-history data with known age and
73 longevity for sufficient individuals that survive to old age. These data are rarely available in wild
74 populations because it is usually difficult to know an individual's age and track their reproductive
75 activities throughout their entire life. Also, it is often difficult to distinguish whether an individual has
76 died or emigrated. Second, the hypotheses concern environmental effects, which are difficult to
77 distinguish from genetic effects in wild populations (Monaghan 2008). For example, if individuals
78 who were provided with more food by their parents when they were young lived longer than those
79 who received less food, one would not know whether it was because they received more food in early
80 life (the silver spoon effect) or because their parents were of better quality, and the offspring inherited
81 the good quality thus lived long.

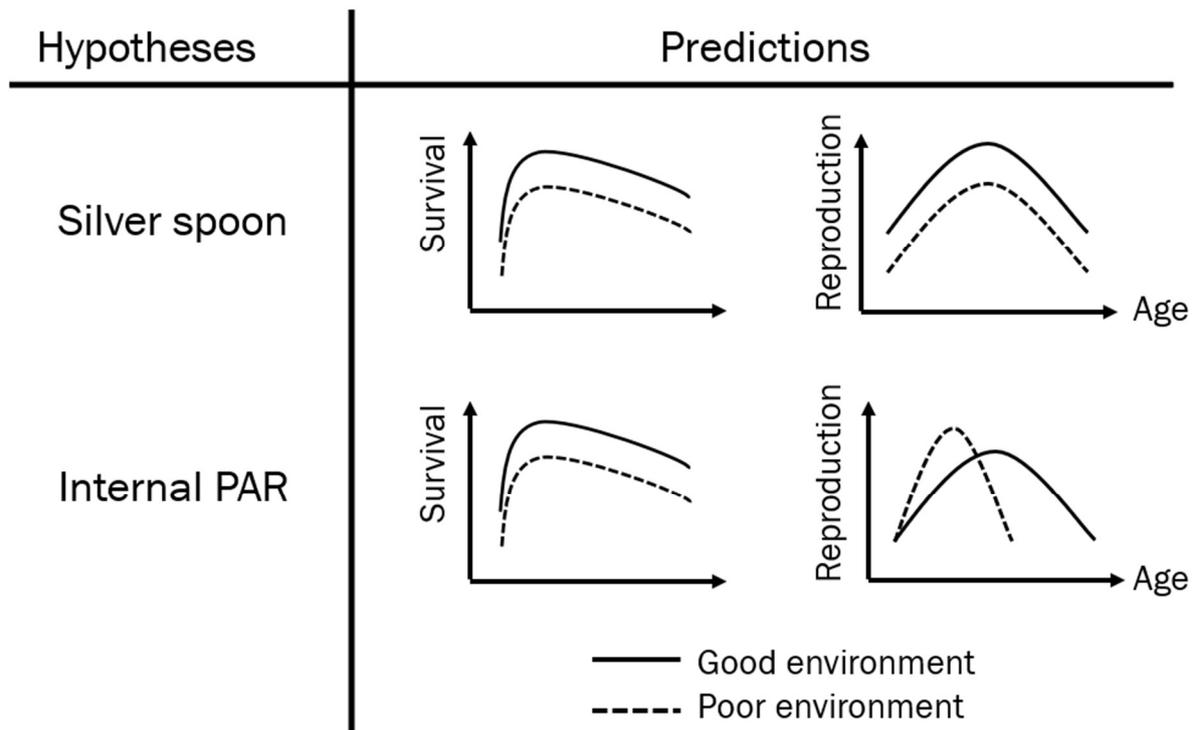
82 Our study tests the silver spoon and the internal PAR hypotheses in a natural study system that has
83 complete life-history data, and allows postnatal environmental effects to be disentangled from genetic
84 effects in a closed, long-term-monitored population of house sparrows (*Passer domesticus*) on Lundy
85 Island in the UK. Because house sparrows are not suited for long-distance flight, immigration and
86 emigration are nearly impossible (Schroeder et al. 2015), which allows us to track virtually every
87 individual until their death. House sparrows are cavity-nesting, peridomestic small passerine birds,
88 and we can closely monitor their breeding events in nest boxes. Therefore, the Lundy house sparrow
89 system provides us with access to complete life-history data. Secondly, cross-fostering experiments
90 have been routinely conducted in this population for 23 years. By cross-fostering chicks right after

91 hatching, we can separate the effects of the postnatal environment from the effects of prenatal factors,
92 including genetic factors. Thirdly, a proportion of breeding sites provide a poor early-life environment
93 as the parents have reduced provisioning rates due to the impact of chronic background noise
94 (Schroeder, Nakagawa, et al. 2012). Chicks reared in this poor environment have lower fledgling
95 success, lower body mass at fledging, and lower recruiting success than chicks reared in a quiet
96 environment (Schroeder, Nakagawa, et al. 2012), demonstrating that the noisy environment is an
97 adverse early-life environment and leads to a poor somatic state. However, it is unknown whether this
98 environment has long-term fitness consequences and whether it is associated with an alteration in the
99 reproductive schedule. Additionally, clutch size differs among broods regardless of the environment.
100 Although parents are expected to optimize the brood size to their resource providing ability, variation
101 in the number of chicks that survive to fledge may still introduce variation in the intensity of within-
102 brood competition (Schroeder, Nakagawa, et al. 2012). Both, the noise presence and the social
103 competition can induce early-life adversity in birds (Nur 1984; Injaian et al. 2019), allowing us to test
104 the silver spoon and internal PAR hypotheses in this wild population.

105 In this study, we investigate survival and reproduction across ages in response to the presence of
106 environmental noise and the number of early-life competitors in Lundy house sparrows, to test the
107 silver spoon and internal PAR hypotheses. (1) The silver spoon hypothesis predicts that an adverse
108 developmental environment has overall negative effects on fitness components; thus, sparrows reared
109 in a noisy environment and/or with more intense within-brood competition are expected to have lower
110 annual adulthood survival and lower annual reproductive output compared with sparrows reared in a
111 quiet environment and/or with less intense within-brood competition. (2) The internal PAR hypothesis
112 predicts that birds reared in an adverse developmental environment have lower adulthood survival,
113 earlier reproductive peaks and higher initial rates of increase and then steeper declines in reproductive
114 success (Figure 1). This study will therefore contribute to our understanding of the effects of early-life
115 environment on long-term fitness in wild populations.

116

117



118

119 **Figure 1** Predictions of the silver spoon and the internal predictive adaptive response (PAR)

120 hypotheses in relation to survival and reproductive success.

121

122

123 **Methods**

124 *Study population*

125 The Lundy house sparrows are free-living and resident on Lundy Island (51°10'N, 4°40'W), UK.
126 Lundy is 19 km from the nearest land, and because house sparrows are not well suited for long-
127 distance flights (Bengtson et al. 2004), the immigration and emigration rates are low (ca. 0.5%
128 immigration rate and three confirmed emigrants 2000–2015; Schroeder et al. 2015). Since 2000, the
129 Lundy house sparrow population has been systematically monitored. Nest boxes and known natural
130 nests have been checked systematically during the breeding season for reproductive activities,
131 sightings and captures have been carried out throughout the breeding season (April–August) and for
132 one or two weeks in the winter. Each bird was ringed with a unique combination of three color-rings
133 and a numbered metal ring from the British Trust for Ornithology. More than 99% of birds were
134 ringed as nestlings, fledglings or in their first year, and are therefore of known age (Schroeder et al.
135 2015). The annual probability of resighting an individual 2001–2008 was 0.90 (minimum 0.72 ± 0.07 ,
136 maximum 1.0 ± 0.0 , Schroeder et al. 2011).

137

138 *Early-life environmental noise*

139 Lundy Island is not connected to the national power grid. Since March 2001, a set of generators has
140 been running 06:00–24:00 h daily (Schroeder, Nakagawa, et al. 2012). These generators produce low-
141 frequency noise that reverberates in the surrounding area – a workshop that is semi-enclosed with
142 stone walls and corrugated roofing, with a permanently open gate and a louvered window that allows
143 the birds access. This physical structure reverberates noise within the workshop but restricts the noise
144 reverberation outside the workshop. The noise level within the workshop was significantly higher
145 than it was outside the workshop (Schroeder, Nakagawa, et al. 2012). Nestbox occupancy, parental
146 body mass, age and reproductive investment did not significantly differ between noisy and quiet
147 areas, suggesting no association between parent quality and the noisy area (Schroeder, Nakagawa, et
148 al. 2012). Both the workshop and the surrounding village and farm buildings contain nest boxes that

149 have fluctuated in number over the past 23 years. In 2008, there were 29 house sparrow nest boxes in
150 the workshop (noisy) and 101 nest boxes elsewhere (quiet) (Schroeder et al. 2012), and in 2023 the
151 numbers were 28 and 88, respectively. In 2013, in response to finding that house sparrow parents
152 provision their offspring less often in noisy conditions (Schroeder et al. 2012), construction was
153 carried out to reduce the average noise level in the workshop from 68 dB(A) to 45 dB(A) (Schroeder
154 et al. 2012 & measurement by YS in 2023, respectively). Therefore, the dataset used in this study only
155 contained birds hatched before 2013 to keep the early-life environmental noise constant. The dataset
156 was then restricted to birds that had been seen after fledging to focus on the long-term effects of early-
157 life environmental noise. This excludes the noise-related reduction in offspring survival between
158 hatching and fledging (Schroeder et al. 2012).

159

160 *Cross-fostering*

161 Chicks were routinely cross-fostered whenever there were enough same-aged broods, with the
162 exceptions of 2008 and 2010, when the population size was too small (Winney et al. 2015). Most
163 chicks were cross-fostered at 2 days old (Cleasby et al. 2010). Broods were cross-fostered entirely or
164 partially, but the original brood size was always left unchanged after cross-fostering. Chicks remained
165 in their foster broods until fledging. Chicks were cross-fostered either within or between noisy and
166 quiet areas opportunistically, depending on where the same-age broods were located. Only cross-
167 fostered individuals were included in this study. The final dataset included 1,057 individuals. The
168 environments where the bird hatched and where they were fostered were hereafter referred to as the
169 natal and rearing environment, respectively.

170

171 *Annual survival*

172 Annual survival data were generated as follows: a bird was observed in a given year if it met any one
173 of these criteria: (1) it was sighted, (2) it was captured, or (3) it had a reproductive record (e.g. genetic
174 pedigree indicated that it produced offspring in that year). When a bird was not observed for two

175 consecutive years, it was considered to have died in the year following the last observation. For
176 example, if a bird was observed in 2005, but not in 2006 and 2007, it was considered to be alive in
177 2005 and dead in 2006. Following this process, all birds in the dataset were classified as dead by the
178 time this dataset was assembled (December 2023), and thus had complete lifespans and lifetime data.
179 The annual survival dataset contained 1,687 observations from 1,057 birds.

180

181 *Annual reproductive output*

182 We used the number of annual genetic recruits as a measure of annual reproductive fitness for all
183 birds that survived until the breeding season following their year of hatching. The number of genetic
184 recruits is the best proxy of long-term fitness (Alif et al. 2022), so we used it to quantify the fitness
185 consequences caused by the early-life environment. A genetic recruit of a focal bird is defined as an
186 individual that is (1) the genetic offspring of the focal bird and (2) is assigned its own offspring in the
187 genetic pedigree. The pedigree was constructed using Cervus 3.0 with up to 23 microsatellite markers
188 (Marshall et al. 1998; Dawson et al. 2012), and contained 9,057 individuals hatched in 1995–2019.
189 The number of annual recruits was first matched to the annual survival data. If a bird survived for a
190 year but did not have an annual recruit record, zero annual recruits were assigned to the bird for that
191 year. The annual reproductive output dataset contained 274 observations from 133 females, and 356
192 observations from 165 males.

193

194 *Statistical analyses*

195 All statistical analyses were conducted in R 4.3.2 (R Core Team 2023).

196 *1. Adult survival*

197 To test the silver spoon and the internal PAR hypotheses, the effects of early-life environmental noise
198 and social competition on survival were tested using a Generalized Linear Mixed Model (GLMM)
199 with a binomial distribution, using *glmmTMB* 1.1.8 (Brooks et al. 2017). An initial model was built

200 with annual survival as the response variable (0 = dead, 1 = survived), and the fixed effects: age
201 (years), age², presence or absence of noise in the rearing environment (0 = noisy, 1 = quiet), presence
202 or absence of noise in the natal environment (0 = noisy, 1 = quiet), the number of fledglings from the
203 brood where the focal bird was reared (continuous), the number of hatchlings from the brood where
204 the focal bird was reared (continuous), sex (0 = female, 1 = male), natal brood order (continuous), and
205 foster brood order (continuous). Age² was included to allow non-linear changes with age. The
206 presence or absence of noise in the natal environment was included to control for prenatal
207 environmental noise effects. The number of hatchlings in the rearing brood was included to control
208 for the quantity of resources that parents provided to a brood, because the parents' provisioning
209 frequencies are positively associated with clutch size (Schroeder et al. 2012). For chicks born in
210 broods with the same numbers of hatchlings, the more fledglings a brood had, the stronger
211 competition the chicks experienced throughout their nestling period. A sparrow can produce 1–5
212 broods in a year, so the orders of natal and foster brood were included to control for potential effects
213 of breeding time and previous breeding attempts (Verhulst et al. 1997; Verhulst and Nilsson 2008).

214 The initial model included all interactions of age and age² with natal environment, rearing
215 environment, and number of fledglings to test the effect of these factors on survival senescence. The
216 interactions of sex with age and age² were also included to control for sex differences in senescence,
217 which are common in vertebrates (Clutton-Brock and Isvaran 2007). Additionally, an interaction
218 between natal and rearing environments was included to test whether a bird hatched in a noisy
219 environment would be less affected by the noise in the rearing environment than a bird hatched in a
220 quiet environment. Males and females can respond to environmental factors differently due to
221 morphological or behavioral dimorphism (Marasco et al. 2019; Sanghvi 2021; Mainwaring et al.
222 2023), therefore the interactions of sex with natal environment, rearing environment, and number of
223 fledglings were included to account for this sex difference.

224 Random effects included in the model were bird ID, year, natal brood ID, and foster brood ID. Bird
225 ID accounted for the nonindependence of the annual survival data across years for the same
226 individual. Year was included because mortality can be year-dependent due to environmental

227 variations such as temperature (MJ Simons et al. preprint from bioRxiv.org). Natal brood ID was
228 included because individuals hatched in the same brood might share genetic factors that influence
229 fitness (Schroeder et al. 2012); foster brood ID was included because individuals reared by the same
230 pair of parents might share parental-care-related factors that also influence fitness (Ivimey-Cook et al.
231 2023).

232 To confirm any age effect detected by the survival model, a post-peak analysis was run using a
233 GLMM, with the dataset restricted to data points after the peak using the following method: annual
234 survival reached the peak at age = 3.4 y, thus observations with age > 3.4 y were used to build a new
235 GLMM (n = 162); the structure of the new GLMM was the same as the final survival model, except
236 that terms involving age² were removed to inspect only the linear relationship between annual
237 survival and age after the peak.

238 2. *Reproductive success*

239 To test the silver spoon and the internal PAR hypotheses, the effects of early-life environmental noise
240 and social competition on reproductive success were tested in two sex-specific GLMMs. Females and
241 males were modelled separately because the reproductive biology and reproductive senescence differ
242 between the sexes (Schroeder, Burke, et al. 2012). In both sexes, the model was fitted with a negative
243 binomial distribution, ensuring the ratio of observed and predicted zeros is within the tolerance range
244 (checked by *performance* 0.13.0, Lüdecke et al. 2021). The initial models were built with the number
245 of annual genetic recruits as the response variable, and the following fixed effects: within-individual-
246 centered age (Δ age, years), Δ age², presence or absence of noise in the rearing environment (0 = noisy,
247 1 = quiet), presence or absence of noise in the natal environment (0 = noisy, 1 = quiet), the number of
248 fledglings in the rearing brood (continuous), the number of hatchlings in the rearing brood
249 (continuous), natal brood order (continuous), foster brood order (continuous), last reproduction (0 =
250 no, 1 = yes), and mean age (years). Last reproduction was included to control for terminal effects (i.e.
251 the last reproduction of birds may have increased or decreased output, Bouwhuis et al. 2009;
252 Schroeder, Burke, et al. 2012). Mean age was the mean of age that each individual appeared in the
253 dataset, and Δ age = age – mean age. With mean age and Δ age in the same model, mean age captured

254 the between-individual effect, and Δage captured the within-individual effect (van de Pol and Wright
255 2009). Δage^2 was included to allow non-linear changes with Δage . The initial models included all
256 interactions of each of Δage and Δage^2 with natal environment, rearing environment, and number of
257 fledglings, as well as the interaction between natal and rearing environments. The reproduction
258 models included the same random effects structure as the survival model. In the female reproduction
259 model, the random effect natal brood ID caused model convergence problems, and was removed as it
260 was associated with problematic eigenvalues indicated by the *diagnose* function in *glmmTMB*.

261 After the initial models were run, non-significant interactions were removed, removing the least
262 significant first until only significant interactions remained. This aids interpretation of first-order
263 effects. The fit of the final models was evaluated by visually inspecting the residual plots generated by
264 *DHARMA* 0.4.6 and ensuring all residual tests performed by the *simulateResiduals* function were
265 passed (Hartig 2022). Collinearity was checked, ensuring that the VIF was <3 (Zuur et al. 2009).
266 Likelihood ratio tests were performed for the final models, and all significant effects detected by the
267 models were confirmed. To ensure the conclusion was not affected by pseudoreplication due to the
268 removal of natal brood ID in the female reproduction model, a data subset containing only one
269 randomly sampled bird from each natal brood was tested again using the same model.

270

271 **Results**

272 *1. Adult survival*

273 In the final adult survival model, the interaction of the number of fledglings in the foster brood and
274 age^2 was statistically significant (Table 1). Adult annual survival first increased then decreased with
275 age except for individuals reared in broods with only one fledgling where there was no later decrease
276 (Figure 2). The more competitors a bird had as a nestling, the steeper its initial increase and later
277 decrease in adult survival was (Figure 2). Neither the effect of noise in the natal nor the rearing
278 environment was statistically significant (Table 1). Adult annual survival in males was higher than in

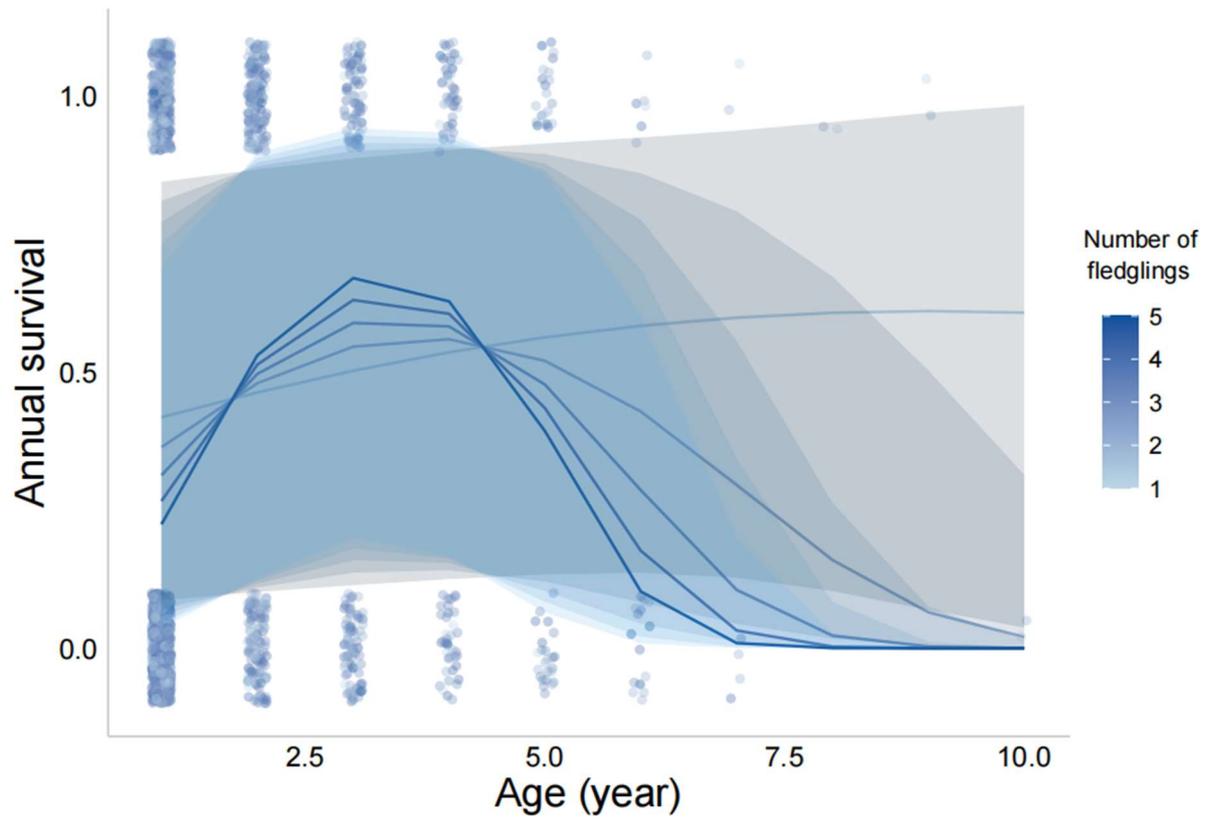
279 females (Table 1). For results of the full model, see Table S1. The post-peak analysis did not detect a
280 decline in adult annual survival in late life (Table S2).

281 **Table 1** Estimates from a GLMM explaining annual adult survival by age in Lundy house sparrows.
 282 Levels and corresponding sample sizes for categorical effects: natal environment: noisy = 351, quiet =
 283 1,336; rearing environment: noisy = 359, quiet = 1,328; sex: female = 797, male = 890. Significant
 284 highest-order fixed effects are in bold.

Fixed effects	Level	Estimate	Std. Error	p
(Intercept)		0.174	0.639	0.785
Age		-0.357	0.403	0.375
Age ²		0.082	0.056	0.142
Natal environment	Quiet	0.117	0.157	0.456
Rearing environment	Quiet	0.035	0.156	0.824
Number of hatchlings		0.019	0.069	0.789
Number of fledglings		-0.710	0.186	<0.001
Sex	Male	0.270	0.119	0.023
Natal brood order		-0.096	0.102	0.347
Foster brood order		-0.097	0.102	0.341
Age × Number of fledglings		0.576	0.154	<0.001
Age² × Number of fledglings		-0.094	0.024	<0.001
Random effects	1,687 observations	Variance		
Bird ID	1,057 individuals	<0.001		
Year	22 years	0.561		
Natal brood ID	459 natal broods	0.180		
Foster brood ID	449 foster broods	<0.001		

285

286



287

288 **Figure 2** Annual adult survival in relationship to age and the number of fledglings in Lundy house
 289 sparrows. Each dot represents an observation, jittered to aid visualization; lines are predicted annual
 290 survival rates for different numbers of fledglings; shaded areas represent 95% confidence intervals;
 291 color saturation indicates the intensity of within-brood competition.

292

293

294

295 2. *Reproductive success*

296 In both females and males that survived to 1 year of age, the number of annual genetic recruits first
297 increased and then decreased with within-individual-centered age (Figure 3). Adult females hatched in
298 a noisy environment produced fewer annual genetic recruits than adult females hatched in a quiet
299 environment, regardless of their age; the noise in the rearing environment did not show a significant
300 effect (Table 2, Figure 3a). The significantly positive effect of mean age implies selective
301 disappearance of low-quality adult females (Table 2). The significant effects of natal environment and
302 mean age were confirmed in the subset where only one bird from each natal brood was modelled to
303 account for pseudoreplication (Table S4).

304 Adult males reared in a noisy environment had an earlier peak in their number of annual genetic
305 recruits produced, relative to their lifespan (Table 2, Figure 3b). The peak for adult males reared in a
306 noisy environment was 1.3 y before the within-individual mean age and for adult males reared in a
307 quiet environment was 0.3 y after. The difference in the timing of the peak was confirmed by
308 bootstrapping (mean difference = 1.6 y, $p < 0.001$). Given that the mean ages of the noisy and quiet
309 groups were 2.2 y and 2.0 y, respectively, the peaks translated into 0.9 y in the noisy group and 2.3 y
310 in the quiet group in chronological age, confirming that adult males reared in a noisy environment had
311 an earlier peak in their annual reproductive output than those reared in a quiet environment. Noise in
312 the natal environment did not have a significant effect (Table 2). The significantly positive effect of
313 mean age implied selective disappearance of low-quality adult males (Table 2). The number of
314 fledglings from the rearing brood did not have a significant effect on the reproduction of females and
315 males that survived the first year of life (Table 2). For results of the full models, see Table S3.

316

317

318 **Table 2** Estimates from the GLMM explaining the number of annual genetic recruits by age in adult Lundy house sparrows. Levels and corresponding sample
319 sizes for categorical effects: natal environment: noisy = 53 (female) and 58 (male), quiet = 221 (female) and 298 (male); rearing environment: noisy = 69
320 (female) and 58 (male), quiet = 205 (female) and 298 (male); last reproduction: no = 159 (female) and 222 (male), yes = 115 (female) and 134 (male).
321 Significant highest-order fixed effects are in bold. Δ age: within-individual-centered age.

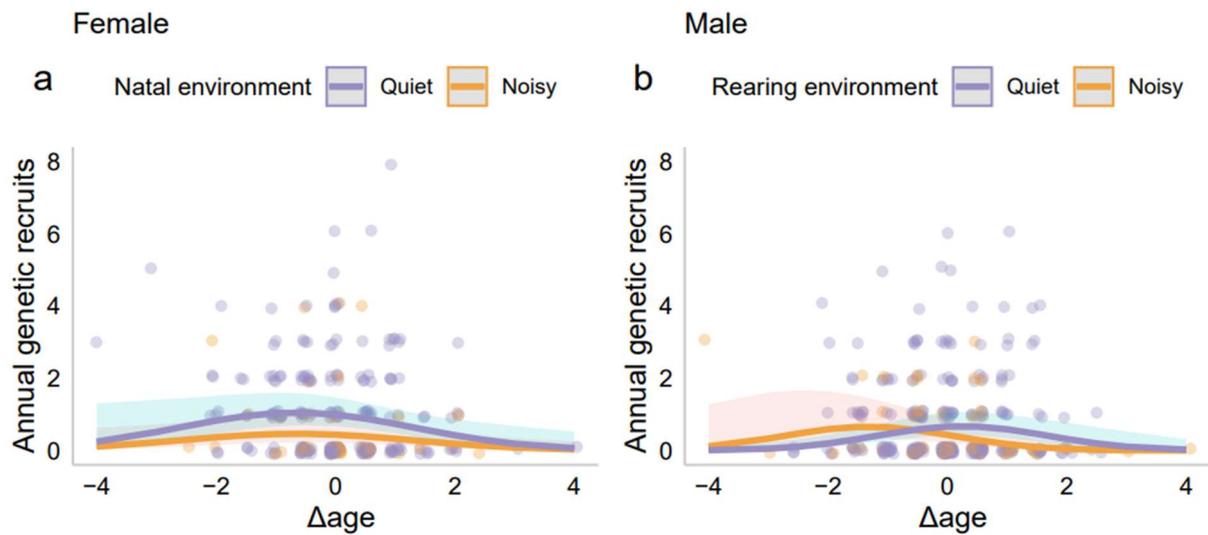
Fixed effects	Level	Estimate	Std. Error	P	Estimate	Std. Error	P
		Female			Male		
(Intercept)		-3.693	0.803	<0.001	-2.412	0.756	0.001
Number of hatchlings		0.218	0.117	0.063	0.034	0.111	0.761
Number of fledglings		-0.068	0.109	0.532	0.080	0.109	0.464
Natal environment	Quiet	0.821	0.341	0.016	-0.114	0.271	0.672
Rearing environment	Quiet	0.458	0.252	0.069	0.431	0.322	0.181
Δ age		-0.169	0.102	0.097	-0.649	0.261	0.013
Δ age ²		-0.130	0.056	0.021	-0.246	0.077	0.001
Natal brood order		0.018	0.176	0.917	-0.029	0.186	0.877
Foster brood order		0.090	0.168	0.591	-0.141	0.170	0.405
Last reproduction	Yes	0.401	0.223	0.072	0.352	0.248	0.155
Mean age		0.709	0.142	<0.001	0.749	0.161	<0.001

Rearing environment × Δage	Quiet			0.773	0.274	0.005
Random effects		274 observations	Variance	356 observations		Variance
Bird ID		133 individuals	<0.001	165 individuals		0.151
Year		20 years	0.335	21 years		0.518
Natal brood ID				148 natal broods		<0.001
Foster brood ID		111 foster broods	0.098	148 foster broods		<0.001

322

323

324



325

326

327

328

329

330

331

332

333

334

335

Figure 3 The number of annual genetic recruits in relationship to within-individual-centered age of adult Lundy house sparrows. The mean ages of birds hatched in a noisy (orange) and quiet (purple) environment were: 1.8 y and 2.0 y for females, and 2.2 y and 2.0 y for males, respectively. Each dot represents an observation; lines are predicted number of annual genetic recruits; shaded areas represent 95% confidence intervals. (a) Females hatched in a noisy environment produced fewer genetic recruits than females hatched in a quiet environment. (b) Males reared in a noisy environment exhibited earlier reproductive peaks relative to their lifespan than those reared in a quiet environment (0.9 y old versus 2.3 y old, respectively).

336 **Discussion**

337 We found sex-specific support for the silver spoon hypothesis in females, and for the internal PAR
338 hypothesis in males, for annual reproductive success but not for survival in a wild population using a
339 multi-year cross-foster experiment.

340

341 *1. Adult survival*

342 We found no support for the silver spoon or the internal PAR hypothesis in our adult annual survival
343 analysis. Since only individuals that survived the first year of life were included in our analysis, the
344 negative effects of a poor early-life environment might be masked by selective disappearance in the
345 first year of life, given that chicks reared in a noisy environment were less likely to fledge and recruit
346 (Schroeder, Nakagawa, et al. 2012), confirming meta-analytic results (Cooper and Kruuk 2018). The
347 absence of the effect on survival could also result from adaptive physiological mechanisms that
348 primarily conserve survival-enhancing traits during development at the cost of reproduction-
349 enhancing traits (Cooper and Kruuk 2018), but further studies are needed to investigate this
350 hypothesis.

351 We found an interactive effect of the number of fledglings on the rates of change in annual adult
352 survival: while statistically controlling for the number of hatchlings, for each additional fledgling in
353 the brood, the quadratic effect of age increased by 0.094 units per year (Table 1). This means that
354 when there was one fledgling from the brood, the change of survival chance with age was mild, but as
355 the number of fledglings increased, the age-related variation became stronger (Figure 2). In this
356 population, a chick's final mass was negatively associated with brood size, suggesting poorer body
357 condition at fledging for birds reared in larger broods (Cleasby et al. 2011). Fledglings in poor body
358 condition could have lower chances of surviving the post-fledging period compared with those in
359 good condition (Perrig et al. 2017). It is possible that in our study, the birds that underwent more
360 intense within-brood competition had a poorer survival right after fledging, but they could improve

361 their body condition to a level of average or above average in mid-life, at the cost of getting fragile
362 more rapidly in late life. To confirm this effect on the decline rate, we ran a post-peak analysis which,
363 however, did not detect a significant decline in late-life survival (Table S2). This is possibly due to the
364 small sample size of individuals that survived to age four (162 observations from 84 individuals), and
365 the sample sizes for extremely small or large numbers of fledglings were even smaller (13
366 observations from 6 individuals for number of fledglings = 1, 10 observations from 4 individuals for
367 number of fledglings = 5). Another possible explanation for the interactive effect of the number of
368 fledglings is that the larger broods might have a larger variation in fledgling quality, and low-quality
369 individuals were quickly eliminated from the population, leading to the reduction of survival right
370 after fledging, while high-quality individuals performed better than average throughout their life.
371 Future studies may examine post-fledging survival in relation to fledgling numbers and consider
372 within-brood variation when investigating its causes.

373

374 *2. Reproductive success*

375 We found sex-specific support for the silver spoon hypothesis and the internal PAR hypothesis with
376 annual reproductive success. The silver spoon effect on annual reproductive success was only
377 observed in females, but it was the noise in their natal environment that reduced their reproductive
378 success, whereas no effect of noise in their rearing environment was detected (Figure 3a). In contrast,
379 the internal PAR was only observed in males, where the noise in their rearing environment
380 accelerated their reproductive schedule (Figure 3b).

381 Noise in the natal environment had an overall negative effect on female annual reproductive output
382 but not in males. Wild-derived zebra finches (*Taeniopygia guttata Castanotis*) also experience a
383 negative effect on reproductive output of prenatal environmental noise, but in both sexes (Meillère et
384 al. 2024). The deleterious effects of prenatal environmental noise also included reductions in
385 embryonic survival and telomere lengths (Meillère et al. 2024). An experiment in domestic chickens
386 (*Gallus gallus domesticus*) also showed that prenatal chronic noise exposure was associated with a

387 decrease in body and brain development (Kesar 2014). All this implies that noise affects embryos in
388 eggs. Alternatively, it could also be the exposure in the first two days after hatching that played a role,
389 given that we cross-fostered the chicks at the age of 2 d. The sex-specificity could be explained by
390 prenatal environmental noise interfering with female germ cell development, given that ovary and
391 female germ cell development occur during incubation, while male germ cell development only takes
392 place after sexual maturation (Aire 2014; Johnson 2014).

393 Our dataset only included individuals that survived the first year of life. Thus, our results do not detect
394 selective disappearance occurring in early life, i.e. our dataset is biased to only those individuals that
395 did survive to the second year, which are potentially of higher quality. Despite this, we found a
396 negative effect of prenatal environmental noise on female reproductive output, suggesting this effect
397 to be strong and acting later in life. However, we could not separate this prenatal environmental effect
398 into genetic and environmental components. Although the overall parental body mass, age and
399 reproductive investment did not differ between quiet and noisy areas, older males (0.3 y difference)
400 were more likely to breed in the noisy area, which, again assuming selective disappearance, means
401 that fathers in the noisy area could be of better quality (Schroeder, Nakagawa, et al. 2012). However,
402 such a genetic effect would only reduce or neutralize the negative effect of the noise; thus, the
403 negative effect of the prenatal environment detected here is a conservative estimate.

404 Males reared in a noisy environment exhibited a reproductive peak more than a year earlier than those
405 reared in a quiet environment (Figure 3b). This is rare support for the internal PAR hypothesis
406 compared with previous studies, which did not find effects (e.g. Weibel et al. 2020, van de
407 Crommenacker et al. 2022) or where the effects were reflected by other aspects such as growth rates,
408 motor skill acquisition and immune function (Berghänel et al. 2016), instead of accelerated
409 reproduction. However, it remains unknown why we only observed this response in males. A
410 possibility is that the response in females was masked by selective disappearance in the first year, and
411 the same selection was not as strong in males. Future studies may investigate sex-specific selective
412 disappearance in relation to rearing environments.

413 Theoretically, postponed reproduction will only evolve when the fitness gain from the increase in
414 annual reproductive success with age outweighs the fitness loss due to annual mortality. Given the
415 high annual mortality (~ 0.5 , Figure 2) and the mild increase in annual reproductive output with age
416 (Figure 3) in Lundy house sparrows, the fitness benefit of postponing reproduction is in theory
417 unlikely. However, variation in the age of reproductive peak was observed in this and previous study
418 (Schroeder, Burke, et al. 2012), suggesting a potential benefit of postponing reproduction. This could
419 be because mortality varies largely by year due to environmental effects, and thus the plasticity in the
420 timing of reproduction could be beneficial as it allows the birds to survive harsh years and breed in
421 good years (MJ Simons et al. preprint from bioRxiv.org).

422

423 *3. Anthropogenic noise*

424 Anthropogenic noise is associated with reduced immediate reproductive success (Halfwerk et al.
425 2011; Kight et al. 2012), greater short-term telomere attrition (Meillère et al. 2015; Injaian et al.
426 2019), altered hormone levels (Injaian et al. 2018; Flores et al. 2019), and reduced body condition
427 (Ware et al. 2015) in wild animals. However, studies focusing on the long-term effects of the noise
428 impact are rare, except for one study in crickets *Teleogryllus oceanicus* (Gurule-Small and Tinghitella
429 2019) and one in zebra finches (Meillère et al. 2024) that found negative effects. Our study shows that
430 the impact of anthropogenic noise experienced in early life can last to late life and lead to lifetime
431 fitness consequences and alteration in life history strategy. This long-term impact on wildlife should
432 be considered when discussing noise-pollution-related questions in urbanization.

433

434 **Conclusion**

435 Using data from a wild bird population, our study found support for the sex-specific silver spoon
436 effect: a reduction in the annual reproductive output of females hatched in an adverse environment.
437 We also found support for sex-specific internal PAR: accelerated reproductive schedules in males

438 reared in an adverse environment. We demonstrate that anthropogenic noise up to and including
439 the first two days of life can affect female birds' long-term fitness, and males age trajectories. We
440 highlight that noise pollution can have long-term impacts on wild animals' fitness and alter their life
441 history strategies.

442

443 **Funding**

444 YS was supported by a double-degree PhD scholarship from the University of Groningen and
445 Macquarie University, and a Heredity Fieldwork Grant from the Genetics Society. HLD was
446 supported by a Rosalind Franklin Fellowship from the University of Groningen. Long-term fieldwork
447 was funded by the Grant CIG PCIG12-GA-2012-333096 from the European Union (to JS) and by
448 Grants NE/F006071/1 and NE/J024567/1 from the UK Natural Environment Research Council (to
449 TB).

450

451 **Acknowledgments**

452 We thank the Lundy company and its staff, Lundy Field Society and Lundy Bird Observatory for their
453 kind help during the fieldwork. We thank members of the Dugdale Research Group and the Schroeder
454 Lab for valuable discussion.

455

456 **Data Availability**

457 Data and code are available at: <https://doi.org/10.5061/dryad.08kpr5dh>.

458

459 **References**

460 Aire TA. 2014. Spermiogenesis in birds. *Spermatogenesis*. 4(3):e959392.
461 doi:10.4161/21565554.2014.959392.

- 462 Alif Ž, Dunning J, Chik HYJ, Burke T, Schroeder J. 2022. What is the best fitness measure in wild
463 populations? A case study on the power of short-term fitness proxies to predict reproductive value.
464 Brown CR, editor. PLoS ONE. 17(4):e0260905. doi:10.1371/journal.pone.0260905.
- 465 Bengtson S-A, Eliassen K, Jacobsen LM, Magnussen E. 2004. A history of colonization and current
466 status of the house sparrow (*Passer domesticus*) in the Faroe Islands. Fróðskaparrit. 51:237–251.
- 467 Berghänel A, Heistermann M, Schülke O, Ostner J. 2016. Prenatal stress effects in a wild, long-lived
468 primate: predictive adaptive responses in an unpredictable environment. Proc R Soc B.
469 283(1839):20161304. doi:10.1098/rspb.2016.1304.
- 470 Bouwhuis S, Sheldon BC, Verhulst S, Charmantier A. 2009. Great tits growing old: selective
471 disappearance and the partitioning of senescence to stages within the breeding cycle. Proc R Soc B.
472 276(1668):2769–2777. doi:10.1098/rspb.2009.0457.
- 473 Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler
474 M, Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated
475 generalized linear mixed modeling. The R journal. 9(2):378–400. doi:10.3929/ETHZ-B-000240890.
- 476 Cleasby IR, Burke T, Schroeder J, Nakagawa S. 2011. Food supplements increase adult tarsus length,
477 but not growth rate, in an island population of house sparrows (*Passer domesticus*). BMC Res Notes.
478 4(1):431. doi:10.1186/1756-0500-4-431.
- 479 Cleasby IR, Nakagawa S, Gillespie DOS, Burke T. 2010. The influence of sex and body size on
480 nestling survival and recruitment in the house sparrow: juvenile survival in the house sparrow. Biol J
481 Linn Soc. 101(3):680–688. doi:10.1111/j.1095-8312.2010.01515.x.
- 482 Clutton-Brock TH, Isvaran K. 2007. Sex differences in ageing in natural populations of vertebrates.
483 Proc R Soc B. 274(1629):3097–3104. doi:10.1098/rspb.2007.1138.
- 484 Cooper EB, Kruuk LEB. 2018. Ageing with a silver-spoon: A meta-analysis of the effect of
485 developmental environment on senescence. Evol Lett. 2(5):460–471. doi:10.1002/evl3.79.
- 486 van de Crommenacker J, Hammers M, Dugdale HL, Burke TA, Komdeur J, Richardson DS. 2022.
487 Early-life conditions impact juvenile telomere length, but do not predict later life-history strategies or
488 fitness in a wild vertebrate. Ecol Evol. 12(6):e8971. doi:10.1002/ece3.8971.
- 489 Crosland A, Rigaud T, Balourdet A, Moret Y. 2022. “Born with a silver spoon in the mouth has bad
490 sides too”: Experimentally increasing growth rate enhances individual quality but accelerates
491 reproductive senescence in females of the mealworm beetle, *Tenebrio molitor*. Front Ecol Evol.
492 10(915054). doi:10.3389/fevo.2022.915054.
- 493 Dawson DA, Horsburgh GJ, Krupa AP, Stewart IRK, Skjelseth S, Jensen H, Ball AD, Spurgin LG,
494 Mannarelli M, Nakagawa S, et al. 2012. Microsatellite resources for Passeridae species: a predicted
495 microsatellite map of the house sparrow *Passer domesticus*. Mol Ecol Resour. 12(3):501–523.
496 doi:10.1111/j.1755-0998.2012.03115.x.
- 497 Flores R, Penna M, Wingfield JC, Cuevas E, Vásquez RA, Quirici V. 2019. Effects of traffic noise
498 exposure on corticosterone, glutathione and tonic immobility in chicks of a precocial bird. Cooke S,
499 editor. Conserv Physiol. 7(1):coz061. doi:10.1093/conphys/coz061.
- 500 Gluckman PD, Hanson MA. 2004. Developmental origins of disease paradigm: A mechanistic and
501 evolutionary perspective. Pediatr Res. 56(3):311–317. doi:10.1203/01.PDR.0000135998.08025.FB.

- 502 Gluckman PD, Hanson MA, Spencer HG. 2005. Predictive adaptive responses and human evolution.
503 Trends Ecol Evol. 20(10):527–533. doi:10.1016/j.tree.2005.08.001.
- 504 Grafen A. 1988. On the uses of data on lifetime reproductive success. Phil Trans R Soc Lond B Biol
505 Sci. 363:1635–1645.
- 506 Gurule-Small GA, Tinghitella RM. 2019. Life history consequences of developing in anthropogenic
507 noise. Glob Chang Biol. 25(6):1957–1966. doi:10.1111/gcb.14610.
- 508 Hales CN, Barker DJP. The thrifty phenotype hypothesis. Br Med Bull. 60(1):5–20.
- 509 Halfwerk W, Holleman LJM, Lessells CM, Slabbekoorn H. 2011. Negative impact of traffic noise on
510 avian reproductive success. J Appl Ecol. 48(1):210–219. doi:10.1111/j.1365-2664.2010.01914.x.
- 511 Injaian AS, Gonzalez-Gomez PL, Taff CC, Bird AK, Ziur AD, Patricelli GL, Hausmann MF,
512 Wingfield JC. 2019. Traffic noise exposure alters nestling physiology and telomere attrition through
513 direct, but not maternal, effects in a free-living bird. Gen Comp Endocrinol. 276:14–21.
514 doi:10.1016/j.ygcen.2019.02.017.
- 515 Injaian AS, Taff CC, Pearson KL, Gin MMY, Patricelli GL, Vitousek MN. 2018. Effects of
516 experimental chronic traffic noise exposure on adult and nestling corticosterone levels, and nestling
517 body condition in a free-living bird. Horm Behav. 106:19–27. doi:10.1016/j.yhbeh.2018.07.012.
- 518 Ivimey-Cook ER, Shorr S, Moorad JA. 2023. The distribution of the Lansing Effect across animal
519 species. Evolution. 77(2):608–615. doi:10.1093/evolut/qpac045.
- 520 Johnson AL. 2014. The avian ovary and follicle development: some comparative and practical
521 insights. Turk J Vet Anim Sci. 38:660–669. doi:10.3906/vet-1405-6.
- 522 Kesar A. 2014. Effect of prenatal chronic noise exposure on the growth and development of body and
523 brain of chick embryo. Int J App Basic Med Res. 4(1):3. doi:10.4103/2229-516X.125666.
- 524 Kight CR, Saha MS, Swaddle JP. 2012. Anthropogenic noise is associated with reductions in the
525 productivity of breeding Eastern Bluebirds (*Sialia sialis*). Ecol Appl. 22(7):1989–1996.
526 doi:10.1890/12-0133.1.
- 527 Kirkwood TBL, Austad SN. 2000. Why do we age? Nature. 408(6809):233–238.
528 doi:10.1038/35041682.
- 529 Lindström J. 1999. Early development and fitness in birds and mammals. Trends Ecol Evol.
530 14(9):343–348.
- 531 Lüdecke D, Ben-Shachar M, Patil I, Waggoner P, Makowski D. 2021. performance: an R package for
532 assessment, comparison and testing of statistical models. JOSS. 6(60):3139. doi:10.21105/joss.03139.
- 533 Mainwaring MC, Tobalske BW, Hartley IR. 2023. Born without a silver spoon: a review of the causes
534 and consequences of adversity during early life. Integr Comp Biol. 63(3):742–757.
- 535 Marasco V, Boner W, Griffiths K, Heidinger B, Monaghan P. 2019. Intergenerational effects on
536 offspring telomere length: interactions among maternal age, stress exposure and offspring sex. Proc R
537 Soc B. 286(1912):20191845. doi:10.1098/rspb.2019.1845.
- 538 Marshall TC, Slate J, Kruuk LEB, Pemberton JM. 1998. Statistical confidence for likelihood-based
539 paternity inference in natural populations. Mol Ecol. 7(5):639–655. doi:10.1046/j.1365-
540 294x.1998.00374.x.

- 541 Meillère A, Brischoux F, Angelier F. 2015. Impact of chronic noise exposure on antipredator
542 behavior: an experiment in breeding house sparrows. *Behav Ecol.* 26(2):569–577.
543 doi:10.1093/beheco/aru232.
- 544 Meillère A, Buchanan KL, Eastwood JR, Mariette MM. 2024. Pre- and postnatal noise directly
545 impairs avian development, with fitness consequences. *Science.* 384(6694):475–480.
546 doi:10.1126/science.ade5868.
- 547 Monaghan P. 2008. Early growth conditions, phenotypic development and environmental change. *Phil*
548 *Trans R Soc B.* 363(1497):1635–1645. doi:10.1098/rstb.2007.0011.
- 549 Nettle D, Frankenhuis WE, Rickard IJ. 2013. The evolution of predictive adaptive responses in human
550 life history. *Proc R Soc B.* 280(1766):20131343. doi:10.1098/rspb.2013.1343.
- 551 Nur N. 1984. The consequences of brood size for breeding blue tits II. Nestling weight, offspring
552 survival and optimal brood size. *J Anim Ecol.* 53(2):497–517.
- 553 Perrig M, Grübler MU, Keil H, Naef-Daenzer B. 2017. Post-fledging survival of Little Owls *Athene*
554 *noctua* in relation to nestling food supply. *Ibis.* 159(3):532–540. doi:10.1111/ibi.12477.
- 555 van de Pol M, Wright J. 2009. A simple method for distinguishing within- versus between-subject
556 effects using mixed models. *Anim Behav.* 77(3):753–758. doi:10.1016/j.anbehav.2008.11.006.
- 557 Sanghvi K. 2021. Sex- and trait-specific silver-spoon effects of developmental environments, on
558 ageing. *Evol Ecol.* 35:367–385. doi:10.1007/s10682-021-10115-y.
- 559 Schroeder J, Burke T, Mannarelli M -E., Dawson DA, Nakagawa S. 2012. Maternal effects and
560 heritability of annual productivity. *J Evol Biol.* 25(1):149–156. doi:10.1111/j.1420-
561 9101.2011.02412.x.
- 562 Schroeder J, Cleasby IR, Nakagawa S, Ockendon N, Burke T. 2011. No evidence for adverse effects
563 on fitness of fitting passive integrated transponders (PITs) in wild house sparrows *Passer domesticus*.
564 *J Avian Biol.* 42(3):271–275. doi:10.1111/j.1600-048X.2010.05271.x.
- 565 Schroeder J, Nakagawa S, Cleasby IR, Burke T. 2012. Passerine birds breeding under chronic noise
566 experience reduced fitness. *PLoS ONE.* 7(7):e39200. doi:10.1371/journal.pone.0039200.
- 567 Schroeder J, Nakagawa S, Rees M, Mannarelli M-E, Burke T. 2015. Reduced fitness in progeny from
568 old parents in a natural population. *Proc Natl Acad Sci USA.* 112(13):4021–4025.
569 doi:10.1073/pnas.1422715112.
- 570 Spagopoulou F, Teplitsky C, Chantepie S, Lind MI, Gustafsson L, Maklakov AA. 2020. Silver-spoon
571 upbringing improves early-life fitness but promotes reproductive ageing in a wild bird. Metcalf J,
572 editor. *Ecol Lett.* 23(6):994–1002. doi:10.1111/ele.13501.
- 573 Verhulst S, Nilsson J-Å. 2008. The timing of birds' breeding seasons: a review of experiments that
574 manipulated timing of breeding. *Phil Trans R Soc B.* 363(1490):399–410.
575 doi:10.1098/rstb.2007.2146.
- 576 Verhulst S, Tinbergen JM, Daan S. 1997. Multiple breeding in the Great Tit. A trade-off between
577 successive reproductive attempts? *Funct Ecol.* 11(6):714–722. doi:10.1046/j.1365-
578 2435.1997.00145.x.

- 579 Ware HE, McClure CJW, Carlisle JD, Barber JR. 2015. A phantom road experiment reveals traffic
580 noise is an invisible source of habitat degradation. *Proc Natl Acad Sci USA*. 112(39):12105–12109.
581 doi:10.1073/pnas.1504710112.
- 582 Weibel CJ, Tung J, Alberts SC, Archie EA. 2020. Accelerated reproduction is not an adaptive
583 response to early-life adversity in wild baboons. *Proc Natl Acad Sci USA*. 117(40):24909–24919.
584 doi:10.1073/pnas.2004018117.
- 585 Wells JCK. 2012. Obesity as malnutrition: The role of capitalism in the obesity global epidemic.
586 *American J Hum Biol*. 24(3):261–276. doi:10.1002/ajhb.22253.
- 587 Winney I, Nakagawa S, Hsu Y, Burke T, Schroeder J. 2015. Troubleshooting the potential pitfalls of
588 cross-fostering. Blackwell P, editor. *Methods Ecol Evol*. 6(5):584–592. doi:10.1111/2041-
589 210X.12341.
- 590 Wu SH, Liu Z, Ho SC. 2010. Metabolic syndrome and all-cause mortality: a meta-analysis of
591 prospective cohort studies. *Eur J Epidemiol*. 25(6):375–384. doi:10.1007/s10654-010-9459-z.
- 592 Zuur A, Ieno E, Walker N, Saveliev A, Smith G. 2009. *Mixed effects models and extensions in
593 ecology with R*. Springer.
- 594