Statement of authorship: The idea was conceived by HLD, JS and YS. YS selected and analysed the data, with input from HLD and JS. YS wrote the first draft of the manuscript, and all authors contributed to revisions. TB and JS manage the long-term study system on which this research was based. TB and JS gained funding for the long-term study, and HLD gained funding for YS' PhD. JS and HLD supervised YS. All authors approved the final submission.

Silver spoon effect: Natal noise exposition is associated with telomere dynamics in adult birds

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

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Abstract

Anthropogenic noise disturbance on wildlife is of growing concern. Environmental noise exposure during incubation can negatively impact fitness in wild birds. Here, we hypothesised that chronic noise introduces stress through oxidative damage to embryos, reflected in short-term fitness reduction and long-term physiological changes. To test this hypothesis, we investigated the effects of chronic natal noise on chick body condition, fledging success, and adult telomere shortening in a wild house sparrow *Passer domesticus* population using 13 years of data. We disentangled the effects of noise in the natal and rearing environments using cross-fostering. We found no evidence for the association between natal noise exposure and chick mass, body condition at fledging, and fledging success. However, adults with shorter telomeres were underrepresented in older age groups if they were incubated in chronic noise conditions, suggesting a silver spoon effect of early-life noise exposure, which has implications for the management of wild populations.

Introduction

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

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

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

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

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

We investigated the short- and long-term effects of natal environmental noise in a wild bird population. We disentangled the effects of natal and rearing environments using a multi-year cross-fostering experiment. We tested short-term effects of natal noise on chick mass, body condition at fledging, and fledging success, predicting that these would be lower in noisy compared to quiet natal environments. We then tested adult telomere shortening in response to the presence of noise in the natal environment, predicting that this would lead to faster telomere shortening in adulthood,

reflecting long-term physiological impacts. We also tested whether the effect on telomere shortening differed between females and males.

Material and methods

Study population

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

Cross-fostering experiments were carried out routinely between same-aged broods during 2000–2012, except in 2008 and 2010 because the breeding population was so small that same-aged broods were not available (Winney et al., 2015). Chicks were typically swapped when they were 2 days old, except that in 2000-2003, cross-fostering took place at 3 days old (Cleasby et al., 2010). Broods were swapped entirely, or partially if that was required to maintain the original brood size. Depending on the location of the same-aged brood(s), cross-fostering occurred within or between noisy and quiet areas. Chicks remained in their foster broods until they fledged. There was no evidence for kin

recognition, and parent birds did not alter their parental care behaviour to cross-fostered broods (Lattore et al., 2019).

Noise impact

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

Data collection

We weighed chicks at the ages of 2, 6 and 12 days with an electronic scale, but occasionally we weighed chicks one day earlier or later or on day 14. We measured tarsus length at the last nest visit (i.e., typically on day 12, occasionally on day 11, 13 or 14). Chicks that survived to the last nest visit were considered fledged. We measured relative telomere length (RTL) from blood samples collected from the birds upon subsequent captures. Sampling frequency for RTL per bird per year ranged between one to five (Chik et al., 2024). Detailed methods for quantifying RTL and the resulting dataset are provided in Chik et al. 2024. In summary, we used a monochrome multiplex quantitative polymerase chain reaction (MMqPCR) and RTL was expressed in a ratio of telomeric signals to that

of a single-copy reference gene (GAPDH; Chik et al., 2024). The intra-plate, between-duplicate repeatability of RTL was 95.7% (s.e. = 0.2%); and the inter-plate repeatability was 97.7% (s.e. = 0.9%; Chik et al., 2024). In this population, RTL declines linearly with age within an individual and its individual repeatability was 14.0% (95% CI: 9.1%-19.9%; Chik et al., 2025).

Statistical analyses

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

Chick mass

We fitted a GLMM with standardised chick mass as the response variable with a Gaussian residual distribution, and the following variables as fixed effects: presence of noise in the natal environment (1 = present, 0 = absent), presence of noise in the rearing environment (1 = present, 0 = absent), age (days), brood size (continuous). Brood size was included to control for the effect that chicks from larger broods were lighter (Cleasby et al., 2011). Sex was not included because the sexes of chicks that died before we blood sampled them were unknown. The model included the following random effects: bird ID, to account for the nonindependence of the mass measured for the same chick at different ages; natal brood ID, to account for the genetic factors that individuals hatched in the same brood might share (Schroeder et al., 2012); cohort, to account for the effects of environmental factors

varying by the year when the chick was hatched. Rearing brood ID was not included because only cross-fostered individuals were included in this dataset, and thus rearing brood ID was perfectly correlated with natal brood ID and would explain the same variance.

Body condition at fledging

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

Fledging success

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

Adult telomere shortening and sex-specific effect

Adult RTL was z-standardised (zRTL) for comparability with other studies (Verhulst, 2020). We modeled zRTL as the response variable, with a skew-normal distribution to account for the skewness of the data (Bürkner, 2021). We fitted the presence of noise in the natal environment (1 = present, 0 = absent) and age as fixed effects, and their interaction (natal environment * age) was fitted to test

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

To examine whether the significant interaction of natal environment * age detected by the previous model was due to a between-individual effect or a within-individual effect, we decomposed age in the final zRTL model into two components: mean age (mean of the ages that each individual appeared in

the dataset) and Δage (age – mean age) (van de Pol & Wright, 2009). This decomposition allowed mean age to capture between-individual differences—i.e., whether individuals that tend to live longer also differ in average RTL—while Δage captures the within-individual change in RTL with age. We included both natal environment * mean age and natal environment * Δage in the model to identify which effect natal environment interacted with. We then removed natal environment * Δage because it was not significant, to facilitate interpretation of first-order effects.

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

Results

Natal noise did not significantly affect chick mass, body condition at fledging, or fledging success (Table 1, Fig. 2). Noise in the rearing environment significantly reduced chick mass and body condition at fledging, and marginally reduced fledging success (Table 1, Fig. 2). The larger the brood was, the lighter the chicks were, but brood size did not predict body condition at fledging or fledging success (Table 1, Fig. 2). Chick mass increased with age (Table 1, Fig. 2a). Males were heavier at

fledging, controlling for tarsus length (Table 1, Fig. 2b).

The age effect on adult RTL at old ages was significantly more positive for birds from a noisy natal environment than it was for birds from a quiet natal environment (Table 2, Fig. 3a). The model using MAC instead of PAC led to the same conclusion (Table S4-5), confirming an environmental effect. The LOO identified two data points with the shape parameter $k > 1$, indicating outsized influence of these observations on the posterior distribution of the model (Vehtari et al., 2017). Removing these two observations let the credible interval (CrI) of the interaction natal environment * age border zero (CrI: [-0.00, 0.17]), but the trend persisted that the age effect was more positive for old birds from a noisy natal environment than it was for those from a quiet natal environment. We kept these data points in the model because they were real observations (Fig. S2).

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

Discussion

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

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

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

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

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

We observed a positive interaction between the effects of natal noise and age on adult telomere length. We revealed that this was due to between-individual differences—i.e., birds that experienced natal noise and that had longer telomeres lived longer, rather than that telomeres lengthened as an individual aged (Fig. 3b & S3). As such, birds with shorter telomeres were more likely to disappear from the population if incubated in the noisy environment. We showed previously that adults with shorter telomeres died earlier, leading to a bias for longer telomeres in older individuals (Sibma, 2021). Given that telomere length is a biomarker of oxidative stress (Reichert & Stier, 2017), our finding suggests that individuals from a noisy natal environment might be more likely to die under oxidative stress of the same intensity than those from a quiet natal environment. Together with the finding that natal noise was associated with reduced annual reproductive output (Sun et al. 2025), this suggests that natal exposure to noise is a cause of lifetime physiological consequences, aligning with the prediction of the silver spoon hypothesis. Our cross-fostering experiments were not conducted until the second day after hatching. It is possible that the disturbance of the parents' provisioning behaviour in the first two days played a critical role, as human studies have shown that provision of nutrition in a very early stage of life could be associated with growth and neurodevelopmental outcome on some occasions (Poindexter et al., 2006). Although the posterior predictive plot showed a suboptimal match to the observed data distribution (Fig. S1), the R-hat parameters and MCSEs

indicated stable posterior estimates, suggesting that the model captured the trend of the data, and parameter estimates and credible intervals can be interpreted with confidence regarding their direction and relative strength.

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

We did not detect a sex-specific effect of natal noise exposure on body condition at fledging or adult telomere length, even though natal noise exposure was associated with a significant reduction specifically in female lifetime reproductive output in this population (Sun et al., 2025). Our results

suggest that the decline in female reproductive performance might not be mediated by a deterioration in somatic condition. A plausible explanation is that individuals allocated more resources to somatic maintenance at the cost of future reproductive success under noise stress during embryonic development to maximise lifetime fitness (Kirkwood, 2002). A meta-analysis showed that the adverse effects of developmental environments were reflected by a faster decline in late-life reproduction instead of survival, presumably due to the same reason (Cooper & Kruuk, 2018). Male reproduction is less energetically demanding than female reproduction, which may explain why it was not detectably affected by natal noise exposure. This life history plasticity to maintain body condition and survival in response to noise stress during development at the expense of adult reproductive output might again be one of the manifestations of the superiority of house sparrows to adapt to human-commensal niches. This might be a direction for future studies to explore.

In conclusion, we found no evidence that natal noise influenced short-term fitness, but it altered the age-telomere relationship in adulthood, indicating potential long-lasting physiological effects. Future studies on the direct effect of noise disturbance on development, as well as studies on long-term consequences of other natal stressors, will be valuable for understanding the nature of these long-lasting effects and the mechanisms underlying them. We also note that the absence of a detectable effect of natal noise on somatic condition in house sparrows may be attributable to their characteristics as a successful human-commensal.

Acknowledgements

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

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Tables

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, and fledging success in Lundy house sparrows. Significant fixed effects are in bold; fixed effects whose 95% CrI borders zero are 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)	(Level)	0.05 [-0.03, 0.13]	0.03 [-0.14, 0.21]	-1.12 [-1.63, -0.63]
	Natal environment	Noisy	-0.03 [-0.06, 0.01]	0.00 [-0.11, 0.12]	0.11 [-0.24, 0.44]
	Rearing environment	Noisy	**-0.04 [-0.08, -0.00]**	**-0.11 [-0.22, -0.01]**	*-0.32 [-0.65, 0.00]*
	Age		**0.92**	-0.02	

			[0.91, 0.93]	[-0.05, 0.01]	
	Brood size		**-0.03**	-0.01	-0.09
			[-0.05, -0.02]	[-0.05, 0.04]	[-0.24, 0.05]
	Tarsus length			**0.80**	
				[0.77, 0.84]	
	Sex	Male		**0.10**	
				[0.04, 0.16]	
Random effects (number of levels)	Bird ID		0.13		
			[0.12, 0.15]		
			(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)

598

599 Table 2. 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) in Lundy house
601 sparrows. Significant fixed effects are in bold. Number of levels for random effects is in brackets. CrI:
602 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^2		0.01 [-0.02, 0.03]
DNA age		**-0.24 [-0.46, -0.01]**
DNA age^2		0.01 [-0.08, 0.10]
Blood age		**-0.27 [-0.48, -0.02]**
Blood age^2		-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]
Natal environment * age	Noisy	**0.09 [0.00, 0.18]**
Random effects		**Estimates (number of levels)**
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)

Table 3. Fixed and random effect estimates with [95% CrI] from the GLMM testing the effect of the natal environmental noise on adult z-standardised relative telomere length (zRTL), with age decomposed into mean age and within-individual-centred age (Δage). Significant fixed effects are in bold; fixed effects whose credible intervals (CrI) borders zero are in italics. PAC: paternal age at conception. For output of the reduced model where the non-significant interaction natal environment * Δage 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]
Δage		-0.01 [-0.05, 0.02]

Δage²		*0.01 [-0.00, 0.03]*
Mean age		-0.01 [-0.06, 0.03]
DNA age		**-0.24 [-0.46, -0.01]**
DNA age²		0.01 [-0.08, 0.10]
Blood age		**-0.26 [-0.47, -0.02]**
Blood age²		-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 * Δage	Noisy	0.02 [-0.06, 0.10]
Natal environment * mean age	Noisy	**0.10 [0.01, 0.19]**
Random effects		**Estimates**
		(number of levels)
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]

		(13)
Plate		0.21 [0.16, 0.28]
		(82)

611

Figures

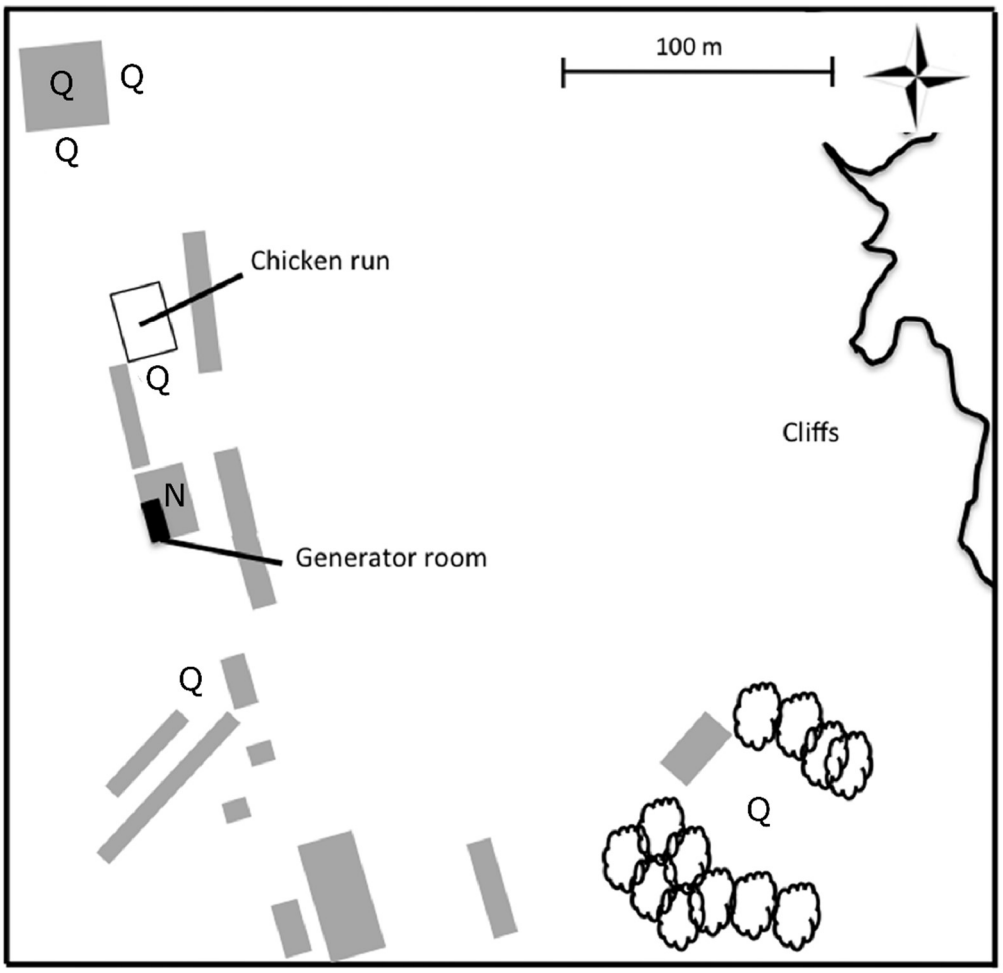

Figure 1. Locations of quiet (Q) and noisy (N) house sparrow breeding sites on Lundy Island. The chicken run was the main feeding site of the house sparrows. Adopted from Sun et al. (2025).

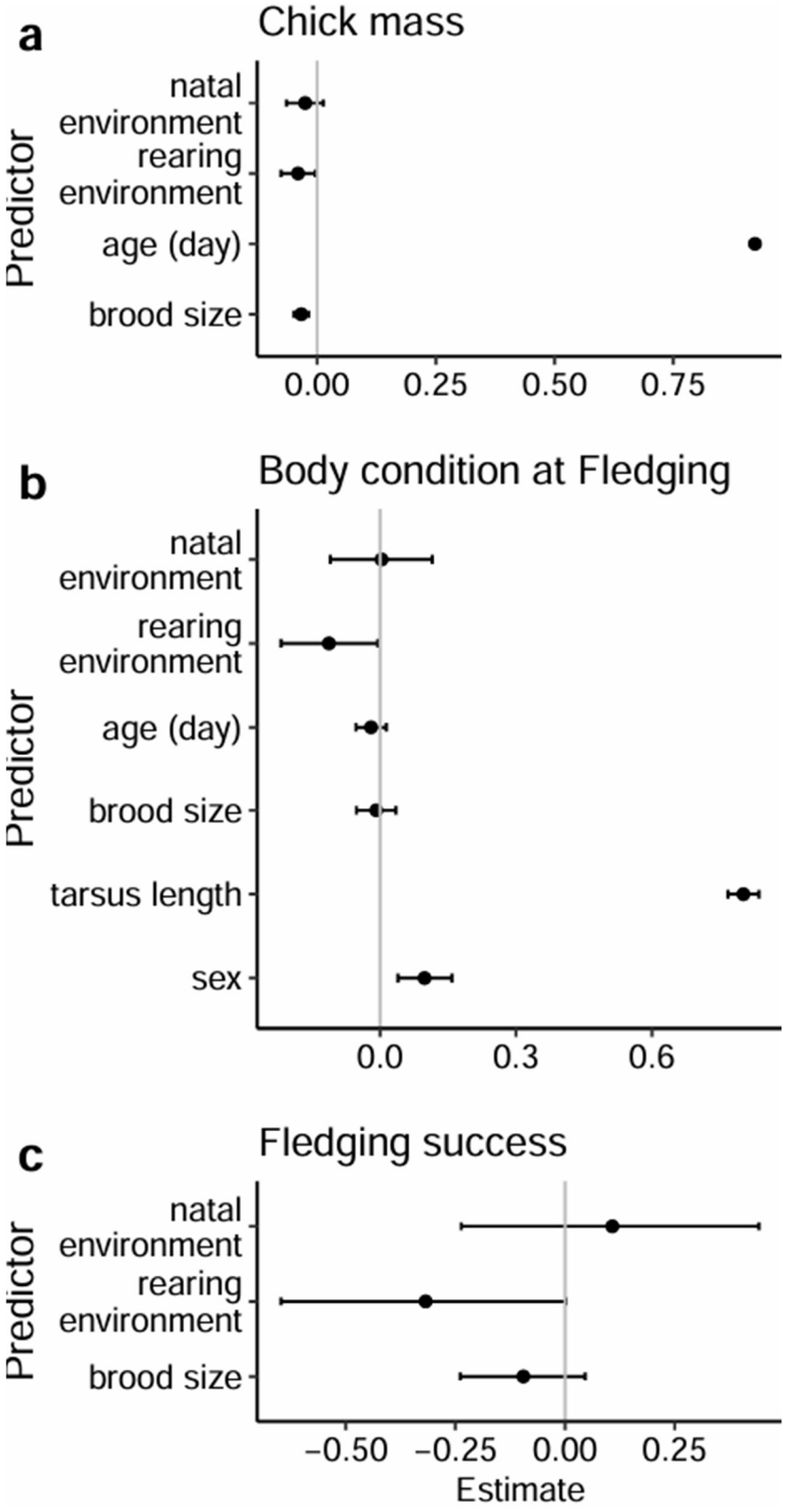

Figure 2. Effect sizes with 95% CrIs of the fixed effects predicting (a) chick mass, (b) body condition at fledging and (c) fledging success.

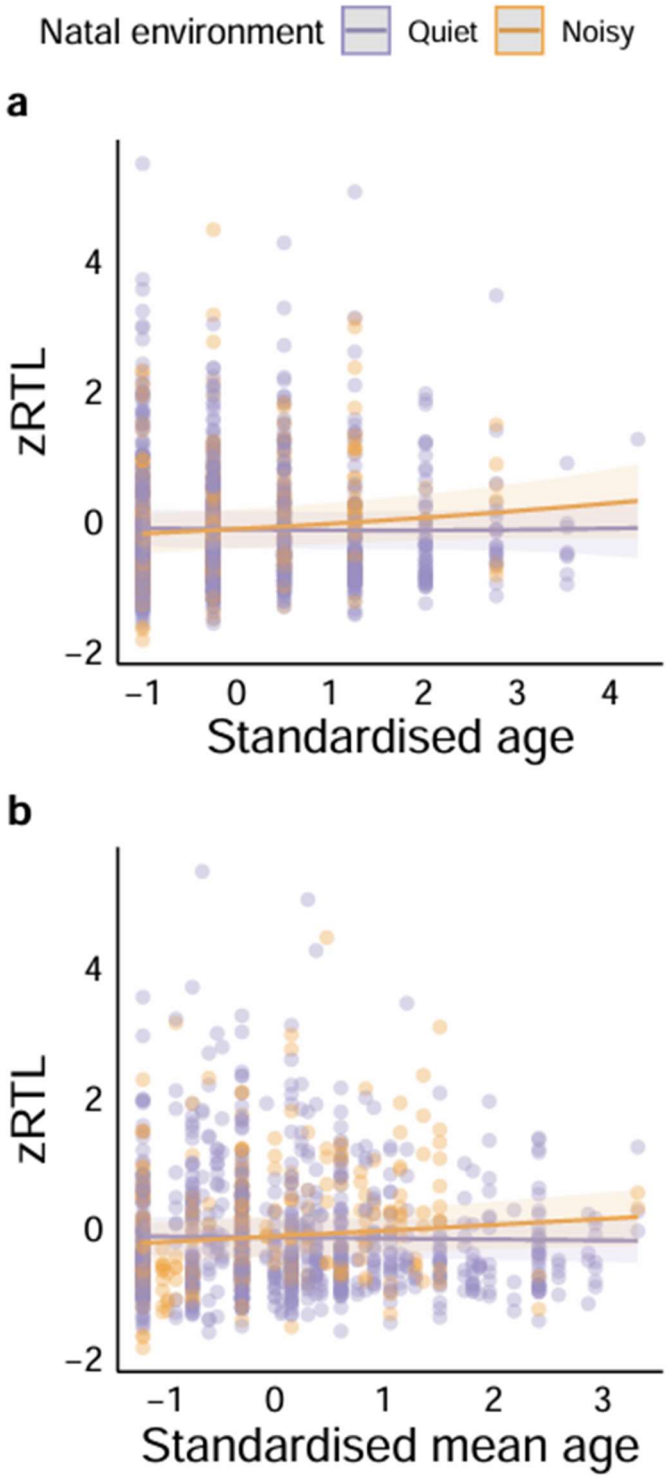

Figure 3. Adult zRTL (z-standardised relative telomere length) in relationship to (a) z-standardised age and (b) z-standardised mean age (mean of the ages that each individual appeared in the dataset) in Lundy house sparrows. Each dot represents an observation; lines are predicted zRTL; shaded areas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

Supplementary materials

Supporting information for:

Silver spoon effect: Natal noise exposition is associated with telomere dynamics in adult birds

Tables S1-S6

Figures S1-S3

Table S1. Priors used for each Bayesian GLMM. zRTL: z-standardised adult relative telomere length.

Model	Class	Priors
Chick body mass Body condition at fledging	Intercept	normal(0, 2)
	b	normal(0, 2)
Fledging success	Intercept	normal(0, 10)
	b	normal(0, 5)
zRTL	Intercept	normal(0, 10)
	b	normal(0, 5)

Table S2. Summary of posterior distribution of the GLMM testing the effect of the natal environmental noise on adult z-standardised relative telomere length (zRTL). CrI: credible intervals. pd: probability of direction. ROPE: region of practical equivalence. ESS: effective sample size. PAC: paternal age at conception.

Parameter	Median	95% CrI	pd	ROPE	% in ROPE	Rhat	ESS
(Intercept)	-0.13	[-0.42, 0.15]	82.74%	[-0.09, 0.09]	34.55%	1.001	2782
Natal environment	0.01	[-0.10, 0.11]	55.91%	[-0.09, 0.09]	96.87%	1.001	8642
Rearing environment	0.00	[-0.10, 0.09]	53.35%	[-0.09, 0.09]	97.84%	1	9002
Age	-0.02	[-0.07, 0.03]	74.67%	[-0.09, 0.09]	100%	1	8102
Age^2	0.01	[-0.02, 0.03]	66.97%	[-0.09, 0.09]	100%	1	9181
DNA age	-0.25	[-0.46, -0.01]	98.08%	[-0.09, 0.09]	6.66%	1.003	2834
DNA age^2	0.01	[-0.08, 0.10]	57.27%	[-0.09, 0.09]	99.17%	1.001	4648
Blood age	-0.27	[-0.48, -0.02]	98.16%	[-0.09, 0.09]	4.82%	1.003	2638
Blood age^2	-0.01	[-0.13, 0.12]	55.25%	[-0.09, 0.09]	88.92%	1.001	4734
PAC	0.01	[-0.02, 0.05]	75.10%	[-0.09, 0.09]	100%	1	11584
Sex	0.04	[-0.03, 0.10]	85.44%	[-0.09, 0.09]	97.61%	1	12071
Technician	-0.03	[-0.20, 0.14]	64.42%	[-0.09, 0.09]	73.21%	1	4237
Natal environment * age	0.09	[0.00, 0.18]	97.96%	[-0.09, 0.09]	47.08%	1	11065

Table S3. Fixed and random effect estimates with [95% CrI] from the GLMM testing the effect of thenatal environmental noise on adult z-standardised relative telomere length (zRTL), with non-significant interactions included. Significant fixed effects are in bold. Number of levels for random effects is in brackets. CrI: credible intervals. PAC: paternal age at conception.

Fixed effects	**Level**	**Estimates**
(Intercept)		-0.13 [-0.42, 0.17]
Natal environment	Noisy	0.07 [-0.08, 0.22]
Rearing environment	Noisy	-0.01 [-0.11, 0.09]
Age		-0.02 [-0.07, 0.03]
Age^2		0.01 [-0.02, 0.03]
DNA age		**-0.24 [-0.46, -0.01]**
DNA age^2		0.00 [-0.09, 0.10]
Blood age		**-0.27 [-0.49, -0.02]**
Blood age^2		-0.01 [-0.14, 0.11]
PAC		0.01 [-0.02, 0.05]
Sex	Male	0.04 [-0.02, 0.08]
Technician	B	-0.03 [-0.20, 0.14]
Natal environment * sex	Noisy * male	-0.09 [-0.25, 0.06]
PAC * sex		-0.04 [-0.11, 0.02]
Natal environment * age		0.11 [-0.00, 0.22]
Natal environment * age^2		-0.02 [-0.08, 0.05]

Random effects	Estimates (number of levels)
Bird ID	0.08 [0.00, 0.17] (652)
Rearing brood	0.09 [0.01, 0.17] (446)
Natal brood	0.08 [0.00, 0.17] (444)
Capture Year	0.30 [0.17, 0.53] (13)
Plate	0.22 [0.16, 0.28] (82)

Table S4. Fixed and random effect estimates with [95% CrI] from the GLMM testing the effect of thenatal environmental noise on adult z-standardised relative telomere length (zRTL), with MAC (maternal age at conception) instead of PAC (paternal age at conception) as a fixed effect and non-significant interactions included. Significant fixed effects are in bold. Number of levels for random effects is in brackets. CrI: credible intervals.

Fixed effects	Level	Estimates
(Intercept)		-0.14 [-0.43, 0.16]
Natal environment	Noisy	0.08 [-0.07, 0.22]

Rearing environment	Noisy	-0.01 [-0.11, 0.09]
Age		-0.02 [-0.07, 0.03]
Age^2		0.01 [-0.02, 0.03]
DNA age		**-0.23 [-0.46, -0.00]**
DNA age^2		0.00 [-0.09, 0.10]
Blood age		**-0.26 [-0.48, -0.01]**
Blood age^2		-0.01 [-0.14, 0.11]
MAC		0.02 [-0.03, 0.07]
Sex	Male	0.06 [-0.03, 0.07]
Technician	B	-0.03 [-0.19, 0.13]
Natal environment * sex	Noisy * male	-0.10 [-0.26, 0.05]
MAC * sex		-0.00 [-0.07, 0.06]
Natal environment * age		0.11 [-0.00, 0.21]
Natal environment * age^2		-0.02 [-0.08, 0.05]
Random effects		**Estimates**
		(number of levels)
Bird ID		0.07 [0.00, 0.17]
		(652)
Rearing brood		0.08 [0.01, 0.17]
		(446)

Natal brood		0.08 [0.00, 0.17]
		(444)
Capture Year		0.30 [0.17, 0.54]
		(13)
Plate		0.22 [0.16, 0.29]
		(82)

Table S5. Fixed and random effect estimates with [95% CrI] from the GLMM testing the effect of thenatal environmental noise on adult z-standardised relative telomere length (zRTL), with MAC (maternal age at conception) instead of PAC (paternal age at conception) as a fixed effect and non-significant interactions removed. Significant fixed effects are in bold. Number of levels for random effects is in brackets. CrI: credible intervals.

Fixed effects	**Level**	**Estimates**
(Intercept)		-0.12 [-0.41, 0.17]
Natal environment	Noisy	0.01 [-0.09, 0.11]
Rearing environment	Noisy	-0.01 [-0.11, 0.09]
Age		-0.02 [-0.07, 0.03]
Age^2		0.01 [-0.02, 0.03]
DNA age		**-0.24 [-0.46, -0.00]**
DNA age^2		0.01 [-0.08, 0.10]
Blood age		**-0.26 [-0.48, -0.01]**

Blood age^2		-0.01 [-0.13, 0.11]
MAC		0.02 [-0.01, 0.06]
Sex	Male	0.04 [-0.03, 0.10]
Technician	B	-0.03 [-0.20, 0.14]
Natal environment * age	Noisy	**0.10 [0.01, 0.18]**
Random effects		**Estimates**
		(number of levels)
Bird ID		0.08 [0.00, 0.17]
		(652)
Rearing brood		0.09 [0.01, 0.17]
		(446)
Natal brood		0.08 [0.00, 0.17]
		(444)
Capture Year		0.31 [0.17, 0.56]
		(13)
Plate		0.22 [0.16, 0.28]
		(82)

Table S6. Fixed and random effect estimates with [95% CrI] from the GLMM testing the effect of the natal environmental noise on adult z-standardised relative telomere length (zRTL), with age decomposed into mean age and within-individual-centred age (Δage) and non-significant interaction

natal environment * Δage removed. Significant fixed effects are in bold; fixed effects whose credible intervals (CrI) border zero are in italics. PAC: paternal age at conception.

Fixed effects	**Level**	**Estimates**
(Intercept)		-0.14 [-0.43, 0.16]
Natal environment	Noisy	0.02 [-0.08, 0.12]
Rearing environment	Noisy	-0.01 [-0.11, 0.09]
Δage		-0.01 [-0.05, 0.03]
Δage^2		*0.01 [-0.00, 0.03]*
Mean age		-0.01 [-0.06, 0.03]
DNA age		*-0.24 [-0.45, 0.00]*
DNA age^2		0.00 [-0.09, 0.10]
Blood age		**-0.26 [-0.48, -0.01]**
Blood age^2		-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, 0.14]
Natal environment * mean age	Noisy	**0.10 [0.01, 0.19]**
Random effects		**Estimates** **(number of levels)**
Bird ID		0.07 [0.00, 0.16] (652)

Rearing brood	0.08 [0.01, 0.17]
	(446)
Natal brood	0.09 [0.00, 0.17]
	(444)
Capture Year	0.31 [0.17, 0.56]
	(13)
Plate	0.21 [0.16, 0.28]
	(82)

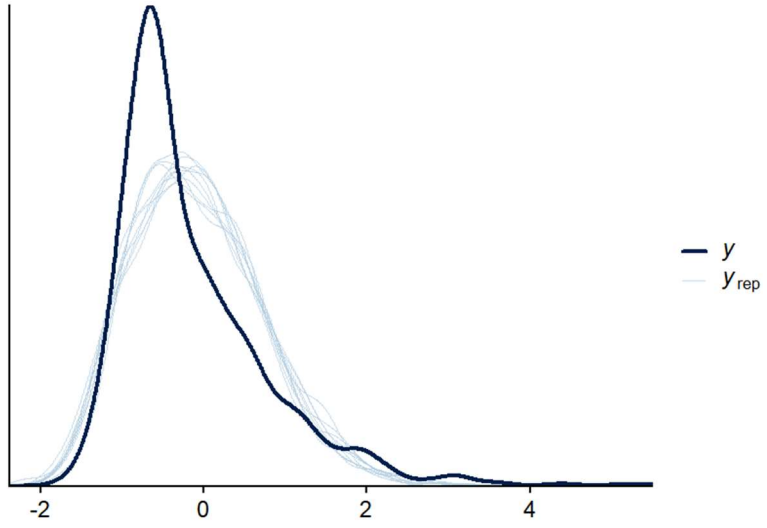

Figure S1. Posterior predictive plot of the zRTL model shows a poor match to the skewed observed data.

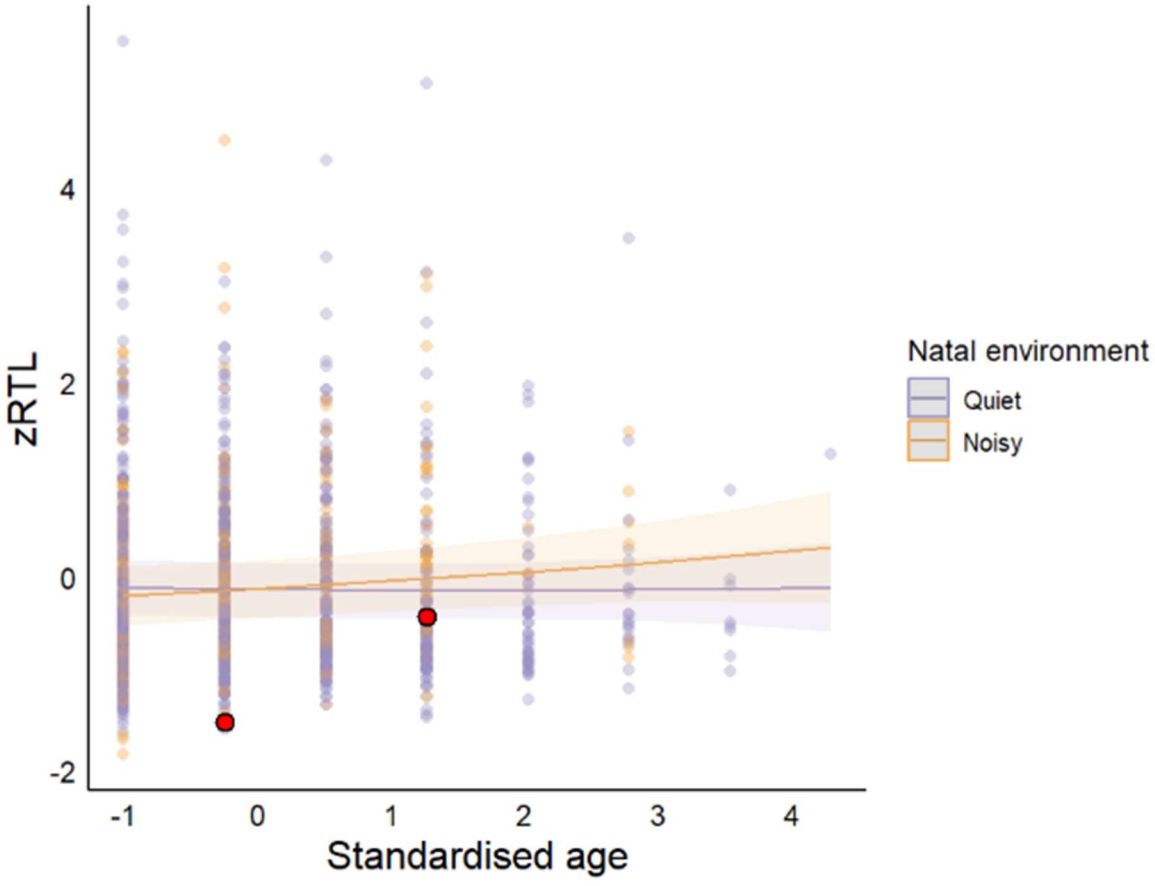

Figure S2. Two outliers in the zRTL model (see main text Fig. 3) marked in red, identified by leave-one-out cross-validation (LOO). Both of the outliers were from the quiet natal environment.

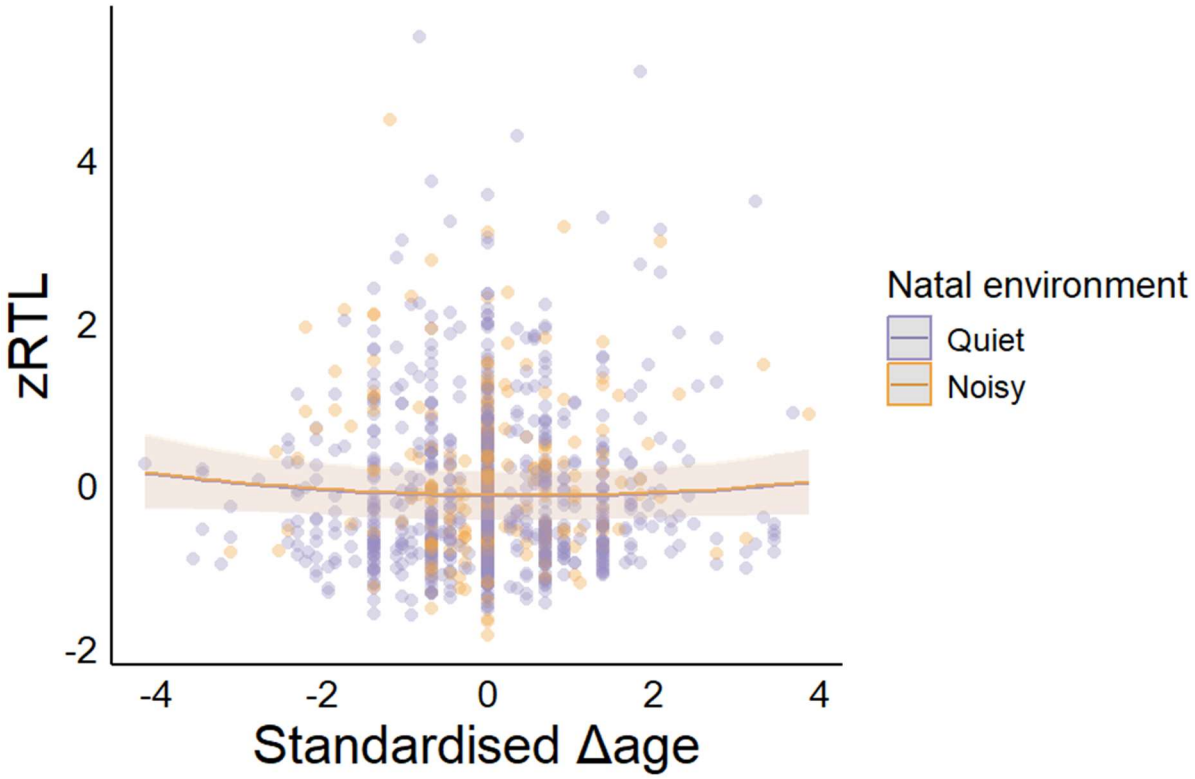

Figure S3. Adult zRTL (z-standardised relative telomere length) in relationship to z-standardised within-individual-centred age (Δage) in Lundy house sparrows. Each dot represents an observation; lines are predicted zRTL; shaded areas represent 95% CrIs.