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## ORIGINAL RESEARCH

# Gas compressor noise does not influence tree swallow nestling condition or immune response

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## Keywords

anthropogenic noise; environmental change; tree swallow; immune response; disturbance effects; *Tachycineta bicolor*; noise pollution; nestling period; gas compressor.

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## Introduction

We live in a noisy world, the result of ever-intensifying urbanization, transportation pathways, and resource extraction practices (Buxton et al., 2017; Francis & Barber, 2013; Gomes et al., 2021). Anthropogenic noise, such as that associated with traffic and industrial machinery like oil and gas compressors (Francis et al., 2012; Kleist et al., 2018), is often louder and more prevalent than natural acoustic stimuli (Popper & Hastings, 2009), leading to increased stress, for example, in humans (Andren et al., 1983; Ising & Kruppa, 2004). Anthropogenic noise pollution has therefore been identified as “an urgent conservation priority” (Francis & Barber, 2013), and work is ongoing to determine its effects on wildlife population dynamics and health.

Studies from a range of avian systems have shown that anthropogenic noise can substantially affect community

## Abstract

Anthropogenic noise pollution, such as that derived from traffic and industrial machinery, has been identified as an urgent conservation priority as it is often louder and more prevalent than natural acoustic stimuli, and can act as a stressor on wildlife. Research in avian systems has shown that anthropogenic noise can affect physiology and reproductive success of adult birds – but effects on juvenile birds have been less-studied despite their being potentially more vulnerable during the nestling period. What studies have been done have shown remarkable variability in juvenile response to anthropogenic noise, suggesting that effects are highly context- and species-specific. Here, we investigate the effects of gas compressor noise, an increasingly prevalent and biologically relevant noise stressor produced during natural gas production, on juvenile tree swallows (*Tachycineta bicolor*). Gas compressors generate considerable sound pressure as they work to pressurize gas pipelines for downstream distribution. We predicted that exposure to increased noise during incubation and the nestling period would result in smaller chicks in poorer body condition and with a dampened immune response. Surprisingly, we found no evidence for any of these predictions, providing further evidence that noise effects on juvenile birds is highly variable, and we explore ways in which individual birds may compensate for the effects of disturbance at the nest.

structure, reproductive success, and short- and long-term stress physiology of adult birds (reviewed in Kight & Swaddle, 2011, Ortega, 2012). Noise pollution has been shown to reduce site occupancy for some species (Francis et al., 2011) and generate differences in the age structure of populations nesting near noise, with younger birds more likely to settle in noisy habitats and experience reduced pairing success (Habib et al., 2007). Chronic noise can affect baseline glucocorticoids, hormones associated with the activation of the vertebrate stress response in birds (Blickley et al., 2012; Kleist et al., 2018) and a range of other vertebrates (Kight & Swaddle, 2011). Elevated glucocorticoid levels are associated with reduced immune response and survival (Crino & Breuner, 2015), and noise pollution studies suggest that birds breeding in disturbed areas generally have reduced reproductive success (Kight et al., 2012), smaller clutches, and smaller broods (Halfwerk et al., 2011).

Juveniles may be more vulnerable to anthropogenic noise effects than adults due to their relative inability to avoid noise, which is important because stress early in life can have life-long impacts on growth and development (Burton & Metcalfe, 2014; Injaian, Taff, & Patricelli, 2018; Kesar, 2014; Strasser & Heath, 2013), ultimately shaping an organism's phenotype in concert with its genetics (Butler & McGraw, 2012; West-Eberhard, 2003). If early life conditions influence phenotype and life-history decisions into adulthood, they have the potential to have multi-generational effects and are therefore a potentially important evolutionary force (Kilner *et al.*, 2015; Wilkin & Sheldon, 2009). For example, anthropogenic noise can influence chick begging (Leonard & Horn, 2008) and increase hormonal stress (Crino *et al.*, 2011; Crino *et al.*, 2013), suggesting the potential for noise effects on growth and physiology in birds. In addition to growth, immunocompetence is impacted by fluctuations in environmental conditions (Martin, 2009), and can be an important predictor of nestling survival (Cichoń & Dubiec, 2005; Hórák *et al.*, 1999). Noise effects on juvenile birds are highly variable across and within species (Crino *et al.*, 2013; Potvin & MacDougall-Shackleton, 2015). However, many studies focus on noise disturbance during only one stage in development (e.g. during provisioning only), meaning that relatively little is known about which stage of development is most vulnerable to noise pollution effects (e.g. incubation or provisioning; but see Williams *et al.*, 2021).

Here, we test the effects of anthropogenic noise throughout development (specifically, natural gas compressor noise) on the growth and immune responses of tree swallow nestlings (*Tachycineta bicolor*) using a natural population in Pennsylvania, USA. Natural gas is a rapidly growing energy source, and the extraction of shale gas resources is expected to increase in the coming decades (U.S. Energy Information Administration, 2018). To collect and transport natural gas for commercial markets, large compressor stations are needed to pressurize gas pipelines, and these stations generate powerful broadband noise with the potential to travel into adjacent habitats (Francis *et al.*, 2009). Importantly, tree swallows nest in cavities which are typically a limited resource, meaning they may be limited in their ability to choose alternate nesting sites during breeding (Winkler *et al.*, 2020), potentially increasing their vulnerability to anthropogenic noise effects. By virtue of their propensity to use nest boxes, tree swallows provide an excellent system to experimentally test for the effects of anthropogenic noise. Gas compressor stations produce chronic noise pollution, running constantly and creating a gradient of noise levels in the surrounding habitat (Francis *et al.*, 2011; Habib *et al.*, 2007; Kleist *et al.*, 2018; Williams *et al.*, 2021), with various negative impacts on wildlife already documented (e.g. Barber *et al.*, 2011; Francis *et al.*, 2009; Kleist *et al.*, 2018). Previous work in this system showed that both eastern bluebirds (*Sialia sialis*) and tree swallows exposed to gas compressor noise at a site with no prior bird population (no nesting sites existed until we built them) or compressor noise selected noisy and quiet nests equally, and that those nesting in noisy nests exhibited decreased hatching success, potentially as a consequence of reduced incubation time

(Williams *et al.*, 2021). Here, we extend this work using the same treatment and population in a second-year to test for effects at the nestling stage (specifically, on nestling immunity and growth) to assess whether successfully hatched chicks nevertheless still pay a cost for noise exposure during development. We predicted that experimentally introduced gas compressor noise at the nest throughout the breeding season would result in (1) reduced nestling growth and body size, (2) decreased nestling immune response, and (3) decreased clutch size, hatching, and fledging success.

## Materials and methods

The research took place at Pennsylvania State University's Russell E. Larson Agricultural Research Center, Rock Springs, Pennsylvania in May and June 2018. We placed 80 nest boxes along small gravel roads and fields in pairs ~1 m apart, with ~100 m between each pair (Williams *et al.*, 2021). This was the second year of experimental noise treatments at this site. Nest boxes were erected in pairs to prevent competition between tree swallows and eastern bluebirds (*S. sialis*) and there was never more than one tree swallow nest in a pair of boxes. This research was approved by Penn State's Institutional Animal Care and Use Committee (protocol #47238).

### Noise disturbance treatment

We subjected 20 of the paired box sites to broadcast recordings of shale gas compressor noise that played continuously 24 h/day from large speakers placed ~1 m behind the nest boxes underneath a black plastic awning. The other 20 control pairs received no noise treatment but still had a black plastic awning on the ground to simulate the same physical disturbance of speakers and batteries. Starting with box 1, we alternated noisy and quiet treatments, ensuring that boxes got the same treatment as in the previous year and study. Experimental playback consisted of 5 h of compressor station recordings (collected using laboratory-grade microphones calibrated to meet Type 1 precision specifications) taken in the field during multiple time points and weather conditions that looped continuously. The sound was played at nests using Boss ATV20 speakers and AGPTek mp3 players powered by 12 V marine deep cycle batteries. Compressors generate acoustic energy up to ~10 000 kHz with considerable power between 0 and 200 Hz. The speakers used in our study had a nominally flat response from 45 Hz to 10 000 kHz, which allowed a large portion of the sound's power to be replicated. We also tested whether noise playback from these speakers was realistic by recording our reproduced sound and confirming that recordings had the same frequency-line structure as the actual compressor noise, and that the level achieved was representative of near-station compressor noise (see Williams *et al.* 2021) for details on noise recordings, spectra, and playback conditions). The experimental noise elevated sound levels above ambient by ~30 dB, simulating noise conditions at ~100 m from an active compressor station (Williams *et al.*, 2021). The noise was introduced in March before tree swallows had returned from

migration and played continuously until all nesting was complete. Boxes were monitored regularly until eggs were laid. Boxes were then checked every 2–3 days to determine their fate. We designated a nest as unsuccessful ( $N = 3$ ) if all eggs failed to hatch (i.e. due to abandonment or predation). Although there is a chance nests were abandoned because of noise treatment, we think this was unlikely as these rare abandonments occurred in both treatments (2 in noisy nests, 1 in quiet nests). Because we were unable to measure any offspring from these nests, they were excluded from further treatment and analysis.

### Chick morphology

On day 7, 2–3 nestlings were selected at random from each nest (2 nestlings from broods of 4, 3 nestlings from broods of 5 and above). Due to logistical constraints, three further boxes were treated on day 8, and 1 on day 9. Nestlings were weighed using an electronic balance (Compass CR, Ohaus Corp., Parsippany, NJ, USA) to the nearest 0.1 g, and the right tarsi were measured using calipers to the nearest 0.1 mm. We used mass and tarsus length to calculate a body condition index (Labocha & Hayes, 2012) which was the residuals of the correlation between  $\log(\text{mass})$  and  $\log(\text{tarsus length})$ ; i.e. a measure of body weight corrected for size.

### Immune response

We implemented a phytohaemagglutinin (PHA) skin test which provides a measure of the cell-mediated immune response: PHA, a plant-derived lectin, is injected into the skin, inducing a swelling response, the magnitude of which is an accurate proxy measurement of the T-lymphocyte response (Tylan & Langkilde, 2017). We first measured the thickness of the injection site (the patagium) in triplicate using a thickness gauge (Mitutuyo 7301 Dial Thickness Gauge 0–10 mm, Mitutuyo America Corp., Aurora, IL) with an accuracy of 0.01 mm. One patagium was then injected with 0.3 mL PHA-L (Sigma L2769, Sigma-Aldrich Corporation, St Louis, MO, USA) suspended in sterile phosphate-buffered saline (PBS: Fisher BP399, Fisher Scientific, Waltham, MA) at a concentration of 0.1 mg/mL. After the initial injection birds were given an aluminum band as an identifier (i.e. to remeasure the correct individuals). After 24 h, the thickness of the injection site was again measured in triplicate. We calculated the swelling response for each individual nestling as the difference between the patagium thickness before injection (mean of three replicate measures), and 24 h post-injection (again, mean of three replicate measures). This was calculated as [post-injection thickness (mm)] – [pre-injection thickness (mm)] such that larger values indicate greater swelling. Note that the PHA skin test is commonly performed without including a vehicle control injection, as this decreases the coefficient of variation due to measuring inaccuracies (Smits *et al.*, 2001). There was no difference between treatment groups in initial patagium thickness ( $T$  test:  $T = -0.41$ ,  $P = 0.68$ ), therefore any difference between treatment groups in swelling response is due to treatment, not

differences in initial patagium thickness. Injections all took place within the same time period (i.e. within a 2 h period) starting at ~9:00 AM as the time of day has been shown to influence common measures of immune function (Zylberberg, 2015).

### Clutch size, hatching, and fledging

We calculated clutch size, the proportion of eggs that hatched (hatching success), the proportion of successfully hatched young that fledged (fledging rate), and the proportion of eggs that produced fledglings (fledging success) from nests where at least one young fledged. Because no nestlings disappeared from boxes before published fledging dates from other studies (Winkler *et al.*, 2020), and all boxes were empty ~25 days post-hatching, we assumed there were no predation attempts and we observed no nest failures.

### Statistical analysis

Whether noise treatment resulted in differences in nestling morphology was tested by setting nestling measures (mass, tarsus length, and body condition) as dependent variables in separate generalized linear mixed models (GLMMs) using the *lme4* package (Bates *et al.*, 2015) in R (R Core Team, 2018). Noise treatment (noisy/quiet) was set as the main categorical explanatory variable of interest. Nest of origin was set as a random term to account for the non-independence of chicks sampled from the same nest. We also included brood size and age at measurement as explanatory variables to account for the small variation we saw in those parameters. We were additionally interested in the potential influence of laying date, as this can be an indicator of parental quality (Winkler *et al.*, 2020), however, laying date was unknown for two nests (4 chicks, both nests from noisy treatment group). We therefore tested the influence of laying date in a model as described above, and then because it did not explain significant variation in any case, removed it as a variable to maximize our sample size of nests (effect of laying date [est  $\pm$  SE] on mass –  $0.08 \pm 0.25$ ,  $T = 0.33$ ,  $P = 0.75$ ; tarsus length –  $0.02 \pm 0.09$ ,  $T = -0.27$ ,  $P = 0.78$ ; body condition  $0.002 \pm 0.01$ ,  $T = 0.11$ ,  $P = 0.91$ ).

Immune response was calculated per nestling as the difference between pre- and post-treatment patagium thickness (i.e. [mean of the three pre-treatment measurements] – [mean of the three post-treatment measures]). Whether noise treatment influenced the immune response was tested as above: swelling response (mm) was set as the dependent variable in a GLMM, again with noise treatment (noisy or quiet) set as the categorical explanatory variable of interest, with brood size and age at measurement as additional explanatory variables, and nest of origin set as a random term to account for non-independence of chicks sampled from the same nest. Again we initially tested the effect of laying date but removed it to maximize sample size as it did not explain significant variation (effect of laying date (est  $\pm$  SE) on PHA response  $0.03 \pm 0.02$ ,  $T = 1.52$ ,  $P = 0.15$ ).

Noise treatment effects on whole-nest measures were tested using generalized linear models (GLM), with nest measures

(clutch size, the proportion of eggs hatched, fledging rate [% chicks fledged], fledging success [% eggs fledged]) set as response variables, and noise treatment as the predictor variable. The clutch size model used a Poisson regression for count data (log link). Proportion data (the remaining three measures) were tested using LMMs with binomial regressions (logit link). In these models, the number hatched/fledged and the number failed were combined as a bound column in each case (using the *cbind* function; for example, one hatched from a nest of three is [1,2]). For hatching success this variable was number hatched/number not hatched; for fledging rate, this variable was number chicks fledged/number chicks not fledged; for fledging success this variable was number eggs fledged/number eggs not fledged. These bound variables can be analyzed as proportion variables using *lme4* but retain information on the number of observations (in this case, clutch or brood size) to perform a weighted regression. Again, we tested the effect of laying date but removed this from the final model as it did not explain significant variation. There were no effects of laying date (est  $\pm$  SE) on clutch size ( $0.01 \pm 0.04$ ,  $Z = -0.20$ ,  $P = 0.84$ ); hatch success ( $0.18 \pm 0.17$ ,  $Z = 1.07$ ,  $P = 0.29$ ); fledging rate ( $0.20 \pm 0.12$ ,  $Z = 1.64$ ,  $P = 0.10$ ); or fledging success ( $0.12 \pm 0.14$ ,  $Z = 0.90$ ,  $P = 0.37$ ).

Model fit was assessed by plotting model residuals – in all cases, residuals were normally distributed indicating good model fit. We additionally calculated the AIC for each model as well as its null model equivalent (e.g. mass  $\sim$  noise treatment + brood size + age measured; mass  $\sim$  1), and from these calculated the  $\Delta$ AIC (AIC null model – AIC full model). As AIC values closer to zero indicate a better model fit the data, positive  $\Delta$ AIC values indicate that the full model describes the data better than the null model;  $\Delta$ AIC values  $<2$  indicate no significant additional variation explained (Symonds & Mousalli, 2011). All means are reported with 1 SD.

## Results

Of the 40 available nest box pairs, 21 were ultimately occupied by tree swallows. Of those that were occupied, 13 were in “noisy” treatment sites, and 8 were in “quiet” (control) sites. This distribution of nests between noisy and quiet treatments was not significantly different from a random distribution (i.e. at an expected 50:50 ratio between the treatments;  $\chi^2 = 1.19$ , d.f. = 1,  $P = 0.28$ ). All nests combined produced a total of 99 chicks (60 from noisy nests, 39 from quiet nests). Three additional nests (one quiet and two noisy) had eggs for a total of 24 nests but they failed shortly into the nesting stage and were not included in the analysis. From the 21 nests, we measured and treated 56 chicks (35 from noisy nests and 21 from quiet nests).

### Nestling morphology

Nest noise treatment did not significantly influence nestling mass, tarsus length, or body condition (Tables 1 and 2; Fig. 1a-c). Age at measurement did not influence any of these measures (Table 2a-d). There was a trend for chicks from larger broods to have a lower mass (Table 2a). Only the model

investigating effects on mass was an improvement on the null model in terms of model fit (from AIC, Table 2a-d).

### Immune response

There was no difference between noisy and quiet nests in pre-treatment patagium thickness ( $T_{1,55} = -0.41$ ,  $P = 0.68$ ). Treatment did not influence immune response (the difference between pre- and post-treatment patagium thickness in the treated wing; Tables 1 and 2; Fig. 1d). There was one major outlier in the noise-treated group (a difference between pre- and post-treated patagium thickness of 1.7 mm, while the mean was  $0.58 \text{ mm} \pm 0.28$ ). However, excluding this individual did not change the lack of effect of treatment ( $T_{1,54} = 0.08$ ,  $P = 0.98$ ).

### Clutch size, hatching, and fledging rates and success

Noise treatment did not affect clutch size; hatching success (the proportion of eggs that successfully hatched); fledging rate (proportion of chicks fledged); or fledging success (proportion of eggs fledged; Tables 1 and 3; Fig. 2a-d). In all cases, the null model was better than the full model according to AIC (Table 3a-d).

## Discussion

Anthropogenic noise is increasingly prevalent in rural as well as urban areas, and has significant potential to impact local animal communities, including birds (Barber *et al.*, 2011; Francis *et al.*, 2011; Kleist *et al.*, 2018; Williams *et al.*, 2021). Natural gas extraction is a rapidly growing enterprise (U.S. Energy Information Administration, 2018) that generates considerable noise pollution with the potential to impact wildlife populations (Barber *et al.*, 2011; Francis *et al.*, 2011; Kleist *et al.*, 2018; Williams *et al.*, 2021). However, we show that tree swallows did not preferentially select quiet nests, despite the availability of quiet nest boxes. A previous study in the same system with the same gas compressor noise treatment demonstrated reduced hatching success in noisy nests (Williams *et al.*, 2021). We are cautious in interpreting our data due to relatively smaller sample sizes; however, we saw no reduction in hatching success in this study. Indeed, developing in a relatively noisy nest did not adversely affect any nestling metrics of condition or immune performance. These results suggest that either the consequences of gas compressor noise at the nest are influenced by variables that we did not test here (e.g. that birds with prior experience may alter their behavior across years), or that adult birds are paying an unseen price for maintaining nestling condition and overall health. These results add to a growing literature on the variability of noise effects on avian reproductive success.

Although a number of studies have shown negative effects of elevated noise on adults and juveniles of this and other species (Kleist *et al.*, 2018), we found no significant effect on metrics of tree swallow reproductive success in this study,

**Table 1** Data summary for all measured variables in the control and noisy treatment groups (mean  $\pm$  SD reported)

| Measure   | Control treatment       | Noisy treatment          |
|---|-------------------------|--------------------------|
|   | <i>N</i> = 21 (8 nests) | <i>N</i> = 35 (13 nests) |
| Mass (g)  | 14.97 $\pm$ 2.75        | 13.95 $\pm$ 3.08         |
| Tarsus length (mm)  | 12.94 $\pm$ 1.10        | 12.82 $\pm$ 1.16         |
| Condition (see text for details)                                  | 0.04 $\pm$ 0.23         | -0.03 $\pm$ 0.16         |
| Change in wing patagium thickness (response to PHA injection, mm) | 0.53 $\pm$ 0.22         | 0.58 $\pm$ 0.28          |
| Clutch size   | 5.75 $\pm$ 0.71         | 5.15 $\pm$ 1.07          |
| Proportion hatch success  | 0.92 $\pm$ 0.13         | 0.94 $\pm$ 0.09          |
| Fledging rate (proportion chicks fledged)                         | 0.81 $\pm$ 0.35         | 0.85 $\pm$ 0.29          |
| Fledging success (proportion eggs fledged)                        | 0.73 $\pm$ 0.32         | 0.81 $\pm$ 0.28          |

PHA, phytohaemagglutinin.

**Table 2** Results from GLMMs investigating noise treatment (vs. control) effects on nestling measures (*N* = 56)

| Chick model                                     | Fixed effects           | Est   | SE   | <i>T</i> | <i>P</i> | $\Delta$ AIC |
|---|-------------------------|-------|------|----------|----------|--------------|
| (a) Mass  | Intercept               | 11.55 | 8.70 | 1.33     | 0.20     | 3.93         |
|   | Noise treatment (noisy) | -1.05 | 1.25 | -0.83    | 0.42     |              |
|   | Day measured            | 1.31  | 1.15 | 1.14     | 0.27     |              |
|   | Brood size              | -1.18 | 0.64 | -1.85    | 0.08     |              |
| (b) Tarsus                                      | Intercept               | 14.44 | 3.23 | 4.47     | 0.0003   | -6.58        |
|   | Noise treatment (noisy) | -0.10 | 0.47 | -0.21    | 0.84     |              |
|   | Day measured            | -0.17 | 0.42 | -0.40    | 0.70     |              |
|   | Brood size              | -0.06 | 0.25 | -0.23    | 0.82     |              |
| (c) Condition                                   | Intercept               | -0.39 | 0.50 | -0.79    | 0.44     | -11.34       |
|   | Noise treatment (noisy) | -0.07 | 0.07 | -0.99    | 0.34     |              |
|   | Day measured            | 0.11  | 0.06 | 1.72     | 0.10     |              |
|   | Brood size              | -0.07 | 0.04 | -1.91    | 0.07     |              |
| d) Difference in PHA-treated patagium thickness | Intercept               | 1.02  | 0.69 | 1.47     | 0.16     | -14.97       |
|   | Noise treatment (noisy) | 0.03  | 0.10 | 0.30     | 0.77     |              |
|   | Day measured            | -0.08 | 0.09 | -0.86    | 0.41     |              |
|   | Brood size              | 0.02  | 0.05 | 0.32     | 0.76     |              |

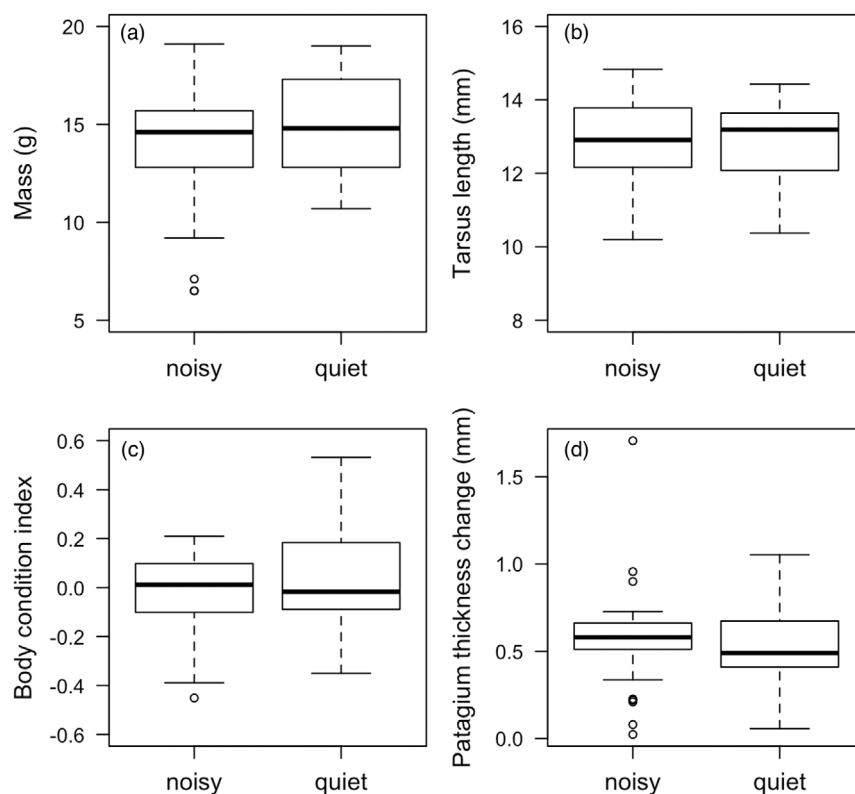
$\Delta$ AIC was calculated as AIC(null mod) - AIC (full mod); values >2 indicate the full model fit the data better than the null model; values <2 indicate the null model fit the data better than the full model.

GLMM, generalized linear mixed models; PHA, phytohaemagglutinin.

from the nest level (no difference in clutch size, hatching, and fledging success), to the chick level (elevated noise levels in our study between days 3 and 15 post-hatch had no effects on tree swallow nestling condition in terms of growth or immune performance). The lack of effect on hatching success is surprising as the same noise treatment gave rise to significant variation in hatching success in the previous year, with tree swallows suffering reduced hatching success in noisy nests (Williams *et al.*, 2021). The reason for this between-year variation is unclear, however, we were unable to repeat the identification and measurements of mothers (which is likely to have generated variation in egg quality or investment), and we did not measure incubation rate, a likely driver of reduced hatching success in year 1. Of course, it is possible that our lower sample size led to increased within-sample variation in noise effects. One alternative explanation is that any returning birds, the number of which we did not quantify, may have habituated to noise more rapidly, resulting in less affected incubation rates and reduced variation in hatching success, masking negative effects on naïve mothers that could have been using noisy boxes. Indeed, given that gas compressor noise is chronic, birds may habituate to it more rapidly than less consistent

stimuli (Francis & Barber, 2013). Alternatively, it is also possible that any experienced returning birds chose to switch nests and use quiet boxes, despite the tendency for returning birds to nest near their previous nesting attempts (Llambias *et al.*, 2008). However, this could lead to enhanced reproductive success compared to noisy nests and we do not see any evidence that quiet-nesting birds performed better.

In common with the previous year's study, we also demonstrated no effect of noise treatment on fledging success *after* hatching: once chicks hatched, they were equally likely to fledge in both studies/years, and in this study, they did not differ in more fine-scale metrics of condition (growth and immune performance). Notably, this is despite extending the noisy period into egg-laying and incubation, as few other studies have done. This suggests minimal effects of this level of noise at the egg as well as the chick stage of development in tree swallows. Our level of noise increase (~30 dB), approximating noise conditions ~100 m from an active compressor station, was relatively modest in comparison to other studies of noise elevation in the same species (Injaian, Taff, & Patricelli, 2018; Leonard & Horn, 2008). Compressor noise in our study may not have been great enough to generate differences



**Figure 1** Compressor noise at the nestbox had no effects on (a) nestling mass, (b) nestling tarsus length, (c) nestling body condition, or (d) response to an immune challenge (phytohaemagglutinin injection into wing web, measured as change in patagium thickness 24 h post-injection).

**Table 3** Results from linear mixed models (LMMs) investigating noise treatment (vs. control) effects on nest measures ( $N = 21$ )

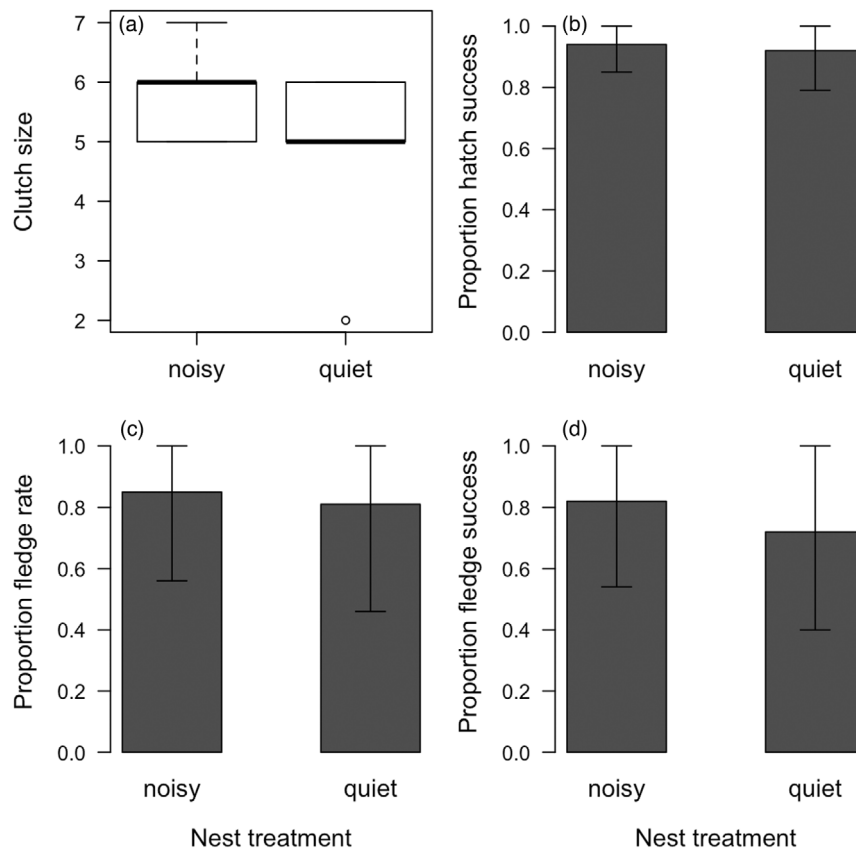
| Nest model           | Fixed effects           | Est   | SE   | Z     | P     | $\Delta$ AIC |
|----------------------|-------------------------|-------|------|-------|-------|--------------|
| (a) Clutch size      | Intercept               | 1.75  | 0.15 | 11.86 | <0.01 | -1.68        |
|                      | Noise treatment (noisy) | -0.11 | 0.19 | -0.57 | 0.57  |              |
| (b) Hatching success | Intercept               | 2.35  | 0.52 | 4.49  | <0.01 | -1.70        |
|                      | Noise treatment (noisy) | 0.41  | 0.73 | 0.55  | 0.58  |              |
| (c) Fledging rate    | Intercept               | 1.30  | 0.38 | 3.46  | 0.001 | -1.48        |
|                      | Noise treatment (noisy) | 0.37  | 0.51 | 0.72  | 0.47  |              |
| (d) Fledging success | Intercept               | 0.93  | 0.33 | 2.84  | 0.004 | -1.19        |
|                      | Noise treatment (noisy) | 0.40  | 0.44 | 0.90  | 0.37  |              |

$\Delta$ AIC was calculated as AIC (null mod) – AIC (full mod); values close to zero (<2) indicate that the null model fit the data as well as the full model.

in growth or parental effort and investment (Leonard & Horn, 2012; Warren *et al.*, 2006).

Though metrics of hatchling conditions did not differ based on the level of noise at their natal nest, it is possible that the parents were paying an extra cost to maintain offspring quality under these conditions. Previous work in this species has indicated that elevated anthropogenic noise at the nest influences the structure of chick begging calls (Leonard *et al.*, 2015; Leonard & Horn, 2008). This may result in increased provisioning of chicks at noisy nests because of enhanced conspicuousness. An increase in provisioning due to elevated noise has been demonstrated in mountain white-crowned sparrows near traffic

(Crino *et al.*, 2011), as well as in tree swallows subjected to experimental traffic noise playback (Injaian, Taff, Pearson, *et al.*, 2018). If parents do in fact overcompensate, that could lead to increased growth masking the true impacts of noise on nestling development. It may also be possible that our increase of ~30 dB is not enough to interfere with chick begging, which translates to increased provisioning. It is possible from either scenario then, that adults are compensating for any reductions in offspring quality associated with noisy conditions—costs that we do not see in the offspring may be passed to them. Because we did not capture adult birds as part of this study, further work is required to determine whether parents



**Figure 2** Compressor noise at the nestbox had no effects on (a) clutch size, (b) hatching success (the proportion of eggs that produced chicks), (c) fledge rate (proportion of chicks that successfully fledged), or (d) fledging success (proportion of eggs that successfully fledged).

are paying the price for noise at the nest. Monitoring proxies of adult fitness in future studies (i.e. body condition) could shed light on the lack of differences we found.

Alternatively, it is possible that our study missed other, more cryptic negative effects that may be important for fitness. For example, traffic noise exposure during incubation and early life in nestling tree swallows is associated with increased baseline levels of corticosterone, a glucocorticoid hormone associated with the stress response (Injaian, Taff, Pearson, et al., 2018); increased oxidative stress (Injaian, Taff, & Patricelli, 2018); and increased telomere attrition (Injaian et al., 2019) relative to controls. These metrics, which we did not measure, can have important implications for individual fitness. Increased oxidative stress in nestlings may not influence the fledging success (Injaian, Taff, Pearson, et al., 2018), but deleterious effects may manifest after the fledging period, for example, on survival (Bize et al., 2008). Similarly, alterations to baseline glucocorticoid levels or reactivity in the hypothalamic-pituitary-adrenal (HPA) axis can have profound effects on future ability to cope with challenges (Wingfield & Romero, 2010). However, in these studies, these effects were accompanied by a reduction in nestling body condition (Injaian et al., 2019; Injaian, Poon et al., 2018; Injaian, Taff, & Patricelli, 2018), which we did not see, so it is potentially unlikely that we would have seen similar effects on physiology in our nestlings. Additionally, the importance of parental effects on

offspring resilience to stressors (e.g. through epigenetic changes to gene expression, Taff et al., 2019) means that without knowing more about parental physiology, in this case, we are limited in our ability to speculate about offspring physiological changes in response to noise.

Our results add to a growing literature showing that the effects of anthropogenic noise on juvenile birds are highly variable. For example, in tree swallows alone, studies have alternately demonstrated no effects (Injaian, Taff, Pearson, et al., 2018; Leonard & Horn, 2008) and negative effects (Injaian et al., 2019; Injaian, Taff, Pearson, et al., 2018). Other studies also show considerable inter-species variability in response to anthropogenic noise, for example, in breeding success (Mulholland et al., 2018), hatching success (Kleist et al., 2018), and size and condition (Crino et al., 2013; Kleist et al., 2018), as well as intra-nest variability, for example, in telomere length in great tits (Grunst et al., 2020). Consequences for offspring appear to be closely linked to noise amplitude (Kleist et al., 2018) and type (i.e. comparable volumes of white and traffic noise had no effect, and deleterious effects, on growth/condition in tree swallows, respectively (Injaian, Taff, Pearson, et al., 2018, Leonard & Horn, 2008)). We note limitations of this study, particularly in terms of sample size; however, more work is clearly required, particularly on the effects of prior experience and the mechanisms driving our observed differences between years in the same population. These questions will bring



an increased understanding of the effects of anthropogenic noise across avian species.

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