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Little parental response to anthropogenic noise in an urban songbird, but evidence for individual differences in sensitivity

Parental responses to anthropogenic noise in an urban songbird

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ABSTRACT Anthropogenic noise exposure has well-documented behavioral, physiological and fitness effects on organisms. However, whether different noise regimes evoke distinct responses has rarely been investigated, despite implications for tailoring noise mitigation policies. Urban animals might display low responsiveness to certain anthropogenic noise regimes, especially consistent noise (e.g. freeway noise), but might remain more sensitive to more diverse noise regimes. Additionally, whether individuals differ in noise sensitivity is a rarely explored issue, which is important to fully understand organismal responses to noise. To address these knowledge gaps, we used a field experiment to measure how urban great tits (*Parus major*) altered parental behaviors in response to two noise regimes: consistent freeway noise, and a diverse anthropogenic noise regime that incorporated variability in noise type and temporal occurrence. We also evaluated whether sex, age, or a well-described personality trait, novel environment exploration behavior, were associated with responses to noise, although our power to assess individual differences in responses was somewhat limited. We found no evidence for mean population-level changes in nestling provisioning behaviors during either noise treatment. However, despite this overall canalization of behavior, there was evidence for individual differences in noise sensitivity, particularly during the diverse noise treatment. Females and birds that explored a novel environment more rapidly (fast explorers) reduced nestling provisioning rate more relative to baseline levels than males and slow explorers during the diverse urban noise, but not during the consistent freeway noise. Furthermore, first year breeders and fast explorers displayed larger increases in latency to return to the nest box relative to baseline conditions during the diverse noise only. Results suggest that urban animal populations might become overall tolerant to anthropogenic noise, but that certain individuals within these populations nonetheless remain sensitive to certain types of noise exposure.

Capsule: In an urban songbird, we found no population-level changes in nestling provisioning behavior during noise exposure, but did find evidence for individual differences in noise sensitivity.

Keywords: Anthropogenic noise; variability; intraspecific variation; personality; exploration behavior; urban ecology, sex differences

1. Introduction Anthropogenic environments present organisms with an array of novel disturbance factors, such as noise, light and chemical pollution, habitat fragmentation, and direct disturbance from human activity (Gaston et al., 2013; Swaddle et al., 2015; Bauerová et al., 2017; Cheptou et al., 2017; Corsini et al., 2017). Animals may adjust their behavior to cope with these stressors, and may also habituate to disturbance such that they either do not perceive these factors as stressors, or respond less strongly to the stimulus, thus potentially mitigating effects on fitness. On the other hand, these novel disturbance factors may overwhelm organismal coping mechanisms, interfere with adaptive patterns of physiology and behavior, and result in declines in individual fitness and population stability (Sih et al., 2011; Sih, 2013; Sol et al., 2013). Anthropogenic noise is particularly pervasive in urban and suburban areas, and also extends its influence into areas that we generally think of as relatively pristine, such as National Parks and reserves (Barber et al., 2011; Buxton et al., 2017). Moreover, the transportation network, and associated noise pollution, is expanding at a rate faster than that of human population (Barber et al., 2009). Thus, noise pollution increasingly threatens the ability of humans and other organisms to maintain homeostasis and health status (Basner et al., 2014; Hammer et al., 2014; Kunc and Schmidt, 2019), deeming understanding of its biological effects particularly urgent.

Anthropogenic noise has been associated with effects on behavior, physiology and fitness across diverse taxa, although many studies are correlational, thus precluding determination of causation (Kight and Swaddle, 2011; Shannon et al., 2016; Kunc and Schmidt, 2019). For instance, exposure to anthropogenic noise has been shown to cause shifts in vocal signals in birds (Brumm and Slabbekoorn, 2005; Slabbekoorn and Ripmeester, 2008; Nemeth and Brumm, 2010; Halfwerk et al., 2011a), insects (Lampe et al., 2012; Orci et al., 2016; Gallego-Abenza et al., 2020), and anurans (Lengagne, 2008; Caorsi et al., 2017), alter glucocorticoid levels (Injaian et al., 2018a; Kleist et al., 2018), and impair communication between parents and offspring (Leonard and Horn, 2012; Leonard et al., 2015; Lucass et al., 2016). Documented effects of anthropogenic noise on fitness include reduced clutch sizes in female great tits (*Parus major*) (Halfwerk et al., 2011b), lighter offspring and fewer recruits in house sparrows (*Passer domesticus*) (Schroeder et al., 2012), reduced offspring survival in a reef fish (*Acanthochromis polyacanthus*) (Nedelec et al., 2017), and reduced spermatophore mold (a sperm delivering structure) mass in male crickets (Bowen et al., 2020). Many documented effects, or correlates, of anthropogenic noise exposure are negative (e.g. Halfwerk et al., 2011b; Schroeder et al., 2012; Dorado-Correa et al., 2018; Injaian et al., 2018a,b,c; Kleist et al., 2018; Zollinger et al., 2019). Yet some studies have found that noise exposure has no effect on the biological variables of interest (Grunst et al., 2014; Angelier et al., 2016; Martínez-Marivela et al., 2018), perhaps due to the emergence of noise tolerance in urban exploiter species (Angelier et al., 2016), or have even documented effects that could be interpreted as positive (Crino et al., 2013; Kleist et al., 2018).

The fact that negative effects of anthropogenic noise exposure are not always observed leads to the important observation that, despite the extensive literature on biological effects of noise, little is known regarding factors contributing to variation in the magnitude of responses. One factor that may affect sensitivity to noise is history of exposure, with individuals potentially developing behavioral insensitivity given repeated, or chronic, exposure (Delaney et al.,1999; Brown et al.,2012; Samson et al., 2014). The extent to which populations of urban animals maintain behavioral patterns under noise exposure remains unclear, because many experimental studies on the effects of noise exposure are performed in rural populations that are relatively naïve to anthropogenic noise and examining the influence of repeated or long-term exposure is challenging, and thus relatively underexplored.

In addition, different noise regimes could evoke different phenotypic responses, but this contingency has rarely been investigated, despite implications for tailoring effective noise mitigation policies. Even in the case of urban animals that might be de-sensitized to noise, some types of noise regimes might be more disruptive than others, and might consequently result in larger magnitude changes in biological responses. For instance, consistent patterns of noise production, such as noise from a freeway, might be less disruptive than more diverse noise regimes that are variable in temporal pattern and sound type (De Boer et al., 1989; Injaian et al., 2018a; Gill et al., 2015; Nichols et al., 2015).

Furthermore, even within populations, individuals may differ in sensitivity to noise exposure on the basis of characteristics such as sex, age and personality type (Harding et al., 2019), with inter-individual variation in responses to noise potentially only emerging under certain types of noise exposure. Studies of intraspecific variation in responses to noise remain relatively limited within free-living animal populations (Candolin, 2019; Harding et al., 2019), and this issue was highlighted as an important area for further research by a recent review (Harding et al., 2019). Considering only mean, population-level responses to noise exposure, or assessing effects of only one type of noise (e.g. traffic noise) may preclude a complete understanding of the biological effects of anthropogenic noise.

To address these important knowledge gaps, we conducted a field experiment to study the effects of two different types of anthropogenic noise regimes on the nestling provisioning behavior of urban great tits (see Fig. 1 for location of study sites). Great tits are a model species in ecology and evolution and feature prevalently in urban ecology studies because they persist across urban gradients (eg. Halfwerk et al., 2011b; Salmón et al., 2016; Charmantier et al., 2017; Raap et al., 2017; de Satgé et al., 2019; Grunst et al., 2019a,b, 2020). We exposed focal individuals breeding at nest boxes within relatively low ambient noise environments within the urban matrix to two different types of anthropogenic noise regimes using a repeated measures design. The noise treatments consisted of: (1) consistent broad band noise recorded from a local freeway, and (2) a noise regime consisting of a diverse array of anthropogenic sound types that occurred at variable temporal intervals, simulating the noise encountered in a busy urban area in which different human activities occur (Table 1; Fig. 2 and 3). We predicted that birds would reduce nestling provisioning rates and increase latency to return to the nest box when exposed to noise. We also predicted that the more diverse noise regime would have larger behavioral effects, since different noise types produced at variable intervals and frequencies might be more likely to startle animals and activate behavioral and physiological self-preservation responses than more consistent noise of an uniform type (e.g. freeway noise) (Blickley et al., 2012; Francis and Barber 2013; Nichols et al., 2015).

In addition, we examined whether individuals differing in sex, age and exploratory personality type displayed different responses to noise . As a caveat, our ability to test relationships with exploratory personality type was limited by the low number of birds with high exploration scores in our sample, and we were also not able to age all individuals. We predicted that females, older birds, and individuals with the tendency to explore a novel environment more rapidly (fast explorers) would be less sensitive to noise exposure. These predictions were based on the greater investment into the clutch and higher certainty of parentage of females relative to males (Clutton-Brock, 1991; Lubjuhn et al., 1999), the lower residual reproductive value of older birds relative to younger birds (Ghalambor and Martin, 2001), and previous research documenting that fast explorers have a less responsive hypothalamus-pituitary-adrenal (HPA) axis than slow explorers and return to nest boxes more rapidly during noise exposure (Stöwe et al., 2010; Baugh et al., 2012; Naguib et al., 2013). We also predicted that intraspecific differences in noise sensitivity might be more pronounced given exposure to the more diverse urban noise regime. Given that diverse noise regimes might be more likely to induce a startle response than more consistent noise (Francis and Barber, 2013), responses might be more closely linked to individual-level variation in stress sensitivity. Our study expands on past research by employing an experimental approach with multiple playback types to elucidate how complexity in anthropogenic noise environments and individual traits could modify responses to noise within urban animal populations.

2. Methods

2.1. Study species and sites: We studied great tits breeding at two sites within the Antwerp, Belgium, metropolitan area (Figure 1). At both areas, Fort 4 (51°10′23.80″ N; 4°27′38.46″ E) and Fort 7 (51°09′52.55″ N; 4°22′40.46″ E), nest boxes were located in gated areas closed from public use. All nest boxes were located in relatively low noise environments (LA_{eq} (continuous A-weighed sound pressure level in decibels): mean ± SE = 48.5 ± 0.381 dB), as determined by recording ambient noise levels, ~3 m from the nest box, for 10 minutes using a CEL633C1 sound level meter (20-140 dB; weight A; NoiseMeters Inc.; see also Grunst et al. 2020) prior to baseline video-recordings. We averaged the measurements obtained for the two baseline recordings taken at each nest box (baseline recordings occurred before both the consistent and diverse noise treatments). This study was approved by the ethical committee of the University of Antwerp (ID number: 2017-90) and conducted in accordance with Belgian and Flemish laws. The Belgian Royal Institute for Natural Sciences (Koninklijk Belgisch Instituut voor Natuurwetenschappen) provided banding licenses for authors and technical personnel.

Figure 1. Location of the two study sites, Fort 7 (F7) and Fort 4 (F4), south of Antwerp, Belgium (top). The small rectangle is enlarged in the second panel to show how the study sites are situated relative to each other. Both study sites are old forts that have been converted into protected areas within the urban matrix. The bottom panel shows the location of the nest boxes within the study sites. Imagery from Google Earth.

2.2. Experimental design: We presented 34 nest boxes (23 at Fort 7 and 11 at Fort 4; Figure 1) with two experimental treatments: noise consisting of consistent broadband noise from a freeway, and noise that was variable in temporal pattern and incorporated diverse sound types. These treatments were presented in balanced, semi-random order on days 10 to 16 of the nestling stage (mean ± SE = 13.5 ± 0.170) . The two treatments occurred on adjacent days or separated by 1 or 2 days (Fig.4). We recorded baseline nestling provisioning behavior for 1-hr using Canon 800/850 camcorders concealed ~5 m from nest boxes. Following the baseline recording, we recorded nestling provisioning behavior for 1-hr in the presence of the noise playback (Fig.4). We chose to always perform the baseline recording first to avoid complications of potential carryover effects of noise exposure into the baseline recording period. To reduce observer effects and standardize between recordings, we only initiated recordings when adults were not visibly or audibly present in the vicinity of the nest box. From video-recordings, we recorded nest box visits, which we used as a proxy for nestling provisioning rate (as in other studies on great tits, such as Naguib et al., 2013). We also calculated latency to return to the nest box following the beginning of the video-recording, when noise playback was also initiated in the case of the noise treatments, and the average amount of time that adults spent in the nest box between arrival and departure (on-bout length). Latency to return to the nest box reflects the bird's initial response to the noise disturbance, whereas nestling provisioning rate, which we averaged over the entire recording period, is reflective of a slightly longer term response, potentially including some degree of habituation. Experiments were completed between April 29 and May 17, 2019 and between 0900 and 1430.

2.3. Noise playback: To create the consistent freeway noise playback, we used an Olympus LS10 audio recorder to obtain three separate, 5 min recordings of consistent, broad band traffic noise from different locations along the local E19 freeway (Table 1; Fig. 1). The consistent noise was played back by setting the recorder on single loop mode. To create the diverse noise recordings, we obtained 30 sec to 1 min audio recordings of human-related sounds with more diverse frequency characteristics off the internet and two 1.5 min recordings of consistent traffic noise (Table 1; Fig. 2). Eleven separate noise files, nine of which differed between recording devices, were placed on two different recorders, and played back using a random shuffle loop. Both recording devices used for the diverse noise playback contained most of the different types of sounds (but different recordings of these sounds), with the exception that only one of the recorders contained construction noise, and only one recorder included weed wacker noise. Sound was playing constantly on the diverse noise recordings, with the recording cycling between the different noise types. Thus, this noise regime included diverse sound types, and since the sounds were played in random order, there was also an element of temporal variability. Since our consistent noise regime was created using different recordings of consistent traffic noise, rather than different types of consistent noise, our results are specifically relevant to comparing behavioral responses to two different types of anthropogenic noise environments: consistent freeway traffic noise and a diverse noise environment within urbanized areas that contains multiple sound types produced at temporally variable intervals. However, we cannot separate the effects of temporal variability and diversity in sound types. Table 1 summarizes the differences between the consistent and diverse noise recordings. See Figure S1-S5 for additional examples of oscillograms, power spectra and sonograms for the diverse noise recordings.

Table 1. Characteristics of the consistent and diverse noise recordings used for the playback experiment.

Playback	Noise type(s)	Playback mode	Amplitude (SPL; ref. level 20μPa)	Frequency variability	Temporal variability
Consistent	Freeway traffic	Single loop	60 dB LA_{eq}	Low	High
Diverse	Chain saw; lawnmower; weed wacker; honking; backing up; brake noise; music; church bell; construction; pseudorandom and consistent traffic	Random shuffle loop	60 dB LA_{max}	High	Low

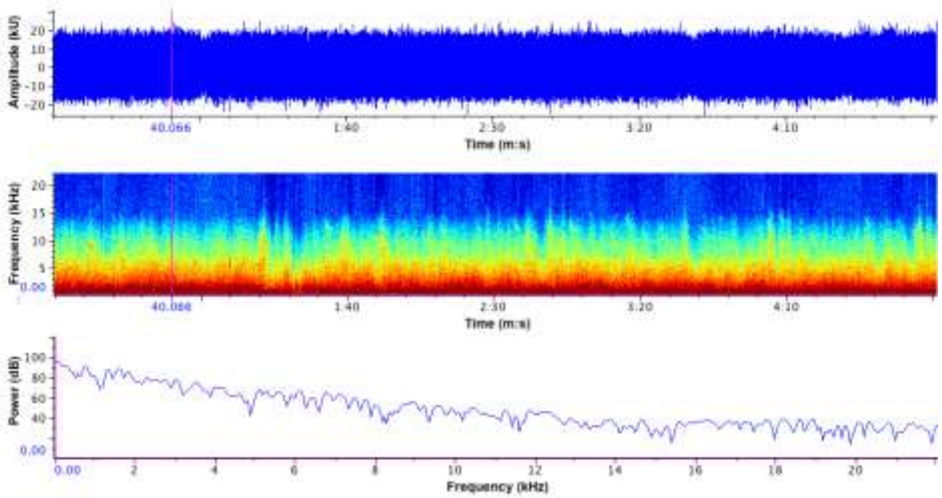

Figure 2. Example oscillogram, spectrogram and power spectrum of the freeway traffic noise used for the consistent noise playback. Created in Raven Pro (Cornell Lab of Ornithology) with a Hann sampling window, window size of 527 samples, and a 3 dB filter bandwidth of 120 Hz. The power spectrum is displayed for the time indicated by the vertical line (40.066 s).

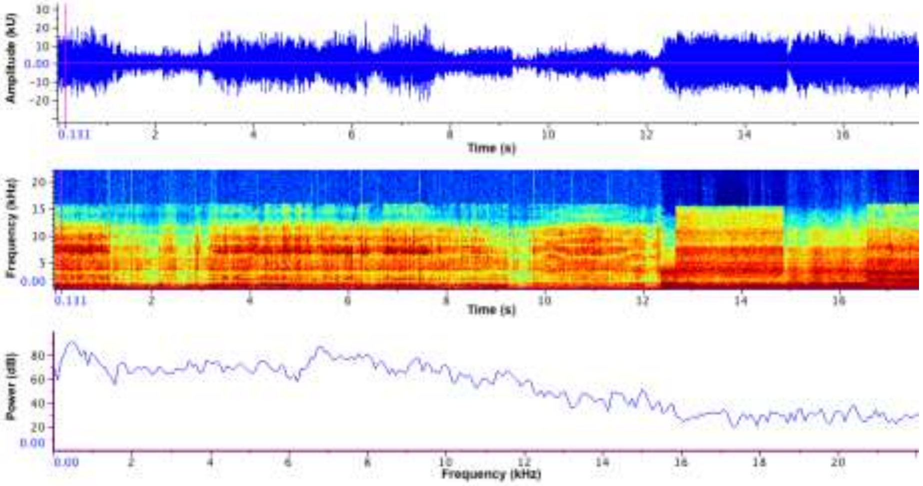

Figure 3. Example oscillogram, spectrogram and power spectrum of the diverse noise recording, including chain saw, traffic and church bell noise. Created in Raven Pro (Cornell Lab of Ornithology) as for Fig. 1. The power spectrum is displayed for the time indicated by the vertical line (0.131 s).

We calibrated the noise playback to 60 dB (SPL; ref. level 20μPa; LA_{eq} for consistent noise; LA_{max} for diverse noise) by holding the sound level meter at the nest box opening, immediately before initiating each experimental session. Sixty dB is typical of sound levels at nest boxes near freeways in our study population, and has been used in other studies investigating the effects of noise exposure on avian behavior and physiology (Injaian et al., 2018a, b). Noise playback was projected using Sony ICD-PX470 recorders secured to trees ~2 m from the nest box opening.

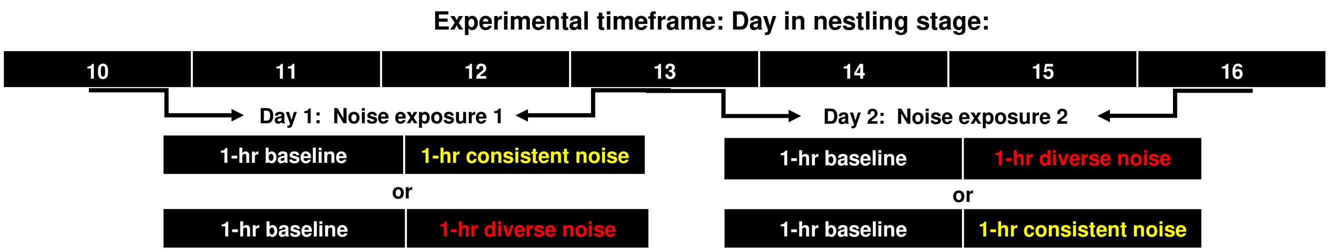

Figure 4. Timeframe of the experiment during the nestling stage. The two noise exposure treatments occurred on adjacent days or 1to 2 days apart.

2.4. Novel environment exploration testing: Great tits were captured in nest boxes between November and March, when roosting in nest boxes at night. Upon capture, birds were removed to captivity for one night, and tested for novel environment exploration behavior the following morning. In brief, we released birds individually into the novel environment exploration room (4.0 × 2.4 × 2.3 m), and tabulated the number of independent hops and flights performed within a 2-minute period (see details in Dingemanse et al., 2002; Thys et al., 2017; Grunst et al., 2018). Exploration behavior is routinely measured in our population and many individuals have been tested multiple times. Exploration behavior is also highly repeatable for a behavioral trait, including in our population (Thys et al., 2017; Grunst et al. 2018). However, past research has shown that repeated testing can affect exploration score, and the score from the time when the bird is first tested represents behavior in a completely novel environment (Dingemanse et al., 2012; Thys et al., 2017). Thus, in this study, we used the exploration score from the time when the bird was first tested (see also Grunst et al., 2019a). Following the exploration test, standard morphometric measurements were taken, and birds were aged (first year breeders or older) and sexed based on plumage characteristics (Svensson, 1984). During the breeding season, adults that had been previously tested for exploration behavior were identified via colored leg rings. Of the birds included in the experiment (34 pairs), 19 males and 19 females were tested for exploration behavior (12 nest boxes with both sexes personality typed; 7 nest boxes each with either the male or female personality typed). The mean exploration score was 9.26 (range: 0 – 61). We were unable to obtain the exploratory personality type for all birds since testing of exploration behavior occurs during the winter when birds are easily captured when sleeping in nest boxes. Restricting measurement of exploration behavior to the winter avoids disruption of breeding behavior and limits seasonal variation in the measurement. However, not all birds sleep in the nest boxes during the winter and some unringed individuals always exist in the breeding population.

2.5. Statistical analyses: We completed statistical analyses in R 3.6.1 (R Core Team, 2019) using linear mixed effect models (R package lme4; Bates et al., 2015) with Satterthwaite approximations for degrees of freedom (R package lmerTest; Kuznetsova et al., 2017). We first predicted nestling provisioning rate (feeding visits per minute) from treatment (baseline, consistent freeway noise, diverse urban noise), without considering variation in individual traits (sex, age, exploratory personality) to look at overall population-level patterns. We entered brood size, time of recording, date of recording, nestling age and recording order (whether the diverse or consistent noise treatment occurred first) as covariates and study site, nest box, individual, recording pair (each baseline recording was paired with a noise treatment), and playback ID as random effects. We used models with the same structure as described above to predict latency to return to the nest box after the recording was initiated (log transformed to normalize model residuals) and the average amount of time spent in the nest box (on-bout length).

We proceeded to incorporate individual traits into the analysis. Specifically, we predicted each behavioral variable (provisioning rate, return latency, on-bout length; separate models) from two-way interactions between treatment and sex, age (first year versus older) and exploratory personality type. We used functions emtrends and emmeans (within R package emmeans; Lenth, 2019) to obtain contrasts between the consistent freeway and diverse noise treatments for significant interactions between exploration score and treatment (continuous predictor variable, so used emtrends) and sex and age and treatment (discrete predictor variables, so used emmeans), and to obtain p-values adjusted for multiple comparisons via the Tukey method.

To further elucidate the intraspecific variation in responses detected in the analyses above, we also constructed separate models predicting the difference in nestling provisioning rate between the baseline and noise treatments from the interactions between noise type (consistent, diverse) and sex and exploration score, with brood size as a covariate and the difference in return latency between the baseline and noise treatments from age and exploration score with brood size and nestling age as covariates (these models only included predictor variables that had significant effects in the models using the raw variables, rather than the difference).

To facilitate interpretation of beta coefficients when including interactions in the model, we centered and standardized all continuous predictor variables (scale function in R; Schielzeth, 2010). We also applied a Helmert contrast, such that beta coefficients are reported across levels of discrete predictor variables (sex, age). To obtain a measure of effect size for models that revealed significant associations between predictor variables and behavior, we used the method of Nakagawa and Schielzeth (2013) (function r2 in R package performance; Lüdecke et al., 2020) to calculate marginal R^2 values. R^2m reflects the proportion of total variance explained by the fixed effects in a mixed effects model. We reduced models via a backwards, step-wise elimination process by first removing non-significant interaction terms, until all variables retained in the model were significant at the $\alpha = 0.05$ level. Full models supported the same conclusions as reduced models (Tables S1-S6).

3. RESULTS

3.1. Nestling provisioning rate: There was no population-level change in the nestling provisioning rate of great tits exposed to either the consistent or diverse noise regime relative to baseline levels, and population-mean provisioning rates also did not differ significantly between the two noise treatments (Table 2; Table S1 for full model). However, we found some evidence for individual differences in sensitivity to the diverse urban noise regime, but not the consistent freeway noise (Table 3). Specifically, how great tits adjusted their nestling provisioning rate when exposed to noise was related to sex and exploratory personality type, and the nature of this response depended on the type of noise regime (Table 3). Although there was a tendency towards age interacting with treatment to predict nestling provisioning rate, this interaction was non-significant (Treatment × Age: $F_{2,85} = 2.92$; $P = 0.059$; Table S1).

Posthoc comparisons indicated that females reduced nestling provisioning rates relative to baseline levels during the diverse noise treatment ($\beta \pm SE = -0.066 \pm 0.023$, $t_{83} = 2.77$, $P = 0.018$; Fig. 5a), and also tended to feed at lower rates during the diverse noise relative to during the consistent noise ($\beta \pm SE = -0.071 \pm 0.031$, $t_{88} = 2.31$, $P = 0.059$; Fig. 5a). Female feeding rate did not differ between the baseline and consistent noise treatments ($\beta \pm SE = 0.006 \pm 0.023$, $t_{85} = 0.246$, $P = 0.967$; Fig. 5a). In contrast, if anything, males tended to feed nestlings at higher rates during the diverse noise relative to during the baseline treatment ($\beta \pm SE = 0.047 \pm 0.023$, $t_{85} = 2.05$, $P = 0.106$; Fig. 5a) and during the consistent noise relative to during the baseline treatment ($\beta \pm SE = 0.051 \pm 0.023$, $t_{85} = 2.22$, $P = 0.073$; Fig. 5a). There was not a significant difference in male provisioning rates between the two noise treatments ($\beta \pm SE = 0.004 \pm 0.031$, $t_{88} = 0.123$, $P = 0.991$; Fig. 5a). There was a trend towards females feeding at lower rates than males during the diverse noise ($\beta \pm SE = -0.099 \pm 0.058$, $t_{35} = -1.73$, $P = 0.092$), whereas feeding rates were not different under baseline conditions ($\beta \pm SE = 0.014 \pm 0.054$, $t_{27} = 0.260$, $P = 0.797$) or during the consistent noise ($\beta \pm SE = -0.031 \pm 0.058$, $t_{34} = -0.547$, $P = 0.587$).

Posthoc comparisons indicated that there was a stronger negative relationship between exploration score and nestling provisioning rate during the diverse noise than in the baseline ($\beta \pm SE = -0.065 \pm 0.016$; $t_{85} = -3.94$; $P < 0.001$; Fig. 5b) and consistent noise ($\beta \pm SE = 0.061 \pm 0.020$; $t_{85} = 2.97$; $P = 0.011$;

Fig. 5b) treatments, but the relationship between exploratory personality and nestling provisioning rate was similar between the baseline and consistent noise treatments (β ± SE = 0.003 ± 0.016; $t_{85} = 0.202$; $P = 0.977$; Table 2; Fig. 5b). The robustness of this result may be affected by the low number of birds with high exploration scores in our sample (Fig. 5b). However, removing one bird with a particularly high exploration score did not qualitatively change the results (see Fig. 5b). Great tit provisioned larger broods at higher rates (Table 3), but date, time, and recording order had no effect on provisioning rate (Table S2).

3.2. Difference in nestling provisioning rate: There was a significant interaction between noise type and sex in predicting the difference in provisioning rate between the baseline and noise exposure treatments ($F = 5.55$, $P = 0.033$), reflecting that females decreased their provisioning rates relative to baseline levels significantly more than males in the case of the diverse (β ± SE = -0.142 ± 0.032, $t_{36} = -4.42$, $P < 0.001$), but not consistent (β ± SE = -0.043 ± 0.032, $t_{36} = -1.35$, $P = 0.186$), noise. There was also a significant interaction between noise type and exploratory personality type in predicting the difference in nestling provisioning rate ($F=6.61$; $P=0.019$), reflecting a significant positive relationship between exploration score and the difference in nestling provisioning rate between the baseline and diverse noise treatments (β ± SE = 0.072 ± 0.018; $t_{23} = 4.06$, $P < 0.001$), but not the baseline and consistent freeway noise treatments (β ± SE = 0.011 ± 0.016; $t_{23} = 0.699$, $P = 0.492$). Therefore, when compared to slow explorers, fast explorers reduced nestling provisioning rates more relative to baseline levels in the case of the diverse noise treatment, but not in the case of the consistent freeway noise treatment.

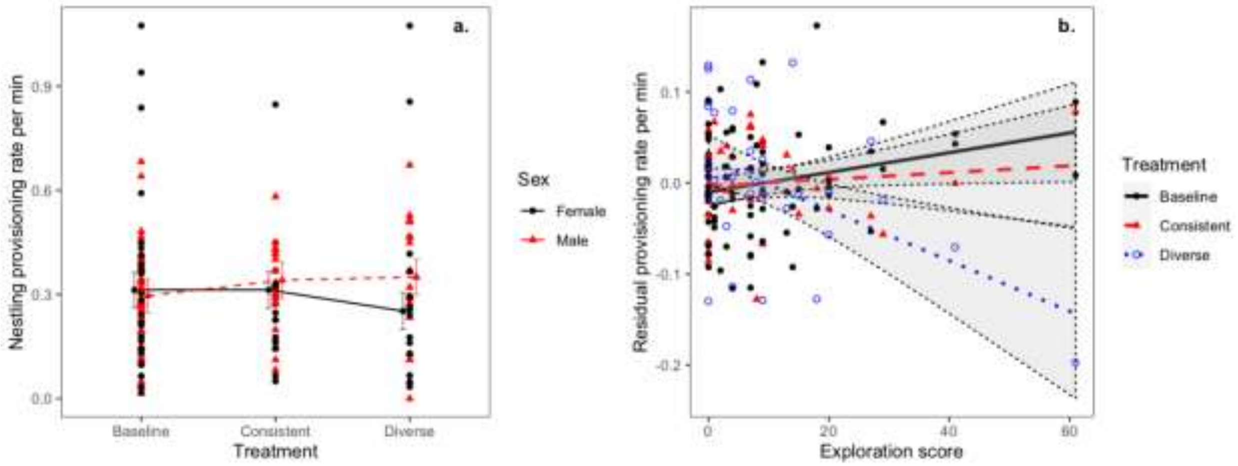

Figure 5. (a) Changes in nestling provisioning rates between baseline conditions and the two noise exposure treatments in female and male great tits. Estimated marginal means from the LMM and individual data points are shown. Bars denote standard error. (b) The relationship between nestling provisioning rate and exploration score under baseline conditions, consistent noise exposure, and diverse noise exposure. Each point represents one bird. There are two baseline treatments for each bird, since a baseline recording was performed before both the consistent and diverse noise exposure. Values are residuals adjusted for the effects of sex, brood size and random effects. Regions enclosed by dotted lines show 95% confidence intervals.

Table 2. Linear-mixed effects model predicting nestling provisioning rate per minute from anthropogenic noise exposure treatment (Baseline, Consistent, Diverse). R^2m = marginal R^2.

	β **± SE**	***Df***	***T***	***P* > (|*t*|)**	***F***	***P* > *F***
Intercept	0.310 ± 0.061	1.09	5.12	0.108		
Consistent noise[a]	0.022 ± 0.018	118	1.23	0.222		
Diverse noise[a]	-0.009 ± 0.016	118	0.076	0.939	0.752	0.475
Nestling age	0.024 ± 0.009	35.9	2.45	**0.019**	5.99	**0.019**
Brood size	0.074 ± 0.002	34.1	3.04	**0.003**	9.24	**0.005**

Random effects	**Variance**	**SD**	**N**
Individual	0.025	0.157	64
Nest box	0.005	0.075	34
Site	0.006	0.074	2
Recording pair	0.001	0.033	66
Playback recording	0.001	0.027	5
Residual	0.011	0.1099	264
R^2m	0.113		

[a] Relative to baseline treatment

Table 3. Linear-mixed effects model predicting nestling provisioning rate per minute from noise treatment (Baseline, Consistent, Diverse) sex and exploration score (ES). R^2m = marginal R^2.

(b)	**β ± SE**	***Df***	***T***	***P* > ($\lvert t \rvert$)**	***F***	***P* > *F***
Intercept	0.293 ± 0.048	1.63	6.05	0.041		
Consistent noise[a]	0.028 ± 0.016	81.9	1.74	0.086		
Diverse noise[a]	-0.009 ± 0.016	81.9	-0.573	0.567	1.69	0.191
Sex[b]	-0.007 ± 0.026	28.7	-0.265	0.792	0.573	0.456
ES	0.004 ± 0.028	33.2	0.141	0.888	0.484	0.492
Brood size	0.092 ± 0.029	37.3	3.13	**0.003**	**9.81**	**0.003**
Consistent noise × Sex	0.022 ± 0.016	82.8	1.42	0.159		
Diverse noise × Sex	0.057 ± 0.016	82.8	3.55	**<0.001**	**6.46**	**0.002**
Consistent noise × ES	-0.003 ± 0.016	83.5	-0.202	0.839		
Diverse noise × ES	-0.065 ± 0.016	83.5	-3.94	**<0.001**	**8.04**	**<0.001**

Random effects	**(a) Variance**	**SD**	**N**

Individual	0.018	0.135	38
Nest box	0	0	27
Site	0.002	0.042	2
Recording pair	0.008	0.091	52
Playback recording	0.003	0.057	5
Residual	0.005	0.072	152
R^2m	0.178		

[a] Relative to baseline treatment

[b] Males relative to females

3.3. Latency to return: We also found no population-mean differences in latency to return to the nest box between the treatment groups (Table 3; Table S3 for full model). However, age and exploratory personality type interacted with noise treatment to predict latency to return to the nest box (Table 4). First year breeders were slower to return during the diverse noise relative to the consistent freeway noise (β ± SE = 0.839 ± 0.274, t_{87} = 3.07, *P* = 0.008; Fig. 6a), tended to return more slowly during the diverse noise relative to during the baseline treatment (β ± SE = 0.514 ± 0.230, t_{103} = 2.24, *P* = 0.070; Fig. 6a), and did not differ in return latency between the baseline and consistent freeway noise treatments (β ± SE = 0.325 ± 0.230, t_{103} = 1.41, *P* = 0.340; Fig. 6a). Posthoc tests indicated no differences in return latencies between treatments for older adults (*P* > 0.60 in all cases), or in return latencies of first year relative to older birds within the treatments (*P* > 0.14 in all cases).

Posthoc comparisons indicated a stronger positive relationship between exploration score and return latency in the diverse noise relative to in the baseline (β ± SE = -0.265 ± 0.112, t_{99} = -2.37, *P* = 0.051) and consistent freeway noise (β ± SE = -0.250 ± 0.132, t_{99} = -1.90, *P* = 0.144) treatments (Fig. 6b), although the first relationship is marginally significant and the second relationship non-significant. There was no difference in this relationship between the baseline and freeway noise treatments ($\beta \pm SE = -0.015 \pm 0.112$, $t_{102} = -0.136$, $P = 0.989$; Fig. 6b).

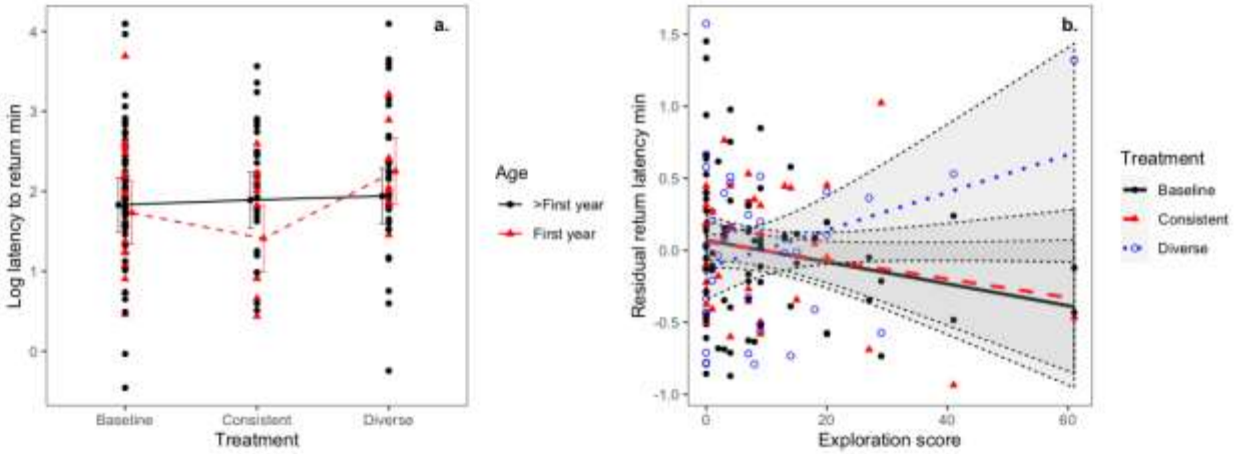

Figure 6. (a) Changes in latency to return to the nest box between baseline conditions and the two noise treatments in older (>first year) and first year breeders. Estimated marginal means from the LMM and individual data points are shown. Bars denote standard error. (b) The relationship between latency to return to the nest box and exploratory personality under baseline conditions, consistent noise exposure, and diverse noise exposure. Each point represents one bird. There are two baseline treatments for each bird, since a baseline recording was performed before both the consistent and diverse noise exposure. Values are residuals adjusted for the effects of age, brood size, nestling age and random effects. Shaded regions show 95% confidence intervals.

Thus, this analysis suggests that fast explorers returned to the nest box after a longer interval of time during the diverse urban noise regime, but not during consistent freeway noise, relative to during the baseline treatment. These results are consistent with, although weaker than, our findings for provisioning rate, but again the robustness of these results is limited by the low number of birds with high exploration scores (Fig. 6b). Indeed, when removing one individual with a particularly high exploration score from the analysis, the interaction between exploration score and treatment became non-significant ($F_{2,102}$ =

0.567; *P* = 0.568). Birds with larger broods and older nestlings also had shorter return latencies (Table 4), whereas other covariates were unrelated to return latency (Table S4).

3.4. Difference in return latency: The difference in return latency between the baseline and noise treatments was negatively related to exploration score (β ± SE = -2.88 ± 1.42, t_{63} = -2.04, *P* = 0.046), but was not related to noise type, age, or the interactions between noise type and age and exploration score ($P>0.50$ in all cases). Thus, this analysis contrasts to the analysis for return latency in which the difference was not calculated, in that it suggests that age is not related to how return latency is affected by noise exposure and that fast explorers increased their return latency more than slow explorers during both the consistent freeway and diverse noise treatments.

Table 4. General linear-mixed effects model predicting return latency (log transformed) from noise treatment (Baseline, Consistent, Diverse). R^2m = marginal R^2.

	***β* ± SE**	***Df***	***T***	***P* > (|*t*|)**	***F***	***P* > *F***
Intercept	1.94 ± 0.239	1.00	8.11	0.078		
Consistent noise[a]	-0.092 ± 0.100	183	-0.921	0.358		
Diverse noise[a]	0.080 ± 0.100	184	0.799	0.425	0.974	**0.380**
Random effects	**Variance**	**SD**	**N**			
Individual	0.354	0.596	64			
Nest box	0.194	0.441	34			
Site	0.079	0.283	2			
Recording pair	0.063	0.250	66			
Playback recording	0	0	5			
Residual	0.412	0.642	264			

R^2m	0.003

[a]Relative to baseline treatment

Table 5. General linear-mixed effects model predicting return latency (log transformed) from noise treatment (Baseline, Consistent, Diverse), age, and exploration score (ES). R^2m = marginal R^2.

(b) Model with intraspecific traits	***β*** **± SE**	***Df***	***T***	***P* > (|*t*|)**	***F***	***P* > *F***
Intercept	1.85 ± 0.334	1.08	5.55	0.099		
Consistent noise[a]	0.060 ± 0.127	105	0.476	0.635		
Diverse noise[a]	0.110 ± 0.127	106	0.862	0.390	4.46	**0.013**
Age[b]	-0.095 ± 0.276	39.7	-0.347	0.730	0.120	0.731
Exploration score	-0.211 ± 0.107	30.1	-1.96	0.058	1.42	0.246
Brood size	-0.276 ± 0.129	19.2	-2.14	0.045	4.57	**0.045**
Nestling age	-0.117 ± 0.055	119	-2.12	0.036	4.47	**0.036**
Consistent noise × Age	-0.385 ± 0.260	105	-1.48	0.141		
Diverse noise × Age	0.404 ± 0.260	105	1.55	0.122	3.46	**0.035**
Consistent noise × ES	0.015 ± 0.111	105	0.138	0.890		
Diverse noise × ES	0.265 ± 0.111	105	2.39	0.018	3.11	**0.048**
Random effects	**Variance**	**SD**	**N**			
Individual	0.170	0.412	38			
Nest box	0.181	0.426	27			
Site	0.179	0.423	2			
Recording pair	<0.001	<0.001	52			
Playback recording	0	0	5			
Residual	0.308	0.554	152			

R^2m	0.295

[a]Relative to baseline treatment

[b]Yearlings relative to older birds

3.5. On-bout length: We found no population-level differences in on-bout length between the treatments (Table S5), and also no evidence for interactions between individual traits and treatment in predicting on-bout length (Table S6). Birds with larger broods had shorter on-bouts ($\beta \pm SE = -0.702 \pm 0.251$, $t_{61} = -2.79$, $P = 0.007$) and there was a tendency for males ($\beta \pm SE = -0.452 \pm 0.253$, $t_{57} = -1.78$, $P = 0.080$) and birds breeding later in the season to have shorter on-bouts ($\beta \pm SE = -0.439 \pm 0.245$, $t_{78} = -1.79$, $P = 0.077$).

4. Discussion

Our results suggest that urban great tits display overall low responsiveness to anthropogenic noise exposure during nestling provisioning. Indeed, we found no population-mean level differences in nestling provisioning rate, return latencies or on-bout length between the two experimental noise treatments and baseline behavioral patterns. This overall low level of responsiveness might be explained by the fact that birds in our study populations are not naïve to anthropogenic noise. Although nest boxes used in our experiments were located in relatively quiet areas within the urban matrix, these territories are nonetheless all relatively close to sources of anthropogenic noise (within ~600 m of roadways, houses, etc.), and birds are thus likely to experience anthropogenic noise in close proximity, for instance while foraging away from the nest box or exploring. As a result, birds in our study populations might be habituated to anthropogenic noise to the extent that many of them maintain nestling provisioning rates under noise exposure. In contrast to our results, Naguib et al. (2013) found overall reductions in parental provisioning rates and latency to return to the nest box in great tits experimentally exposed to noise. The difference with our results may reflect the more rural nature of the study area where Naguib et al. (2013) conducted their research, which could have deemed birds in their study population less familiar with noise exposure. However, other studies have also reported low parental responsiveness to noise exposure. For instance, Injaian et al. (2018b) found a modest positive, rather than negative, effect of traffic noise exposure on parental feeding rate in tree swallows, and an earlier study on tree swallows found no effect of ambient noise levels on feeding rate (Leonard et al., 2015). Due to the high importance of sustained parental care to reproductive fitness, selection may be strong to maintain parental behavior, even in the face of perturbations such as anthropogenic noise. Indeed, especially in our urban study population, maintaining parental behavior in the face of anthropogenic disturbance factors that truly pose little threat may elevate fitness, with the caveat that reduced responsiveness to disturbance may tradeoff against adaptive responsiveness to life-threatening situations (e.g. predation) (Ghalambor and Martin, 2001; Partecke et al., 2006; Brown et al., 2012).

Lack of a strong behavioral response during nestling provisioning also does not preclude other negative effects of anthropogenic noise on these birds, for instance increases in stress hormone levels and changes in health status (Injaian et al., 2018a; Kleist et al., 2018). For example, Injaian et al. (2018b) found reduced body size and delayed fledging in tree swallow nestlings exposed to noise, and these effects could not be explained by differences in parental behavior. In addition, behavior and physiology during different activities or life-stages could be more strongly affected by noise exposure than parental behavior during the nestling stage. For example, we recently documented significant changes in sleep behavior in urban great tits experimentally exposed to traffic noise (Grunst et al. *In Review*), and shortened telomeres (a marker of biomolecular aging rate) in the smallest nestlings of great tit broods located on noisy urban territories (Grunst et al. 2020).

Moreover, despite the lack of population-level responses, our analyses suggest that some individuals within our urban study populations are more sensitive to noise exposure than others, especially in the case of exposure to a diverse urban noise regime, consisting of multiple sound types and temporal unpredictability. Specifically, when exposed to the diverse noise regime, but not to consistent freeway noise, females and fast explorers reduced nestling provisioning rates more relative to baseline conditions than males and slow explorers. Although these results were less robust, we also found some evidence that, compared to slow explorers, fast explorers increased their return latency more relative to baseline conditions during the noise exposure. This pattern only emerged during the diverse urban noise regime when using repeated measures of return latency across all treatments, but existed in both noise regimes when the analysis was conducted using the difference in return latency as the dependent variable. Similarly, when using repeated measures of return latency, first year breeders appeared more sensitive to the diverse noise regime, but not consistent freeway noise, as compared to older breeders. As a caveat, the difference in return latency in response to noise exposure was not significantly related to age.

The more pronounced effect of the diverse noise regime on the behavior of certain subsets of birds could have arisen because more temporally unpredictable patterns of noise production are perceived as more threatening or are harder to habituate to (Wysocki et al., 2006; Blickley et al., 2012; Nichols et al., 2015), or because certain sound types present in the diverse noise recordings had greater behavioral effects than consistent freeway noise. To simulate patterns of noise produced in a busy urban area that experiences different sources of noise, we incorporated both temporal variability and diverse sound types into the diverse noise playbacks. A limitation of this study design is that it does not allow us to separate effects of temporal unpredictability versus diversity in sound type. Indeed, a single sound type on the diverse noise recordings could have driven differences in responses between the two noise treatments. Previous research on differential responses to specific noise types are not common, but Delaney et al. (1999) found that chain saw noise was more disruptive to Mexican spotted owls (*Strix occidentalis lucida*) than helicopter noise at a comparable distance, demonstrating that the acoustical properties of specific anthropogenic noise types may have non-trivial effects on the magnitude of organismal responses. The diverse noise regime that we used included some noises of higher frequency, and sounds with certain frequency characteristics might be perceived as more threatening, depending on the auditory sensitivity of the species (Francis and Barber, 2013; Mancera et al., 2017). Higher frequency noises could also have interfered with high frequency great tit calls, and thus disrupted communication (great tit calls are produced at 2 to 8 kHz; Templeton et al. 2016), although why such effects would have been specific to certain classes of individuals is not apparent. Our results illustrate that experimentally testing for effects of only one type of anthropogenic noise (e.g. traffic noise), and focusing on population-mean patterns alone, might lead to failure to reveal the full scope of effects of anthropogenic noise on organisms. Future studies should incorporate additional noise exposure treatments to parse apart the effects of variability in different attributes of the noise regime. Importantly, temporal variability may have different biological implications than diversity in noise types. For instance, noise regimes that are more temporally intermittent include more intervals of silence, and may thus potentially interfere less with communication than consistent noise (Blom et al., 2019).

Our results were in part consistent with the prediction that a more diverse noise regime might have larger behavioral effects, in that evidence for individual differences in noise sensitivity were only detected in the case of the diverse noise regime. Past research has also suggested that, as compared to more consistent noise, temporally intermittent or variable noise regimes can have larger magnitude effects on biological response variables, such as lek attendance in greater sage-grouse (*Centrocercus urophasianus*) and cortisol levels in fresh water and coastal marine fish (Wysocki et al., 2006; Blickley et al., 2012; Nichols et al., 2015). However, our results with respect to which classes of individuals were more responsive to the noise exposure were not all as expected.

Contrary to predictions, females reduced nestling provisioning rates more than males under conditions of diverse urban noise, whereas we had predicted the opposite due to greater female investment in broods (Clutton-Brock, 1991; Lubjuhn et al., 1999). Why we observed the opposite pattern is unclear, but male and female great tits both invest extensively into nestling provisioning (Smith et al., 1988), and past studies have found inconsistent results with respect to sex-differences in noise sensitivity (see Harding et al., 2019 for review). One possible explanation for our results is that sex role separation increased under the more diverse noise regime, with females redirecting effort towards nest guarding and males in some cases compensating by increasing nestling provisioning rates. Consistent with this hypothesis, male nestling provisioning rates tended to increase in the diverse noise treatment relative to baseline levels.

Also contrary to predictions, our results suggested higher sensitivity of fast explorers to the diverse urban noise regime, when considering both nestling provisioning rates and return latencies. We had predicted that slow explorers would respond more to noise exposure because slow explorers have more reactive HPA axes than fast explorers (Stöwe et al., 2010; Baugh et al., 2012), which might translate into greater sensitivity to disturbance. Consistent with this prediction, Naguib et al. (2013) reported that slow explorers took longer to resume nestling provisioning during exposure to traffic noise. Yet, consistent with our findings, Naguib et al. (2013) initially predicted that fast explorers would be more sensitive to noise, because some past research suggests that slow explorers display greater flexibility in behavioral responses and better cope with environmental change (Verbeek et al., 1994; Guillette et al., 2010; Exnerová et al., 2009). In addition, Naguib et al. (2013) found that slow-exploring males, but fast-exploring females, reduced nestling provisioning more when exposed to noise, with the reason for this sex difference unclear. Further research using larger sample sizes that can robustly test interactive effects is needed to better resolve the relationship between exploratory personality type and noise sensitivity, especially given that our current study was based on a relatively small sample size of personality-typed birds.

Consistent with predictions, we found some evidence that, when compared to older birds, first year breeders displayed greater increases in latency to return to the nest box during the diverse noise relative to during the consistent freeway noise or under baseline conditions. Senescence has been shown to occur in the great tit (Bouwhuis et al., 2009), suggesting that older birds could have reduced residual reproductive value, and increased incentive to care for the brood as compared to younger birds, especially under conditions of environmental stress or unpredictability. In addition, older individuals could have more prior experience with diverse types of anthropogenic noise, and could thus be less responsive to noise exposure. In parallel to these results, a past study reported that younger birds avoided a phantom road to a greater extent than older adults during migration (McClure et al., 2017).

Our study has some additional limitations. First, although we used a repeated-measures design, which increases statistical power, our sample size was relatively small. Thus, we again urge further research using larger sample sizes, especially into the factors underlying individual differences in sensitivity to anthropogenic noise. Second, due to financial limitations, we used relatively low-tech recording devices to project the noise playback rather than professional loudspeakers. Thus, the noise projected is likely to have been somewhat distorted relative to the actual noise type that it was meant to emulate, although we do not believe that this distortion was large enough to be highly problematic. Finally, our study could have benefited from additional physiological (e.g. corticosterone levels obtained from blood samples) or behavioral (e.g. rate of alarm calling) measurements that would be indicative of stress.

5. Conclusions In conclusion, we found no population-level responses in the nestling provisioning behavior of urban great tits exposed to either a consistent or more diverse anthropogenic noise regime, indicating that the population contains many individuals that do not change nestling provisioning behavior under noise exposure. This result may reflect the fact that individuals within this urban population commonly encounter anthropogenic noise in the environment, such that many individuals display canalized behavior in the face of noise exposure. Indeed, animals may elevate fitness by maintaining parental behavior in the face of disturbances that truly pose little threat. However, despite overall low responsiveness to noise exposure, certain classes of individuals within the urban population nonetheless appeared to remain sensitive to the diverse urban noise regime. Specifically, females, first year breeders, and fast explorers displayed more pronounced behavioral responses (decreased nestling provisioning rates or increased latency to return to the nest box) to the diverse noise regime than males, older breeders and slow explorers. These results suggest that anthropogenic noise may have the potential to exert selection and affect population dynamics, and that focusing experiments only on one type of anthropogenic noise regime (e.g. traffic noise), and only on population-mean responses, may result in failure to appreciate the full scope of biological effects arising from anthropogenic noise exposure. Notably, noise mitigation policies often focus on reducing freeway noise, whereas our results suggest that policy makers should also attempt to reduce other sources of anthropogenic noise pollution. We urge further research to better elucidate the sources of intraspecific variation in responses to anthropogenic noise, and to parse apart the effects of different components (different sound types, temporal predictability) of diverse urban noise regimes.

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Data accessibility Data will be made available via the Dryad Digital Repository.

References

Angelier, F., Meillère, A., Grace, J.K., Trouvé, C., Brischoux, F., 2016. No evidence for an effect of traffic noise on the development of the corticosterone stress response in an urban exploiter. Gen. Comp. Endocrinol. 232, 43–50. doi: 10.1016/j.ygcen.2015.12.007.

Barber, J.R., Crooks, K.R., Fristrup, K.M., 2009. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. 25, 180-189. doi: 10.1016/j.tree.2009.08.002.

Barber, J.R., Burdett, C.L., Reed, S.E., Warner, K.A., Formichella, C., Crooks, K.R., Theobald, D.M., Fristrup, K.M., 2011. Anthropogenic noise exposure in protected natural areas: estimating the scale of ecological consequences. Landscape Ecol. 26, 1281. doi: 10.1007/s10980-011-9646-7.

Basner, M., Babisch, W., Davis, A., Brink, M., Clark, C., Janssen, S., Stansfeld, S., 2014. Auditory and non-auditory effects of noise on health. Lancet 383, 1325-1332. doi:10.1016/S0140-6736(13)61613-X.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Software 67, 1-48. doi:10.18637/jss.v067.i01.

Bauerová, P., Vinklerová, J., Hraníček, J., Čorba, V., Vojtek, L., Svobodová, J., Vinkler, M., 2017. Associations of urban environmental pollution with health-related physiological traits in a free-living bird species. Sci. Tot. Environ. 601-602, 1556-1565. doi: 10.1016/j.scitotenv.2017.05.276.

Baugh, A.T., Schaper, S.V., Hau, M., Cockrem, J.F., de Goede, P., van Oers, K., 2012. Corticosterone responses differ between lines of great tits (Parus major) selected for divergent personalities. Gen. Comp. Endocrinol. 175, 488–494. doi: 10.1016/j.ygcen.2011.12.012.

Blickley, J.L., Blackwood, D., Patricelli, G., 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conserv. Biol. 26, 461-471. doi: 10.1111/j.1523-1739.2012.01840.x.

Blom, E-L., Kvarnemo, C., Dekhla, I., Schöld, S., Andersson, M.H., Svensson, O., Amorim, M.C.P., 2019. Continuous but not intermittent noise has a negative impact on mating success in a marine fish with paternal care. Sci. Rep. 9, 5494. doi.org/10.1038/s41598-019-41786-x.

Bouwhuis, S., Sheldon, B.C., Verhulst, S., Charmantier, A., 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proc. Roy. Soc. B. 276, 2769-2777. doi: 10.1098/rspb.2009.0457.

Bowen, A.E., Gurule-Small, G., Tinghitella, R.M., 2020. Anthropogenic noise reduces male reproductive investment in an acoustically signaling insect. Behav Ecol Sociobiol. 74, 103. doi: 10.1007/s00265-020-02868-3.

Brown, C.L., Hardy, A.R., Barber, J.R., Fristrup, K.M., Crooks, K.R., Angeloni, L.M., 2012. The effect of human activities and their associated noise on ungulate behavior. Plos One 7, e40505. doi: 10.1371/journal.pone.0040505.

Brumm, H., Slabbekoorn, H., 2005. Acoustic communication in noise. Adv. Study Behav. 35, 151–209. doi: 10.1016/S0065-3454(05)35004-2.

Buxton, R.T., McKenna, M.F., Mennitt, D., Fristrup, K., Crooks, K., Angeloni, L., Wittemyer, G., 2017. Noise pollution is pervasive in U.S. protected areas. Science 356, 531-533. doi: 10.1126/science.aah4783.

Candolin, U., 2019. Why study intraspecific variation: a comment on Harding et al. Behav. Ecol. 30, 1515-1516. doi: 10.1093/beheco/arz162.

Caorsi, V.Z., Both, C., Cechin, S., Antunes, R., Borges-Martins, M., 2017. Effects of traffic noise on the calling behavior of two Neotropical hylid frogs. PLoS ONE 12, e0183342. doi: 10.1371/journal.pone.0183342.

Charmantier, A., Demeyrier, V., Lambrechts, M., Perret, S., Grégoire, A., 2017. Urbanization is associated with divergence in pace-of-life in great tits. Front. Ecol. Evol. 5, 53. doi: 10.3389/fevo.2017.00053.

Cheptou, P.O., Hargreaves, A.L., Bonte, D., Jacquemyn, H., 2017. Adaptation to fragmentation: evolutionary dynamics driven by human influences. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 372, 20160037. doi: 10.1098/rstb.2016.0037.

Clutton-Brock, T.H., 1991. The Evolution of Parental Care. Princeton, NJ. Princeton University Press.

Corsini, M., Dubiec, A., Marrot, P., Szulkin, M., 2017. Humans and tits in the city: quantifying the effects of human presence on great tit and blue tit reproductive trait variation. Front. Ecol. Evol. 5, 82. doi: 10.3389/fevo.2017.00082.

Crino, O.L., Johnson, E.E., Blickley, J.L., Patricelli, G.L., Breuner, C.W., 2013. Effects of experimentally elevated traffic noise on nestling white-crowned sparrow stress physiology, immune function and life history. J. Exp. Biol. 216, 2055–2062. doi: 10.1242/jeb.081109.

Delaney, D.K., Grubb, T.G., Beier, P., Pater, L.L., 1999. Effects of helicopter noise on Mexican spotted owls. J. Wild. Mang. 63, 60-76. doi: 10.2307/3802487.

De Boer, S.F., Van Der Gugten, J., Slangen, J.L., 1989. Plasma catecholamine and corticosterone responses to predictable and unpredictable noise stress in rats. Physiol. Behav. 45, 789-795. doi: 10.1016/0031-9384(89)90296-5.

De Satgé, J., Strubbe, D., Elst, J., De Laet, J., Adriaensen, F., Matthysen, E., 2019. Urbanization lowers great tit *Parus major* breeding success at multiple spatial scales. J. Avian Biol. 50. doi: 10.1111/jav.02108.

Dingemanse, N.J., Both, C., Drent, P.J., van Oers, K., van Noordwijk, A.J., 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. Anim. Behav. 64, 929–937. doi: 10.1006/anbe.2002.2006.

Dingemanse, N.J., Bouwman, K.M., van de Pol, M., van Overveld, T., Patrick, S.C., Matthysen, E., Quinn, J.L., 2012. Variation in personality and behavioural plasticity across four populations of the great tit Parus major. J. Anim. Ecol. 81, 116–126. doi: 10.1111/j.1365-2656.2011.01877.x.

Dorado-Correa, A.M., Zollinger, S.A., Heidinger, B., Brumm, H., 2018. Timing matters: traffic noise accelerates telomere loss rate differently across developmental stages. Front. Zool. 15, 29. doi: 10.1186/s12983-018-0275-8.

Drent, P.J., van Oers, K., van Noordwijk, A.J., 2003. Realized heritability of personalities in the great tit (Parus major). Proc. R. Soc. Lond. B 270, 45–51. doi: 10.1098/rspb.2002.2168.

Exnerová, A., Svadova, K.H., Fucikova, E., Drent, P., Stys, P., 2009. Personality matters: individual variation in reactions of naive bird predators to aposematic prey. Proc. R. Soc. B. 277, 723-728. doi: 10.1098/rspb.2009.1673.

Francis, C.D., Barber, J.R., 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. Front. Ecol. Environ. 11, 305–313. doi: 10.1890/120183.

Gallego-Abenza, M., Mathevon, N., Wheatcroft D., 2020. Experience modifies an insect’s response to anthropogenic noise. Behav Ecol. 31, 90-96. doi:10.1093/beheco/arz159.

Gaston, K.J., Bennie, J., Davies, T.W., Hopkins, J., 2013. The ecological impacts of nighttime light pollution. Biol. Rev. 88, 912-927. doi: 10.1111/brv.12036.

Ghalambor, C.K., Martin, T.E., 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292, 494-497. doi: 10.1126/science.1059379.

Gill, S.A., Job, J.R., Myers, K., Naghshineh, K., Vonhof, M.J., 2015. Towards a broader characterization of anthropogenic noise and its effects on wildlife. Behav Ecol. 26, 328-333. doi: 10.1093/beheco/aru219.

Grunst, M.L., Rotenberry, J.T., Grunst, A.S., 2014. Variation in adrenocortical stress physiology an condition metrics within a heterogenous urban environment in the song sparrow *Melospiza melodia*. J Avian Biol. 45, 574-583. doi: 10.1111/jav.00459.

Grunst, A.S., Grunst, M.L., Thys, B., Raap, T., Daem, N., Pinxten, R., Eens, M., 2018. Variation in personality traits across a metal pollution gradient in a free-living songbird. Sci. Tot. Environ. 630, 668-678. doi: 10.1016/j.scitotenv.2018.02.191.

Grunst, A.S., Grunst, M.L., Pinxten, R., Eens, M., 2019a. Personality and plasticity in neophobia levels vary with anthropogenic disturbance but not toxic metal exposure in urban great tits. Sci. Tot. Environ. 656, 997-1009. doi: 10.1016/j.scitotenv.2018.11.383.

Grunst, M.L., Grunst, A.S., Pinxten, R., Bervoet, L., Eens, M., 2019b. Carotenoid- but not melanin-based plumage coloration is negatively related to metal exposure and proximity to the road in an urban songbird. Environ. Pollut. 256, 113473. doi: 10.1016/j.envpol.2019.113473.

Grunst, M.L., Grunst, A.S., Pinxten, R., Eens, M., 2020. Anthropogenic noise is associated with telomere length and carotenoid-based coloration in free-living nestling songbirds. Environ. Pollut. 26, 114032. doi: 10.1016/j.envpol.2020.114032.

Grunst, M.L., Grunst, A.S., Pinxten, R., Eens, M., *In Review*. Variable and consistent traffic noise negatively affect the sleep behavior of free-living songbirds.

Guillette, L.M., Reddon, A.R., Hoeschele, M., Sturdy, C.B., 2010. Sometimes slower is better: slow-exploring birds are more sensitive to changes in a vocal discrimination task. Proc. R. Soc. B. 278, 767-773. doi: 10.1098/rspb.2010.1669.

Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., ten Cate, C., Slabbekoorn, H., 2011a. Low-frequency songs lose their potency in noisy urban conditions. Proc. Natl. Acad. Sci. USA 108, 14549-14554. doi: 10.1073/pnas.1109091108.

Halfwerk, W., Holleman, L.J.M., Lessells, C.M., Slabbekoorn, H., 2011b. Negative impact of traffic noise on avian reproductive success. J. Appl. Ecol. 48, 210–219. doi: 10.1111/j.1365-2664.2010.01914.x.

Hammer, M.S., Swinburn, T.K., Neitzel, R.L., 2014. Environmental noise pollution in the United States: developing an effective public health response. Environ. Health Perspect. 122, 115–119. doi: 10.1289/ehp.1307272.

Harding, H., Gordon, T.A.C., Eastcott, E., Simpson, S.D., Radford, A., 2019. Causes and consequences of intraspecific variation in animal responses to anthropogenic noise. Behav. Ecol. 30, 1501-1511. doi:10.1093/beheco/arz114.

Injaian, A.S., Taff, C.C., Pearson, K.L., Gin, M.M.Y., Patricelli, G.L., Vitousek, M.N., 2018a. Effects of experimental chronic traffic noise exposure on adult and nestling corticosterone levels, and nestling body condition in a free-living bird. Horm. Behav. 106, 19-27. doi: 10.1016/j.yhbeh.2018.07.012.

Injaian, A.S., Taff, C.C., Patricelli, G.L., 2018b. Experimental anthropogenic noise impacts avian parental behaviour, nestling growth and oxidative stress. Anim. Behav. 136, 31-39. doi: 10.1016/j.anbehav.2017.12.003.

Injaian, A.S., Poon, L.Y., Patricelli, G.L., 2018c. Effects of experimental anthropogenic noise on avian settlement patterns and reproductive success. Behav. Ecol. 29, 1181–1189. doi.org/10.1093/beheco/ary097.

Kight, C.R., Swaddle, J.P., 2011. How and why environmental noise impacts animals: an integrative, mechanistic review. Ecol. Lett. 14, 1052–1061. doi: 10.1111/j.1461-0248.2011.01664.x.

Kleist, N.J., Guralnick, R.P., Cruz, A., Lowry, C.A., Francis, C.D., 2018. Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. Proc. Natl. Acad. Sci. 115, E648-E657. doi: 10.1073/pnas.1709200115.

Kunc, H.P., Schmidt, R., 2019. The effects of anthropogenic noise on animals: a meta-analysis. Biol. Lett. 15, 20190649. doi: 10.1098/rsbl.2019.0649.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. J. Stat. Software 82, 1-26. doi: 10.18637/jss.v082.i13.

Lampe U, Schmoll T, Franzke A, Reinhold K. 2012. Staying tuned: grasshoppers from noisy roadside habitats produce courtship signals with elevated frequency components. Funct Ecol. 26, 1348–1354. doi: 10.1111/1365-2435.12000.

Lengagne, T., 2008. Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. Biol Conserv. 141, 2023-2031. doi: 10.1016/j.biocon.2008.05.017.

Lenth, R., 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.3.01. https://CRAN.R-project.org/package=emmeans

Leonard, M.L., Horn, A.G., 2012. Ambient noise increases missed detections in nestling birds. Biol. Lett. 8, 530-532. doi: 10.1098/rsbl.2012.0032.

Leonard, M.L., Horn, A.G., Oswald, K.N., McIntyre, E., 2015. Effect of ambient noise on parent-offspring interactions in tree swallows. Anim. Behav. 109, 1-7. doi: 10.1016/j.anbehav.2015.07.036.

Lubjuhn, T., Strohbach, S., Brün, J., Gerken, T., Epplen, J.T., 1999. Extra-pair paternity in great tits (Parus major) - A long term study. Behaviour 136, 1157-1172. doi: 10.1163/156853999501810.

Lucass, C., Eens, M., Müller, W., 2016. When ambient noise impairs parent-offspring communication. Environ. Pollut. 212, 592-597. doi: 10.1016/j.envpol.2016.03.015.

Lüdecke, D., Makowski, D., Waggoner, P., Patil, I., 2020. performance: Assessment of Regression Models Performance. R package version 0.4.7. https://CRAN.R-project.org/package=performance

Mancera, K.F., Lisle, A., Allavena, R., Phillips, C.J.C., 2017. The effects of mining machinery noise of different frequencies on the behaviour, faecal corticosterone and tissue morphology of wild mice (*Mus musculus*). Applied Anim. Behav. Sci. 197, 81-89. doi: 10.1016/j.applanim.2017.08.008.

Martínez-Marivela, I., Morales, M.B., Iglesias-Merchán, C., Delgado, M.P., Tarjuelo, R., Traba, J., 2018. Traffic noise pollution does not influence habitat selection in the endangered little bustard. Ardeola 65, 261-270. doi: 10.13157/arla.65.2.2018.ra5.

McClure, C.J.W., Ware, H.E., Carlisle, J.D., Barber, J.R., 2017. Noise from a phantom road experiment alters the age structure of a community of migrating birds. Anim. Conserv. 20, 164–172. doi.org/10.1111/acv.12302.

Naguib, M., van Oers, K., Braakhuis, A., Griffioen, M., de Goede, P., Waas, J.R., 2013. Noise annoys: effects of noise on breeding great tits depend on personality but not on noise characteristics. Anim. Behav. 85, 949-956. doi: 10.1016/j.anbehav.2013.02.015.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. doi:10.1111/j.2041-210x.2012.00261.x.

Nedelec, S.L., Radford, A.N., Pearl, L., Nedelec, B., McCormick, M.I., Meekan, M.G., Simpson, S.D., 2017. Motorboat noise impacts parental behaviour and offspring survival in a reef fish. Proc. R. Soc. B 284, 20170143. doi:10.1098/rspb.2017.0143.

Nemeth, E., Brumm, H., 2010. Birds and anthropogenic noise: are urban songs adaptive? Am. Nat. 176, 465-475. doi: 10.1086/656275.

Nichols, T.A., Anderson, T.W., Širović, A., 2015. Intermittent noise induces physiological stress in a coastal marine fish. PLoS ONE 10, e0139157. doi:10.1371/journal.pone.0139157.

Orci, K.M., Petróczki, K., Barta, Z., 2016. Instantaneous song modification in response to fluctuating traffic noise in the tree cricket *Oecanthus pellucens*. Anim Behav. 112, 187-194. doi: 10.1016/j.anbehav.2015.12.008.

Partecke, J., Schwalb, I., Gwinner, E., 2006. Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. Ecol. 87, 1945-1952. doi:10.1890/0012-9658(2006)87[1945:satcua]2.0.co;2.

R Core Team., 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Raap, T., Pinxten, R., Casasole, G., Dehnhard, N., Eens, M., 2017. Ambient anthropogenic noise but not light is associated with the ecophysiology of free-living songbird nestlings. Sci. Rep. 7, 2754. doi:

10/1038/S41598-017-02940-5.

Salmón, P., Nilsson, J.F., Nord, A., Bensch, S., Isaksson, C., 2016. Urban environment shortens telomere length in nestling great tits, Parus major. Biol. Lett. 12, 20160155. doi:10.1098/rsbl.2016.0155.

Samson, J.E., Mooney, T.A., Gussekloo, S.W.S., Hanlon, R.T., 2014. Graded behavioral responses and habituation to sound in the common cuttlefish *Sepia officinalis*. J. Exp. Biol. 217, 4347-4355. doi: 10.1242/jeb.113365.

Schielzeth, H., 2010. Simple means to improve the interpretability of regression coeficients. Methods Ecol. Evol. 1, 103-113. doi: 10.1111/j.2041-210X.2010.00012.x.

Schroeder, J., Nakagawa, S., Cleasby, I.R., Burke, T., 2012. Passerine birds breeding under chronic noise experience reduced fitness. PLoS ONE 7, e39200. doi: 10.1371/journal.pone.0039200.

Shannon, G., McKenna, M.F., Angeloni, L.M., Crooks, K.R., Fristrup, K.M., Brown, E., Warner, K.A., Nelson, M.D., White, C., Briggs, J., McFarland, S., Wittemyer, G., 2016. A synthesis of two decades of research documenting the effects of noise on wildlife. Biol. Rev. 91, 982–1005. doi: 10.1111/brv.12207.

Sih, A., Ferrari, M.C.O., Harris, D.J., 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evol. Appl. 4, 367-387. doi: 10.1111/j.1752-4571.2010.00166.x.

Sih, A., 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. Anim. Behav. 85, 1077-88. doi: 10.1016/j.anbehav.2013.02.017.

Slabbekoorn, H., Ripmeester, E.A.P., 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Mol. Ecol. 17, 72–83. doi: 10.1111/j.1365-294X.2007.03487.x.

Smith, H.G., Källander, H., Fontell, K., Ljungström, M., 1988. Feeding frequency and parental division of labour in the doubly-brooded great tit *Parus major*. Behav. Ecol. Sociobiol., 22, 447-453. doi: 10.1007/BF00294983.

Sol, D., Lapiedra, O., González-Lagos, C., 2013. Behavioural adjustments for life in the city. Anim. Behav. 85, 1101–12. doi: 10.1016/j.anbehav.2013.01.023.

Stöwe, M., Rosivall, B., Drent, P.J., Möstl, E., 2010. Selection for fast and slow exploration affects baseline and stress-induced corticosterone excretion in great tit nestlings, Parus major. Horm. Behav. 58, 864-871. doi: 10.1016/j.yhbeh.2010.08.011.

Stuber, E.F., Araya-Ajoy, Y.G., Mathot, K.J., Mutzel, A., Nicolaus, M.,Wijmenga, J.J., Mueller, J.C., Dingemanse, N.J., 2013. Slow explorers take less risk: a problem of sampling bias in ecological studies. Behav. Ecol. 24, 1092–1098. doi: 10.1093/beheco/art035.

Svensson, L., 1984. Identification Guide to European Passerines. Edn. 3. British Trust for Ornithology, Stockholm.

Swaddle, J.P., Francis, C.D., Barber, J.R., Cooper, C.B., Kyba, C.C., Dominoni, D.M., Shannon, G., Aschehoug, E., Goodwin, S.E., Kawahara, A.Y., Luther, D., Spoelstra, K., Voss, M., Longcore, T., 2015. A framework to assess evolutionary responses to anthropogenic light and noise. Trends Ecol. Evol. 30, 550-560. doi: 10.1016/j.tree.2015.06.009.

Templeton, C.N., Zollinger, S.A., Brumm, H., 2016. Traffic noise drowns out great tit alarm calls. Curr. Biol. 26, R1173-R1174. doi: 10.1016/j.cub.2016.09.058.

Thys, B., Pinxten, R., Raap, T., De Meester, G., Rivera-Gutierrez, H.F., Eens, M., 2017. The female perspective of personality in a wild songbird: repeatable aggressiveness relates to exploration behaviour. Sci. Rep. 7, 7656. doi: 10.1038/s41598-017-08001-1.

Van Oers, K., Drent, P.J., de Goede, P., van Noordwijk, A.J., 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. Proc. R. Soc. Lond. B 271, 65-73. doi: 10.1098/rspb.2003.2518.

Verbeek, M.E.M., Drent, P.J., Wiepkema, P.R., 1994. Consistent individual differences in early exploratory behaviour of male great tits. Anim. Behav. 48, 1113-1121. doi: 10.1006/anbe.1994.1344.

Wysocki, L.E., Dittami, J.P., Ladich, F., 2006. Ship noise and cortisol secretion in European freshwater fishes. Biol. Conserv. 128, 501–508. doi: 10.1016/j.biocon.2005.10.020.

Zollinger, S.A., Dorado-Correa, A., Goymann, W., Forstmeier, W., Knief, U., Bastidas-Urrutia, A.M., Brumm, H., 2019. Traffic noise exposure depresses plasma corticosterone and delays offspring growth in breeding zebra finches. Conserv. Physiol. 7, coz056. doi: 10.1093/conphys/coz056.