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Variable and consistent traffic noise negatively affect the sleep behavior of a free-living songbird

Running title: Traffic noise affects sleep behavior

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ABSTRACT Anthropogenic noise is an ubiquitous disturbance factor, which, owing to the extensive nature of transportation networks, and ability of sound waves to penetrate distances, has wide-reaching impacts on biological communities. Research effort on biological effects of anthropogenic noise is extensive, but has focused on waking behavior, and to our knowledge, no published experimental study exists on how noise affects sleep in free-living animals. Sleep plays vital functions in processes such as cellular repair and memory consolidation. Thus, understanding the potential for noise to disrupt sleep is a critical research objective. Whether different noise regimes exert distinct effects on behavior also remains poorly understood, as does intraspecific variation in noise sensitivity. To address these knowledge gaps, we used a repeated-measures field experiment involving broad-casting traffic noise recordings at great tit (*Parus major*) nest boxes over a series of consecutive nights. We evaluated whether increasing the temporal variability and amplitude of traffic noise increased deleterious effects on sleep behavior in free-living great tits, and whether individuals differed in the magnitude of responses.

We found that traffic noise reduced sleep duration, proportion, and bout length, and induced birds to exit nest boxes earlier in the morning. There was some support for a stronger effect of more variable noise, and relative to lower amplitude noise, higher amplitude noise resulted in less and more fragmented sleep. Effects of noise on sleep duration were stronger in older adults, and substantial, repeatable variation existed in individual responses. We demonstrate for the first time that anthropogenic noise can have strong effects on sleep in free-living animals, which may have cascading effects on waking behavior, physiology and fitness. Results suggest that reducing the amplitude of traffic noise may be an effective mitigation strategy, and that differences in individual sensitivity are important to consider when evaluating effects of noise exposure.

Capsule: Experimental exposure to temporally variable and consistent traffic noise negatively affected sleep behavior in a free-living songbird.

Keywords: Anthropogenic noise, sleep, variability, amplitude, intraspecific variation, great tit, *Parus major*

1. Introduction Anthropogenic activities introduce environmental stimuli which can pose significant challenges for diverse facets of organismal life (Kempenaers et al., 2010; Gaston et al., 2013; Swaddle et al., 2015; Bauerová et al., 2017). Anthropogenic noise is particularly pervasive and has wide-reaching effects on biological systems, from individuals to communities (Barber et al., 2009, 2011; Francis et al., 2009; Kight and Swaddle, 2011; Francis et al., 2012). The transportation network is extensive, and sound waves can travel considerable distances before attenuating in the environment (Francis and Barber, 2013). Thus, anthropogenic noise can affect animals across urban-rural interfaces and even within protected areas, such as National Parks and reserves (Barber et al., 2009; Buxton et al., 2017; Francis et al., 2017).

Most studies in free-living animals focus on how anthropogenic noise affects behavioral patterns of animals during the waking phase (Siemers and Schaub, 2011; Francis and Barber, 2013; Voellmy et al., 2014; Luo et al., 2015; Shannon et al., 2016; Injaian et al., 2018; Jerem and Mathews, 2020). For example, anthropogenic noise can disrupt communication, impair cognition, interfere with predatory-prey interactions and alter habitat use, with implications for individual fitness, population dynamics and community organization (Brumm and Slabbekoorn, 2005; Patricelli and Blickley, 2006; Jones, 2008; Chan et al., 2010; Kight and Swaddle, 2011; Bracciali et al., 2012; Francis et al., 2012; Nemeth et al., 2013; Rosa and Koper, 2018). However, noise pollution increasingly occurs across the 24-hour period, and thus could also have important effects during the night, including on nocturnal sleep (Francis and Barber, 2013). In fact, anthropogenic noise may be particularly disruptive at night, which has historically been a relatively quiet period. Sleep is a widely conserved characteristic of organismal existence that fulfills critical functions in cellular repair and memory consolidation (Cirelli and Tononi, 2008; Diekelmann and Born, 2010; Rattenborg et al., 2011; Vorst and Born, 2015), and sleep deprivation has been associated with cognitive impairment, pathology and fitness declines in humans and other animals (Cirelli and Tononi, 2008; Gallicchio and Kalesan, 2009; Cappuccio et al., 2011). Thus, disruptive effects of noise on sleep could have non-trivial fitness effects.

Owing in part to limited research effort, a number of significant knowledge gaps remain regarding how anthropogenic noise affects the sleep behavior of animals. First, although considerable research indicates negative effects of artificial light at night and anthropogenic noise on sleep duration and quality in humans (Griefahn and Spreng, 2004; Hume et al., 2012; Halperin, 2014; Cho et al., 2015; Touitou et al., 2017), little is known about how anthropogenic disturbance factors in general, and noise in particular, affects sleep in free-living animals (Kight and Swaddle, 2011; Francis and Barber, 2013; but see Aulsebrook et al., 2018 for a review on artificial light at night). Our research group has demonstrated that exposure to light at night inside nest boxes has pronounced effects on the sleep behavior of a common European songbird, the great tit (*Parus major*) (Raap et al., 2015, 2016, 2017), and Aulsebrook et al. (2020) demonstrated that artificial light at night affects the quantity and quality of sleep in domestic pigeons (*Columba livia*) and wild-caught Australian magpies (*Cracticus tibicen tyrannica*) in captivity. On the other hand, a study on the combined effects of light and noise pollution on sleep in free-living great tits reported no effects of ambient pollution levels (Caorsi et al., 2019). To our knowledge, whether anthropogenic noise modifies the sleep behavior of wild animals has not been experimentally investigated. However, considerable research suggests that anthropogenic noise exposure advances the timing of dawn song, which is indirect evidence that noise may affect sleep behavior (Dominoni et al., 2016; Dorado-Correa et al., 2016; Hennigar et al., 2019).

Second, whether different anthropogenic noise regimes exert distinct effects on behaviors, including sleep, remains poorly understood. A substantial number of human studies, and a few studies in animals, suggest that properties of noise regimes besides average loudness, such as intermittency and frequency-mediated differences in detectability, can affect responses to noise, including changes in sleep (Gill et al., 2015; but see Wysocki et al., 2006; Blickley et al., 2012; Nichols et al., 2015). The human auditory system more easily adjusts to consistent noise than intermittent noise (Westman and Walters, 1981), and intermittent noise can produce more annoyance, distraction and cognitive decline (Szalma and Hancock, 2011; Brink et al., 2019). Research in humans and laboratory animals also suggests that variable noise disrupts sleep more than consistent noise (Öhrström and Rylander, 1982; Öhrström et al., 1988; Carter, 1996; Rabat, 2007). Broadband, consistent noise can even enhance sleep in humans by masking other environmental sounds (Messineo et al., 2017). In free-ranging animals, a few studies have found that variable noise has larger behavioral and physiological effects than consistent noise. For instance, semirandom traffic noise reduced the lek occupancy of greater sage grouse (*Centrocercus urophasianus*) more than consistent noise from a natural gas drilling rig (Blickley et al., 2012), and intermittent, but not consistent, ship noise increased cortisol levels in four fish species (Wysocki et al., 2006). Whether temporally variable noise could also have different effects than consistent noise on the sleep of wild animals has not been tested.

Third, individual-level variation in noise sensitivity is well-documented in humans (Belojević et al., 1997; Dang-Vu et al., 2010; Shepherd et al., 2015), but less so in other animals (Harding et al., 2019). Animal personality traits, which are repeatable and can have a genetic component (Dingemanse et al., 2002; Sih et al., 2004; Réale et al., 2010), may affect stress responsiveness (Koolhaas et al., 1999; Atwell et al., 2012; Baugh et al., 2012) and responses to noise (Harding et al., 2019), including during sleep (Rabat, 2007). For instance, rat personality, measured by activity in a novel environment, was negatively related to noise sensitivity during sleep, reflecting distinct neurochemical and neuroendocrine characteristics of different personality types (Rabat et al., 2005). In humans, personality traits have also been linked to noise sensitivity (Belojević et al., 1997; Shepherd et al., 2015), and sleep disruption by noise (Zaharna and Guilleminault, 2010). Sex and age could also affect sensitivity to noise due to effects on neurochemistry, neuroendocrinology and brain activity. Research suggests that older people are more disrupted by noise during sleep than younger individuals (Wilkinson and Campbell, 1984; Rabat, 2007), but comparable data are lacking for free-living animals. Individual differences in sensitivity to noise are non-trivial, as they have implications for understanding how noise exposure affects population and community dynamics (Radford et al., 2016; Harding et al., 2019). For instance, increased predation risk in noise polluted areas could be mediated through loss of risk-sensitive and vigilant individuals from populations, with implications for population stability (Francis and Barber, 2013).

We used a repeated-measures field experiment to address the knowledge gaps outlined above, using free-living great tits (*Parus major*) as a study species. Our primary objective was to experimentally test for an effect of anthropogenic noise on sleep behavior in free-living animals for the first time. Our second objective was to explore whether different noise regimes had distinct effects on sleep behavior. We specifically explored whether more temporally variable (intermittent and unpredictable in timing), and higher amplitude traffic noise regimes had larger effects on sleep behavior relative to temporally consistent and lower amplitude noise regimes. Our third objective was to elucidate sources of intraspecific variation in responses to noise by assessing individual repeatability and analyzing whether birds differing in exploratory personality type, age, or sex displayed differential sensitivity to noise. We predicted that noise would disrupt sleep more in individuals that less rapidly explored a novel environment (slow explorers) and older individuals. The prediction regarding exploratory personality type was based on past evidence from rats (Rabat et al., 2005), and studies wherein slow versus fast exploring great tits displayed higher stress responsiveness (Baugh et al., 2012) and took longer to resume nestling provisioning when exposed to noise (Naguib et al., 2013). The prediction regarding age was based on the human literature. We did not have specific predictions regarding sex differences in noise sensitivity. We also predicted that individual differences in sleep disruption by noise might be more pronounced in the variable versus consistent noise regime, because more variable noise may have more potential to activate stress responses (e.g. Wysocki et al., 2006), and phenotypic variation can be magnified in the context of environmental stress (Badyaev, 2005). We lacked a sufficient sample size to test a parallel prediction for higher amplitude noise. Finally, our fourth objective was to assess the extent to which sleep behavior would recover within a single night after noise exposure, a phenomenon that has rarely been studied in animals (but see Aulsebrook et al., 2020). We predicted that sleep behavior would rebound after the noise playback ceased, but that disruption would persist to a greater extent for the variable and loud noise treatments, with the rationale being that these noise regimes could elevate stress hormone levels to a greater extent, with enduring effects (Francis and Barber, 2013). However, we reasoned that the converse could also be true, since greater initial disruption of sleep by temporally variable or high amplitude noise might leave more scope for recovery. Our study provides new insights into the effects of anthropogenic noise on sleep in free-living animal. These insights are particularly valuable in our increasingly unquiet world.

2. Materials and methods

2.1. Study site and species: We studied effects of anthropogenic noise on sleep behavior in a suburban nest box population of great tits (on and near University of Antwerp's campus Drie Eiken; Wilrijk, Belgium; 51°9'44"N, 4°24'15"E). This population has been studied since 1997 (e.g. Van Duyse et al., 2000, 2005; Rivera-Gutierrez et al., 2010, 2012; Raap et al., 2016, 2017; Vermeulen et al., 2016) and is monitored throughout the year. Great tits sleep in nest boxes between November and March. For this study, we used 26 nest boxes located in areas with relatively low ambient noise levels (LA_{eq}; average A-weighted sound levels over 3-mins: (mean ± SE): 50.1 ± 0.743 [range: 44.2-61.3]), taken between 1700 and 1830 on two weekdays shortly after the experiment (February 14 and 17, 2020) using a CEL633C1 sound level meter (20-140 dB; weight A; NoiseMeters Inc.). These noise levels are not that low (levels as low as 40 dB have been shown to disrupt animals; see Shannon et al., 2016), which indicates that the birds used in our experiment were not naïve to anthropogenic noise. The moderate ambient noise levels in our study area perhaps deem it less likely that habituation would cause the observed effects of noise exposure on sleep to diminish over time. 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 provided banding licenses.

2.2. Experimental design: We exposed sleeping great tits to noise during 2 time periods: December 16-26, 2019, and February 4-8, 2020. Across the experimental period, sunrise time advanced from 840 to 809 and sunset time progressed from 1634 to 1744, with the largest difference being between the December and February experimental period. We controlled for variation in daylength by including recording period (December versus February) in statistical models (see below). Our sample included 26 individuals (20 males, 6 females, 8 yearlings, 18 older adults; 13 tested each period). All birds were already fitted with passive integrated transponder (PIT) tags, which allowed us to detect birds in nest boxes with a handheld transponder reader (GR-250 RFID Reader, Trovan, Aalten, Netherlands). We selected birds representing a range in exploratory personality type (mean ± SE: 8.65 ± 2.04; range: 0-34), for which all birds had been previously tested (see details provided below). We first surveyed nest boxes using the handheld transponder reader to locate personality-typed individuals. Great tits commonly sleep in the same nest box on consecutive nights (Raap et al., 2015, 2016, 2017). Beginning the night after the initial survey, we recorded sleep behavior for three nights using infrared cameras (Pakatak PAK-MIR5, Essex, UK) installed under the nest box lid (Raap et al., 2015, 2016). Cameras recorded both video and audio, which allowed us to confirm that the noise playback was functioning, and to determine the exact time at which the playback turned on and off. First, we recorded baseline sleep behavior in absence of noise (Fig. 1; Raap et al., 2015, 2016, 2017). The following night, we recorded sleep in the presence of either consistent or variable traffic noise at an amplitude of 70 dB. The third night, we recorded sleep behavior in the presence of the other noise regime (Fig 1). The order of the noise treatments was determined in a semirandom, balanced fashion. We always performed the control treatment on the first night to avoid potential carryover effects of the noise treatments on sleep behavior the following night. We have also employed this methodology in past studies on the effect of artificial light at night on sleep behavior (Raap et al., 2015, 2016). If a bird was not in the nest box (N = 2), or the camera failed (N = 6), we repeated the trial the following night. During February, we recorded sleep behavior on a fourth night, using higher amplitude noise (80 versus 70 dB) (*N* =12; half exposed to each noise regime).

We installed cameras in nest boxes between 1200 and 1500, on the day preceding the night of the experiment, when they commenced recording. We removed cameras around 930 am at the earliest to ensure they recorded the bird's exit. Each night, we visited nest boxes shortly after sunset and used the transponder reader to confirm that the target bird was in the nest box. For noise treatments, we also started the noise recording at this time (range in start times: 1649 to 1847 for the entire experiment; 1649 to 1751 in December; 1733 to 1847 in February).

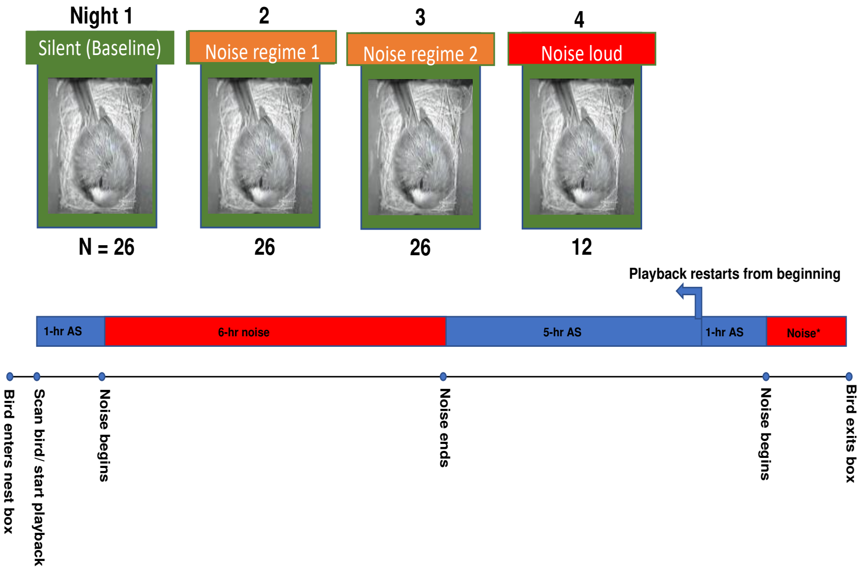

Figure 1. The experimental design (top) and timeframe of the playback showing periods of noise and ambient sound (AS)(below). *The morning noise exposure varied in length since birds exited the nest box at variable times after the noise restarted. Photo credit: Thomas Raap.

2.3. Noise playback: We used Audacity 2.3.1 to create traffic noise playbacks. Playbacks began with a 1-hr block of silence, such that the noise started 1-hr after we visited the nest box (Fig. 1). This allowed time for birds to resume sleep behavior after potential disturbance by the researcher before the noise commenced. Noise used to create playbacks was obtained with a Olympus LS10 audio recorder using the internal microphone (20 Hz to 21 kHz frequency response). Playbacks were recorded in PCM format (16-bit amplitude encoding; 44.1 kHz sampling frequency). Autogain was not used and manual gain remained constant throughout each recording. We created three recordings of consistent noise using different 5-min recordings of noise obtained from a local freeway (E19; 5 lanes in each direction) during steady traffic flow at a distance of ~50-100 m (Fig. 2 depicts recorded freeway noise; see Supplementary Fig. S1 for a comparison of playback versus recording). We repeatedly pasted the 5-min recordings into Audacity, for a duration of 6-hrs. Three temporally variable noise playbacks were created using 36 clips of semirandom traffic noise recorded from local 2 lane roads (traffic flow of ~2 cars per minute) and silence. We randomly shuffled the 36 recordings repeatedly, in different ways for the three playbacks, for a duration of 6-hrs (Fig. 3). We removed loud amplitude noise events using Audacity's click removal function (threshold of 154; max spike width of 20). We did not use a fade function when compiling the variable noise playback, such that this playback contains rapid onset and offset of sound that is not characteristic of traffic noise. This feature of the variable noise treatment increased our expectation of observing a more pronounced disruption of sleep in the variable relative to consistent noise. After the 6-hrs of noise, we inserted 5-hrs of silence, which combined with the 1-hr of silence at the beginning (the playback started over) to create 6-hrs of silence in which we assessed the extent to which sleep behavior returned to normal under ambient sound levels after the noise playback ceased (Fig. 1). The noise resumed in the morning after the 6-hrs of silence, allowing us to assess the effect of morning traffic noise on exit time (Fig. 1). Sound files (16-bit amplitude encoding; 44.1 kHz sampling frequency) were saved in MP3 format in Audacity (170-210 kbps).

We used a MIFA F10 bluetooth speaker with a 32 GB microSD card inserted to playback noise. The speaker was secured to the nest box latch, facing against the side of the nest box. We calibrated consistent noise playbacks to 70 dB LA_{eq} (80 dB for higher amplitude treatment) prior to placement in the field, using a sound level meter held inside an empty nest box at the level of the sleeping bird for a duration of 2 min. For variable noise recordings, calibration occurred during a period of noise and LA_{max} (maximum A-weighted sound level within the time period) was used instead of LA_{eq} (Blickley et al., 2012). We chose to design the playback in this way to minimize the difference in maximum noise levels between the treatments, which was the case since there was low variability in sound levels on the consistent noise playback. However, as a result, the variable noise treatment had lower average sound levels than the consistent noise treatment. Thus, we tradeoff consistency in maximum noise levels against consistency in average noise levels. LA_{max} for the 70 dB consistent noise treatment averaged 71.2 dB and LA_{eq} for the 70 dB variable noise treatment averaged 65 dB, when assessed three times over 10-mins.

2.4. Analyzing sleep behavior: We extracted metrics of sleep behavior which have been used in past studies on great tits: average sleeping bout length, total sleep duration, proportion of time inactive (asleep), sleep bout frequency, and exit time (Raap et al., 2015, 2016, 2017). Although these behaviors are all significantly correlated (Supplementary Table S1), we follow past work in assessing independent effects on these variables (Raap et al., 2015, 2016, 2017), rather than eliminating some variables or combining the variables using a principal components analysis. This facilitates comparisons to past studies, and also allows us to more easily assess not only whether sleep behavior changes in response to noise exposure, but also how it changes. In two cases, the camera stopped recording before the bird exited, precluding calculation of exit time, total sleep duration and sleep proportion. Sleeping great tits adopt a characteristic posture, with the head tucked under the scapular (Fig 1.; Raap et al., 2015, 2016, 2017). The transition between the behavioral sleeping and waking state is distinct and has been well described by previous studies (Raap et al., 2015, 2016, 2017). We analyzed videos using the VLC media player (version 3.0.8), in which it was possible to precisely record the time at which the transitions between the sleeping and active state occurred.

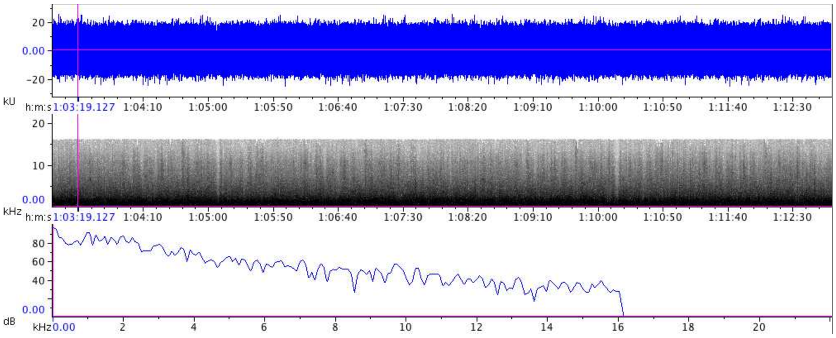

Figure 2. Oscillogram, spectrogram and power spectrum of an excerpt from the temporally consistent traffic noise recording. Created in Raven Pro (Cornell Lab of Ornithology) with a Hann sampling window, window size of 527 samples, and 3 dB filter bandwidth of 120 Hz. The power spectrum is displayed for the time indicated by the vertical line (1:03:19).

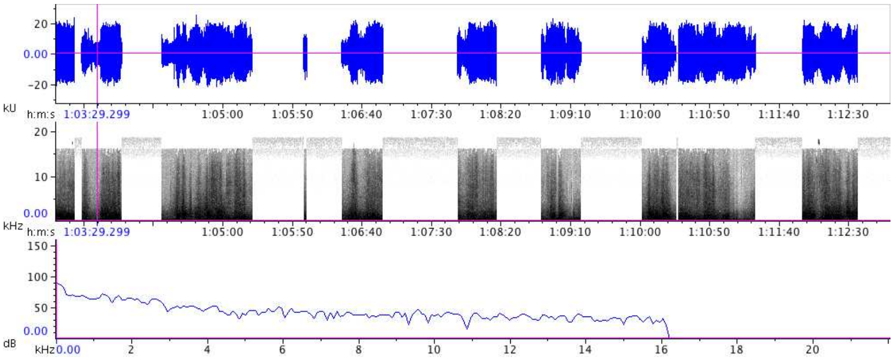

Figure 3. Oscillogram, spectrogram and power spectrum of an excerpt from the temporally variable traffic noise recording. Created in Raven Pro (Cornell Lab of Ornithology) with a Hann sampling window, window size of 527 samples, and 3 dB filter bandwidth of 120 Hz. The power spectrum is displayed for the time indicated by the vertical line (1:03:29).

2.5. Novel environment exploration behavior: All birds were tested for exploration behavior prior to the experiment (early December 2019, or November-February of a previous year). In great tits, exploratory personality is repeatable within multiple populations (Verbeek et al., 1994; Dingemanse et al., 2012; Stuber et al., 2013; Thys et al., 2017), has a genetic component (Dingemanse et al., 2002; Quinn et al., 2009; Nicolaus et al., 2012), and is linked to physiological (glucocorticoid stress response; Baugh et al., 2012) and behavioral (neophobia; Grunst et al., 2019) metrics of stress responsiveness. Although highly repeatable, exploration score increases with repeated testing (Dingemanse et al., 2012). Therefore, we used the score from the first time each bird was tested in analyses. The novel environment exploration test is routinely performed by our research group and procedures are described in detail elsewhere (Thys et al., 2017; Grunst et al., 2018). In brief, birds were captured in nest boxes while roosting overnight and removed to captivity for one night. The following morning, each bird was independently tested for exploration behavior by counting the number of movements performed for the first 2-min following release into the novel environment room.

2.6. Statistical analysis: We performed statistical analyzes in R 3.6.1 (R Core Team, 2019). First, to assess the effect of the consistent and variable noise treatments on sleep behaviors, we constructed separate linear mixed effects models (LMMs; R package lme4; Bates et al., 2015) predicting each of the sleep behaviors (sleep duration, proportion of time asleep, average sleep bout length, and frequency of sleep bouts per hour (log-transformed), exit time) calculated across the entire night. These models included the main effects and three two-way interactions between treatment (baseline, consistent noise, variable noise), exploration score, age and sex. We entered recording session (December or February) and recording order (consistent noise first or second) as covariates, and individual as a random effect. We also tested whether individual differences in sleep disruption by noise were more pronounced in the variable, versus consistent, noise regime by calculating the difference between sleep behaviors measured under baseline conditions and in each noise treatment and then using a paired sample variance test to assess homogeneity of variance.

We constructed a second set of models to examine whether higher amplitude noise had a more pronounced effect on each of the sleep behaviors. Since the high amplitude treatment was only conducted in February, we only used data from the second recording session in this analysis, and hence recording session was not included as a covariate in these models. We entered the main effects and interaction between noise type (consistent, variable) and amplitude (70 or 80 dB) and individual as a random effect. We did not include additional interactions since we had a lower sample size for this analysis.

We next assessed whether the temporal variability of the noise exposure or amplitude affected how sleep behavior changed during the period of noise versus ambient sound as the night progressed. To this end, we constructed a third and fourth set of models. The third set of models predicted each sleep behavior (excluding exit time) from the main effects and interaction between treatment (baseline, consistent noise, variable noise) and period (noise versus ambient sound; for baseline recordings, periods corresponded in time to when the periods would have occurred for a noise treatment). The fourth set of models consisted of the main effects and two-way interaction between amplitude (70 or 80 dB) and period (noise, ambient sound). We did not include noise type in the fourth set of models because, with the exception of exit time, the effect of noise type was non-significant in the second set of models. Since sleep duration and proportion are equivalent for the fixed-duration periods of noise and ambient sound, we only performed the third and fourth set of models for sleep proportion, and not duration. These analyses used the first 6-hr period of noise and following 6-hr period of ambient sound levels. We did not analyze effects of noise on behaviors measured during the morning period of noise, since individuals left the nest box at variable times after the morning noise commenced. We only included covariates that were significant ($\alpha = 0.05$) in the first and second set of models, and again included individual as a random effect.

We performed repeatability analyses using R package rptR (Stoffel et al., 2017). To gain insight into individual consistency and variation in sleep, we calculated repeatability across the entire recording period and across treatment types, while including treatment and recording session in the model. To gain insight into whether the response to noise was repeatable, we calculated the difference in sleep behaviors between the baseline and noise treatments and repeated the analysis.

We standardized exploration score (the only continuous predictor variable) to a mean of zero and a standard deviation of 1 to facilitate interpretation of beta coefficients when including interactions in models (Schielzeth, 2010), and estimated degrees of freedom using Satterthwaite approximations (R package lmerTest; Kuznetsova et al., 2016). We also applied a Helmert contrast for models involving interactions, such that beta coefficients for main effects are reported across levels of discrete predictor variables (age, sex). We performed posthoc comparisons via the Tukey method (R package emmeans; Lenth, 2019). For significant effects of noise exposure treatment and noise amplitude, we report p-values both before and after controlling for the false discovery rate (FDR) using the Benjamini-Hochberg method (p.adjust function in R; Benjamini and Hochberg, 1995). Models were reduced using backwards, step-wise elimination by first removing non-significant interaction terms ($\alpha = 0.05$). Model diagnostics were performed using R package DHARMa (Hartig, 2019), and all model assumptions were met.

3. Results

3.1. Variable versus consistent traffic noise: Relative to baseline levels, great tits exposed to traffic noise slept for a lesser amount and proportion of time, had shorter sleep bouts, and exited the nest box earlier in the morning, but did not differ in sleep bout frequency (Fig. 4a-e; Table 1). Variable and consistent noise had similar effects on sleep behaviors, but the effect on sleep proportion and sleep bout length was only significantly different from baseline in the case of variable, and not consistent noise (Fig. 4b,c; Table 1; the effect of variable noise on sleep bout length is only marginally significant after correction for FDR). None of the sleep behaviors differed between the noise treatments (Fig. 4a-e; Table 1).

Age and treatment interacted to predict the amount of time great tits spent asleep, with variable noise reducing sleep duration in older, but not first-year birds (Table 1). Consistent noise had a similar effect on sleep duration in the two age classes, but this effect was only significantly different from baseline in older adults, and not yearlings (Table 1). No other interaction between treatment and individual traits predicted any sleep behavior, and exploratory personality type was also non-significant in all cases (*P* >

0.05). Independent of noise exposure, males had more frequent sleep bouts than females and yearlings tended to have less frequent sleep bouts than older birds. Great tits slept less and exited the nest box earlier in February than in December (Table 1), but sleep proportion ($\beta = 0.012 \pm 0.011$, $t_{23} = 1.16$, $P = 0.256$), sleep bout length ($\beta = -0.001 \pm 0.017$, $t_{24} = -0.078$, $P = 0.939$), and sleep bout frequency ($\beta = -0.346 \pm 0.888$, $t_{24} = -0.390$, $P = 0.700$) did not differ between the recording sessions. Recording order was not related to any sleep behavior ($P > 0.05$).

Variance in individual responses to noise treatments (measured as change in sleep behaviors between baseline conditions and noise exposure) did not differ between the variable and consistent noise treatment for any sleep behavior ($P > 0.05$ in all cases).

Table 1. Results from linear mixed effects models predicting sleep behaviors across the entire night from noise exposure treatment (baseline (BL), consistent noise (CN), variable noise (VN); reference level listed first) and covariates (Age; A=Adult, Y = Yearling; Recording session; F = February, D = December; Sex; M = Male, F = Female; reference level listed first). N = 26 individuals; 76 observations. P_{adjust} = P values corrected for FDR using the Benjamini-Hochberg method.

	β±SE	**T**	**df**	**P**	**P_{adjust}**	**$F_{2,\sim49}$**	**P**	**P_{adjust}**
(a) Sleep duration (hr)								
Treatment BL-CN	0.411 ± 0.114	4.24	46.0-	0.002	0.010			
Treatment BL-VN	0.401 ± 0.116	3.48	46.3	0.003	0.010			
Treatment CN-VN	-0.009 ± 0.116	-0.086	46.3	0.995		8.43	<0.001	<0.001
Age A-Y	0.071 ± 0.113	0.626	46.0	0.534				
Recording session F-D	-1.15 ± 0.175	-6.52	23.1	<0.001				
Age × Treatment BL-CN	-0.0005 ± 0.114	-0.004	46.1	0.997				
Age × Treatment BL-VN	0.329 ± 0.116	2.85	46.5	0.006		5.35	0.008	
Contrasts within interaction								
Age A BL-CN	0.411 ± 0.139	2.96	46.8	0.016				
Age A BL-VN	0.731 ± 0.145	5.03	46.0	<0.001				
Age A CN-VN	0.319 ± 0.140	2.82	46.8	0.068				
Age Y BL-CN	0.412 ± 0.184	2.24	46.0	0.075				
Age Y BL-VN	0.073 ± 0.184	0.874	46.0	0.918				
Age Y CN-VN	-0.339 ± 0.184	-1.84	46.0	0.167				
(b) Sleep proportion								
BL-CN	0.016 ± 0.007	2.16	49.0	0.088	0.146			
BL-VN	0.026 ± 0.007	3.34	49.3	0.004	0.010			
CN-VN	0.009 ± 0.007	1.23	49.3	0.436		5.77	0.005	0.008
(c) Sleep bout length (hr)								
BL-CN	0.015 ± 0.009	1.54	49.0	0.284	0.355			
BL-VN	0.024 ± 0.009	2.45	49.3	0.047	0.058			
CN-VN	0.009 ± 0.009	0.933	49.3	0.622		3.07	0.055	0.068
(d) Sleep bout freq/hr								
BL-CN	-0.106 ± 0.077	-1.36	48.0	0.370	0.370			

BL-VN	-0.132 ± 0.079	-1.65	48.8	0.239	0.239			
CN-VN	-0.026 ± 0.079	-0.326	48.8	0.946		1.57	0.218	0.218
Sex M-F	0.333 ± 0.133	2.51	23.1	0.020				
Age A-Y	0.238 ± 0.116	2.05	22.5	0.052				
(e) Exit time (hr)								
BL-CN	0.082 ± 0.025	3.29	48.0	0.005	0.012			
BL-VN	0.076 ± 0.025	2.96	48.5	0.012	0.020			
CN-VN	-0.005 ± 0.025	-0.232	48.5	0.971		6.62	0.003	0.007
Recording session F-D	-0.614 ± 0.044	-14.1	24.1	<0.001				

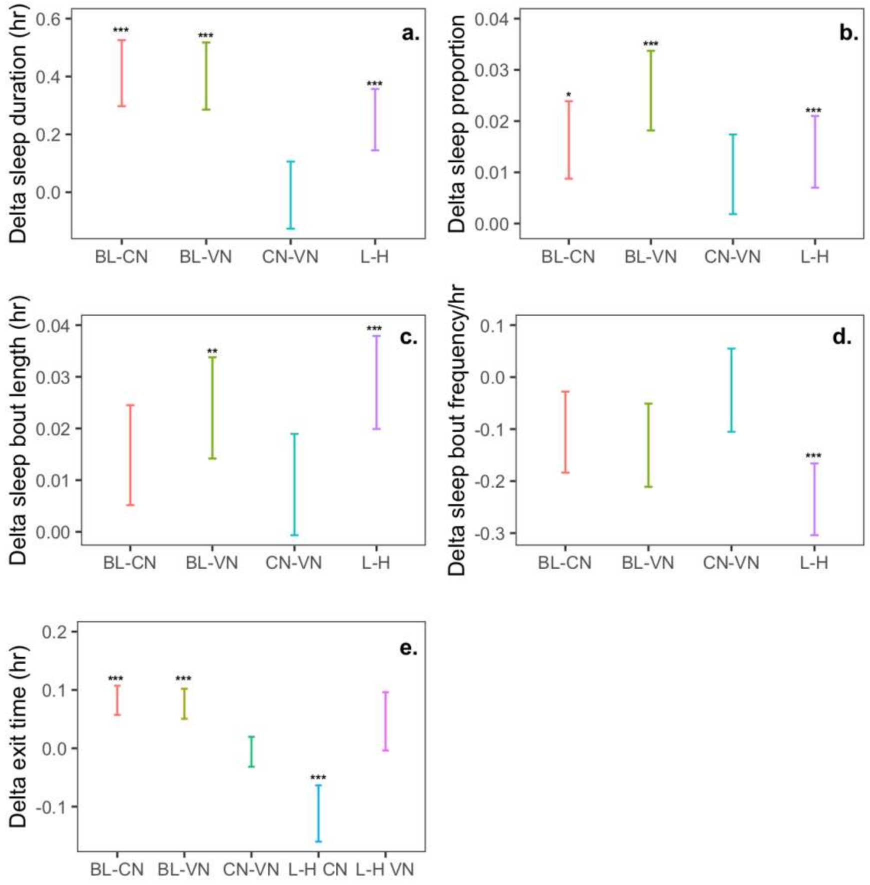

Figure 4. Differences (effect sizes) in sleep behaviors between the baseline and consistent noise (BL-CN), baseline and variable noise (BL-VN), two noise treatments (CN-VN), and the low (70 dB) and high (80 dB) amplitude levels (L-H). For exit time, the L-H comparison is shown within the CN and VN treatments, because there was an interaction between amplitude and noise type. Estimates are from linear mixed effect models with individual as a random effect. ***=significant (<0.05) after correction for FDR,

**=marginally significant after correction for FDR (<0.10), *=marginally significant before correction for FDR. Bars denote standard error.

3.2. Noise amplitude: Relative to when exposed to 70 dB noise, great tits exposed to 80 dB noise slept for a lesser amount (lower sleep duration) and proportion of time, and had shorter more frequent sleep bouts (Fig. 4a-d; Table 2). The interactions between noise type (variable, consistent) and amplitude were non-significant for sleep duration, sleep proportion, sleep bout length and sleep bout frequency ($P >$ 0.10). However, noise type (variable, consistent) and amplitude interacted to predict the effect of noise on exit time (Table 2). Birds exposed to 80 dB consistent noise stayed in the nest box longer than birds exposed to 70 dB consistent noise or 80 dB variable noise. There was no difference between the exit time of birds exposed to 70 or 80 dB variable noise or the two noise types at 70 dB (Fig. 4e; Table 2).

Table 2. Results from linear mixed effects models predicting sleep behaviors across the entire night from noise type (consistent noise (CN), variable noise (VN)) and noise amplitude (L(low) = 70 dB; H(high) = 80 dB; L as reference level). N =13 individuals; 36 observations. P_{adjust} = P values corrected for FDR using the Benjamini-Hochberg method.

	β±SE	**T**	**df**	**P**	**P_{adjust}**
(a) Sleep duration (hr)					
Amplitude L-H	0.251 ± 0.106	2.36	22.7	0.027	0.033
(b) Sleep proportion					
Amplitude L-H	0.015 ± 0.007	2.10	22.4	0.047	0.047
(c) Sleep bout length (hr)					
Amplitude L-H	0.028 ± 0.009	3.16	23.4	0.004	0.010
(d) Sleep bout freq/hr					
Amplitude L-H	-0.235 ± 0.069	-3.37	22.5	0.002	0.010
(e) Exit time					
Amplitude L-H	-0.055 ± 0.023	-2.35	23.2	0.027	0.033
Treatment CN-VN	0.082 ± 0.036	2.31	25.2	0.029	
Amplitude × Noise type CN-VN	0.079 ± 0.036	2.22	25.3	0.035	
Contrasts within interaction					
CN L-H	-0.112 ± 0.048	2.32	22.9	0.029	
VN L-H	0.046 ± 0.050	0.928	23.2	0.363	
H CN-VN	0.161 ± 0.062	2.58	26.7	0.015	
L CN-VN	0.003 ± 0.038	0.083	20.7	0.934	

3.3. Sleep behavior in the periods of noise and ambient sound: Sleep proportion and sleep bout length increased, and sleep bout frequency decreased, during the 6-hrs of ambient sound levels following the first 6-hr period of noise exposure. However, the interactions between treatment and period were non-significant in all cases ($P > 0.20$), indicating that the sleep behaviors changed similarly between the period of noise and ambient sound during the baseline treatment and during the noise exposures. Treatment significantly predicted sleep proportion and sleep bout length, with both being significantly lower than under baseline conditions in the variable, but not consistent, noise treatment (Table 3). Sleep bout frequency tended to be higher relative to baseline conditions during the variable, but not consistent, noise (Table 3). None of the sleep behaviors differed between the two noise exposure treatments (Table 3).

Sleep proportion was lower and sleep bout frequency higher in the high (80 dB) amplitude noise and during the period of ambient sound (Table 4), but there was no interaction between noise amplitude and period in predicting sleep proportion or sleep bout frequency ($\beta = -0.017 \pm 0.019$, $t_{59} = -0.870$, $P = 0.388$; $\beta = -0.216 \pm 0.148$, $t_{59} = -1.47$, $P = 0.148$), indicating that sleep proportion and sleep bout frequency changed similarly between the periods of noise and ambient sound in both the 70 and 80 dB noise exposures. On the other hand, there was a significant interaction between amplitude and period in predicting sleep bout length (Table 4). This interaction reflected the fact that sleep bout length was only significantly greater in the low relative to high amplitude levels during the period of ambient sound, and not during the period of noise (Table 4). Although sleep bout length increased in the period of ambient sound in both amplitude levels, the beta estimate was ~2x larger for the low relative to high amplitude level (Table 4).

Table 3. Results from linear mixed effects models predicting sleep behaviors from treatment (baseline (BL), consistent noise (CN), variable noise (VN); reference level listed first) and period (noise (N), ambient sound levels (AS); N as reference level). N = 26 individuals, 155 observations. P_{adjust} = P values corrected for FDR using the Benjamini-Hochberg method.

	β±SE	**$T_{\sim126}$**	**P**	**P_{adjust}**	**$F_{2,\sim49}$**	**P**	**P_{adjust}**
(b) Sleep proportion							
BL-CN	0.007 ± 0.008	0.855	0.669				
BL-VN	0.020 ± 0.008	2.49	0.037	0.055			
CN-VN	0.013 ± 0.008	1.64	0.233		3.20	0.044	0.066
Period N-AS	-0.034 ± 0.007	-5.08	<0.001				
(c) Sleep bout length (hr)							
BL-CN	0.017 ± 0.012	1.32	0.385				

BL-VN	0.040 ± 0.013	3.14	0.005	0.015			
CN-VN	0.023 ± 0.012	1.84	0.161		4.98	0.008	0.024
Period N-AS	-0.094 ± 0.010	-9.09	<0.001				
(d) Sleep bout freq/hr							
BL-CN	-0.071 ± 0.073	-0.966	0.599				
BL-VN	-0.158 ± 0.074	-2.13	0.088	0.088			
CN-VN	-0.087 ± 0.074	-1.16	0.475		2.26	0.107	0.107
Period N-AS	0.555 ± 0.060	9.11	<0.001				

Table 4. Results from linear mixed effects models predicting sleep from noise amplitude (L(low) = 70 dB; H(high) = 80 dB; L as reference level) and period (noise (N), ambient sound (AS); N as reference level). N =13 individuals, 74 observations. P_{adjust} = P values corrected for FDR using the Benjamini-Hochberg method.

	β±SE	$T_{\sim 58}$	P	P_{adjust}
(a) Sleep proportion				
Amplitude L-H	0.020 ± 0.010	2.05	0.045	0.045
Period N-AS	-0.044 ± 0.009	-4.78	<0.001	
(c) Sleep bout length (hr)				
Amplitude L-H	0.023 ± 0.005	4.11	<0.001	<0.001
Period N-AS	-0.047 ± 0.005	8.61	<0.001	
Amplitude × Period N-AS	-0.015 ± 0.005	2.82	0.006	
Contrasts within interaction				
Period N L-H	0.015 ± 0.015	0.941	0.351	
Period AS L-H	0.077 ± 0.016	4.91	<0.001	
Amplitude L N-AS	-0.126 ± 0.13	-10.0	<0.001	
Amplitude H N-AS	-0.064 ± 0.13	-3.52	<0.001	
(d) Sleep bout freq/hr				
Amplitude L-H	-0.309 ± 0.075	-4.11	<0.001	<0.001
Period N-AS	-0.710 ± 0.069	-10.2	<0.001	

3.3. ***Individual variation and repeatability***: Sleep behaviors measured across treatments, and the change in sleep behaviors between baseline conditions and the noise exposure treatments, were all significantly repeatable (*P*< 0.001; Table 5). See Table S2 for mean ± SE and range of sleep behaviors and Fig. S3 for reaction norms depicting how sleep behaviors changed between baseline conditions and the noise treatments for each individual.

Table 5. Repeatability estimates ± SE [95% CI] for sleep behaviors measured across treatments and change in sleep behaviors in the noise exposure treatments relative to baseline levels.

	Overall behavior	Change in behavior
Sleep duration (hr)	0.454 ± 0.071 [0.230, 0.679]	0.502 ± 0.132 [0.249, 0.77]
Sleep proportion	0.424 ± 0.117 [0.198,0.652]	0.554 ± 0.121 [0.313, 0.773]
Sleep bout length (hr)	0.373 ± 0.119 [0.144, 0.609]	0.541 ± 0.123 [0.292, 0.78]
Sleep bout frequency/hr	0.537 ± 0.102 [0.344, 0.732]	0.622 ± 0.112 [0.382, 0.825]
Exit time (hr)	0.481 ± 0.114 [0.253, 0.703]	0.570 ± 0.117 [0.341, 0.794]

4. Discussion Traffic noise exposure had pronounced negative effects on the sleep behavior of free-living great tits, with sleep duration and proportion being reduced, and the length of sleep bouts shortened. In addition, great tits exposed to noise left the nest box earlier in the morning, which could help explain past observations of earlier outset of dawn song in noisy areas and with experimental noise exposure (Dominoni et al., 2016; Dorado-Correa et al., 2016; Hennigar et al., 2019). Thus, traffic noise can significantly interfere with sleep in a wild animal, which may have repercussions for behavior during the waking phase, maintenance of body condition, and fitness. Evidence linking sleep deprivation to deleterious downstream effects in wild animals is largely lacking. However, sleep deprivation related to exposure to light at night elevated the probability of malarial infection in great tits, suggesting potential impacts of sleep debt on disease dynamics (Ouyang et al., 2017). Furthermore, human and laboratory studies on sleep disruption or deprivation document wide-spread deleterious effects of sleep debt, including impaired cognition, reduced performance and compromised health status (Cirelli and Tononi, 2008). Due to the pervasive quality of anthropogenic noise, effects of nighttime noise pollution may be present across urban-rural interfaces, and even within protected areas, such as national parks and reserves (Barber et al., 2011; Buxton et al., 2017; Francis et al., 2017). Thus, there is an urgent need for studies to further elucidate effects of nighttime noise exposure in free-ranging animals, and to characterize the mechanistic pathways involved.

We hypothesized that temporally variable traffic noise would have larger deleterious effects on sleep behavior than consistent traffic noise. This hypothesis was based on evidence from humans and laboratory animals suggesting greater effects of intermittent noise on sleep (Öhrström and Rylander, 1982; Öhrström et al., 1988; Carter, 1996; Rabat, 2007), and studies in free-ranging animals documenting larger behavioral or physiological effects of intermittent, or unpredictable noise (Wysocki et al., 2006; Blickley et al., 2012). There was some support for this hypothesis, in that effects of traffic noise on sleep proportion and sleep bout length were only significantly different from baseline in the variable noise treatment. In addition, in the analyses examining effects of treatment on sleep behaviors within the periods of noise and ambient sound, the variable, but not consistent, noise treatment significantly reduced sleep proportion and bout length and increased bout frequency relative to baseline levels. However, there was not a significant difference between any aspect of sleep behavior during the two noise treatments. In addition, we also found no evidence that exposure to temporally variable noise induced more variation in individual responses than exposure to consistent noise. Thus, more research is needed to evaluate the possibility that temporally variable noise is more disruptive to sleep and other behaviors than consistent noise (see further discussion below).

There was a clear effect of noise amplitude on sleep behavior. Relative to 70 dB amplitude noise, great tits exposed to 80 dB amplitude noise had lower sleep duration and proportion, and displayed more fragmented sleep consisting of shorter, more frequent sleep bouts. We also found an interaction between noise type and amplitude in predicting exit time, with birds exposed to 80 dB consistent noise staying in the nest box longer than birds exposed to 70 dB consistent noise, but amplitude having no effect within the variable noise treatment. This result is in the opposite direction to the overall effect of noise exposure on exit time, suggesting involvement of different causal pathways. The overall advance in exit time could reflect an effect on wakefulness, whereas higher amplitude consistent noise could have deemed birds hesitant to leave the nest box. For the analysis comparing the 70 and 80 dB amplitude noise level, we only used data from the February recording session. Thus, hormonal differences between the recording sessions (for instance, associated with increasing daylength) are not implicated in the reported results.

We also found evidence for intraspecific differences in sensitivity to noise. Specifically, variable traffic noise reduced total sleep duration in older birds, but not in first-year breeders, and there was a similar, but non-significant, pattern for consistent noise. These results are consistent with research in humans suggesting that older people are more vulnerable to sleep disruption by noise (Wilkinson and Campbell, 1984; Rabat, 2007). Nevertheless, we view this result with some caution, given our larger sample size of older adults relative to yearlings. We found no other differences in how noise exposure affected the sleep of individuals differing in age, sex or exploratory personality, suggesting that sleep disruption was largely independent of these intraspecific traits. Earlier, we also found that exploratory personality was unrelated to the effect of artificial light at night on sleep behavior in great tits (Raap et al., 2018b), suggesting that exploratory personality may have little effect on sensitivity of individuals to sleep disturbance. However, especially for sex (*N* = 6 females), we had somewhat limited power to test these relationships. Thus, we urge further research to investigate whether these, or other, intraspecific traits modify the extent to which noise disrupts sleep behavior.

Indeed, we found considerable variability and high individual repeatability in sleep behaviors calculated across treatments and in change in sleep behaviors between baseline and noise exposure treatments. These results indicate that consistent differences in individual sleep behavior (independent of noise exposure) and consistent individual responses to noise (independent of the level of temporal variability) exist. Thus, despite lack of strong associations between the individual-level traits measured and sleep disruption, the sleep behavior of some individuals was consistently more insensitive to noise exposure, whereas others were more disrupted by noise. A past study on the sleep behavior of great tits also reported relatively high individual repeatability (Stuber et al., 2014). However, another study by the same research group found much lower repeatability when there was a larger temporal interval between recordings, prompting the authors to conclude that there was limited scope for a between-individual 'sleep syndrome' (Stuber et al., 2016). The high individual repeatability in sleep behaviors and sensitivity to noise detected in our study could reflect variation in state variables (e.g. body condition, need for sleep) that are stable over the short term. More research would be needed to determine whether these differences persist over a longer time frame.

We also assessed how noise treatment (baseline, consistent noise, variable noise) and amplitude (70 versus 80 dB) affected the fashion in which the sleep behaviors changed between the initial 6-hr period of noise exposure and the following 6-hrs at ambient sound levels. From this analysis it was evident that sleep increased later in the night (as indicated by higher sleep proportion and bout length and decreased frequency of sleep bouts) across treatment types, regardless of whether birds were exposed to noise. Given that the sleep behavior of great tits does change across the night independent of noise exposure, it could be informative to evaluate the effect of shifting the timing of noise exposure across the nocturnal period. The lack of an interaction between treatment and period in predicting sleep variables suggests that sleep similarly increased across the night in the baseline versus noise exposures, and that sleep did not recover during the period of ambient sound, but instead remained compromised. Similar to these results, although for a different disturbance factor, Aulsebrook et al. (2020) found that rapid eye movement (REM) sleep in Australian magpies remained compromised in the 4-hrs following 4-hrs of exposure to white light at night. There was also no interaction between amplitude and period in predicting sleep proportion or sleep bout frequency, suggesting that amplitude level did not modify the extent to which these behaviors changed between the period of noise and ambient sound. On the other hand, amplitude and period interacted to predict sleep bout length, with sleep bout length being significantly longer in the low (70 dB) amplitude as compared to high (80 dB) amplitude, but only during the period of ambient sound. This interaction could reflect differential recovery of sleep bout length contingent upon amplitude level, since the increase in sleep bout length during the period of ambient sound was ~2x greater in the case of the 70 dB noise treatment.

Interestingly, we only observed two occasions in which great tits did not sleep in the same nest box the night following the first noise exposure treatment, despite the deleterious impacts of noise on sleep. This may have been because the noise only started after the birds had already made the decision to enter the nest box, but could also reflect limited behavioral plasticity. If birds are unwilling to shift the location in which they are sleeping when confronted with noise disturbance, perhaps due to familiarity, or are unable to find another suitable and unoccupied sleeping location (e.g. there are a limited number of nest boxes), this could elevate negative effects arising from sleep deprivation.

Past research on the effect of anthropogenic noise on avian sleep is minimal. However, similar to our study, a recent electroencephalographic study on captive Australian magpies found pronounced effects of experimental noise exposure on sleep, with sleep bouts being shorter and more fragmented (Connelly et al., 2020). On the other hand, in contrast to our study, the only other study that has investigated effects of noise on sleep in great tits found no effects (Caorsi et al., 2019). To our knowledge, this is also the only other study on the effects of anthropogenic noise on sleep in free-living birds. This study was correlational, had a low sample size, and consequently lacked power. Nevertheless, the study suggests that anthropogenic noise exposure may have little effect on sleeping great tits at levels commonly experienced by natural populations.

Indeed, when interpreting our results, it is important to note that the noise levels that we used for our experimental manipulations were relatively high. Studies on terrestrial wildlife have documented effects of anthropogenic noise on behavior at levels as low as 40 dB, which is orders of magnitude lower than those used in our study (Shannon et al., 2016). In fact, the ambient noise levels in our population exceed the 40 dB threshold at which biological effects have been observed, although the threshold for effects may also vary between populations differentially exposed to noise. To further put our experimental noise levels in context, average nighttime LA_{eq} and LA_{max} levels measured outside nest boxes near the highway in our population were 58.7 ± 2.43 dB (A) (range: 55.9-65.6 dB (A)) and 69.6 ± 3.66 dB (A) (range: 64.6-78.7 dB (A)), respectively (see Grunst et al. 2020 for details). Therefore, our "low" (70 dB) amplitude treatment reflects extreme values of LA_{eq} and mean values of LA_{max} in our population during the night and our "high" (80 dB) amplitude treatment reflects the upper limit of LA_{max} observed. In the other study on sleep behavior of free-living great tits, which was also conducted in an urban area, ambient noise levels ranged from 36 to 76 dB (A) (mean 56.9 dB (A)) (Caorsi et al., 2019), again suggesting that our experimental treatments represent the upper margins of noise exposure. Nevertheless, it is conceivable that birds experience these sound levels, especially given that some individuals will not be sleeping inside nest boxes or in cavities, which are limited in number. In addition, there is habitat closer to the freeway than the nest boxes at which these sound levels were measured. Although avoidance behavior could occur, habitat saturation might force some birds to occupy poor quality habitat along the margin of the freeway. We do not believe that the sound levels used in our experiment were so high as to guarantee a response, since some individuals were actually quite unresponsive to the playback (see Supplementary Fig. S3). However, further work, both in quieter ambient noise environments and using lower amplitude playback, is needed to fully elucidate the extent to which effects of anthropogenic noise on sleep occur in free-ranging animal populations.

Another consideration with respect to our playback design is that we calibrated sound levels for the consistent noise treatment to LA_{eq}, but used LA_{max} when calibrating the variable noise treatment (see also Blickley et al., 2012). We chose to design the playback in this way so that the maximum noise levels would differ minimally between the two treatments, which was the case since variance in sound levels was relatively low for the consistent noise treatment. However, as a result, and given the periods of silence within the variable noise treatment, the average sound levels (LA_{eq}) experienced were lower for the variable noise treatment, which could have mitigated the potentially more deleterious effects of temporal variability and explain why we did not see pronounced differences between the two types of noise regimes. Indeed, average amplitude and temporal pattern are both likely important to the biological response to noise, and temporal patterning may have dominated the effect on sleep for the variable noise condition, whereas average amplitude may have dominated for the consistent noise treatment. Importantly, when considering traffic noise regimes, more variable patterns of noise production (e.g. produced by smaller roads versus freeways) are usually associated with lower LA_{eq} due to the intervals between passing vehicles. Further work would be needed to parse apart the effects of average amplitude and temporal variability on sleep.

Furthermore, since we did not use a fade function when creating our playbacks, the variable noise playback also included instantaneous onset and offset of traffic noise (see Fig. 3; this was only the case at the very beginning and end of the consistent noise playback). We acknowledge that instantaneous onset and offset is not characteristic of actual patterns of traffic noise, and that our variable noise playback lacked realism in this respect. Given the abrupt onset and offset of noise within the variable noise playback, it is even more surprising that the birds did not show a more pronounced response to the variable noise treatment (even given the consideration with respect to average amplitude levels, discussed above). Indeed, we would predict that abrupt changes in sound levels would elicit startle-type responses to a greater extent than the gradual onset and offset of changes in sound levels associated with passing vehicles (e.g. Francis and Barber, 2013).

As a final caveat, we measured effects of noise on sleep using behavioral metrics, rather than through electroencephalography. These behavioral metrics are well-described in great tits, and have been used by numerous past studies (Stuber et al., 2015, 2017; Caorsi et al., 2019), including by our research group (Raap et al., 2015, 2016, 2017, 2018a,b). However, we can only indirectly infer effects of noise on sleep as defined by brain wave activity, and cannot comment on effects on sleep intensity, or different sleep states (non-REM versus REM). Differential effects of the two noise regimes could also have been more pronounced if electrocephalographic measures of sleep could have been assessed. We are aware of only one study that has assessed effects of noise on avian sleep as measured by brain activity (Connelly et al., 2020), and of no study in wild animals. Assessing effects of noise pollution on electrocephalographic measures of sleep in free-living animals is an area for future research. Further research is also needed to identify physiological, behavioral and genetic bases underlying intraspecific variation in sensitivity to noise, to assess interactive effects between noise and other anthropogenic disturbance factors (light, chemical pollution) on sleep (Dominoni et al., 2020), and explore the many downstream effects that could arise from sleep disruption by noise. In addition, over a longer period, great tits may habituate to noise, which could help explain the lack of effect observed in the correlational study on great tits (Caorsi et al., 2019). Future experimental studies are needed to determine whether habituation to noise decreases effects on sleep, and the timeframe over which the process may take place.

5. Conclusions From our research, we can conclude that both temporally consistent and variable traffic noise have the potential to disrupt the sleep behavior of free-living animals, such that both types of noise regimes should be addressed by mitigation efforts. However, targeted mitigation efforts could consider that higher amplitude traffic noise had a more pronounced effect on sleep. In addition, there was some evidence that more temporally variable traffic noise may have a larger derogatory effect on sleep than consistent noise, although more research is needed to assess this contingency. Our analysis also suggested that sleep of older individuals was more sensitive to noise exposure than sleep of younger birds, and that repeatable individual differences in responses to noise exist. Thus, considering individual differences in sensitivity to noise may be critical to understanding the full scope of responses and elucidating effects on population dynamics. Given the pervasive, increasing, and global nature of the problem, our results provide motivation for measures to reduce anthropogenic noise, and to buffer wildlife and human populations from its effects.

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