Original Article

Impact of chronic noise exposure on antipredator behavior: an experiment in breeding house sparrows

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Over the last century, expanding urbanization has led to a strong increase in the levels of background noise. This noise pollution has been shown to negatively affect wildlife (e.g., reduced species diversity and density, reduced breeding success), especially birds. Most research addressing the effects of anthropogenic noise has focused on avian communication and, to date, very little is known regarding the impact of chronic noise exposure on nonvocal behavior such as antipredator behavior. Here, we exposed free-living house sparrows (*Passer domesticus*) breeding in nest-boxes to either a playback of traffic noise (disturbed birds) or the rural background noise of the study site (no playback: control birds) during their first breeding attempt. We tested whether one of the female's antipredator behaviors (i.e., flushing distance) was affected by exposure to chronic noise and investigated the impact of chronic noise on reproductive performances. Disturbed females flushed more rapidly than controls, suggesting that birds may compensate for reduced ability to detect predators with increased vigilance. However, we found no significant effect of exposure to chronic noise on reproductive performances. Our findings show, for the first time, that chronic noise exposure can affect the antipredator behavior of a breeding bird.

Key words: anthropogenic noise, antipredator behavior, flushing distance, house sparrow, reproductive performance.

INTRODUCTION

Since the development of cities, urban sprawl has reached unprecedented levels and is expected to continue to increase at an alarming rate (United Nations 2012). Urban areas are highly modified environments, which undergo significant structural changes (e.g., fragmentation, degradation, and loss of natural habitat; Saunders et al. 1991; Marzluff and Ewing 2001), increased disturbances (e.g., noise, light pollution, and human activities; Schlesinger et al. 2008; Barber et al. 2010; Kempenaers et al. 2010), and typically have higher levels of pollution than rural areas (e.g., gases, fine particles, and heavy metals; Roux and Marra 2007; Grimm et al. 2008). Although urban life poses difficult and restrictive conditions that can have detrimental effects on wildlife (McKinney 2002), identifying and understanding causal mechanisms through which urbanization affects biodiversity remains limited because of numerous confounding factors.

Among all the major urban-associated factors, anthropogenic noise has recently received considerable attention. Expanding urbanization has led to an increase in the levels of background noise (Slabbekoorn and Ripmeester 2008), and there is rapidly accumulating evidence that noise pollution can have harmful effects on wildlife (Warren et al. 2006; Barber et al. 2010) and especially birds because most of their life cycle relies on acoustic communication (Patricelli and Blickley 2006; Kociolek et al. 2011; Slabbekoorn 2013). Indeed, urbanization creates a novel and complex acoustic environment in which high noise level can mask songs and other important avian communication signals (Slabbekoorn and Peet 2003; Fuller et al. 2007; Bermúdez-Cuamatzin et al. 2011; Halfwerk et al. 2011; Leonard and Horn 2012; Arroyo-Solis et al. 2013; Brumm and Zollinger 2013; McLaughlin and Kunc 2013; Proppe et al. 2013; Gil and Brumm 2014). Because birds use acoustic communication to attract mates, to establish social dominance, and to communicate with their brood and partner (Catchpole and Slater 2008), masking these acoustic signals can have a detrimental impact on territorial defense (Mockford and Marshall 2009), mating success (Habib et al. 2007), pair bonds (Swaddle and Page 2007), and reproductive performances (i.e., clutch size and fledging success; Halfwerk et al. 2011). Accordingly, female house sparrows reduce their brood provisioning rate and, therefore, raise fewer chicks when breeding under chronic noise conditions (Schroeder et al. 2012).

Noise pollution may also alter the ability of birds to perceive threats, such as the sound made by an approaching potential predator (Barber et al. 2010). Predation can have dramatic effects on individual

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fitness (direct killing), but it can also have indirect effects on fitness because the perception of predation risk itself may affect reproductive performance (Zanette et al. 2011). For instance, increased predation risk (without predation) indirectly reduces the breeding success of song sparrows (*Melospiza melodia*) by affecting the time-activity budget of parents that spent less time provisioning their brood (Zanette et al. 2011). Furthermore, some authors have suggested that anthropogenic disturbance stimuli, including noise, are similar to predation risk (Gill et al. 1996; Frid and Dill 2002), and thus, urban noise could possibly increase the perceived risk of predation (Owens et al. 2012).

Surprisingly, the influence of anthropogenic noise exposure on the antipredator behavior of breeding birds has not been investigated, to date, and it remains unknown how parents adjust their behavior to the risk of predation when exposed to chronic noise. First, anthropogenic noise could reduce the bird's ability to detect an approaching predator (called hereafter "the reduced detectability hypothesis"). The noise could mask the sound made by the predator's approach (masking effect; Klump 1996; Barber et al. 2010) or provide distracting stimuli and force birds to reallocate some of their finite attention away from predator detection (distracting effect; Chan et al. 2010; Chan and Blumstein 2011; Blumstein 2014). Under this hypothesis, anthropogenic noise would prevent birds from responding to an approaching predator, resulting in a direct fitness cost. Alternatively, breeding birds may compensate for compromised ability to detect predators by lowering their threshold for response ("the increased threat hypothesis"; Owens et al. 2012). For instance, parents could increase their vigilance (i.e., antipredator behavior; Quinn et al. 2006; Rabin et al. 2006) to compensate for lost auditory awareness.

It was within this context that we investigated the effect of chronic anthropogenic noise exposure on antipredator behavior of breeding birds. Specifically, we exposed free-living house sparrows (*Passer domesticus*), breeding in nest-boxes, to either a playback of chronic traffic noise (disturbed birds) or the rural background noise of the study site (no playback: control birds) during their first breeding attempt. First, we tested if house sparrows changed one of their antipredator behaviors when breeding under chronic noise exposure by measuring the flushing distance (i.e., the distance at which the breeding bird leaves the nest when an observer is approaching; Barash 1975; Jiménez et al. 2011), a variable that provides an appropriate indicator of risk-taking by the breeding parent and its susceptibility to disturbance (Beale and Monaghan 2004; Møller 2008; Boukhriss and Selmi 2010; Møller 2014). Then, we tested whether disturbed birds had impaired reproductive performances relative to controls. We predicted that disturbed house sparrows should be less able to perceive an approaching predator and should therefore flush when the observer is closer to their nest (i.e., shorter flushing distance) relative to controls (prediction 1, "the reduced detectability hypothesis"). Alternatively, disturbed sparrows could increase their vigilance and therefore their flushing distance if they compensate for a reduced ability to detect predators by lowering their threshold of response (prediction 2, "the increased threat hypothesis"). Finally, we predicted that disturbed birds should have a lower breeding success than controls because chronic noise should alter the ability of parents to provide appropriate care to their broods (prediction 3).

METHODS

Study population

This study was conducted during the 2013 breeding season in a free-living population of house sparrows breeding in nest-boxes in a rural environment at the Centre d'Etudes Biologiques de Chizé (46°09′N, 0°24′W), France (see Leloutre et al. 2014). In the study site, 67 nest-boxes (measuring $27 \times 17 \times 15$ cm) are fixed on building walls (south- or east-oriented), 3 m above the ground and at an average distance of 2 m from each other. All nest-boxes were checked every 2 days to determine laying dates, clutch sizes, hatching dates, and brood sizes. Most of the birds are color banded at this site, and nest-box owners were identified from their color-band combinations using spotting scopes. The study site is characterized by a low predation pressure although this parameter was not precisely monitored during the study.

Experimental design

Urban noise measurements and traffic noise recording
Prior to the initiation of the study, we measured sound pressure levels in several urban sites where house sparrows breed to determine a reference level of urban noise for the experiment. For this purpose, noise levels have been measured at 6 locations in 2 medium-sized cities (Niort [46°19′N, 0°27′W] and La Rochelle [46°09′N, 1°09′W], France) during 10 surveys (at different hours of the day and different days—weekdays and weekends—chosen randomly for each survey). For each survey, 15 measurements were performed per site using a Voltcraft® SL-200 digital sound meter (Voltcraft, Hirschau, Germany), and we used average noise level from these pilot measurements as urban noise reference level (around 61 dB(A), see below). We recorded traffic noise using a Zoom H4n recorder with onboard stereo condenser microphones (Zoom Corporation, Tokyo, Japan), 5 m from a 4-lane highway near Paris (48°44′52N, 2°11′49E; around 2200 vehicles/h at a speed of approximately 90 km/h). The traffic noise recording consisted of a 2-min-long digital sound file (44.1 kHz sampling rate, 16 bits) that we edited for playback using Audacity 2.0.3 (Free Software Foundation, Boston, MA).

Experimental noise exposure
We experimentally exposed house sparrows breeding in nest-boxes in the rural site to 2 different sound treatments: traffic noise ("disturbed": $\mathcal{N} = 21$ nest-boxes) and control (rural background noise: "control": $\mathcal{N} = 46$ nest-boxes) during their first breeding attempt (April–July 2013). The traffic noise recording was delivered by an iPod shuffle (Apple Inc., Cupertino, CA) connected to Logitech LS11 stereo speakers (Logitech, Fremont, CA; frequency response 70–20 000 Hz) and was played in a loop 6 h a day (from 9 to 12 AM and from 2 to 5 PM). The speakers were hidden approximately 3–4 m from the nest-boxes (2 speakers for 4–5 neighboring nest-boxes), around 1 m above the ground and oriented toward them. Our experiment, therefore, simulated traffic noise in the vicinity of the nest-box only and did not modify the ambient noise in the whole home range of the sparrows. The volume of the playback was adjusted to our urban noise reference level using the sound level meter at the position of the nest-box (average amplitude around 63 dB(A), see below). The traffic noise exposure produced low frequency noise (see Figure 1 for example of spectrograms and power spectra of background noise at a disturbed and a control nest). Similar to urban noise measurements, we recorded noise levels at the nest-boxes 10 times during the experimental period to characterize differences in the acoustic background between disturbed and control nests. Noise levels measured at the disturbed and control nest-boxes and in urban sites were compared using a 1-way analysis of variance (Anova) and Tukey's Honestly Significant Difference test (Tukey's HSD) as a multiple comparison procedure. Sound treatment produced different noise levels as measured at the nest-boxes (Anova: $F_{2,24} = 153.8$, $P < 0.001$, Figure 2). Noise exposure for disturbed birds was significantly higher than for control birds (Tukey's HSD—$P < 0.001$: disturbed: 63.32 ± 1.65 dB(A), 95%
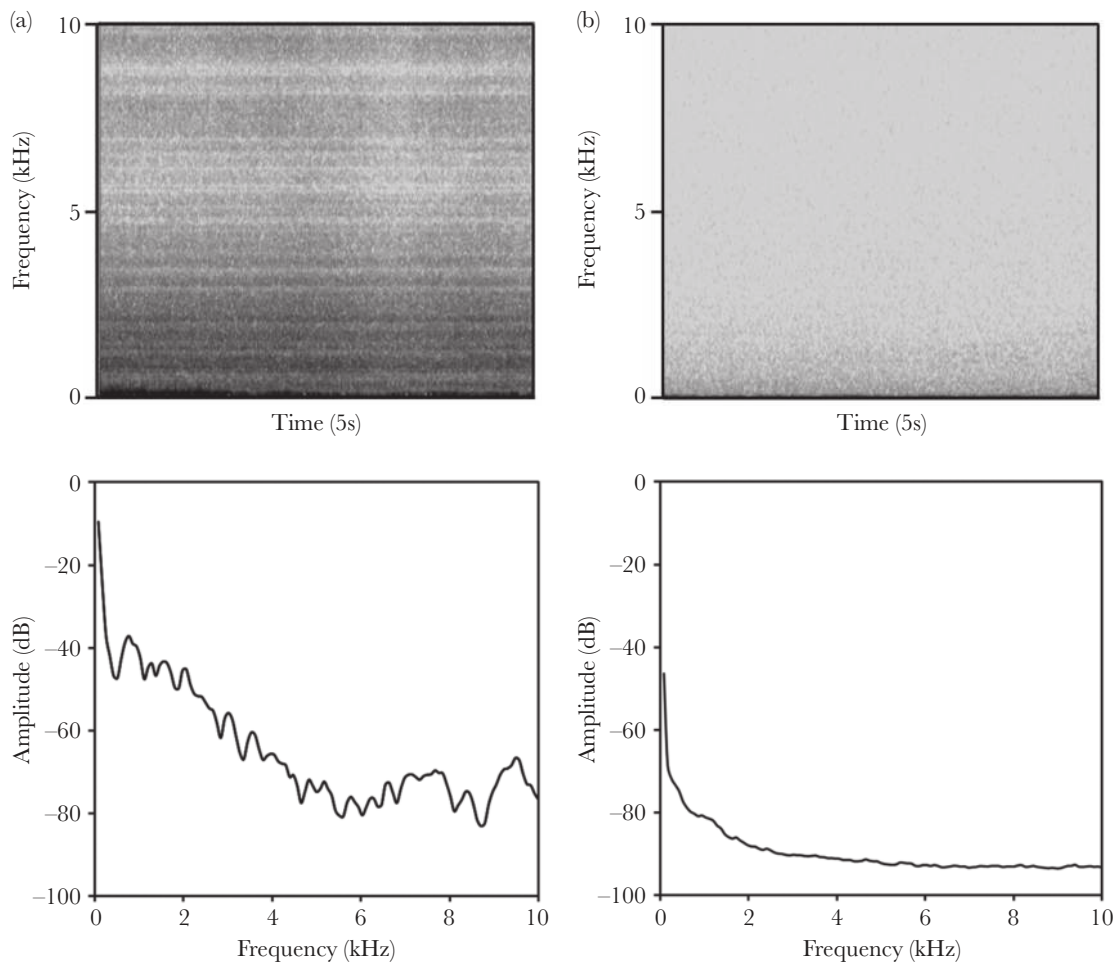
Figure 1
Example of spectrogram and power spectra of 5-s background noise recorded at (a) a disturbed nest and (b) a control nest. Darker colors on the spectrogram indicate higher amplitude. Disturbed nests were exposed to the traffic noise recording that produced low frequency sound (concentration of energy below 2 kHz). Control nests were only exposed to the rural background noise of the study site (main source of noise: wind, birds, and insects). Spectrograms and power spectra were produced using Audacity 2.0.3.

confidence interval [CI]: 61.07–65.56 dB(A); controls: 43.04 ± 0.47 dB(A), 95% CI: 41.46–44.63 dB(A)) but similar to the noise level experienced by birds breeding in urban environments (Tukey's HSD—$P = 0.45$: urban: 61.35 ± 1.21 dB(A), 95% CI: 58.93–63.78 dB(A)). Disturbed and control nest-boxes were located in the same site, limiting the confounding effect of other environmental factors. Except for the level of background noise, all other factors were similar among the monitored nests (e.g., size, height, and orientation of the nest-boxes; vegetation; access to food; human activity; and predation pressure), and thus, the effects of noise were likely separated from other confounding variables.

Flushing distance measurements

Twenty-one nest-boxes were occupied and, thus, monitored, during this experiment ("disturbed nests": $\mathcal{N} = 7$; "control nests": $\mathcal{N} = 14$). The sound treatments started on the 1 April 2013, before sparrows had begun to build their nest (settlement dates: mean ± standard error [SE]: 19 April 2013 ± 3 days) and started laying eggs (laying dates: mean ± SE: 6 May 2013 ± 3 days). For each nest, we experimentally evaluated 1 antipredator behavioral response of parents by measuring the flushing distance in response to human approach (Barash 1975). Contrary to other species (see McIntyre et al. 2014 for an example),

female house sparrows do not adopt any obvious behavior to defend their nest after they flush (Anderson 2006). The flushing distance was used as a metric to quantify sparrow's response to sound treatment. Flushing behavior is known to depend on various factors such as the sex of the breeding adult, the reproductive stage, and the time of the breeding season (Boukhriss and Selmi 2010). Thus to avoid confounding effects, we only recorded female flushing distance during their first breeding attempt. Behavioral observations of females were performed twice during the breeding period while the traffic noise recording was played (between 9 and 12 AM): in early incubation (first 5 days after clutch completion) and early brooding (first 3 days after hatching). An observer walked slowly and silently toward the nest-box starting at least 30 m away. When the female flushed from the nest-box, the distance between the observer and the nest was measured to the nearest 1 m. To avoid bias due to multiple observers, all flushing distances were recorded by the same person (A.M.).

Data analysis

All statistical analyses were performed with R 3.1.0 (R Core Team 2014). First, we used Pearson's chi-squared test to test the influence of the sound treatment on nest-box occupancy rates. Differences in clutch size and laying date among disturbed and control nests were
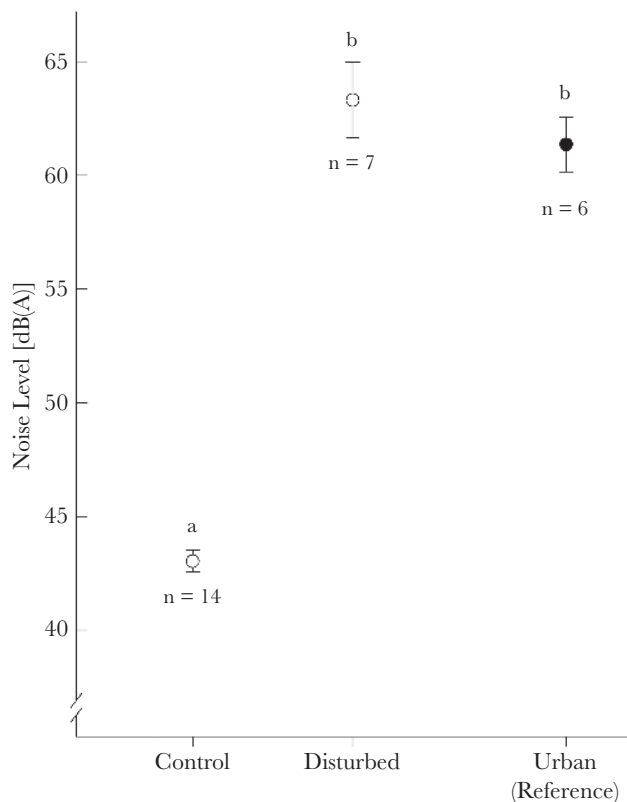
Figure 2
Mean (±SE) noise level (dB(A)) measured at nest-boxes in the 2 sound treatments (white circles) and in urban areas (black circle). Differing letters indicate statistical difference (Tukey's HSD test).

tested using the Wilcoxon–Mann–Whitney test and Student's *t*-test, respectively. Second, we used linear mixed models to examine the effects of noise exposure on female's flushing behavior (normal errors and identity link function). Because flushing distance was recorded twice during the breeding period, we included bird identity as a random factor to control for temporal pseudoreplication. We tested an effect of "sound treatment" (disturbed birds vs. controls), breeding "stage" (early incubation vs. early brooding), and their interaction on flushing distance of breeding females. Because flushing distance of breeding birds can be influenced by the reproductive value of current reproduction (Forbes et al. 1994; Albrecht and Klvana 2004), we then used generalized linear models (normal errors and identity link function) separately for each breeding stage to assess the effects of clutch and brood size on flushing distance. We, therefore, tested an effect of "sound treatment" (disturbed birds vs. controls), "clutch size" for incubating birds (or "brood size" for chick-rearing birds), and their interaction on flushing distance of breeding females. Flushing distances were $\log_{10}(X + 1)$ transformed to ensure the normality of model residuals, but we present nontransformed values to facilitate interpretation. Finally, we used generalized linear models (binomial errors and logit link function) to examine the effects of noise exposure on female's breeding success: hatching success (proportion of eggs that hatched) and fledging success (proportion of chicks that fledged). We tested an effect of "sound treatment" (disturbed birds vs. controls), "clutch size" (or "brood size"), and their interaction on female's hatching and fledging success, respectively.

We used an information-theoretic approach to select the best models (Burnham and Anderson 2002). Criteria used in model selection included the Akaike's information criterion corrected for small sample size (AICc), the difference in AICc between each candidate model, and the model with the lowest AICc (ΔAICc) and Akaike weights (wi). The best model was taken to be the one with the smallest AICc, and other models with ΔAICc < 2 were considered as receiving strong support (Burnham and Anderson 2002; Burnham et al. 2011). Akaike weights represent the relative likelihood of a model and indicate the probability that the model is the best among the whole set of models considered. To test the strength of the variables, we also calculated each variable's relative importance (VI) by summing the AICc weights of all models, which included that variable (Burnham and Anderson 2002). Selected models were finally checked for assumptions (constancy of variance and residual normality) and parameters' estimates (±SE), and 95% CIs were given for models with the highest AICc weight.

RESULTS

Occupancy, laying date, and clutch size

Occupancy rates were similar among the 2 sound treatments (Pearson's chi-squared test: $\chi_1^2 = 0.08$, $P = 0.77$). Clutch size did not differ between control and disturbed birds (Wilcoxon–Mann–Whitney test: $\mathcal{Z} = -1.12$, $P = 0.27$), and laying dates were also similar among the 2 sound treatments (*t*-test: $t = 0.88$, $P = 0.39$).

Effect of chronic noise exposure on female's flushing distance

Variation in female's flushing distance was best explained by the sound treatment (Table 1, VI = 0.998). Sound treatment was included in the 3 best fitting models, suggesting a strong effect of noise exposure on female flushing distance. Overall, flushing distances of disturbed females were significantly increased (Table 1: parameter estimates; disturbed birds: 9.41 ± 1.46 m, controls birds: 2.80 ± 0.50 m). Flushing distance was, however, not affected by the breeding stage (Table 1, VI = 0.396). Although the second best model includes this variable and has a relatively high AICc weight, flushing distance did not significantly differ between incubating and brooding birds (parameter estimates [log]—brooding vs. incubating: 0.01 ± 0.07 [CI: −0.14 to 0.15], $t = 0.11$, $P = 0.92$; incubation: 5.63 ± 1.35 m; brooding: 4.37 ± 0.69 m).

When breeding stages were analyzed separately, variation in female's flushing distance was also best explained by the sound treatment (Table 2a and b, VI = 0.994 and 0.943, respectively). Flushing distance of incubating disturbed females was significantly increased in comparison to controls (Table 2a: parameter estimates, Figure 3a). There was also a significant positive effect of sound treatment on flushing distance of brooding females (Table 2b: parameter estimates, Figure 3b). Although the second best models include either the clutch or the brood size and have relatively high AICc weights (Table 2a and b, VI = 0.405 and 0.361, respectively), flushing distance was not influenced by the clutch (parameter estimates [log]: 0.12 ± 0.09 [CI: −0.07 to 0.31], $t = 1.32$, $P = 0.20$) or the brood size (parameter estimates [log]: 0.01 ± 0.05 [CI: −0.11 to 0.12], $t = 0.13$, $P = 0.90$).

Effect of chronic noise exposure on female's breeding performances

Although the model with the lowest AICc includes sound treatment as a variable (Table 3a, VI = 0.572), this model was only very slightly better than the null model (ΔAICc = 0.20), indicating that very little variance in hatching success was explained by the sound treatment. The proportion of eggs that hatched did not significantly differ between disturbed and control birds (Figure 4a, parameter estimates

Table 1

Model selection using the AICc to determine the best model explaining variation in (log transformed) flushing distance of female house sparrows

Model	K	Log likelihood	AICc	ΔAICc	wi
Sound treatment	**2**	**−4.23**	**17.5**	**0**	**0.603**
Sound treatment, Stage, Sound treatment × Stage	4	−2.54	19.5	1.94	0.229
Sound treatment, Stage	3	−4.23	20.1	2.57	0.166
Null model	1	−11.41	29.5	11.92	0.002
Stage	2	−11.41	31.9	14.35	0.000
Selected model	Parameter	Estimate ± SE	t	P	CI
Sound treatment	Intercept	0.48±0.06	7.86	<0.001	0.36–0.61
	Sound treatment (disturbed)	0.47±0.10	4.43	<0.001	0.25–0.69

All models (linear mixed models) include bird identity as a random factor. The 5 most competitive models are represented and ranked according to their AICc (selected model in bold). *K* indicates the number of parameters. The second part of the table includes the parameter estimates and 95% CIs for the selected model.

Table 2

Model selection using the AICc to determine the best model explaining variation in (log transformed) flushing distance of female house sparrows for the (a) incubation stage and (b) brooding stage

Model	K	Log likelihood	AICc	ΔAICc	wi
(a) Early incubation					
Sound treatment	**2**	**−4.19**	**15.8**	**0.00**	**0.593**
Sound treatment, Clutch size	3	−3.21	16.9	1.14	0.336
Sound treatment, Clutch size, Sound treatment × Clutch size	4	−3.09	20.2	4.39	0.066
Clutch size	2	−9.34	26.1	10.29	0.003
Null model	1	−11.07	26.8	11.02	0.002
Selected model	Parameter	Estimate ± SE	t	P	CI
Sound treatment	Intercept	0.44±0.08	5.27	<0.001	0.26–0.61
	Sound treatment (disturbed)	0.60±0.14	4.19	<0.001	0.30–0.90
(b) Early brooding					
Sound treatment	**2**	**0.26**	**6.9**	**0.00**	**0.594**
Sound treatment, Brood size, Sound treatment × Brood size	4	2.57	8.9	1.97	0.221
Sound treatment, Brood size	3	0.27	10.0	3.07	0.128
Null model	1	−3.69	12.1	5.17	0.045
Brood size	2	−3.65	14.7	7.83	0.012
Selected model	Parameter	Estimate ± SE	t	P	CI
Sound treatment	Intercept	0.53±0.07	7.9	<0.001	0.39–0.67
	Sound treatment (Disturbed)	0.34±0.12	2.95	<0.01	0.10–0.59

The 5 most competitive models (generalized linear models) are represented and ranked according to their AICc (selected models in bold). *K* indicates the number of parameters. Parameter estimates and 95% CIs are given for the selected models.

[logits]—disturbed vs. control: −1.22±0.76 [CI: −2.86 to 0.25], $z = -1.60$, $P = 0.11$). The model including clutch size as a predictor has a much larger AICc than the null model, suggesting that there was no effect of clutch size on hatching success (Table 3a, VI = 0.313).

Two models with similar AICc were identified as the best models to explain female's fledging success (Table 3b). Both models include brood size as a variable (VI = 0.999), and fledging success was significantly affected by the number of chicks at hatching (Table 3b: parameter estimates), with the proportion of chicks that fledged decreasing with increasing brood size. Although the second best model includes sound treatment as a variable and has a relatively high AICc weight (Table 3b, VI = 0.543), female's fledging success did not significantly differ between disturbed and control birds (Table 3b: parameter estimates, Figure 4b).

DISCUSSION

In this study, we experimentally showed for the first time that anthropogenic noise can affect one antipredator behavior of a wild bird species during the parental phase. Contrary to the "reduced detectability hypothesis" (prediction 1, Chan et al. 2010; Chan and Blumstein 2011; Blumstein 2014), we found that parent house sparrows increased their flushing distance when breeding under chronic noise. This suggests that chronic noise raised the perceived level of threat and that disturbed sparrows increased their vigilance in order to compensate for reduced ability to detect predators (the "increased threat hypothesis," prediction 2, Quinn et al. 2006; Rabin et al. 2006; Owens et al. 2012). Surprisingly, despite this large impact of chronic noise exposure on behavior and contrary to previous studies (Halfwerk et al. 2011; Hayward et al. 2011; Kight et al. 2012; Schroeder et al. 2012), we did not find any significant effect of our noise manipulation on the reproductive performances of female house sparrows. This suggests that the impact of chronic noise exposure on breeding success may also depend on other ecological parameters. Importantly, this also suggests that important changes in antipredator behavior may not always affect reproductive performances in wild birds.
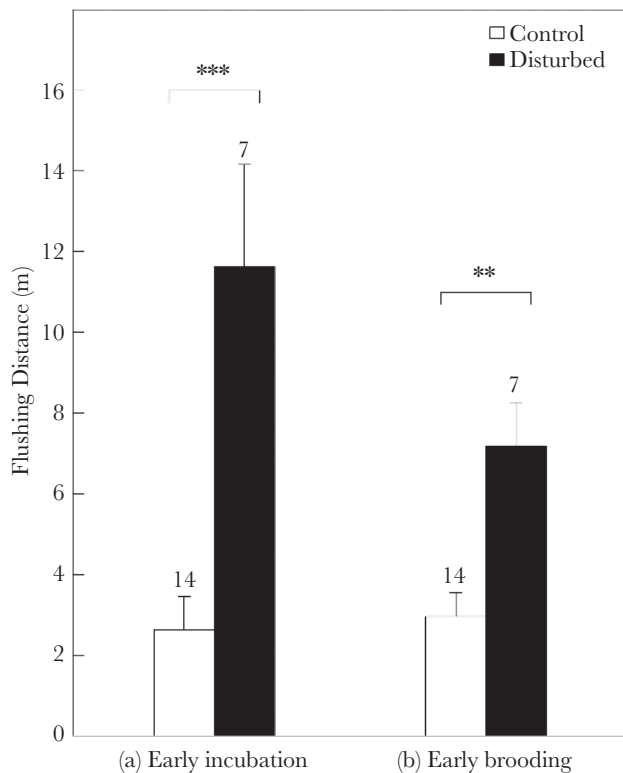
Figure 3
Effect of noise exposure on female's flushing distance at the (a) early incubation and (b) early brooding stages. Significant effects of experimental treatment are symbolized: **$P < 0.01$, ***$P < 0.001$. Vertical bars denote SE and numbers above bars indicate sample size.

Impact of chronic noise exposure on the initiation of reproduction

Anthropogenic noise has been shown to reduce avian reproductive performance, and several hypotheses, mostly related to signal masking, have been suggested to explain the possible mechanisms leading to this reduced fitness (Halfwerk et al. 2011; Schroeder et al. 2012). Among these hypotheses, many rely on an effect of noise exposure on the early steps of the reproduction (i.e., establishment of a breeding territory, pairing success). For instance, some studies have shown that breeding pairs avoid establishing their breeding territory in areas exposed to a chronic noise because they probably perceive such a disturbed territory as being of poor quality (Reijnen and Foppen 1994; Habib et al. 2007; Francis et al. 2009). This was apparently not the case in our experiment as we found similar occupancy rates between the 2 sound treatments. Although low-quality and/or less experienced birds could have been excluded from control nest-boxes by high-quality and/or experienced sparrows (Habib et al. 2007), this seems unlikely because many undisturbed nest-boxes remained unoccupied. Noise may also interfere with female's acoustic assessment of mate quality and, as a result, females may reduce their parental investment (e.g., breed later, allocate less energy to the eggs; Holveck and Riebel 2010; Halfwerk et al. 2011). In our study, we did not report any difference in laying date and clutch size between disturbed and control nests, suggesting that pairing success and females' initial reproductive investment were not significantly affected by our experimental noise exposure.

Impact of chronic noise exposure on flushing distance

According to our hypotheses, we found a strong and highly significant behavior effect of our experimental treatment on females' flushing distance. In our experiment, the observer could not be totally blind because he could hear the sound treatment while measuring the flushing distance. However, we found an important difference in flushing distance between disturbed and control birds (incubation stage: 11.64 ± 2.52 m for the disturbed birds vs. 2.63 ± 0.82 m for the control birds; brooding stage: 7.18 ± 1.09 m for the disturbed birds vs. 2.96 ± 0.60 m for the control birds), and this magnitude was too important to be linked only to an observer bias. Furthermore, the control nest-boxes were only exposed to the natural ambient background noise of the study site and did not receive a playback. Thus, one could argue that the sound treatment was potentially confounded by the presence of the loudspeaker and playback device and that this alone might have affected flushing behaviors. However, we are confident that this was not the case in our experimental design for the following reasons: First, the speakers were not directly visible in the environment of the disturbed nest-boxes. They were placed in order to minimize disturbance effect while producing an acoustic environment equivalent in amplitudes for all the nest-boxes in the area. Second, the sound treatment started before sparrows had begun to build their nest. Therefore, the speakers could not be considered as novel and distracting objects as the sparrows were used to them since they settled.

We found that female house sparrows increased their flushing distance when exposed to noise, supporting the "increased threat hypothesis" (prediction 2). Because anthropogenic noise can interfere with the ability of an individual to detect an approaching danger and can increase the perceived level of threat (Gill et al. 1996; Frid and Dill 2002; Barber et al. 2010; Owens et al. 2012), females may have responded to the traffic noise exposure by increasing their vigilance behavior to compensate for lost auditory awareness. Because of this increased vigilance, female house sparrows may then have detected the observer earlier than controls despite a louder background noise. This would explain their increased flushing distance (the "flush early to avoid the rush" theory, Blumstein 2010; Samia et al. 2013). Such impact of background noise on antipredator behavior has also been reported in foraging chaffinches (*Fringilla coelebs*), which increased the time spent to predator detection when foraging in a noisy environment (Quinn et al. 2006). Importantly, our results do not support the "reduced detectability hypothesis" (prediction 1, Chan et al. 2010; Chan and Blumstein 2011; Blumstein 2014) because experimental sparrows did not decrease their flushing distance relative to controls. This suggests that an increase of background noise (up to 60–70 dB(A)) does not totally preclude house sparrows from perceiving an approaching predator.

Interestingly, we found that both incubating and brooding female house sparrows increased their flushing distance when exposed to noise. Moreover, the flushing distance of incubating birds did not differ from that of brooding birds in both groups. This result demonstrates that the effect of chronic noise exposure on flushing distance is apparent during the whole parental phase and is not limited to the first days of chronic noise exposure when individuals are confronted to a noisy situation. The lack of difference between flushing by incubators and brooders also demonstrates that, in our study, female sparrows did not habituate to the flushing distance protocol throughout the study period.

Table 3

Model selection using the corrected version of AICc to determine the best model explaining (a) female's hatching success (proportion of eggs that hatched) and (b) fledging success (proportion of chicks that fledged)

Model	K	Log likelihood	AICc	ΔAICc	wi
(a) Hatching success					
Sound treatment	2	−14.14	32.9	0.00	0.361
Null model	1	−15.47	33.1	0.20	0.326
Sound treatment, Clutch size	3	−13.79	35.0	2.05	0.130
Clutch size	2	−15.40	35.5	2.53	0.102
Sound treatment, Clutch size, Sound treatment × Clutch size	4	−12.71	35.9	2.98	0.081
(b) Fledging success					
Brood size	**2**	**−23.65**	**52.0**	**0.00**	**0.457**
Sound treatment, Brood size	**3**	**−22.36**	**52.1**	**0.16**	**0.422**
Sound treatment, Brood size, Sound treatment × Brood size	4	−22.06	54.6	2.65	0.121
Null model	1	−33.94	70.1	18.12	0.000
Sound treatment	2	−32.98	70.6	18.66	0.000
Selected models	Parameter	Estimate ± SE	z	P	CI
Brood size	Intercept	5.82 ± 1.95	2.98	<0.01	2.36 to 10.17
	Brood size	−1.74 ± 0.47	−3.68	<0.001	−2.80 to −0.91
Sound treatment, Brood size	Intercept	6.25 ± 2.03	3.08	<0.01	2.68 to 10.79
	Sound treatment (disturbed)	−1.12 ± 0.73	−1.52	0.13	−2.73 to 0.23
	Brood size	−1.74 ± 0.47	−3.68	<0.001	−2.81 to −0.92

The 5 most competitive models (generalized linear models) are represented and ranked according to their AICc (selected models in bold). K indicates the number of parameters. Parameter estimates and 95% CIs are given for the selected models of fledging success.
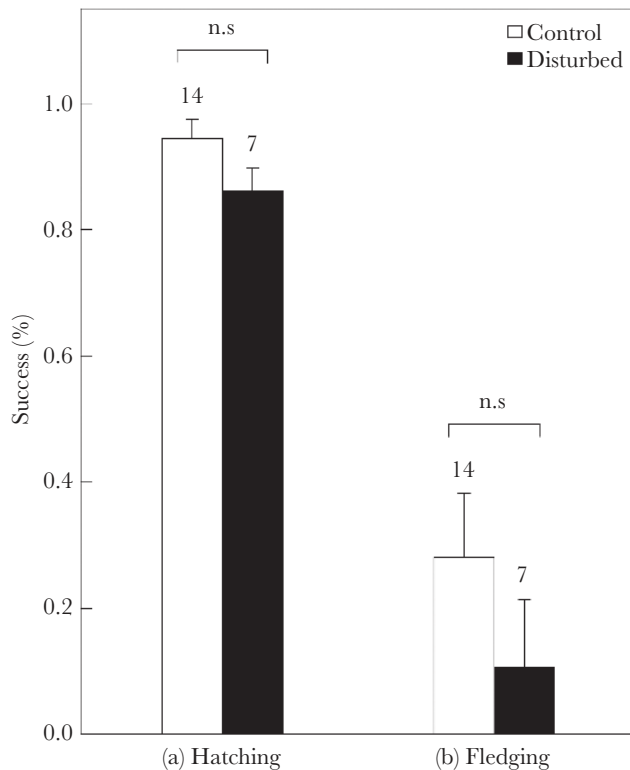
Figure 4

Effect of noise exposure on female's (a) hatching and (b) fledging success. Vertical bars denote SE and numbers above bars indicate sample size. "n.s" indicates nonsignificant differences in our variable of interest (hatching or fledging success) between disturbed and control birds (generalized linear models with binomial errors and logit link function).

Surprisingly, this result is not entirely consistent with an important prediction of the parental investment theory (Barash 1975; Roff 1992; Stearns 1992; Albrecht and Klvana 2004). Indeed, parental investment, and therefore, risk-taking behavior should be influenced by a broods' current reproductive value (Seltmann et al. 2012). Thus, flushing distance should decrease as breeding stage progresses (from incubation to brooding) because the reproductive value of the current breeding episode increases with time. For the same reasons, flushing distance should decrease with increasing clutch and brood size (Forbes et al. 1994; Albrecht and Klvana 2004). Contrary to this, our results suggest that the relationship between flushing distance and parental investment may not be so obvious in natural conditions because flushing distance probably depends on many other variables (e.g., environment, Lima and Dill 1990, this study; individual quality, Møller 2014) that may mask this relationship.

Impact of chronic noise exposure on breeding performances

One would expect our experiment to induce reduced breeding success because increased vigilance may alter parental behavior (Lima 2009). Although vigilance behavior can improve survival by reducing risk-taking in parents (Møller 2014), this behavior requires much time, and increased vigilance is done at the expense of other activities, such as foraging or parental care (Brick 1998; Caro 2005). For instance, the presence of a predator is not only associated with increased vigilance but also with an important reduction in chick provisioning in passerines (Whittingham et al. 2004; Fontaine and Martin 2006; Fernández-Juricic et al. 2007; Tilgar et al. 2011; Pascual and Senar 2013). Although we were not able to measure parental behavior (incubation commitment

and chick provisioning), we predicted that an increased flushing distance and a chronic exposure to anthropogenic noise should have decreased the time spent incubating the eggs or provisioning the chicks and, therefore, should have resulted in reduced breeding success. Surprisingly, reproductive performances did not differ between disturbed and control birds. How can we explain this similarity in breeding success between disturbed and control sparrows? First, the frequency of predator attack may interact with flushing distance to affect reproductive performances. Although we found that experimental birds flushed earlier than controls when confronted with a risk of predation, the actual cost of flushing earlier may only be apparent when individuals are frequently and repeatedly confronted with a potential predation risk while the predation pressure and human disturbance are very low in our study site. Therefore, female sparrows may have flushed from their nest only on a few occasions during the study period, and overall, incubation commitment and chick provisioning may not have differed enough between treatments to induce a significant effect on reproductive performance. Second, the year of study was characterized by very poor conditions for European passerines (low temperatures and high precipitations) and, therefore, by delayed breeding and reduced breeding success (Gładalski et al. 2014). Most chicks were in very poor conditions, and breeding success was very low at our site (Figure 4). These extreme environmental conditions may have obscured a potential relationship between flushing distance and reproductive performance because all chicks—experimental and control—may have suffered from these conditions.

More generally, our study shows that chronic noise exposure can dramatically affect the behavior of a breeding bird species, independently from direct interference on acoustic communication. However, contrary to our predictions, disturbed females displayed similar breeding success to controls. Although we did not detect a direct effect of anthropogenic noise on the parameters we examined, exposure to chronic noise may have subtly affected nestlings during their development (e.g., physiology, Crino et al. 2013; begging calls, Leonard and Horn 2008). Future experiments are, therefore, needed to investigate whether chronic noise exposure affects nestling phenotype.

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