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ORIGINAL ARTICLE

Bursts of white noise trigger song in domestic Canaries

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Abstract

Acoustic communication is fundamentally constrained by noise. In birds, the masking of mating signals (songs) may reduce fitness and, hence, they have evolved various mechanisms to maintain communication in noise. One of these tactics is the adjustment of song timing to avoid overlap with masking sounds, but previous studies yielded contrasting results regarding the occurrence and magnitude of this behavioural plasticity. Here, we investigated how temporal noise avoidance varies with noise intensity. We exposed singing Canaries (*Serinus canaria*) to playbacks of masking noise of varying amplitude [60–80 dB(A) SPL]. Contrary to our prediction, the birds did not shift song onsets to the silent intervals between noise bursts at high noise amplitudes, nor did they increase singing outside the playback period. Rather, we found that noise generally triggered the onset of song: the Canaries preferentially sang during the noise bursts independent of the noise amplitude. This behaviour is somewhat paradox because it leads to the most unfavourable signal-to-noise ratios. Our results, together with findings from the current literature, indicate marked species differences in the noise-induced song plasticity of birds. Therefore, we suggest a more comprehensive conception of noise that incorporates both supressing and stimulating effects.

Keywords Animal communication · Acoustic masking · Behavioural plasticity · Bird song · Noise · *Serinus canaria*

Zusammenfassung

Impulse von weißem Rauschen lösen Gesang bei domestizierten Kanarienvögeln aus

Akustische Kommunikation wird durch Rauschen im Übertragungskanal stark beschränkt. Bei Singvögeln kann eine akustische Maskierung von sexuellen Signalen (Gesang) die Fitness reduzieren und daher haben sie verschiedene Mechanismen entwickelt, um sich auch bei Lärm zu verständigen. Eine solche Strategie ist die zeitliche Anpassung des Gesangs, um Überlappungen mit maskierenden Geräuschen zu vermeiden. Frühere Studien haben allerdings widersprüchliche Ergebnisse hinsichtlich des Auftretens und des Ausmaßes dieser Verhaltensplastizität hervorgebracht. In der vorliegenden Studie untersuchten wir an domestizierten Kanarienvögeln (*Serinus canaria*), in wie weit die zeitliche Lärmvermeidung

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mit der Lärmintensität zusammenhängt. Dazu setzten wir singende Männchen einem Rauschen, das den Gesang maskiert, mit unterschiedlicher Amplitude [60–80 dB(A) SPL] aus. Die Auswertung zeigte überraschenderweise, dass die Vögel bei hohen Lärmamplituden den Beginn ihres Gesangs nicht in die stillen Intervalle zwischen den Rauschimpulsen verlegten und auch nicht häufiger außerhalb des Playbacks sangen. Wir fanden hingegen, dass das Rauschen allgemein Gesang auslöste: Die Männchen sangen bevorzugt während der Rauschimpulse, unabhängig von deren Lautstärke. Diese Verhaltensweise ist einigermaßen paradox, da dies zu einem höchst ungünstigen Signal-Rausch-Abstand führt. In der Zusammenschau mit der Literatur weisen unsere Ergebnisse auf deutliche Artunterschiede in der lärminduzierten Gesangsplastizität von Singvögeln hin. Daher schlagen wir eine umfassendere Betrachtungsweise des Einflusses von Lärm auf die Kommunikation vor, die sowohl unterdrückende als auch stimulierende Wirkungen umfasst.

Introduction

Many animals rely on acoustic communication to establish and maintain their social relationships. Acoustic signals propagate very quickly and over long distances (Bradbury and Vehrencamp 2011), but with increasing transmission distances, they get more and more attenuated and degraded by the environment (Wiley and Richards 1978). Attenuation of acoustic signals in natural environments is mainly the result of atmospheric absorption and scattering and attenuation by vegetation, whereas degradation refers to reverberations and amplitude fluctuations induced by reflection from objects and the effects of wind on sound propagation (Wiley and Richards 1978). In addition, acoustic communication is strongly constrained by masking noise, which limits the active range of a signal (Brumm and Slabbekoorn 2005; Wiley 2015). Such noise may include, for example, the sounds produced by wind, rain or flowing water, the vocalisations of other species, and, to an ever-increasing degree, anthropogenic noise pollution (Luther and Gentry 2013).

Birds use acoustic signals (songs) for crucial functions, such as mate attraction, mate choice, and territory defence (Catchpole and Slater 2008). Therefore, impairment of song communication is likely to have major fitness consequences for birds and thus, in turn, one may expect strong selection on vocal and other behavioural faculties for efficient song transmission in noise (Brumm and Naguib 2009). In fact, birds have evolved a whole array of different vocal production mechanisms to mitigate acoustic masking by noise (Brumm and Zollinger 2013). These mechanisms can be roughly categorised into two groups: on the one hand, increasing the signal level and, on the other, indirectly decreasing the level of noise, both of which eventually help maintaining favourable signal-to-noise ratios for communication. To increase their signal level in noise, all bird species tested so far regulate their vocal amplitude depending on the background noise level. This capacity is a basic form of noise-dependent vocal plasticity in birds and mammals, known as the Lombard effect (Brumm and Zollinger 2011). The Lombard effect is often accompanied by additional changes in other signal parameters, e.g. some bird species may also increase the redundancy of their vocalisations in noise by producing longer and more repetitive signal series (Potash 1972; Lengagne et al. 1999; Brumm and Slater 2006), adjust their signal duration (Osmanski and Dooling 2009), or change the frequency of their vocalisation (Goodwin and Podos 2013; Osmanski and Dooling 2009). From all of these noise-induced signal changes, increasing vocal amplitude is by far the most effective to maintain signal detectability in noise (Nemeth and Brumm 2010; Luo et al. 2015). However, physiological and physical constraints limit bird song (like any other animal vocalisation) to a certain maximum amplitude (Suthers and Zollinger 2008).

An alternative tactic to increase signal-to-noise ratios in fluctuating noise is to shift vocal output to periods when noise levels are low. Birds are known to deploy this tactic by shifting the timing of their songs from a few seconds to larger, diel levels (Brumm and Zollinger 2013). Common Nightingales (*Luscinia megarhynchos*), for example, increase the variability of their song onset intervals by a few seconds to fit their songs in the silent intervals between the songs of other birds, thereby avoiding masking by the heterospecific songs (Brumm 2006). Birds in noise-polluted areas may advance their singing to take advantage of earlier times during the day when noise levels are lower (Dorado-Correa et al. 2016). One such example comes from European Robins (*Erithacus rubecula*), which have been found to shift their singing activity in urban areas from the early morning into the night to avoid overlap with traffic noise (Fuller et al. 2007). Bird habitats close to airports are exposed to extreme levels of noise pollution and in these areas entire bird communities begin singing 4–45 min earlier in the morning, probably to gain more time for uninterrupted singing before aircraft operations start (Gil et al. 2015; Dominoni et al. 2016; Sierro et al. 2017; de Framond and Brumm 2022). Chaffinches (*Fringilla coelebs*) were found not only to sing earlier at airports, but they also avoided singing during aircraft take-offs when the noise exceeded 78 dB(A) SPL (Dominoni et al. 2016). Taken together, these findings indicate that not only the presence of noise but also its temporal pattern as well as the noise intensity are crucial for triggering shifts of singing activity on different time scales in birds.

While the sound level of noise is an important factor for song adjustments, only few experimental studies examined how noise-mitigation behaviour varies with noise intensity. One of them found that calling rates in domestic chicken (*Gallus gallus*) are increased in moderate noise (probably to maintain information transfer by increased redundancy), but supressed by high noise levels, indicating that noise effects may not be linear (Brumm et al. 2009). This observation, just like the chaffinch study mentioned in the previous paragraph, suggests a noise-level threshold that triggers suppression of vocal signal production. Understanding the conditions and noise characteristics that elicit behavioural plasticity is important to better apprehend the effects of noise pollution on animals and thus may help to improve noise-mitigation measures. To this end, we investigated noise-related timing of vocalisations in a passerine bird, the domesticated Canary (*Serinus canaria*). Song production and vocal control in this species have been well-studied (Leitner and Catchpole 2004; Suthers et al. 2012), including the Lombard effect (Hardman et al. 2017), as well as the function of male song in mate attraction and mate stimulation (Voigt and Leitner 2008; Leitner et al. 2001; Leboucher et al. 2012). During the breeding season, the mean duration of individual Canary songs is 8.6 s and the singing rate culminates at about 5.4 songs per minute at the peak of the season (Voigt and Leitner 2008; Leitner et al. 2015). To investigate noise-induced song plasticity in Canaries, in particular temporal noise avoidance behaviour, we tracked the singing activity of individual males while broadcasting intermittent white noise for ten hours per day, roughly mimicking the patterns of noise pollution at an airport (Dominoni et al. 2016). We predicted that the Canaries would avoid singing during the noise bursts depending on the noise amplitude. According to the findings of non-linear changes in chicken vocalisations (Brumm et al. 2009), we expected that vocal production may be stimulated by low-amplitude noise and suppressed at high amplitudes. We also predicted that, over the course of the experiment, the Canaries would shift their singing activity to the quiet period in the morning before the onset of the noise playback, similar to what has been observed in birds at airports.

Methods

Subjects

We studied 34 male outbred domesticated Canaries, all of which were sexually mature (aged between nine months to five years). The birds were bred and raised in aviaries at the Max Planck Institute for Ornithology (Seewiesen, Germany). Experiments were performed under a 14:10 h light:dark cycle (lights on from 07:00 to 21:00). The birds had constant access to ad libitum food and water, supplemented with fresh vegetables, cuttlebones, and grit. The study was conducted under a licence by the Government of Upper Bavaria (permit number 55.2-2532.Vet_02-18-133).

Apparatus

The males were recorded individually in cages (42 × 120 cm and 42 cm high) in acoustically shielded boxes (55 × 149 cm and 61 cm high). Using nine sound boxes, we tested up to nine males simultaneously in one experimental round. In the interests of animal welfare and to motivate the males to sing, each male was paired with one of 17 different females, so that each cage in each box contained one male and one female. The cages were each equipped with four perches and a nest bowl and nesting material to further induce breeding motivation (and thus singing). The doors of the sound boxes were not tightly shut so that birds could (faintly) hear each other (which further increased the general singing motivation), but most birds in a given experimental round did not sing at the same time (Table S1). Noise playbacks were broadcast from a PC connected to an amplifier (Apart Champ 4) and then to two loudspeakers (Kenwood KFC-1789ie) that were mounted in the short sides of the sound box facing the centre of the cage. Each box was equipped with an omni-directional microphone (Monacor ECM-3005) mounted vertically above the cage, which was connected through a Pro Audio PR8E preamplifier to an external soundcard (Edirol UA-101) and the PC. The birds' vocalisations were constantly monitored with the software Sound Analysis Pro [v. 2011.113, (Tchernichovski et al. 2000)]. We used an amplitude threshold to trigger the recording (sample rate of 44.1 kHz and 16-bit accuracy). It was adjusted by hand for each noise amplitude to be just above the playback noise amplitude but not to miss any Canary songs (given the high amplitude of Canary song and the placement of the microphones close to the perches and perpendicular to the loudspeakers ensured that the noise amplitude was always lower at the position of the microphones than the peak amplitude of the bird songs). Recordings files were set to be 5 s long at maximum. We chose this short recording duration because longer files may can contain several songs. A previous study showed that the mean duration of Canary song in the breeding season was 8.6 ± 1.0 s (Voigt and Leitner 2008). Since we analysed recordings based on a file unit, it was easier to reconstruct a long song from several contiguous short recordings than to separate several songs in a longer recording. We added a 2-s pre-buffer period to make an overlap with contiguous recordings and to make sure that the onset of a song was recorded. We used the automatic classifier in Sound Analysis Pro to discard recordings that did not contain bird vocalisations (cage noise, calls, flight noise, etc.). For this, we applied a threshold of 420 ms for the longest syllable (or syllable bout), above which the entire file was saved. This setting is very conservative and thus did not reject all non-song recordings (which were then discarded by hand), but we chose it to ensure that all songs were detected.

Playback noise

The playback was generated in R (v. 4.1.2, The R Foundation for Statistical Computing) with the package *seewave* (v. 2.1.8). We synthetized 40 s of white noise (0–22 kHz, sample rate of 44.1 kHz, 16 bits accuracy) followed by 40 s of silence. We chose a duration of 40 s because this is longer than typical male Canary songs in the breeding season (Voigt and Leitner 2008) and theoretically would allow the birds to insert their songs into the silent periods between the noise. The noise had a 0.1-s fade-in and 0.1-s fade-out to prevent the loudspeaker of producing a clicking sound due to a sudden signal onset. We further band pass-filtered the noise (0.10–10.0 kHz) to restrict it to the spectral range of Canary songs. In addition, we used a band-stop filter to make a small spectral "window" between 3.5 and 4.0 kHz, which allowed us to better see the Canary song syllables in the high-level noise.

Procedure

At the beginning of each experimental round, we let each male and female get accustomed to the new keeping environment in the sound box for one to three days (except for Round 1, in which the birds were habituated for 19 days). After that, the birds were accustomed to the noise playback by several hours of noise at low amplitude (40–60 dB(A) SPL, all dB values in this article refer to a reference of 20 µPa). On the following day, we began an experimental period of five consecutive days. On each of these five days, noise of a different amplitude [60, 65, 70, 75, and 80 dB(A), measured at the perch with a CASELLA CEL-24X sound level meter] was broadcast between 09:00 and 19:00. The order of these noise treatments was systematically varied so that each bird was exposed to each of the five levels. In total, we carried out four experimental rounds between 5 April and 20 May 2022, which is in the breeding season of Canaries (Voigt and Leitner 2008). Due to a technical error, the playback did not start on 2 days (day 3 of Round 2 and day 2 of Round 3). The recordings from these days were discarded and we repeated the respective treatments on a sixth experimental day, so that all birds experienced five days of noise playbacks.

Song analysis

The recordings were screened with Avisoft SASLab Lite (v. 3.5.01, Avisoft Bioacoustics, Berlin, Germany) to identify songs by visual inspection of spectrograms (Hann window, FFT-length: 256 points, resolution: 172 Hz). Following a definition of previous studies (Voigt and Leitner 2008; Leitner et al. 2001), we considered vocalisations longer than 1.5 s and containing no pauses longer than 0.4 s as song. However, since the recordings files were 5 s long, they could theoretically contain two short song vocalisations with a gap between 0.4 and 2.0 s between them. Thus, our operational definition of song includes performances with such silent intervals between two consecutive vocalisations. According to these criteria, we found that 22 males sang at least one song. In total, we recorded 1842 songs consisting of 2959 recording files. We counted the number of song onsets in noise and in the silent intervals between noise periods. The time of song onset was defined as the onset time of the 5-s recording that contained the onset of the song.

Statistical analysis

All subsequent statistical analyses were performed in R (v. 4.1.2, The R Foundation for Statistical Computing). We investigated the impact of noise level and the total duration of intermittent noise exposure (number of experimental days) on the onset of songs using four generalised linear mixed models and one linear mixed model (Table 1), built with the package *lme4* (v. 1.1.29). In model 1.1 and model 1.2, we investigated the probability of birds to start singing during a 40-s noise burst or in the silent periods between the noise burst over the course of the experiment (fixed effect: experimental day, from 1 to 5) and according to the noise level [fixed effect: playback noise level in dB(A)]. To account for circadian changes in their song activity, we included the time since the start of playback (in hours) as a fixed effect. Whether birds started the song in the noise or not was treated as a binomial variable and modelled using a logistic regression. Since previous studies showed that singing or calling activity may increase with moderate noise levels and then decrease at higher noise levels (Brumm et al. 2009; Díaz et al. 2011; Brumm and Zollinger 2013), we expected the probability of birds to start singing in the noise to follow the same pattern. Therefore, in model 1.2, the noise amplitude was fitted as a polynomial term of degree 2. We compared model 1.1 and model 1.2 using an ANOVA to determine whether the polynomial term in model 1.2 improved model fit significantly. Since birds in acoustically polluted areas shift their daily song onsets to earlier times in the morning (da Silva et al. 2014; Gil et al. 2015; Dominoni et al. 2016), we investigated whether the time of the first song per day changed over the course of the experiment (model 2). The time at which the first song was emitted was measured relative to the onset of light and log-transformed to achieve normality and then modelled using a linear mixed model. Following the notion that the advancement of singing activity would allow birds to sing more before the onset

Table 1 Summary of five models investigating the singing activity of Canaries in a noise-playback experiment

Model	family	Dependant variable	Fixed predictors	Random predictors	Sample size
Model 1.1 Short-term adjustment of song onset (linear)	Binomial GLMM (logit link)	Song onset in the noise (Yes/No)	Noise level Experimental day Time since start of playback Experimental round	Bird ID	1658
Model 1.2 Short-term adjustment of song onset (quadratic)	Binomial GLMM (logit link)	Song onset in the noise (Yes/No)	Noise level Squared noise level Experimental day Time since start of playback Experimental round	Bird ID	1658
Model 2 First song in the morning	Gaussian LMM	Log (onset time of first song in a day)	Experimental day Experimental round	Bird ID	72
Model 3 Song in the morning before playback	Binomial GLMM (logit link)	Song onset before the playback period, i.e. before 09:00 (Yes/No)	Experimental day Experimental round	Bird ID	1842
Model 4 Song in the evening after playback	Binomial GLMM (logit link)	Song onset after the play-back period, i.e. after 19:00 (Yes/No)	Experimental day Experimental round	Bird ID	1842

of the noise (e.g. Arroyo-Solís et al. 2013; Dominoni et al. 2016), we tested this with additional analyses that investigated whether the Canaries shifted their singing activity to the silent period before or after the playback. For this purpose, we calculated the proportion of songs that were emitted before the playback started (model 3) and the proportion of songs that were emitted after the end of the playback period (model 4). Whether a song was emitted before (1) or after (0) the start (model 3) or end (model 4) of the playback period was treated as a binomial variable and modelled against the experimental day using a logistic regression. In all models, we additionally added the unique identifier of the experimental round as a fixed effect to account for the time within the breeding season. Bird identity was used as a random effect in all models to consider individual differences. Quality of model fit was assessed by visual inspection of the residual distributions. No signs of heteroscedasticity and no obvious trend in the residuals were detected. Following Abbey-Lee et al. (2016), we generated posterior distributions for each model by simulating them 1000 times using the package *arm* (v. 1.12.2). Estimates and credible intervals were defined at the mean, 0.025 and 0.975 percentile of the posterior distribution.

Results

On average, the birds produced 84 songs over the course of the experiment (range: 1–402 songs), but not every bird sang in every treatment. In cases where birds sang more than one song per day, the intervals between them were not random. As can be seen in Fig. 1, there was a marked 80-s cycle, which corresponds to the start-start interval of the noise bursts (i.e. the duration of the noise burst and the following silent period).

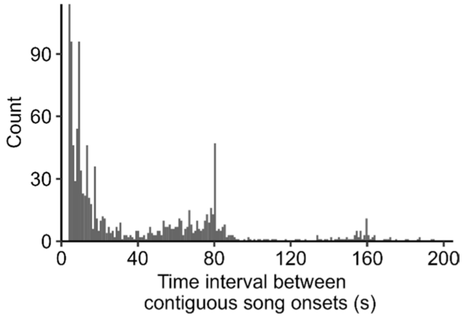

Fig. 1 Distribution of the time interval between contiguous song onsets of 22 male Canaries. Intervals exceeding 200 s are not shown

Model 1: Short-term adjustment of song onset

The probability that Canaries started a song during a noise burst was very high in all noise levels (mean = 0.86, Fig. 2a) and at all times of the day (mean = 0.88, Fig. 2b), indicating that the birds preferred to sing during the noise bursts, independently of the noise amplitude (Table 2). Including the squared noise amplitude in the model did not improve model fit (AIC for model 1.1 = 1107.8, AIC for model 1.2, with the quadratic term = 1107.2, ANOVA p-value = 0.10). The birds' preference for singing in the noise seemed to slightly increase the longer they were exposed to the noise during the day, but the effect was very small (Table 2).

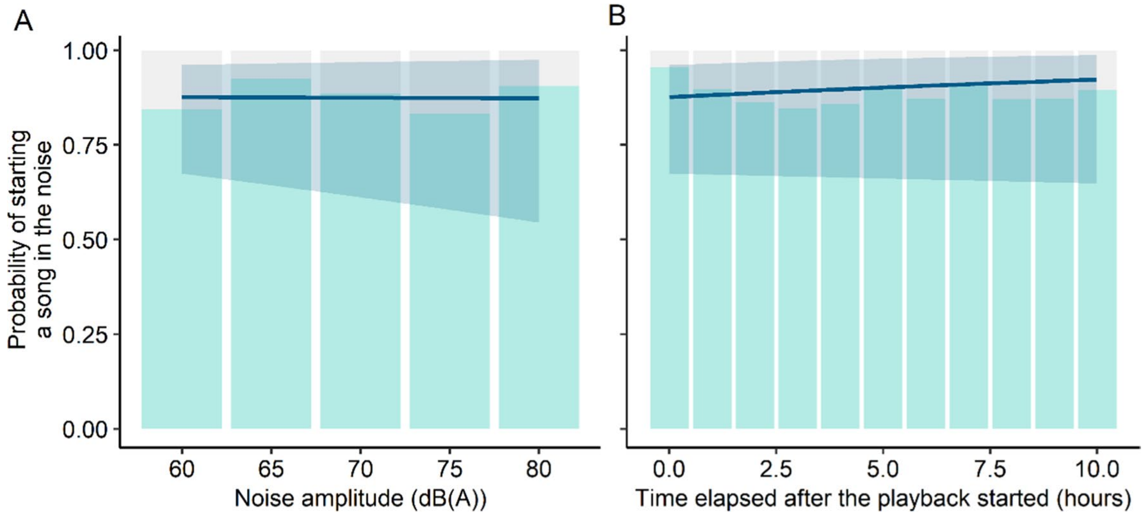

Fig. 2 Canaries started a song preferably during a noise burst. Estimate (dark blue lines) and 95% credible interval (dark blue shaded areas) of the probability that a Canary starts a song during the noise as a function of (**A**) noise amplitude and (**B**) time elapsed after the playback started. Predicted values are derived from Model 1.1: "Short-term adjustment of song onset (linear)". The proportion of song onsets in the noise (light blue bar) and outside the noise (grey bar) are shown in the bar plot

Table 2 Estimates and 95% credible intervals of the GLMM and LMM measuring the effect of noise playback on Canary singing behaviour

Model	Predictor	Estimate (95% credible interval)
Model 1.1 Short-term adjustment of song onset (linear)	(Intercept)	1.94 (0.68, 3.20)
	Noise amplitude	– 0.01 (– 0.23, 0.23)
	Experimental day	0.07 (– 0.06, 0.19)
	Time of day	0.05 (– 0.01, 0.12)
	Round 2	0.34 (– 1.42, 2.18)
	Round 3	– 2.28 (– 4.032, – 0.21)
	Round 4	0.56 (– 1.34, 2.50)
Model 2 First song	(Intercept)	1.25 (0.50, 2.00)
	Experimental day	– 0.02 (– 0.18, 0.15)
	Round 2	– 0.46 (– 1.14, 0.19)
	Round 3	– 0.44 (– 1.23, 0.35)
	Round 4	– 0.04 (– 0.75, 0.65)
Model 3 Song in the morning before playback	(Intercept)	– 5.51 (– 7.26, – 3.76)
	Experimental day	– 0.01 (– 0.17, 0.16)
	Round 2	3.14 (0.95, 5.29)
	Round 3	2.43 (– 0.15, 5.07)
	Round 4	1.91 (– 0.55, 4.24)
Model 4 Song in the evening after playback	(Intercept)	– 3.87 (– 6.22, – 1.59)
	Experimental day	– 0.27 (– 0.45, – 0.09)
	Round 2	1.49 (– 1.81, 4.88)
	Round 3	0.18 (– 4.43, 4.93)
	Round 4	0.84 (– 2.76, 4.59)

Because the birds in a given experimental round could potentially hear each other, we tested whether they triggered each other to sing and found that this was only the case in a small fraction of songs (4.5%, see Supplement). The fact that a few songs were not timed independently did not bias our result of noise stimulating song, as leaving out interacting birds when refitting model 1.1 yielded the same result (Table S2).

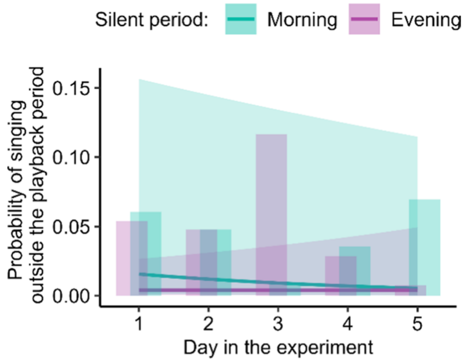

Fig. 3 Canaries did not shift their singing activity outside the noise-playback period. Estimate and 95% credible interval of the probability that Canaries sing before (morning) or after the playback period (evening) as a function of the day in the experiment (models 3 and 4). The proportions of song onsets outside the playback period are shown in the bar plots

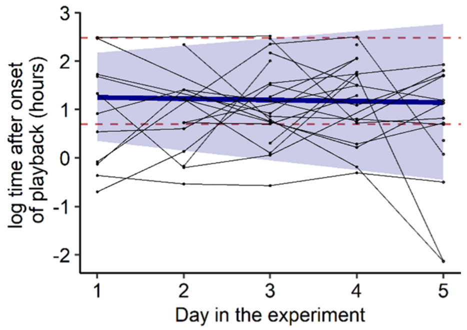

Fig. 4 Canaries did not begin singing earlier in the morning over the course of the experiment. Predicted (Estimate and 95% credible interval, model 2 “First song”) log time of the first song of a day in relation to the day in the experiment (blue line). Raw data points are indicated by black dots, black lines connect data points of a given individual. The red dashed lines indicate the start and end times of the playback (i.e. 09:00 and 19:00)

Models 2 and 3: first song and morning activity

The time at which Canaries started singing in a day did not change over the course of the experiment (Fig. 3, Table 2, model 2), and birds did not shift their singing activity to the morning (Table 2, model 3). Overall, the probability of singing before 9:00 was very low (mean = 0.004, Fig. 4). These results suggest that birds did not take advantage of the noise-free window in the morning to reduce acoustic masking. Variability in morning activity among birds was high [variance of model 3 = 2.30 (1.35, 3.59)], and it seemed that the birds of group 2, 3, and 4 tended to sing more often in the noise-free window than birds of group 1 (Table 2, model 3).

Model 4: evening activity

Birds did not shift their singing activity to the silent period after playback, rather, the probability of singing in the evening remained very low over the course of the experiment (Table 2, model 4, Fig. 3). If anything, there was a slight decrease of singing activity in the silent period after the playback. Variability in evening song activity among birds was high [variance of model 4 = 7.89 (4.68, 12.03)].

Discussion

We found that Canaries did not avoid starting to sing in noise. Contrary to our predictions, the tested birds did not reduce song onsets in noise depending on the noise amplitude nor did they shift their singing activity to the silent period before or after the noise playback. Rather we found that the birds generally preferred to start singing during noise bursts irrespective of the noise amplitude [ranging from 60 to 80 dB(A)].

The observed lack of noise avoidance is somewhat puzzling because noise mitigation is a basic mechanism in the evolution of animal communication systems (Brumm and Zollinger 2013; Wiley 2013). Frogs, for instance, call preferentially in the silent intervals between synthetic noise bursts (Zelick and Narins 1985) or heterospecific calls (Schwartz and Wells 1983). Similarly, nightingales have been found to fit their songs into the silent gaps between the songs of other species (Brumm 2006). The silent gaps between noise bursts in our experiment were longer than the normal duration of Canary song, thus allowing the birds to potentially insert their songs into these silent intervals. However, unlike frogs and nightingales, the tested Canaries did not shift song onsets into the gaps but started singing preferentially during the noise. Based on previous studies that indicated that constant noise at amplitudes above 70 dB SPL suppresses vocalisations in birds, whereas moderate noise levels between 60 and 70 dB SPL have the opposite effect of facilitating vocal production (Brumm et al. 2009; Díaz et al. 2011), we predicted that increasing noise levels would first stimulate and then inhibit song production. However, this was not supported by our data either, as the high proportion of Canary song onsets in noise remained constant across all tested noise levels.

Temporal adjustments to shift signals to quiet periods is not the only way in which animals counteract acoustic masking by noise. Perhaps Canaries rely primarily on increased song amplitudes in noise and less so on temporal adjustments. This seems conceivable as wild Canaries breed in small breeding territories close to each other (Voigt and Leitner 1998) where they are probably exposed to extended periods of masking songs from conspecifics. The Lombard effect is triggered in Canaries within a few hundred milliseconds (Hardman et al. 2017), thus the birds can quickly increase signal-to-noise ratios by increasing their vocal amplitude. Since metabolic costs for increased vocal amplitudes are low in songbirds (Zollinger and Brumm 2015), the Lombard effect is a simple, yet efficient way to reduce acoustic song masking. However, as is typical for birds (Brumm and Zollinger 2013), the Lombard effect in Canaries does not fully compensate reduced signal-to-noise ratios in high-amplitude noise (Hardman et al. 2017). Thus, the observed lack of temporal noise avoidance leads to a reduced active space of Canary songs in noisy environments and it would be interesting to know how this affects mating behaviours and male–male interactions, as successful song transmission is crucial for both (Amy and Leboucher 2009; Leboucher et al. 2012).

Whether Canaries do not show any temporal song adjustments in response to intermittent noise at all cannot be answered by our experiment. Perhaps our experimental noise was not loud enough to induce temporal shifts. We expected to see an effect at 80 dB(A) based on a previous study on chaffinches that indicated overlap avoidance at noise levels above 78 dB(A) (Dominoni et al. 2016). However, the amplitude thresholds at which birds avoid overlapping with sounds varies between species and the type of noise. For instance, common nightingales avoided overlap with heterospecific songs already at 55 dB(A) (Brumm 2006), whereas Eurasian wrens (*Troglodytes troglodytes*) did not avoid temporal overlap with traffic noise between 50 and 66 dB(A) nor with white noise at 64 dB(A) (Yang et al. 2014). If Canaries have even higher noise thresholds for than chaffinches, then this would explain the lack of effect observed in this study. Anyhow, our results, synthesised together with the findings from the current literature, suggest that there are marked species differences in the noise-induced behavioural song plasticity of birds.

Contrary to our prediction, the Canaries also did not shift their singing activities to the quiet period before or after the playback period. Several studies found that birds in heavily noise-polluted areas, such as airports, advance their singing activity to early times in the morning when environmental noise levels were still low (Gil et al. 2015; Dominoni et al. 2016). Hence, birds gain more time of uninterrupted singing. In our study, however, this could not be replicated, although the broadcasted noise levels matched the noise measured near airports (Dominoni et al. 2016). Given that the Canaries preferred to start singing in noise, it is not surprising that they did not shift their singing activity outside of the noise playback. Moreover, a recent study suggests that the advanced singing activity at airports is based on behavioural plasticity in some songbird species and on long-term, population-wide changes in others (de Framond and Brumm 2022). If Canaries belong to the second group, they may only be able to advance singing activity over several generations under strong selection for early song. Future studies, drawing on bigger samples of different species, may relate species-specific noise-mitigation strategies to ecological and behavioural traits of different bird groups.

One potential candidate for such an ecological trait could be the environmental acoustics of the habitat a species has evolved in. The wild ancestors of our study subjects occurred on Atlantic islands and while islands are not necessarily noisier than mainland habitats (Robert et al. 2019), Canary breeding habitats are often exposed to constant high levels of abiotic noise caused by strong winds and the sound of surf (Leitner pers. observation). In an environment with constant noise over considerable time periods, shifts in song timing may not be useful and environmental selection has perhaps driven Canaries to lose the faculty of short-term timing shifts that is found in other songbirds. It remains unclear though whether any potential adaptation to noisy habitats has been further intensified during domestication in this species and thus comparisons with wild-type Canaries would be worthwhile.

That the birds preferred to start singing in the experimental noise even at noise levels as high as 80 dB(A) was somewhat surprising. Moreover, the probability of starting a song in the noise even increased with time after the playback onset. Both observations indicate that the noise triggered song onset in Canaries. It is known that moderate noise may induce bird vocalisations (Brumm et al. 2009; Díaz et al. 2011; Brumm and Zollinger 2013). Indeed, sound playbacks (e.g. radio play) are sometimes used by aviculturists to induce singing in captive birds or as environmental enrichment in zoos. For instance, a study reported that birds in a zoo increased vocalisation in the presence of natural sounds of a rainforest (Robbins and Margulis 2016). But birds typically increase their vocal activity only until a certain level of moderate noise around 60–70 dB(A), above which song is supressed (Brumm et al. 2009; Díaz et al. 2011). In our study, however, all experimental noise levels [from 60 to 80 dB (A)] triggered song to the same degree. Because of this, we found a clear 80-s period of song onsets in our experiment, which means that the birds started their songs at the same time of each noise burst, indicating a very robust song trigger with negligible habituation, if any at all.

In view of noise eliciting bird vocalisations, we advocate a more comprehensive conception of noise that incorporates both supressing as well as stimulating effects. In the past, bird song studies have regarded noise chiefly as a masking problem and hence examined how birds increase the signal-to-noise ratio of their vocalisations (Brumm and Zollinger 2013). However, for reasons yet unknown, the tested Canaries generally chose to sing during short noise bursts, which led to the most unfavourable signal-to-noise ratios for communication. A better understanding of this paradox will deepen our knowledge about vocal control mechanisms in songbirds (Brenowitz 1997), which ultimately may constrain song evolution (Podos et al. 2004). In addition, more insight into the mechanism and potential functions of noise-induced singing will also be valuable for conservation issues, as our findings raise the possibility that anthropogenic noise may have unexpected effects on animal behaviour and, in turn, on resulting ecological processes.

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