Anthropogenic noise affects vocal interactions

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Abstract

Animal communication plays a crucial role in many species, and it involves a sender producing a signal and a receiver responding to that signal. The shape of a signal is determined by selection pressures acting upon it. One factor that exerts selection on acoustic signals is the acoustic environment through which the signal is transmitted. Recent experimental studies clearly show that senders adjust their signals in response to increased levels of anthropogenic noise. However, to understand how noise affects the whole process of communication, it is vital to know how noise affects the receiver's response during vocal interactions. Therefore, we experimentally manipulated ambient noise levels to expose male European robins *(Erithacus rubecula)* to two playback treatments consisting of the same song: one with noise and another one without noise. We found that males responding to a conspecific in a noise polluted environment increased minimum frequency and decreased song complexity and song duration. Thus, we show that the whole process of communication is affected by noise, not just the behaviour of the sender.

1. Introduction

Communication plays a crucial role in many species as it is used in sexual selection through both female choice and male-male competition, in parental care among parents and their offspring, and in predator prey interaction (Bradbury and Vehrencamp, 2011). Animal communication in its simplest form involves a sender producing a signal that conveys information, and a receiver making a decision on how to respond to that signal (Bradbury and Vehrencamp, 2011). During such vocal interactions individuals exchange information about their quality, status or motivation (Todt and Naguib, 2000; Vehrencamp, 2000). Thus, for the process of communication to be completed, it is vital that the sender is able to successfully transmit the signal across the environment to the receiver.

The shape of a signal is determined by different constraints. Sexually selected traits, such as bird song, are shaped by an interaction between sexual selection and other natural selection pressures. Sexual selection favours the elaboration of traits, whereas the elaboration of a trait might be counteracted by natural selection processes optimizing both transmission and detectability of signals (e.g. Wiley and Richards, 1982; Patricelli and Blickley, 2006). One environmental factor that exerts selection pressure on acoustic signals is ambient noise, which can mask the information in a signal (Ryan and Brenowitz, 1985). A relatively novel form of ambient noise is anthropogenic noise.

A growing number of experimental studies have demonstrated that senders adjust their signals to anthropogenic noise. In birds, one strategy to avoid masking of signals by low-frequency anthropogenic noise is through an increase in minimum frequency (Halfwerk and Slabbekoorn, 2009; Gross et al., 2010; Verzijden et al., 2010; Bermudez-Cuamatzin et al., 2011; Hanna et al., 2011; McLaughlin and Kunc, 2013; Montague et al., 2013). A similar response to increasing noise levels was reported in anura where individuals called at higher dominant frequencies when experimentally exposed to anthropogenic noise (Cunnington and Fahrig, 2010). Thus, increasing anthropogenic noise levels have a clear impact on the signalling behaviour of the sender. These changes in signal characteristics also affect the response of receivers. Great tits, for example, respond differently to conspecific songs recorded in noisy areas than in quiet areas when background noise was removed (Mockford and Marshall, 2009). However, to understand how noise affects the whole process of communication, it is vital to know how noise affects song during vocal interactions.

In the European robin, *Erithacus rubecula*, males produce complex songs, and they use their song to interact with conspecifics (Hoelzel, 1986; Brindley, 1991). Recent studies showed that robins also adjust their songs to increasing noise levels. Robins recorded in noisy locations sang songs at higher minimum frequencies, which were less complex and shorter in duration as songs recorded in quiet locations. These observational findings were then confirmed by noise exposer experiments (McLaughlin and Kunc, 2013; Montague et al., 2013). Thus, robins provide an ideal model to test also how individuals during a vocal interaction are affected by anthropogenic noise.

The aim of this study was to investigate how noise affects responses during vocal interactions. We experimentally manipulated ambient noise levels to expose male European robins *(Erithacus rubecula)* to two playback treatments consisting of the same song: one with noise and another one without noise (Fig. 1). If vocal interactions were affected by changes in noise during the playbacks we predicted a different response to the two treatments.

2. Materials and Methods

2.1. Recording and Noise Playback Protocol

The experiment was conducted on European robins between February and June 2011 in Northern Ireland. To create playback stimuli, we recorded the songs of 18 European robin males in quiet areas using a solid state recorder (Marantz PMD660, .wav format, sample frequency 44.1 kHz, resolution 16 bit) connected to a Sennheiser ME 66/K6 microphone. From each of the 18 recordings, songs for playback were selected from sonograms (sample frequency = 44.1 kHz, FFT = 512, overlap = 93.75%, time resolution = 5.8 ms) generated with Avisoft SASlab Pro (R. Specht, Berlin). To simulate an average singing male with a song rate of 7 songs/min (Montague et al., 2013), we randomly selected 21 songs of each recording to create playback files of 3 min duration. Songs for each playback were arranged in Audacity (1.2.6) and normalised to the peak amplitude. A copy of each playback file was merged with a standardised traffic noise recording obtained from motorway bridges during rush hours (for details see (Gross et al., 2010).

The experiment comprised two treatments: playbacks of the same stimulus songs with and without traffic noise. As subjects we chose males in quiet areas, different from those recorded to create the stimuli. Each of the 18 subjects received both treatments, separated by a 3 minute silent interval. Each subject's singing behaviour was recorded during the two three minute playback treatments with the same equipment as described above. Treatment order was randomised, with the constraint that treatments were balanced (Milinski, 1997). Background noise levels (dB(A)) were measured with a digital sound-level metre SL-100 (Voltcraft, Hirschau). Background noise levels in territories where experiments were conducted were below 50 dB(A).

Stimuli were played from a Marantz PMD660 connected to a SME-AFS loudspeaker (Saul Mineroff Electronics, USA) positioned 15-20 m from the subject's song post, facing the subject, without obstacles in between. The volume of the stimuli was adjusted before playback to 80 dB(A) at 1 m, as measured with the sound-level meter. To analyse singing responses of the 18 subjects, we randomly selected 10 songs from each recording in both treatments (McLaughlin and Kunc, 2013). For each song, we measured (i) minimum frequency (kHz), i.e. the lowest frequency of any syllable in the song; (ii) song complexity, i.e. the number of different elements; (iii) song length (seconds); and (iv) song rate, i.e. the number of songs per minute. For a detailed description of acoustic measurements see (Slabbekoorn and Peet, 2003; Hu and Cardoso, 2009; Verzijden et al., 2010; Francis et al., 2011; McLaughlin and Kunc, 2013; Montague et al., 2013).

It is important to note that the aim of our study was to test how noise affects the receiver's response during a vocal interaction, and not how singing behaviour differs between an individual singing on its own during low and high levels of noise (c.f., Halfwerk and Slabbekoorn, 2009; Gross et al., 2010; Verzijden et al., 2010; Bermudez-Cuamatzin et al., 2011; Hanna et al., 2011; McLaughlin and Kunc, 2013; Montague et al., 2013).

2. 2. Statistical Analysis

To test whether the presence of ambient noise affected receivers' responses, we used paired t-tests in R (2011) for each song parameter.

3. Results

Males' singing behaviour differed between the two playback treatments. During the playback of song with noise, males sang at a higher minimum frequency ($t_{17} = -7.1$, $p < 0.001$, Fig. 2a) than during the playback of song without noise. Males also sang less complex songs ($t_{17} = 2.7$, $p = 0.01$, Fig. 2b), and shorter songs ($t_{17} = 3.3$, $p = 0.004$, Fig. 2c) during the playback of song with noise than during the playback of song without noise. However, song rate did not differ significantly between the two treatments ($t_{17} = 1.5$, $p = 0.2$, Fig. 2d).

4. Discussion

To our knowledge, this is the first experimental evidence in the wild that changes in ambient noise levels affects vocal interactions. Thus, the whole process of communication is affected by noise, not just the behaviour of the sender. Adjustments to changes in the acoustic environment can affect the outcome of communication, because even slight signal adjustments decrease transmission efficiency as well as individual or species recognition (Wiley and Richards, 1982; Nelson, 1989; Mockford and Marshall, 2009; Mockford et al., 2011).

The adjustments of different song parameters may affect the outcome of male-male competition and female choice. In some species, for example, low-frequency song is correlated with fighting ability, and females prefer males singing at lower frequencies (ten Cate et al., 2002; Cardoso, 2012). Moreover, complex and/or long songs are advantageous in repelling opponents as well as in attracting females (Catchpole and

Slater, 2008). Therefore, males responding to a rival in a noisy environment face a human-generated trade-off between producing a signal that is effective at repelling other males and attracting females, versus a signal that is effective in noisy conditions. However, we show that ambient noise causes the receiver to respond to an opponent with less complex and shorter songs. Thus, changes in the acoustic environment affect both the signal of the sender (Cunnington and Fahrig, 2010; Gross et al., 2010; Verzijden et al., 2010; Bermudez-Cuamatzin et al., 2011; Hanna et al., 2011; Montague et al., 2013) but also the receiver's response to the signaller. These changes in signal characteristics of both sender and receiver could have far reaching consequences because animals exchange information about their quality, status or motivation during vocal interactions (Todt and Naguib, 2000; Vehrencamp, 2000). Changes in the dynamics of such interactions may affect the ability of males to mediate conflicts between each other and the choice of females (Mennill, Ratcliffe and Boag, 2002; Mennill et al., 2003; Kunc, Amrhein and Naguib, 2006; Schmidt et al., 2006; Kunc et al., 2007). This is in line with a recent finding in fish, where agonistic behaviour was influenced by anthropogenic noise (Sebastianutto et al. 2011). Thus, environmental changes may affect not only sexually selected traits, such as bird song per se, but also social interactions between individuals.

Adjustments to changing environmental conditions can occur through either phenotypic plasticity or micro-evolutionary responses to natural selection (West-Eberhard, 1989; Pigliucci, 2005; Charmantier et al., 2008). A growing body of experimental studies show that adjustments of the sender in signalling to changes in the acoustic environment are based on phenotypic behavioural plasticity (e.g. Gross et al., 2010; Verzijden et al., 2010; Bermudez-Cuamatzin et al., 2011; Hanna et al., 2011; Montague et al., 2013). In contrast to previous noise exposure experiments which were confined to playback of anthropogenic noise we additionally played back the song of a conspecific. Therefore, receivers also show a plastic response over a remarkably short time scale to changes in the acoustic environment. Interestingly, the adjustments in song characteristics found in this study are similar to the adjustments reported recently in robins when singing alone (McLaughlin and Kunc, 2013; Montague et al., 2013). This suggests that the adjustments in song characteristics during vocal interactions and in situations in which an individual is singing alone have a similar underlying mechanism.

Regarding the behavioural adjustments observed in our experiment, a number of possible mechanisms may be involved. Birds may increase the minimum frequency in response to increasing noise levels (Slabbekoorn and Peet, 2003), and/or they may sing louder (Brumm 2004; Nemeth and Brumm, 2010). A correlational study showed that in blackbirds amplitude is positively correlated with minimum frequency and peak frequency (Nemeth et al. 2013). A recent experimental study, however, demonstrates that birds can adjust the frequency of their song independently of the songs amplitude (Potvin and Mulder, 2013). A more complex analysis including more song characteristics, although not song amplitude, has shown that the plastic response of minimum frequency in response to increasing noise level restricts the elaboration of other song characteristics such as song complexity (Montague et al. 2013). Taken all these results together, birds adjust their songs in response to increasing noise levels irrespective of whether they sing on their own or whether they are involved in a vocal interaction. This suggests that vocal responses are more affected by changes in the acoustic environment rather than by the sender's signal.

In conclusion, our study provides evidence that individuals adjust their signals during vocal interactions to changes in the acoustic environment. Anthropogenically induced changes in acoustic signals may have fundamental consequences, because animals exchange information on their quality, status or motivation during vocal interactions. Therefore, changes in the entire communication process have to be considered to understand how species are affected by anthropogenic changes in the acoustic environment.

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References

Bermudez-Cuamatzin, E., Rios-Chelen, A. A., Gil, D., Macıas Garcia, C., 2011. Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. Biol. Lett. **7**, 36-38.

Bradbury, J. W., Vehrencamp, S. L., 2011. *Principles of Animal Communication*. 2nd edn. . Sunderland: Sinauer Associates.

Brindley, E. L., 1991. Response of European robins to playback of song: neighbour recognition and overlapping. Anim. Behav. **41**, 503-512.

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. J. Anim. Ecol. **73**, 434-440.

Cardoso, G. C., 2012. Paradoxical calls: the opposite signaling role of sound frequency across bird species. Behav. Ecol. **23**, 237-241.

Catchpole, C. K., Slater, P. J. B., 2008. Bird song: Biological themes and variation. 2nd. Cambridge: Cambridge University Press.

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., Sheldon, B. C., 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science **320**, 800-803.

Cunnington, G. M., Fahrig, L., 2010. Plasticity in the vocalizations of anurans in response to traffic noise. Acta Oecologica **36**, 463-470.

Francis, C. D., Ortega, C. P., Cruz, A., 2011. Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. Proc. Roy. Soc. B **278**, 2025-2031.

Gross, K., Pasinelli, G., Kunc, H. P., 2010. Behavioral plasticity allows short-term adjustment to a novel environment. Am. Nat. **176**, 456-464.

Halfwerk, W., Slabbekoorn, H., 2009. A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. Anim. Behav. **78**, 1301-1307.

Hanna, D., Blouin-Demers, G., Wilson, D. R., Mennill, D. J., 2011. Anthropogenic noise affects song structure in red-winged blackbirds (*Agelaius phoeniceus*). J. Exp. Biol. **214**, 3549-3556.

Hoelzel, A. R., 1986. Song characteristis and response to playback of male and female robins *Erithacus rubecula*. Ibis **128**, 115-127.

Hu, Y., Cardoso, G. C., 2009. Which birds adjust the frequency of vocalizations in urban noise? Anim. Behav. **79**, 863-867.

Kunc, H. P., Amrhein, V., Naguib, M., 2006. Vocal interactions in nightingales, *Luscinia megarhynchos*: more aggressive males have higher pairing success. Anim. Behav. **72**, 25-30.

Kunc, H. P., Amrhein, V., Naguib, M., 2007. Vocal interactions in common nightingales (*Luscinia megarhynchos*): males take it easy after pairing. Behav. Ecol. Sociobiol. **61**, 557-563.

McLaughlin, K. E., Kunc, H. P, 2013. Experimentally increased noise levels change spatial and singing behaviour. Biol. Lett. **9**, 20120771.

Mennill, D. J., Boag, P. T., Ratcliffe, L. M., 2003. The reproductive choices of eavesdropping female black-capped chickadees, *Poecile atricapillus*. Naturwiss. **90**, 577-582.

Mennill, D. J., Ratcliffe, L. M., Boag, P. T., 2002. Female eavesdropping on male song contests in songbirds. Science **296**, 873-873.

Milinski, M., 1997. How to avoid seven deadly sins in the study of behavior. Adv. Stud. Behav. **26**, 159-180.

Mockford, E. J., Marshall, R. C., 2009. Effects of urban noise on song and response behaviour in great tits. Proc. Roy. Soc. B **276**, 2979-2985.

Mockford, E. J., Marshall, R. C., Dabelsteen, T., 2011. Degradation of rural and urban great tit song: testing transmission efficiency. PLoS ONE **6**, e28242.

Montague, M. J., Danek-Gontard, M., Kunc, H. P., 2013. Phenotypic plasticity affects the response of a sexually selected trait to anthropogenic noise. Behav. Ecol. **24**, 343-348

Nemeth E, Brumm H., 2010. Birds and Anthropogenic Noise: Are Urban Songs Adaptive? Am. Nat. 176:465–475.

Nelson, D. A., 1989. Song frequency as a cue for recognition of species and individuals in the field sparrow (*Spizella pusilla*). J. Comp. Physiol. **103**, 171-176.

Patricelli, G. L., Blickley, J. L., 2006. Avian communication in urban noise: causes and consequences of vocal adjustment. Auk **123**, 639-649.

Pigliucci, M., 2005. Evolution of phenotypic plasticity: where are we going now? Trends Ecol. Evol. **20**, 481-486.

Potvin, D. A., Mulder, R. A. 2013. Immediate, independent adjustment of call pitch and amplitude in response to varying background noise by silvereyes (*Zosterops lateralis*). Behav. Ecol. **24**, 1363–1368.

Ryan, M. J., Brenowitz, E. A., 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. Am. Nat. **126**, 87-100.

Schmidt, R., Kunc, H. P., Amrhein, V., Naguib, M., 2006. Responses to interactive playback predict future pairing success in nightingales. Anim. Behav. **72**, 1355-1362.

Sebastianutto, L., Picciulin, M., Costantini, M., Ferrero, E. A. 2011. How boat noise affects an ecologically crucial behaviour: the case of territoriality in *Gobius cruentatus (Gobiidae)*. Environ. Biol. Fish. 92:207-215.

Slabbekoorn, H., Peet, M., 2003. Ecology: Birds sing at a higher pitch in urban noise - Great tits hit the high notes to ensure that their mating calls are heard above the city's din. Nature **424**, 267-267.

R Development Core Team, 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org/.

ten Cate, C., Slabbekoorn, H., Ballintijn, M. R., 2002. Birdsong and male-male competition: Causes and consequences of vocal variability in the collared dove (*Streptopelia decaocto*). Adv. St. Behav. **31**, 31-75.

Todt, D., Naguib, M., 2000. Vocal interactions in birds: the use of song as a model in communication. Adv. St. Behav. **29**, 247-296.

Vehrencamp, S. L., 2000. Handicap, index, and conventional signal elements of bird song. In *Animals Signals: Signal design in animal communication*. Espmark, Y., Amundsen, T., Rosenqvist, G. (Eds.). Trondheim: Tapir Academic Press.

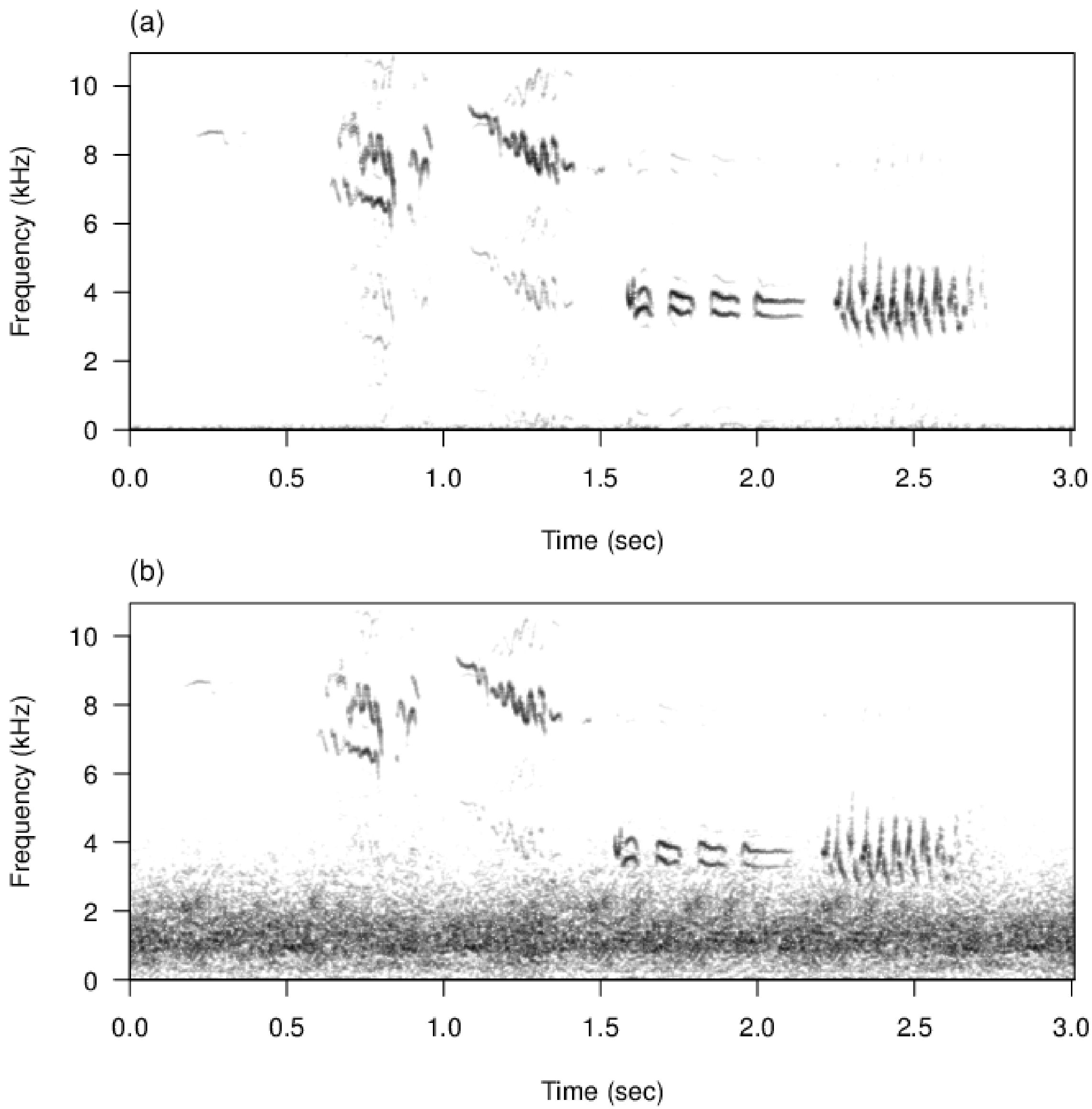
Verzijden, M. N., Ripmeester, E. A. P., Ohms, V. R., Snelderwaard, P., Slabbekoorn, H., 2010. Immediate spectral flexibility in singing chiffchaffs during experimental exposure to highway noise. J. Exp. Biol. **213**, 2575-2581.

West-Eberhard, M. J., 1989. Phenotypic Plasticity and the Origins of Diversity. Ann. Rev. Ecol. Syst. **20**, 249-278.

Wiley, R. H., Richards, D. G., 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In *Acoustic communication in birds*: 131-181. Kroodsma, D. E., Miller, E. H. (Eds.). New York: Academic Press.

Fig. 1 Sonagrams of song stimuli used of a European robin played back as (a) song without anthropogenic noise and (b) song with anthropogenic noise.

Fig. 2 Mean ± SE (a) minimum frequency, (b) song complexity, (c) song duration, and (d) song rate of individuals responding to playback of conspecific song without (white bars) and with anthropogenic noise (grey bars).


(a)
Frequency (kHz)
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(b)
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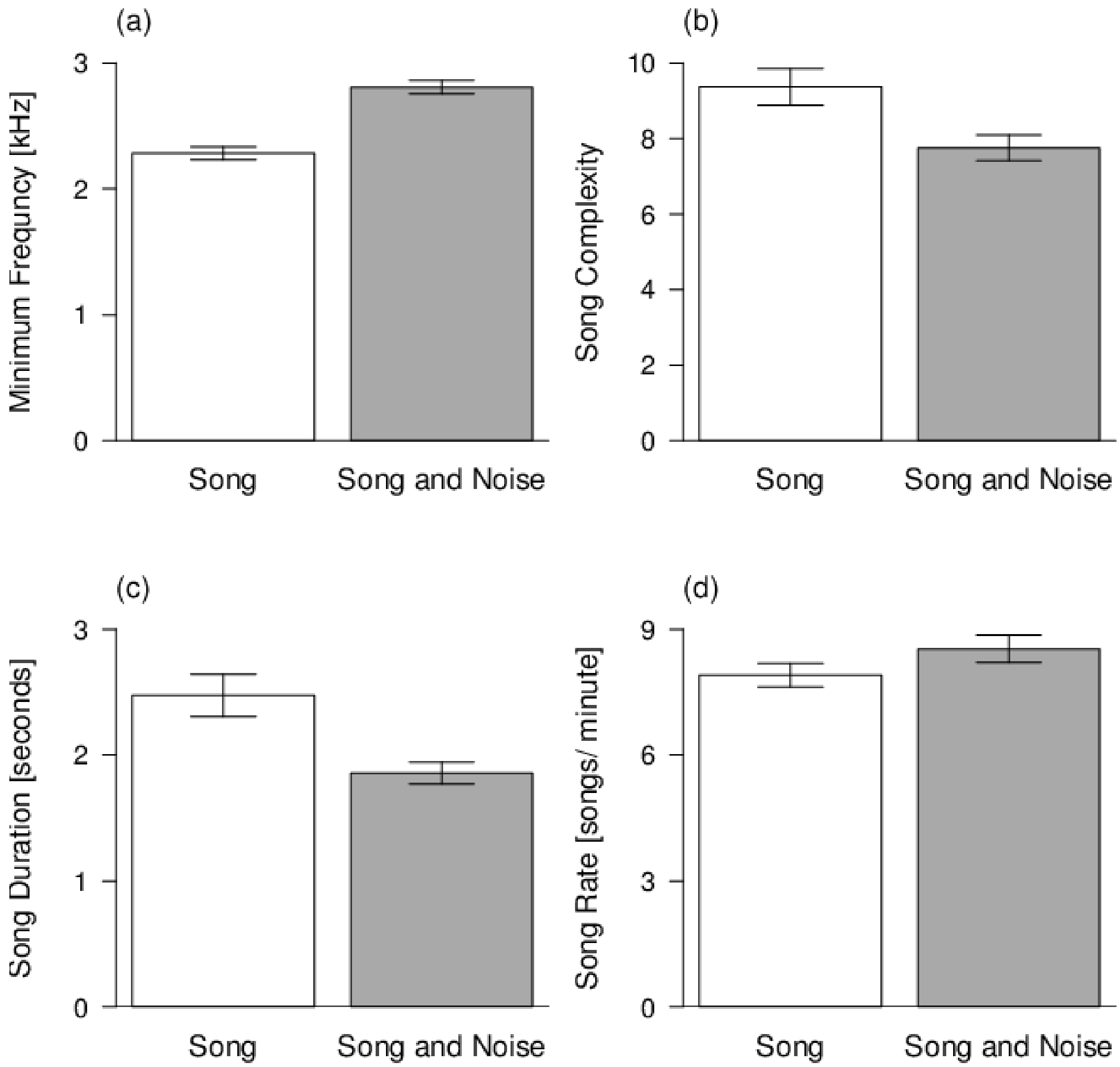
(a)
Minimum Frequncy [kHz]
3
2
1
0
Song
Song and Noise
(b)
Song Complexity
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8
6
4
2
0
Song
Song and Noise
(c)
Song Duration [seconds]
3
2
1
0
Song
Song and Noise
(d)
Song Rate [songs/ minute]
9
6
3
0
Song
Song and Noise

331