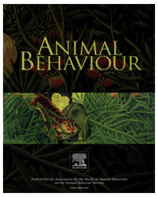
Animal Behaviour 92 (2014) 111–116

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Can animals detect differences in vocalizations adjusted for anthropogenic noise?

David Luther*, Jessica Magnotti

Biology Program, George Mason University, Fairfax, VA, U.S.A.

ARTICLE INFO

Article history:
Received 10 October 2013
Initial acceptance 2 December 2013
Final acceptance 18 March 2014
Published online
MS. number: A13-00844R3

Keywords:
animal communication
anthropogenic noise
birdsong
Cardinalis cardinalis
northern cardinal

Most animals use vocalizations to attract mates and defend territories. Many species alter these signals in the presence of anthropogenic noise, such as rush-hour traffic. Yet, little is known about how intended receivers (territorial rivals, potential mates) respond to these altered signals. Here we investigated responses of free-living male northern cardinals, *Cardinalis cardinalis,* to computer-generated songs that mimicked (1) the population's average minimum-frequency song ('average frequency' song) and (2) songs that had been shifted to have a higher minimum frequency ('shifted-frequency' song), as occurs in the presence of loud anthropogenic noise. Males gave stronger responses to songs of average frequency than to songs with a shifted frequency. At low levels of background noise, differences in responses to two song types were greatest, but as the amplitude of anthropogenic noise increased, differences in responses to the two song types diminished, and at the highest amplitudes, males had almost equal responses to the two song types. Since the shifted-frequency songs received weaker responses than the average-frequency songs, the shifted-frequency songs do not seem advantageous in terms of communication efficacy, especially at low levels of background noise. Songs with a higher minimum frequency are not necessarily beneficial for signal efficiency and might not be adaptive despite potential benefits of masking avoidance, which could have important consequences for mate selection and resource defence among populations in urban areas.

Most animals use acoustic signals to communicate to intended receivers, such as potential mates and territorial rivals (Bradbury & Vehrencamp, 1998). Human-generated noise, which is predominately lower than or in the same bandwidth as the communication signals of most vertebrate animals, is known to disrupt animal communication both in terrestrial and aquatic environments (Barber, Crooks, & Fristrup, 2010; Francis, Ortega, & Cruz, 2011; Goodwin & Shriver, 2011; Lampe, Schmoll, Franzke, & Reinhold, 2012; Nowacek, Thorne, Johnston, & Tyack, 2007). Animals including whales, birds, insects and frogs adjust their acoustic signals, presumably to avoid interference from human-generated noise and to improve their communication efficiency (Lampe, et al., 2012; Nemeth & Brumm, 2009; Nowacek et al., 2007; Parris, Velik-Lord, & North 2009; Patricelli & Blickley, 2006; Slabbekoorn & den Boer-Visser, 2006; Slabbekoorn & Peet, 2003).

One of the most widespread and consistent adjustments observed in animal vocalizations is to raise the minimum frequency in the presence of anthropogenic noise (Hu & Cardoso, 2010; Nemeth & Brumm, 2009; Patricelli & Blickley, 2006; Slabbekoorn & den Boer-Visser, 2006; Slabbekoorn & Peet, 2003; Wood & Yezerinac, 2006), which could increase the signals' contrast with anthropogenic background noise. Alternatively, animals could increase the amplitude of their vocalization to be heard above the din of background noise. Or, an animal could increase the amplitude and shift the frequency to increase the signal-to-noise ratio and improve signal detection (Nemeth & Brumm, 2010; Nemeth et al., 2013). Increased contrast with background noise should improve detection and discrimination by intended receivers (Klump, 1996; Luther & Gentry, 2013; Wiley, 1994, 2006). However, adjustments to the minimum frequency of acoustic signals could have negative consequences for signallers. The perceived quality of the signaller and the information in adjusted signals could elicit different responses from intended receivers, such as potential mates and territorial rivals, compared with responses to nonadjusted signals. If intended receivers can perceive the difference between these signals, there could be fitness consequences for the signaller, such as possible cuckoldry (Halfwerk et al., 2011) or reduced pairing success (Francis & Barber, 2013; Francis, Kleist, Davidson, Ortega, & Cruz, 2012).

---

* Correspondence: D. Luther, Biology Program, George Mason University, Fairfax, VA 22030, U.S.A.

E-mail address: dluther@gmu.edu (D. Luther).

http://dx.doi.org/10.1016/j.anbehav.2014.03.033
0003-3472/© 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Despite several studies that have documented adjustments of acoustic signals in the presence of anthropogenic noise, there are surprisingly few studies on the responses of intended receivers to the adjusted signals (but see Halfwerk et al., 2011; Luther & Derryberry, 2012; Mockford & Marshall, 2009; Ripmeester, Mulder, & Slabbekoorn, 2010). The true test of the adaptive value of a signal with a higher minimum frequency is to investigate how intended receivers respond to the altered signal. The functional compromise hypothesis states that signals adjusted for anthropogenic noise, such as those with a higher minimum frequency, could be beneficial for detection by avoiding masking from low-frequency anthropogenic noise, but could be functionally detrimental if the lower frequencies of the signal carry important information that is lost when the signal is altered. Therefore, signallers face a potential trade-off of signalling at a higher frequency to improve the detection of their signals or signalling with a lower minimum frequency to convey important information within their signal (Gross, Pasinelli, & Kunc, 2010; Slabbekoorn, 2013; Slabbekoorn & Ripmeester, 2008). To make matters even more complicated, these decisions could be noise dependent, as under quiet and noisy conditions animals might vocalize differently.

In this paper, we tested whether northern cardinals, *Cardinalis cardinalis*, respond differently to signals that are adjusted to have a higher minimum frequency (a ‘shifted frequency’) than they do to signals that are not adjusted (population ‘average frequency’). If shifted-frequency signals are beneficial, we hypothesized that, under noisy conditions, shifted-frequency signals would be advantageous compared to average-frequency signals because shifted-frequency signals should be better for signal detection. However, if shifted-frequency signals are functionally detrimental but more beneficial for detection, then average-frequency signals should elicit stronger responses than shifted-frequency signals in quiet conditions and equal responses in louder conditions. Finally, the shifted-frequency signals could be beneficial both functionally and for signal detection; if true, then shifted-frequency signals would elicit stronger responses under both quiet and noisy conditions. Therefore, receivers might have stronger responses to the shifted-frequency signals compared to the average-frequency signals, which would reinforce the adjustment in the presence of anthropogenic noise.

METHODS

Study Population

Research was conducted at sites throughout the greater Washington, D.C. metropolitan area. Study sites were part of the Smithsonian Neighborhood Nestwatch citizen science project (http://nationalzoo.si.edu/ConservationAndScience/MigratoryBirds/Research/Neighborhood_Nestwatch), as well as other locations in the vicinity of the campus of George Mason University, Fairfax, VA, U.S.A. At each study site, we measured ambient noise level using a RadioShack Realistic digital sound level meter, A weighted, fast response. Ambient noise measurements were taken from the centre of each northern cardinal territory, the same location as the playback, for 4 min total in four directions, north, south, east and west, and the average readings in each direction were recorded and averaged among the four directions. We took readings within 5 min of the presentation of the songs, between 0630 and 1000 hours, on the same day that songs were presented at the site.

The northern cardinal is a year-round resident in much of the eastern portion of North America. It is quite common in and around suburban and urban regions, as well as more natural locations (Halkin & Linville, 1999). Northern cardinals are an excellent subject for this research as they are easily observed, vocally active and have been observed to adjust the minimum frequency of their songs in the presence of anthropogenic noise (Dowling, Luther, & Marra, 2012).

Song Synthesis

We synthesized northern cardinal songs in Matlab using the average timing and frequency characteristics of wild songs. We recorded 14 northern cardinal songs in the greater Washington, D.C. region using a Sony TCM-5000EV tape recorder and a Sennheiser ME 66 shotgun microphone. Recordings were digitized and analysed with Wildspectra at a sampling rate of 22 050 Hz, a frequency resolution of 344 Hz and a temporal resolution of 2.9 ms (see Dowling et al., 2012). We averaged the timing and frequency parameters, such as minimum, maximum and dominant frequency, song duration, note length and time between notes to create an average song type for the northern cardinal population in the greater Washington, D.C. region. Synthesized songs were frequency-modulated swept sine waves; the range of frequencies, the shape of the sweep and the timing of notes and note intervals all reflect the population average of northern cardinals in the greater Washington, D.C. region based on the aforementioned recordings. In addition, we created a song with a higher minimum frequency to represent the adjustment that northern cardinals make in the presence of anthropogenic noise (see Dowling et al., 2012). The altered song had a minimum frequency that was 345 Hz higher than that of the synthesized population average song, but was the same as the population average song in every other way (Fig. 1).

Playback Experiments

We presented each treatment to 30 territorial northern cardinal males. All playbacks were conducted between 0630 and 1000 hours. Both treatments were in the same location near the centre of a male’s territory with a RadioShack amplified speaker connected to 5 m cable and an iPod. Once the speaker was in place and the male cardinal had been located and silent for 3 min, we selected one of the two treatments at random and played it in a loop for 1 min. Behavioural observation lasted for 10 min after the song played. Treatments were separated by at least 48 h to minimize any carryover effects from previous trials. We did not test territorial neighbours on the same day. Both trials had overlapping ambient noise conditions with a difference of less than 1 dB, as measured within 5 min of the playback. However, at four sites, the difference in sound pressure level between the two trials was greater than 1 dB for each trial, and responses of males at these four sites were excluded from the analysis. Each subject received treatments in a random order. We adjusted the peak amplitude of all playbacks to approximate that of natural songs (81 dB at 1 m, Realistic digital sound level meter, A weighted, fast response).

We recorded (1) closest distance of the subject to the speaker (in m), (2) time from the start of playback to the subject’s first song (latency of song in min), (3) number of songs sung by the subject, (4) number of flights by the subject within 1 m of the speaker and (5) number of duets. Low values for measures 1 and 2 and high values for measures 3–5 indicated strong responses to playback. Response variables were used in matched-pairs t tests to compare individual responses to the average-frequency and shifted-frequency songs. We used Bonferroni correction to address the use of multiple comparisons (adjusted $\alpha = 0.01$).

To determine whether there was an interaction between background noise level and playback song type, we used an ANCOVA on each of two response variables, number of songs and number of flights past the speaker. In paired t tests, these two variables had the