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Immediate, independent adjustment of call pitch and amplitude in response to varying background noise by silvereyes (*Zosterops lateralis*)

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Many birds raise the pitch of their vocalizations in urban environments, a shift generally attributed to avoidance of low frequencies vulnerable to masking by anthropogenic noise (acoustic adaptation hypothesis [AAH]). However, high frequencies could just be an incidental byproduct of singing more loudly (Lombard hypothesis). If birds cope with background noise by singing more loudly and increases in frequency are byproducts of increased amplitudes, they should respond with louder songs (and increased pitch) to either high- (HFN) or low-frequency noise (LFN) of similar amplitude. However, if birds adaptively adjust frequency to minimize interference, they should increase frequency in response to LFN but decrease it in response to HFN. We exposed silvereyes (*Zosterops lateralis*), which use higher songs and calls in urban areas, to high- and low-frequency background noise of standardized amplitude. Silvereyes from both rural and urban areas exposed to HFN responded by lowering the minimum frequencies of their calls, and this shift was independent of call amplitude, which increased in all noise treatments. These findings support the AAH. Calls during HFN treatments were also longer than those made during quiet treatments. Our results suggest that silvereyes are capable of flexible adjustments of call frequency, amplitude, and duration to maximize signal-to-noise ratio in noisy environments.

Key words: **behavioral flexibility, contact calls, silvereyes, *Zosterops lateralis*.**

INTRODUCTION

There are 2 competing hypotheses to explain why songbirds raise the lowest frequencies of their songs in urban habitats (Slabbekoorn and Peet 2003; Brumm 2006; Wood et al. 2006; Nemeth and Brumm 2009; Francis et al. 2011b; Potvin et al. 2011). The acoustic adaptation hypothesis (AAH; Morton 1975) proposes that animals adaptively shift song or call frequency (pitch) to improve broadcast fidelity in noisy environments. In urban areas, where anthropogenic noise is concentrated in the low-frequency range (1–4 kHz), the AAH predicts that birds should shift song pitch upwards to avoid masking or interference (Slabbekoorn and den Boer-Visser 2006). Changes in pitch shifts of urban bird songs have consistently been attributed to the AAH, and evidence for both real-time flexibility of songs as well as cultural evolution (the transmission of adaptive memes between generations) in this context have been observed (Halfwerk and Slabbekoorn 2009; Verzijden et al. 2010; Bermudez-Cuamatzin et al. 2011; Cardoso and Atwell 2011a; Potvin and Parris 2012). An alternative hypothesis, the Lombard hypothesis (LH; Brumm and

Naguib 2009; Nemeth and Brumm 2010) instead proposes that animals increase the amplitude (loudness) of their acoustic signals when in a noisy environment because any improvement in transmission gained by shifting pitch is negligible compared with that gained from shifting amplitude (Nemeth and Brumm 2010). Increasing the amplitude of a vocalization may result in a pitch shift upwards in birds (Beckers et al. 2003), possibly explaining why higher-pitched songs (and calls) are found in urban environments.

We attempted to distinguish between these hypotheses with a novel experiment on the silvereye (*Zosterops lateralis*), a native Australian bird that sings and calls at higher frequencies in urban areas (Potvin et al. 2011). We recorded vocal (contact call) responses of silvereyes to experimental playback of 1) a simulated quiet environment, 2) an environment with low-frequency noise (LFN), and 3) an environment with high-frequency noise (HFN). The LH predicts increases in call amplitude to all noise treatments, which should be manifested in an upward shift in call frequency across all treatments (Beckers et al. 2003). In contrast, if birds are capable of flexibly adjusting vocalization frequency to the current environment, this predicts a shift in frequency of calls away from the source of interference; that is, upwards in response to LFN (e.g., urban noise) and downwards in response to HFN (e.g., other bird or insect vocalizations), regardless of call amplitude.

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Our test assumes that birds are capable of adjustments in both amplitude and frequency. But if contact calls are inflexible, individuals may not be able to react to noise with observable shifts. If so, calls would remain consistent within individuals, yet we might observe consistent differences in the frequencies of calls across treatments depending on their source (urban vs. rural). For instance, if urban birds have acoustically adapted over generations to their environment, we may see a difference between call frequencies of urban and rural birds regardless of experimental treatment. To account for this, we sourced birds from both rural and urban populations for our experiment.

METHODS

Experimental set-up and procedure

In November and December 2011, we caught wild silvereyes from an urban (Darebin Parklands, Melbourne: −37.78, 145.03) and a rural site (Lerderderg State Park, Victoria: −37.55, 144.41). We measured sound levels for 1 min at 10 locations within a 200 m diameter at each site at 06:00, 09:00, and 12:00 h using a Lutron SL-4001 sound level meter. We used a slow response measurement with "A" weighting to measure background noise. Average background noise level was 60.67 dB(A) for the urban site and 50.38 dB(A) for the rural site. Each silvereye was banded with a numbered Australian Bird and Bat Banding Scheme (ABBBS) aluminum leg band and a unique combination of color bands for identification. Groups of between 5 and 12 birds from the same site were housed together for up to 2 weeks. Birds were kept in an outdoor aviary (average background noise level 57.78 dB[A]) at the University of Melbourne with ad libitum food (fruit, nectar, and fat/protein mix) and water.

We acclimatized each group to the testing space for 30 min per day for more than 2–3 days (without noise). The testing space consisted of a 2.5- × 2- × 2.5-m room built with double-layer noise-mitigating board walls. Baseline background noise levels (tested with a Lutron SL-4001 Sound Level Meter) at the center of the room were 30–40 dB, similar to a quiet rural natural environment (Potvin et al. 2011). Inside the room were 2 eucalypt saplings for perching, extra perches, lighting, food, and water (Figure 1). Three wireless omnidirectional speakers (5th room) were placed on 3 walls, and a small (30 × 60 × 30 cm) cage with perches, food, and water was placed against the remaining wall for the focal bird. We installed a Sennheiser ME67 directional microphone inside the cage to record calls of the focal bird at 48-kHz sampling rate onto a Marantz Professional PMD Solid State Digital Recorder.

On testing days, we released a group of 5–12 silvereyes from the same original population in the testing space around 07:00 h. One focal silvereye was placed in the small cage with the microphone, able to see and communicate with the other silvereyes in the room. We then presented 3 noise treatments consecutively in random order to the whole room through the speakers: quiet (no sound through speakers; 30–40 dB at center of room); LFN (1–4 kHz recorded traffic noise at 65 dB); and HFN (5–8 kHz simulated traffic noise at 65 dB). Each treatment was played for 4 min. We recorded the focal individual's contact calls in response to all treatments. Testing days consisted of 1–4 sessions per group with a minimum of 10 min between sessions. We tested 25 focal rural and 20 focal urban birds. All birds emitted calls during all treatments. We also video recorded the testing space during all experiments to monitor movements of the birds. After testing, we released the birds at their site of capture.
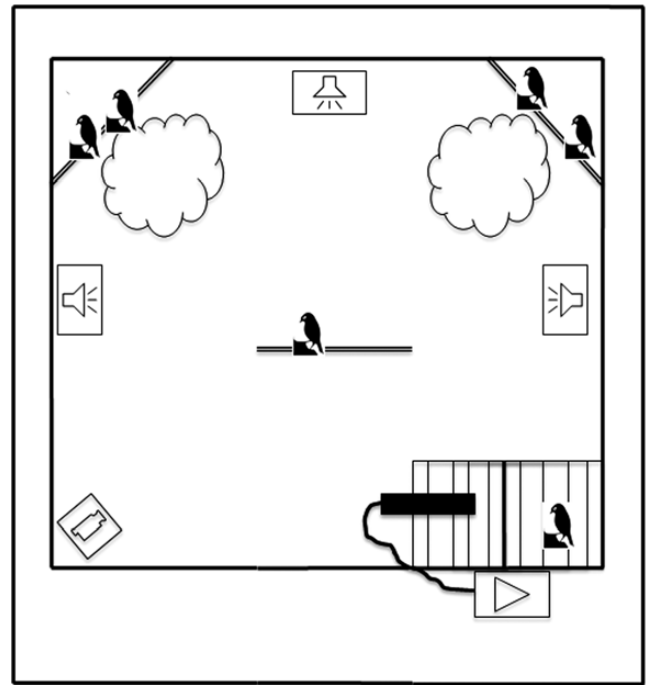

Figure 1
Experimental set-up, including 2 trees, 3 speakers (playing background noise), 3 perches, camera, focal cage, microphone, and focal bird.

Call analysis

We generated both spectrograms and waveforms of each recording in RavenPro 1.4 (www.birds.cornell.edu/raven) to calculate the average frequency, peak frequency, frequency range, and duration of each call. An example of a silvereye contact call is shown in Figure 2. Using the power spectrum view, we automatically calculated the likely minimum and maximum frequency of each call by measuring the frequency at which signal amplitude dropped by a value of 20 dB at each extreme of the call. Because recordings were made at a standard close (20–30 cm) distance to the bird, signal-to-noise ratios were large enough to be confident in these measurements. Additionally, we extracted the average power and the root mean square (RMS) amplitude of each call. Because all calls were compared with each other only, rather than to a baseline, we could then determine whether birds were calling louder (with more energy) based on treatment type or origin. Recordings were analyzed blind to the identity of the bird. We also tallied the number of calls given by each bird for each treatment to obtain a measure of call rate (calls/min). For statistical analyses, we used the mean values for each individual's calls during each treatment.

Recently, there have been criticisms of current methods of analyzing bird vocalizations that are recorded with background noise or are used to compare sounds made in noisy versus quiet sites (Zollinger et al. 2012). However, while analysis of frequency and amplitude from such recordings may present difficulties in precision (i.e., the measurement of an absolute maximum and minimum frequency of a signal if the amplitude of these outer limits is low), we postulate that detection of such low-amplitude fragments of signals would be similarly indiscernible by other individuals. Because it is unknown as to how a directional microphone and recorder compare directly with the hearing and signal-processing apparatus of a silvereye, we have presented
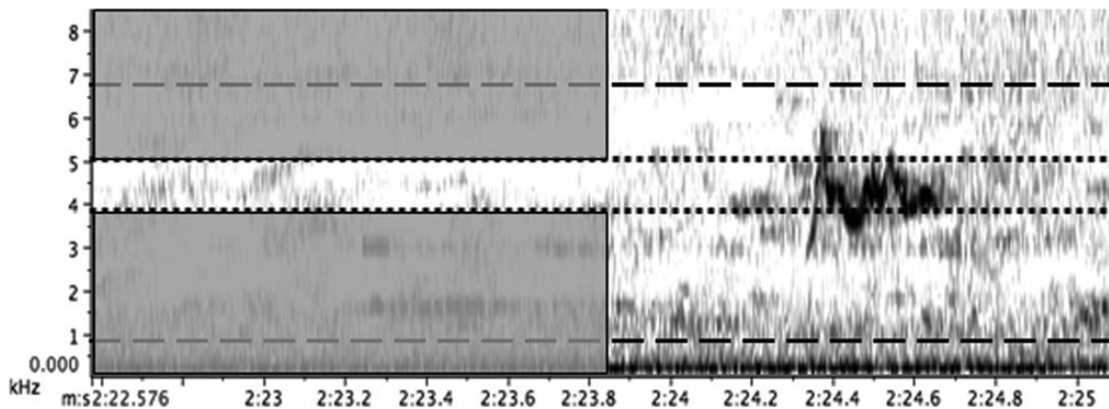
Figure 2
A sonogram of a silvereye contact call. Black dashed lines indicate the uppermost and lowest limits of the calls recorded. Areas enclosed by the shaded areas demonstrate the acoustic space occupied by the high- and low-frequency experimental background noise.

results as analyzed with the best precision and accuracy available. Furthermore, the automatic independent calculation of amplitude, power, and frequency using software ensured that if precision was low, detectability of any shifts would be low, and therefore, any interpretation of these results would need to take this possible Type II error into consideration.

Statistics

We used OpenBUGS to generate 2-way analysis of variance (Anova) Bayesian models using interactions to test for interactions between origin of bird and treatment type as well as treatment type and treatment order (McCarthy 2007). We also analyzed whether the order of the individual birds tested affected call characteristics in order to rule out effects of potential sensitization. We ran 200 000 runs discarding the first 100 000 as a burn-in. We used the quiet treatment as a reference class and rural origin as a (random) reference class. If no interactions were found (i.e., the 95% credible intervals [CI] encompassed zero), then a simple 2-way Anova model was generated as the most parsimonious model. A model was generated for each response variable described previously, testing for any effect of order, origin of bird, and treatment on the call variable. We then tested whether relative energy of the call (RMS amplitude or average power) was correlated with minimum frequency by running an additional Bayesian regression model, with RMS amplitude and average power being the predictive variables and minimum frequency being the response variable. Means (difference between the reference class and the treatment for the Anova, effect size for the regression analysis) with 95% CI are reported.

Ethical note

All capturing and handling procedures were undertaken with the approval of the animal ethics committee at the University of Melbourne and the ABBBS.

RESULTS

Minimum frequencies of calls were on average 112.4 Hz lower during the HFN compared with quiet (95% CI = −262.3, 84.77) treatment. This effect was most prominent when HFN was played last of the 3 treatments (mean = −295.3, 95% CI = −698.1, 103.5), although this interaction effect was small. Consistent with our previous findings (Potvin et al. 2011), the minimum frequency in response to LFN also

tended to be higher, though this effect was small (mean shift upwards of 79.91 Hz, 95% CI = −198.1, 361.0; Figure 3).

There were no important shifts of maximum frequencies, average frequencies, or peak frequencies between treatments, nor was there an effect of the order of individual testing on these characteristics. Lower minimum frequencies meant that the range of call frequencies used during the HFN treatment was higher than for the quiet treatment (mean = 186.5 Hz, 95% CI = −76.14, 451.3).

Silvereyes called more loudly in both noise treatments, as shown by increases in both RMS amplitude (mean in LFN = 947.9, 95% CI = −2.79, 1889.0; mean in HFN = 1334.0, 95% CI = 379.5, 2284.0) and average power (mean in LFN = 2.232 dB, 95% CI = −1.25, 5.72; mean in HFN = 14.61 dB, 95% CI = 11.13, 18.08; Figure 4). RMS amplitude and average power were both negatively correlated with minimum frequency across treatments; however, the effect sizes were negligible, with decreases of between 0–8 Hz with each increase in call decibel, or a drop in frequency of 0.002–2.1% over the entire amplitude range.

Calls made during HFN playback were about 14% longer than during quiet treatment (mean = 0.02, 95% CI = 0.001, 0.036). This effect was absent in the LFN treatment compared with the quiet treatment (mean = 0.005, 95% CI = −0.012, 0.023). Although all the above results were consistent between urban and rural birds (i.e., no origin effect was found on the above variables), the magnitude of the shifts differed between urban and rural birds, with urban birds consistently using shorter calls during both noise treatments than rural birds (treatment/origin interaction effect for LFN treatment: mean = −0.022, 95% CI = −0.058, 0.012; for HFN treatment: mean = −0.024, 95% CI = −0.060, 0.011). Finally, although overall call rates were not affected by noise treatment, urban birds decreased call rates in LFN (interaction effect: mean = −14.62 calls/min, 95% CI = −40.73, 11.39). Notably, nonfocal birds called only from perches and did not approach the cage during testing, as video analysis revealed. Additionally, the focal bird called from the perch in the cage in all cases.

DISCUSSION

Silvereyes appear to be capable of bidirectional adjustments to their call frequencies that are independent of changes in amplitude and in a direction that is consistent with adaptive minimization of interference. In the presence of high- or low-frequency background
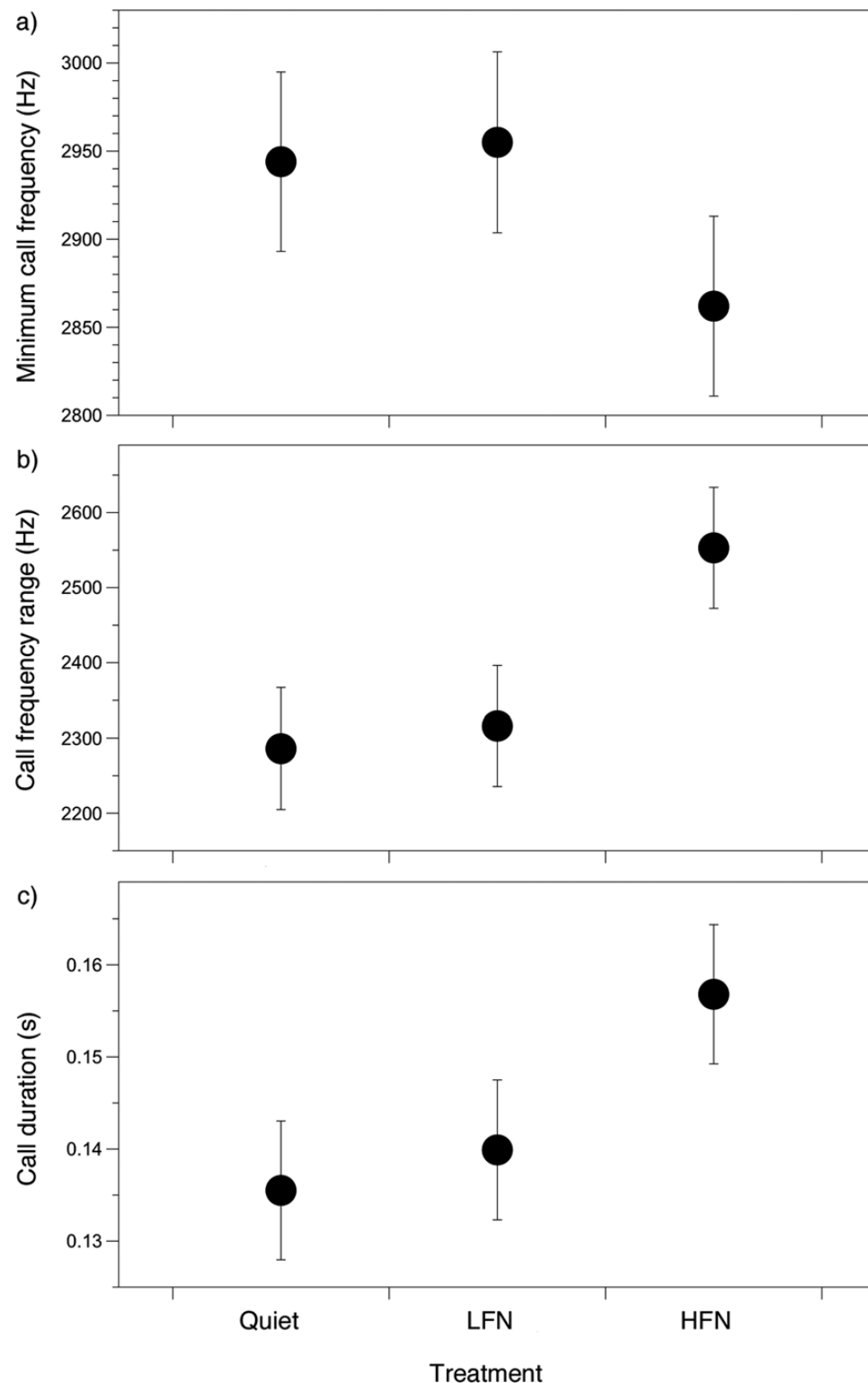
Figure 3

Effect of treatment type (quiet, low-, and high-frequency background noise) on (a) call minimum frequency (Hz), (b) call frequency range (Hz), and (c) call duration (s) of all birds. Error bars represent 95% CI.

noise, silvereyes adjusted their calls to exploit spectrally favorable (i.e., noninterfering) frequencies, which differed from those they used under quiet conditions. Silvereyes in both noise treatments called with increased energy compared with the quiet treatments, but this was not correlated with an increase in the minimum frequency of calls as predicted by the LH. Because responses to LFN involved increases in both amplitude and frequency, they are consistent with either the AAH or the LH. However, in response
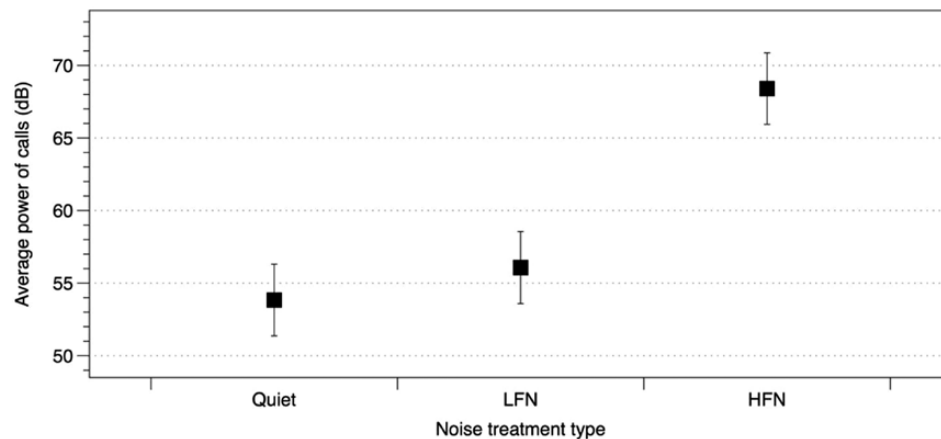
Figure 4

Effect of treatment type (quiet, low-, and high-frequency background noise) on call amplitude (average power; dB). Error bars represent 95% CI.

to HFN, both urban and rural silvereyes lowered the minimum frequency of their calls while increasing amplitude, as predicted only by the AAH. If this shift in pitch were due to the LH, both noise treatments should have prompted an upward shift in pitch of the call as a byproduct of calling more loudly (Nemeth and Brumm 2010).

Silvereyes appeared to adjust pitch only with respect to minimum frequency, and thus achieved improved signal-to-noise ratio of contact calls by decreasing the bandwidth of their calls in response to LFN and increasing bandwidth in response to HFN. In a similar experiment, Halfwerk and Slabbekoorn (2009) exposed captive great tits *Parus major* either to "city noise" (LFN) or "inverse city noise" (HFN). Although relatively few birds (41%) responded to the treatments, great tits switched to song types with decreased high-note frequencies in HFN and increased low-note frequencies in LFN, thus achieving increased signal-to-noise ratios by reducing frequency bandwidth in both treatments. Increasingly, tonality by decreasing frequency bandwidth should improve the efficiency of signal transmission in noisy environments (Lohr et al. 2003; Hanna et al. 2011), so it is curious that silvereyes did not also reduce frequency bandwidth in the presence of HFN. This might reveal limitations in mechanical flexibility in the vocal apparatus, or alternatively, functional constraints on omission of elements of the call that have high information content value.

The upward shifts we measured in minimum frequency were smaller than the differences we measured between rural and urban bird calls in a previous study (Potvin et al. 2011). Although we cannot be certain of the cause of this difference, the birds participating in this study were sampled from a restricted geographic area (Melbourne, with the rural site located within 50 km of the urban site), compared with the multiple locations around Eastern Australia we used for our previous study. If these subpopulations show reduced spectral flexibility compared with others, this might explain why they showed limited changes in frequency in response to LFN. Depending on whether birds adjusted call frequency using internal or external feedback mechanisms (Brumm and Slabbekoorn 2005; Peake et al. 2005), limited vocal frequency range in the call frequencies of stimulus individuals could have influenced the responses of focal birds.

In response to HFN alone, silvereyes also increased the duration of their calls. Longer song phrases may be easier to detect and potentially reduce overlap with competing signals. Longer songs are used by great tits *P. major* (Hamao et al. 2011; although

see Slabbekoorn and den Boer-Visser 2006), gray vireos *Vireo vicinor* (Francis et al. 2011a), and house finches *Carpodacus mexicanus* (Bermudez-Cuamatzin et al. 2011) in noisy areas, and longer calls are also used by common marmosets *Callithrix jacchusin* (Brumm et al. 2004) and killer whales *Orcinus orca* (Foote et al. 2004) in the presence of noise. In silvereyes, differences in call duration were especially noticeable when the noise was novel—silvereyes called for longer in response to HFN than LFN, and rural birds (unaccustomed to loud noise in general) used longer calls than urban birds in both noise treatments. Again, it is unclear why silvereyes adjusted signal duration only in response to HFN, given the hypothesized advantages of longer calls in terms of signal transmission.

We found no evidence that silvereyes employed other mechanisms for diminishing the effects of acoustic masking, such as switching to a different call type (Bermudez-Cuamatzin et al. 2009; Dunlop et al. 2010). Likewise, we found no effect of noise on call rates of silvereyes. In fact, most animals that have been tested tend to decrease their calling or singing rates when loud background noise is present, possibly to avoid masking by timing calls appropriately when noise has abated (Sun and Narins 2005; Parks et al. 2007; Thierry 2008; Halfwerk and Slabbekoorn 2009), but see Díaz et al. (2011).

Wild dark-eyed juncos (*Junco hyemalis*; Cardoso and Atwell 2011b) also show independent adjustment of amplitude and frequency in response to noise, but in songs rather than calls. The ability of silvereyes to flexibly adjust contact calls is somewhat surprising because songs are often learned, whereas calls are sometimes assumed to be innate (Marler 2004). However, some plasticity has also been identified in adult contact calls (budgerigars *Melopsittacus undulatus*; Farabaugh et al. 1994) and in begging calls (tree swallows *Tachycineta bicolor*; Leonard and Horn 2008) of passerines.

Our study adds to a growing body of evidence for diverse forms of plasticity in avian vocalizations in response to anthropogenic noise, including adaptive adjustment to vocalization type (Bermudez-Cuamatzin et al. 2009), frequency (Slabbekoorn and Peet 2003), amplitude (Pytte et al. 2003), duration (Halfwerk and Slabbekoorn 2009), and tonality (Hanna et al. 2011). Our finding that silvereyes can furthermore adjust frequency independently of amplitude demonstrates that birds are capable of sophisticated adjustments to calls to maximize signal-to-noise ratios in noisy environments. This finding provides support for the AAH under controlled experimental conditions and sheds light on the variety of

ways birds may communicate in—and cope with—environments with high levels of human-generated noise.

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