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Silvereyes decrease acoustic frequency but increase efficacy of alarm calls in urban noise

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Many passerines adjust song attributes to avoid potential masking by anthropogenic noise. The costs of masking should be particularly high for vocalizations important for survival (e.g. alarm calls), but few studies have investigated how such calls are affected. We compared urban and rural silvereye, *Zosterops lateralis*, alarm calls across southeastern Australia, and found that urban calls had lower average, peak and maximum frequencies than rural calls. The average, peak and maximum frequency of alarm calls also decreased linearly with increasing background noise. The direction of this frequency shift runs contrary to expectations and previous findings of higher-pitched avian vocal signals in urban habitats, including higher-pitched song and contact calls in urban silvereyes. However, assuming no change in call amplitude, acoustic modelling indicates that the observed frequency shift would lead to a 20% increase in the predicted active space of alarm calls (i.e. the distance over which the calls can be detected by a conspecific bird) in urban noise, and therefore may be potentially adaptive. Our findings highlight the importance of considering behavioural and ecological contexts in urban acoustic-adaptation studies.

According to the ‘acoustic adaptation hypothesis’ (Morton, 1975), animals should adaptively respond to the acoustic backdrop against which they communicate, by altering their vocalizations to maximize transmission and clarity. This hypothesis has been invoked to explain why some birds vocalize at higher frequencies in urban environments, where low-frequency traffic noise tends to mask communication signals (Bermudez-Cuamatzin, Rios-Chelen, Gil, & Garcia, 2011; Brumm, 2006; Cardoso & Atwell, 2011b; Slabbekoorn & den Boer-Visser, 2006). While the direction of such shifts is consistent with the acoustic adaptation hypothesis, alternative explanations for such changes in signal frequency, especially in unlearned vocalizations (Parris, Velik-Lord, & North, 2009; Potvin, Parris, & Mulder, 2011) have been less thoroughly investigated. For example, differences between urban and rural vocalizations might result from stress, interrupted auditory feedback, differences in male density, or impaired cognitive or vocal development during the early life of urban birds (Hamao, Watanabe, & Mori, 2011; Lercher, Evans, & Meis, 2003; Partecke, Schwabl, & Gwinner, 2006; Wright et al., 2007).

To date, studies investigating differences between urban and rural vocalizations of birds have been predominantly focused on song. This work has shown that songbirds are able to make real-time adjustments to a range of song attributes in response to increasing background noise (Gross, Pasinelli, & Kunc, 2010; McMullen, Schmidt, & Kunc, 2014; Montague, Danek-Gontard, & Kunc, 2013) that increase the detectability of songs in noisy environments. These responses include switching songs or syllable types (Cardoso & Atwell, 2011a; Halfwerk & Slabbekoorn, 2009; Potvin & Parris, 2013), increasing vocalization duration (Montague et al., 2013; Potvin & Mulder, 2013), increasing amplitude (Brumm, 2004) or shifting frequency (McMullen et al., 2014; Potvin & Mulder, 2013). Such modifications require variability and plasticity in the affected vocalization; songs are learned, and therefore are generally considered to be more flexible than other vocalizations (Catchpole & Slater, 2008; Kroodsma, 2004).

In contrast, there has been little research on ways in which unlearned avian vocalizations may differ between rural and urban environments. Urban noise appears to have the greatest effect on avian vocal signals with frequencies below 3 kHz (Hu & Cardoso, 2009, 2010; Parris & Schneider, 2009), although signals up to 6.5 kHz are expected to suffer some acoustic interference in urban noise with a reduction in active space (communication distance) of 20–30% (Parris & McCarthy, 2013). Many unlearned or less flexible vocalizations such as alarm calls fall into this part of the frequency spectrum. Given that such calls are important for survival, they should be under particularly strong selection for optimal transmission and detectability. It is therefore surprising that they have

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rarely been studied in this context (although see Leonard & Horn, 2008; McIntyre, Leonard, & Horn, 2014; Skiba, 2000).

Alarm calls are used by almost all avian species, in the context of a potential threat such as presence of a predator. Given that urban birds may be undergoing physiological, morphological or even microevolutionary changes (Badyaev, Young, Oh, & Addison, 2008; Bonier et al., 2007; Chace & Walsh, 2006; Evans, Gaston, Sharp, McGowan, & Hatchwell, 2009; Evans et al., 2012; Gavett & Wakeley, 1986; Møller, Erritzoe, & Karadas, 2010; Mueller, Partecke, Hatchwell, Gaston, & Evans, 2013), innate or unlearned vocalizations such as alarm calls may undergo changes independent of those affecting learned vocalizations such as song. We assessed this hypothesis by investigating potential differences in silvereye, *Zosterops lateralis*, alarm calls in urban and rural habitats. This native Australian songbird adjusts both its songs and contact calls in response to urban noise (Potvin et al., 2011). These changes are flexible and involve syllable selectivity (Potvin & Parris, 2013), tempo, duration and frequency adjustments (Potvin & Mulder, 2013; Potvin et al., 2011). In silvereyes, alarm calls are made by both males and females in distress (including threats to the nest) and induce mobbing by neighbours (D. A. Potvin, personal observation), and their acoustic structure is characteristic of mobbing calls by being repetitive, of wide bandwidth and easily locatable (Fig. 1; Marler & Slabbekoorn, 2004). Although the exact information encoded in silvereye alarm calls is unknown, many alarm calls contain crucial information about context, such as the level of threat or the type of predator (Klump & Shalter, 1984; Leavesley & Magrath, 2005). Therefore, changes to alarm calls to increase their transmission may be costly, making them potentially highly conserved and inflexible.

We assessed the frequency, duration and tempo of silvereye alarm calls in multiple urban and rural populations to determine how much these call properties varied with habitat type (urban or rural) and/or the level of background noise. As the frequencies of silvereye alarm calls overlap with typical frequencies of urban noise, we would expect an upward shift in frequency if the calls are subject to (and being shaped by) acoustic adaptation and are behaviourally flexible (Potvin & Mulder, 2013). Alternatively, a finding of no substantial difference in call frequency might suggest that this call type is highly conserved and inflexible.

METHODS

Study Species

Silvereyes are common native Australian passerines that inhabit a variety of environments, including urban areas. Silvereye songs and contact calls in city environments are higher in pitch than those in rural habitats (Potvin et al., 2011). Silvereyes also utter alarm calls, which are broadband in nature and consist of a fundamental frequency and a number of emphasized harmonics (Fig. 1).

Study Sites

Each pair of study sites was located at the following specific geographical areas in southeastern Australia, with one site of each pair in a city and the other situated in a rural area within 150 km: Melbourne, Victoria (37°30′S, 144°30′E; Darebin Parklands and Lerderderg State Park); Adelaide, South Australia (35°S, 138°30′E; Glenalta and Coorong National Park); Sydney, New South Wales (35°S, 151°E; Poulton Park and Munghorn Gap Nature Reserve); Grafton, New South Wales (30°S, 153°E; Susan Island and Lamington National Park); Brisbane, Queensland (27°30′S, 153°E; Kingfisher Park and Mount Coot-Tha State Forest); Hobart, Tasmania (43°S, 147°30′E; Seven Mile Beach/Hobart Airport and Mount

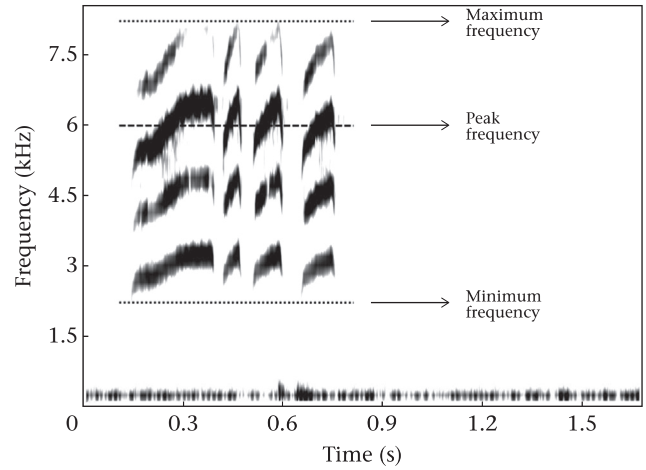

Figure 1. An example of a silvereye, *Zosterops lateralis*, alarm call. Pictured is a spectrogram of a call with a duration of 0.75 s, four notes and four formants.

Wellington Reserve); Canberra, A.C.T. (35°S, 149°E; Australian National Botanic Gardens and Namadgi National Park). Silvereyes are breeding residents at all sites.

Field Methods

Fieldwork was conducted between September 2009 and February 2010. Silvereyes were captured in mist nets over 2–8 days. Each captured individual was fitted with an ABBBS (Australian Bird and Bat Banding Scheme) aluminium numbered band and three colour bands for individual identification, and released within 10 min. We used Marantz Professional PMD660 solid-state recorders and Sennheiser ME67 directional microphones to subsequently record alarm calls from banded individuals at a sampling rate of 48 kHz. Alarm calls were obtained from two to five individuals (for a total of 34 individuals and 281 calls) between dawn and 1200 hours at each site. We also measured sound levels for 1 min at 10 locations within a 200 m diameter at each site at 0600 hours, 0900 hours and 1200 hours using a Lutron SL-4001 sound level metre, using a slow response measurement with ‘A’ weighting to measure background noise. Average levels of background noise were then calculated for each site. To produce a noise spectrum for urban and rural habitats, we recorded the background noise at one typical urban (Darebin Parklands, Melbourne, Australia) and one typical rural (Lerderderg State Park, Australia) site at which birds were caught. Recordings of background noise were taken for 5 min at 0600 hours during one morning within the field season, using the same microphone and digital recorders used to record calls.

Call Analysis

Figure 1 shows an example of a typical silvereye alarm call. We analysed spectrograms of calls in RavenPro 1.4 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) blind to the source of the call. For each call, we determined minimum frequency, peak frequency (the frequency with the most energy, also known as the dominant frequency), maximum frequency, average frequency, number of formants, call duration and tempo (notes/s; Fig. 1) and then averaged values for each individual. There was sufficiently high signal-to-noise ratio in each recording to enable use of an automated threshold for the minimum frequency values: minimum frequencies were demarcated at the point on the frequency spectrum