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Traffic noise drives an immediate increase in call pitch in an urban frog

V. Higham, N. D. S. Deal, Y. K. Chan, C. Chanin, E. Davine, G. Gibbings, R. Keating, M. Kennedy, N. Reilly, T. Symons, K. Vran & D. G. Chapple

School of Biological Sciences, Monash University, Clayton, VIC, Australia

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Correspondence
David G. Chapple, School of Biological Sciences, Monash University, Clayton VIC 3800, Australia.
Email: David.Chapple@monash.edu

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Abstract

Noise pollution is an underappreciated component of global environmental change and can impact species that have a strong reliance on acoustic communication. In urban areas, traffic noise can interfere with the ability of animals to communicate and complete essential aspects of their daily lives. We investigated the impact of traffic noise on the calling behaviour of the brown tree frog (*Litoria ewingii*) in south-eastern Melbourne, the fastest-growing human population centre in Australia. We placed six acoustic recorders at increasing distances from a busy suburban road and recorded the calling behaviour (call pitch and call rate) of brown tree frogs immediately before and after loud traffic noises, and in response to different chorus sizes. Traffic noise resulted in a significant, but short-term, increase in call pitch in the brown tree frog. Both call pitch and call rate decreased with increasing distance from the road, yet traffic noise still resulted in increased call pitch even 200–300 m from the road. Conversely, although traffic noise increased call pitch across all chorus sizes of the brown tree frog, larger chorus sizes were associated with decreased call pitch. Our study highlights the pervasive, and sustained, impact that anthropogenic noise can have on urban frog populations.

Introduction

The Anthropocene has been characterized by the rapid transition of natural habitats into human-dominated landscapes (Seddon *et al*., 2016). This shift has been driven by both accelerated population growth and the increased concentration of humans into cities and urban regions (Steffen *et al*., 2015). Such urbanization has had a profound impact on biodiversity (McKinney, 2006; Concepción *et al*., 2015), exposing species to habitat loss and fragmentation, invasive species, overexploitation and environmental pollution (Diamond, 1984). Noise pollution is an underappreciated component of global environmental change (McGregor *et al*., 2013) and is concentrated in urban areas as a result of human activities, particularly those related to transportation (e.g. roads, railway lines, airports and shipping ports) (Alberti *et al*., 2003). Anthropogenic noise has been associated with decreased species diversity (Eigenbrod, Hecnar & Fahrig, 2008; Francis, Ortega & Cruz, 2009), impaired cognitive abilities (Potvin, 2017), modified mate choice (Halfwerk *et al*. 2019) and altered immune function (Tennessen *et al*., 2018).

Anthropogenic noise can also have a significant impact on animal behaviour, particularly for species that have a strong reliance on acoustic communication (Candolin & Wong, 2012, 2019; Wong & Candolin, 2015; Slabbekoorn *et al*, 2018). Human-generated noise has been demonstrated to alter the communication behaviours of a diverse range of animal groups including fishes (Hawkins & Popper, 2018), amphibians (Roca *et al*., 2016; Simmons & Narins, 2018), birds (Nemeth & Brumm, 2009; Roca *et al*., 2016) and mammals (Buckstaff, 2004; Slabbekoorn *et al*., 2018). In urban areas, anthropogenic noise can interfere with the ability of animals to communicate effectively, make decisions regarding food selection or detect predators (Chan & Blumstein, 2011). For tasks involving acoustic communication, species may respond to the presence of anthropogenic noise by altering aspects of their calls, such as duration, frequency, intensity or pitch in order to be heard (McGregor *et al*., 2013; Roca *et al*., 2016; Caorsi *et al*., 2017).

Anurans are a group that are predicted to be strongly impacted by anthropogenic noise, as they rely heavily on acoustic communication for both social and reproductive behaviours (Simmons & Narins, 2018). Thus, if noise from anthropogenic activities inhibits their communication, it may negatively influence key aspects of anuran biology (McGregor *et al*., 2013; Caorsi *et al*., 2017). However, studies across a range of anuran species have demonstrated a capacity to respond to anthropogenic noise by avoiding the source of the noise (Caorsi *et al*., 2017) or altering components of their calls (Roca *et al*., 2016; Simmons & Narins, 2018). Frog species may temporally adjust their calling behaviour, and/or adjust their call rate, length, frequency, pitch or amplitude (Sun &

Narins, 2005; Cunnington & Fahrig, 2010; Alloush *et al.*, 2011; Halfwerk *et al.* 2016; Kruger & Du Preez, 2016; Caorsi *et al.*, 2017). However, different anuran species may exhibit divergent or inconsistent responses to the same anthropogenic noise, even within the same habitat (Simmons & Narins, 2018). For instance, in Thailand, three frog species decreased their call rate in response to airplane and motorbike noise, but one increased its call rate (Sun & Narins, 2005). Several frog species have demonstrated the capacity for immediate, short-term shifts in aspects of their calling behaviour in response to traffic or aircraft noise, returning to normal soon after cessation of the noise (Cunnington & Fahrig, 2010; Kruger & Du Preez, 2016).

Melbourne is the fastest-growing population centre in Australia (Mestres, 2019; Australian Bureau of Statistics, 2019). The rapid urbanization of the greater Melbourne region has had a substantial impact on the resident fauna (Hale *et al.*, 2013; Gravolin, Key & Lill, 2014; Keely *et al.*, 2015; Vines & Lill, 2016). The traffic noise from the extensive network of suburban roads, particularly bordering remnant patches of bushland or native habitat, has been demonstrated to alter the calling behaviour of frogs (Parris, Velik-Lord & North, 2009). This is particularly the case for the brown tree frog (*Litoria ewingii*), the most common anuran species in the greater Melbourne region (Museum Victoria, 2006), which calls at a higher pitch in response to traffic noise (Parris *et al.*, 2009).

Here we investigate the impact of traffic noise on brown tree frog calling behaviour in the Jock Marshall Reserve, a remanent bushland reserve on the Clayton campus of Monash University in south-eastern Melbourne. As brown tree frogs have previously been shown to call at a higher pitch in response to traffic noise, we examined whether (1) this represents an immediate, or long-term, change in calling behaviour, (2) calling behaviour is influenced by the distance from a major road and (3) chorus size influences calling behaviour, and its interaction with traffic noise. Based on previous anuran studies (e.g. Cunnington & Fahrig, 2010; Kruger & Du Preez, 2016), we predicted that the change in call pitch would be an immediate, short-term response to traffic noise and that the influence of traffic noise would decrease with distance from a major road. Similarly, we predicted that increased chorus size (i.e. natural noise from conspecifics) would also result in an increase in call pitch, especially in the presence of traffic noise.

Materials and methods

Frog call audio recording

Six acoustic recorders (Song Meter SM4 Acoustic Recorder, Wildlife Acoustics, Maynard, USA) were placed within the Jock Marshall Reserve (Fig. 1), on the Clayton campus of Monash University, Melbourne, Australia (37.9095°S, 145.1401°E). Each recorder employs omnidirectional microphones with 16 and 26 dB of gain for the amplifier and preamplifier respectively. The sample rate was 24 kHz/s which was deemed suitable for capturing the calls of brown tree frog calls which are typically ~2.5 kHz and thus well below the Nyquist frequency. The audio recorders were set to record for 5 min periods at 1 am, 5 am and 9 pm each day over a seven day period during July 2017. The acoustic recorders were placed at different distances from Blackburn Road, a busy suburban road that runs along the eastern boundary of the Clayton Campus (Fig. 1). However, the audio recordings from site 1 were excluded from our study (Fig. 1), as the brown tree frog calls were inaudible above the vehicle noise from Blackburn Road.

Frog call analysis

To determine the pre- and post-vehicle brown tree frog call pitch, Audacity audio editing software (Version 2.1.3; available from https://www.audacityteam.org/) was used to produce frequency spectrum plots (via fast Fourier transform of size 1024 with a Hann window, and thus frequency resolution of 47 Hz) for the 20-sec intervals immediately prior to and following all occurrences of heavy vehicle noise (i.e. trucks, motorbikes and large engine cars). These occurrences of heavy vehicle noise were detected by a human listener, within each audio recording. A total of 602 spectral plots were generated, with 301 plots generated per time period (i.e. pre- and post-vehicle). For each spectral plot, the frequency (Hz) of the highest peak (db) between 2000 and 3000 Hz (corresponding with the dominant frequency of the middle note in brown tree frog calls: Littlejohn, 1965; Parris *et al.*, 2009; Smith, Oliver & Littlejohn, 2012) was recorded. Where the pre-vehicle interval overlapped with the post-vehicle interval of a previous vehicle, the data were excluded. To ensure that non-relevant sounds did not skew the call pitch measures, Audacity's noise removal tool was also used to reduce non-relevant background sounds (i.e. bird calls, frog calls other than those of brown tree frogs, other human activities) from the audio recordings prior to analysis.

Chorus size was also quantified to assess whether the social environment influenced frog call behaviour. Chorus size was estimated by identifying the number of brown tree frog individuals calling in chorus (i.e. calling concurrently) within each pre- and post-vehicle interval. The number of frogs calling concurrently was determined by a human listener, who identified the number of frog call/s initiated during the first frog call occurrence for each pre- and post-vehicle interval and confirmed each frog call initiation event visually within the waveform plot generated by Audacity. Finally, the distance of the recorder locations from the vehicle noise source was determined via Google Maps, to be utilized as an estimation of vehicle noise intensity.

To assess whether the amount of vehicle noise across each recording influenced frog call behaviour we also quantified the number of frog calls and loud vehicle noises in each recording. To determine the call rate, we identified all brown tree frog calls within each of the 105 recordings and divided the number of these calls by the duration of the recording (i.e. 5 min). The number of frog calls in each audio recording was determined by a human listener, who visually confirmed the occurrence of each call within the waveform plot generated by Audacity.

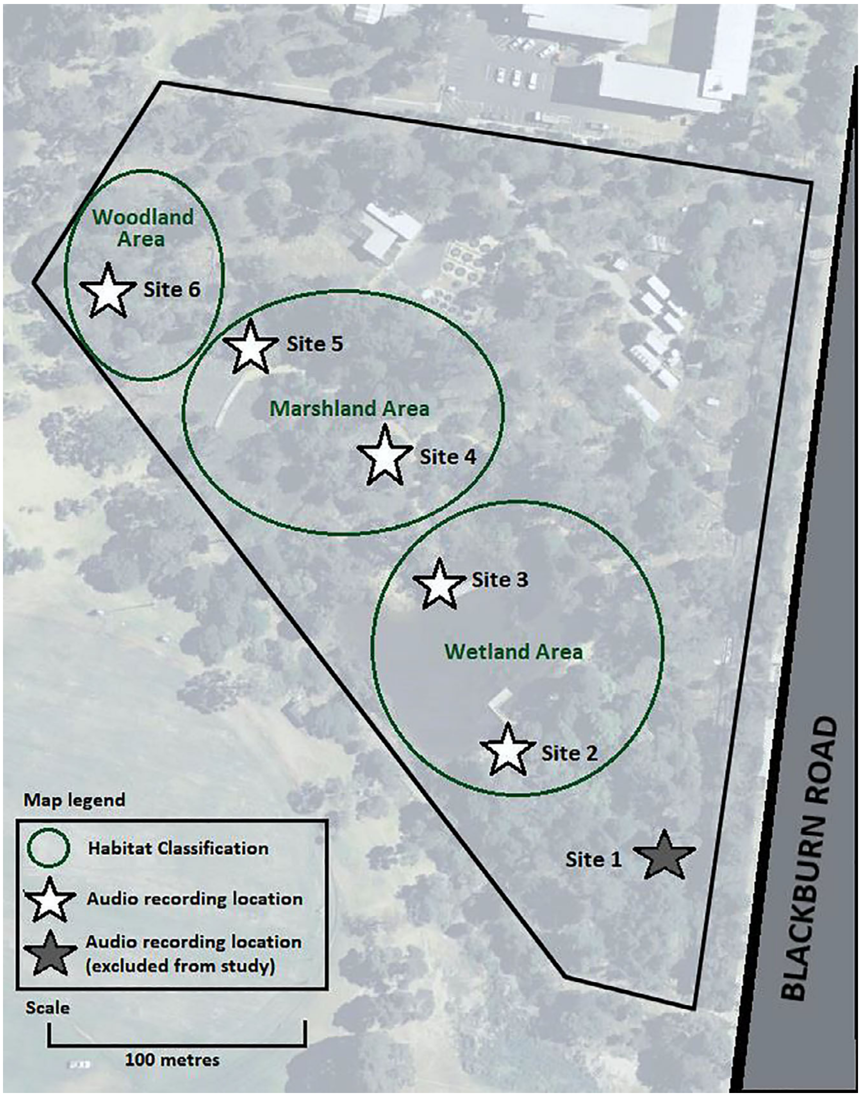

Figure 1 Map of Jock Marshall Reserve, indicating the location of the six acoustic recorders. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

Similarly, the incidence of loud vehicle noises was calculated by dividing the total number of listener identified heavy vehicle noises by the recording duration.

Statistical analyses

R version 3.2.3 (R Development Core Team, 2018) and RStudio (Version 0.99.879) were used for statistical analyses. A linear mixed effect model was performed, using the lme4 package (Bates *et al*., 2015), to assess whether the variation in call pitch (Hz) was associated with the vehicle interval (i.e. whether the call preceded or followed a loud vehicle noise), distance from the road, chorus size and the interactions between vehicle interval and distance from the road, and vehicle interval and chorus size. A linear mixed effect model was also utilized to assess whether the observed variation in call rate was associated with the vehicle noise incidence, distance from the road and the interaction between vehicle noise incidence and distance from the road. Within both models, variation attributable to the time, day and an interactive effect of day and time was partitioned from that of the main effects by including day, time and the interaction between day and time as random effects. Furthermore, within the linear mixed effect model assessing variation in call pitch (Hz), the recording identity (unique to each recording made at a specific recording site on a specific date and time) and an identification number allocated to each pair of calls that preceded and followed a particular heavy vehicle sound were also included as random effects. Visual inspection of diagnostic plots indicated that the assumptions of normality and equal variances were met. All significance was tested at 0.05 level using Type II Wald chi-square tests.

Results

Effects of vehicle noise on call pitch

Overall, we found that the pitch of those frog calls measured following vehicle noise was significantly higher than the calls that preceded it (Fig. 2); specifically, the mean call frequency (Hz) was significantly greater during the post-vehicle interval compared to the pre-vehicle interval ($\chi^2 = 76.42$, $df = 1$, $P < 0.001$; Table 1).

Frog call pitch was also significantly associated with the distance from the road ($\chi^2 = 6.89$, $df = 1$, $P = 0.009$; Table 1). We found a moderate negative correlation between mean call pitch and distance from the road ($r = -0.73$, $R^2 = 0.535$), in which the mean pitch of the frog calls tended to decrease with increasing distance from the road (Fig. 3). This pattern appeared to be consistent for both calls measured prior to and after vehicle noise, with no significant interaction between call interval timing relative to vehicle noise and distance from the road ($\chi^2 = 0.11$, $df = 1$, $P = 0.737$; Table 1; Fig. 4).

Frog call pitch was also significantly influenced by chorus size ($\chi^2 = 11.06$, $df = 2$, $P = 0.004$; Table 1). We found that the mean call pitch was greater when a single frog was calling, compared to when 2–3 frogs or more than three frogs were calling concurrently (Fig. 5). Additionally, chorus size was shown to significantly influence the effects of vehicle noise on frog call pitch ($\chi^2 = 6.27$, $df = 2$, $P = 0.043$; Table 1). While the pitch of the frog calls increased in response to vehicle noise across all chorus sizes, we found that the magnitude of the increase was substantially greater when 2–3 frogs were calling concurrently, and moderately greater when more than three frogs were calling concurrently, compared to the magnitude of the increase when only a single frog was calling (Fig. 6).

Effects of vehicle noise incidence on call rate

The number of vehicles per minute was not shown to significantly impact the call rate of the frogs ($\chi^2 = 0.69$, $df = 1$, $P = 0.407$; Table 2). However, call rate was shown to be impacted by distance from the road; our results indicated that call rate significantly decreased with increasing distance from the road (Fig. 7; $\chi^2 = 9.44$, $df = 1$, $P = 0.001$; Table 2).

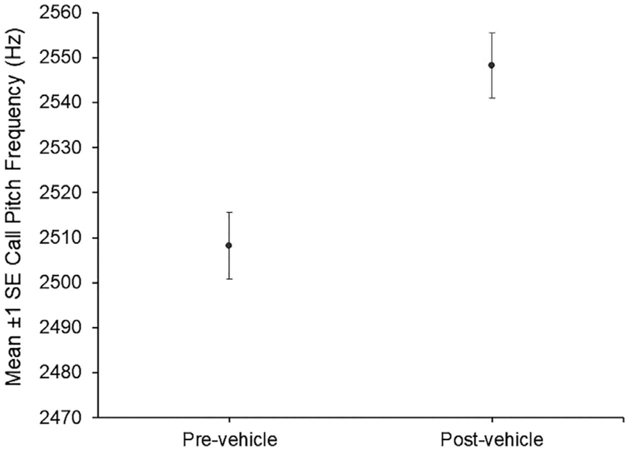

Figure 2 Comparison of pitch frequencies (Hz; mean ± SE) of *Litoria ewingii* calls pre- and post-vehicle noise.

Table 1 Results of linear mixed effect model with call pitch (Hz) as the dependent variable performed using Type II sum of squares chi-square ANOVA

Fixed effects	χ^2-value	df	*P*-value
Period (Pre- vs Post-Vehicle)	76.42	1	**<0.001***
Distance from road ($\sqrt{m}$)	6.89	1	**0.009***
Chorus Size	11.06	2	**0.004***
Period: Distance from Road	0.11	1	0.737*
Period: Chorus Size	6.27	2	**0.043***

Random effects	Variance (%)
Recording ID	29.78
Call Pair ID	19.87
Day: Time	8.87
Day	22.32
Time	0
Residual	19.16

*Significance at 0.05 level.

Discussion

Our study demonstrates that traffic noise has a substantial influence on the calling behaviour of the brown tree frog and highlights the complexities and pervasiveness of its impact in suburban Melbourne. Loud traffic noise results in a significant, but short-term, increase in call pitch. Yet, although both call pitch and call rate decreased with increasing distance from a major road, traffic noise still resulted in an increased call pitch even 200–300 m from the road. Conversely, larger chorus size led to a decreased call pitch, especially in smaller (2–3 frogs) choruses. Nevertheless, traffic noise resulted in an increase in call pitch across all chorus sizes. Below we discuss the implications of these findings.

Brown tree frog calls following traffic noise are higher in pitch

As predicted, traffic noise resulted in an increased call pitch in the brown tree frog. Our result is consistent with a previous study of the brown tree frog (Parris *et al.*, 2009), and with most studies that have been conducted on avian and anuran species worldwide (Roca *et al.*, 2016). However, given that we observed that the pitch of the brown tree frog calls increased in the period immediately after a traffic noise event, our results suggest that traffic noise from Blackburn Road induced an immediate, short-term elevation in call pitch. Similarly, Kruger & Du Preez (2016) reported that male Pickersgill's reed frogs (*Hyperolius pickersgilli*) increased their call rate during, and shortly after, aircraft noise, returning to baseline levels within 15 min. Such immediate, short-term responses in aspects of calling behaviour have been documented in frog assemblages

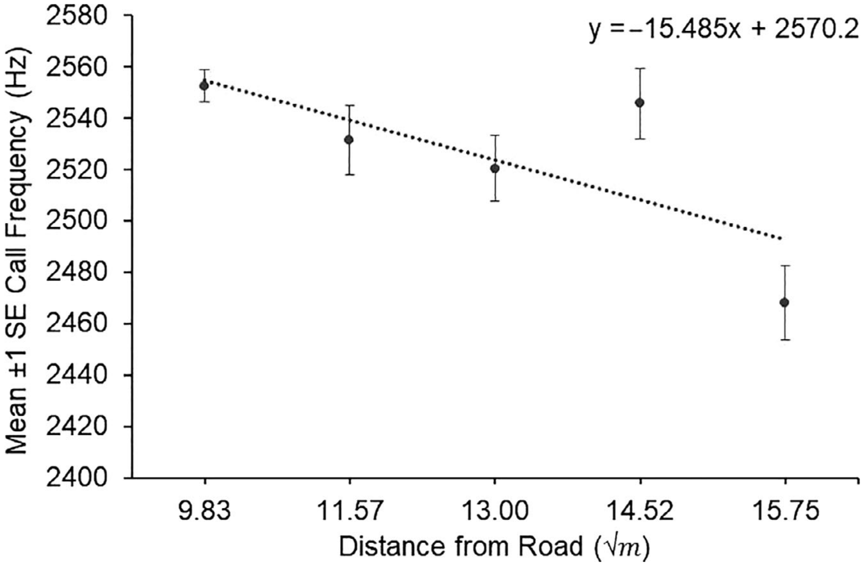

Figure 3 Association between pitch frequency (Hz; mean ± SE) of *Litoria ewingii* calls and distance from Blackburn road traffic noise ($\sqrt{m}$), with fitted regression line and regression equation.

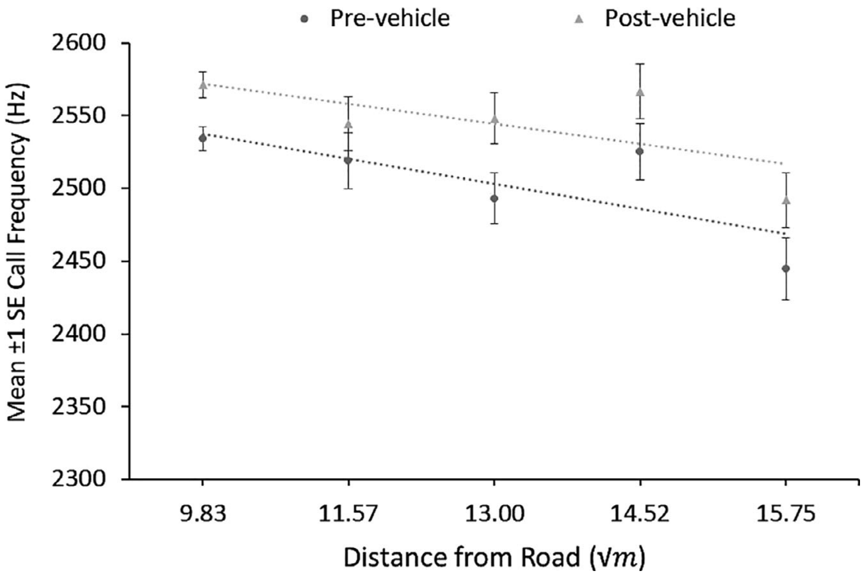

Figure 4 Association between pre- and post-vehicle noise call pitch frequency (Hz; mean ± SE) of *Litoria ewingii* and distance from Blackburn road traffic noise ($\sqrt{m}$), with fitted regression lines.

from North America (Cunnington & Fahrig, 2010) and South America (Caorsi *et al*., 2017). In the case of the brown tree frogs we report on here, it remains unclear whether the observed increased call pitch represents individual frogs altering the pitch of their calls in response to vehicle noise or instead differences in the cohorts of frogs that call before and after vehicle noise. However, the former explanation appears likely given the immediacy of the effect and reports of anurans altering call pitch characteristics in response to other acoustic stimuli, including conspecific calls (e.g. Wagner, 1989; Morais, Siqueira & Bastos, 2015; reviewed in, Bee, Reichert & Tumulty, 2016) and background white noise (Zhao *et al*., 2018). Regardless of the exact mechanism, however, our results for the brown tree frog further emphasize the remarkable plasticity in call behaviour that anurans are capable of exhibiting in response to anthropogenic noise.

Call pitch decreases with increasing distance from a major road

Both the call pitch and call rate of the brown tree frog decreased with increasing distance from Blackburn Road. While it was anticipated that the distance from traffic noise would influence both call pitch and call rate (e.g. Sun & Narins, 2005; Halfwerk *et al*. 2016), our finding that traffic noise could invoke an immediate increase in call pitch up to 200–300 m away from the road was unexpected. Consequently, although some frog species (e.g. *Boana bischoffi*, *B. leptolineata*) have been recorded moving away from anthropogenic noise, our findings indicate the vast distances that individuals would need to disperse to escape the impact of traffic noise. In many systems, the limited dispersal capacity of frogs, or the small remnant habitat patches that frogs occur in, could restrict the potential for individuals to move away

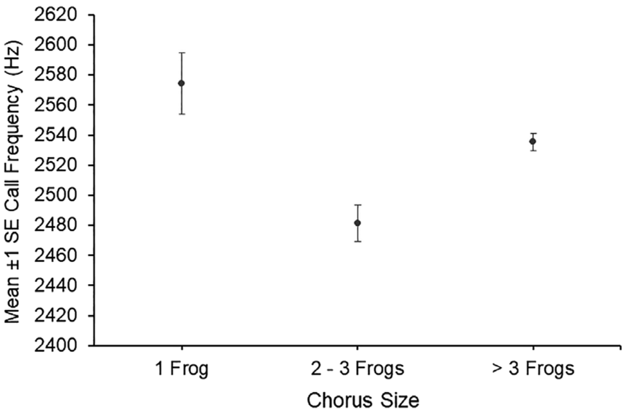

Figure 5 Comparison of pitch frequencies (Hz; mean ± SE) of *Litoria ewingii* calls across different chorus sizes.

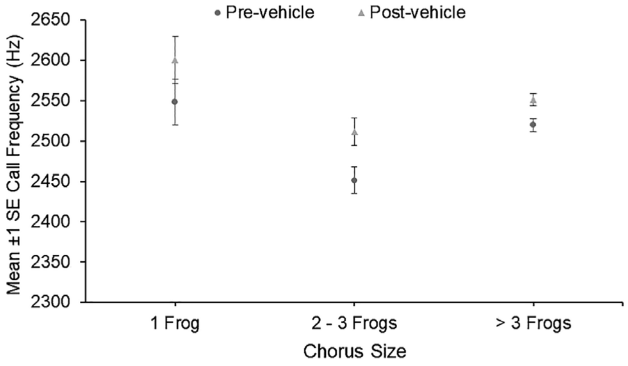

Figure 6 Comparisons of pre- and post-vehicle noise call pitch frequency (Hz; mean ± SE) of *Litoria ewingii* across differing chorus sizes.

from anthropogenic noise. Thus, the inability to escape such a constant stressor provides important context for studies that have reported altered immune function (Tennessen *et al*., 2018), modified mate choice (Halfwerk *et al*. 2019) and decreased species diversity (Eigenbrod *et al*., 2008) in areas of high anthropogenic noise.

Divergent impacts of traffic noise and chorus size on call pitch

The chorus size of brown tree frogs had a significant influence on call pitch whereby choruses of multiple frogs resulted in a decrease in call pitch, with the magnitude of the decrease greater in small choruses (2–3) rather than larger (3+) choruses. Similarly, Grenat *et al*. (2019) reported that impacts of traffic noise on the frequency of male common lesser escuerzo frog calls (*Odontophrynus americanus)* were elevated when frogs participated in chorus. Taken together with our other findings, these results indicate that frogs may adjust the pitch of their calls in opposing ways in response to anthropogenic traffic noise and conspecific calls. Such variation in responses may reflect different functional purposes of call modification in response to each of these stimuli. Whilst adoption of higher pitch calls in response to traffic noise may help to reduce masking of the call and facilitate signal transmission, it may be that lower pitch calls are employed in the presence of conspecifics as a means to adjust the information conveyed by the signal. Specifically, since large body size is often linked to lower pitch calls in anurans, it may be that in the presence of competing calling males it is important for males to indicate (honestly or dishonestly) large size with low pitch calls to invoke potential mate choice benefits or deter rival males (Wells, 2007). Indeed, prior research in several other species has reported such a response to conspecific calls (eg., Wagner, 1989; Bee & Perrill, 1996; Bee & Bowling, 2002). Alternatively, it may be that observed changes in call pitch could reflect changes in chorus composition. Perhaps individuals with high-pitched calls opportunistically call in situations in where competition from lower-pitched conspecifics may be diminished, such as when few other frogs are calling or immediately after disruptive traffic noise. Importantly, the influence of heavy vehicle noise still resulted in an immediate, short-term elevation of call pitch across all chorus sizes in the brown tree frog. However, the change in call pitch following this noise was most pronounced in the social conditions that otherwise favoured low pitch calls (i.e. small choruses). This finding, along with recent reports in other anurans that anthropogenic noise can reduce male participation in choruses (Alloush *et al*., 2011) or reduce female discrimination of male call spectral properties (Wollerman & Wiley, 2002), highlight the need to further explore the potential alteration or diminishment of sexual selection by noise pollution and the ramifications of this for population dynamics and demographics.

Table 2 Results of linear mixed effect model with call rate as the dependent variable performed using type II sum of squares chi-square ANOVA

Fixed effects	χ^2-value	df	*P*-value
Vehicles per minute	0.69	1	0.407
Distance	9.44	1	**0.001***
Vehicles per minute: Distance	1.58	1	0.209

Random effects	Variance (%)
Day: Time	13.28
Day	<0.001
Time	50.60
Residual	36.12

*Significance at 0.05 level.

Implications of call pitch differences for the reproductive ecology of urban frog populations within noisy environments

The observed increase in call frequency would likely increase the audibility of these vocalizations by reducing overlap with lower-frequency vehicle noise (Nemeth & Brumm, 2009; Roca *et al*., 2016). While increasing call amplitude provides an alternative method for male frogs to overcome the auditory masking effects of traffic noise, it has been previously reported that

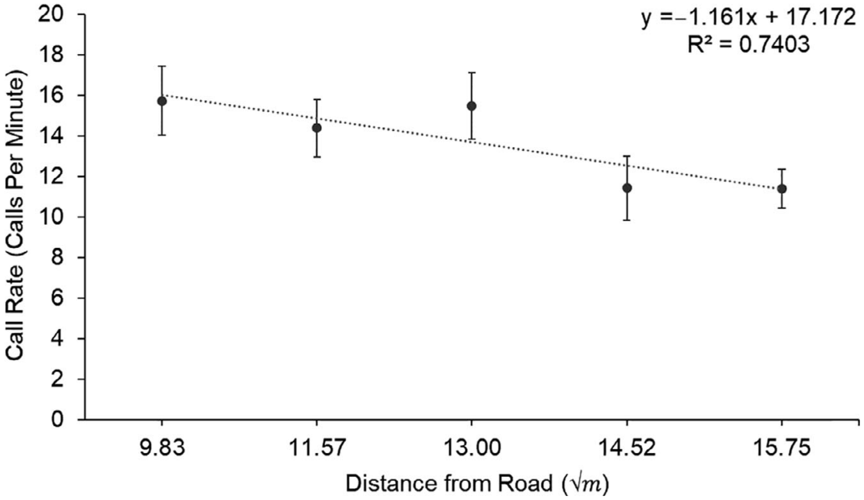

Figure 7 Association between call rate (number of calls per minute; mean ± SE) of *Litoria ewingii* and distance from Blackburn road traffic noise ($\sqrt{m}$), with fitted regression line, regression equation and R^2 value.

increasing call amplitudes incurs greater energetic costs than increasing call frequency in the brown tree frog (Parris *et al.*, 2009). Parris *et al.* (2009) report that increasing call amplitude to a level that achieves a release from auditory masking effects comparable to those of a 123 Hz call frequency increase, total nightly energy expenditure would increase by 37%. While the shift in call frequency that we observed was lower than previously reported, such a shift in call frequency would nevertheless decrease the energetic costs required to overcome the masking effects of traffic noise, relative to the costs of amplitude modification.

In species, such as anurans, whose reproductive success is dependent upon males attracting mates with their advertisement calls (Wells, 2007), anthropogenic noise pollution interferes with the capacity of potential female mating partners to receive and assess male advertisement calls. Increased traffic noise has been previously reported to be associated within decreased orientation towards the target signal and increased response latency amongst females when exposed to simulated advertisement calls (Bee and Swanson, 2007). Thus, utilizing increased call frequencies to enhance audibility of advertisement calls would provide males with a method to increase the probability of signal detection by potential female mating partners within habitats with anthropogenic noise pollution.

However, while increasing call frequency appears to be a cost-effective method to increase the probability of signal detection, it may have significant negative impacts upon mate-attraction. Lode & Le Jacques (2003) report that for the midwife toad *(Alytes obste)* male call frequency was associated with reproductive success, with lower call frequencies leading to an increased number of successful matings and hatching outcomes for males. Furthermore, Gerhardt (1991) demonstrated that grey treefrog *(Hyla versicolor)* and green treefrog *(Hyla cinerea)* females preferred male advertisement calls of the dominant frequency for each species and that a 200 Hz increase or decrease in call frequency led to a 20–40% decrease in female choice. Notably, female choice was found to be impacted with even a 50 Hz shift in call frequency (Gerhardt, 1991). Thus, males that increase the frequency of their advertisement calls, even slightly, may be perceived as less attractive by females, and consequently experience decreased reproductive success. Such a situation presents an important trade-off between audibility and reproductive success; males that invest heavily in enhanced audibility may be perceived as less attractive, whilst those who invest in attractiveness are likely to be detected by less potential female mates.

Conclusions

Amphibians are the most threatened group of terrestrial vertebrates, with 40% of species listed as threatened under the IUCN Red List of Threatened Species (Stuart *et al.*, 2004; Wake & Vredenburg, 2008; Greenberg & Mooers, 2017; IUCN, 2019). Anurans are susceptible to a broad range of threatening processes, particularly chytrid fungus (O'Hanlon *et al.*, 2018). Our study highlights the pervasive impact that anthropogenic noise can have on urban frog populations. Anthropogenic noise represents an additional threat to anurans due to its potential to disrupt communication and reproduction. While many anuran species exhibit short-term, plastic shifts in their calling behaviour (Roca *et al.*, 2016; this study), the sustained and inescapable nature of anthropogenic noise has the capacity to result in increased stress, decreased immune function and reduced species diversity (Eigenbrod *et al.*, 2008; McGregor *et al.*, 2013; Tennessen *et al.*, 2018; Slabbekoorn *et al.*, 2018).

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Conflict of interest

The authors declare no conflicts of interest.

Author contributions

All authors were involved in the conceiving and designing the experiments. VH, YKC, CC, ED, GG, RK, MK, NR, TS and KV performed the experiments. VH and NDSD analysed the data. DGC and VH wrote the paper, with editorial input from all other authors.

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