

When sounds collide: the effect of anthropogenic noise on a breeding assemblage of frogs in Belize, Central America

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Summary

Many organisms depend on acoustic communication for myriad functions, and have evolved behaviours to minimize effects of naturally occurring acoustic interference. However, as habitats are subject to increased alteration, anthropogenic noise becomes unavoidable, and how animals overcome such interference is not well understood. In most ecosystems, only a subset of frog species is associated with disturbed habitats; the ability of these species to overcome exogenous noise suggests that habitat associations may be related to species' response to noise. We tested the hypothesis that frogs associated with largely undisturbed forest habitat would be less likely to increase call output in response to exogenous noise than would those associated with disturbed or open habitat. While this relationship was not significant, we

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found a slight trend supporting the hypothesis. We then asked whether anthropogenic noise affects chorus tenure at individual- or at chorus-levels. Male frogs exposed to anthropogenic noise decreased both the number of days present at the chorus and the nightly chorus duration relative to controls. Because females generally join choruses late at night to breed, the effects of noise shown here are likely to substantially decrease frog reproductive success; thus, the acoustic environment may play an important role in shaping population dynamics and in amphibian declines.

Keywords: amphibian, anuran, chorus tenure, *Dendropsophus microcephalus*, urban noise.

1. Introduction

Naturally occurring biotic noise produced by both con- and heterospecifics is often pervasive as well as spatiotemporally structured and so may shape the local species assemblage (Bourne & York, 2001; Amézquita et al., 2006). Interference from noise is a ubiquitous phenomenon which all acoustically communicating organisms must overcome, as it generally decreases the ability of a receiver to respond to information in a sender's message (Narins & Zelick, 1988) and many species exhibit behavioural and physiological adaptations to process signals in naturally occurring noise (Narins, 1982; Brumm & Slabbekoorn, 2005). With anthropogenic habitat alteration now affecting most biomes in a variety of ways (Ellis & Ramankutty, 2008), one of the more poorly understood consequences of such alteration is the effect of the introduction of anthropogenic noise, such as traffic noise, on acoustically communicating animals. Some species of birds have been shown to avoid habitats near roads (Forman & Alexander, 1998) or to alter spectral or temporal properties of calls when presented with anthropogenic noise (Slabbekoorn & Peet, 2003; Slabbekoorn & den Boer-Visser, 2006; Wood & Yezerinac, 2006). Although frogs are among the most vocal vertebrates (Narins, 1982), only recently have they become a focus for studies of behavioural responses to exogenous noise. These studies have shown that noise affects frog breeding patterns by altering mate preferences in females (Bee & Swanson, 2007), and may more directly impact communication behaviour by causing males to modulate their call rate or call frequency (Sun & Narins, 2005; Kaiser & Hammers, 2009; Parris et al., 2009).

Frogs are associated with a variety of natural habitats, from intact forest to disturbed areas, and this association may partially determine their ability to respond to anthropogenic noise. Roads, for example, may have many impacts on amphibians (Kentula et al., 2004), including introducing high levels

of traffic and engine noise to natural areas which are otherwise largely undisturbed. Life history and communication traits that facilitate animal communication in naturally occurring noise may also be major predictors of a species' ability to persist in the face of anthropogenic noise. However, explicit tests to determine if the effects of anthropogenic noise on amphibian calling are habitat dependent are lacking (Pellet et al., 2004; Eigenbrod et al., 2008).

Moreover, amphibian vocalizations may increase aerobic metabolism up to 22 times resting rates, making calling one of the most energetically costly activities frogs undertake (Taigen & Wells, 1985; Wells & Taigen, 1989). Given the physiological costs associated with frog vocalizations, species that increase calling effort in response to anthropogenic noise may alter other behaviours to compensate for increased energy expenditure associated with increased vocal output (e.g., call duration or call rate). Such behavioural changes may have impacts on breeding success. In particular, the best predictor of male mating success for prolonged breeding frogs (*sensu* Wells, 1977) is chorus tenure, traditionally defined as the number of nights a male is present in a chorus (Greer & Wells, 1980; Ryan et al., 1981; Godwin & Roble, 1983); one way for male frogs to compensate for increased call energy expenditure is for individuals to decrease time spent in choruses. The cumulative effect of such behavioural changes over time may be to negatively affect population growth and persistence. It is unknown whether changes in individual calls in response to anthropogenic noise have any cumulative impact on chorus tenure.

To understand how amphibian species respond to the encroachment of anthropogenic noise on their habitats, we asked two questions: (1) Do frog species associated with naturally disturbed habitats more readily modify their calling behaviour in response to anthropogenic noise than do species associated with undisturbed habitats? To answer this, we studied an entire species assemblage of vocalizing anurans. In any group of species, correlations among species' traits may be affected by their relative degree of phylogenetic relatedness (Harvey & Pagel, 1991). To account for such structure, we also tested whether our hypothesis of habitat-associated response to noise could be better explained by relatedness of species rather than habitat association. We then asked (2) Do frog species that modify their calling behaviour in response to noise and, thus, exhibit increased energetic expenditure during individual calls, also decrease chorus tenure? For our second objective,

we focused on a single species known to increase its call rate in response to anthropogenic noise, and asked whether there was a decrease in individual- and chorus-level chorus tenure.

2. Materials and methods

2.1. Site selection and study species

This study was conducted from 27 June through 19 August, 2008 in the vicinity of Las Cuevas Research Station (LCRS), Chiquibul Forest Reserve, Belize (16°44'N, 88°59'W). Vehicular traffic at the site was primarily in the form of diurnal movement to and from the station, and the occasional military or Belize Forest Department patrol. As a result, even the frogs at ponds near the main logging road in this region are generally naïve to nocturnal anthropogenically-produced sounds such as automobile noise. Playback experiments were conducted with calling males of seven species (Table 1).

2.2. Stimulus preparation

We selected 10 3-min recordings of different automobiles that met two criteria: the stimulus had energy reaching at least 7 kHz, as most sound energy from vehicular traffic falls within the lower frequencies (Lewis, 1973). To ease comparison among trials, we also chose recordings in which stimulus dominant frequency was within 15% of the mean of all stimuli. We used Audition (Adobe v. 2.0) to pitch shift each file ± 1 , 2 and 3 semitones using the PitchShifter plugin, generating a total of 70 sound files. All species were also presented with a positive control stimulus consisting of continuous white noise and a negative control, consisting of a silent track. White noise was generated within Audition. All stimuli were then calibrated using Vibro Toolbox (Gridi-Papp, 2006–2007) to compensate for the acoustic profile of the speaker, ensuring equivalent levels for all stimuli (Figure A1).

2.3. Playback experiments

We conducted playback experiments at a total of 11 sites around LCRS, ranging from 100 m to approx. 6 km from the field station. Natural biotic background noise at the breeding sites was measured using a sound level meter with C-weighting (Radio Shack 33-2055). C-weighting allows the

sound level meter to measure lower frequencies without as much attenuation as A-weighting, although at very high frequencies, can attenuate slightly more. Measurements included in analyses were taken between 1830–1945 h.

For all species, all recordings of vocalizing males were made between 1900 and 2300 h. To avoid multiple recordings of individuals, in dense choruses, we collected each male after a recording, and held them in individual bags. At the end of the recording session, all frogs were released at their point of capture. In sparse choruses (fewer than five individuals of a species), we worked systematically through a chorus to avoid multiple recordings from the same individual. For community-wide experiments, the recording protocol consisted of five 3-min blocks per focal male: pre-stimulus baseline of spontaneous calling, anthropogenic noise, positive control, negative control and post-stimulus. We rotated through breeding sites in the area, returning to a site only after a minimum of 2.5 weeks had passed.

For the focal species *Dendropsophus microcephalus*, two types of playback experiments were conducted. The first consisted of five 3-min blocks: pre-stimulus baseline of spontaneous calling, anthropogenic noise at 70 dB SPL, anthropogenic noise at 90 dB SPL, negative control, and post-stimulus. The second protocol consisted of four 3-min blocks: pre-stimulus baseline of spontaneous calling, anthropogenic noise at 90 dB SPL, positive control, and post-stimulus. Within a trial in each experiment, the order of control and noise stimuli was randomized. Immediately following a recording, individuals of *D. microcephalus* were captured and individually marked using visual implant alpha tags (Northwest Marine Technology, Shaw Island, WA, USA; Kaiser et al., 2009) or identified by a previous marking. Only one set of recordings from each individual was used in the analyses.

Within a species, each frog was presented with a different anthropogenic noise stimulus, and no stimulus was used more than once for a given species (McGregor et al., 1992). Stimulus amplitudes were calibrated to 90 dB SPL at 1 m using the sound level meter and presented to focal animals using an iPod and a powered loudspeaker (CalRad 20-257) at a distance of 1 m; for individuals of *A. moreletii*, stimuli were broadcast at 70 dB to facilitate detection of their calls. Frog calls were recorded using a directional microphone (Audio Technica AT-815b or AT-835b) and a digital recorder (Marantz PMD670). Sample size for each species varied (Table 1).

Table 1. Habitat associations and sample sizes of species included in this study.

Species	Habitat	<i>N</i>
<i>Agalychnis callidryas</i>	Forest	12
<i>Agalychnis moreletii</i>	Forest	11
<i>Dendropsophus ebraccatus</i>	Forest	13
<i>Dendropsophus microcephalus</i>	Open/disturbed	39
<i>Incilius valliceps</i>	Open/disturbed	9
<i>Tlalocohyla loquax</i>	Open/disturbed	12
<i>Tlalocohyla picta</i>	Open/disturbed	14

2.4. *Chorus tenure*

Due to a paucity of comparable ponds, as well as safety constraints, chorus tenure experiments were limited to two ponds. Study ponds were approx. 5–6 km from LCRS, separated by 1 km, and matched for amphibian species composition, canopy cover and vegetation. Both ponds were within 1 km of a logging road which experienced approx. 1–2 vehicle transits per day, but was not generally used at night. Vehicular noise during the day measured at the ponds was less than 50 dB SPL; nighttime ambient noise levels at ponds were above 60 dB SPL.

All male *D. microcephalus* encountered at both ponds were individually marked using VIE ($N = 57$; Kaiser et al., 2009). Measurement of air temperature, time of chorus start and end, and identification of all calling individuals present at both ponds were carried out each night of the study. We randomly designated one pond as the experimental pond for the duration of the study; here, we broadcast engine noise (Figure A1) for at least one hour per night. The stimulus consisted of a mix of anthropogenic noise stimuli from *D. microcephalus* playback experiments. The order of the different audio stimuli differed each night to prevent habituation. Noise was broadcast using the system described above, with an amplitude of 90 dB SPL at 1 m. The speaker was placed at the same location each night, opposite the perch sites of most calling *D. microcephalus*. Depending on call site, the estimated SPL of the noise stimulus at the frogs was approx. 60–70 dB SPL. At the control pond, (a) noise was never broadcast, and (b) noise from the experimental pond was less than 50 dB SPL. Surrounding breeding aggregations were monitored periodically for immigration of marked individuals.

2.5. Analyses

We analyzed call rates using Audacity (Audacity, sv 1.2.6) and Audition (Adobe Systems, v. 2.0). Call duration measurement (Audition) was limited to *Incilius valliceps* and *Tlalocohyla picta*, species with vocalizations having short attack and decay times, to ensure accurate estimates of call onsets and offsets. Call rate response was normalized across species, using the transform $\ln(\text{stimulus response}/\text{pre-stimulus response})$. This transform assured that all individuals and species were compared in terms of proportional response to stimulus. Analyses on transformed data were carried out using a linear mixed model to account for repeated measures across nights. For post-hoc comparison among stimuli not tested in the model, we used chi-squared tests. We used Bonferroni corrections to alpha levels to test for significance in all post-hoc tests. For *D. microcephalus*, a total of six comparisons were made, and for all other species, a total of five; alpha levels were, thus, set to 0.008 and 0.01, respectively. We tested for a dependence of species' call rate response upon habitat using ANOVA, also using transformed data. Habitat associations were based on Lee (2000; Table 1) and validated by our own observations. To account for phylogenetic relatedness among species, we further tested for habitat associations using two methods. First, we used a phylogenetic ANOVA (Garland Jr. et al., 1993), which simulates evolution of a continuous character along a phylogenetic tree relating the species of the frog assemblage, using the GEIGER package within R (Harmon et al., 2008). We also used a generalized least-squares method as described in Paradis (2006) which uses a Brownian correlational structure to express phylogenetic relatedness among species. We did not have branch lengths for our phylogenetic tree, so we performed all tests against trees having branch lengths transformed each of four ways: a 'punctuational' transformation with all branches of equal length; and three forms of Grafen transformations with power 0.5, 1 and 2, which results in all leaves being equidistant from the base of the tree, with diversification rates at leaves in comparison to earlier interior nodes occurring more slowly, at the same rate, or more rapidly (Grafen, 1989).

Chorus tenure analyses were conducted using Wilcoxon rank-sum tests and were restricted to frogs initially marked at least one month prior to the end of census. Frogs never recaptured (19.2% of total at the experimental pond and 18.3% of total at the control pond) were not included in chorus tenure analyses. These statistical analyses were carried out in StataIC 10.0 (StataCorpLP, 2008).

3. Results

3.1. Background biotic noise

Background noise levels in forest habitats were not significantly different ($T = 0.825$, $N_1 = 5$, $N_2 = 37$, $p = 0.414$) than in open habitats during the period just after dusk when chorusing first began (between 1830 and 1945 h). Frequency spectra of forest and open habitats were generally similar, with most sound energy below 8 kHz, but with some low-level background insect noise from 1 kHz up to approximately 17 kHz.

3.2. Call rate

Of the seven species tested, three did not change call rate at all in response to noise: *Agalychnis moreletii*, *Tlalocohyla picta* and *Incilius valliceps*. In contrast, *A. callidryas*, *T. loquax* and *Dendropsophus microcephalus* all increased call rate in response to anthropogenic noise and to white noise (Figure 1); in these species, white-noise and anthropogenic-noise responses did not differ significantly from each other. In each of these species, the negative control stimulus had no significant effect on call rate, and pre- and post-stimulus treatments did not differ significantly from each other. Furthermore, the increase in call rate observed in male *D. microcephalus* in response to anthropogenic noise did not differ whether noise was broadcast at 70 or 90 dB SPL ($T = -2.2472$, $DF = 16$, $p = 0.0391$; $\alpha = 0.008$). *Dendropsophus ebraccatus* was the only species for which the model was significant but no treatment contrasts were significant. There was a trend toward a decrease in call rate during negative control stimulus and post-stimulus blocks (negative control: $Z = -1.99$, $p = 0.047$; post stimulus: $Z = -2.25$, $p = 0.025$), although with corrected alphas for multiple comparisons ($\alpha = 0.01$), these were not significant. Due to the fact that we recorded multiple individuals from a pond on a given night, it is likely that neighbouring males within a pond overheard the stimulus within a night. Although we were unable to control for this, generally consistent results across individuals within a species suggest this did not substantially affect results.

3.3. Call length

Only *I. valliceps* and *T. picta* were included in this analysis. *Tlalocohyla picta* did not change call length in response to noise ($N = 10$, $\chi^2 = 3.87$,

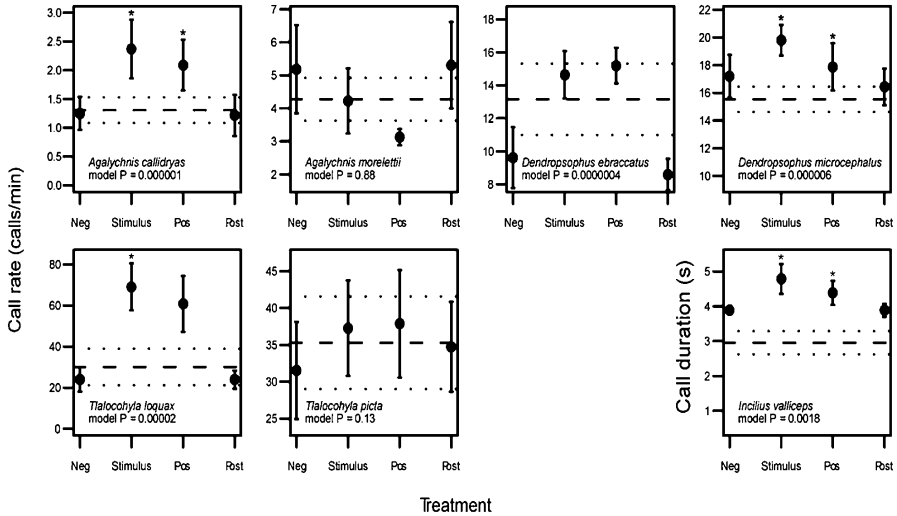


Figure 1. Species responses to noise treatments. Significance of the overall repeated-measures model is indicated by the *p* value. Significantly different treatments as indicated by post-hoc tests are indicated by an asterisk. Call rates are shown for all species but *I. valliceps*, for which call duration is shown. Treatments are shown relative to pre-treatment baseline call rate (dashed line) and its 95% confidence intervals (dotted lines); no species increased call rate during negative silent control (Neg) or in post-stimulus spontaneous calling (Post). Species which significantly increased vocal output in response to anthropogenic noise (Stimulus) also tended to increase in response to positive white noise control (Pos). Error bars are SE.

p = 0.424), but *I. valliceps* increased duration significantly (*N* = 11, $\chi^2 = 0.0003$, *p* = 0.0001).

3.4. Habitat association and call rate response

Within the ANOVA analysis, there was no significant relationship between a species' habitat association and its response to anthropogenic noise ($F_{5,1} = 0.47$, *p* = 0.52). Accounting for phylogenetic context (Figure 2), regardless

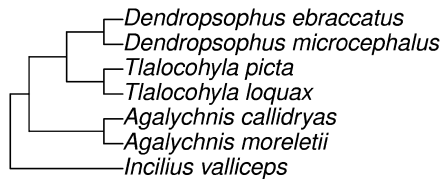


Figure 2. Phylogenetic relatedness of species in frog assemblage. For this figure, branch lengths were transformed using Grafen's (1989) method with power 1.

of branch length transformation, none of the phylogenetic ANOVAs were significant (all $p > 0.64$), nor were the results of the generalized least-squares analysis with phylogenetic correlational structure (all $p > 0.62$). However, the power of our ANOVA analyses was limited by sample size (number of species). It is particularly notable that only one of three forest species increased call rate in response to noise, while three of four disturbed-habitat species increased call rate (Figure 1). Taken together, this suggests a likely general association between a species' habitat preference and its call rate response, such that species associated with more open or disturbed habitats can respond to anthropogenic noise more readily than can species associated with more pristine habitats. Unfortunately we lacked statistical power to demonstrate this conclusively.

3.5. *Chorus tenure*

The number of nights an individual participated in chorusing was reduced, and frogs were detected for a shorter period at the experimental pond than at the control pond (Wilcoxon rank-sum test: $Z = -2.626$, $N_1 = 19$, $N_2 = 38$, $p = 0.0086$; Figure 3). Additionally, frogs were captured less frequently at the experimental pond than at the control pond ($Z = -2.434$, $N_1 = 19$, $N_2 = 38$, $p = 0.0150$; Figure 3). Only one marked individual was observed to move between focal ponds, and no marked individuals were ever observed at surrounding ponds.

3.6. *Chorus length*

The aggregated effect of anthropogenic noise on individuals resulted in shorter choruses. Start times of *D. microcephalus* choruses at the two ponds did not differ throughout the season ($Z = 0.290$, $N_1 = 28$, $N_2 = 33$, $p = 0.7721$). Moreover, when the analysis was restricted to the first ten data-nights, before the onset of noise broadcasts, chorus lengths at the two ponds were not significantly different ($Z = 0$, $N_1 = N_2 = 12$, $p = 1.00$). This demonstrates that chorus lengths at the two ponds were similar before the introduction of exogenous noise, and that chorus end times only diverged once the treatments began. However, when data from the entire season were analyzed, chorus lengths at the experimental pond were significantly shorter ($Z = 4.175$, $N_1 = 28$, $N_2 = 29$, $p < 0.0001$), and ended significantly earlier ($Z = 4.455$, $N_1 = 28$, $N_2 = 29$, $p < 0.0001$) than those at the control pond (Figure 4). Frogs at the experimental pond ending calling on average

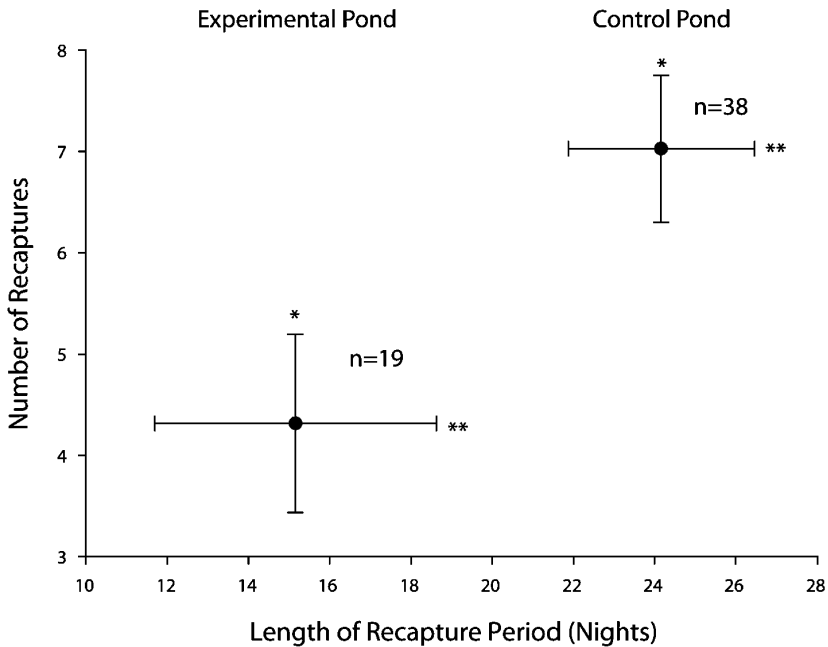


Figure 3. Noise exhibits individual level effects on frogs. The number of frog recaptures during the sampling period as a function of the length of recapture period (total time recaptured from first night marked to final night recaptured, in nights). Frogs at the experimental pond were captured significantly less frequently and over a significantly shorter period than those at the control pond. Error bars are SE (* $p < 0.01$; ** $p < 0.001$).

at 2232 h, and as early as 2020 h; frogs at the control pond ended at 2329 h on average and did not end earlier than 2208 h. Notably, chorus start times throughout the field season after the noise treatments commenced remained statistically equivalent at each pond. Thus, the demonstrated effect is in fact due to the noise treatment and not due to chance differences between the two ponds.

4. Discussion

We found that, within the assemblage we studied, despite similar background noise levels during frog calling in forest and open habitats, species associated with open habitats were likely to increase, not decrease, call output. The response to noise, thus, generally followed the predicted pattern based on habitat use in this region, although due to our limited sample size (number

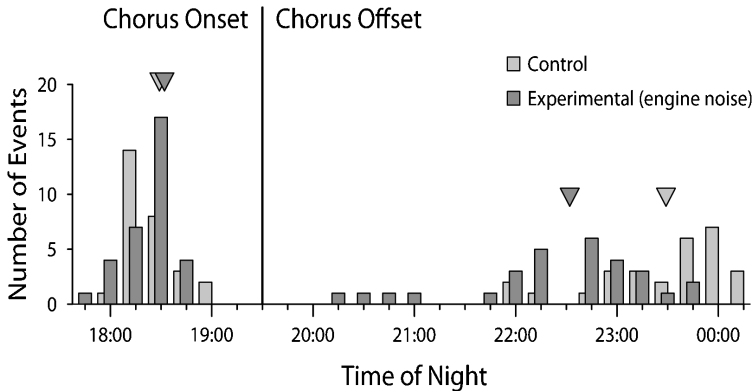


Figure 4. Chorus tenures at control and experimental ponds. Mean chorus start times at the two ponds did not differ significantly, whereas chorus end times were significantly earlier at the experimental pond ($p < 0.0001$). Arrows indicate means of distributions.

of species), this result was not significant. Two species did not follow predicted behavioural patterns. *Agalychnis callidryas* increased call rate in response to noise, but observed call rates were low, and the increase evoked by noise was correspondingly low: approximately one call per minute. Whether this change is of physiological relevance to males or of behavioural relevance to females was beyond the scope of this study. *Tlalocohyla picta*, an open/disturbed habitat dweller, was predicted to increase call rate in response to noise, but did not. Thus, two of three forest species and three of four open/disturbed habitat species followed the predicted patterns of call response to noise.

Furthermore, we have shown that increasing vocal output in response to noise may have consequences at both the individual- and the chorus-level. Previous studies have focused on a single species or a selection of species (Sun & Narins, 2005; Kaiser & Hammers, 2009); this is the first assessment of the response of an entire species assemblage to anthropogenic noise. However, these results are indicative of the immediate behavioural responses only. Prediction of the long-term effects of exposure to anthropogenic noise will require understanding of additional factors including behavioural energetics, chorus-level dynamics, and intra- and inter-species dynamics.

Although the frogs in our study were naïve to exogenous anthropogenic noise, man-made noise levels in animal habitats can be quite high. Measurements of these levels as they relate to animal behaviour are starting to be recorded: night time anthropogenic noise levels in bird habitats in Sheffield,

England were lower (49 dB SPL) than in daytime (57 dB SPL; Fuller et al., 2007). Nighttime noise levels measured in two wetlands in Minnesota, USA, averaged 75 dB SPL, and remained consistent from 1800 to 0000 h (Bee & Swanson, 2007). Habitat loss and alteration has now impacted over 4000 amphibian species (IUCN et al., 2008); as anthropogenic habitat change continues, exogenous noise will become ever more prevalent. Thus, the need to overcome disruptive noise is universal: a signal presented in the absence of other sounds will be the exception rather than the rule. Indeed, individuals of many species have developed a diversity of ways to accommodate decreased signal-to-noise ratios (reviewed in Gerhardt & Huber, 2002). However, because of the structural and temporal differences between natural and anthropogenic noise, the efficacy of these mechanisms against this new form of exogenous noise will vary.

Other studies have examined the effect of frog life history traits on species distributions, the likelihood of persistence after catastrophic declines, or on habitat choice (i.e., common to forest or to pasture; Lips et al., 2003; Bielby et al., 2008; Hawley, 2008). No study has included bioacoustic parameters in their assessments. The integration of multiple parameters, such as bioacoustic responses, into one unifying model to determine those factors driving species occupancy of disturbed habitats requires substantially more data on species' responses to noise, but may be extremely useful in understanding how the acoustic environment contributes to the shaping of local species assemblages, species distributions, or in understanding the effect, if any, of anthropogenic noise on amphibians.

Given the energetic costs of calling in frogs (Wells & Taigen, 1989), the consequences of increased vocal output in response to noise for frogs are clear. A frog that increases its vocal output in response to anthropogenic noise will use more of its energy reserves, and require more foraging time between chorus nights, resulting in decreased individual chorus tenure. Other frog species may respond to anthropogenic noise by increasing call rate (Sun & Narins, 2005; Kaiser & Hammers, 2009) or call frequency (Parris et al., 2009). In addition, *Hyla chrysocelis* has been shown to increase call duration in response to increased chorus noise, while keeping calling effort relatively constant (Love & Bee, 2010); whether this species would respond to anthropogenic noise similarly remains to be tested. It is unknown whether the energetic costs of behavioural compensation for anthropogenic noise requires other tradeoffs in reproductive traits, such as reduced sperm quality or

quantity. While we did not test the effect of chorus size here, Kaiser & Hammers (2009) showed that the responses of the frog *Dendropsophus triangulum* to chorus noise and anthropogenic noise playbacks at 75 dB SPL were not significantly different. We suggest, however, that this does not diminish the impact of anthropogenic noise on frogs: chorus size may fluctuate, but as anthropogenic encroachment on habitats increases, anthropogenic noise is likely to simply grow ever more constant.

Anthropogenic noise negatively impacts (at least male) fitness by decreasing male chorus-level tenure. In many species, males arrive at breeding sites early in the evening and chorus to attract females. Females typically arrive at ponds later than do males: in one study, males of *D. microcephalus* began calling at 1830 h, but females arrived, on average, at 2315 h (Bevier, 1997). Anthropogenic noise can cause male choruses to end earlier than they otherwise would, and prior to female arrival. Therefore, the introduction of noise causes not only individual-level and chorus-level components of chorus tenure to decrease, but also reduces the synchronicity between male calling and female presence in the chorus. This ultimately reduces mating opportunities for both sexes. Thus, we propose a redefinition of chorus tenure as a predictor of mating success is in order. Traditionally, chorus tenure has been defined as the number of nights a male spends in a chorus, calling to attract females (Greer & Wells, 1980; Godwin & Roble, 1983; Gerhardt et al., 1987). Because non-calling males ('satellite males') generally have a lower chance of mating than do callers (Roble, 1985), it behooves all frogs in the chorus to call, and to call for as long as possible, within the constraints imposed by energetic costs. As a result, chorus tenure can be thought of as having two components: (a) an individual-level component: the number of nights an individual frog returns to a chorus and (b) a chorus-level component: the total amount of time an aggregation spends chorusing on a given night. This supercedes previous definitions (Godwin & Roble, 1983; Gerhardt et al., 1987), which included only an individual-level component.

While we lacked replication for testing chorus-level effects, these results are consistent with noise having large-scale effects on male amphibians. The response of female frogs will undoubtedly also affect the outcome of male behavioural shifts to anthropogenic noise and the resulting changes in male chorus behaviour. In many species of frogs, females prefer males with higher call rates; thus, females may prefer males with a greater behavioural response

to anthropogenic noise. Female frequency preference is more complex. Females often prefer low frequency calls to higher frequencies; as frequency is generally correlated with body size, this preference favours larger males (Gerhardt, 1994). In species where either size-assortative mating or large-male advantage exists, preferred males generally have higher fertilization success relative to small males (reviewed in Gerhardt, 1994). However, animals that alter call frequencies to avoid anthropogenic noise shift calls up in pitch, where the noise energy begins to decrease (Slabbekoorn & Peet, 2003; Parris et al., 2009). How females respond to changes in call intensity or call frequency is unknown.

Our results show that the role of anthropogenic noise has been under-represented in the current literature on amphibian behaviour and declines. Although the effect of anthropogenic noise on anuran calling behaviour has gained attention more recently, there has been less focus on the ecological and conservation ramifications of this work (Fahrig et al., 1995; Fahrig & Rytwinski, 2009). Our results add to the growing body of research which indicates that species which communicate vocally need acoustic protection to survive anthropogenic encroachment. While species may, and likely do, have multiple mechanisms for coping with acoustic interference, such mechanisms may not serve to allow organisms to overcome anthropogenic noise, which differs from naturally occurring noise in many important ways. Due to the realistic constraints on most field studies, we suggest that future studies should focus on replication of these experiments with other forest and disturbed habitat species. The power needed to detect trends of responses associated with habitat or other factors will likely come from various authors, and be in the form of meta-analysis. Noise has been shown to be detrimental to birds and may be even more detrimental to frogs, which are less vagile and are less able to distance themselves from an anthropogenic noise source. For these species, anthropogenic disturbance to the acoustic environment may be as important as disturbance to the physical environment.

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Appendix

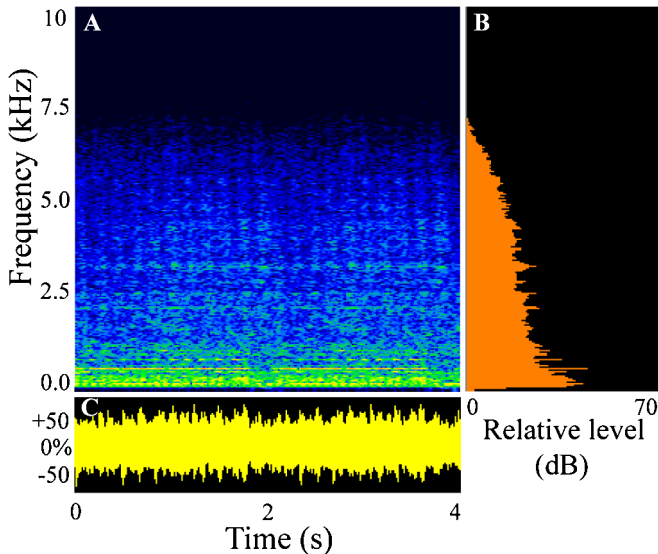


Figure A1. Attributes of noise stimulus used. (A) Sound spectrogram of the stimulus recording, in which colour intensity encodes sound intensity. (B) Relative amplitude spectrum of recording. (C) Waveform of noise stimulus. This figure is published in colour in the online edition of this journal, which can be accessed via <http://www.brill.nl/beh>