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Original article

Plasticity in the vocalizations of anurans in response to traffic noise

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ABSTRACT

Many species use acoustic signals to attract mates, and such signals can be degraded by anthropogenic noise. Anuran abundance has been shown to be negatively correlated with road traffic which could be due in part to the interruption of mate attraction by traffic noise. However, this impact could be small if anurans can alter their vocalization characteristics to avoid masking of their calls by traffic noise. We predicted that: (i) anuran vocalization characteristics (dominant frequency, mean amplitude and call rate) should be different in areas with different traffic noise levels; (ii) increases in traffic noise can cause immediate changes in amphibian vocalization characteristics; (iii) these altered vocalizations are similar to those at high traffic sites. To test the first prediction we compared vocalizations of four species of anuran at breeding sites in locations with low traffic noise vs. sites with high traffic noise. For the second prediction we broadcast traffic noise at low traffic (quiet) sites, and compared the anuran vocalizations before vs. during the broadcast traffic noise. For the third prediction we compared vocalizations at high traffic sites to those produced at low traffic sites while broadcasting traffic noise. Three species of anurans found at locations with low traffic noise produced vocalizations with different characteristics than individuals of the same species found in locations with high traffic noise. Broadcast traffic noise immediately altered amphibian vocalization characteristics such that they became similar to those of the same species found in locations with high traffic noise. We conclude that plasticity in the vocalizations of anurans allows for the maintenance of acoustic communication in the presence of traffic noise.

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1. Introduction

The spread of urban centres can have large effects on the natural environment. One such effect is anthropogenic noise ('noise pollution'), which can be harmful to animals, interfering with their acoustic signalling for communication (Slabbekoorn and Peet, 2003; Sun and Narins, 2005). The effectiveness of an acoustic signal depends on the distance a receiver is from the signal's origin (Forrest, 1994), the acoustic properties of the signal, and the degree to which the environment disrupts signal transmission through, for example, background interference (Ryan and Rand, 1993; Castellano et al., 2003). If animals in a particular area are unable to communicate due to background interference, the habitat quality in that area is effectively reduced; this may result in declines in species density and distribution (Sun and Narins, 2005).

It has been estimated that globally one-third of amphibian species are experiencing population declines (Stuart et al., 2004). Beebe and

Griffiths (2005) listed habitat alteration, environmental contaminants, UV-B irradiation, disease, introduced species, exploitation and climate change as the primary factors explaining these declines. Roads are an additional possible cause. Amphibian abundance is known to be negatively correlated with road traffic (Fahrig et al., 1995; Carr and Fahrig, 2001), and amphibian species richness is negatively correlated with the density of paved roads (Findlay and Houlahan, 1997; Houlahan and Findlay, 2003). Several authors have suggested that traffic mortality (road kill) is the main reason for these negative relationships (Fahrig et al., 1995; Hels and Buchwald, 2001; Mazerolle, 2004). However, it is also possible that roads reduce amphibian abundance through disruption of vocalization-based mate attraction by traffic noise (Barrass, 1985; Forrest, 1994; Warren et al., 2006; Lengagne, 2008). Bee and Swanson (2007) suggest that traffic noise acts to reduce the effective transmission distance (ETD) of a vocalization, resulting in vocalizations becoming lost in the noise such that females cannot orient themselves towards a breeding chorus (Narins, 1982). On the other hand, if males can alter their vocalizations to avoid masking by traffic noise, there may be no net effect on reproductive success. While differences in vocalization characteristics in areas with and without traffic noise have been observed in several species of birds (Slabbekoorn and Peet, 2003;

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Brumm, 2004; Parris et al., 2009) and anurans (Bee, 2000; Lardner and bin Lakim, 2002; Penna and Hamilton-West, 2007; Parris et al., 2009) it is not yet known whether this is a plastic or fixed response.

The purpose of this study was to test the predictions that: (i) anuran vocalization characteristics (dominant frequency, mean amplitude and call rate) are different in areas with different traffic noise levels; (ii) increases in traffic noise cause immediate changes in amphibian vocalization characteristics; (iii) these altered vocalizations are similar to those observed at high traffic (noisy) sites. To test the first prediction we compared vocalizations of anurans at breeding sites with low traffic noise vs. at sites with high traffic noise. For the second prediction we broadcast traffic noise (mean 76 dBA) at low traffic (quiet) sites, and compared the anuran vocalizations before vs. during the broadcast noise. For the third prediction we compared vocalizations of anurans at breeding sites with high traffic noise to the vocalizations produced at low traffic sites while broadcasting traffic noise.

2. Materials and methods

We tested these predictions using four species of anurans in eastern Ontario: green frogs (*Rana clamitans*), northern leopard frogs (*Rana pipiens*), gray treefrogs (*Hyla versicolor*), and American toads (*Bufo americanus*). We also included spring peepers (*Pseudacris crucifer*) but these data had to be omitted (see below for explanation). Sample sites in Eastern Ontario, located south of Ottawa and north of highway 401 between Brockville and Long Sault, were selected from National Topographic Data Base (NTDB) maps using Geographic Information System software. Sites consisted of wetlands, ponds and ditches (Fig. 1). Sample sites were selected to provide the greatest distribution of locations across the region given the limitations imposed by the locations of high and low traffic roadways. Sampling locations were a minimum of 3 km apart to avoid pseudoreplication (Eigenbrod et al., 2008a). If no anurans of a particular species were found calling at a sampling location, the site was removed from the study for that species. Sites were divided into two categories (HIGH and LOW noise) and were selected such that they represented the greatest possible difference in traffic noise levels between categories. LOW sites were those with traffic noise not exceeding 50 dBA while HIGH sites were those with traffic noise exceeding 60 dBA (Fig. 2). We obtained traffic noise levels from audio recordings (see below). Forty-four LOW and 39 HIGH sites were sampled between May 1 and August 1, 2007, between half an hour after sunset and midnight.

At each sampling location we made audio recordings of the vocalizations produced by a single male anuran with a digital sound recorder (Sampson Zoom H4 with stereo unidirectional electret condenser microphone) using a sampling rate of 96 kHz, at 1.5 m above the ground placed at the water's edge. At HIGH locations audio recordings were made for 3 min. Vocalizations at LOW sites were recorded for a total of 6 min. Three minutes into the recording at LOW sites, we broadcast traffic noise (mean 76 dBA at 5 m) from stereo speakers (Altec Lansing, Model – VS4121BLK), located directly below the recording equipment, for 3 min. This resulted in a 3-minute recording of vocalizations before the broadcast of traffic noise (BEFORE) and a 3-minute recording of vocalizations during the broadcast (TREATMENT) at the low traffic sites. The sampling unit was the vocalization of a single male at a given site, found within 5 m of the recording equipment. Vocalizations attenuate with increasing distance from their source (Martin et al., 1977); however, the attenuation rate over a 'hard' boundary such as water is very low (Forrest, 1994). Therefore, we assumed that anuran vocalizations produced at the water surface did not attenuate appreciably over this short distance. During the initial 3 min recording, a sound meter (Galaxy Audio, Model – CM-130) was

used to record the mean amplitude of the site background noise. If there was more than one anuran species calling at a given site, we returned to that site for successive nights, such that each night an individual of a different species was recorded. This was done to limit the exposure of individuals to the broadcasted traffic noise at LOW sites while collecting the BEFORE recording. The number of calling bouts recorded per species varied due to the innate characteristics of each species call. For species with long calls (e.g. American Toads) we recorded between six and 10 bouts per sample while species with shorter calling bouts (e.g. Green frogs and Leopard frogs) allowed for the recording of a greater number of bouts (4–33 bouts) within the same 3 min sampling period.

2.1. Vocalization characteristics

All recordings were amplified using Raven Pro v1.3 (Cornell Lab of Ornithology, 2007), until the mean site noise level within the recording was equal to that of the reading from the sound meter during recording. The use of a digital recorder with a stereo microphone results in the production of audio files with two channels (Left and Right). We used the channel with the lowest traffic noise levels to extract our vocalizations. The remaining channel was used to determine the site level traffic noise (see below). Raven Pro v1.3 was used to isolate calls produced by individual males from each recording. For TREATMENT recordings, the interactive signal detector tool was used to remove the traffic noise from the recording. This tool allows the software to identify the known traffic noise and remove it, leaving behind the male vocalizations for analysis. Recordings that were found to have traffic noise levels higher than the amplitude of anuran vocalizations were subjected to multiple runs through the signal detection software, and any remaining traffic noise was filtered out of the recording manually. We also listened to each recording during processing to ensure no vocalizations were removed by the detector tool.

Extraction of vocalization characteristics of the calls produced by individual males was completed in Raven Pro (v1.3). Individual calls were subjected to a Fourier transformation to define signal frequency and magnitude. Each Fourier coefficient was then squared and the resulting values were used to produce columns of pixels within a spectrogram (Charif et al., 2008). The values of the power spectrum between the lower and upper frequency bounds of the call were summed, and then divided by the number of frequency bins in the call to provide a mean amplitude value in dB for a given call (Charif et al., 2008). Mean amplitude values for all calls taken from a three minute recording were then averaged to produce the mean amplitude for an individual male. This process was repeated to produce a single dominant frequency value for an individual male. The spectrogram and playbacks of a recording were used to determine the number of calls per minute, i.e., the number of calls divided by three (minutes of recording).

2.2. Site specific traffic noise

To obtain a measure of the site specific traffic noise we selected the channel from each recording that contained the highest traffic noise level. As traffic noise is known to be composed of primarily low frequencies, the mean amplitude of all elements below 400 Hz contained within each recording was used as a measure of the traffic noise at each location. Sounds below 400 Hz are below that of vocalizations produced by the species in this study (Fig. 3).

2.3. Broadcast traffic noise

Traffic noise for broadcasting was obtained by recording traffic from Provincial Highway 401, 5 m from the edge of the paved road

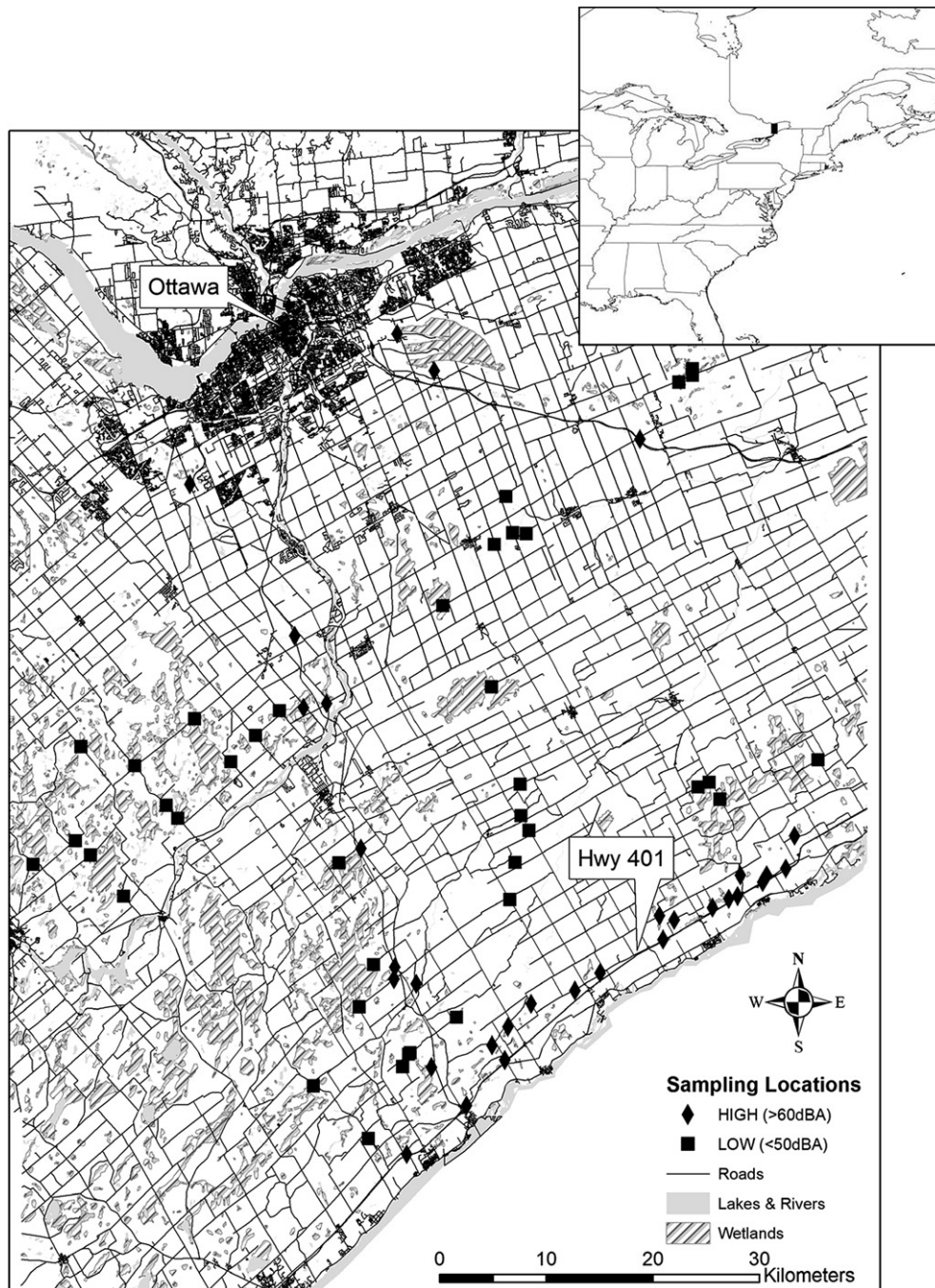


Fig. 1. Sampling locations with traffic noise >60 dBA (HIGH) and <50 dBA (LOW) in Eastern Ontario. Inset shows location of study within Eastern North America.

surface at a height of 1 m. Highway 401 connects the two largest cities in Canada—Toronto and Montreal—and forms the southern boundary of the study area. At the point of recording, Highway 401 is a four-lane divided highway with an average traffic volume of 18,300 vehicles/day, including a high proportion of transport trucks (Eigenbrod et al., 2008b); it offers the highest traffic noise level in our region. A sound level meter (Galaxy Audio, Model – CM-130) was used to measure the mean amplitude (dBA) of the traffic noise during recording (76 dBA). During broadcast, the sound volume of the traffic recording was set such that the mean amplitude at 5 m was 76 dBA.

2.4. Analysis

Temperature is known to affect the vocalization characteristics of anurans (Parris et al., 2009). We compared the median ambient temperature at HIGH and LOW sites using a Mann–Whitney U test, to ensure this variable was not contributing to any observed differences in vocalization characteristics. This test was conducted separately for each species, using the subset of sites at which each species was present. Results were considered significant at $\alpha = 0.05$.

To test the prediction that anuran vocalization characteristics (dominant frequency, mean amplitude and call rate) are different in

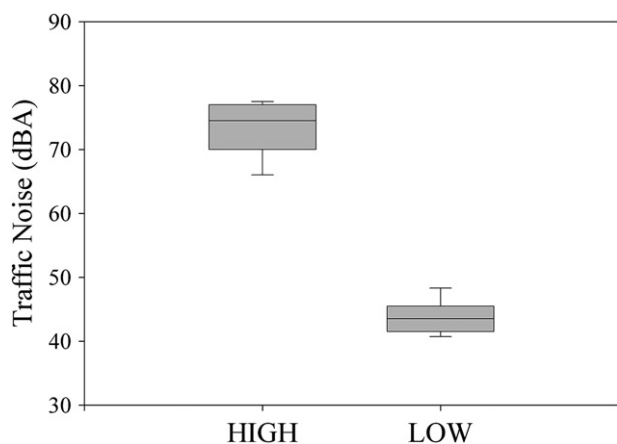


Fig. 2. Traffic noise levels (dBA) at HIGH sites and LOW sites. Lines within boxes represent the median values, upper and lower limits of boxes represent the 75th and 25th percentiles, and upper and lower whiskers represent the 90th and 10th percentiles.

sites with different traffic noise levels, we compared vocalization characteristics at LOW sites before noise was broadcast (BEFORE) to vocalization characteristics at HIGH sites using Mann–Whitney U tests. To test the prediction that traffic noise causes immediate responses in amphibian vocalization characteristics, we compared vocalization characteristics at LOW sites before traffic noise was broadcast (BEFORE) to vocalization characteristics at the same sites during the 3-minute broadcast of traffic noise (TREATMENT), using Wilcoxon’s signed ranks tests. To determine if the experimentally altered vocalizations are similar to those at high traffic sites, we compared vocalization characteristics from TREATMENT at LOW sites to vocalization characteristics at HIGH sites using the Mann–Whitney U test. Significance for the comparison of vocalization characteristics was then corrected by the Benjamini–Hochberg procedure for controlling false positives in multiple

comparisons (Thissen et al., 2002). All statistical analyses were conducted with SPSS (v13.0).

3. Results

Mean traffic noise was 43.8 dBA (SD = 2.66) at LOW sites and 73.2 dBA (SD = 4.91) at HIGH sites (Fig. 2). Temperature was not significantly different between the LOW and HIGH sites where green frogs, leopard frogs, gray treefrogs or American toads were sampled (Table 1). However, ambient temperature was significantly higher at the LOW sites than at the HIGH sites where spring peepers were sampled (Table 1). Due to the confounding nature of temperature on the vocalization characteristics of anurans and the difference in ambient temperatures between the LOW and HIGH spring peeper sites, the spring peeper data were removed from further analyses. The spectral signatures of vocalizations produced at quiet sites by green frogs and leopard frogs overlapped the traffic noise spectrum, whereas the vocalizations produced by American toads and gray treefrogs did not (Fig. 3).

3.1. Prediction 1: vocalizations at low traffic vs. high traffic sites

The call rates of green frog, leopard frog and gray treefrog vocalizations were significantly lower at LOW sites than at HIGH sites (Fig. 4, Table 2). Green frogs produced vocalizations with significantly lower mean amplitude and significantly higher dominant frequency at HIGH sites compared to LOW sites (Table 2, Fig. 4). Leopard frogs did not show significant differences in the mean amplitude of their vocalizations (Table 2) but did demonstrate a significantly higher dominant frequency of vocalizations at HIGH sites than LOW sites (Table 2, Fig. 4). Gray treefrogs did not produce vocalizations with significantly different mean amplitude or dominant frequency at LOW vs. HIGH sites (Table 2, Fig. 4). No significant differences were observed in any of the American toad vocalization characteristics at LOW vs. HIGH sites (Table 2, Fig. 4).

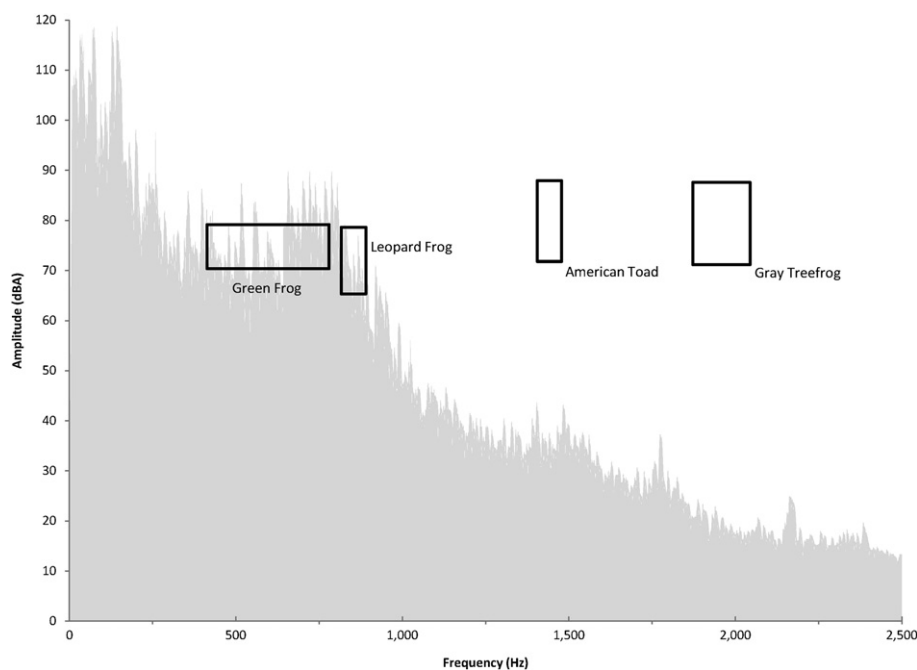


Fig. 3. Spectral overlap of the broadcast highway noise and vocalizations of four species of anurans from sites with low traffic noise. Rectangles represent the range of acoustic characteristics of species vocalizations.

Table 1

Median temperatures (*T*) and number of males recorded (*n*) at LOW (<50 dBA) and HIGH (>60 dBA) traffic noise locations for five species of anuran. Sample sizes differ among species because each species was present at a subset of sites. Only one male of each species was recorded at a given site.

Species	LOW sites		HIGH sites		Mann–Whitney U (LOW vs. HIGH T)	
	Median T	<i>n</i>	Median T	<i>n</i>	Z	<i>p</i>
Green Frog	20.0	25	20.0	23	-1.103	0.270
Leopard Frog	12.5	12	10.0	5	-1.377	0.195
Gray Treefrog	20.0	11	21.0	8	-0.840	0.968
American Toad	14.5	14	10.5	6	-1.255	0.239
Spring Peeper	17.0	17	11.0	11	-2.650	0.007

3.2. Prediction 2: vocalizations at low traffic sites before vs. during broadcast of traffic noise

Green frog and leopard frog vocalizations during the TREATMENT sampling period had significantly lower call rates and mean amplitudes than during the BEFORE sampling period (Table 2, Fig. 4). Both green and leopard frogs produced vocalizations with significantly higher frequencies during the TREATMENT sampling period when compared to the BEFORE period (Table 2, Fig. 4). Gray treefrog call rates during the TREATMENT sampling period were significantly reduced compared to the BEFORE sampling period; however, there was no significant difference in the mean amplitude or dominant frequency of their vocalizations between these two sampling periods (Table 2, Fig. 4). When exposed to broadcast

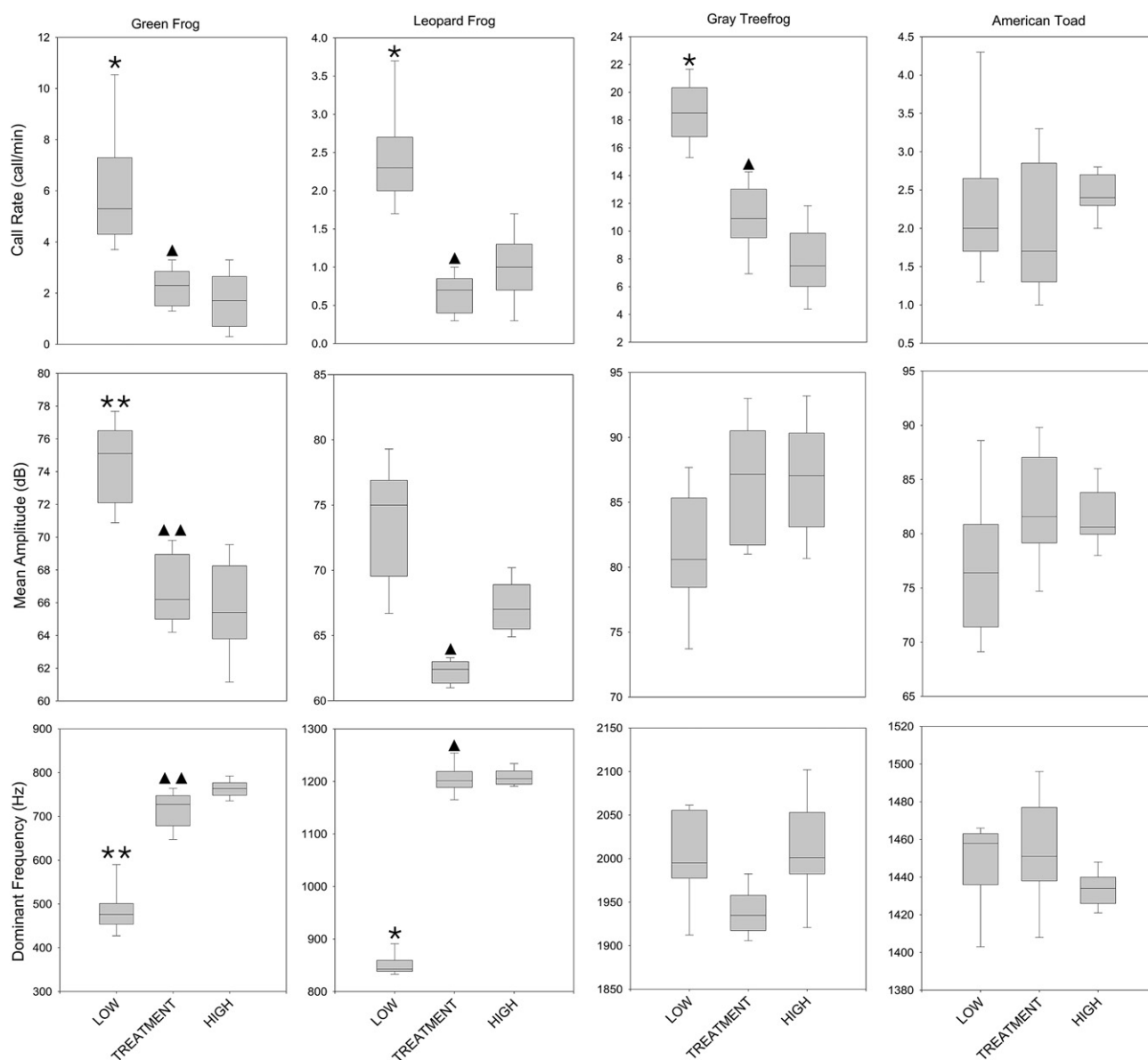


Fig. 4. Vocalization characteristics of four species of anuran at low-traffic sample sites (noise levels ≤ 50 dBA), before (LOW) and during (TREATMENT) the broadcast of traffic noise (mean 76 dBA at 5 m), and at high-traffic sample sites (noise levels > 60 dBA) (HIGH). * indicates a significant difference between LOW and HIGH (* $p < 0.05$, ** $p < 0.001$), ▲ indicates a significant difference between LOW and TREATMENT (▲ $p < 0.05$, ▲▲ $p < 0.001$), and ● indicates a significant difference between TREATMENT and HIGH (● $p < 0.05$, ●● $p < 0.001$). Upper and lower limits of boxes represent the 75th and 25th percentiles. Lines within the boxes represent the median values and upper and lower whiskers represent the 90th and 10th percentiles.

Table 2

Comparisons of vocalization characteristics for four species of anuran at LOW (<50 dBA traffic noise) vs. HIGH (>60 dBA traffic noise) sites, at LOW sites before the broadcast of traffic noise vs. during the broadcast of traffic noise (TREATMENT) and at LOW sites during the broadcast of traffic noise (TREATMENT) vs. at HIGH sites. Sample sizes for each treatment are indicated in Table 1. Note that sample sizes for LOW and TREATMENT are equal. *P*-values have been corrected by the Benjamini-Hochberg procedure for controlling false positives in multiple comparisons.

	LOW vs. HIGH		LOW vs. TREATMENT		TREATMENT vs. HIGH	
	Z	<i>p</i>	Z	<i>p</i>	Z	<i>p</i>
<i>Green Frog</i>						
Call rate	-2.728	0.009	-2.837	0.009	-0.486	0.634
Mean amplitude	-4.419	<0.001	-3.374	<0.001	-0.566	0.671
Dominant frequency	-5.351	<0.001	-4.341	<0.001	-2.915	0.233
<i>Leopard Frog</i>						
Call rate	-2.294	0.032	-2.563	0.023	-1.010	0.464
Mean amplitude	-1.868	0.110	-2.646	0.024	-1.470	0.244
Dominant frequency	-2.842	0.023	-2.646	0.036	-0.490	0.730
<i>Gray Treefrog</i>						
Call rate	-3.125	0.006	-2.521	0.048	-0.755	0.596
Mean amplitude	-1.620	0.362	-0.700	0.544	-0.811	0.695
Dominant frequency	-0.463	0.694	-1.260	0.374	-1.390	0.426
<i>American Toad</i>						
Call rate	-1.245	0.408	-1.309	0.429	-0.856	0.586
Mean amplitude	-1.179	0.490	-1.423	0.464	-0.236	0.864
Dominant frequency	-1.887	0.597	-0.474	0.715	-1.887	0.299

traffic noise, American toads did not significantly change their vocalizations (Table 2, Fig. 4).

3.3. Prediction 3: vocalizations at high traffic sites vs. at low traffic sites during the broadcast of traffic noise

There were no significant differences in calling characteristics between HIGH sites and LOW sites during TREATMENT periods for any of the four species (Table 2, Fig. 4).

4. Discussion

The results of our experimental field-based study of four anuran species indicate that (a) three species of anurans found at locations with low traffic noise produce vocalizations with different characteristics than individuals of the same species found in locations with high traffic noise; (b) experimentally broadcasting traffic noise elicits immediate changes in amphibian vocalization characteristics in the same three species; and (c) these experimentally altered vocalizations are similar to those of the same species found in locations with high traffic noise.

To the best of our knowledge, our study is the first demonstration that anuran vocalization characteristics respond immediately to increased traffic noise, and that these altered vocalizations are similar to the vocalizations anurans make at sites with chronically high traffic noise. Our results suggest that these species employ a plastic vocalization response to contend with communication difficulties associated with anthropogenic noise. It has long been recognized that such plasticity allows individuals to have a broader tolerance to environmental conditions and therefore higher fitness in multiple or highly variable environments (Padilla and Adolph, 2005; Ghalambor et al., 2007; Wells and Schwartz, 2007). Natural noise levels in the anuran environments in our area are variable in space and time due to noise sources such as rapids/waterfalls, wind, and noise produced by conspecifics, other chorusing anuran species, and other vocal taxa. Therefore, it seems likely that the plasticity we observed in anuran vocalizations is an adaptive response to this spatio-temporal variability in ambient noise.

This interpretation is in contrast to previous studies which suggested that spatial differences in calling characteristics are “dialects”, or fixed adaptive responses to local noise conditions (Ryan and Wilczynski, 1988). In our area it is unlikely that populations (within species) are genetically distinct. The total area covered by our sites has a diameter of about 65 km, and anuran habitats – wetlands, streams, forests – are well-distributed and common in the area. Dispersal ranges of our study species are on the order of 1–6.5 km (Smith and Green, 2005). Therefore, frequent genetic mixing across our region is likely, such that genetically determined dialects are unlikely to develop. It seems possible that previously identified “dialects” in other regions are simply the expression of a plastic response to local environmental noise.

One possible confounding variable that we were unable to measure is the effect of body size on the dominant frequency of calls. It is well documented that larger anurans produce calls with lower dominant frequencies (Forester and Czarowsky, 1985; Wells, 2007). If HIGH traffic sites contained smaller males than LOW traffic sites, this could explain our first result (above). We do not have information on body sizes of individuals at our sites so we cannot test this possibility directly. However, given that individuals from LOW traffic sites increased the dominant frequency of their vocalizations and produced calls more similar to those found at HIGH traffic sites when exposed to artificial traffic noise (TREATMENT), differences in body size are likely not responsible for our results.

It is also possible that our results are confounded by population sizes of anurans near vs. far from high-traffic roads. Anuran populations are known to be reduced near high-traffic roads (Eigenbrod et al., 2009), so at these sites the number of individuals and species of chorusing anurans should be lower. This means that the differences in calling characteristics between LOW and HIGH could be due to a response to differences in chorus sizes rather than a response to the traffic noise. However, again, given that individuals from LOW traffic sites produced calls more similar to those found at HIGH traffic sites when exposed to artificial traffic noise (TREATMENT), differences in chorus sizes are likely not responsible for our results.

If elevated levels of (low-frequency) traffic noise cause individuals to produce calls with a higher dominant frequency, it is possible that the largest males in the population (those with the lowest call frequencies) could be at a disadvantage in attracting females. While previous research indicates that female anurans prefer male vocalizations with lower dominant frequencies (Gerhardt, 1994; Howard and Palmer, 1995), recent studies suggest that females become less choosy in the presence of traffic noise. Wollerman and Wiley (2002) suggested that in noisy environments, female anurans switch from discriminating among available male vocalizations to simply locating a male. In environments dominated by low frequency noise, males with higher dominant frequencies may be more easily located by females and be chosen instead of the males that females would normally choose, i.e., the larger males with lower call frequencies. This shift in mating towards smaller males could result in lower genetic quality of offspring. Alternatively, a shift in mating towards smaller males could result in an increase in genetic variation among populations. These hypotheses have yet to be tested.

It is of interest to note that the two species in our study with the shortest breeding seasons, the gray treefrog and American toad, did not alter the dominant frequency of their vocalizations, and demonstrated limited or no alteration of their calling characteristics in response to traffic noise (Fig. 4). The time period over which these two species breed is primarily influenced by water availability (Lengagne, 2008), resulting in an explosive breeding strategy. If vocalizations are only required to attract mates over a short time during which there is only limited spatio-temporal

variability in ambient noise, and males of these species actively search for mates (Howard and Young, 1998), these species may not need the same plasticity in vocalization characteristics as species with longer breeding seasons. On the other hand, the lack of observed plasticity in vocalization characteristics in these species may simply be due to the fact that their innate vocalizations are not masked by ambient noise (Fig. 3). It would therefore be interesting to see whether these species alter their vocalizations in the presence of higher frequency noises.

Previous work on calling energetics in frogs has revealed that calling is probably the most energetically expensive activity a male frog undertakes during his lifetime (Pough et al., 1992). Wells and Schwartz (2007) suggest that due to the energetic costs of calling, individuals should use vocalizations that conserve energy while maximizing the effective transmission distance. It is possible that the observed acoustical responses to traffic noise by green frogs and leopard frogs in our study are the result of a trade-off. The reductions in call rate and mean amplitude are coupled with significant increases in the call frequency (Fig. 4). An increase in the dominant frequency of a vocalization comes at an increased energetic cost; however, this cost is considerably less than that of increasing the mean amplitude or calling rate of the vocalization (Parris, 2002). The associated reduction in calling rate and power could result in a vocalization with no net increase in energetic expenditure for the increased dominant frequency.

Two primary hypotheses have been developed to explain how species attempt to overcome the masking effects of their environment: the Lombard effect hypothesis and the acoustic adaptation hypothesis (AAH). The Lombard effect hypothesis states that in noisy environments individuals should increase the power of their vocalizations (Pick et al., 1989). The AAH states that the environment in which acoustic communication takes place should favour vocalization characteristics that minimize attenuation and distortion (signal degradation) with distance (Brown and Handford, 2000). The AAH predicts that individuals should increase the frequency of their vocalizations such that they are not masked by lower frequency noise (e.g. Slabbekoorn and Peet, 2003; Rabin et al., 2003) or that individuals should alter the temporal characteristics of their calls (Lengagne et al., 1999) such that they are not masked by other noise in the environment. Both green frogs and leopard frogs significantly altered multiple calling characteristics in response to increased levels of traffic noise (Fig. 4), suggesting that they are attempting to produce vocalizations that minimize attenuation of the acoustic signal, in support of the AAH.

It remains unclear whether the alterations in calling characteristics we observed compensate for possible effects of traffic noise on breeding. Without data on reproductive success in the presence of traffic noise, it is not possible to determine whether traffic noise contributes to amphibian population declines (Warren et al., 2006). Although previous studies have examined the impact of traffic noise on species that use vocalizations to attract mates (Narins, 1982; Slabbekoorn and Peet, 2003; Brumm, 2004; Sun and Narins, 2005; Parris et al., 2009), two key questions remain unanswered: (1) how effective are altered vocalizations at attracting potential mates? and (2) are there costs associated with altered vocalizations that affect the survival of individual males? Future efforts should focus on determining whether a reduction in breeding success occurs in the presence of traffic noise or alterations in vocalization characteristics by amphibians in the presence of noise are truly compensatory.

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