Mate attraction by male anurans in the presence of traffic noise

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Abstract

We previously found that males of two anuran species – *Hyla versicolor* and *Rana clamitans* – alter their mating calls in response to traffic noise. To test whether these alterations compensate for an effect of traffic noise on mate attraction, we (1) recorded a male calling at a quiet site; (2) played traffic noise at the same male and recorded its altered call; (3) used these recordings to attract females to a trap at sites either with or without broadcast traffic noise. The calls produced without traffic noise attracted fewer females when they were played at sites with traffic noise than when they were played at sites without noise. However, the calls of the same individuals produced with traffic noise attracted as many females at sites with noise as at sites without noise, and they attracted as many females as did the call of the same male made without noise and played at sites without noise (the 'natural' situation). Therefore, for these species, traffic noise does not affect mate attraction; males change their calls to compensate for a potential effect of traffic noise on mate attraction. A third species – *Bufo americanus* – does not alter its call in response to traffic noise, and its call made in the absence or presence of traffic noise was equally able to attract females in the absence or presence of traffic noise, indicating that traffic noise does not negatively affect mate attraction. Therefore, it appears that traffic noise does not negatively affect mate attraction in these three species of anurans. We suggest that, if our results apply to anurans in general, the previously documented negative effects of roads on anuran populations are likely caused mainly by road mortality. If this is true, road mitigation for anurans should focus mainly on reducing this mortality.

Introduction

Many studies have shown negative effect of roads on anuran (frog and toad) abundance and distribution (Fahrig *et al*., 1995; Vos & Chardon, 1998; Carr & Fahrig, 2001; Houlahan & Findlay, 2003; Pellet, Guisan & Perrin, 2004; Nyström *et al*., 2007; Skidds *et al*., 2007; Eigenbrod, Hecnar & Fahrig, 2008, 2009; reviewed in Fahrig & Rytwinski, 2009). Most authors assume that the negative effects of roads on anurans are due to road mortality. This is a reasonable assumption because very high anuran mortality rates have been recorded on roads. For example, Ashley & Robinson (1996) documented over 30 000 road-killed amphibians over a 4-year period on a 3.6-km stretch of road; Hels & Buchwald (2001) estimated that roads can kill as much as 25% of an adult amphibian population annually; and Bouchard *et al*. (2009) found that 28% of frogs attempting to cross a low-traffic road were killed by vehicles.

In addition to direct mortality, some authors have suggested that roads could affect anuran populations indirectly if traffic noise interferes with the ability of calling males to attract females (Warren *et al*., 2006; Bee & Swanson, 2007;

Lengagne, 2008). On the other hand, several studies have shown that anuran males of some species alter their mating calls in the presence of traffic noise (Penna, Pottstock & Velásquez, 2005; Penna & Hamilton-West, 2007; Parris, Velik-Lord & North, 2009; Cunnington & Fahrig, 2010). It is possible that such alterations compensate for a potential negative effect of traffic noise on the ability of males to attract mates; however, to date, there are no studies of the effect of traffic noise on mate attraction in anurans.

In a previous study (Cunnington & Fahrig, 2010), we recorded the calls of individual males of three anuran species, first in the absence of traffic noise and then while we played traffic noise at the same individuals. Two species, the gray treefrog *Hyla versicolor* and the green frog *Rana clamitans*, altered their calls in the presence of traffic noise, while the third species, American toad *Bufo americanus*, did not. Here, we hypothesize that gray treefrogs and green frogs change their calls in the presence of traffic noise to reduce negative effects of traffic noise on the ability of males to attract mates. We further hypothesize that American toads do not change their calls in the presence of traffic noise because traffic noise does not interfere with their ability to
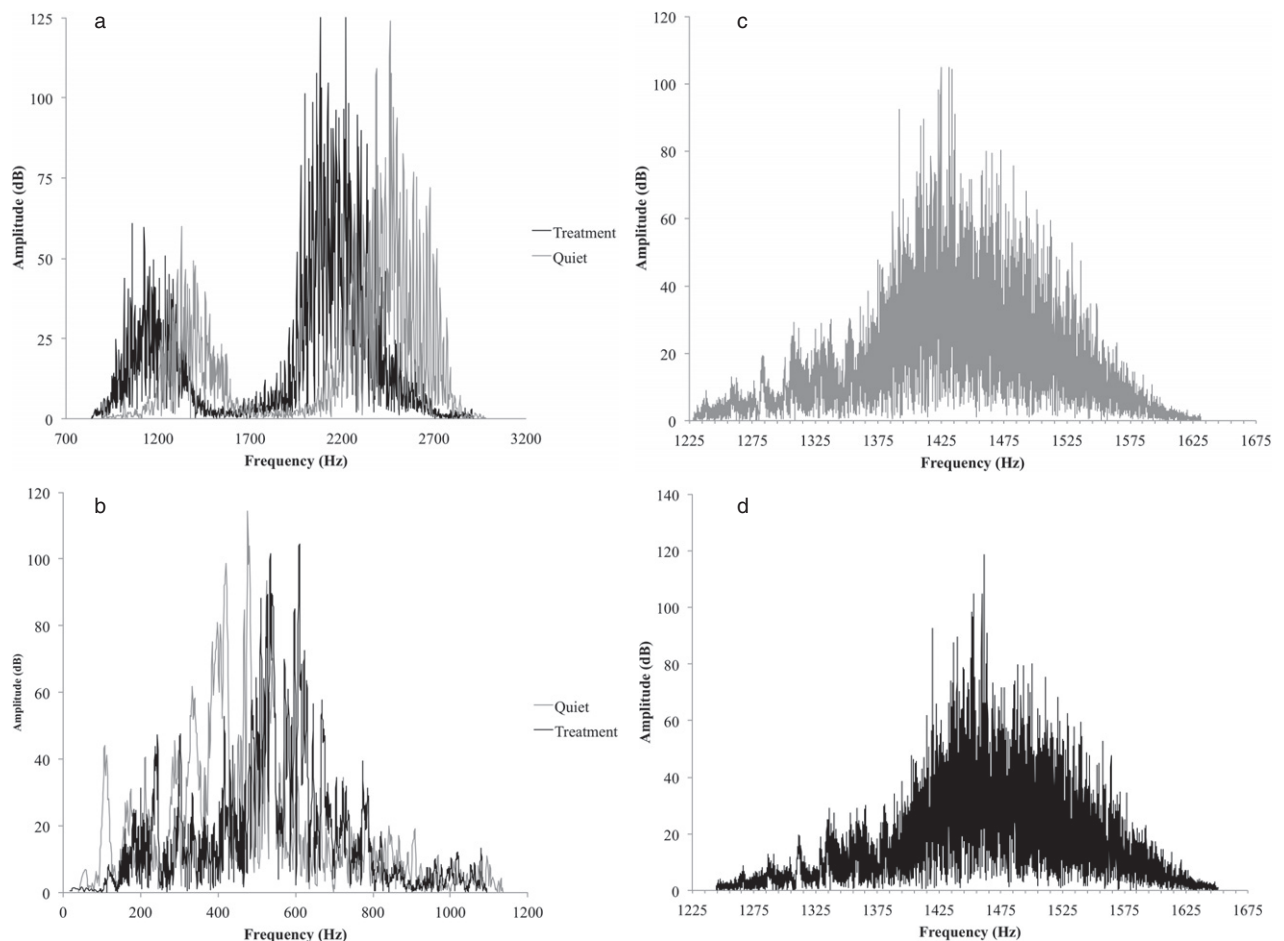
Figure 1 Power spectra of the broadcast calls of male anurans used to attract females, recorded in waveform audio format (96 kHz, 24 bits). Spectra were generated by fast Fourier transformation of a single advertisement call. Grey lines are the calls in the absence of traffic noise and black lines are the calls of the same individuals in the presence of broadcast traffic noise: (a) gray treefrog *Hyla versicolor*, (b) green frog *Rana clamitans*, and (c,d) American toad *Bufo americanus*.

attract mates. The purpose of the current study was to test these hypotheses.

Materials and methods

To test for the effects of traffic noise on mate attraction in the gray treefrog, green frog and American toad, we used the recorded mating calls of a typical individual male (of each species) from our previous study (Cunnington & Fahrig, 2010). These were 24-bit recordings in waveform audio (WAV) format made using a Sampson Zoom H4 recorder (Samson Technologies, Hauppauge, NY, USA), with stereo unidirectional electret condenser microphone at a sampling rate of 96 kHz. The individual's call was recorded (in the field) first in the absence of noise and then while we played traffic noise at it. For the current study, we selected a single representative male of each species, using its recorded call without traffic noise and then with traffic noise, to attract females in the absence or presence of traffic noise. Using a single male of each species allowed us to

control for other factors that affect recorded calls such as distance from the recorder, vegetation height, and wind speed and direction. Power spectra of the recorded calls (Fig. 1) were created through fast Fourier transformation using Sigview (2.4; SignalLabs, Pforzheim, Germany); call characteristics in comparison with the means are shown in Table 1.

Here, we refer to calls produced by a male in the absence of traffic noise as 'CAN' and calls produced by the same male in the presence of traffic noise as 'CPN'. Our overall design was to broadcast the CAN and CPN, to attract females to box traps, either in the absence or presence of traffic noise (NT and T, respectively; Table 2), during the breeding seasons of each of the three species (Table 3). Based on our hypotheses (previously stated), we made the following predictions. First, for the gray treefrog and the green frog, the number of females captured should be lowest in the CAN-T treatment because the call is not adjusted to compensate for traffic noise. Furthermore, if the adjusted calls *completely* compensate for the traffic noise, we pre-

Table 1 Vocalization characteristics of the individual males used in the experiment, in the presence and absence of broadcast traffic noise (see also Fig. 1)

	Mean frequency (Hz)		Mean power (dB)		Mean call rate (calls min⁻¹)	
	No traffic noise	Traffic noise broadcast	No traffic noise	Traffic noise broadcast	No traffic noise	Traffic noise broadcast
Gray treefrog	1976 (1994)	1957 (1945)	78.3 (81.5)	85.3 (84.4)	11.3 (18.5)	6.7 (10.2)
Green frog	497 (489)	738 (724)	72.6 (74.8)	62.0 (65.9)	4.7 (5.2)	2.7 (2.0)
American toad	1426 (1448)	1451 (1454)	79.2 (79.8)	81.6 (82.2)	2.0 (2.3)	1.3 (2.0)

Values in parentheses are the mean values across individuals, from Cunnington & Fahrig (2010).

Table 2 Treatments applied to determine if alteration of calls in the presence of traffic noise compensates for potential negative effects of traffic on mate attraction in anurans

Treatment name	Male call	Traffic noise broadcast at the trapping site?
CAN-T	Male recorded in the absence of traffic noise	Yes
CPN-T	Male recorded in the presence of traffic noise	Yes
CAN-NT	Male recorded in the absence of traffic noise	No
CPN-NT	Male recorded in the presence of traffic noise	No

Male calls, produced in either the absence or presence of traffic noise, were broadcast to attract females at four different sites, with treatments rotating through sites across sampling dates (see Table 3). Traffic noise was broadcast at mean of 76 dB at 5 m.

dicted that there would be about the same number of females attracted in the CAN-NT and CPN-T treatments. In addition, if the altered calls made by these two species do not carry a cost in terms of mate attraction, we predicted that there should be about the same number of females attracted to the CAN-NT and CPN-NT treatments. For the American toad, we predicted no differences in the number of females attracted in any of the treatment combinations because we hypothesized that the reason this species does not adjust its call in the presence of traffic noise is that traffic noise does not interfere with mate attraction.

We selected four study sites in Eastern Ontario, *c*. 40 km south-west of Ottawa. All sites were vegetated wetlands previously known to contain all three focal species during their respective breeding seasons and had traffic noise levels not exceeding 50 dB, a level of traffic noise corresponding to traffic volumes shown to have no detectable effect on the abundance of these anuran species (Eigenbrod *et al.*, 2008). The recorded male calls were then broadcast at the four trapping locations, where the treatments (Table 2) were cycled through the trapping locations through time (Table 3). Note that calls of only one species were used each night (Table 3). Each night, two trapping locations were exposed to the CPN broadcast and two locations to the CAN broadcast. Within each pair of locations, traffic noise was broadcast at one location, while no traffic noise was broadcast at the other. Calls were broadcast from a portable Ultra Hydra 1 GB portable media player (Ultra Components and Technologies, Fletcher, OH, USA) through a waterproof marine speaker (Pyramid MDC7, Pyramid Audio, Brooklyn, NY, USA) mounted to the lid of a 2.5-L plastic container (Fig. 2d). The broadcasts consisted of a 3-min recording of a calling male (Fig. 1, Table 1), which was broadcast in a continuous loop for the whole 4-h trapping period (below). In treatments involving broadcast

traffic noise (CPN-T and CAN-T), a second portable media player and speaker were used to broadcast traffic noise on the edge of the wetland. The amplitude of the broadcast traffic noise and the broadcast calls were adjusted until values measured using a sound meter (Galaxy Audio, model e CM-130, Galaxy Audio Inc., Wichita, KS, USA) matched the amplitude of the recorded traffic noise and calls (Cunnington & Fahrig, 2010). The traffic noise broadcast was set at a mean of 76 dB at 5 m and the amplitudes of the broadcast male calls at 5 m are shown in Table 1.

Note that because use of MP3 as a file type would have resulted in the loss of some sound elements, we made the original recordings in WAV format. However, the portable media players we used did not recognize WAV format. They did recognize Windows Media Audio (WMA) format, which retains more information than does MP3 format. Therefore, the WAV-format field recordings of traffic noise and of individual male calls were converted to WMA format for the broadcasts. We suggest that this change in file format did not have a substantive effect on our results, as the spectral characteristics of the two audio files were similar, apart from a small reduction in amplitude in the conversion from WAV to WMA (Fig. 3), which was corrected in the field using a sound meter (see above). In our previous study using the same recorder and players (Cunnington & Fahrig, 2010), we found that the vocal responses of these anurans to this broadcast traffic noise were the same as their vocal responses to actual traffic noise. Therefore, despite the alterations to the signal, the anurans appear to 'hear' them in the same way that they hear the actual traffic noise, at least for the portion of sound that is relevant to their responses to traffic noise. There was still the possibility that this conclusion cannot be extrapolated to the female responses to broadcast male calls; it is possible that females hear a real calling male differently from the broadcast of the

Table 3 Dates on which trapping of three species of anurans was conducted at the four sites (A, B, C and D)

Species	Date	Site/Treatment			
GTF	30 May	B/CAN-NT	A/CPN-T	D/CPN-NT	C/CAN-T
GTF	31 May	B/CPN-T	D/CAN-T	C/CAN-NT	A/CPN-NT
GTF	1 Jun	A/CPN-T	B/CAN-NT	D/CPN-NT	C/CAN-T
GTF	2 Jun	C/CPN-NT	A/CAN-NT	B/CAN-T	D/CPN-T
GTF	4 Jun	C/CAN-NT	B/CPN-T	A/CPN-NT	D/CAN-T
GTF	9 Jun	D/CAN-T	C/CAN-NT	B/CPN-T	A/CPN-NT
GTF	11 Jun	A/CAN-T	D/CAN-NT	C/CPN-T	B/CPN-NT
GTF	12 Jun	C/CPN-NT	B/CAN-T	D/CPN-T	A/CAN-NT
GTF	16 Jun	D/CAN-T	A/CPN-NT	C/CAN-NT	B/CPN-T
GTF	23 Jun	A/CAN-T	C/CPN-T	B/CPN-NT	D/CAN-NT
GTF	24 Jun	B/CAN-T	D/CPN-T	A/CAN-NT	C/CPN-NT
GTF	25 Jun	D/CAN-T	C/CAN-NT	A/CPN-NT	B/CPN-T
GF	1 July	B/CPN-NT	A/CAN-T	D/CAN-NT	C/CPN-T
GF	2 July	B/CAN-T	D/CPN-T	C/CPN-NT	A/CAN-NT
GF	4 July	A/CPN-T	B/CPN-T	D/CAN-T	C/CAN-NT
GF	7 July	C/CAN-T	A/CPN-T	B/CAN-NT	D/CPN-NT
GF	8 July	C/CAN-NT	B/CPN-T	A/CPN-NT	D/CAN-T
GF	9 July	D/CPN-T	C/CPN-NT	B/CAN-T	A/CAN-NT
GF	14 July	A/CPN-T	D/CPN-NT	C/CAN-T	B/CAN-NT
GF	15 July	C/CPN-T	B/CPN-NT	D/CAN-NT	A/CAN-T
GF	16 July	D/CAN-T	A/CPN-NT	C/CAN-NT	B/CPN-T
GF	17 July	A/CPN-T	C/CAN-T	B/CAN-NT	D/CPN-NT
GF	21 July	B/CPN-NT	D/CAN-NT	A/CAN-T	C/CPN-T
GF	22 July	D/CAN-T	C/CAN-NT	A/CPN-NT	B/CPN-T
AT	21 May	B/CPN-NT	A/CAN-T	D/CAN-NT	C/CPN-T
AT	22 May	B/CAN-NT	D/CPN-NT	C/CAN-T	A/CPN-T
AT	23 May	A/CAN-NT	B/CAN-T	D/CPN-T	C/CPN-NT
AT	24 May	C/CAN-NT	A/CPN-NT	B/CPN-T	D/CAN-T
AT	25 May	C/CAN-T	B/CAN-NT	A/CPN-T	D/CPN-NT
AT	26 May	D/CAN-NT	C/CPN-T	B/CPN-NT	A/CAN-T
AT	27 May	A/CAN-NT	D/CPN-T	C/CPN-NT	B/CAN-T
AT	28 May	D/CAN-T	C/CAN-NT	A/CPN-NT	B/CPN-T

Treatments are defined in Table 2. The sequence of site treatments (left to right) within each date indicates the order in which the treatments began (and ended, 4 h later). AT, American toad; GF, green frog; GTF, gray treefrog.

same male call. We could not test this directly, but, in retrospect, given the support for our predictions (see the Results section), the assumption seems to have been reasonable. If the male broadcasts were 'noise' and not representative of actual male calls, we should not have seen the predicted differences in female attraction for the different treatments and species.

A single box trap (Fig. 2a) was placed in the water 5 m from the edge of the wetland (and the broadcast traffic noise) at each of the four sample sites. The speaker broadcasting the male call was placed inside the screened portion of the trap and was therefore floating in the water. Individuals approached the trap (in the open position) by first sitting on the large flat area; to get closer to the recorded call, they would cross over the raised lip (which was sloped towards the centre of the trap) and enter the central screened area. The screened area was open only at the top, and the lip around the top edge retained trapped individuals. Traps were placed such that the water line was level with the large flat area of the trap and therefore with the base of the screened lip (Fig. 2c).

Traps were placed in the trapping sites 1 week before the onset of sampling to allow individuals to become acclimatized to their presence. The treatment at a given site on a given night was systematically selected such that no site was exposed to successive nights of the same treatment and each of the four treatments was conducted for the same number of nights for a given species at a given site (Table 3). As broadcasts could not be started simultaneously at all four sites, trap sites were visited consecutively to begin trapping, with the same order being repeated at the end of the trap night. The consecutive visits to trap sites resulted in a 20-min difference between the start of trapping at the first site and the start of trapping at the fourth site; however, by repeating the same order of visits to sites at the end of each trap night, we standardized the trapping time (effort) across locations. To ensure that no bias in effort was created by the lag time, we systematically selected the starting site (i.e. of sites A–D) for each trap night such that each site began the trap night an equal number of times (Table 3).

Trap nights began 30 min after sunset and lasted for *c*. 4 h during the focal species breeding season. Traps were emptied at the end of each night. Individuals were considered captured if they were found on or in any portion of the trap. Traps were closed at the end of each night to ensure no individuals were captured outside of the trapping period (Fig. 2b). The air temperature of each trap site for each night of sampling was obtained by averaging the temperature recorded at the beginning and end of each night.

As no site received the same treatment two nights in a row (Table 3), we used each night as an independent sample in our analysis. Because of the relatively high proportions of nights with zero captures (54–59%; see the Results section), logistic regression was the appropriate modeling framework. The results represent the probability of the treatment attracting at least one female. We modeled the occurrence of captures (presence/absence of at least one female) in a logistic regression analysis, separately for each species, with predictor variables *treatment* (CPN-T, CAN-T, CPN-NT and CAN-NT; Table 2) and *site* (A, B, C and D) as factors, and *temperature* as a covariate; we included the interaction effect between *treatment* and *site*. We modeled site and *site × treatment* as fixed effects rather than random effects because there were only four levels of the site variable, that is, four sites (Bolker *et al.*, 2009). We also conducted post-hoc pairwise comparisons of treatment effects using the least significant difference (LSD) method for logistic regression. Note that, because we were comparing responses within species (for different treatments), not between species, it was not necessary to assume that the traps were equally effective at capturing the three species. In addition, by rotating the treatments through the same four sites (Table 3) and including *site* and *site × treatment* in the analyses, we controlled for site variables (e.g. local abundance) that could affect the numbers of females attracted to the traps.

Figure 2 Box trap (a – open position, b – closed position, c – closed *in situ*) and broadcast equipment (d) used to attract and capture three species of anuran in Eastern Ontario. The speaker broadcasting the male call was placed inside the screened portion of the trap and was therefore floating in the water. Individuals approached the trap (in the open position) by first sitting on the large flat area; to get closer to the recorded call, they would cross over the raised lip (which was sloped towards the centre of the trap) and enter the central screened area. The screened area was open only at the top, and the lip around the top edge retained trapped individuals. Traps were placed such that the water line was level with the large flat area of the trap and therefore with the base of the screened lip.
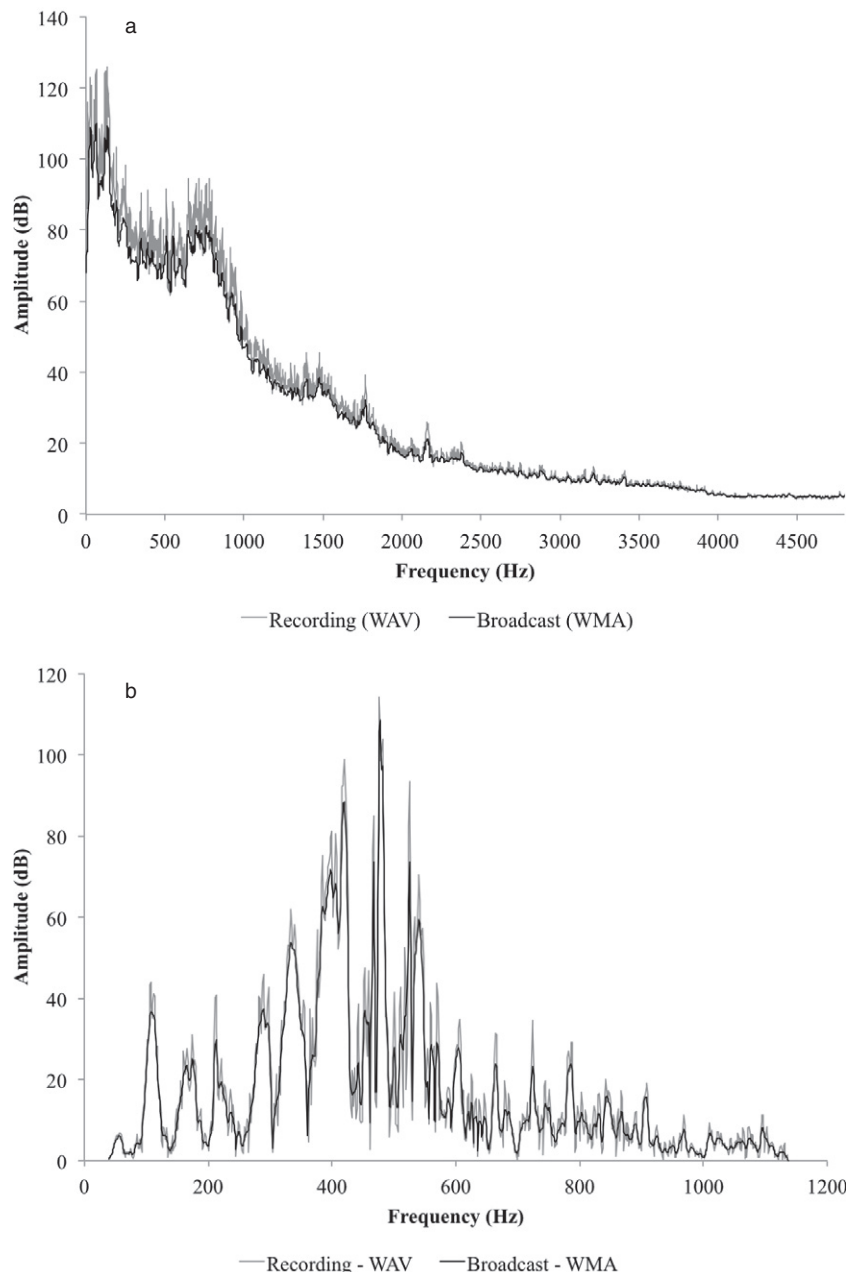
Results

We captured gray treefrogs on 22 of 48 trap nights, green frogs on 20 of 48 trap nights and American toads on 13 of 32 trap nights. The raw data, showing numbers of captures per night, are given in Supporting Information Appendix S1. The probability of capture of gray treefrog females and of green frog females was lower when broadcasting the mating call made in the absence of traffic noise at sites when traffic noise was broadcast (CAN-T) than in the other three treatments (Fig. 4). For the gray treefrog, the overall *P*-value for the treatment effect was 0.055 (Table 4); in the post-hoc LSD pairwise comparisons, the probability of capture for CAN-T was significantly lower than for all the other treatments ($P < 0.001$ for all comparisons), and the other treatments were not significantly different from each other ($P \geq 0.99$ for all comparisons). For the green frog, the overall *P*-value for the treatment effect was 0.014 (Table 4);

in the post-hoc LSD pairwise comparisons, the probability of capture for CAN-T was significantly lower than for all the other treatments ($P \leq 0.005$ for all comparisons), and the other treatments were not significantly different from each other ($P \geq 0.3$ for all). There was no effect of *treatment* on the probability of capture of American toads [overall *P* for *treatment* = 0.74 (Table 4); $P > 0.99$ in all post-hoc LSD pairwise comparisons]. The significance level of the treatment effect did not change substantially for any species when simpler models were considered, although some simpler models were more parsimonious than the full models (Table 5).

Discussion

To the best of our knowledge, this study is the first test of the hypothesis that alteration of mating calls by anurans compensates for effects of traffic noise on mate attraction. Our

Figure 3 Comparison of the power spectra of the field recordings in waveform audio (WAV) format (black line) to the broadcast files in Windows Media Audio (WMA) format (grey line). (a) Traffic noise. (b) Male green frog *Rana clamitans* call.

results support the predictions that, for the species whose males alter their calls in the presence of traffic noise (gray treefrog and green frog; Cunnington & Fahrig, 2010): (1) calls made in the absence of traffic noise should attract fewer females in the presence of traffic noise than do calls made in the presence of traffic noise; (2) calls made in the presence of traffic noise should attract as many females in the absence of traffic noise as do calls made in the absence of traffic noise. These results support the hypotheses that (1) the alteration of male mating calls in the presence of traffic noise completely compensates for the effect of traffic noise on mate attraction; (2) the altered calls do not carry a cost for mate attraction. In addition, our results support the prediction

that, for a species whose males do not alter their calls in the presence of traffic noise (American toad; Cunnington & Fahrig, 2010), there should be no difference between the mate attraction ability of male calls made in the presence or absence of traffic noise, played at sites with or without traffic noise. This supports the hypothesis that the species that does not alter its call does not need to alter it because its unaltered call is effective in attracting mates in the presence of traffic noise. Therefore, it seems that, when necessary to do so, male anurans are able to change their calls to attract females in the presence of traffic noise, such that traffic noise has no effect on mate attraction, at least for the species we have studied.
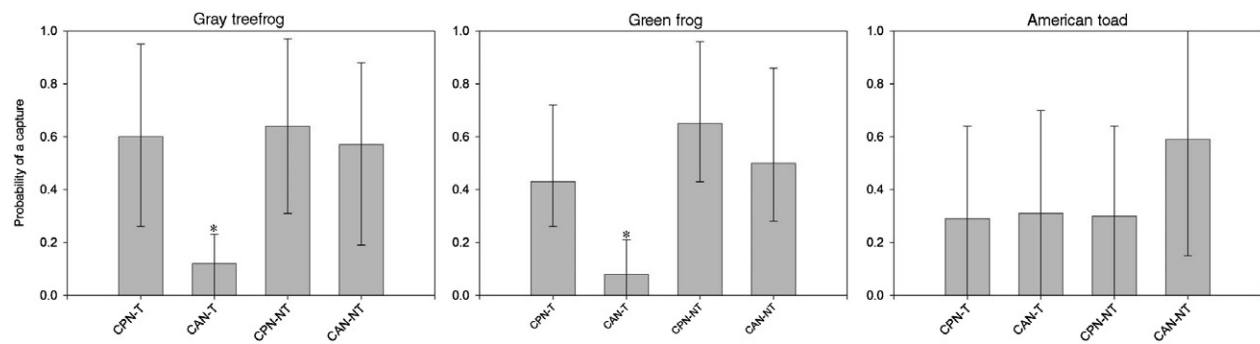
Figure 4 Proportion of nights with a capture (with 95% confidence intervals) of three species of anuran in each of four experimental treatments (see Table 2 for definitions of treatments). Post-hoc pairwise comparisons, using the least significant difference method for logistic regression, revealed that the CAN-T treatment for gray treefrog *Hyla versicolor* and green frog *Rana clamitans* differed significantly from all three other treatments ($P \le 0.005$, indicated by * above CAN-T). There were no other significant pairwise differences.

Table 4 Results of multiple logistic regressions estimating the probability of capturing at least one female (per night per site), on temperature, site, treatment, and treatment × site for each of the three study species

Species	Predictor		Coefficient	X^2	P-value
Gray treefrog	Site			1.457	0.692
		1	0.584		
		2	−23.262		
		3	−21.898		
		4	0		
	Treatment			7.585	0.055
		CPN-T	1.097		
		CAN-T	−22.032		
		CPN-NT	23.411		
		CAN-NT	0		
	Temperature		0.344	7.164	0.007
	Site × Treatment			19.002	0.025
Green frog	Site			0.000	1.000
		1	23.396		
		2	1.450		
		3	−21.823		
		4	0		
	Treatment			10.584	0.014
		CPN-T	−0.265		
		CAN-T	−21.802		
		CPN-NT	1.482		
		CAN-NT	0		
	Temperature		0.088	0.110	0.740
	Site × Treatment			11.015	0.275
American toad	Site			7.657	0.054
		1	0.271		
		2	−0.155		
		3	−0.039		
		4	0		
	Treatment			1.259	0.739
		CPN-T	−22.273		
		CAN-T	−0.077		
		CPN-NT	−0.271		
		CAN-NT	0		
	Temperature		0.155	0.309	0.578
	Site × Treatment			7.391	0.596

The reference site was site 4 and the reference treatment was CAN-NT; the other coefficients are relative to the references. Treatments are defined in Table 2.

Table 5 AIC values and *P*-values for significance tests of the treatment effect ('treat'; see Table 2 for treatments), for increasingly complex logistic regression models

Model	Treat	Treat + temp	Treat + temp + site	Treat + temp + site + treat × site
Gray treefrog				
AIC	68.050	65.1	70.6	69.6
P for treatment	0.104	0.077	0.074	0.055
Green frog				
AIC	61.4	63.4	66.8	73.8
P for treatment	0.012	0.012	0.007	0.014
American toad				
AIC	49.5	51.1	52.2	62.8
P for treatment	0.943	0.935	0.933	0.739

The response variable was the capture of at least one female (per site per night). AIC, Akaike information criterion; temp, temperature.

We hypothesize that our results may apply to anurans in general and not just to the species we studied. Studies of anuran mating calls in the presence of background noise have found that males alter their calls in response to noise in a variety of ways. Species shown to alter their calls include *Microhyla butleri*, *Rana nigrovittata*, *Kaloula pulchra*, *Rana taipehensis* (Sun & Narins, 2005), *Litoria ewingii* (Parris *et al.*, 2009), *Eupsophus calcaratus*, *Eupsophus emiliopungini* (Penna *et al.*, 2005; Penna & Hamilton-West, 2007), *H. versicolor* and *R. clamitans* (Cunnington & Fahrig, 2010). At least for *H. versicolor* and *R. clamitans*, this is a flexible behaviour, such that the male changes its call when the noise begins. We hypothesize that this flexibility in mating calls has evolved as a response to natural variability in space and time in background noise levels because of waterfalls and rapids, wind and noise made by conspecifics and other species. For example, *Hyla ebraccata* (Schwartz & Wells, 1983*a*,*b*) and *Hyla chrysoscelis* (Love & Bee, 2010) decrease their calling rate in response to chorus noise, a response similar to the response to traffic noise of *H. versicolor* (Cunnington & Fahrig, 2010). A flexible call allows males to attract females in various noise environments.

We suggest that the reason traffic noise does not reduce mate attraction by the non-altered American toad call (CAN) is that its 'natural' call characteristics already avoid potential masking by traffic noise. American toad calls naturally occur at frequencies well above that of traffic noise (American toad ~1430 Hz, traffic ~400 Hz), which should facilitate their detection by females. On the other hand, gray treefrogs, which do adjust their calls in the presence of traffic noise (Cunnington & Fahrig, 2010), also call at frequencies well above that of traffic noise, suggesting that call frequency is not the entire explanation for the American toad results. A second aspect of the natural American toad call that could make it immune to traffic noise is its long duration. Toads have much longer calls than other anurans in our area, including gray treefrogs and green frogs. Because shorter calls are more likely to be masked by time-varying noise, the long calls of American toads

may make them relatively immune to effects of traffic noise on female attraction. It has been shown in some anuran species, including gray treefrogs, that call duration is an important component of mate selection (Schwartz, Buchanan & Gerhardt, 2001; Gerhardt & Brooks, 2009), and that males increase call duration while simultaneously reducing call rate, in response to chorus noise (Wells & Taigen, 1986; Martinez-Rivera & Gerhardt, 2008). In our previous work (Cunnington & Fahrig, 2010), we found reduced call rates for gray treefrogs and green frogs in the presence of traffic noise, which could indicate an associated increase in call duration (not measured) in these species, if they respond to traffic noise in a similar way as to chorus noise. In contrast, American toads did not show a change in call rate (Cunnington & Fahrig, 2010), so probably did not changed their call duration, again supporting the idea that their natural call is already sufficiently long to avoid masking by traffic noise.

It is particularly surprising that in the absence of traffic noise, the altered calls (CPN) of gray treefrogs and green frogs attracted as many females as did their unaltered calls (CAN). This is surprising because many laboratory studies have demonstrated female choice for particular male call characteristics in anurans (Gerhardt, 2005; Castellano & Rosso, 2006; Höbel & Gerhardt, 2007; Bee, 2008; Marquez, Bosch & Eekhout, 2008; Richardson *et al.*, 2010), including in *H. versicolor* (Schwartz *et al.*, 2001, 2010; Gerhardt & Brooks, 2009). It would therefore seem reasonable to assume that calls that are altered because of traffic noise should be less attractive to females in the absence of traffic noise than are 'normal' calls, as the alterations should move them away from the optimum for female choice. One possible explanation for the lack of reduced attractiveness is that the alterations to the calls because of traffic noise may not compromise the particular call components that females cue in on for mate selection. Species vary widely in the call components that females select on, but, at least in the case of *H. versicolor*, as mentioned previously, call duration appears to be an important element of mate choice by females (Schwartz *et al.*, 2001; Gerhardt & Brooks, 2009). If call duration is unaffected or even increases in response to traffic noise, as seen in response to chorus noise for some species (e.g. Wells & Taigen, 1986; Martinez-Rivera & Gerhardt, 2008), this could explain why the altered calls remain successful in attracting females even in the absence of traffic noise. An alternative possible explanation is that the assumption of strong female choice based on call characteristics may not apply in the field; studies conducted in the field often indicate rather weak or even random mate choice by females (Schwartz *et al.*, 2001; Friedl & Klump, 2005; Bee, 2008; but see Pröhl, 2003), possibly because of interference from background noise (Wollerman & Wiley, 2002). Whatever the explanation, our results indicate that the alteration to calls in response to traffic noise does not affect female attraction to them, at least in the species we studied.

There is the possibility that the individuals attracted to the calls in our experiment included both males and females. Males are known to use other males' calls to locate breeding

aggregations and to gain access to the females there (Bee, 2007), including in *R. clamitans* (Bee & Perrill, 1996). We suggest that even if males were attracted to our male calls, it is very unlikely that this could produce artefactual results, that is, altered male calls (CPN) actually do not compensate for the effect of traffic noise on mate attraction. Such a bias would require that males are *more* attracted to the CPN calls than to the CAN calls, even in the absence of traffic noise, which could mask a reduced attraction by females to the CPN calls. Because this scenario seems unlikely, we suggest that the possible occurrence of males within our samples did not bias our results.

The sample size in our study was constrained by the limited calling seasons of the species and the number of ponds that we could study in a single night (four). Therefore, the sample size was 8–12 trials per treatment per species. In this context, we decided to create the treatment recordings using a single male for each species. We used our previous study (Cunnington & Fahrig, 2010) to select a single male whose calling characteristics, recorded in the field, were typical of the average for that species in the absence of traffic noise, and whose call changed in response to traffic noise (also recorded in the field) in a manner typical for that species. We acknowledge that the use of a single male for each species limits the inferential strength of our study, but we suggest that it was appropriate to use our previous knowledge on the calling characteristics of these species to select a single typical individual, thus eliminating variation in the response that would be caused by variation in distance of individuals from the recorder, wind direction, vegetation height and density, and other factors.

Although our study indicates, in three species of anurans, that mate attraction is not affected by traffic noise, and that the alteration of male calls in response to traffic noise does not carry a cost to mate attraction, it is still possible that traffic noise lowers fitness in these species. Males using altered calls may have lower survival, if production of these calls requires more energy. Taigen & Wells (1985) suggested that calling represents the most energetically expensive activity a male frog undertakes during his lifetime. Male gray treefrogs have been shown to experience significant weight loss after only a few nights of calling (Fellers, 1976). Parris (2002) indicated that an increase of 3 dB in the mean amplitude of a call resulted in a doubling of the energy required to produce the call. Ideal calls would have an optimal balance between the conservation of energy and maximization of the call transmission distance (Pough *et al.*, 1992); in altered calls, conservation of energy may be reduced in favour of maintaining a longer transmission distance. Again, further research would be required to determine whether there is a net energetic cost associated with altered calls and whether this cost translates into a negative effect at the population level.

In conclusion, the results of our study indicate that alteration of calling characteristics by anurans is compensatory, eliminating potential negative effects of traffic noise on mate attraction, at least for the three species we studied. Given this result, we suggest that the previously documented nega-tive effects of roads on anuran populations (Fahrig *et al.*, 1995; Ashley & Robinson, 1996; Findlay & Houlahan, 1997; Carr & Fahrig, 2001; Hels & Buchwald, 2001; Houlahan & Findlay, 2003; Mazerole, 2004; Nyström *et al.*, 2007; Eigen-brod *et al.*, 2008) are likely due mainly to road mortality. If this inference is correct, it provides clear direction for miti-gation of road effects on anurans. It implies that the main objective of such mitigation should be to keep anurans off roads, thereby eliminating road mortality. At least for the species we studied, measures to remove or reduce traffic noise (e.g. noise barriers) are apparently unnecessary, or at most of secondary importance relative to measures, such as fencing and ecopassages, aimed at keeping anurans off roads.

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Supporting Information

Additional Supporting Information may be found in the online version of this paper:

Appendix S1. Raw data. For definitions of treatments, see Table 2.