

Evidence for selective avoidance of traffic noise by anuran amphibians

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Keywords

vocalization; phantom road; road ecology; traffic noise; urban ecology; anurans; noise pollution; *Anaxyrus quercicus*.

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Abstract

Roads create many challenges for conservation, and amphibians are particularly vulnerable to their negative effects. This experiment evaluates the impact that traffic noise has on amphibian populations, specifically anurans (frogs and toads). It is thought that traffic noise may act to reduce population abundances; however, it is difficult to disentangle the impact of noise from other road effects, such as roadkill and chemical pollution. To test this, we created a 'phantom road' by playing different traffic noise treatments in three roadless areas and measured resulting anuran abundance using vocalizations as a proxy. We also tested the vocalizations of one species, the Oak Toad *Anaxyrus quercicus* for changes in response to noise. We found that broadcasting traffic noise caused a significant reduction in vocalizations heard, but, intriguingly, we did not observe this effect when the traffic noise was digitally altered to remove frequencies that overlap with anuran vocalizations. This suggests that avoidance of traffic noise could be a tactic that increases the success of communication with conspecifics. We also found that Oak Toads increase the redundancy of their calls in response to traffic noise, but not in response to the altered noise.

Introduction

Roads are associated with reduced abundances of many animal species, from arthropods to mammals (reviewed in Fahrig & Rytwinski, 2009), and it is hypothesized that avoidance of traffic noise is a contributing factor (Francis & Barber, 2013). Due to the logistical challenges, there are few studies which have experimentally tested the effects of noise on wildlife abundance. In contrast, there are innumerable observational studies which suggest that noise affects abundance (reviewed in Potvin, 2016), but these studies are confounded by other road effects, such as direct mortality via roadkill or chemical and light pollution (e.g. Reijnen *et al.*, 1995; Eigenbrod, Hecnar & Fahrig, 2009).

One way to circumvent these confounding factors is to use a 'phantom road' approach (McClure *et al.*, 2013; Ware *et al.*, 2015), in which pre-recorded traffic noise is broadcast in an otherwise roadless area. This type of approach has shown that traffic noise causes certain frog species to modify their vocalizations (Cunnington & Fahrig, 2010); that traffic noise may impede detection of calling male frogs by females (Bee & Swanson, 2007; Tennessen, Parks & Langkilde, 2014) and increases individuals' stress levels (Tennessen *et al.*, 2014). Regarding the impact of noise on animal abundance, the phantom road approach has been used to show that migratory birds spend less stop-over time in areas with low to moderate levels of road noise (McClure *et al.*, 2013).

However, to date, this approach has not been used to study the effect of traffic noise on site occupancy by non-volant species.

In this project, we broadcast traffic noise in roadless areas to observe the effect on anuran (frog and toad) abundance as measured by recordings of vocalizations. We chose to use vocalizations as a proxy for abundance (rather than trapping individuals) to increase sampling effort, and because number of vocalizations has been found to correlate with number of anuran individuals (Nelson & Graves, 2004). We measured the number of vocalizations heard in three different treatments: (1) control (no noise); (2) unaltered traffic noise; and (3) traffic noise that was digitally altered to not overlap with anuran vocalizations. We predicted that if anurans avoid anthropogenic noise in general, they would show similar avoidance of unaltered and altered traffic noise; however, if they avoid noise that interferes with their ability to communicate, they would not avoid the altered traffic noise.

This method produced a library of vocalization recordings, which we used to assess whether traffic noise induces changes in anuran vocalizations. It has long been known that many songbird species alter properties of their vocalizations, such as frequency, amplitude, duration, and song type, in response to traffic noise (reviewed in Slabbekoorn, 2013 and Potvin, 2016). While several studies have experimentally tested for this in anurans (Sun & Narins, 2005; Lengagne, 2008; Cunnington & Fahrig, 2010, 2013; Hanna *et al.*,

2014), they have produced conflicting results. Given the wide diversity in vocalization properties displayed by anuran species around the world, it is unsurprising that there is a diversity of responses to masking noise, and our study provides another piece of information that may help uncover a broad pattern.

Materials and methods

Study sites

To determine whether traffic noise alone negatively impacts anuran abundance, we broadcast traffic noise at roadless pine flatwoods sites in Tosohatchee Wildlife Management Area (Christmas, FL, USA), a habitat that supports at least 20 anuran species (pers. obs.), one of which is federally threatened (Gopher Frog, *Rana capito*). Due to Florida's subtropical climate, anurans can be found calling almost year-round. We selected three sites within Tosohatchee that are at least 1000 m from each other and 1000 m from any paved roads. One thousand meters is the maximum road-effect zone recorded for anurans, that is the distance that the effects of a paved road extend into the landscape (Eigenbrod *et al.*, 2009). By selecting sites beyond this range, we attempted to eliminate any confounding factors from paved roads or from our other study sites. Though there are dirt roads in Tosohatchee near the study sites, they are not frequently traveled and experience a traffic volume of fewer than 50 cars/day. In addition, the park is closed after sunset (which is when sampling occurred), so we consider any noise effects from these unpaved roads to be negligible, if present.

At each of the three sites, we buried an open-top cattle tank (8 ft. circular diameter, 2 ft. deep) filled with dechlorinated water to ensure that there would always be a water source for breeding anurans, since many species seek out fishless water in which to lay their eggs. Although all three sites flood seasonally, the ponds were installed in case of dry-down events. The ponds were installed in early June 2015 and were stocked with native aquatic vegetation. Though we expected that anurans may have been slow to recognize these ponds as viable breeding spots, anurans and tadpoles had been observed in some of the ponds as early as July 2015.

Traffic noise playback

Beginning in May 2016, we began broadcasting traffic noise treatments from a point source at each of the three pond sites and surveying for adult anuran abundance. Treatments were played back using car stereos (XO Vision) connected to 40-watt coaxial marine speakers (SeaWorthy). The stereo and speakers at each site were powered by a group 24 marine battery connected to a 5-watt solar battery maintainer.

The traffic noise stimulus was a digital compilation of individual vehicle pass-by events (as in McClure *et al.*, 2013). With the stimulus, we sought to recreate the conditions on State Road 528, a highway that runs east to west through Tosohatchee (5 km south of the closest sampling

site). The speed limit on S.R. 528 is 70 mph (~113 km/h) and maintains a relatively high traffic volume even at night, when anurans are more actively calling. Between 19:00 and 00:00 hours, the average traffic volume is 1126 vehicles/hour (standard deviation 476.3 vehicles/h). McClure *et al.* (2013) found significant negative effects of traffic noise on bird abundance at traffic volumes of 720 vehicles/h.

Although the traffic volume was based on S.R. 528, which bisects Tosohatchee, we recorded cars on State Road 50, which forms part of its northern boundary. We chose to record on S.R. 50 because it has a lower traffic volume, which was not only safer but allowed us to obtain cleaner recordings. We made recordings of individual cars travelling between 60 and 70 mph (~97–113 km/h) on April 30, 2015. The microphone (Sennheiser MKH 50 P48, with wind guard) was placed 7 m perpendicular to the edge of the road at a height of 1.1 m and we used a Marantz PMD670 solid-state recorder. We chose 9 of these individual car pass-by recordings based on their clarity and normalized them to a common peak amplitude in (Audacity Team 2014). These recordings were digitally combined to create a looping sound file that played back 1120 vehicle pass-by events per hour without shuffling (similar to the methods of McClure *et al.*, 2013).

At any given time, each site received one of three traffic noise treatments: (1) control (no noise), (2) traffic, and (3) non-masking. The traffic treatment was played at 65–70 dB (A) measured at 5 m from the speaker, which is comparable to the ambient noise experienced standing 30 m from a busy highway (Reijnen *et al.*, 1995). Non-masking noise was also played at 65–70 dB(A), but we digitally filtered the noise with the result that signal's amplitude was concentrated at frequencies below 2 kHz; this removed the frequencies of the noise that overlap with many anuran vocalizations (Fig. 1). It was not possible to filter out additional frequencies without sacrificing broadcast amplitude. Study site anurans all vocalize with minimum frequencies above 400 Hz, and many above 2 kHz (Cunnington & Fahrig, 2010). Including non-masking noise allowed us to test whether anurans avoid all noise, or just noise that interferes with breeding communication. If they only avoid noise that masks their vocalizations, we predicted that abundance should be lower in the traffic treatment than in the non-masking.

We played one treatment at each site for 24 hours, turning the noise on in the morning (between 08:00 and 09:00) and off the next morning. Playing the noise for longer periods of time was impossible due to battery limitations; however, some bird species have shown immediate decreases in abundance in response to experimental traffic noise (McClure *et al.*, 2013). We sampled one night per week, swapping treatments among sites using a Latin square design that accounts for carry over effects (Wang, Wang & Gong, 2009). We sampled over 13 weeks from May 2016– August 2016. Due to technical difficulties, the stimulus broadcast was sometimes cut short (so that the noise was present in daytime recordings but absent from evening recordings at that site), so those dates could not be included in analysis and resulted in an unbalanced dataset (Table 1).

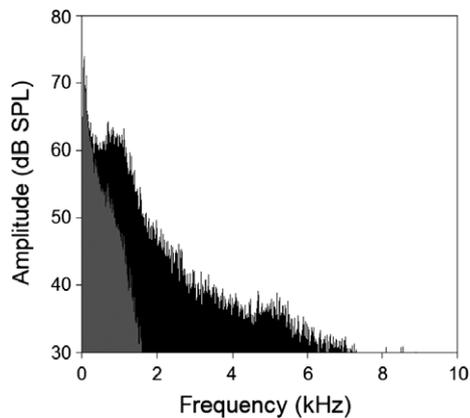


Figure 1 Power spectrum showing the difference between the traffic noise (black) and non-masking noise (gray) treatments (the non-masking treatment is the traffic treatment with higher frequencies removed and is in the foreground; the shape of its spectrum perfectly overlaps with the traffic treatment at the lowest frequencies). Anuran species whose vocalizations have a minimum frequency above 2 kHz did not face interference from the non-masking noise.

Measuring anuran abundance

Field recorders (Raspberry Pi computers connected to a microphone) were set out at each site to passively log anuran calls. The devices recorded continuously, but we subsampled by restricting the sampling hours to between 20:00 and 02:00 (when anurans are most likely to be calling; Bridges & Dorcas, 2000; North American Amphibian Monitoring Program protocol). To prevent undercounting of species whose vocalizations are masked by traffic noise, we counted the number of calling individuals during 15-min silent periods built into the traffic noise stimuli. These silent periods occurred once per hour, creating 45-min blocks of treatment followed by 15-min blocks of silence.

We counted calling individuals during six different hours per night because anuran activity varies by species throughout the night (Bridges & Dorcas, 2000). However, it was impossible to know whether or not calls heard in a different hour represent different individuals. To prevent spurious inflation of our dataset, we used the greatest number of individuals heard in one of the sampled hours as the number of individuals calling per site per night. For example, if we recorded three individual Oak Toads *Anaxyrus quercicus* between 20:00 and 21:00, one individual between 22:00 and 23:00, and two individuals between 1:00 and 2:00, the total number of oak toads heard at that site at that night would be recorded as three individuals, not six.

It is important to note that we indirectly measured anuran abundance using calls as a proxy. However, Green Frog *Rana clamitans* abundances measured using mark-recapture are positively correlated with calling index and calls per minute (Nelson & Graves, 2004). Though only males produce calls, male and female frog abundances are positively correlated (Nelson & Graves, 2004). Therefore, we expected

Table 1 Number of sampling events by site and treatment

Treatment	site 1	site 2	site 3
Control	3	3	5
Non-masking	1	4	3
Traffic	3	3	2

that any differences in number of calling individuals reflect a true difference in abundance.

Modeling the effects of traffic noise

We tested whether species richness and total abundance (number of individuals encountered, regardless of species) varied with noise treatment in R (v. 3.3.1). Because of our conservative counting method and because 2016 was a relatively dry year at Tosohatchee, we recorded too few individuals of each species (no more than three individuals/species/site/night) to perform analyses of abundance for individual species. We modeled the effects of noise treatment on species richness and abundance using generalized linear models because the amount of samples from each treatment combination were unbalanced (Table 1) and using a Poisson distribution because the dependent variables (species richness and total abundance) were counts.

We created candidate model sets to explain richness and total abundance using combinations of treatment, site, humidity, temperature, and ordinal date as explanatory variables, as well as a null model. By including site as a variable we controlled for potential pseudoreplication caused by sampling at each site multiple times. Although site could be considered a random factor, because there were only three levels we treated it as a fixed factor, as is recommended when the number of levels is small (Gelman & Hill, 2007; Bolker *et al.*, 2009). Humidity and temperature were measured at the Tosohatchee weather station and found to be somewhat collinear (Pearson correlation = 0.66) so the candidate sets did not include models with both factors. We also considered ordinal date separately from weather variables, because in some cases seasonality is a stronger predictor of anuran call rates (Steen, McClure & Graham, 2013). Ordinal date, as expected, was collinear with both humidity and temperature (Pearson correlations = 0.72 and 0.81, respectively) so it was not included in candidate models with either of those variables.

When building our candidate sets, we wished to include only interaction terms which we could justify ecologically. Given that our sites occurred over a relatively small spatial scale, we did not expect the effects of site to interact with humidity, temperature, or ordinal date. We also did not expect the effect of noise treatment to interact with these variables. Therefore, the only interaction terms included in our candidate sets were between treatment and site. This resulted in a candidate set of 20 models each for species richness and total abundance.

The candidate models were tested for overdispersion (R package AER, function 'dispersiontest') and were found to meet the assumptions of the Poisson distribution. We used

model selection (AICc; R package MuMIn) to determine the models that explained most of the variance in species richness and total abundance.

Effects of traffic noise treatments on vocalization properties

We used our recorded vocalizations to test whether any properties of the vocalizations change when individuals are exposed to traffic noise. Changes in various properties of bird and anuran vocalizations have been observed in response to traffic noise, though response varies greatly between species (reviewed in Slabbekoorn, 2013; Gil & Brumm, 2014; Potvin, 2016). The most well-documented change is an increase in the minimum frequencies of notes, possibly to reduce the amount of the vocalization that overlaps with (and is masked by) low-frequency traffic noise or as a side effect of singing louder to compensate for the noisy environment (Halfwerk & Slabbekoorn, 2009). However, proper assessment of this phenomenon requires recordings made from individuals whose vertical position is known and that are relatively close to the recording equipment, because frequencies of a signal attenuate (are lost) depending on the distance between the signal and receiver and the height at which the signal is produced (Marten & Marler, 1977).

Because our recordings were made passively, without knowledge of the distance from the microphone and position of each individual frog, it was not possible to accurately measure the frequencies of calls. A similar problem occurs when trying to measure the amplitude (loudness) of calls; to do so accurately, the distance between the calling individual and microphone must be known. Therefore, we measured three properties that could be easily identified from a spectrogram (a visual representation of sound which plots frequency in kHz on the *y*-axis vs. time on the *x*-axis; for example, Fig. 2): the duration of the call, number of notes per call, and number of notes per second (rate). Spectrograms were visualized using the program Syrinx.

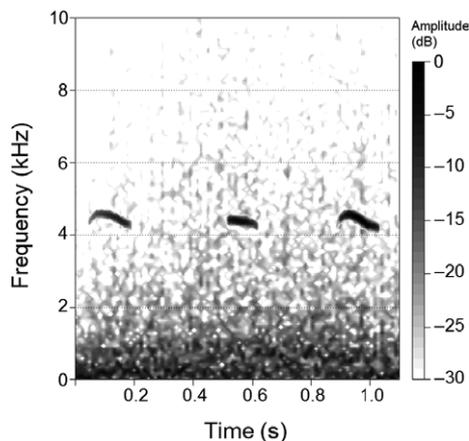


Figure 2 Spectrogram showing three high-amplitude Oak Toad notes easily distinguishable against the background of traffic noise. Spectrogram generated using R version 3.3.1.

This analysis was limited to one species, the Oak Toad *Anaxyrus quercicus*, because it was the most abundant species observed. Oak Toad calls are high enough in frequency and amplitude (100 dB at 100 cm, Gerhardt, 1975) to remain both audible and visible on a spectrogram even if there is interference from traffic noise (Fig. 2).

Because there was no way to identify whether one individual called throughout the night, or if different individuals called during different hours, we only measured calls recorded during one hour per site per night to prevent pseudoreplication. If oak toads called during more than one hour of the night, we chose the hour closest to the peak in oak toad calling activity (22:00–23:00), which we determined by summing the number of individual oak toads found to be calling during each hour over every night in our sampling period. In the given hour, we measured the duration, number of notes, and notes/s for all calls for 5 min during the treatment (traffic, non-masking, or control). Calls were considered subsamples and all values within one-five-minute period were averaged to determine the average value for the sampling occasion.

We compared the average values for call duration, number of notes per call, and notes per second from the different noise treatments using ANOVA. Visual inspection indicated that variances between treatments were not equal for call duration and number of notes per call. Therefore, call duration and notes per call were natural log-transformed to meet this assumption. The assumption of normality was met for all treatment groups for the natural log-transformed duration and notes/call, as well as for the untransformed call rate (notes/s).

Results

Anuran species observed

From the recordings, we identified 16 anuran species from 5 different families; however, some species were much more common than others (Table 2).

Effect of traffic noise on species richness

Overall, we recorded a mean of 3.89 species/site/night (± 1.67 SD, median 4). Model selection found that humidity and ordinal date were both significant predictors of species richness, but noise treatment was not (Table 3). Considering the output of the top model, humidity was significantly positively correlated with species richness ($P = 0.0295$, Fig. 3)

Effect of traffic noise on total abundance

Overall, we recorded on average 5.44 individuals/site/night (this number considers individuals of all species; ± 3.29 SD, median 5). Unlike with species richness, total anuran abundance was best explained by a model that included treatment and humidity as factors (Table 4, Fig. 3). The model output (Table 5) shows that overall abundance was significantly lower in the traffic treatment than in the control treatment,

but the non-masking treatment was not significantly different from the control.

Effects of traffic noise on vocalization properties

Call duration was on average 1.53 seconds longer in the traffic treatment than in the control treatment (Tukey's post-hoc test, $P = 0.0388$; Table 6) but there was no significant difference between the control and non-masking treatment. There was a trend for number of notes per call to be higher (average 1.30 notes more) in the traffic treatment than the control treatment (Tukey's post-hoc test, $P = 0.0745$; Table 6), and there was no significant difference in call rate (notes/s) between treatments (Table 6).

Discussion

This study was the first to examine how traffic noise affects anuran species richness and abundance. It has been widely observed that traffic noise is correlated with reduced bird species richness and abundance (e.g. Reijnen *et al.*, 1995; Potvin, 2016), an effect that has also been shown experimentally (McClure *et al.*, 2013). Anurans are similar to birds in that they rely heavily on vocal communication, and we expected that they would be affected similarly by traffic noise. It is known that anurans are one of the taxa most threatened by roads and that their abundances are reduced near roads (Fahrig & Rytwinski, 2009), and the effect of roads on abundance varies with life history (Grace, Smith & Noss, 2017). However, no research has attempted to address

Table 2 Species identified by their calls from the recordings, reported with the number of independent sampling occasions during which the species was observed

Species binomial	Common name	Family	# of sites/night species observed (out of 27 possible)
<i>Anaxyrus quercicus</i>	Oak toad	Bufoidea	21
<i>Anaxyrus terrestris</i>	Southern toad	Bufoidea	4
<i>Eleutherodactylus planirostris</i>	Greenhouse frog	Eleutherodactylidae	22
<i>Acris gryllus</i>	Cricket frog	Hylidae	4
<i>Hyla cinerea</i>	Green treefrog	Hylidae	4
<i>Hyla femoralis</i>	Pinewoods treefrog	Hylidae	4
<i>Hyla gratiosa</i>	Barking treefrog	Hylidae	3
<i>Hyla squirella</i>	Squirrel treefrog	Hylidae	22
<i>Osteopilus septentrionalis</i>	Cuban treefrog	Hylidae	5
<i>Pseudacris crucifer</i>	Spring peeper	Hylidae	1
<i>Pseudacris nigrita verrucosa</i>	Florida chorus frog	Hylidae	3
<i>Pseudacris ocularis</i>	Little grass frog	Hylidae	19
<i>Gastrophryne carolinensis</i>	Eastern narrow-mouthed toad	Microhylidae	3
<i>Rana catesbeianus</i>	American bullfrog	Ranidae	2
<i>Rana grylio</i>	Pig frog	Ranidae	2
<i>Rana sphenoccephala</i>	Southern leopard frog	Ranidae	15

Table 3 Subset of candidate models for species richness. Only weighted models are shown here (out of 20 total candidate models, see Materials and methods)

Model	d.f.	logLik	AICc	Δ AICc	Weight
Humidity	2	-50.7	106.0	0.0	0.358
Date	2	-51.6	107.7	1.8	0.148
1 (null)	1	-53.2	108.5	2.6	0.098
Temperature	2	-52.1	108.6	2.7	0.094
Site + humidity	4	-49.5	108.9	2.9	0.083
Treatment + humidity	4	-49.9	109.6	3.6	0.058
Site + date	4	-50.5	110.7	4.8	0.033
Treatment + date	4	-50.6	110.9	5.0	0.030
Site	3	-52.3	111.7	5.7	0.021
Treatment + site + humidity	6	-47.8	111.8	5.9	0.019
Site + temperature	4	-51.1	112.0	6.1	0.017
Treatment + temperature	4	-51.2	112.2	6.3	0.016
Treatment	3	-52.6	112.3	6.4	0.015
Treatment + site + date	6	-48.9	114.0	8.0	0.006
Treatment + site	5	-51.6	116.0	10.0	0.002
Treatment + site + temperature	6	-49.9	116.0	10.1	0.002

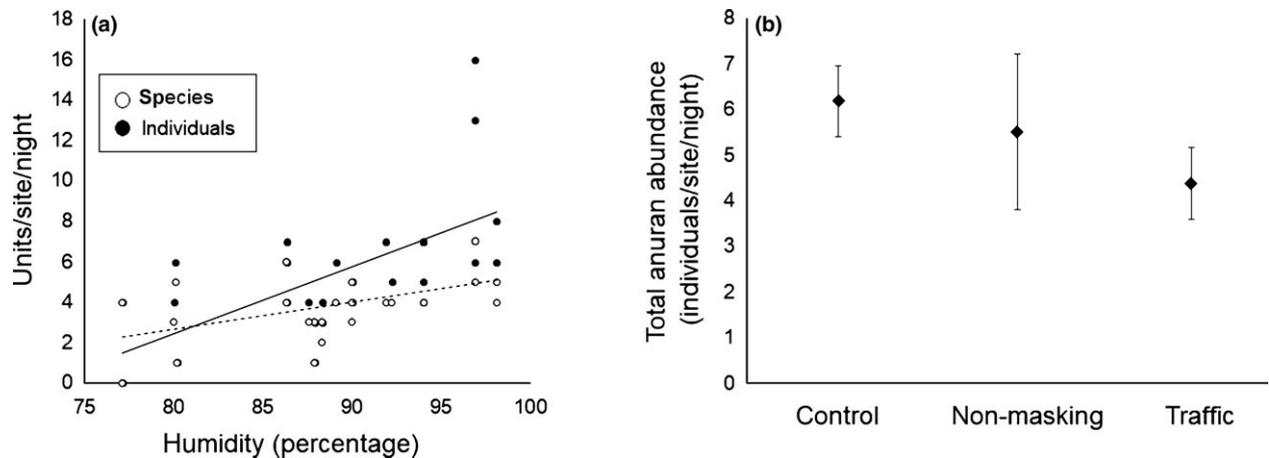


Figure 3 Visualization of the factors influencing species richness and abundance. (a) Humidity was a significant predictor of both species richness and total anuran abundance. (b) Traffic noise significantly impacted total anuran abundance, with fewer individuals observed in the traffic noise treatment. Error bars represent standard error.

Table 4 Subset of candidate models for total abundance of anurans. Only weighted models are shown here (out of 20 total candidate models, see Materials and Methods)

Model	d.f.	logLik	AICc	Δ AICc	Weight
Treatment + humidity	4	-56.9	123.6	0.0	0.530
Humidity	2	-59.9	124.3	0.7	0.380
Treatment + site + humidity	6	-55.9	128.0	4.4	0.059
Site + humidity	4	-59.8	129.5	5.9	0.028
Treatment + date	4	-62.7	135.2	11.6	0.002
Date	2	-65.4	135.3	11.7	0.002

Table 5 Output from the top model in the candidate set explaining anuran abundance. Estimates of effect sizes comparing the listed treatments to the control are given

	Estimate	SE	Z	Pr(> z)
Intercept	-4.75	1.42	-3.34	8.34e ⁻⁰⁴
Non-masking treatment	-0.08	0.19	-0.40	0.692
Traffic treatment	-0.49	0.21	-2.33	0.020
Humidity	0.07	0.02	4.71	2.47e ⁻⁰⁶

how traffic noise contributes to this pattern, either correlatively or experimentally. Eigenbrod *et al.* (2009) found evidence for species-specific 'road effect zones', distances from roads within which anuran abundance is reduced, which parallels the findings of Reijnen *et al.* (1995) in birds. Traffic intensity (e.g. vehicles/day), which is presumably linked to traffic noise amplitude, has been shown to negatively impact abundance of some anuran species (Fahrig *et al.*, 1995; Carr & Fahrig, 2001; Eigenbrod, Hecnar & Fahrig, 2008). However, these studies considered increased mortality, not increased levels of noise, to be the cause.

In our experiment, playback of traffic noise significantly reduced the total number of anurans observed compared to the control treatment, an effect previously observed in migrating birds (McClure *et al.*, 2013). Due to the low

Table 6 ANOVA outputs comparing vocalization properties across treatments

		d.f.	Sum Sq.	Mean Sq.	F	Pr(>F)
ln (duration)	treatment	2	0.79	0.39	3.88	0.0378
	residuals	20	2.03	0.10		
ln (notes/call)	treatment	2	0.32	0.16	3.16	0.0643
	residuals	20	1.01	0.05		
call rate (notes/s)	treatment	2	0.50	0.25	0.99	0.389
	residuals	20	5.05	0.25		

overall abundance of anurans during the 2016 field season, the observed difference was small- an effect size of roughly one individual fewer- but the fact that this pattern was detected despite low sample sizes indicates that it is probably an ecologically significant pattern. The low sample size is due to a relatively dry field season in 2016 during which the wet flatwoods did not flood, compared to flooding observed during site selection in 2015. There was not a significant difference in number of individuals observed between the control and non-masking treatments, however, it is possible that our study simply lacked the power to detect a difference. Therefore, we are not willing to say that anurans are unaffected by noise that does not overlap with their vocalizations; however, this study did not provide evidence to the contrary. We therefore call for continued study of this phenomenon across regions and species to fully understand how traffic noise is impacting anuran communities around the world.

We also observed that both anuran abundance and species richness, assessed from calls, were positively correlated with humidity, stronger than the effects of either temperature or ordinal date. Previous studies have found both temperature and ordinal date to be important predictors of calling behavior (e.g. Saenz *et al.*, 2006; Steen *et al.*, 2013). However, those studies were conducted over either larger temporal

scales (i.e. three years, Steen *et al.*, 2013) or with greater variation in temperature (Saenz *et al.*, 2006). Due to the short-term nature of our study (less than 3 months) and relatively small variation in temperature across the study period (19.9–26.8°C), it makes sense that humidity would emerge as an important predictor. However, it is likely that if this study had been conducted over a longer time period, temperature and season would have emerged as important predictors.

Oak toads produced longer calls at traffic noise sites than at control sites, an effect that appears to be due to an increase in number of notes per call rather than an increase in call rate (notes/s). The fact that increased call duration did not occur at non-masking noise sites indicates that it is a response to the decreased signal-to-noise ratio of oak toad calls experienced during the traffic, but not the non-masking, treatment. This was a curious result, because previous work on anurans has found the exact opposite pattern: Green Frogs *Rana clamitans* and Northern Leopard Frogs *Rana pipiens* reduce call rate (calls/min) and amplitude but increase dominant frequency in response to traffic noise; Gray Treefrogs *Hyla versicolor* also reduce call rate (Cunnington & Fahrig, 2010). European Tree Frogs *Hyla arborea* reduce the length of their calling bouts when exposed to traffic noise (Lengagne, 2008), as do Spring Peepers *Pseudacris crucifer* exposed to masking noise (Hanna *et al.*, 2014). These responses suggest that these species expend less energy calling when there is interference from traffic noise, which makes sense from a theoretical standpoint; calling is one of the most energetically expensive activities frogs perform (Pough *et al.*, 1992), and therefore males should spend more time calling at times when the effective transmission distance of those calls will be greater (Wells & Schwartz, 2007).

However, not all anuran species decrease call duration in response to anthropogenic noise. Sun & Narins (2005) found that while three species of co-occurring frogs in Thailand *Microhyla butleri*, *Rana nigrovittata*, and *Kaloula pulchra* vocalized less during airplane flyovers, another species found in the pond assemblage, *Rana taipehensis*, consistently increased calling effort during flyovers. Sun and Narins hypothesize that *R. taipehensis* was exploiting the reduction from interspecific calls during the airplane flyovers, and it is possible that the same thing is happening here; however, our data were not collected for answering that question. It is also possible that Oak Toads are exhibiting another adaptive strategy: increasing signal redundancy to increase the probability that the signal will be communicated (Shannon & Weaver, 1949). This adaptation is well documented in birds; Japanese Quail (Potash, 1972) and King Penguins (Lengagne *et al.*, 1999) increase the number of syllables per call as background noise increases, and Silvereyes *Zosterops lateralis* and Chaffinches *Fringilla coelebs* increase call duration in response to noise playback (Brumm & Slater, 2006; Potvin & Mulder, 2013). Though our study was the first to observe increased redundancy of anuran calls in response to traffic noise, redundancy has been observed in many (but not all) species as a response to

anuran chorusing (reviewed in Schwartz & Bee, 2013), which has been studied far more extensively than anurans' response to traffic noise. Anurans often increase the duration and/or number of notes in noisy chorus situations, so it makes sense that the behavior could be a response to other noisy situations like traffic noise.

Amphibians are facing an extinction crisis worldwide (Houlahan *et al.*, 2000; Stuart *et al.*, 2004) and it is therefore critical to understand the factors contributing to their decline. The impact of road mortality is extremely high for amphibians (e.g. Gibbs & Shriver, 2005; Glista, DeVault & DeWoody, 2008), and as a result there has been an increase in ecopassages designed specifically for reptiles and amphibians. However, if traffic noise has a deterrent effect on wildlife, then these crossings, which are expensive and difficult to maintain, may not be the best option for conservation of certain species. Given the rapid increase in the amount of paved roads predicted in the next few decades (Laurance *et al.*, 2014), it is imperative that more research is done to understand how the resulting increases in traffic and traffic noise will impact these sensitive taxa.

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