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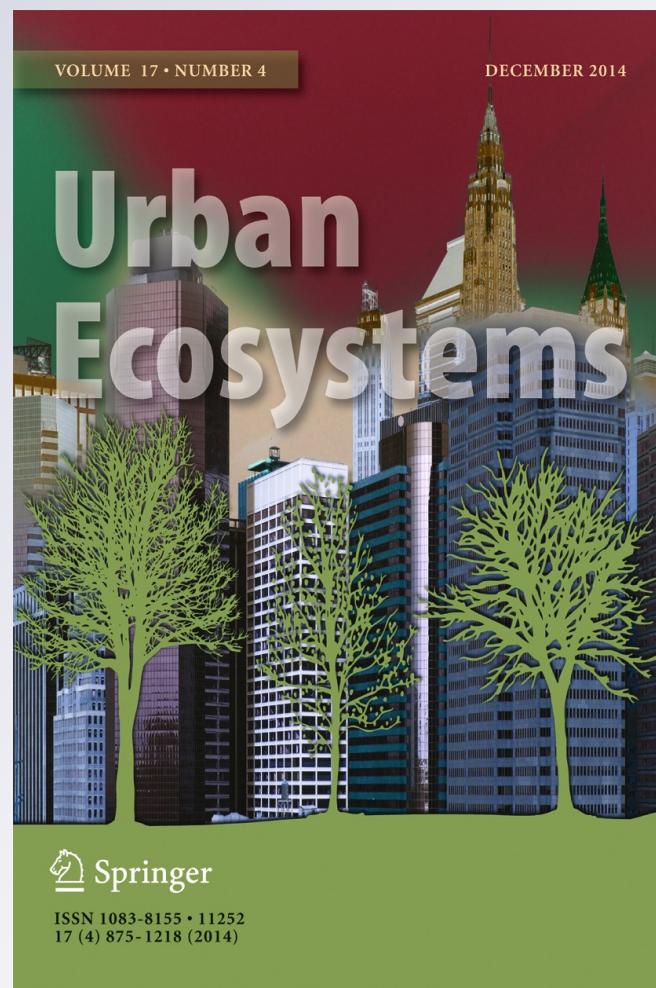
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Does traffic noise alter calling time in frogs and toads?
A case study of anurans in Eastern Ontario, Canada

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Abstract In habitats disturbed by anthropogenic noise, acoustically communicating species may develop behavioral responses that help them transmit information and overcome signal masking. We studied four anuran species breeding in wetlands, ponds, and ditches near a highway in eastern Ontario, Canada, to test whether they called more often when traffic noise intensity was lower, and stopped calling when the noise intensity increased (i.e., gap calling behavior). We made call recordings between April and July 2011, and compared the traffic noise intensity (sound pressure level) between times when the anurans were calling and times when they were not calling. We found that the two species with the highest call peak frequency (American toad, gray treefrog) called randomly with regard to traffic noise intensity. In contrast, the two species with the lowest call peak frequency (green frog, bullfrog) called more often when traffic noise intensity was low. The behavioral response in the two latter species likely represents a short-term strategy that enhances their signal-to-noise ratio thereby increasing the chance of effective communication. Our results support predictions derived from the acoustic adaptation hypothesis: low-frequency signals are more prone to be masked by anthropogenic noise and therefore require behavioral adjustments (in this study gap-calling behavior) to ameliorate this effect.

Keywords Acoustic communication · Amphibian conservation · Anthropogenic noise · Anurans · Masking interference · Road ecology

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Introduction

Communication between individuals is critical for several fitness-related processes such as species recognition, mate choice, attraction of heterospecifics, and defense of resources (Szekely et al. 2010; Schaefer and Ruxton 2011). Thus, individuals sending communication signals should adapt the signal to maximize information transfer to the receptor. Numerous factors can reduce the efficacy of information transfer from senders to receivers. In species that communicate acoustically, signals emitted by senders may not be perceived by receivers due to background noise in their habitat; this phenomenon is known as masking (Gerhardt and Klump 1988; Brumm and Slabbekoorn 2005). Masking of acoustic signals can occur from natural sources (e.g., rain, wind, conspecific and interspecific communication, etc.) or from anthropogenic sources (e.g., vehicular traffic, industrial noise) (Rabin et al. 2003; Slabbekoorn et al. 2010; Ortega 2012).

There are long- and short-term mechanisms by which senders can reduce masking of auditory signals: evolutionary changes in call traits and reversible behavioral adjustments, respectively (Brumm and Slabbekoorn 2005). One such short-term mechanism is called "call alternation behavior". This occurs when individuals producing a call time their vocalizations to coincide with periods of low masking noise. When two individuals are in close proximity, they effectively take turns calling (Cade and Otte 1982; Schwartz 1987). Call alternation is thought to reduce the masking of signals by conspecifics (Sismondo 1990; Zelick and Narins 1982; Grafe 1996) or heterospecifics (Ficken et al. 1974; Popp et al. 1985; Brumm 2006; Wong et al. 2009).

The same mechanism can explain so-called "gap calling behaviour" in which animals call during lower-noise periods within abiotic noise, either natural (Douglas and Conner 1999) or anthropogenic (Sun and Narins 2005; Vargas-Salinas and Amézquita 2013). The intensity of anthropogenic noise can vary over short periods. For example, near roads, the noise level produced by truck traffic is higher than that produced by smaller vehicles (Fig. 1). Animals can adjust to this variation shifting the timing of calls to coincide with the periods of lower noise levels (Fuller et al. 2007; Cartwright et al. 2013). Calling during these gaps should increase the contrast between the calling signals and the abiotic background noise, acting to reduce the potential for signal masking, thereby improving communication. This should increase reproductive success and ultimately population viability (Bee and Swanson 2007; Francis et al. 2011a).

Understanding how and why some species are more susceptible to negative effects of anthropogenic noise whereas others appear unaffected is important for determining the situations in which mitigation is needed (Francis et al. 2011a, 2011b; Summers et al. 2011; Cunnington and Fahrig 2013). Thus, the purpose of this study was to test for the occurrence of gap calling behavior in four anuran species exposed to variation in the intensity of anthropogenic noise in breeding sites adjacent to a highway. We predicted that anurans would tend to call when the noise intensity at the calling sites was relatively low, and cease calling when noise intensity increased.

Materials and methods

To test our prediction we used four species of anurans in Eastern Ontario, Canada (Fig. 2): American toad (*Anaxyrus americanus*), gray treefrog (*Hyla versicolor*), green frog (*Lithobates clamitans*), and bullfrog (*Lithobates catesbeianus*). Nineteen sample sites (wetlands, ponds and ditches) were located near Highway 401 between the intersection with Highway 416
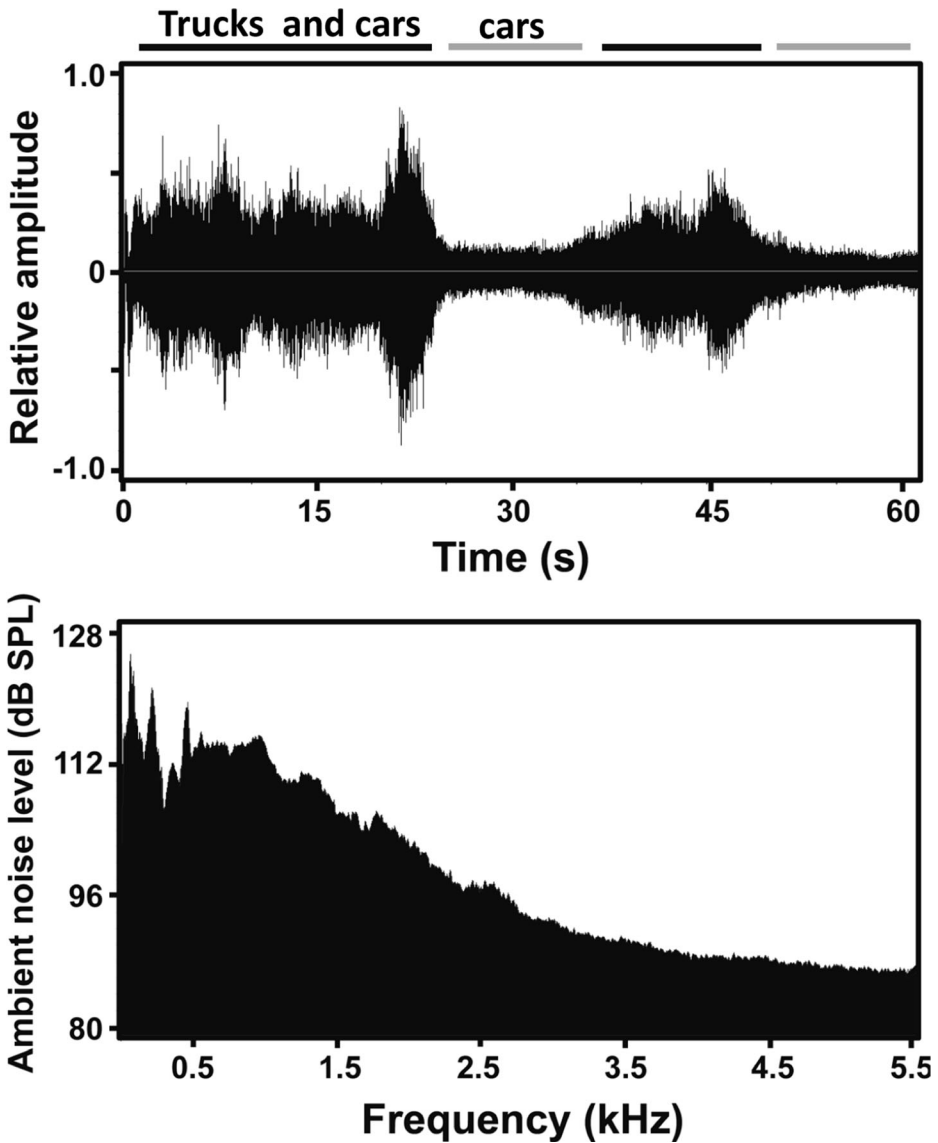
Fig. 1 Representative oscillogram (above) and power spectrum (below) showing the background noise characteristics at locations where anurans were recorded (wetlands, ponds, and ditches) near Highway 401, Eastern Ontario, Canada. The oscillogram shows temporal variation in noise intensity mainly due to the presence (upper black lines) or absence (upper gray lines) of trucks passing near the recording site

(44°45'34"N; 75°28'21" W) and the intersection with County Road 14 (45°00'39"N; 74°59'56" W) (Fig. 3). We selected sites where individuals of the focal species were known to breed (Cunnington and Fahrig 2010). The average distance from the sampling sites to Highway 401 was approximately 20 m (range=~10–60) while the minimum distance between individual sampling sites was > 100 m. Traffic density on Highway 401 is ~18300 vehicles/day, and traffic represents the most important source of anthropogenic noise at the sample sites

Fig. 2 Calling individuals of the four species of anurans recorded during this study: American toad *Anaxyrus americanus* **a**, gray treefrog *Hyla versicolor* **b**, green frog *Lithobates clamitans* **c**, and bullfrog *Lithobates catesbeianus* **d**

(Eigenbrod et al. 2008). The area contains a relatively low human population density with most area covered by farms and forest (Fig. 3).

We conducted nocturnal recordings of males' calling activity on windless nights between April 10 and July 30, 2011. Recordings were made in the absence of wind, to avoid microphone interference. We used an omnidirectional microphone (Sennheiser ME62/K6) connected to a digital recorder (Marantz PMD661; sampling rate 44.1 kHz). The frequency responses of the recorder and the microphone were 20Hz−24kHz and 20Hz−20kHz, respectively. We did not filter recordings post-processing. The microphone was located in a fixed position at 60−100 cm from the calling male. Calling males were recorded for 3 min (American toad, gray treefrog) or 5 min (green frog, bullfrog). We performed longer recordings for the latter two species because they call at lower rates than the first two species. Often, we recorded several males per species at the same sample site. Therefore, to prevent pseudoreplication, we recorded frogs of the same species at any single site just during one single night. Dispersal ranges of our study species are on the order of 1 to 6.5 km (Smith and Green 2005), but we considered unlikely that we recorded the same individual twice at different sampling sites given the short duration of our study.

Potential masking of calls by heterospecifics was not a concern in our study because our focal species' calling activity is temporally and spatially segregated (Harding 1997). For instance, American toads typically breed in ditches and small ponds of shallow water without emergent vegetation, while gray treefrogs select areas with abundant emergent vegetation, and bullfrogs and green frogs select open areas in permanent ponds. The species also vary in the timing of their breeding seasons resulting in only one or two species being found actively calling during the collection of each recording. Finally, the call peak frequency (i.e., the frequency at which a call contained most energy; hereafter call peak frequency) does not overlap among species pairs (see table 1).
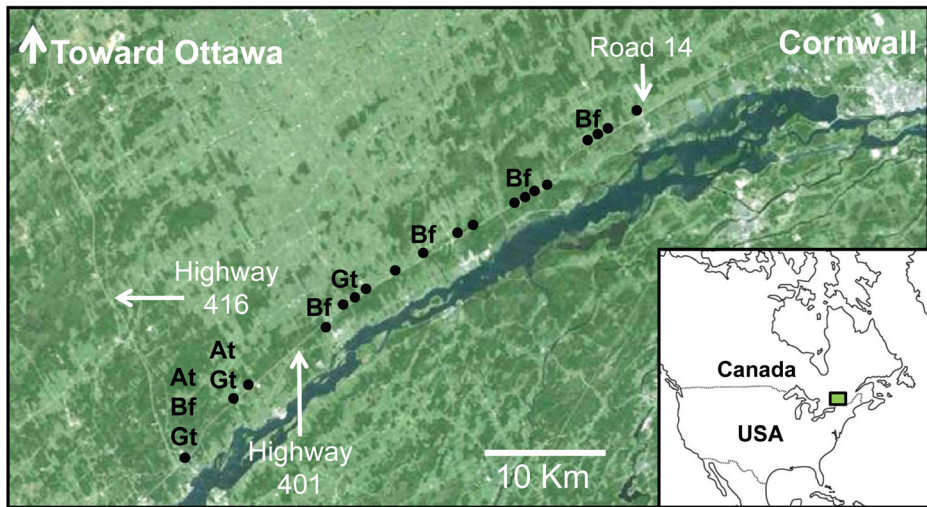
Fig. 3 Study area and locations of sampling sites (wetlands, ponds, ditches) in Eastern Ontario, Canada. Letters adjacent to sampling sites (black points) refer to anuran species recorded there; green frog was present in all sampling sites except the second- and third-most westerly sites. At: American toad, Bf: bullfrog, Gt: gray treefrog. Image edited from www.maps.google.es

To test whether individuals called randomly with regard to traffic noise, or exhibited gap calling behavior, we compared traffic noise when the individual was calling to traffic noise when it was not calling. We measured the mean call peak frequency from power spectra (Raven software, Bioacoustics Research Program 2011; Window: Blackman, Discrete Fourier Transform [DFT]=2048 samples). For green frogs, gray treefrogs and bullfrogs we calculated the call peak frequency by Fourier transform of the entire call. The call of American toad consists of long pulse trills, so for this species we calculated call peak frequency by Fourier transform of a 2-s section in mid-call (see Cocroft and Ryan 1995). For each species we calculated at the mean call peak frequency, the relative background noise intensity (hereafter traffic noise; dB, re 20 µPa) when the individual was calling and the relative traffic noise when the individual was not calling. Traffic noise during calling was calculated as the mean of values taken one second immediately before and after each call of each individual. Traffic noise at non-calling times was calculated using one-second intervals every 10 s for the whole 3–5 min of recording, excluding periods when the male was calling. Since sound pressure levels (SPL) were measured in dB, which represents a logarithmic scale, we used non-parametric statistical

Table 1 Number of males (sample size) and calls recorded, along with call peak frequencies, for anuran species recorded in wetlands, ponds, and ditches near Highway 401, Eastern Ontario, Canada

Species	Number males recorded	Number of calls recorded	Mean and range of number of calls per recording	Mean (±SD) of call peak frequency
American toad	14	97	6.9 (5–10)	1587.86 ± 106.51
Gray treefrog	16	619	38.7 (11–61)	2126.4 ± 73.38
Green frog	15	172	10.9 (6–19)	869.34 ± 382.01
Bullfrog	16	467	28.6 (10–62)	270.81 ± 39.42

analyses based on median instead of mean values. A Wilcoxon test for related samples was used to compare the noise intensity at calling times to the noise intensity at non-calling times.

Results

We collected 61 recordings over 28 nights of surveys resulting 1355 recorded calls of the four species (Table 1). There was no significant difference between the traffic noise intensity during calling and non-calling times for American toads ($Z=-1.161$, $P=0.245$, $N=14$) or gray treefrogs ($Z=-1.164$, $P=0.245$, $N=16$) (Fig. 4). In contrast, both green frogs and bullfrogs called more often during periods of lower-intensity traffic noise (green frog $Z=-2.613$, $P=0.009$, $N=15$; bullfrog $Z=-2.947$, $P=0.003$, $N=16$; Fig. 4). The statistical difference found for both green frogs and bullfrogs persisted when we applied Bonferroni's correction, $\alpha< 0.05/4=0.0125$ for multiple tests (4).

Discussion

Both green frogs and bullfrogs called more often when the level of traffic noise was relatively low and stopped calling when traffic noise was relatively high (Fig. 4); this behavioral response was not observed in American toads and gray treefrogs. As traffic noise energy is concentrated at low frequencies, low frequency calls are especially prone to masking (Slabbekoorn and Peet 2003; Brumm and Slabbekoorn 2005; see Fig. 1 for our study system). Accordingly, our results suggest gap calling behavior in the species with the lower call frequencies (green frog, bullfrog), but not in those with the higher call frequencies (American toad, gray treefrog). By calling at times when traffic noise intensity is relatively
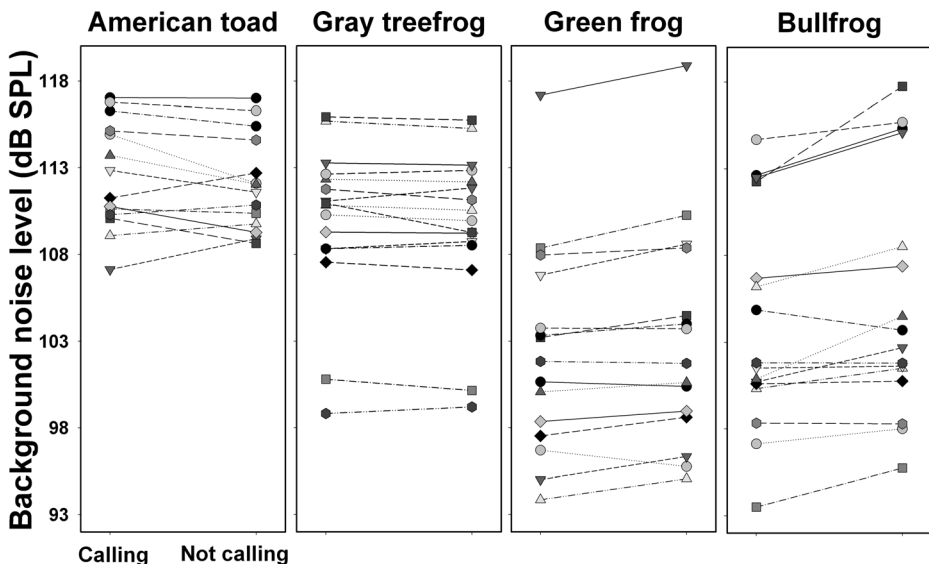

Fig. 4 Relative traffic noise intensity (dB SPL) measurements during calling and non-calling times for four anuran species in wetlands, ponds and ditches near highway 401 in Eastern Ontario, Canada. Symbol pairs united by a line denote the same individual

low, green frogs and bullfrogs likely increase their signal-to-noise ratio (Zelick and Narins 1982; Douglas and Conner 1999; Sun and Narins 2005).

We do not believe that our results are simply due to our inability to detect green frog and bullfrog calls made during high traffic noise periods. As each recording was made in close proximity to the focal individual, it was always was possible to see and hear when it was calling, and to distinguish calls from background noise in our recordings (Fig. 2). We also do not believe that variation in distance from traffic noise to the focal individuals can explain our results. Almost all recordings were made within 30 m of the paved shoulder of Highway 401.

The difference in traffic noise intensity between calling and non calling times in our study system (0.74 dB SPL for green frog and 1.48 dB SPL for bullfrog) is less than reported previously in a tropical anuran species (3.4 dB SPL; Vargas-Salinas and Amézquita 2013). In both studies, noise was produced by cars and trucks; however, the traffic volume was much higher at the current study site: ~18300 vehicles/day on Highway 401, Canada (Eigenbrod et al. 2008) vs. ~3200 vehicles/day on a road in the Colombian Andes (Vargas-Salinas and Amézquita 2013). As traffic density increases, a reduction in acoustic windows is expected. Therefore, anurans will have increasingly limited opportunities for selecting noise-free periods for gap calling behavior.

In addition to their gap calling behavior, other characteristics of green frog and bullfrog calls may allow them to communicate in the presence of traffic noise. Green frogs can increase their call peak frequency in response to traffic noise (Cunnington and Fahrig 2010); this behavioural plasticity may explain the relatively high variability of call peak frequency for this species in our results (Table 1). Also, the peak sound pressure level (SPL) of green frogs' calls may be enough to prevent masking by traffic noise: call intensities at a distance of 50 cm from a focal male are 96 dB SPL (Ryan 1985) whereas the mean traffic noise intensity in our sample sites is 73 dB SPL (Cunnington and Fahrig 2010). Similar to green frogs, the sound peak pressure of the bullfrog call (85 dB SPL at 1 mt distance; Both and Grant 2012) may be high enough to overcome traffic noise background over short distances. Furthermore, the effect of behavioral adjustments mentioned here in the signal-to-noise ratio would be accentuated by the spatial separation between individuals and the noise source (Nityananda and Bee 2012, and Citations therein).

Despite the lack of gap-calling behaviour we observed in the American toad and the gray treefrog, these species may nonetheless be capable of this behaviour when necessary. It is likely not necessary in the context of traffic noise where the high-frequency calls of these species would limit masking by traffic noise (Cunnington and Fahrig 2010; but see Vargas-Salinas and Amézquita 2013). In addition, the American toad exhibits explosive breeding with scramble breeding behavior. Under these conditions, the mating success of males is mainly influenced by active searching and physical struggling instead, of by attractiveness of individual calls (Wells 2007 and Citations therein). With respect to the gray treefrog, we collected recordings within dense choruses, where individuals tend to alternate their calls in reaction to the calls of conspecific neighbors (Halliday and Tejedo 1995; Gerhardt and Huber 2002). For both species the behavioural activity of conspecifics may be a more important factor modulating calling time than is the noise generated by the highway. Future research of the potential interaction effect between conspecific calling and anthropogenic noise on gap calling behavior in these two species is warranted.

This and previous studies (Sun and Narins 2005; Vargas-Salinas and Amézquita 2013) suggest that anthropogenic noise can promote gap calling behavior in anurans. Since call alternation behavior has been observed in diverse taxa (e.g. Roy et al. 2011; Sismondo 1990; Zelick and Narins 1982; Brumm 2006; Römer 2013; for a review see Brumm 2013), gap calling might well be widespread in acoustically communicating vertebrates and possibly

invertebrates living in habitats disturbed by anthropogenic noise. Gap calling behavior is expected to be particularly common in species with relative low signal frequencies similar to those found in anthropogenic noise. Finally, reduced effectiveness of gap calling behavior is likely with increasing traffic density and the associated reduction of available acoustic windows.

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