RESEARCH PAPER

ethology　WILEY

Traffic noise differentially impacts call types in a Japanese treefrog (*Buergeria japonica*)

Henry D. Legett[1] 🆔　|　Ryan P. Madden[1]　|　Ikkyu Aihara[2]　|　Ximena E. Bernal[1,3]

[1]Department of Biological Sciences, Purdue University, West Lafayette, IN, USA

[2]Graduate School of Systems and Information Engineering, University of Tsukuba, Tsukuba, Japan

[3]Smithsonian Tropical Research Institute, Balboa, Panama

Correspondence
Henry D. Legett, Department of Biological Sciences, Purdue University, West Lafayette, IN, USA.
Email: hlegett@purdue.edu

Abstract

Acoustic noise from automobile traffic impedes communication between signaling animals. To overcome the acoustic interference imposed by anthropogenic noise, species across taxa adjust their signaling behavior to increase signal saliency. As most of the spectral energy of anthropogenic noise is concentrated at low acoustic frequencies, species with lower frequency signals are expected to be more affected. Thus, species with low-frequency signals are under stronger pressure to adjust their signaling behaviors to avoid auditory masking than species with higher frequency signals. Similarly, for a species with multiple types of signals that differ in spectral characteristics, different signal types are expected to be differentially masked. We investigate how the different call types of a Japanese stream breeding treefrog (*Buergeria japonica*) are affected by automobile traffic noise. Male *B. japonica* produce two call types that differ in their spectral elements, a Type I call with lower dominant frequency and a Type II call with higher dominant frequency. In response to acoustic playbacks of traffic noise, *B. japonica* reduced the duration of their Type I calls, but not Type II calls. In addition, *B. japonica* increased the call effort of their Type I calls and decreased the call effort of their Type II calls. This result contrasts with prior studies in other taxa, which suggest that signalers may switch to higher frequency signal types in response to traffic noise. Furthermore, the increase in Type I call effort was only a short-term response to noise, while reduced Type II call effort persisted after the playbacks had ended. Overall, such differential effects on signal types suggest that some social functions will be disrupted more than others. By considering the effects of anthropogenic noise across multiple signal types, these results provide a more in-depth understanding of the behavioral impacts of anthropogenic noise within a species.

KEYWORDS
acoustic communication, anthropogenic noise, frogs, noise pollution, road effect

1 | INTRODUCTION

As the human transportation network continues to expand into natural areas, it is accompanied by high levels of anthropogenic acoustic noise from automobile traffic (Barber, Crooks, & Fristrup, 2010).

In addition to inducing stressful physiological responses (Crino, Johnson, Blickley, Patricelli, & Breuner, 2013; Slabbekoorn et al., 2010; Tennessen, Parks, & Langkilde, 2014), such noise can impair communication, reducing the detectability and discriminability of acoustic signals (Bee & Swanson, 2007; Lohr, Wright, & Dooling,

2003; Templeton, Zollinger, & Brumm, 2016) and carrying energetic costs for signalers (Alloush et al., 2011). High levels of traffic noise can, therefore, negatively affect species that depend on acoustic communication to mediate behaviors such as mating and avoiding predation (Bee & Swanson, 2007; Templeton et al., 2016). Thus, in the presence of traffic noise, many species adjust their signaling behavior to increase the signal-to-noise ratio and signal saliency (Brumm, 2013).

Frogs and toads are particularly susceptible to acoustic interference from anthropogenic noise, as many species rely heavily on acoustic signals for reproduction. Anurans, however, lack the vocal plasticity of other acoustically sensitive taxa (Lengagne, 2008; Roca et al., 2016). Many species of birds and mammals, for instance, can partially overcome elevated noise levels by increasing the amplitude of their acoustic signals by singing or calling more intensely (Brumm & Zollinger, 2011). This response to background noise, known as the Lombard effect, allows signalers to shift the signal-to-noise amplitude ratio increasing the probability of detection by the receiver. While there are some studies that claim anurans may also exhibit the Lombard effect in response to noise (Halfwerk, Lea, Guerra, Page, & Ryan, 2016; Shen & Xu, 2016), it is questionable whether this strategy is available to anuran species (Love & Bee, 2010; Zhao et al., 2018). In the presence of traffic noise, however, anurans can adjust other aspects of their signaling behavior, changing the spectro-temporal

properties of their calls such as production rate, duration, and spectral frequency (Schwartz & Bee, 2013). Whether these changes are enough to overcome acoustic interference imposed by traffic noise, and the corresponding negative consequences, is unclear (Parris, Velik-Lord, North, & Function, 2009).

Not all acoustic signals, however, are predicted to be impacted by traffic noise. Most of the spectral energy of traffic noise is concentrated at low acoustic frequencies, below 1,000 Hz (Bee & Swanson, 2007; Cho & Mun, 2008; Cunnington & Fahrig, 2010; Lewis, 1973), masking lower frequency signals more than higher frequency signals. Thus, for species with signal repertoires of multiple types of calls, lower frequency call types are expected to be more acoustically masked compared to higher frequency call types. Indeed, different effects of traffic noise on different call types have been shown in birds (Brumm & Slater, 2006; Halfwerk & Slabbekoorn, 2009; Wood & Yezerinac, 2006), mammals (Holt, Noren, & Emmons, 2011), and reptiles (Brumm & Zollinger, 2017). As a result, in response to anthropogenic noise, individuals from species in these taxa may switch to using different song or call types that are less susceptible to auditory masking (Bermúdez-Cuamatzin, Ríos-Chelén, Gil, & Garcia, 2010; Brumm & Zollinger, 2017; Halfwerk & Slabbekoorn, 2009). Whether this strategy of switching call type is widespread or effective, however, is debatable (Zollinger, Slater, Nemeth, & Brumm, 2017). Many anuran species also have signal repertoires with call types that vary
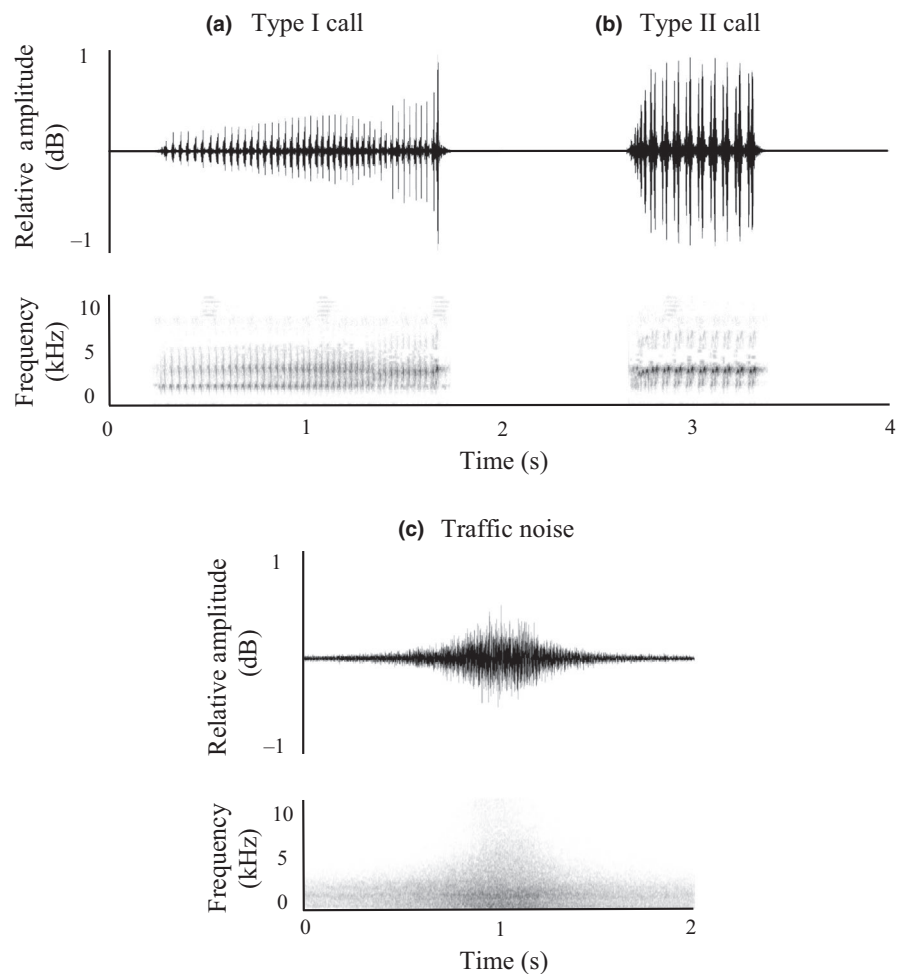

FIGURE 1 Oscillograms (top) and spectrograms (bottom) of *Buergeria japonica* mating calls, Type I (a) and Type II (b), and traffic noise (c) recorded from a single car pass on Prefectural Road 215, Iriomote Island. Type I calls have two frequency peaks, one around 2 kHz and another around 3.1 kHz. Type II calls have a single peak around 3.1 kHz

in their acoustic properties. Yet, despite studies comparing the impact of traffic noise on the calling behavior of different anuran species (e.g., Caorsi, Both, Cechin, Antunes, & Borges-Martins, 2017; Cunnington & Fahrig, 2010; Sun & Narins, 2005), the within-species effects of traffic noise on call types have remained unconsidered.

Here, we examine how the production of call types in the Japanese stream breeding treefrog (*Buergeria japonica*), also known as the Ryukyu Kajika frog, is differentially affected by traffic noise. Choruses of this species are directly exposed to traffic noise, as males often call along roadside ditches. Male *B. japonica* produce two main call types (Kuramoto, 1986; Tang, 2009; Figure 1a,b) that differ in susceptibility to acoustic interference from traffic noise. Although their exact social functions are unknown, both are suspected to play a role in attracting mates (Tang, 2009; Wang et al., 2017). One call (Type I) has dominant spectral elements that greatly overlap with the low dominant frequencies of traffic noise, while the other call (Type II) has less spectral overlap with traffic noise (Figure 1c). Thus, we predict that *B. japonica* will respond to noise by adjusting the spectro-temporal properties of their Type I calls more than Type II calls. We also assess whether males switch to using the higher frequency Type II calls in the presence of noise, a strategy that may be used by birds (Bermúdez-Cuamatzin et al., 2010) and reptiles (Brumm & Zollinger, 2017), but has yet to be observed in anurans.

2 | MATERIALS AND METHODS

2.1 | Study site

We collected traffic noise recordings and conducted acoustic playback experiments on Iriomote Island, Okinawa Prefecture, Japan (24°17′33″N 123°51′43″E). The island is 289.62 km² in area (Geospatial Information Authority of Japan, 2017) with a population of approximately 2,500 (Taketomi Town, 2018). The only major infrastructure is a coastal road (Prefectural Road 215) which partially rings the island. Large frog choruses, often multi-species in composition, form in ditches along the side of this road following heavy rains. These choruses typically include *B. japonica*, the ornate narrow-mouth frog (*Microhyla ornata*), and the Asian grass frog (*Fejervarya sakishimensis*). Abundance of these species peaks in July and August, overlapping with the rainy season (Watanabe, Nakanishi, & Izawa, 2005). All data, including the audio recordings of traffic noise and frog vocalizations, were collected from July to August 2016. For the duration of this study, temperature ranged from 26.6 to 29.5°C, relative humidity from 82.4% to 97.4%, and wind speed from 0.0 to 4.5 m/s.

2.2 | Traffic noise

We collected three audio recordings of a passing vehicle to use for the playback experiments. This traffic noise was recorded from different sites along the Prefectural Road 215 using a Marantz Professional digital recorder (Model PMD660) and a Sennheiser microphone (Model ME66—K6) placed 1 m from the edge of the road at ground level. A Brüel & Kjær digital sound level meter (Type 2,250) was also placed next to the microphone (C-weighting, fast RMS response). The audio files of traffic were edited using COOLEDIT2000 (Syntrillium Software) so that the sound of a single car pass was broadcast at a controlled rate of once every 8 s to simulate nighttime suburban traffic flow (Baker, Dowding, Molony, White, & Harris, 2007; Barrass & Cohn, 1984; Fahrig, Pedlar, Pope, Taylor, & Wegner, 1995; Okamura, Watanabe, & Watanabe, 2000).

2.3 | Acoustic playbacks

To assess changes in male *B. japonica* vocalizations in response to traffic noise, we conducted acoustic playbacks broadcasting our recorded traffic to 40 males selected haphazardly from two choruses at roadside ditches on the northern side of Iriomote Island. Following previously established methods (McGregor et al., 1992), a focal male was chosen within the chorus and his calling behavior was recorded over three consecutive 5-min intervals: (a) a silent pre-noise period to assess natural calling behavior, (b) a treatment period of broadcast traffic noise, and (c) a silent post-noise period. Playbacks were broadcast using a Pignose portable amplifier speaker (Model 7–100; Pignose-Gorilla) at amplitudes paired to the original traffic recordings (70–80 dB SPL re. 20 μPa), measured at ground level 1 m from the speaker (C-weighting, fast RMS response; Brüel & Kjær Type 2,250 digital sound level meter). Both the speaker and microphone for vocal recordings were placed at ground level 1 m from the focal male frog. Playback experiments were started 1 hr after sunset, alternating between the different choruses to minimize the exposure of non-focal frogs to broadcast noise. For each focal male, all calls of each call type (I and II) were counted within each of the three recording intervals (pre-noise, traffic noise, and post-noise) to measure call effort (calls/min). In addition, up to the first ten calls of each call type (I and II) in each recording interval (≤ 30 calls per male total) were measured for call duration (s) and dominant frequency (kHz). All call properties were analyzed using Raven Pro 1.5 (Cornell Lab of Ornithology; Hanning type spectrograms, sample rate of 0.012 s, FFT size 8,192, a frequency resolution of 5.38 Hz). To avoid measurement artifacts from acoustic interference, duration and dominant frequency were only measured for calls that did not temporally overlap with the traffic noise or calls from other males in the chorus. In addition, only males that produced at least one call in each recording interval were included in the analyses of call duration and dominant frequency. The dominant frequency of each call was computed as a measurement of the power spectral density, the variation of the signal energy at different frequencies. Call effort was measured as the number of calls per min over the 5-min recording interval. Overall, 1,618 Type I calls (40.5 ± 41.5 calls per male) and 366 Type II calls (9.2 ± 7.7 calls per male) were recorded and counted from 40 focal males to calculate call effort. Out of those calls, 412 Type I calls from 21 males (19.6 ± 9.0 calls per male) and 124 Type II

calls from 15 males (8.3 ± 2.8 calls per male) were analyzed for dominant frequency and duration.

2.4 | Statistical analysis

All statistical analyses were conducted using program R v. 3.5.2 (R Development Core Team: www.R-project.org). All three call properties (call effort, duration, and dominant frequency) for each *B. japonica* call type (Type I and Type II) were analyzed separately using the generalized linear mixed-effect model function in the *glmmTMB* package (Brooks et al., 2017). Recording interval (pre-noise, traffic noise, and post-noise) was included as a fixed factor, traffic noise playback (noise ID) as a random factor, and male frog (subject) as a random factor nested within noise ID. A gamma error structure and a log link function were used in the call duration and dominant frequency models. A Tweedie error structure and a log link function were used in the call effort models. Models were fit based on AIC following procedures described in Bolker et al. (2009). Model fits were evaluated using residual plots (Zuur & Ieno, 2016) in the *DHARMa* package (Hartig, 2018), and assumptions of homoscedasticity for each model were additionally assessed using Levene's tests. Post hoc Tukey contrast tests were performed, and least square means calculated, using the *emmeans* package (Searle, Speed, & Milliken, 1980). Effect sizes were calculated as the difference in least squares, estimated marginal means. The relative call effort of each call type was compared using a two-tailed Kendall tau correlation analysis. Data sets supporting these analyses are available in the supporting informations 1 and 2.

3 | RESULTS

The recorded traffic noise had an average amplitude of 74 ± 5 dB(C) and was broadband with more spectral energy at low acoustic frequencies, below 1,200 Hz (Figure 1c). This was similar to traffic noise recorded in other geographic areas where anuran behavioral studies have been performed (Cunnington & Fahrig, 2010; Parris et al., 2009). Males significantly increased their Type I call effort in response to traffic noise (Figure 2a), producing 5.65 ± 11.50 more calls/min during traffic noise playbacks compared to the pre-noise interval (t (113) = −2.79, p = .017, effect size = 0.43) and 5.88 ± 15.01 more calls/min compared to the post-noise interval (t (113) = −2.56, p = .031, effect size = 0.39). In addition, males significantly shortened Type I calls following noise playbacks (Figure 2c), reducing call duration by 0.13 ± 0.80 s during post-noise compared to the pre-noise interval (t (406) = −2.92, p = .010, effect size = 0.12) and by 0.13 ± 0.81 s compared to the noise interval (t (406) = −2.74, p = .018, effect size = 0.12).

In contrast to their lower frequency Type I calls, males significantly reduced the call effort of their higher frequency Type II calls from the pre-noise to the post-noise interval (Figure 2b), producing 1.55 ± 4.05 fewer calls/min following the traffic noise playbacks (t

(113) = −2.80, p = .016, effect size = 0.49). There was no change in Type II call duration (p > .05 and/or effect size <.01 for all combinations; Figure 2d) and no change in dominant frequency for either call type (p > .05 and/or effect size <.01 for all combinations; Figure 2e, f). The relative call effort of Type I and Type II calls was weakly, negatively correlated (τ = −0.23, z = −3.42, p < .001).

4 | DISCUSSION

The traffic noise recorded on Iriomote Island is similar to traffic noise from other areas (Cunnington & Fahrig, 2010; Parris et al., 2009) and, characteristically, contains more energy at lower spectral frequencies (Bee & Swanson, 2007). Given the spectral properties of traffic noise, higher frequency acoustic signals should have a greater signal-to-noise ratio than lower frequency signals. Although studies on the abilities of animals to alter their calls in the presence of traffic noise have been limited, in some taxa, signalers may switch to producing higher frequency call types in response to traffic noise (birds: Halfwerk & Slabbekoorn, 2009; Bermúdez-Cuamatzin et al., 2010; reptiles: Brumm & Zollinger, 2017). We found, however, that male *B. japonica* decrease the call effort of their higher frequency Type II calls and increase the call effort of their lower frequency Type I calls in response to traffic noise. Instead of switching to a higher frequency call type, our results suggest that male *B. japonica* use a different strategy, increasing signal redundancy. By producing the lower frequency Type I calls more often, the males may increase the chance of successful signal transmission, temporally avoiding auditory masking. Such adjustments in signal redundancy in response to noise have been observed in birds (Brumm & Slabbekoorn, 2005).

In addition to changing call effort, we found that male *B. japonica* also slightly reduced Type I call duration following playbacks. While it is unlikely that such a reduction in call duration is biologically meaningful, similar small changes of only a few pulses within a call have been shown to influence female call preference (Gerhardt, Tanner, Corrigan, & Walton, 2000). To better assess this impact, however, further studies are needed to understand the responses of female *B. japonica* for variation in call duration.

Overall, we found that *B. japonica* call types are differentially affected by traffic noise. Type I calls increased in call effort and decreased in duration while Type II calls decreased in call effort. In addition, the duration of the effect of traffic noise differed between call types. The increase in Type I call effort was a short-term response to noise, returning to pre-playback levels immediately following the traffic noise, while reduced Type II call effort persisted after the presentation of the noise. These differential effects of traffic noise on call types suggest that some social functions may be disrupted more than others. However, the specific functions of *B. japonica* Type I and Type II calls are currently unknown. Both are likely relevant to mating (Tang, 2009; Wang et al., 2017), but it is intriguing that their relative use changes between *B. japonica* populations (Kuramoto, 1986; Wang et al., 2017). The lack of the expected switch to the higher frequency call type in the
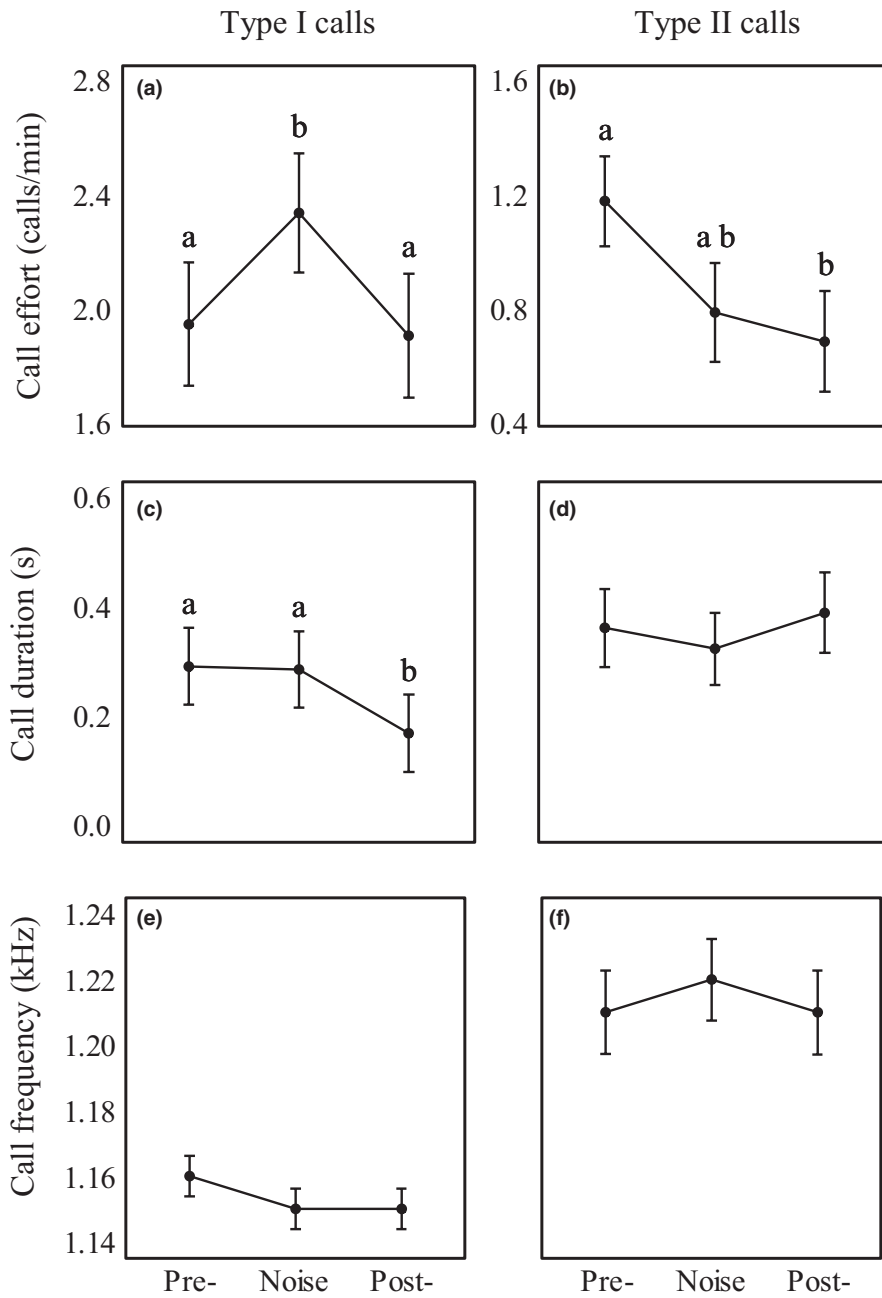
FIGURE 2 Call effort (a, b), call duration (c, d), and dominant frequency (e, f) of Type I and Type II calls, compared across the pre-noise, traffic noise playback, and post-noise recording intervals. Values are least square means, bars show standard error, letters above bars indicate statistically significant ($p < .05$) differences. For call effort, 1618 Type I calls (40.5 ± 41.5 per male) and 366 Type II calls (9.2 ± 7.7 per male) were recorded and counted from 40 focal males. For call duration and frequency, 412 Type I calls (19.6 ± 9.0 per male) were analyzed from 21 males and 124 Type II calls (8.3 ± 2.8 per male) were analyzed from 15 males

presence of acoustic interference suggests these call types may have different functions. That is, the social function of a call type may prevent males from using one call type more than the other. Different call types in frogs can have a variety of social functions within and beyond mating including courtship, aggressive interactions with other males, release, and distress (Toledo et al., 2015). Future studies investigating call type function in *B. japonica*, and how different populations respond to traffic noise, may provide insights into the social impacts of traffic noise in this species and their calling repertoire.

Our results for *B. japonica* fall within the variation of previously reported anuran responses to traffic noise, which includes both increases and decreases in calling rate and effort (Cunnington & Fahrig, 2010; Sun & Narins, 2005; Vargas-Salinas, Cunnington, Amézquita,

& Fahrig, 2014), call duration (Caorsi et al., 2017; Grace & Noss, 2017), and dominant frequency (Hoskin & Goosem, 2010; Lukanov, Simeonovska-Nikolova, & Tzankov, 2014; Nelson et al., 2017; Parris et al., 2009) across different species. Until now, however, only the responses of single call types have been examined for a given species. Even then, previous studies have found inconsistencies in response within species. Male European treefrogs (*Hyla arborea*), for example, decreased the rate and duration of their calling bouts in response to playbacks of traffic noise (Lengagne, 2008). The same species (*H. arborea*), however, did not change calling behavior when examined in a different study (Lukanov et al., 2014). Similarly, gray treefrogs (*Hyla versicolor*) decreased their calling rates in response to noise in one study (Cunnington & Fahrig, 2010), but not in another (Vargas-Salinas et al., 2014). Overall, these studies highlight the

need for more detailed studies addressing within-species variation in response to traffic noise. In addition, understanding how males vocally respond to traffic noise is only one half of the picture when studying anthropogenic noise and communication. As male frogs adjust calling behavior to overcome acoustic masking from noise, female choice experiments are also needed to examine the effectiveness of these strategies (e.g., Senzaki, Kadoya, Francis, Ishiyama, & Nakamura, 2018; Wollerman & Wiley, 2002). Studies, therefore, that aim to address the interaction between male responses to noise and female choice in noise across multiple call types would provide a more in-depth understanding of the impacts of anthropogenic noise on anuran species.

5 | CONCLUSION

Just as species with lower frequency calls can be more affected by traffic noise than species with higher frequency calls (Cunnington & Fahrig, 2010), our results suggest that the behavioral impacts of traffic noise could also be different for lower and higher frequency call types within a species. In addition, while we expected males to switch to higher frequency call types in response to traffic noise, male *B. japonica* instead increased the call effort of their lower frequency Type I calls. Why male *B. japonica* respond in this seemingly counterintuitive way is still unclear. However, by producing Type I calls more often, males may be increasing signal redundancy, temporally avoiding masking from traffic noise as opposed to spectral avoidance. Finally, the differential impact of traffic noise on acoustic signal types within species suggests that some social functions may be affected more than others. As many species rely on acoustic signals, often using repertoires of numerous signal types, uneven effects of anthropogenic noise on communication systems are expected across and within taxa.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ORCID

Henry D. Legett https://orcid.org/0000-0001-9005-8641

REFERENCES

Alloush, M., Scofield, D., Marczak, S., Jones, R., Kaiser, K., Oliva, M., ... Martineau, K. (2011). When sounds collide: The effect of anthropogenic noise on a breeding assemblage of frogs in Belize, Central America. *Behaviour*, *148*, 215–232. https://doi.org/10.1163/000579510X551660

Baker, P. J., Dowding, C. V., Molony, S. E., White, P. C., & Harris, S. (2007). Activity patterns of urban red foxes (*Vulpes vulpes*) reduce the risk of traffic-induced mortality. *Behavioral Ecology*, *18*, 716–724. https://doi.org/10.1093/beheco/arm035

Barber, J. R., Crooks, K. R., & Fristrup, K. M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution*, *25*, 180–189. https://doi.org/10.1016/j.tree.2009.08.002

Barrass, A., & Cohn, L. (1984). Variation of the spacing of calling male *Bufo woodhousei* and *Hyla cinerea* near roadway noise. *American Zoologist*, *24*, A15.

Bee, M. A., & Swanson, E. M. (2007). Auditory masking of anuran advertisement calls by road traffic noise. *Animal Behaviour*, *74*, 1765–1776. https://doi.org/10.1016/j.anbehav.2007.03.019

Bermúdez-Cuamatzin, E., Ríos-Chelén, A. A., Gil, D., & Garcia, C. M. (2010). Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. *Biology Letters*, *7*, 36–38. https://doi.org/10.1098/rsbl.2010.0437

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*, 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., ... Bolker, B. M. (2017). *glmmTMB* balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*, 378–400. https://doi.org/10.3929/ethz-b-000240890

Brumm, H. (2013). *Animal communication and noise*. Berlin, Germany: Springer.

Brumm, H., & Slabbekoorn, H. (2005). Acoustic communication in noise. *Advances in the Study of Behavior*, *35*, 151–209. https://doi.org/10.1016/S0065-3454(05)35004-2

Brumm, H., & Slater, P. J. (2006). Ambient noise, motor fatigue, and serial redundancy in chaffinch song. *Behavioral Ecology and Sociobiology*, *60*, 475–481. https://doi.org/10.1007/s00265-006-0188-y

Brumm, H., & Zollinger, S. A. (2011). The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour*, *148*, 1173–1198. https://doi.org/10.1163/000579511X605759

Brumm, H., & Zollinger, S. A. (2017). Vocal plasticity in a reptile. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170451. https://doi.org/10.1098/rspb.2017.0451

Caorsi, V. Z., Both, C., Cechin, S., Antunes, R., & Borges-Martins, M. (2017). Effects of traffic noise on the calling behavior of two Neotropical hylid frogs. *PLoS ONE*, *12*, e0183342. https://doi.org/10.1371/journal.pone.0183342

Cho, D. S., & Mun, S. (2008). Study to analyze the effects of vehicles and pavement surface types on noise. *Applied Acoustics*, *69*, 833–843. https://doi.org/10.1016/j.apacoust.2007.04.006

Crino, O. L., Johnson, E. E., Blickley, J. L., Patricelli, G. L., & Breuner, C. W. (2013). The effects of experimentally elevated traffic noise on nestling white-crowned sparrow stress physiology, immune function, and life-history. *Journal of Experimental Biology*, *216*, 2055–2062. https://doi.org/10.1242/jeb.081109

Cunnington, G. M., & Fahrig, L. (2010). Plasticity in the vocalizations of anurans in response to traffic noise. *Acta Oecologica*, *36*, 463–470. https://doi.org/10.1016/j.actao.2010.06.002

Fahrig, L., Pedlar, J. H., Pope, S. E., Taylor, P. D., & Wegner, J. F. (1995). Effect of road traffic on amphibian density. *Biological Conservation*, *73*, 177–182. https://doi.org/10.1016/0006-3207(94)00102-V

Geospatial Information Authority of Japan (2017). *2017 Area Size by Prefectural Municipalities*. Retrieved from http://www.gsi.go.jp/KOKUJYOHO/MENCHO/201710/f3_shima.pdf

Gerhardt, H. C., Tanner, S. D., Corrigan, C. M., & Walton, H. C. (2000). Female preference functions based on call duration in the gray tree frog (*Hyla versicolor*). *Behavioral Ecology*, *11*, 663–669. https://doi.org/10.1093/beheco/11.6.663

Grace, M. K., & Noss, R. F. (2017). Evidence for selective avoidance of traffic noise by anuran amphibians. *Animal Conservation*, *21*, 343–351. https://doi.org/10.1111/acv.12400

Halfwerk, W., Lea, A. M., Guerra, M. A., Page, R. A., & Ryan, M. J. (2016). Vocal responses to noise reveal the presence of the Lombard effect in a frog. *Behavioral Ecology*, *27*, 669–676. https://doi.org/10.1093/beheco/arv204

Halfwerk, W., & Slabbekoorn, H. (2009). A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. *Animal Behaviour*, *78*, 1301–1307. https://doi.org/10.1016/j.anbehav.2009.09.015

Hartig, F. (2018). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. R package, (2), 6.

Holt, M. M., Noren, D. P., & Emmons, C. K. (2011). Effects of noise levels and call types on the source levels of killer whale calls. *The Journal of the Acoustical Society of America*, *130*, 3100–3106. https://doi.org/10.1121/1.3641446

Hoskin, C. J., & Goosem, M. W. (2010). Road impacts on abundance, call traits, and body size of rainforest frogs in northeast Australia. *Ecology and Society*, *15*, 15.

Kuramoto, M. (1986). Call structures of the rhacophorid frogs from Taiwan. *Scientific Report of the Laboratory for Amphibian Biology*, *8*, 45–68. https://doi.org/10.15027/363

Lengagne, T. (2008). Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. *Biological Conservation*, *141*, 2023–2031. https://doi.org/10.1016/j.biocon.2008.05.017

Lewis, P. T. (1973). The noise generated by single vehicles in freely flowing traffic. *Journal of Sound and Vibration*, *30*, 191–206. https://doi.org/10.1016/S0022-460X(73)80113-0

Lohr, B., Wright, T. F., & Dooling, R. J. (2003). Detection and discrimination of natural calls in masking noise by birds: Estimating the active space of a signal. *Animal Behavior*, *65*, 763–777. https://doi.org/10.1006/anbe.2003.2093

Love, E. K., & Bee, M. A. (2010). An experimental test of noise-dependent voice amplitude regulation in Cope's grey treefrog, *Hyla chrysoscelis*. *Animal Behaviour*, *80*, 509–515. https://doi.org/10.1016/j.anbehav.2010.05.031

Lukanov, S., Simeonovska-Nikolova, D., & Tzankov, N. (2014). Effects of traffic noise on the locomotion activity and vocalization of the Marsh Frog, *Pelophylax ridibundus*. *North-Western Journal of Zoology*, *10*, 359–364.

McGregor, P. K., Catchpole, C. K., Dabelsteen, T., Falls, J. B., Fusani, L., Gerhardt, H. C., … Weary, D. M. (1992). Design of playback experiments: The Thornbridge Hall NATO ARW consensus. In P. K. McGregor (Ed.), *Playback and studies of animal communication* (pp. 1–9). New York, NY: Plenum Press.

Nelson, D. V., Klinck, H., Carbaugh-Rutland, A., Mathis, C. L., Morzillo, A. T., & Garcia, T. S. (2017). Calling at the highway: The spatiotemporal constraint of road noise on Pacific chorus frog communication. *Ecology and Evolution*, *7*, 429–440. https://doi.org/10.1002/ece3.2622

Okamura, H., Watanabe, S., & Watanabe, T. (2000). An empirical study on the capacity of bottlenecks on the basic suburban expressway sections in Japan. *Proceedings of the 4th International Symposium on Highway Capacity*, *12*, 120–129.

Parris, K. M., Velik-Lord, M., North, J. M., & Function, L. (2009). Frogs call at a higher pitch in traffic noise. *Ecology and Society*, *14*, 25. https://doi.org/10.5751/ES-02687-140125

Roca, I. T., Desrochers, L., Giacomazzo, M., Bertolo, A., Bolduc, P., Deschesnes, R., … Proulx, R. (2016). Shifting song frequencies in response to anthropogenic noise: A meta-analysis on birds and anurans. *Behavioral Ecology*, *27*, 1269–1274. https://doi.org/10.1093/beheco/arw060

Schwartz, J. J., & Bee, M. A. (2013). Anuran acoustic signal production in noisy environments. In V. M. Janik, & P. K. McGregor (Eds.), *Animal communication and noise* (pp. 91–132). Berlin, Germany: Springer.

Searle, S. R., Speed, F. M., & Milliken, G. A. (1980). Population marginal means in the linear model: An alternative to least squares means. *The American Statistician*, *34*, 216–221. https://doi.org/10.1080/00031305.1980.10483031

Senzaki, M., Kadoya, T., Francis, C. D., Ishiyama, N., & Nakamura, F. (2018). Suffering in receivers: Negative effects of noise persist regardless of experience in female anurans. *Functional Ecology*, *32*, 2054–2064. https://doi.org/10.1111/1365-2435.13130

Shen, J. X., & Xu, Z. M. (2016). The Lombard effect in male ultrasonic frogs: Regulating antiphonal signal frequency and amplitude in noise. *Scientific Reports*, *6*, 27103. https://doi.org/10.1038/srep27103

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., & Popper, A. N. (2010). A noisy spring: The impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution*, *25*, 419–427. https://doi.org/10.1016/j.tree.2010.04.005

Sun, J. W., & Narins, P. M. (2005). Anthropogenic sounds differentially affect amphibian call rate. *Biological Conservation*, *121*, 419–427. https://doi.org/10.1016/j.biocon.2004.05.017

Taketomi Town (2018). *Taketomi Town population dynamics*. Retrieved from https://www.town.taketomi.lg.jp/userfiles/files/11matu.pdf

Tang, W. (2009). *The chorus sound charateristics and phonotactic behavior of* Buergeria japonica. Tainan City, Taiwan: National Cheng Kung University.

Templeton, C. N., Zollinger, S. A., & Brumm, H. (2016). Traffic noise drowns out great tit alarm calls. *Current Biology*, *26*, R1173–R1174. https://doi.org/10.1016/j.cub.2016.09.058

Tennessen, J. B., Parks, S. E., & Langkilde, T. (2014). Traffic noise causes physiological stress and impairs breeding migration behaviour in frogs. *Conservation Physiology*, *2*, cou032. https://doi.org/10.1093/conphys/cou032

Toledo, L. F., Martins, I. A., Bruschi, D. P., Passos, M. A., Alexandre, C., & Haddad, C. F. (2015). The anuran calling repertoire in the light of social context. *Acta Ethologica*, *18*, 87–99. https://doi.org/10.1007/s10211-014-0194-4

Vargas-Salinas, F., Cunnington, G. M., Amézquita, A., & Fahrig, L. (2014). Does traffic noise alter calling time in frogs and toads? A case study of anurans in Eastern Ontario, Canada. *Urban Ecosystems*, *17*, 945–953. https://doi.org/10.1007/s11252-014-0374-z

Wang, Y. H., Hsiao, Y. W., Lee, K. H., Tseng, H. Y., Lin, Y. P., Komaki, S., & Lin, S. M. (2017). Acoustic differentiation and behavioral response reveals cryptic species within Buergeria treefrogs (Anura, Rhacophoridae) from Taiwan. *PLoS ONE*, *12*, e0184005. https://doi.org/10.1371/journal.pone.0184005

Watanabe, S., Nakanishi, N., & Izawa, M. (2005). Seasonal abundance in the floor-dwelling frog fauna on Iriomote Island of the Ryukyu Archipelago, Japan. *Journal of Tropical Ecology*, *21*, 85–91. https://doi.org/10.1017/S0266467404002068

Wollerman, L., & Wiley, R. H. (2002). Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Animal Behaviour*, *63*, 15–22. https://doi.org/10.1006/anbe.2001.1885

Wood, W. E., & Yezerinac, S. M. (2006). Song sparrow (*Melospiza melodia*) song varies with urban noise. *The Auk*, *123*, 650–659. https://doi.org/10.1093/auk/123.3.650

Zhao, L., Sun, X., Chen, Q., Yang, Y., Wang, J., Ran, J., … Cui, J. (2018). Males increase call frequency, not intensity, in response to noise, revealing no Lombard effect in the little torrent frog. *Ecology and Evolution*, *8*, 11733–11741. https://doi.org/10.1002/ece3.4625

Zollinger, S. A., Slater, P. J., Nemeth, E., & Brumm, H. (2017). Higher songs of city birds may not be an individual response to noise. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170602. https://doi.org/10.1098/rspb.2017.0602

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, *7*, 636–645. https://doi.org/10.1111/2041-210X.12577

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.