

Anthropogenic sounds differentially affect amphibian call rate

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Abstract

The effects of airplane flyby noise and playbacks of low-frequency motorcycle sounds on calling activity were examined in a mixed-species anuran calling assemblage in central Thailand. In response to these stimuli, three of the most acoustically active pond-edge species (*Microhyla butleri*, *Rana nigrovittata* and *Kaloula pulchra*) significantly decreased their calling rate. Yet under the identical stimulus regime, *Rana taipehensis* consistently increased its calling rate. Moreover, during the occasional natural lulls in the chorus in which males collectively stop calling, resulting in a conspicuous reduction in chorus intensity, calls of *R. taipehensis* would appear to emerge from the background noise. These results suggest that man-made acoustic interference may affect anuran chorus behavior either directly by modulating call rates of the chorus participants or indirectly, by suppressing calling behavior of one set of species which in turn stimulates calling in other species. The results of our playback experiment coupled with the natural calling behavior of these species support the latter hypothesis.

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1. Introduction

The past two decades have seen an emergence of interest and concern in the decline of amphibian populations throughout the world (Barinaga, 1990; Wyman, 1990; Ingram, 1990; Blaustein and Olsen, 1991; Blaustein et al., 1994; Marsh and Trenham, 2001). As a direct result, conservationists have concentrated their attention on such potentially negative effects of human activities on amphibians, as habitat modification and destruction, global climate change and chemical contaminants (Blaustein and Wake, 1990; Phillips, 1990; Wyman, 1990; Pechmann et al., 1991; Fahrig et al., 1995; Laurance, 1996; Vos and Chardon, 1998; Alexander and Eischeid, 2001; Hels and Buchwald, 2001; Blaustein and Kiesecker, 2002). Yet one aspect that is poorly understood is the interaction between man-made

sound and amphibian biology. Increased frequency and intensity of sounds produced by airplanes, motorcycles, boats and other vehicles may have deleterious effects on acoustically communicating species. While recent studies have examined the consequences of exogenous sounds on population size and behavior in marine mammals, birds and fish (Richardson et al., 1985; Malme et al., 1988; Richardson and Würsig, 1997; Winker, 2000; Houser, 2001; Perry et al., 2002; Wilson and Dill, 2002; Slabbekoorn and Peet, 2003), very few have explored the effects of man-made acoustical disturbances on amphibians (Barrass, 1985).

This study was motivated by a series of observations of calling behavior in an Old World tropical frog community. At the pond-edge, males of *Rana taipehensis* would exhibit conspicuous vocal sac movements, yet no calls appeared to be emitted. It was not until several other syntopic species drastically reduced their calling rate in response to an airplane flying overhead, that *R. taipehensis* produced a series of rapid, squeak-like calls audible to the human ear.

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The aim of our experiments was to demonstrate the differential effects of anthropogenic sounds on calling rate, and to predict the potential impact they may have on the survival and reproductive success of a multi-species frog community. Because it is well-established that individual reproductive success is directly proportional to calling effort in numerous frog species (e.g., Whitney and Krebs, 1975; Davies and Halliday, 1977; Ryan, 1980; Gerhardt, 1982; Halliday, 1983; Sullivan, 1983; Arak, 1983, 1988; Wells and Schwartz, 1984; Robertson, 1986; Schwartz, 1986; Klump and Gerhardt, 1987; Dyson et al., 1992; Witte et al., 2001), we deduce that anthropogenic sounds that affect calling rate may impact fitness by altering reproductive behavior in this species.

2. Methods

2.1. Study area and focal species

This study was conducted in a small semi-permanent pond located in a semi-evergreen rainforest in Khao Yai National Park, Thailand (14°24'N, 101°22'E, altitude 765 m) from 13 to 22 May 2001. Located about 20 m from a park road, the study site was populated by several species of frogs and toads actively calling at the start of the breeding season. Exogenous sounds, specifically engine noises produced by airplane flyovers, passing motorcycles and automobiles were quite evident at the study site.

At the start of this study, the pond was approximately 15 m long by 10 m wide. Temperatures ranged from 22.5 to 25.5 °C, and relative humidity varied between 85% and 100% throughout the study period. All measurements were taken between 19:30 and 23:30 h when calling was most active.

Rana taipehensis, the focal species of this study, is a small, conspicuous ranid frog present in high densities at the study site. Males call from the pond-edge and are characterized by a snout-vent length of less than 30 mm and the lack of distinct stripes on the inner side of the latero-dorsal folds on the back (Ohler and Mallick, 2002). Both color morphs (green and brown) were actively calling at this site. Like other ranid frogs, this locally abundant species is threatened by the overuse of agricultural pesticides in Asia. Declining numbers have resulted in them being reclassified as “vulnerable” and “threatened” in Taiwan and Hong Kong, respectively (Dahmer et al., 2001).

2.2. Field recordings and playbacks

We recorded calling activity of *R. taipehensis* and several other syntopic frog species before (Fig. 1(a)), during (Fig. 1(b) and (c)) and after lulls in background noise-evoked by airplane overflights and playbacks of motorcycle engine noise. Vocalizations were recorded with an audiocassette recorder (Sony TC-D5M) and directional microphone (Sennheiser ME88) equipped with a windscreen placed within 50 cm of a calling male.

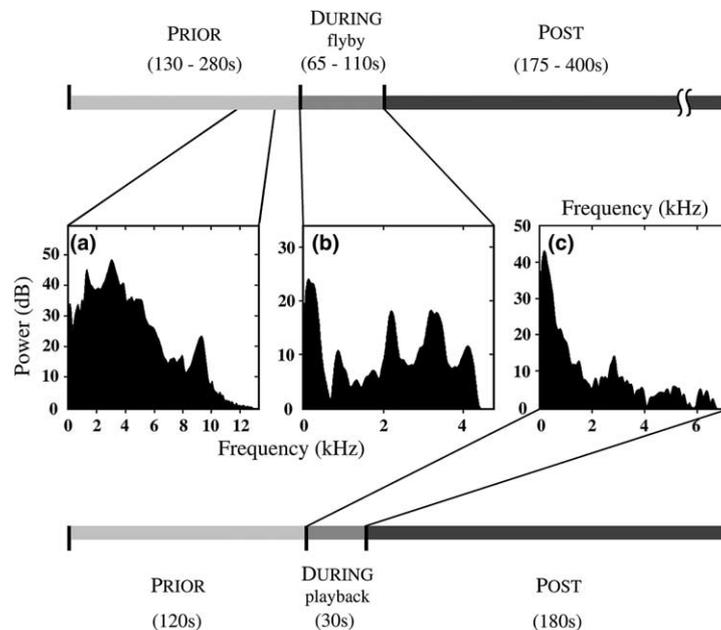


Fig. 1. Observation period prior, during and post-airplane overflight (top time line) and motorcycle stimulus (bottom time line); recording time given in seconds. The power spectra (a) of the ambient noise at the pond prior to flyby, (b) during flyby and (c) of the motorcycle engine noise stimulus are shown. The ambient noise power spectra for the post-stimulus periods (data not shown) are similar to those in (a).

A dynamic stereo headphone (Sony MDR-V250) was used to monitor recordings.

To capture call rate changes of *R. taipehensis*, it was necessary to find a stationary male vocalizing for an extensive period of time. Because both the time of occurrence and the duration of the airplane flyby were unpredictable, recording times differed for each individual frog (Fig. 1(b)). A portable sound level meter (Realistic 33–2050, C-weighting) was used to measure the overall intensity of the background noise of the pond before, during and after a passing plane.

To study the vocal response of *R. taipehensis* to more locally generated anthropogenic noise, a playback stimulus was created by holding a directional microphone (Sennheiser ME88) connected to an audiocassette recorder (Sony TC-D5M) 1 m away from a running motorcycle engine. Playback of this high-intensity, low-frequency sound (duration 29.7 s) complemented the airplane flyby observations and was used to experimentally induce call rate modulation of the frog species at the pond. Prior to presenting the stimulus, a microphone was placed within 3–5 cm of a focal male to record its spontaneous calling for 120 s. The stimulus was then broadcast from a powered speaker system (Sony SRS-A21) placed 1 m from the male under test (Fig. 1(c)). Playback levels were adjusted by ear to simulate, as nearly as possible, actual motorcycle engine noise levels. Recording continued for 180 s post-playback.

2.3. Data analysis

Representative recordings from six individuals were chosen to characterize vocalizations of *R. taipehensis*. Call structure and parameters were examined using Canary software (version 1.2.4, Cornell University, Laboratory of Bioacoustics). Sound spectrograms of the calls were constructed using a 699.40 Hz analysis filter bandwidth and clipping levels set to –80 dB.

To analyze the vocal behavior of individual frogs during an airplane- or experimentally-induced lull in background noise, calls emitted in the time periods before, during and after an airplane flyby or playback of the motorcycle stimulus tape were displayed (Wild-Spectra v. 001217) and counted. Calling rate was then calculated and graphed for each time period. To assess overall response differences in calling rate before, during and after the acoustic stimulus, we used a Friedman's non-parametric ANOVA test (SPSS 10.0). When significant differences were detected, a Wilcoxon signed-ranks test (two-tailed) was used to specify which time periods differed. We used the same procedure to measure calling rate of *R. taipehensis* and the dominant background species (DBS) to make direct comparisons between their call rates during a flyby- or a playback-evoked lull.

3. Results

3.1. Flyby-evoked lull

Background noise levels at the pond were taken on the second and third night of recordings when four airplanes flew overhead. In the absence of airplanes, the overall sound level measured 1 m above the pond-edge ranged from 80 to 86 dB SPL peak. During four airplane flyovers, the sound levels at the pond dropped to a minimum of 76, 70–72, 70–72, and 68 dB SPL peak, respectively.

A total of seven airplane overflights was observed in the field (average duration = 91.1 ± 18.0 s). Call rates of *R. taipehensis* significantly differed in time periods before, during and after airplane overflights (Friedman's test, $\chi^2 = 10.89$, $df = 2$, $P = 0.004$, $n = 7$). Males increased calling rate during overflights as opposed to periods before (Wilcoxon signed-ranks test: $Z = 2.366$, $P = 0.018$) or after ($Z = 2.366$, $P = 0.018$). *Microhyla butleri*, the dominant background species in most cases, also responded differently in the three time periods (Friedman's test, $\chi^2 = 7.6$, $df = 2$, $P = 0.022$, $n = 5$), but instead, called less during the overflight than periods before (Wilcoxon signed-ranks test: $Z = 2.023$, $P = 0.043$) or after ($Z = 2.023$, $P = 0.043$). Overall, as a group, the two recorded dominant background species (*M. butleri* and *Rana nigrovittata*) called at lower rates during airplane overflights than periods before or after (Friedman's test, $\chi^2 = 10.57$, $df = 2$, $P = 0.005$, $n = 7$; Wilcoxon signed-ranks test: $Z = 2.366$, $P = 0.018$) (see Fig. 2).

3.2. Motorcycle-evoked lull

Fig. 1(c) shows the sound spectrum of the motorcycle playback stimulus. The motorcycle engine noise is composed of a series of broadband clicks, each encompassing a frequency range between 0 and 7 kHz. The dominant energy in this stimulus was below 500 Hz.

In all playback experiments, *R. taipehensis* exhibited overall call rate differences in periods before, during and after a motorcycle playback was presented (Friedman's test: $\chi^2 = 28.8$, $df = 2$, $P < 0.001$, $n = 19$). Males significantly increased their calling rate in the post-stimulus period compared to the pre-stimulus period (Wilcoxon signed-ranks test: $Z = 3.826$, $P < 0.001$). Calling rates were also different for the dominant background species (*M. butleri*, *Rana miopus* and *R. nigrovittata*) in the three time periods (Friedman's test: $\chi^2 = 16.53$, $df = 2$, $P < 0.001$, $n = 19$), decreasing their calling rate during the stimulus compared to pre- (Wilcoxon signed-ranks test: $Z = 3.705$, $P < 0.001$) or post- ($Z = 3.101$, $P < 0.001$) stimulus calling activity (Fig. 3).

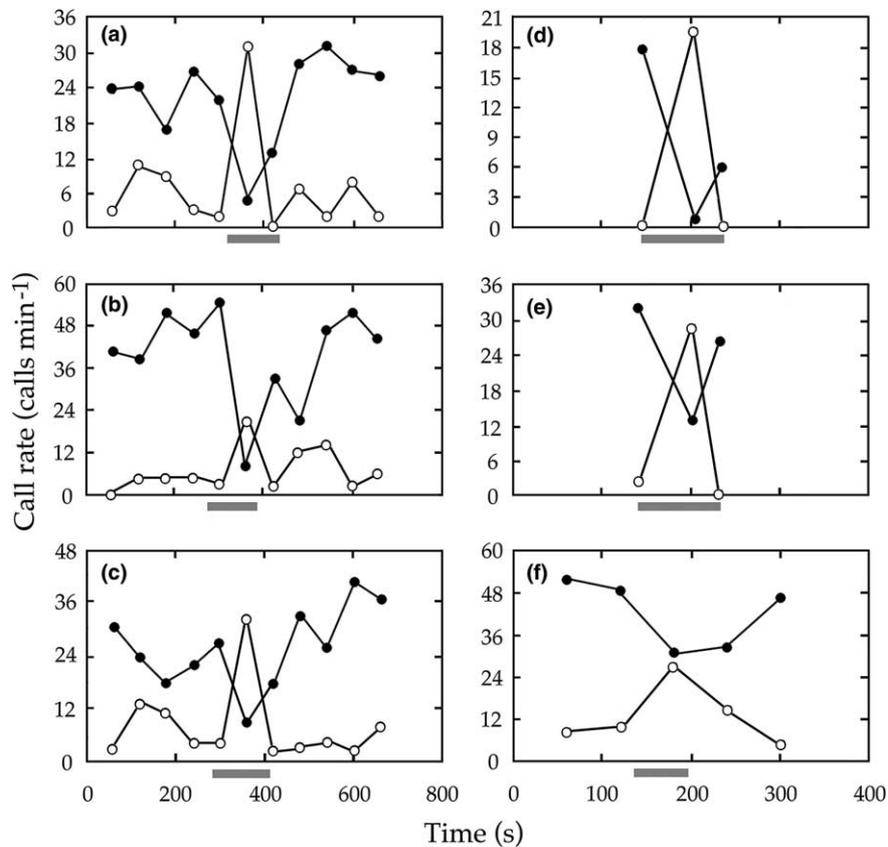


Fig. 2. Representative calling rates prior to, during and after an airplane overflight (black bars) for *R. taipehensis* (○) and the dominant background species, DBS (●): (a)–(d) *M. buleri*; (e)–(f) *R. nigrovittata*. Since flyby durations were unpredictable, recording times varied as well.

3.3. Vocal repertoire

Because south-east Asian ranid frogs typically exhibit a high-degree of color polymorphism (P.P. van Dijk, pers. commun.), we treated the two color morphs of *R. taipehensis* operationally as one population of the same species. All calls in Fig. 4 are present in the vocal repertoire of both color morphs. Within this repertoire is a continuum of calls containing frequency components ranging from 0.5 to 9.5 kHz (Fig. 4). Clearly influenced by the background noise level in the pond, *R. taipehensis* produced certain calls at different times. At background sound levels ≥ 80 dB SPL, males emitted multi-harmonic calls with a duration range from approximately 20 to 70 s (Fig. 4(f), (h) and (i)). However, during noise lulls evoked by airplane overflights, males of *R. taipehensis* almost exclusively produced a series of rapid, low-intensity squeak-like calls. (Fig. 4(a)–(d) and (g)). For instance, of 42 low-intensity squeaks produced by an individual calling male, 39 were emitted during airplane flybys when ambient noise dropped by 11 dB relative to the time period prior to or post-flyby. In playback experiments, calling rates for low-intensity squeaks differed in different time periods (Friedman's test: $\chi^2 = 34.02$, $df = 2$, $P < 0.001$, $n = 19$). Males increased squeak calling rates in the post-stimulus period

relative to the time period before (Wilcoxon signed-ranks test: $Z = 3.904$, $P < 0.001$) or during ($Z = 3.904$, $P < 0.001$) playback. Other calls were produced only infrequently, regardless of background noise levels (e.g., Fig. 4(e)).

4. Discussion

Anurans have been generally promoted as reliable indicators of environmental degradation (Barinaga, 1990; Andreone and Luiselli, 2000). The results presented here illustrate anurans' sensitivity to noise pollution. Specifically, the emission of anthropogenic sounds has led *R. taipehensis* and other frogs in this pond community to exhibit rather novel calling behavior in response to a complex and dynamic acoustic environment.

4.1. Call parameters

Our findings suggest that successful communication among *R. taipehensis* is facilitated by the design and structure of their call notes. In multi-species calling assemblages of anuran amphibians, background noise levels may reach 86 dB SPL or higher, measured at 1 m,

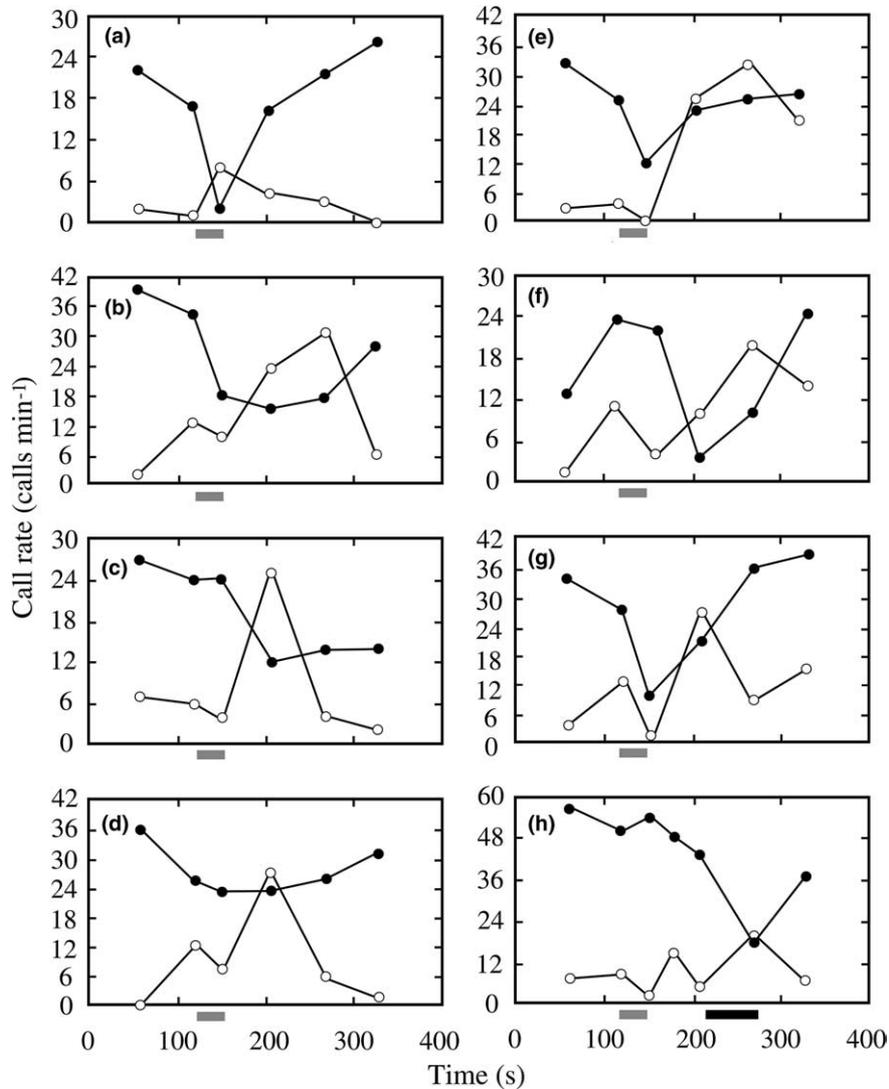


Fig. 3. Representative calling rates for *R. taipehensis* (○) and the dominant background species (DBS) (●): (a), (f) and (g) *M. butleri*; (b)–(d) *K. pulchra*; (e) *R. miopus*; (h) *R. nigrovittata*, prior to, during and after a motorcycle stimulus (gray bar) was broadcast from one meter above the calling male. In (h), *R. taipehensis* increased its calling rate following the relatively short duration motorcycle stimulus and again during an unexpected, longer airplane flyby (black bar) while the DBS responded to the latter stimulus with a greatly reduced calling rate.

representing a formidable obstacle for species-specific communication (Narins, 1982; Schwartz and Wells, 1983a,b; Wells, 1988; Wollerman and Wiley, 2002; this study). Therefore, heterospecific background noise could mask a male’s advertisement call and diminish its ability to communicate readiness for mating (Wells, 1977; Narins and Capranica, 1976; Wells and Greer, 1981; Gerhardt and Schwartz, 1995). To avoid this, some male frogs have adopted a series of repetitive clicks or short notes that contrast acoustically with the background noise (Schwartz and Wells, 1984), much like the repetitious, low-intensity short calls emitted by *R. taipehensis* (Fig. 4(a) and (g)). The contrast would therefore, aid females in detecting and localizing males more efficiently. Repeating call notes also increases the probability of their detection in noisy environments (Narins, 1982; Wiley and Richards, 1982).

4.2. Calling strategy: temporal and spectral separation

Additional means for ensuring successful acoustic communication in noisy environments include reducing acoustic interference by temporal and spectral separation (Narins, 1982; Drewry and Rand, 1983; Gerhardt and Schwartz, 1995; Garcia-Rutledge and Narins, 2001). Each airplane flying overhead or motorcycle passing by on the park road, triggered a dramatic reduction in the intensity of the background noise at the pond. Increased calling of *R. taipehensis* in response to lulls in background noise-evoked by exogenous sounds may be viewed as short-term temporal separation, one of several adaptive behaviors for avoiding acoustic interference. Since *M. butleri* males possess high-intensity advertisement calls and are particularly sensitive to the sounds produced by airplane flybys, reduction in their call rate

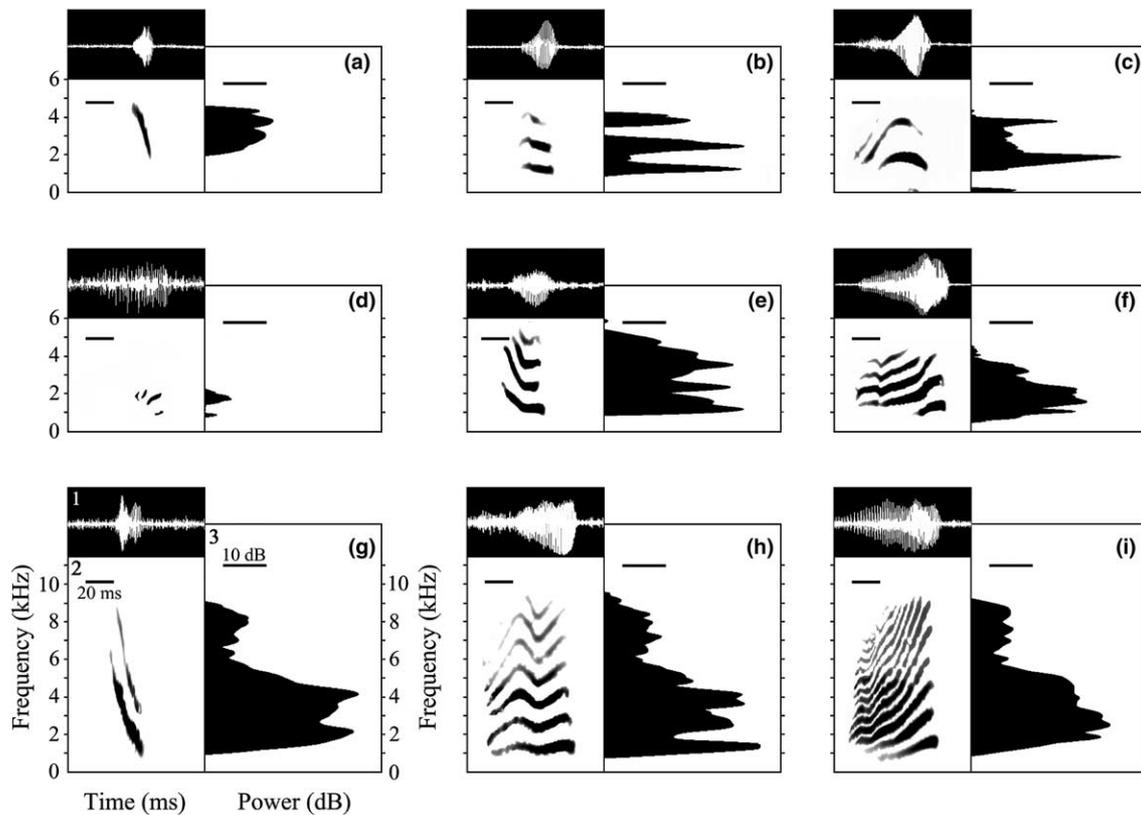


Fig. 4. Spectrographic analysis of nine representative vocalizations from the vocal repertoire of *R. taipehensis*. For each call type, the waveform (amplitude vs. time) is shown in (1), the spectrogram (frequency vs. time) in (2) and the power spectrum (power vs. frequency) in (3). The 20-ms time scale bar applies to both panels (1) and (2). See text for analysis settings. Temperature during all recordings ranged from 22.5 to 25.5 °C. Low-intensity calls (a)–(d) and (g) were produced primarily during lulls in background noise whereas higher-intensity calls (f), (h), and (i) were exclusively produced in ambient sound levels greater than 80 dB SPL. Call (e) was produced at all background sound levels.

contributes significantly to the decrease in overall background sound level. As a result, noise levels at the pond during airplane overflights were the lowest measured. In contrast, when lulls were artificially evoked by the (relatively short duration) motorcycle engine playback stimulus, noise levels were lowest immediately following the stimulus. In both these situations, *R. taipehensis* individuals increased their calling rate in response to transient lulls in ambient sound levels, and in doing so, may have improved their chances of being detected. Experiments with New World frogs *Eleutherodactylus coqui* and *Hyla ebraccata* have demonstrated similar behavior. For example, males of *E. coqui* will preferentially place their calls in the period immediately following reductions in background noise level as small as 2 dB (Zelick and Narins, 1983). In addition, in some mixed-species assemblages, *Hyla microcephala* inhibit calling activity of *H. ebraccata* males (Schwartz and Wells, 1983a,b; Gerhardt and Schwartz, 1995).

Spectral separation may also reduce acoustic interference, and partially explain the lack of calling rate reduction by *R. taipehensis* during a flyby. Several workers have demonstrated that spectral partitioning of advertisement calls in mixed-species anuran breeding

communities may contribute to reduction in cross-species acoustic interference (Drewry and Rand, 1983; Zimmerman and Bogart, 1988; Garcia-Rutledge and Narins, 2001). It is clear that *R. taipehensis* is able to distinguish itself acoustically by occupying a much higher-frequency calling niche than most if not all other frog species in the local pond community. We suggest that the increased calling during airplane flybys may be related to its high-frequency call. Because seismic vibrations generated from a passing airplane are likely to be sub-threshold due to the impedance mismatch between the air and the substrate, the assumption was made that it is the low-frequency airborne sounds from the airplane engine that suppressed calling in most other species of frogs. These sounds likely inhibit calling of frogs sharing a frequency range similar to the airplane engine (Zelick and Narins, 1983; Wollerman, 1999). As the airplane (or low-frequency) sound diminishes, most species at the pond gradually resume their pre-stimulus calling rates. Males of *R. taipehensis* increase their calling rate when they detect a drop in sound level during heterospecific call reduction.

However, males of *R. taipehensis* did not increase their calling rate during low-frequency playback, but

rather following the broadcast of the low-frequency stimulus. In one fortuitous playback experiment, an airplane flew overhead about 1 min after the motorcycle stimulus was broadcast, thereby creating two noise lulls in succession (Fig. 3(h)). Prior to the flyby, the stimulus was delivered and as expected, the focal male increased his calling rate. Approximately 1 min later, he had lowered his calling rate to pre-stimulus levels. When the airplane flew overhead, males of the dominant background species (*R. nigrovittata*) dramatically decreased their calling rate, and the focal male increased his calling rate once again. Such results suggest that males of *R. taipehensis* are not necessarily detecting a drop in the background noise level of the pond as a whole, but rather a decrease in the noise generated by frogs calling within their vicinity. By using a speaker to broadcast the motorcycle recordings during playback experiments, we created a noisy area surrounding the calling male which may have directly inhibited his calling during the stimulus. In addition, calling males of *Kaloula pulchra* significantly decreased their calling rate during the playback, so that when the motorcycle playback ended, there was a slight lull in background noise before these frogs increased calling rates back to pre-stimulus levels. By placing their calls in the relatively quiet interval following the motorcycle playback, *R. taipehensis* increased the probability of its call being detected. The observed calling behavior could also be due, in part, to the relatively short duration of the playback stimulus (29.7 s) in comparison to airplane overflights (average duration = 91.4 ± 17.6 s, $n = 7$). In other words, *R. taipehensis* may have increased calling during the playback period if the stimulus and average airplane overflight durations had been comparable.

4.3. Implications for conservation

Changes in amphibian calling behavior in response to airplane and motorcycle noises are a clear indication of the effect of the anthropogenic noise stemming from the growing number of vehicles throughout the world. Despite the empirical difficulties in linking human activity to changes in animal behavior, industrial sounds have already been shown to alter migration patterns, mating and communication in several species of whales, fish and other aquatic life (Richardson et al., 1985; Houser et al., 2001; Patenaude et al., 2002; Wilson and Dill, 2002), suggesting a potential need to limit human aquatic activity. Birds have also shown a response to urban noise pollution by singing at a higher minimum frequency to prevent call masking (Slabbekoorn and Peet, 2003). While the direct consequences of vehicles on amphibians, such as road kills have been examined (Fahrig et al., 1995; Hels and Buchwald, 2001), the acoustical effects of these man-made machines remain poorly understood. To the best of our knowledge, only one study of the

effect of highway traffic noise on amphibian reproductive behavior in two North American frog species, has been conducted (Barrass, 1985).

Although our results reveal a relationship between exogenous sounds and changes in calling behavior, causative links to changes in reproductive success and survival have yet to be demonstrated in this species. However, previous experiments have successfully linked calling effort with increased fitness, leading us to believe that similar principles can be applied to the pond community we studied in Thailand. The reduction in heterospecific calling evoked by man-made sounds may be indirectly increasing *R. taipehensis*'s likelihood of mating while simultaneously reducing that of other species. Perhaps this helps explain why this species is not only able to survive in an acoustically formidable environment, but reproduces rather successfully as reflected in the high-density of calling males at the study site.

To date, conservation studies have focused predominantly on the detrimental impact of humans on the environment. Few of these have addressed the consequences of anthropogenic sounds on animal populations, and even fewer have examined them in amphibians. Our experiments not only document the impact of exogenous sounds on anuran amphibian choruses, but also bring to light the possibility of a human disturbance differentially affecting members of a multi-species community. Future long-term studies that correlate individual calling levels with reproductive success in human-affected amphibian populations are needed to determine the quantitative fitness consequences of anthropogenic sounds and thus better inform management policies.

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Appendix A. Density measurements

A square wooden frame measuring 30.5 cm on a side was placed at 34 sampling points around the pond on

five consecutive nights. To determine density, the number of frogs of each species present within the borders of the frame at each sampling point was counted. The density of each species at all 34 points was calculated and an average density was determined by taking mean values for each species over five nights.

Our results show that *R. taipehensis* and *M. butleri* had the highest average density values per sampling plot around the pond (13.9 and 3.4 frogs m⁻², respectively) for five nights. Other species recorded had relatively lower average densities: *Polypedates leucomystax* (0.8 frogs m⁻²), *Microhyla heymsi* (0.7 frogs m⁻²), *R. nigrovittata* (0.3 frogs m⁻²), *Occidozyga lima* (0.2 frogs m⁻²), *Kaloula pulchra* (0.1 frogs m⁻²), *Philautus hanseanae* (0.1 frogs m⁻²) and *Philautus nongkhorensis* (0.1 frogs m⁻²).

Post-hoc comparisons revealed that the densities of *R. taipehensis* and *M. butleri* are significantly higher than the other seven species of frogs calling at the pond. Nevertheless, there is a significant difference between the densities of *R. taipehensis* and *M. butleri* ($P = 0.001$). No one sampling plot had a significantly different density than any other sampling plot ($P > 0.05$); thus, density was sampling plot-independent.

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