

Ultrasonic frogs call at a higher pitch in noisier ambiance

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Abstract The ultrasonic communication in Concave-eared torrent frogs *Odorrana tormota* is believed to be an adaptation to avoid masking by the intense low-frequency noise of the rushing stream in their habitat. The acoustic adaptation hypothesis for ultrasonic origin predicts that some organisms subjecting to persistent acoustic interference from broadband, low-frequency environmental noise, might shift their signal frequency upward into frequency bands with lower noise energy. In other words, low-frequency environmental noise might cause upward shifts of species' vocalization frequencies making their signals more conspicuous. Presently, it is unclear whether male *O. tormota* adjust their signal features in response to a change in the ambient noise level. We tested the prediction of the acoustic adaptation hypothesis by recording the vocalizations of male *O. tormota* inhabiting two streams with different background noise levels in Huangshan in central China and comparing their call features including the fundamental frequency (F0). Results showed that the spectrotemporal characteristics of the vocal signals of males in the two habitats were indifferent, except the duration of the call harmonic segments and three parameters related to the call fundamental frequency (F0). In terms of the F0, the pooled and individual frog data showed that frogs inhabiting the noisier habitat tended to emit calls having higher F0. The higher F0 increases the signal-to-noise ratio, thus benefiting the detection of vocalization. Thus, similar to several anuran species, concave-eared torrent frogs also display noise-dependent adjustment of vocal pitch in their vocalizations for making them more audible [Current Zoology 61 (6) : 996–1003, 2015].

Keywords Acoustic adaptation, Ambient noise, *Odorrana tormota*, Sound communication

Sound communication plays a vital role regulating the reproductive behavior of various animals from anurans, to birds and mammals (Ryan, 1985). For this communication to be effective, senders must emit signals that are conspicuous and distinct from other biotic sound, such as the signals produced by heterospecifics and conspecifics, as well as abiotic sound, such as the sounds associated with wind, water streams, and traffic on roads, etc. (Feng and Schul, 2007; Brumm and Naguib, 2009). Also, the signals emitted must be robust enough to withstand degradation during propagation (Vargas-Salinas and Amézquita, 2013).

The sound produced by rapidly flowing water represents a major source of background noise for anurans inhabiting alongside streams. When the noise spectrum overlaps with that of frog calls, masking may disrupt information transfer between senders and receivers, and communication may break down (Nemeth et al., 2013). To increase the signal-to-noise ratio, males of those species could simply increase the intensity of their calls, but calling louder is energetically very costly (Love and Bee, 2010). Alternatively, as the sound energy of stream-generated noise is concentrated at low frequencies (Dubois and Martens, 1984), to conserve energy,

stream-breeding anurans may adapt to stream noise by evolving high frequency calls (Feng et al., 2006; Boekle et al., 2009).

It has been suggested that long-term adaptation to habitat-specific noise, especially to persistently high level low-frequency background noise, may be a powerful selective force causing upward shifts of vocalization frequencies among species (Slabbekoorn and Peet, 2003), which effectively increases the signal-to-noise ratio of their vocal signals (Arch and Narins, 2008). Indeed, studies in *O. tormota* have revealed that males of this species have evolved calls whose harmonics extend well into the ultrasonic range and specialized ear structure and auditory sensitivity to ultrasound which enable them to communicate acoustically in the presence of intense but predominantly low frequency stream noise (Narins et al., 2004; Feng et al., 2006; Shen et al., 2011). The acoustic adaptation hypothesis predicts that long-term exposure to low-frequency background noise might result in upward shift in vocalization frequencies. We opted to test this prediction, namely, that male *O. tormota* evolve calls at higher frequencies at elevated ambient noise level.

Results of earlier studies on acoustic adaptation in

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anurans have been mixed. Parris and colleagues (2009) reported that southern brown treefrogs call at a higher pitch amidst traffic noise (Parris et al., 2009). For two lineages of poison frogs living along noisy streams, males closer to the stream emit calls at higher frequencies compared to those living away from that noise source (Vargas-Salinas and Amezcuita, 2013). In contrast, other studies looking for acoustic adaptation to environmental conditions have produced negative results (Penna and Solis, 1998; Kime et al., 2000; Penna et al., 2006; Jang et al., 2011). Thus, unlike avian (Brumm and Slabbekoorn, 2005), acoustic adaptation is not uniform across anuran species and likely species dependent. We expect our study to also contribute to the body of literature on acoustic adaptation in anurans. In the present study, we compared the vocalizations of male *O. tormota* occupying habitats with differential noise characteristics and we predict that the call frequency of males is adaptive to the ambient noise level, similar to the condition reported in southern brown treefrogs and the poison frogs (Parris et al., 2009; Vargas-Salinas and Amezcuita, 2013).

1 Materials and Methods

1.1 Study sites

We recorded the advertisement calls of male *O. tormota* along two parallel streams having differential ambient noise levels, i.e., Fu Creek and Taohua Creek, in Huangshan (a mountain in Anhui Province in Central China) during the months of April through May. The two study sites were: Site-1 - Fu Creek; 118° 8' 44.89", 30° 5' 1.61" N; Elevation: 600 m; Site-2 - Taohua Creek; 118° 10' 8.45", 30° 6' 10.19"; Elevation: 640 m. The local ambient temperature and humidity fell in the same narrow ranges, namely, from 15.5 to 19.0°C and from 38% to 100%, respectively. During the study period, male concave-eared torrent frogs called practically nightly between 18:30 and 24:00 h from low-level vegetations and boulders along short stretches of the respective streams.

Along each stream, we identified 6–8 segments where males tended to aggregate nightly; these segments were separated by a distance of over 50 m. Each segment had its characteristic rock formations and rapids, and therefore its own noise characteristics. At each segment, we recorded as many calls as possible from 1–2 males over the 5+ hours of a single night. Afterward, the frog's snout vent length was measured with a calliper, and the frog was released to the wild. In instances where more than one male vocalized concur-

rently at a calling locus we used simultaneous video recordings (see below) to sort their vocal signals. To minimize the possibility of repeated sampling from any one frog, no further recordings were carried out at that segment in the ensuing evenings.

1.2 Sound recordings

Males' calls were recorded using a digital audio recorder (Sound Devices 702, Sound Devices, WI, USA; frequency range: 10 Hz–96 kHz) and a miniature omni-directional condenser microphone with a flat frequency response over 20–20,000 Hz and a drop of a mere 10 dB at 30,000 Hz (AKG model C417, AKG Acoustics, Vienna, Austria), using a sampling rate of 96 kHz and 16-bit accuracy. The AKG microphone was chosen over an extra wideband condenser microphone in light of its reliable performance in high humidity environments. Use of the AKG microphone has no effect on the measurements and comparisons of the basic spectral and temporal characteristics of the calls of different individuals of *O. tormota* (for which the call fundamental frequency is below 10 kHz); the only impact was on measurements and comparisons of the call's higher harmonics beyond 20 kHz, but this was not a focus of the present study.

During the recording sessions, oral comments were made to the same recording track with particular attention paid to the identity of the vocalizing frog. When multiple frogs emitted calls from the vicinity of a calling male, the frog's vocal behavior was additionally captured on a camcorder (Canon HF M40). Sorting was made post hoc for verification of signal source.

1.3 Call analysis and noise analysis

Methods of call analysis adhered to that of Feng et al. (2009). Briefly, initial analysis of vocal signals was based on narrow-band spectrogram of the signal using SELINA, a custom-designed software program (Feng et al., 2006; Shen et al., 2008). Criteria for categorizing a call into a unique entity (i.e., call-type) were the call duration, F0 range and the presence of small interruptions (breaks). Breaks are periods of silence of 10–200 ms; breaks longer than 200 ms were taken as gaps between separate calls. If one or more breaks were present the call was categorized as a multi-note call type. Two of the call-types were categorized as 'long calls', comprising high-intensity single- and multi-note calls having a duration of > 200 ms. As long calls carry individual signatures (Feng et al., 2009), we focused all our further analysis on long calls.

The ambient noise levels of the frog's calling loci along Fu Creek and Taohua Creek were recorded nightly.

From the recorded noise signals, we measured the peak noise level at each locus using SELINA, through analytical comparison of the peak spectral level in the ambient noise with that of a “standard” signal (1 kHz, 94 dB SPL RMS, or 97 dB SPL peak) from a sound level calibrator (Bruel and Kjaer, 4230). From these measurements we obtained the average ambient noise levels of the various calling loci within the two study sites for the duration of the study. The level and power spectrum of stream noise varied with the location along the stream, the proximity of rapids, the steepness of the ravines on its banks, as well as the weather – a rain locally, or at higher elevation, increased the rush of water stream markedly, thereby elevating the noise level and broadening its bandwidth.

We first identified the different temporal segments of a call on the basis of their acoustic regimes with PRAAT (Boersma and Weenick, 2008). Segmentation was based on visual inspection of narrowband spectrograms and associated Fourier frequency spectra. Segment borders were positioned at the boundaries between different dynamic regimes (see details in Feng et al., 2009). Regimes were categorized as no phonation, harmonic phonation, subharmonics, biphonation, deterministic chaos and breaks (for definitions see Feng et al., 2009). After segmentation was completed, the time and frequency of occurrence of each segment were noted. In addition, total call duration, duration of the breaks, and durations of the harmonic, subharmonic, biphonic and chaotic segments were measured (all in ms).

For each harmonic segment, the F0 was tracked using the ‘pitch tracking’ mode in PRAAT at 1-ms intervals. F0 analysis was not carried out for nonlinear segments, thus F0 values in a call refer strictly to the F0 in the harmonic segments. The mean, maximum and minimum F0, and the difference between the maximum and minimum values (and together with 6 temporal parameters for complete sake) were measured for each call.

1.4 Statistical analysis

The goal of the present study is to determine whether or not the frequency of frog’s vocal signals is higher with increasing background noise level. For this, we compared the vocal signals, with a focus on the call frequency, of male *O. tormota* along a creek (Fu Creek - Site-1) to those along a second creek (Taohua Creek - Site-2). The call data for the Fu Creek were derived from seven males and those from the Taohua Creek from eight males. The data for each creek were initially

pooled to obtain the grand averages – the averages for the two creeks were then compared.

We first calculated and compared the within-creek (CV_w) as well as the inter-creek (CV_b) coefficients of variation for each acoustic parameter. We next performed univariate ANOVAs to determine which if any of the various call parameters for the two creeks differed significantly. As one of the acoustic parameters that differed significantly between the two creeks was F0, we additionally performed post hoc Tukey’s HSD (Honest Significance Difference) test to validate the statistical difference in the F0s.

To assess whether the difference in F0 is related to a difference in the background noise level, we pooled the F0 data from individual males and plotted the average F0 for each frog against the average background noise level at its calling locus. We then employed an ANCOVA model to perform a linear regression of these data in order to determine whether there was a correlation between the F0 and the background noise level.

2 Results

Representative sound spectrograms and power spectra of the ambient noise for the two study sites are shown in Fig. 1. A constant feature of the power spectra is showing a peak at below 240 Hz (range: 44–234 Hz at Site-1; 19–39 Hz at Site-2), with a progressive decay in energy with increasing frequency. The average peak noise level at Site-1 (67.32 ± 4.856 dB SPL; range: 62.0–77.6 dB SPL) was ~ 7 dB higher than that at Site-2 (60.27 ± 4.21 dB SPL; range: 55.7–68.2 dB SPL).

Similar to frog calls recorded from the Taohua Creek (Feng et al., 2009), the vocal signals of male *O. tormota* along Fu Creek were diverse and could be classified into seven distinct call-types: single- and multi-note calls having short (< 200 ms) or long (> 200 ms) duration, low-level ‘meow’ calls, low-level ‘infant’ calls and staccato calls. Our subsequent analysis focused on single- and multi-note long calls (Fig. 2) – these are high-intensity calls having a total call duration of > 200 ms.

The long calls were heterogeneous, as evidenced by the large values of CV_w for all acoustic parameters examined (Table 1). Among the acoustic parameters analyzed, two temporal parameters (i.e., total duration and duration of harmonic segments) and four spectral parameters (i.e., average F0, $F0_{\min}$, $F0_{\max}$, and $F0_{\max} - F0_{\min}$) had CV_w of $< 25\%$, indicating that these were relatively less variable compared to the other parameters. As shown in Figure 2, the timing, the duration, and the frequency of occurrence of harmonic and nonlinear

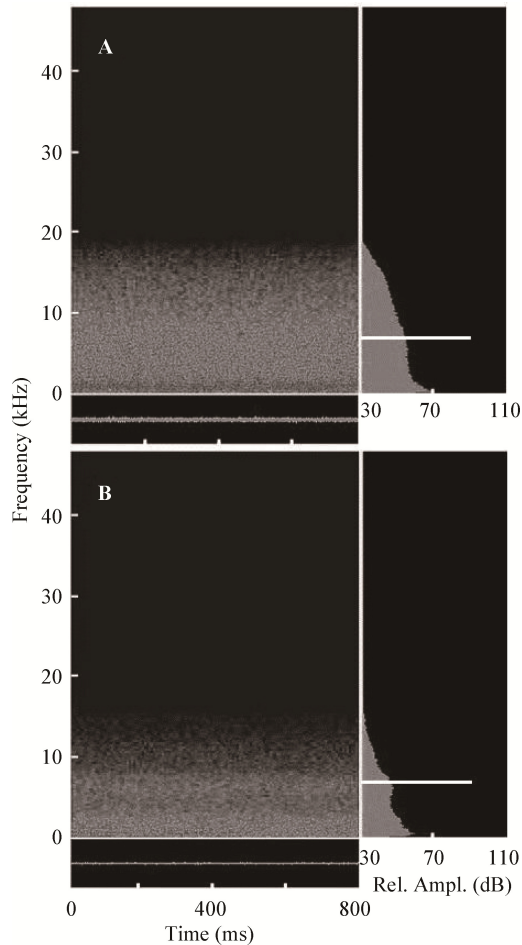


Fig. 1 Ambient noise at the two study sites

Shown are representative sound spectrograms (top left panel), waveforms (bottom panel), and power spectra (top right panel) of the ambient noise at Site-1 (**A**) and Site-2 (**B**). The ambient noise is dominated by the sound of the rushing mountain stream and therefore its level, bandwidth and power spectra vary with the onset of rain locally or at higher elevations. A constant feature of the power spectra is having a peak at below 240 Hz, with a progressive decay in energy with increasing frequency. In the power spectra panel of Site-1 (**A**) and Site-2 (**B**), we inserted a hypothetical tone of 7 kHz at ~ 90 dB SPL (approximating a frog call at this frequency) for the purpose of illustrating how an upward shift in the call frequency effectively increases the signal-to-noise ratio.

segments (namely, subharmonic, chaos, frequency-jump and biphonation) and of segment-breaks, varied greatly from one call to the next. Also, the depth, rate and pattern of frequency modulation were highly variable.

A comparison of CV_w and CV_b of long calls for the two creeks revealed that CV_b/CV_w were near unity for four of six temporal parameters and one spectral parameter, indicating that for them, the variations between creeks having differential background noise levels were no greater than the within-creek variations. In contrast, for two temporal parameters (i.e., total duration and duration of harmonic segments) and three parameters

associated with F_0 (i.e., the average F_0 , $F_{0_{\min}}$, and $F_{0_{\max}} - F_{0_{\min}}$), they had a ratio of > 1.14 , indicating that they may be specific to the creek.

Univariate ANOVAs of long calls of individual frogs from the two creeks ($n = 7$ from Site-1 and $n = 8$ from Site-2) revealed that, other than the duration of the harmonic segments, all temporal parameters (i.e., the total call duration and the durations of breaks, subharmonic, chaotic and biphonic segments) were statistically similar (Table 2). In contrast, other than the $F_{0_{\max}}$, all spectral parameters associated with F_0 , i.e., the average F_0 , $F_{0_{\min}}$, and $F_{0_{\max}} - F_{0_{\min}}$, differed significantly. In particular, the average F_0 for Site-1 (7.75 ± 0.92 kHz) was 1.11 kHz higher than that for Site-2 (6.64 ± 0.93 kHz). Post hoc Tukey's HSD test showed that the average F_0 s for the two creeks with differential background noise levels were significantly different ($F = 124.75$; $P < 0.001$).

It is possible that the differences in F_0 parameters are related to differences in the background noise levels at the recording loci. To assess this possibility we pooled the F_0 data from 15 males and plotted the average F_0 for individual frogs against the average background noise level at the frog's calling locus (Fig. 3). The linear regression of such scatter plot showed that there was a trend for the F_0 to increase with increasing background noise level ($P < 0.05$).

3 Discussion

For the animals that use sound to communicate, as shown in several species of birds and frogs (Slabbekoorn and Peet, 2003; Narins et al., 2004; Feng et al., 2006; Parris et al., 2009; Nemeth and Brumm, 2009; Vargas-Salinas and Amezcuita, 2013), modulation of frequencies at noisy locations was one of the solutions to the problem of acoustic signal masking (Schuster et al., 2012). Moreover, noise-related changes in signal structure are found on different timescales from evolutionary to ontogenetic adaptation (Brumm and Slabbekoorn, 2005; Luther and Baptista, 2010). This adaptation represents an evolved response and allows animals to communicate effectively in the presence of intense ambient noise.

Our study shows that the spectrotemporal characteristics of vocal signals of male *O. tormota* along two separate creeks in the mountain range of Huangshan are similar in various aspects. The divergence occurs primarily in the spectral domain, i.e., in the average F_0 , $F_{0_{\min}}$, and $F_{0_{\max}} - F_{0_{\min}}$ (Table 2). In the time domain, only the duration of the harmonic segments is

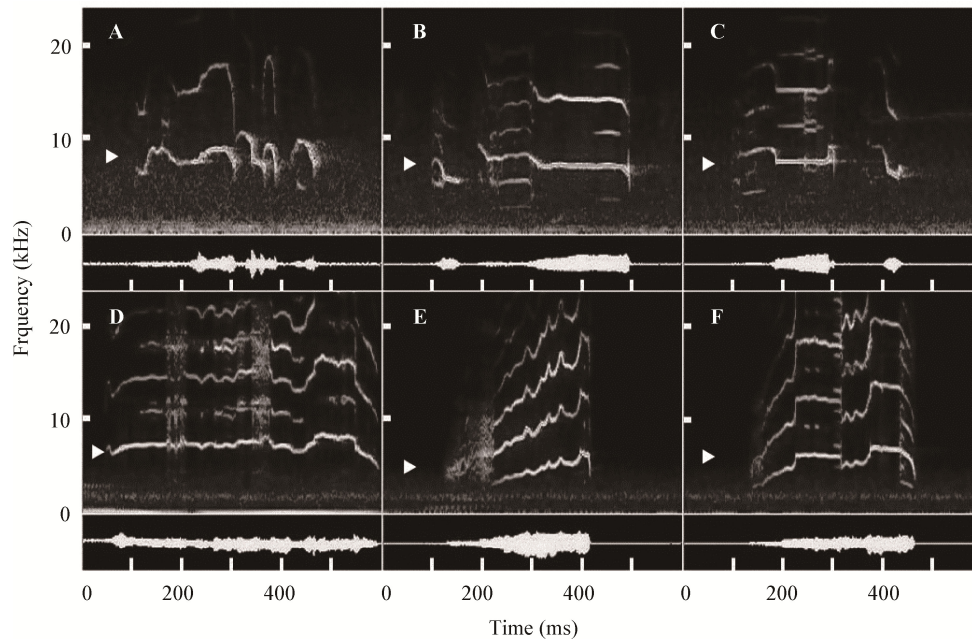


Fig. 2 Vocalizations of male *O. tormota* are extraordinarily diverse and complex

Representative spectrograms of vocal signals of a male *O. tormota* in Site-1 (A–C) and a male in Site-2 (D–F). Calls contain harmonic segments, as well as non-harmonic segments (i.e., chaotic, subharmonic, biphonic and frequency jump) - See Feng et al., 2009 for definitions of these terms. One call differs from the next in terms of the timing and frequency of occurrence of various harmonic and nonharmonic segments as well as segment breaks, and of the frequency modulation pattern in the harmonic segments. Arrow heads represent the average F0s of the calls.

Table 1 Within- and between- Creek coefficients of variations of 10 sound parameters

Parameter	Mean CV _w	CV _b	CV _b /CV _w
Total duration	15.89 (11.82–19.96)	18.69	1.18
Duration of Ha	21.45 (14.36–8.54)	25.54	1.19
Duration of Sh	64.10 (54.00–74.2)	65.72	1.03
Duration of Bp	124.89 (70.61–179.17)	119.56	0.96
Duration of Ch	95.61 (95.67–96.56)	92.95	0.97
Duration of Br	62.70 (58.45–66.95)	60.19	0.96
Average F0	12.98 (11.92–14.03)	14.83	1.14
Maximum F0	11.52 (9.51–13.53)	11.44	0.99
Minimum F0	13.33 (10.88–15.79)	24.39	1.83
F0max – F0min	18.17 (13.84–22.49)	42.42	2.33

Shown are the coefficient of variations of within (CV_w) and between (CV_b) the males inhabiting Fu Creek (Site-1) and Tauhua Creek (Site-2) for 10 different call parameters, as well as the ratios of the CV, the CV_b/CV_w, for these parameters. Abbreviations: Ha = harmonic segment; Sh = Subharmonic segment; Bp = Biphonation segment; Ch = Chaotic Segment; Br = Break.

statistically significant different for the two creeks (Table 2) – this difference indicates that the calls of males along Tauhua Creek are more tonal compared to those of males along Fu Creek.

The spectral divergence in calls of males along the two creeks is not likely attributed to a difference in the

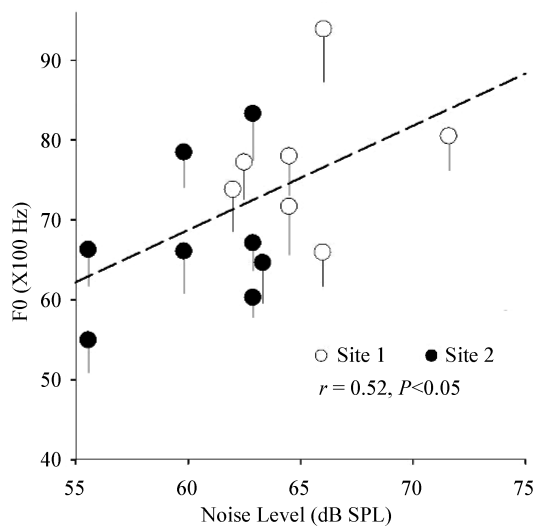
ambient temperature (see Feng et al., 2009 for the lack of temperature effect on individual call signatures), the altitude or latitude of the frog's habitat, or to differential body size (Gerhardt and Huber, 2002; Bernal et al., 2005). The ambient temperature range at times of audio recording overlapped extensively for the two studies (i.e., 15.5–19.0°C in Fu Creek versus 15.0–20.0°C in Tauhua Creek). The latitudes of the two study sites are essentially identical, and their altitudes (averaging 600 and 640 m above sea level) overlap extensively. Finally, the body size of calling frogs along the two creeks are not statistically different, having snout-vent lengths of 3.40 ± 1.61 cm and 3.25 ± 1.53 cm for male frogs in Sites-1 and -2, respectively. As body size is negatively correlated with call frequency (Gerhardt and Huber, 2002), the slight difference in the frog's snout-vent length argues against it having any role in the differential F0, as males in Site 1 are slightly bigger than those in Site 2, and yet emit calls having higher F0.

Results of our correlational study indicate that the differential ambient noise is likely a contributor to the spectral divergence. First, the average F0 is higher for males inhabiting the stream with higher average background noise level. Stream noise is characterized by having a peak energy at low frequency (< 240 Hz) (Dubois and Martens, 1984; Feng et al., 2006), with

Table 2 Univariate ANOVAs. Results of univariate ANOVAs showing whether and which if any of the 10 call parameters from two study sites differ significantly (Site-1 and Site-2, $n = 15$, $df = 1$)

Parameter	Average (Site 1)	Average (Site 2)	F	P
Total duration (ms)	313.95 \pm 37.12	369.1 \pm 73.69	3.19	0.097
Duration of Ha (ms)	167.97 \pm 47.94	233.26 \pm 33.50	9.56	0.009
Duration of Sh (ms)	22.24 \pm 16.50	40.04 \pm 21.62	3.13	0.100
Duration of Bp (ms)	3.30 \pm 5.39	3.39 \pm 2.39	0.08	0.787
Duration of Ch (ms)	37.61 \pm 35.94	44.52 \pm 42.59	0.11	0.742
Duration of Br (ms)	42.33 \pm 28.34	47.41 \pm 27.71	0.12	0.732
Average F0 (kHz)	7.75 \pm 0.92	6.64 \pm 0.93	5.33	0.038
F0max (kHz)	8.73 \pm 0.83	8.52 \pm 1.15	0.160	0.696
F0min (kHz)	6.89 \pm 0.75	4.59 \pm 0.72	36.26	< 0.01
F0max – F0min (kHz)	1.85 \pm 0.26	3.93 \pm 0.88	35.90	< 0.01

See Table 1 for abbreviations.

**Fig. 3 Average F0 increases with increasing average background noise level**

A plot of average F0 of long calls for 15 frogs versus the average peak background noise level at their calling loci (empty circles represent individual frog's data from Fu Creek, and filled circles represent individual's data from Taohua Creek). The vertical bar represents the standard deviation of the data from each frog. Linear regression of the data set (dashed line) shows a significant correlation between the two variables ($r = 0.52$, $P < 0.05$).

progressively decreasing noise energy with increasing frequency (Fig. 1). Thus, an upward shift in the F0 effectively increases the signal-to-noise ratio, reducing acoustic interference of the background noise and making the signal more conspicuous. Second, the individual's data from 15 frogs show a trend for individuals occupying noisier habitats to emit calls having higher F0 (Fig. 3). These data are suggestive that *O. tormota* exposed to persistently high levels of low-frequency background noise generally call at higher frequencies, thereby elevating the signal-to-noise ratio and making their signals

more audible.

Other than changing the spectrum of the vocalizations (Slabbekoorn and Peet, 2003; Narins et al., 2004; Feng et al., 2006; Parris et al., 2009; Nemeth and Brumm, 2009; Vargas-Salinas and Amezcua, 2013), various studies have also shown that animals adopt many different strategies to avoid masking by ambient noise (see Brumm and Slabbekoorn, 2005; Schwartz and Bee, 2013 for a review). A common strategy is adjustment of vocal amplitude through a so-called Lombard effect (Brumm et al., 2009). Alternatively, sender may increase signal duration (Schwartz et al., 2008; Brumm et al., 2009), repetition rate (Sun and Narins, 2005), and employ temporal windowing (Handford, 1988), or spatial separation (Feng and Ratnam, 2000), to avoid noise interference.

In light of the abundance of masking avoidance strategies, numerous issues remain unresolved for the concave-eared torrent frogs. For example, it remains to be determined whether or not *O. tormota* utilizes the Lombard effect, or an increase in the repetition rate, to counter the high-level stream noise in their habitat. Also, future research is needed to determine whether or not males exhibit vocal plasticity (Halfwerk and Slabbekoorn, 2009; Cunnington and Fahrig, 2010; Montague et al., 2013), namely, adjusting their call frequency in response to a change in the ambient noise level, or whether the vocal plasticity and the time it takes to respond to changes in the ambient noise level are individual specific.

In addition, a caveat of the present study is the limited sample size, i.e., only 15 males from two streams were sampled, and the number of males in each stream from which we obtained their vocal signals is below 10. Obviously, a greater sample size would have been more

conclusive. The limitation is a consequence of males' tendency to emit many different call-types, and on average evening, it is rare that they produce > 10 long calls (i.e., a meaningful sample size from a frog). Nevertheless, the current study still revealed that *O. tormota* call at a higher pitch in noisier ambiance, which is consistent with the masking avoidance hypothesis and with the prediction of the acoustic adaptation hypothesis.

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