

Evolution of high-frequency communication in frogs

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ABSTRACT

Background: Two species of frog are currently known to produce high-frequency or even partly ultrasonic vocalizations, *Odorrana tormota* and *Huia cavitympanum*. Both possess special adaptations to their hearing system that extend their hearing into the high-frequency range. Typical stream-dwelling species of frog are not known to use high frequencies.

Goal: To investigate the environmental conditions that may have led to the evolution of very high-frequency communication in some frog species.

Method: Study auditory communication in *Huia masonii*, a frog of habitats next to fast-flowing streams on the island of Java, Indonesia. Study the tympanums of all members of the genus *Huia*. Measure the acoustic characteristics of fast-flowing water. Calculate water noise levels (amplitudes) at different distances from streamside.

Results: All four members of the genus *Huia* possess a modified tympanal membrane, suggesting that high-frequency communication is present in all members. All frogs using high-frequency communication live along turbulent perennial streams. They all appear to be solitary callers and experience low encounter rates between partners. The high frequencies used by *Huia* improve signal detection and discrimination but only within 103 m of a noisy river; they are unsuited for long-range detection. Beyond 103 m of noisy rivers, communication using normal (low) frequencies is more advantageous.

Keywords: acoustic, communication, evolution, frog, *Huia masonii*, ultrasonic.

INTRODUCTION

Two species of frog are currently known to produce high-frequency or even partly ultrasonic vocalizations, *Odorrana tormota* and *Huia cavitympanum*, both of which have a specially adapted hearing system (Arch *et al.*, 2009). The use of high-frequency communication in frogs has been interpreted as being adaptive to the acoustical conditions near fast-flowing streams (Dubois, 1974; Dubois and Martens, 1984; Feng *et al.*, 2006). However, in Indonesia, many species of frog living close to or in fast-flowing rivers use calls that appear similar to those of other members of their genus and do not show any signs of frequency changes: *Phrynoidis aspera* and *Odorrana hosii* in Java; *Hylarana crassiovis*, *H. kampeni*, *H. picturata*, *H. signata*,

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P. aspera, and *P. juxtaspera* in Sumatra; *Limnonectes microtympalum* in Sulawesi; and *Staurois latopalmatus*, *S. natator*, *S. tuberinguis*, and *Hylarana signata* in Borneo. For this reason, it remains unclear why some frogs have evolved a high-frequency communication system, whereas others have not.

Here, we show that yet another species of the genus *Huia*, *H. masonii*, uses high-frequency signals for its communication and that all members of the genus have a recessed tympanal membrane, thought to extend the hearing into the high-frequency range (Feng *et al.*, 2006).

To investigate the acoustic benefits of using high-frequency communication, we measured more precisely than previously the acoustic characteristics of fast-flowing water and calculated the amplitude at different distances. In this way we were able to assess precisely if and how frequency shifts can help frogs to communicate more efficiently at specific distances from a noisy river.

Our calculations suggest that specific conditions may have to apply to force the evolution of high-frequency communication in frogs.

METHODS

Locations

Huia masonii and *Odorrana hosii* were recorded and photographed at Curug Nangka (6°40'14.0"S, 106°43'29.8"E; 640 m above sea level), Java, Indonesia. Individuals of *Huia modiglianii* were photographed in Bukit Tapan, Kerinci Seblat National Park, Sumatra (2°05'52.0"S, 101°14'57.7"E; 550 m above sea level) and *H. modiglianii* in Ketenong, Kerinci Seblat National Park, Sumatra (1°39'6.6"S, 106°14'41.4"E; 800 m above sea level).

Recordings

Sounds of frogs and water were recorded with an Audio Technica AT875R microphone, which has a linear frequency response between 90 Hz and 20 kHz. The linearity of this microphone is better than that of the custom-made microphone of the PC-Tape system used in previous measurements of water noise (Feng *et al.*, 2006). All sounds were registered on a Fostex FR 2LE in wave format with a sampling frequency of 88.2 kHz and a bit rate of 24 bits. The high sampling frequency ensured that practically no information was lost in the digitization process. We measured the noise of water at close range at different streams to obtain the loss in power (dB/kHz, see below). The noise of water was also measured at different distances at one stream (3, 5, 8, 13, 17, 20, 26, and 31 m) with the microphone pointing to the river along an unobstructed path.

Sound analysis

The sounds of frogs were analysed using Batsound (Pettersson Elektronik). The sound of rustling water (strong, moderate, and calm water) was analysed using Matlab (Natick, MA). To measure the power spectral density (dB/Hz) of the water, we first applied a power spectral density estimate using Welch's method, with a window size of 512 points and an overlap of 99.6%. We then measured the frequency of the strongest amplitude (peak frequency) and performed a linear regression over the power spectrum from the peak

frequency to 20 kHz (the maximum linear frequency of the microphone). The slope of this regression represents the loss in power (in dB) per kilohertz increase of frequency.

To measure the noise level of the water at different distances, root mean square and peak values of recordings were calculated using Matlab. As the trend with distance of the two measures was virtually identical, root mean square values only were used in further calculations. These values were converted into decibels using: $20\log_{10}(\text{value3m}/\text{valueX})$, with valueX representing the values measured at the other distances from the river.

Calculations

We used sound attenuation values of $0.2 \text{ dB} \cdot \text{m}^{-1}$ at 15 kHz and $0.005 \text{ dB} \cdot \text{m}^{-1}$ at 1 kHz (90% humidity) in our calculations. For the calls of frogs we treated the frog as a point source and therefore assumed a loss of 6 dB per doubling of distance (spherical spreading). Source levels (in dB SPL) of a fast-flowing stream were taken to be 80 dB SPL at 1 m (Boeckle *et al.*, 2009). We used the same value for frogs, based on literature values for many other loud frog species (for an overview, see Wells, 2007). The decrease of river noise with distance was measured in the field (see above). The noise level data with distance were fitted with an exponential function ($R^2 > 0.98$ for all fits), extrapolated from 1 to 40 m and normalized to 80 dB SPL at 1 m (see above). The noise level data of the river at 15 kHz are the same data with 20 dB subtracted (see Results) and compensated for excess sound attenuation (see above). We verified these calculations by comparing them to plotted power (dB) at 15 kHz from a Fast Fourier Transform (2048 points) of the sound samples at different distances and the correspondence was nearly perfect.

RESULTS

Frog vocalizations

Calls of *Huia masonii* consisted of single warbles (duration: 60–200 ms) usually modulated up and down several times within a frequency span of 2–6 kHz. The carrier frequency of individual calls was mostly around 12 kHz, but calls from 4.5 to 16.5 kHz were also recorded. The second harmonic of the high calls was completely ultrasonic. Recordings with an ultrasonic detector revealed no calls with the first harmonic being completely ultrasonic (above 20 kHz). Most intensity was usually present in the first harmonic, unless it had an extremely low frequency (Fig. 1a, middle). Figure 1a even suggests that frequencies below 5 kHz may be suppressed selectively, although series of impulses (buzzes) with energy still around 4–5 kHz have also been recorded (Fig. 1c). A buzz consists of about 5–9 impulses, each with duration of ~8 ms, 15 ms apart.

Warbles are highly variable and none are 100% identical. In the field, calling males appeared to stimulate others to join. During such calling bouts, many males were heard to call. During a calling bout, typically lasting 1–1.5 min, each male would utter about 6–8 individual warbles, and one series of closely spaced warbles (Fig. 1a). The closely spaced warbles (3–4) were typically delivered at 200–350 ms intervals, whereas single harmonic warbles mostly occurred at intervals of 5–11 s. Calling bouts occurred about every 20 min, but later in the evening even intervals of 60 min were recorded. Individual males may therefore only emit about 180 warbles on a single night, suggesting a very low calling effort.

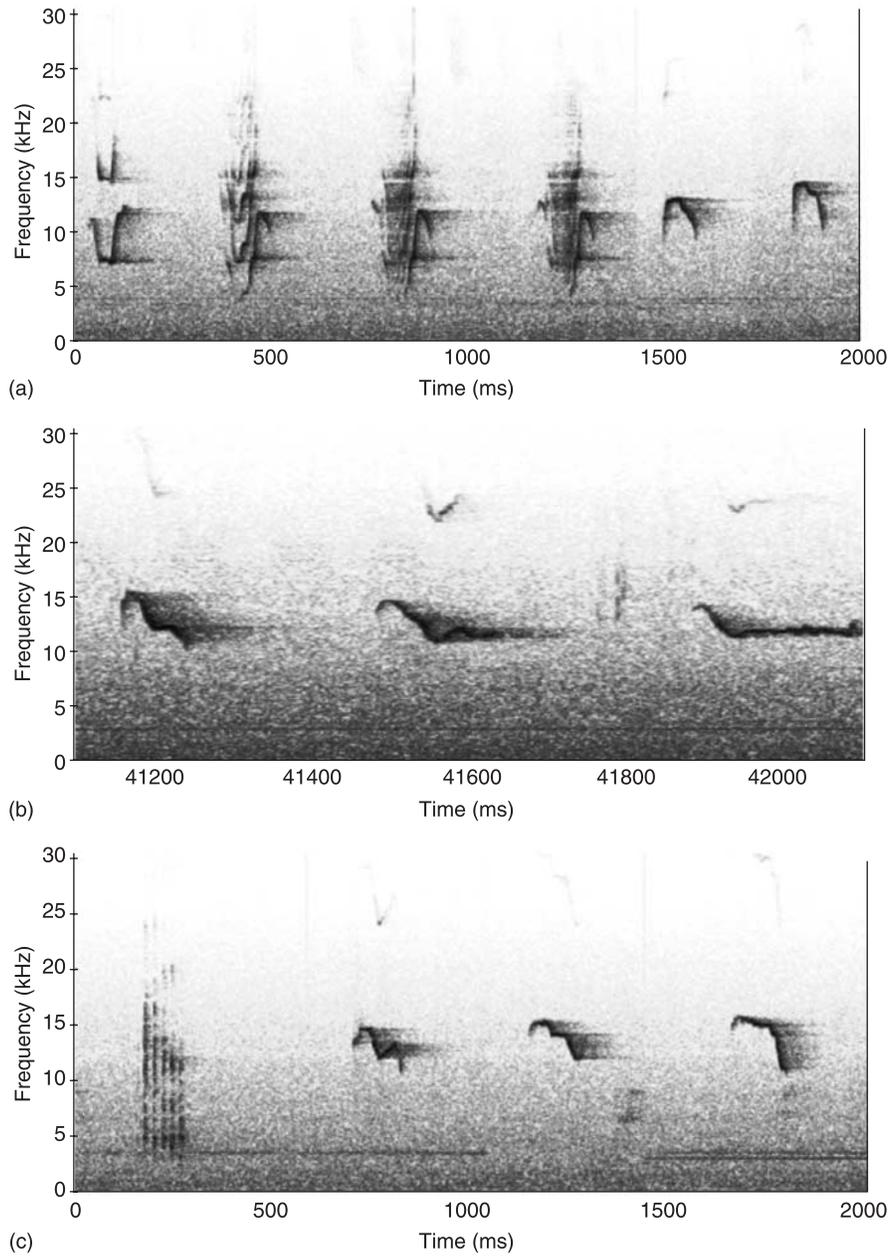


Fig. 1. (a) A series of densely packed harmonics in four warbles (first harmonic low) in real time, followed by two single harmonic warbles that occurred at much longer time intervals than on the display. (b) An example of three warbles with ultrasonic second harmonics. The warbles were given in quick succession (300-ms intervals). (c) An example of a low-frequency call (series of impulses). The three warbles were delivered at intervals of many seconds and the time between them has been shortened for the purpose of display.

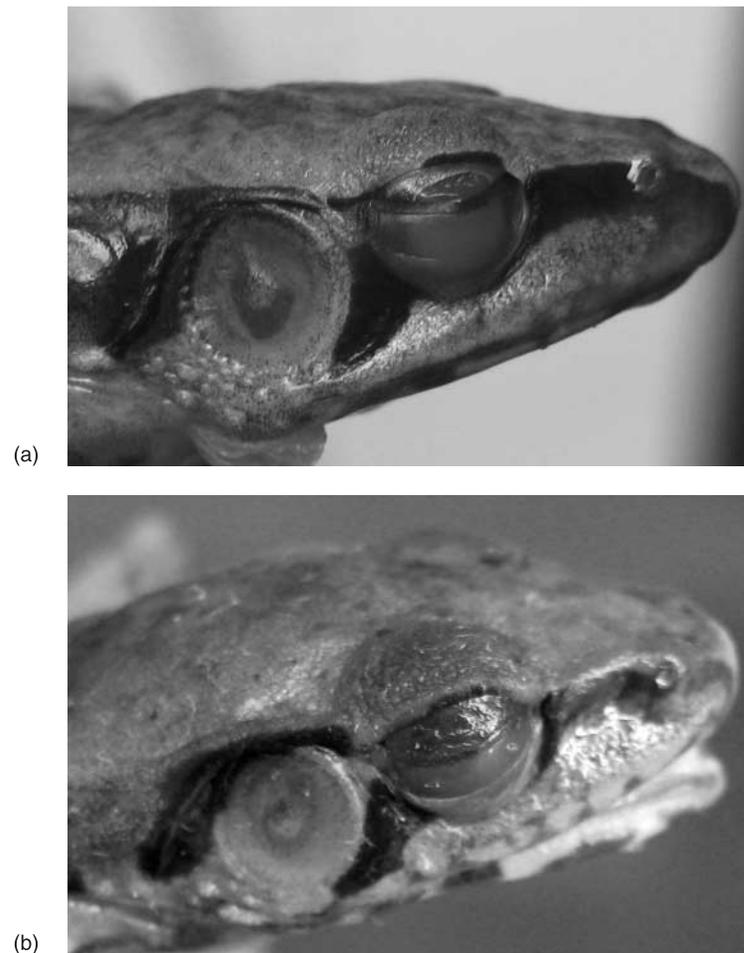


Fig. 2. Lateral view of (a) an adult male *H. masonii* and (b) an adult male *H. sumatrana*.

Tympanic membrane in *Huia*

To learn more about the structure of the tympanic membrane in other members of *Huia*, we used previously photographed specimens and specimens that have been preserved in alcohol (Fig. 2). The photographs show the recessed tympanic membrane that is believed to be used in receiving high frequencies.

Basics of stream noise

Figure 3 shows the power spectral density of a calm rushing stream recorded at close range. The graph shows a small gap at the very low frequencies (below 861 Hz). We found that this gap ended at 689 Hz for more turbulent water and was absent in recordings of extremely rough water. We calculated the decrease of power from low to high frequencies for each of the streams and found -1.4 dB/kHz for calm rushing water, -1.8 dB/kHz for more turbulent

water, and -1.6 dB/kHz for extremely rough water ($R > 0.98$) for all fits. This slope means that river noise at a frequency of 15 kHz is around 19.6–25.2 dB quieter than it is at 1 kHz (the normal frequency of frog communication). To be on the conservative side, we use 20 dB throughout this paper.

Transition distance

We wished to investigate the maximum distance at which the use of high frequencies is still profitable to attract females. To do this we had to calculate the frog call level relative to the noise level of the stream at different distances for 1 kHz and for 15 kHz. At 1 kHz the losses in both frog and river noise are 0.005 dB · m⁻¹, and at 15 kHz they are 0.2 dB · m⁻¹. There are also losses due to spreading effects of the sound, but they are identical for the 1-kHz and 15-kHz cases and can therefore be ignored. However, the river noise is 20 dB lower if 15 kHz is used (Fig. 3). So the maximum profitable distance, x , satisfies $0.2x - 0.005x = 20$, yielding $x = 102.6$ m. This means that at distances further than 102.6 m from a noisy river, frogs would have a better signal-to-noise ratio if they used 1-kHz sounds compared with 15-kHz sounds.

Calculations with empirical data on river noise

We wished to determine whether and where the use of high frequencies is advantageous to frogs. With this aim in mind, we followed the procedure outlined in the Methods to calculate the absolute sound pressure levels (SPL) of river and frog at different distances from a stream. We calculated these data for a normal (low-frequency: 1 kHz) frog and a high-frequency frog (15 kHz) (Fig. 4). We calculated the case for a male frog calling from within the stream while the female listens 1–40 m away. We also calculated the case for when a male

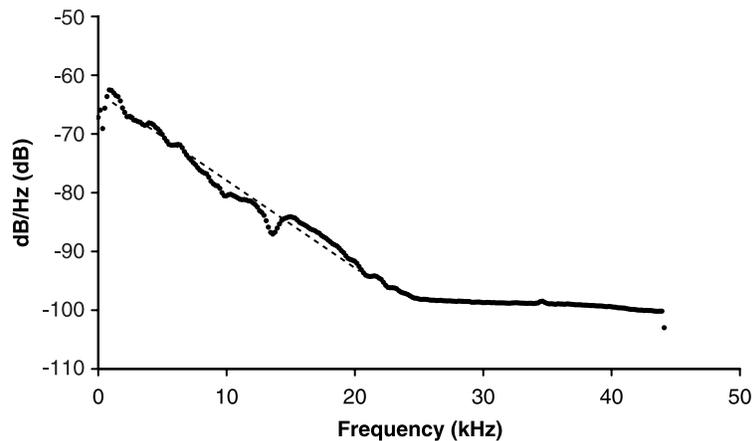


Fig. 3. Typical power spectrum of calm river noise recorded at close range. At 25 kHz, the river noise becomes equal to other noise in the microphone output. At 44.1 kHz, the sound is filtered abruptly by the recorder. The peak frequency is at 861 Hz. Between 861 Hz and 20 kHz, the power of the water noise diminishes by 1.4 dB/kHz (regression line). At the location of the recording, frogs would therefore gain in audibility by $1.4 \times 14 = 19.6$ dB when raising their frequency by 14 kHz [from 1 kHz (normal frogs) to 15 kHz (*Huia*)].

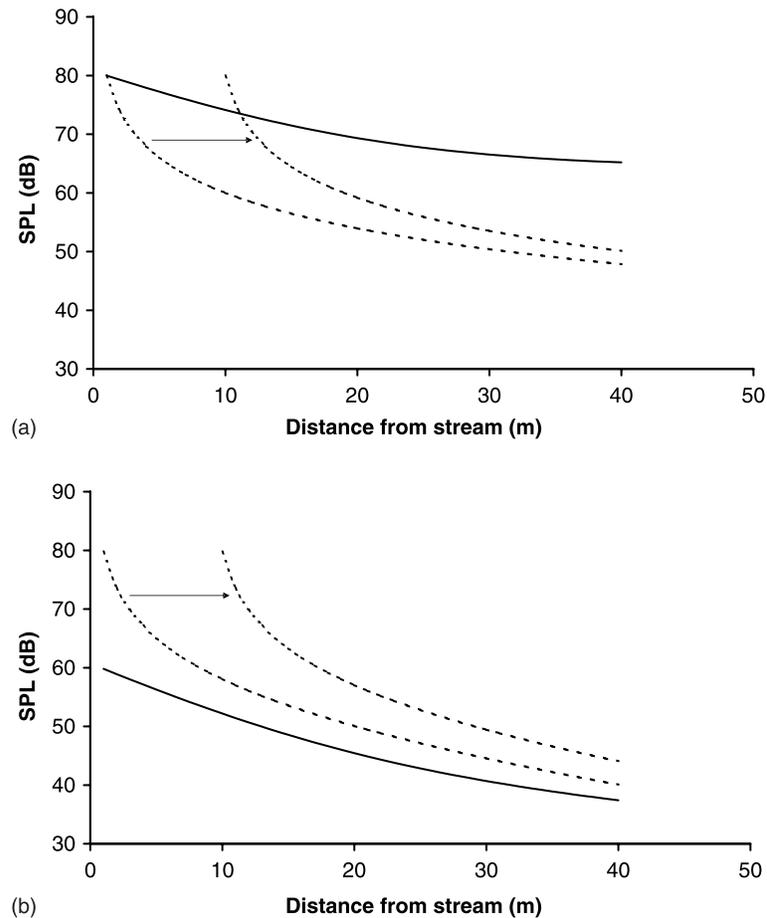


Fig. 4. (a) Hearing at normal frequencies (1 kHz). Thick continuous line represents noise level of the stream. Dotted lines represent the sound pressure levels of a male frog as received by a female frog if the male frog is calling from the river (left) or further from the river (right). In both cases, each dot of the line represents an increasing distance from female to male (1–40 m and 1–30 m respectively) and at the same time an increasing distance from the river (1–40 and 11–40 m respectively). The x-axis shows the distance from the river to the listening female. The graph shows that females must either enter the river to detect the males or the males must move out of the river (arrow) to increase their detection probability by approaching females. (b) Same as (a) but for a frog calling and listening at a high frequency only (15 kHz). The noise level of the same stream is perceived to be much weaker (thick continuous line). Male frogs are therefore clearly audible when calling from the stream or in its vicinity. Within 20 m of the river, the male's signal is clearly (>4.5 dB) above the noise. Further away than 20 m, the male's calls may still be detected, but with more difficulty. The arrow again indicates the frog's detectability when calling further away from the stream.

calls 10 m from the river while the female is 1–30 m from him (i.e. she is 11–40 m from the river). The arrow in each graph shows how to move the curve to simulate the male calling at an increasing distance from the river. The curve having been shifted to the right represents the sound pressure level received by a female frog of a male frog that has moved away from

the river by the distance the curve was shifted to the right. The absolute distance of the female to the river can be read from the x-axis. The distance from the female to the male is the same distance but with the shift to the right subtracted.

DISCUSSION

In this study, we showed that *Huia masonii* uses a communication system with very high frequencies similar to *Huia cavitympanum*. Based on specimen observation, all four species of *Huia* (*H. cavitympanum*, *H. masonii*, *H. modiglianii*, and *H. sumatrana*) possess a specially adapted sunken tympanal membrane as described for *Huia cavitympanum*, thought to be part of the high-frequency hearing system. Therefore, probably all species of the genus *Huia* use very high-frequency sounds.

Huia masonii also produces warbles, similar to *Odorrana tormota* and *Huia cavitympanum*. It has been shown that due to their subtle frequency modulations, such warbles have the potential to use individual vocal signatures and hence enable individual recognition between male frogs in *Odorrana* (Feng *et al.*, 2002, 2009a, 2009b). This shows that warble sounds, as used by *Huia masonii*, are far from stereotypical and part of their evolution may have been driven by the need to advertise individuality.

Our calculations and measurements of water noise show that signalling at 15 kHz instead of at 1 kHz (other frogs) improves partner detection 1–40 m distant from a stream within noisy environments (Fig. 4). Between 1 and 20 m from streams, the calls of males are clearly above river noise (> 4.5 dB). At longer distances from the river, this difference diminishes. Our calculations show that beyond 103 m, the normal (low) frequencies that other frogs use become more effective for attracting mates. This means that between 40 and 103 m from the river, high-frequency communication is still preferable to using low frequencies, but the detection of calls will strongly depend on the frog's ability to filter out calls from the noise. At long distances from the river (and sender), therefore, high-frequency signals mainly facilitate the process of *detection*. At much shorter distances to the sender, the received signals will be clearly above the river noise (Fig. 4) and therefore become very obvious to the receiver. The main process in the auditory system of the frog will therefore no longer be detection, but here we suggest it may well be *discrimination* and *phonotaxis*. The use of high frequencies is still helpful close to the emitter because (1) individual signal *discrimination* has been shown to play an important role in warbling frogs (Feng *et al.*, 2009a; see above), and (2) Shen *et al.* (2008) showed that thanks to the use of high frequencies, angular resolution in the frog *Odorrana tormota* is extremely good and improves female phonotaxis compared with frogs that use low-frequency sounds.

Our calculations show that for whatever signal processing purpose, high-frequency signals are advantageous in noisy stream habitats, probably up to a distance of 103 m. Low-frequency signals (1 kHz) that other frogs use only become advantageous beyond 103 m of streams. On the basis of these facts, it is quite remarkable that so few species of frog that live in or close to streams have raised their frequencies (see also Boeckle *et al.*, 2009), as our data show that, theoretically, every kilohertz gives the frog about 1.5 dB gain (Fig. 3). Even within a single family (Hylidae), species that prefer to call from streams do not produce calls that are higher than those of other members of their genus (Hoskin *et al.*, 2009). How is it possible that evolution has radically altered the hearing and vocalization system of only some stream frogs, whereas it seems to have had no effect on most other wild water frogs? It may be hypothesized that in areas with changing precipitation where river beds may

temporarily become dry, long-distance communication to attract females (hence using low frequencies) may be essential. Furthermore, if the frogs are terrestrial and female abundance is high, the probability of a male approaching within 1 m or closer (so its calls can be heard) is high. In this situation, the reported preference of females for low-frequency males (Bosch *et al.*, 2002) or simply phylogenetic constraints (Bosch and De la Riva, 2004) may inhibit a shift to higher frequencies.

The above arguments suggest that high-frequency communication in frogs is a special case that may be driven by the following factors: (1) the presence of a permanent river system; (2) a low abundance of females; and (3) the males do not form aggregations and the call type used has the potential to be individualized (i.e. can be individually different).

The logic of requirement (1) is described above. Requirement (2) follows from the fact that a low probability to come close to a calling frog will make it necessary to make its calls more detectable and easier to be guided to. Requirement (3) is logical because if males are spread, calling from branches or rocks, vocalizations are likely to play a key role in guidance and mate selection (or recognition of a rival) over some distance, for which high frequencies are essential in stream habitats. In this scenario, male frogs are likely to compete acoustically, leading to acoustic differences between males. However, vocal individuality may not always simply evolve when required. In frogs, phylogenetic calling constraints are high (Bosch and De la Riva, 2004) and not all signal types are equally suited to express individuality as warbles are. In some permanent stream habitats in the world, frogs that have been present for a long time during evolution may use rapid series of impulses (FM) making the frequency content rather fixed and whose temporal occurrence is usually a static feature (see below) and therefore has little potential to be individualized. Such a call design would make acoustic competition hard, driving males to find non-acoustical means to be more successful than others.

Interestingly, we found the three conditions that apply in all species of *Huia* also seem to apply to *Meristogenys orphnocnemys*, which uses a relatively high-frequency communication system [7.3 kHz (Boeckle *et al.*, 2009)]. Similar to *Huia*, the sex ratio in river habitats in this species is extremely skewed towards males [227:8 (R.F. Inger and F.L. Tan, personal communication)]. In this respect, it is interesting that in other stream frogs that share their habitat with *Huia masonii*, such as *Odorrana hosii*, males are often surrounded by females at close range and the frequencies used by *Odorrana hosii* are in the normal range for frogs.

The warbles of *Huia* enable male frogs to stand out from a choir in a way other than using calling rate or intensity, as in many other frog species (Gerhardt, 1988; Wells, 1988; Gerhardt and Huber, 2002). High calling rates are energetically costly and would be largely lost on *Huia* females because they are mostly not present. Typically, a choir of *Huia masonii* was heard for only 1–2 min in intervals of 20–60 min, indicating a remarkably low calling rate. Second, if mate selection takes place over relatively long distances in *Huia*, it is virtually impossible for a female to estimate call intensity of each individual, as each of them calls from a different distance and position relative to her. Because *Huia* uses warbles, calls that go up and down in frequency, it can play with frequency and time (two dimensions) simultaneously, making it easier for males to make their calls different from each other. Not all families of frogs may be blessed with a sound system that allows individual males to excel acoustically. In frogs such as *Microhyla* that use short impulses, the playroom within a species is mainly one-dimensional: variation in impulse rate, which is likely a so-called static parameter and therefore constrained due to female preference (Gerhardt, 1991; Castellano and Giacoma, 1998). The use of warbles (long, narrowband signals) as employed by *Huia* to communicate in a noisy

environment is a logical adaptation since long signals match the neural integration time of frogs (Dunia and Narins, 1989) and narrowband signals can potentially increase the signal-to-noise ratio in a receiver.

It has been suggested that high-frequency communication in frogs is energetically more favourable than the use of low frequencies since the shorter wavelengths of high-frequency signals match more closely the dimensions of the frogs' vocal sac than do low-frequency signals. However, this argument is probably based on a misconception. The vocal sac of frogs probably does act as a resonator, but not in the way as is commonly assumed (Purgue, 1997). Most likely, the air within the sac only has the function to control the tension of the sac membrane. The wavelength of a 1-kHz sound in air is far longer than the dimensions of the vocal sac, so as stated frequently, the resonance coupling is very poor. However, it has been shown in three genera of frog that the sound probably travels *within* the membrane of the sac. Because of the membrane properties, the wavelength is much smaller and in fact does fit the dimensions of the sac well, resulting in an efficient resonance (Purgue, 1997). Note that in this context experiments with helium have failed to show any frequency changes in the vocalizations, which should have been the case if the air in the vocal sac formed a resonance chamber (Rand and Dudley, 1993). It would therefore be interesting to conduct helium experiments with *Huia* frogs to check if their vocal apparatus does use an air resonance system, but the improved coupling argument to explain the evolution of high-frequency communication could still not be made.

Our measurements and calculations suggest that quite specific key conditions are necessary to drive the evolution of high-frequency communication in frogs, explaining why many stream-associated species in the world mostly use sounds typical of their genus.

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