Advertisement Calls of Two Horned Frogs, *Megophrys kuatunensis* and *M. huangshanensis*, from China (Anura, Megophryidae)

Rongchuan XIONG[1,2], Masafumi MATSUI[3], Kanto NISHIKAWA[3], and Jianping JIANG[1]*

[1]*Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, CHINA*
[2]*Department of Life Science, Liupanshui Normal College, Liupanshui 553004, CHINA*
[3]*Graduate School of Human and Environmental Studies, Kyoto University, Kyoto 606–8501, JAPAN*

Abstract: Animals communicating by sound face interference from biotic and abiotic sources. Contrasting strategies have been reported in different taxa in the presence of prolonged noise. Some torrent-living frogs of the genera *Odorrana* and *Huia* emit ultrasounds to avoid masking by environment noise. That strategy, however, might not be the only mode of acoustic communication for inhabiting along fast-flowing streams. To examine this possibility, we analyzed call structures of two horned toads, *Megophrys kuatunensis* and *M. huangshanensis*, which inhabit along streams in eastern China. We investigated variation in call properties within and between the two species and found that the two species show similar call structures but significantly differ in note duration and inter-note interval. Both of the two species concentrate energy on a single, wide harmonic band, and this might be an acoustic strategy against environmental noise.

Key words: Acoustic communication; Advertisement calls; Anurans; Horned frogs; Stream breeding

INTRODUCTION

It is commonly believed that acoustic cues are important for attracting conspecifics and for mediating spacing between individuals and groups of diverse animals such as primates, birds, tailless amphibians, and insects (Altmann, 1959; Marler, 1972; Whitney and Krebs, 1975; Campbell and Shipp, 1979; Doolan and Mac

Nally, 1981; Brenowitz et al., 1984; Robertson, 1984). The vocalization of frogs is an important biological characteristic among extant amphibians, and the mating or advertisement call of male frogs is the medium through which frogs conduct their reproductive activities. However, communicating by sound always faces interference from biotic and abiotic sources since the acoustic signals must first be transmitted through the environment in order to play a role in communication.

Confronting this noise interference, animals have evolved different strategies including

---

* Corresponding author. Tel: +86–28–82890789;
Fax: +86–28–82890288;
E-mail address: jiangjp@cib.ac.cn

changes in vocalization amplitude (Cynx et al., 1998; Pytte et al., 2003; Brumm, 2004; Kaiser et al., 2011), emission rate (Lengagne et al., 1999; Sun and Narins, 2005), duration (Kaiser et al., 2011; Martinez-Rivera and Gerhardt, 2008), inter-call interval (Martinez-Rivera and Gerhardt, 2008), and frequency structure (Katti and Warren, 2004; Parris et al., 2009), and adjustments in the timing of emissions to intervals when the interference decreases or is absent (Greenfield, 1988).

Stream-dwelling frogs face interference from the wide-band background noise of local, fast-flowing torrents. To avoid masking by that noise, some *Odorrana* and *Huia* frogs communicate with bird-like melodic calls with pronounced frequency modulations that often contain spectral energies in the ultrasonic range (Feng et al., 2006; Arch et al., 2009; Boonman and Kurniati, 2011; Shen et al., 2011). The frog *O. tormota* was demonstrated to produce and detect ultrasounds, and this is the first case of non-mammalian ultrasonic communication. *Huia cavitympanum*, which is phylogenetically remote from *O. tormota* (Pyron and Wiens, 2011), can even use pure ultrasound to communicate between conspecific males (Arch et al., 2009). The convergence of call characteristics of these species implies that similar habitats might be an important factor in shaping the call structures of fast-flowing stream-dwelling frogs.

Basic mating call structures of some horned frog species of the genus *Megophrys*, which also occur around streams, have been reported (e.g., Wang et al., 2014), but to our knowledge no reports have associated their mating call structures with stream noises. In order to understand such associations, we studied *Megophrys kuatunensis* and *M. huangshanensis*, which live along streams and whose males call there in breeding seasons under noisy conditions (Fei et al., 2012).

Female frogs in many species choose mates, at least in part, by recognizing the species-specific component of male calls (Gerhardt, 1994a,b). For accurate recognition, calls of each species must differ from those of the other

sympatric species (Wollerman and Wiley, 2002). Various studies have shown that the advertisement call represents a premating isolating mechanism in anurans (Duellman and Trueb, 1986; Hoskin et al., 2005), which makes it a valuable tool in taxonomy (Matsui, 2006; Matsui et al., 2009; Hertz et al., 2012).

On the other hand, some call components show substantial variation within a single population (Sullivan and Wagner, 1988; Briggs, 2010) or even within a single individual (Gerhardt, 1991). As a result, traits can be classified as static (low within-male variation) or dynamic (high within-male variation) call properties, and the variability found in dynamic properties may account for their importance in mate choice (Gerhardt, 1991, 1994b). Static call traits include dominant frequency, which is not expected to change greatly because it is a function of body size (Gerhardt, 1991). Dynamic call properties like call rate and call duration are typically the products of both abiotic and biotic factors (Gerhardt, 1991).

In the present study, both static (dominant frequency) and dynamic (note duration, inter-note interval) call properties of male advertisement calls of two stream-dwelling horned frogs, *M. kuatunensis* and *M. huangshanensis*, were investigated. Based on the spectral structures, we examined how the stream-dwelling *Megophrys* species employ specific acoustic communication modes. Those may be different from the acoustic modes of sympatric *Odorrana* species, which can extend some harmonic energy into the ultrasonic range. We also conducted statistic comparisons within and between species to explore the call traits associated with species recognition and individual variation.

MATERIALS AND METHODS

Study site

The study of *M. kuatunensis* was conducted from 16 to 23 March 2011 at the locality of Guadun Village (27°44′41″N, 117°38′05″E, 1360 m asl) in Wuyishan City, Fujian Province,

China, which is the type locality of this species (Pope, 1929). The air temperature varied between 12.5 and 18C. All recordings were carried out between 19:45 and 0:30 h, when calling activity was most intense.

The study of *M. huangshanensis* was carried out on 21 July 1992 (one individual) near the type locality (Fei and Ye, 2005), and from 26 July to 1 August 2011 (three individuals) and from 18 to 22 July 2012 (one individual) at Fuxi Village (30°05'3"N, 118°08'46"E, 563 m asl) in Huangshan City, Anhui Province, China, about 4 km southwest to the type locality (Fei and Ye, 2005). The air temperature fluctuated between 17 and 22C. All recordings were carried out between 18:45 and 0:30 h, during the most intensive calling activities. Recordings were made sequentially for each individual encountered, and the temporary number and the time of recording were also noted for later analyses. We did not measure body sizes of frogs.

Acoustic recording and call digitization

Vocalizations of *M. kuatunensis* (48 calls from two males) and *M. huangshanensis* (134 calls from five males) were recorded and digitized using a Portable Linear PCM Recorder (Sony PCM-D50). Exceptionally, recording of one *M. huangshanensis* (36 calls) was made using a cassette tape recorder (Sony TC-D5), and the vocalizations were digitized at 16-bits and 44 kHz like other digitized recordings. Sounds were later transferred onto a PC (Lenovo Windows 7 PC), where recordings were stored at a sampling rate of 44.1 kHz.

Calls were then categorized according to the degree of frequency modulation and harmonic structure (Feng et al., 2009). The call properties were extracted with PRAAT software (Boersma and Weenink, 2009). Call attributes, following the definition of Matsui (1997), included mean note duration, mean inter-note interval between separate notes, mean dominant frequency (mean DF), and minimum and maximum dominant frequencies (MinDF and MaxDF) for each male. A note is defined as a complete sequence of pulses separated from the next note by a notable gap (inter-note interval). Dominant frequency of a call is defined as the harmonic frequency that carries the most energy.

Analysis and statistics

Differences among groups were analyzed by a Kruskal-Wallis ANOVA on ranks because the data were not normally distributed. All multiple comparison tests were two-tailed. Direct comparisons between two groups were performed with the nonparametric Mann-Whitney U test. We conducted pair-wise comparisons of call traits among all the individuals using Dennett's post hoc test because equal variances were not assumed. All statistical analyses were performed using SPSS statistical software (SPSS 17.0 for Windows, Release 17.0.0, SPSS Inc., Chicago, IL).

RESULTS

Call characteristics

We recorded and analyzed spontaneous vocalizations from five males of *M. huangshanensis* and two of *M. kuatunensis*. Just one basic call type was observed (Figs. 1 and
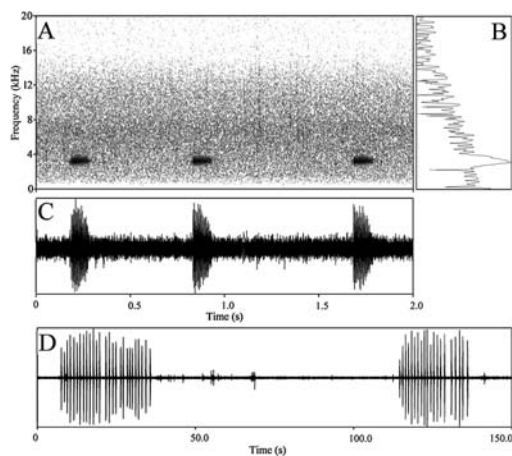

FIG. 1. Sound spectrograms (A) and waveforms (C) of three notes within a call, a slice amplitude spectrum (B), and waveforms of two calls within a call bout (D) of *Megophrys kuatunensis*; vocalizations recorded at Guadun Village.
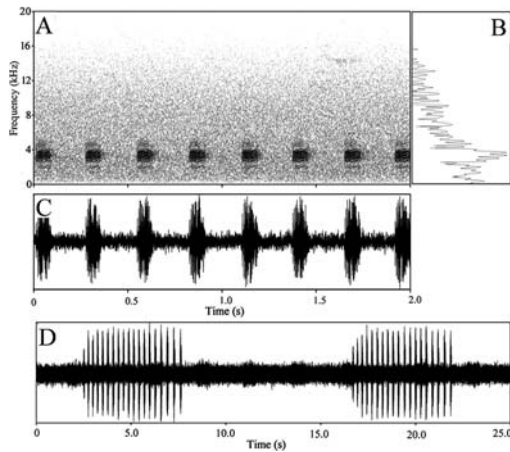
Fig. 2. Sound spectrograms (A) and waveforms (C) of eight notes within a call, a slice amplitude spectrum (B), and waveforms of two calls within a call bout (D) of *Megophrys huangshanensis*; vocalizations recorded at Fuxi Village.

2): short tonal multi-calls within a call bout that contain shallow or no frequency modulation (FM). The energy of the call was concentrated in one wide frequency band.

The call characteristics of *M. kuatunensis*, based on the calls from two individuals recorded at Guadun Village, were: mean (±SE) note duration=0.11±0.01 s (n=48); inter-note interval: 0.71±0.14 s (n=45); MinDF: 3.23±0.02 kHz (n=48); MaxDF: 3.40±0.15 kHz (n=48); and mean DF: 3.27±0.02 kHz (n=48).

The call characteristics of *M. huangshanensis*, based on the calls from five individuals, are: mean note duration=0.10±0.02 s (n=168); inter-note interval: 0.18±0.04 s (n=159); MinDF: 3.24±0.23 kHz (n=168); MaxDF: 3.40±0.223 kHz (n=168); and mean DF: 3.31±0.22 kHz (n=168).

Analysis and statistics

There were significant differences between *M. kuatunensis* and *M. huangshanensis* in the note duration and inter-note interval (P<0.01, Mann-Whitney test). However, there was no significant difference between them in MinDF (P=0.16, Mann-Whitney test), MaxDF (P=0.42, Mann-Whitney test), or mean DF

Table 1. P values in Dunnett's post hoc test for pairwise comparisons of call traits among two individuals of *Megophrys kuatunensis* (K1, K2) and five individuals of *M. huangshanensis* (H3–H7). For abbreviations, see text.

Combination			Note duration	Inter-note interval	MinDF	MaxDF	MeanDF
K1	vs	K2	<0.001	1	0.999	<0.001	0.001
H3	vs	H4	<0.001	<0.001	<0.001	<0.001	<0.001
H3	vs	H5	<0.001	<0.001	<0.001	<0.001	<0.001
H3	vs	H6	0.003	<0.001	<0.001	<0.001	<0.001
H3	vs	H7	<0.001	0.997	<0.001	<0.001	<0.001
H4	vs	H5	0.013	0	<0.001	<0.001	<0.001
H4	vs	H6	<0.001	0.996	<0.001	<0.001	<0.001
H4	vs	H7	<0.001	<0.001	<0.001	<0.001	<0.001
H5	vs	H6	0.021	<0.001	<0.001	<0.001	<0.001
H5	vs	H7	<0.001	<0.001	<0.001	<0.001	<0.001
H6	vs	H7	<0.001	<0.001	1	<0.001	<0.001
K1	vs	H3	<0.001	<0.001	<0.001	1	<0.001
K1	vs	H4	<0.001	<0.001	<0.001	<0.001	<0.001
K1	vs	H5	<0.001	<0.001	<0.001	0.263	<0.001
K1	vs	H6	<0.001	<0.001	<0.001	<0.001	<0.001
K1	vs	H7	<0.001	<0.001	<0.001	<0.001	<0.001
K2	vs	H3	<0.001	<0.001	<0.001	<0.001	<0.001
K2	vs	H4	0.049	<0.001	<0.001	<0.001	<0.001
K2	vs	H5	1	<0.001	<0.001	<0.001	<0.001
K2	vs	H6	0.291	<0.001	<0.001	<0.001	<0.001
K2	vs	H7	<0.001	<0.001	<0.001	1	<0.001

(P=0.11, Mann-Whitney test).

Within *M. kuatunensis*, the note duration (P<0.01, Mann-Whitney test), MaxDF (P<0.01, Mann-Whitney test), and mean DF (P<0.01, Mann-Whitney test) showed significant variation between individuals, but the inter-note interval (P>0.05, Mann-Whitney test) and MinDF (P>0.05, Mann-Whitney test) did not differ. In contrast, within *M. huangshanensis,* all the above traits showed significant differences among individuals (P<0.01, Kruskal-Wallis test).

We conducted pair-wise comparisons of call traits among all of the individuals using Dunnett's post hoc test, without assuming equal variances. Each individual was numbered, numbers 1 and 2 for *M. kuatunensis*, and numbers 3–7 for *M. huangshanensis.* There were no significant intraspecific differences between individuals 1 and 2 in the inter-note interval or MinDF, between individuals 4 and 6 in the inter-note interval, between individuals 3 and 7 in the inter-note

interval, or between individuals 6 and 7 in MinDF (Table 1). In interspecific comparisons, there were no significant differences between individuals 1 and 3, between 1 and 5, or between 2 and 7 in MaxDF; or between individuals 2 and 5, or between 2 and 6 in note duration (Table 1). The remaining pair-wise comparisons all resulted in significant differences (P<0.05, Dunnett's post hoc test).

DISCUSSION

Acoustic signals of male frogs usually contain information regarding species identity, size, fighting ability (Gerhardt and Huber, 2002), quality of parental care (as in some birds; Welling et al., 1997; Buchanan and Catchpole, 2000), and/or species' adaptation to their acoustic environment. In this study, we report results from statistical analyses of advertisement calls of *M. kuatunensis* and *M. huangshanensis*, which showed possible traits related to acoustic adaption, species identity, and individual condition.

Adaptation to the acoustic environment

Communication is shaped in part by the external environment. Signal detectability not only depends on the receiver's sensory system (Narins and Capranica, 1976; Arch et al., 2012) but also on the signal design of the sender and the conditions of the environment (Endler, 1992; Grafe et al., 2012). During sound transmission through the environment, signals are subject to masking from abiotic and biotic noise (i.e., signals of other noisy animals, including vocal signals of conspecifics). For riparian anurans, a major source of abiotic noise is that of rapidly flowing streams or waterfalls,

Narins (1982) concluded six strategies by which a calling frog could improve its ability to communicate in a noisy environment: 1) spectral separation strategy, namely employing unusual frequencies; 2) temporal separation strategy, calling when the environment is relatively quiet; 3) calling at a greater intensity than its neighbors; 4) producing a periodic,

stereotyped call to reduce its variability and hence facilitate localization; 5) adjusting its auditory receptors to match the spectral and temporal features of the species-specific vocalizations; and 6) possessing a high degree of frequency resolution for extracting the species' call from the background noise.

By combining strategies 1 and 5, two *Odorrana* species, *O. tormota* and *O. graminea*, use ultrasonic communication in loud stream environments (Feng et al., 2006; Shen et al., 2011), where males can produce calls with prominent energy distribution on high frequency harmonics, in line with their high frequency sensitivity (Feng et al., 2006).

Although we did not analyze environmental noise at the sites of recording, environmental noise of the streams of Huangshan, where *M. huangshanensis* sympatrically occurs with *O. tormota*, have a peak around 0.1 kHz, substantial amplitudes over 0.2–10 kHz, and a progressive decline from 11–22 kHz (Feng et al., 2006). *Megophrys kuatunensis* is also sympatric with the *Odorrana* species, but the two megophryids completely differ in acoustic characteristics from the *Odorrana*. First, the dominant frequencies of the two megophryids are lower than those of the two sympatric *Odorrana* species (Feng et al., 2006; Shen et al., 2011) (strategy 1). Second, the two *Megophrys* species produce a periodic, stereotyped call to reduce its variability and hence facilitate the localization (strategy 4). Finally, the most conspicuous strategy is to concentrate their spectral energy in a single frequency band, which might subserve calling at a greater intensity than the background noise (strategy 3). Thus, it is conceivable that these two megophryid species adopt a combination of these strategies to mask the background noises in a different way from two *Odorrana* species.

Species identity

As mentioned above, each species' calls must differ from those of other species for accurate recognition of conspecifics (Wollerman and Wiley, 2002). Although having similar

acoustic traits, the two *Megophrys* species studied showed significant differences from each other in the note duration and inter-note interval. Statistical comparisons showed that the duration and dominant frequency (including minimum, maximum, and mean) all showed large overlap between the two species. Only the inter-note interval showed clear separation between them. Resemblance in duration and dominant frequency in the two species may be due to phylogenetic constraint. However, our results differ from those reported by Wang et al. (2014) in this regard. For *M. huangshanensis*, they showed note duration of 0.09 s and inter-note interval of 0.17 s, only slightly smaller than our values of 0.10 s and 0.18 s, respectively. In contrast, their values for *M. kuatunensis* (note duration=0.21 s, inter-note interval=1.00 s) are much larger than ours (0.11 s and 0.71 s, respectively). Reasons for the discordance in these temporal characteristics are unknown, but may partly be due to possible differences in temperatures at the time of recording, which they did not provide. Wang et al. (2014) also showed highest and lowest frequencies and the means of such values approximate our results.

Individual variation

Frogs' acoustic signals usually exhibit variation among intraspecific individuals (Gerhardt, 1991; Feng et al., 2009; Briggs, 2010; Chakraborty et al., 2010). On one hand, this intraspecific variation may confer information about an individual's condition. For example, males of some frog species can assess the size and fighting ability of rivals based on size-related variation in spectral properties of the calls (review in Gerhardt and Bee, 2006). Other studies of sexual selection and female choice have shown that female frogs commonly prefer the low-frequency calls of larger males or differentiate traits that potentially depend on a male's condition, such as call duration and calling rate (Gerhardt and Huber, 2002; Bee et al., 2010; Richardson et al., 2010). On the other hand, call diversity may be caused by the senders' acoustic regula-

tion when they encounter variable conditions. For example, some male frogs will change their pulse rate (Schwartz and Wells, 1984; Owen and Gordon, 2005), duration, and interval (Martinez-Rivera and Gerhardt, 2008) when they encounter a conspecific male, and dominant frequency when they encounter background noise (Parris et al., 2009).

Since no aggregation or chorus was observed for either species in this study, the recorded calls are judged to be courtship calls. Intraspecific variations might have been affected by differences in surrounding temperatures that varied somewhat at the time of recording, and variations in body size, which we did not accurately measure. In addition to these possibilities, varied individual condition or calling adjustments to their microhabitat cannot be ruled out. These potential factors need further studies in the future.

Literature Cited

Altmann, S. A. 1959. Field observations on a howling monkey society. *Journal of Mammalogy* 40: 317–330.

Arch, V. S., Grafe, T. U., Gridi-Papp, M., and Narins, P. M. 2009. Pure ultrasonic communication in an endemic Bornean frog. *PLoS ONE* 4: 1–8.

Arch, V. S., Simmons, D. D., Quiñones, P. M., Feng, A. S., Jiang, J.P., Stuart, B. L., Shen, J.-X., Blair, C, and Narins, P. M. 2012, Inner ear morphological correlates of ultrasonic hear-

ing in frogs. *Hearing Research* 283: 70–79.

BEE, M. A., COOK, J. M., LOVE, E. K., O'BRYAN, L. R., PETTITT, B. A., SCHRODE, K., AND VELEZ, A. 2010. Assessing acoustic signal variability and the potential for sexual selection and social recognition in boreal chorus frogs (*Pseudacris maculata*). *Ethology* 116: 564–576.

BOERSMA, P. AND WEENINK, D. 2009. *Praat: doing phonetics by computer, Version 5.1. 44*. http://www.praat.org/

BOOMAN, A. AND KURNIATI, H. 2011. Evolution of high-frequency communication in frogs. *Evolutionary Ecology Research* 13: 197–207.

BRENOWITZ, E., WILCZYNSKI, W., AND ZAKON, H. 1984. Acoustic communication in spring peepers. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 155: 585–592.

BRIGGS, V. S. 2010. Call trait variation in Morelett's tree frog, *Agalychnis moreletii*, of Belize. *Herpetologica* 66: 241–249.

BRUMM, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology* 73: 434–440.

BUCHANAN, K. L. AND CATCHPOLE, C. K. 2000. Song as an indicator of male parental effort in the sedge warbler. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267: 321–326.

CAMPBELL, D. J. AND SHIPP, E. 1979. Regulation of spatial pattern in populations of the field cricket *Teleogryllus commodus* (Walker). *Zeitschrift für Tierpsychologie* 51: 260–268.

CHAKRABORTY, M., MANGIAMELE, L. A., AND BURMEISTER, S. S. 2010. Neural activity patterns in response to interspecific and intraspecific variation in mating calls in the Tungara frog. *PLoS ONE* 5: 1–10.

CYNX, J., LEWIS, R., TAVEL, B., AND TSE, H. 1998. Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*. *Animal Behaviour* 56: 107–113.

DOOLAN, J. M. AND MAC NALLY, R. C. 1981. Spatial dynamics and breeding ecology in the cicada *Cystosoma saundersii*: the interaction between distributions of resources and intraspecific behaviour. *Journal of Animal Ecology* 50: 925–940.

DUELLMAN, W. E. AND TRUEB, L. 1986. *Biology of Amphibians*. Johns Hopkins University Press, London.

ENDLER, J. A. 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist* 139: 125–153.

FEI, L., YE, C. Y., AND JIANG, J.-P. (Eds.). 2012. *Colored Atlas of Chinese Amphibians and Their Distributions*. Sichuan Publishing House of Science and Technology, Chengdu.

FENG, A. S., NARINS, P. M., XU, C. H., LIN, W. Y., YU, Z. L., QIU, Q., XU, Z. M., AND SHEN, J. X. 2006. Ultrasonic communication in frogs. *Nature* 440: 333–336.

FENG, A. S., RIEDE, T., ARCH, V. S., YU, Z., XU, Z. M., YU, X. J., AND SHEN, J. X. 2009. Diversity of the vocal signals of concave eared torrent frogs (*Odorrana tormota*): evidence for individual signatures. *Ethology* 115: 1015–1028.

GERHARDT, H. C. 1991. Female mate choice in treefrogs: static and dynamic acoustic criteria. *Animal Behaviour* 42: 615–635.

GERHARDT, H. C. 1994a. Selective responsiveness to long-range acoustic signals in insects and anurans. *American Zoologist* 34: 706–714.

GERHARDT, H. C. 1994b. The evolution of vocalization in frogs and toads. *Annual Review of Ecology and Systematics* 25: 293–324.

GERHARDT, H. AND BEE, M. 2006. Recognition and localization of acoustic signals. p. 113–146. *In*: P. M. Narins, A. S. Feng, R. R. Fay, and A. N. Popper (eds.), *Hearing and Sound Communication in Amphibians*. Springer, New York.

GERHARDT, H. C. AND HUBER, F. 2002. *Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions*. University of Chicago Press, Chicago.

GRAFE, T. U., PREININGER, D., SZTATECSNY, M., KASAH, R., DEHLING, J. M., PROKSCH, S., AND HODL, W. 2012. Multimodal communication in a noisy environment: A case study of the Bornean rock frog *Staurois parvus*. *PLoS ONE* 7: e37965.

GREENFIELD, M. D. 1988. Interspecific acoustic interactions among katydids *Neoconocephalus*: inhibition-induced shifts in diel periodicity. *Animal Behaviour* 36: 684–695.

HERTZ, A., HAUENSCHILD, F., LOTZKAT, S., AND KÖHLER, G. 2012. A new golden frog species of the genus *Diasporus* (Amphibia, Eleutherodactylidae) from the Cordillera Central, western Panama. *ZooKeys* 196: 23–46.

HOSKIN, C. J., HIGGIE, M., McDONALD, K. R., AND MORITZ, C. 2005. Reinforcement drives rapid allopatric speciation. *Nature* 437: 1353–1356.

KAISER, K., SCOFIELD, D. G., ALLOUSH, M., JONES, R. M., MARCZAK, S., MARTINEAU, K., OLIVA, M. A., AND NARINS, P. M. 2011. When sounds collide: the effect of anthropogenic noise on a breeding assemblage of frogs in Belize, Central America. *Behaviour* 148: 215–232.

KATTI, M. AND WARREN, P. S. 2004. Tits, noise and urban bioacoustics. *Trends in Ecology & Evolution* 19: 109–110.

LENGAGNE, T., AUBIN, T., LAUGA, J., AND JOUVENTIN, P. 1999. How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266: 1623–1628.

MARLER, P. 1972. Vocalizations of East African monkeys II: black and white colobus. *Behaviour* 42: 175–197.

MARTINEZ-RIVERA, C. C. AND GERHARDT, H. C. 2008. Advertisement-call modification, male competition, and female preference in the bird-voiced treefrog *Hyla avivoca*. *Behavioral Ecology and Sociobiology* 63: 195–208.

MATSUI, M. 1997. Call characteristics of Malaysian *Leptolalax* with the description of two new species (Anura: Pelobatidae). *Copeia* 1997: 158–165.

MATSUI, M. 2006. Three new species of *Leptolalax* from Thailand (Amphibia, Anura, Megophryidae). *Zoological Science* 23: 821–830.

MATSUI, M., BELABUT, D. M., AHMAD, N., AND YONG, H. S. 2009. A new species of *Leptolalax* (Amphibia, Anura, Megophryidae) from Peninsular Malaysia. *Zoological Science* 26: 243–247.

NARINS, P. M. 1982. Effects of masking noise on evoked calling in the Puerto Rican coqui (Anura: Leptodactylidae). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural,* *and Behavioral Physiology* 147: 439–446.

NARINS, P. M. AND CAPRANICA, R. R. 1976. Sexual differences in the auditory system of the tree frog *Eleutherodactylus coqui*. *Science* 192: 378–380.

OWEN, P. C. AND GORDON, N. M. 2005. The effect of perceived intruder proximity and resident body size on the aggressive responses of male green frogs, *Rana clamitans* (Anura : Ranidae). *Behavioral Ecology and Sociobiology* 58: 446–455.

PARRIS, K. M., VELIK-LORD, M., AND NORTH, J. M. A. 2009. Frogs call at a higher pitch in traffic noise. *Ecology and Society* 14: 25.

POPE, C. H. 1929. Four new frogs from Fukien Province, China. *American Museum Novitates* 352: 1–5.

PYRON, R. A. AND WIENS, J. J. 2011. A large-scale phylogeny of Amphibia including over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution* 61: 543–583.

PYTTE, C. L., RUSCH, K. M., AND FICKEN, M. S. 2003. Regulation of vocal amplitude by the blue-throated hummingbird, *Lampornis clemenciae*. *Animal Behaviour* 66: 703–710.

RICHARDSON, C., JOLY, P., LENA, J. P., PLENET, S., AND LENGAGNE, T. 2010. The challenge of finding a high-quality male: a treefrog solution based on female assessment of male calls. *Behaviour* 147: 1737–1752.

ROBERTSON, J. G. M. 1984. Acoustic spacing by breeding males of *Uperoleia rugosa* (Anura: Leptodactylidae). *Zeitschrift für Tierpsychologie* 64: 283–297.

SCHWARTZ, J. J. AND WELLS, K. D. 1984. Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*. *Behavioral Ecology and Sociobiology* 14: 211–224.

SHEN, J. X., XU, Z. M., FENG, A. S., AND NARINS, P. M. 2011. Large odorous frogs (*Odorrana graminea*) produce ultrasonic calls. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 197: 1027–1030.

SULLIVAN, B. K. AND WAGNER, W. E. 1988. Variation in advertisement and release calls, and social influences on calling behavior in the

Gulf Coast toad (*Bufo valliceps*). *Copeia* 1988: 1014–1020.

SUN, J. W. C. AND NARINS, P. M. 2005. Anthropogenic sounds differentially affect amphibian call rate. *Biological Conservation* 121: 419–427.

WANG, Y.-Y., ZHAO, J., YANG, J.-H., ZHOU, Z.-X., CHEN, G.-L., AND LIU, Y. 2014. Morphology, molecular genetics, and bioacoustics support two new sympatric *Xenophrys* toads (Amphibia: Anura: Megophryidae) in Southeast China. *PLoS ONE* 9: e93075.

WELLING, P. P., RYTKONEN, S. O., KOIVULA, K. T., AND ORELL, M. I. 1997. Song rate correlates with paternal care and survival in willow tits: Advertisement of male quality? *Behaviour* 134: 11–12.

WHITNEY, C. L. AND KREBS, J. R. 1975. Spacing and calling in Pacific tree frogs, *Hyla regilla*. *Canadian Journal of Zoology* 53: 1519–1527.

WOLLERMAN, L. AND WILEY, H. 2002. Possibilities for error during communication by neotropical frogs in a complex acoustic environment. *Behavioral Ecology and Sociobiology* 52: 465–473.