



Signal Synchrony and Alternation Among Neighbor Males in a Japanese Stream Breeding Treefrog, *Buergeria japonica*

Authors: Legett, Henry D., Aihara, Ikkyu, and Bernal, Ximena E.

Source: Current Herpetology, 39(1) : 80-85

Published By: The Herpetological Society of Japan

URL: <https://doi.org/10.5358/hsj.39.80>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Signal Synchrony and Alternation Among Neighbor Males in a Japanese Stream Breeding Treefrog, *Buergeria japonica*

HENRY D. LEGETT^{1*}, IKKYU AIHARA², AND XIMENA E. BERNAL^{1,3}

¹Department of Biological Sciences, Purdue University, 915 W State St, West Lafayette, IN 47907, USA

²Graduate School of Systems and Information Engineering, University of Tsukuba, Tenoudai 1–1–1, Tsukuba science city, Ibaraki 305–8573, JAPAN

³Smithsonian Tropical Research Institute, Luis Clement Avenue, Bldg. 401 Tupper, Balboa, Ancón, Panama, REPUBLIC OF PANAMA

Abstract: Animals that aggregate in leks to attract mates often time the production of their mating signals against the signals of neighboring conspecifics. Such signal timing usually falls into general patterns within these aggregations, which can be categorized based on the amount of overlap between the signals. In many species, individuals produce signals in an alternating pattern, avoiding signal overlap to reduce interference and increase mate attraction. In contrast, individuals in some species produce signals in synchrony, maximizing overlap and interference. The prevalence and function of signal synchronization is still unknown in many species. Here we examine the call timing strategies of the Ryukyu Kajika frog (*Buergeria japonica*). Using acoustic playback experiments we characterize a divergence in timing patterns between the two call types in this species, one produced in alternation and one in synchrony. Specifically, male *B. japonica* responded to playbacks of the first call type (Type I calls) with delayed Type I calls, avoiding overlap with the playbacks. In contrast, males responded to playbacks of the second call type (Type II calls) with synchronized Type II calls, overlapping their calls with the playbacks. Such variation in temporal signaling strategies within a species provides insights into how social and environmental pressures shape signal timings.

Key words: Acoustic communication; Audio playback; *Buergeria japonica*; Call timing; Synchronized signals

INTRODUCTION

Many animals aggregate in large groups when producing mating signals. In such aggregations,

signals produced at the same time can interfere with one another, reducing the ability of receivers to discriminate between individual signals (Gerhardt and Klump, 1988; Wollerman, 1999). This challenge of communicating in groups is most notable in the leks of many insect and anuran species, where female receivers select a preferred

*Corresponding author.

E-mail address: hlegett@purdue.edu

signaling male from aggregations of sometimes hundreds of signalers (Gerhardt and Huber, 2002). Indeed, there are numerous behavioural adaptations for group communication (Brumm and Slabbekoorn, 2005; Bee and Micheyl, 2008). One strategy is for signalers to avoid overlapping the timing of signal production with the signals of nearby signalers. By avoiding interference from other signals, non-overlapping signalers are more conspicuous and are thus expected to attract more mates (Greenfield, 1994). When competing signalers mutually offset the timing of their signals in this way, it results in a pattern of signal alternation. This antiphonal signal timing strategy has been broadly observed within acoustically sensitive taxa, including birds (Farabaugh, 1982), insects and anurans (Gerhardt and Huber, 2002).

Alternation of signals in aggregations of animals is widespread. There is, however, considerable variation in signal timing strategies across chorusing species (Wells and Schwartz, 2007). As an extreme opposite to alternation, males of some species produce calls in synchrony, where two or more individuals signal at the same time, maximizing the degree of signal overlap. In anurans, for example, synchronized signaling has been described in a handful of species (*Smilisca sila*: Tuttle and Ryan, 1982; *Dendropsophus ebraccata*: Wells and Schwartz, 1984; *Cochranella granulosa*: Ibáñez, 1993; *Kassina fusca*: Grafe, 1999; *Kassinia kuvagenus*: Grafe, 2003; *Hyla arenicolor*: unpublished data reviewed in Gerhardt and Huber, 2002; *Assa darlingtoni*: Clulow et al., 2017; *Diasporus diastema*: Capshaw et al., 2018). In contrast to the function of signal alternation, increased mate attraction, the function of signal synchrony in these species is less understood (Greenfield, 1994; Gerhardt and Huber, 2002). Prior studies, however, have only examined species that exclusively use one signal timing strategy.

Here we report on the call timing strategies of the Ryukyu Kajika frog (*Buergeria japonica*), a species complex ranging from Taiwan

through the Ryukyu Archipelago of Japan. In this species group, specific call properties vary between populations in the region, from island to island (Wang et al., 2017). In most cases, however, calls are generally divided into two distinct types. The first call type (Type I) is a trill that builds in intensity and frequency, from 1.8 kHz to 3 kHz, over its' duration (Fig. 1a). The second call type (Type II) is a higher dominant frequency (3 kHz) trill of constant intensity, comprised of notes similar to the high frequency notes found at the end of Type I calls (Fig. 1b). Duration is highly variable for both call types, ranging from short bursts, <0.5 s, to prolonged trills, >3.0 s (Kuramoto, 1986). Most notably, field observations suggested that while Type I calls are produced in alternation with neighboring males, Type II calls are produced in synchrony. We followed on these observations by using acoustic playbacks of calls to further determine the timing of the two call types and assess the degree of overlap between synchronized Type II calls. Ultimately, we discuss the selective pressures that might have driven this divergence in timing strategy between Type I and Type II calls in *B. japonica*.

MATERIALS AND METHODS

All observational and experimental data was collected from 7 July to 26 July 2015 at *B. japonica* choruses on Iriomote Island, Japan (24°23'30.3"N, 123°52'48.8"E), located approximately 200 km east of Taiwan in southern Okinawa. Chorus wide call effort (calls/min) of synchronized Type II calls was measured over 10 min intervals (n=11 nights). Acoustic playback experiments were used to assess male *B. japonica* response latencies to Type I and Type II calls. Playbacks were broadcast using a Pignose portable amplifier speaker (Model 7-100) placed 1 m from a focal male frog in a chorus, at an amplitude of 80 dB SPL re. 20 μ P (Brüel and Kjær digital sound level meter Type 2250) at 1 m from the speaker at ground level. Starting 30 min after sunset, a single call, either Type I

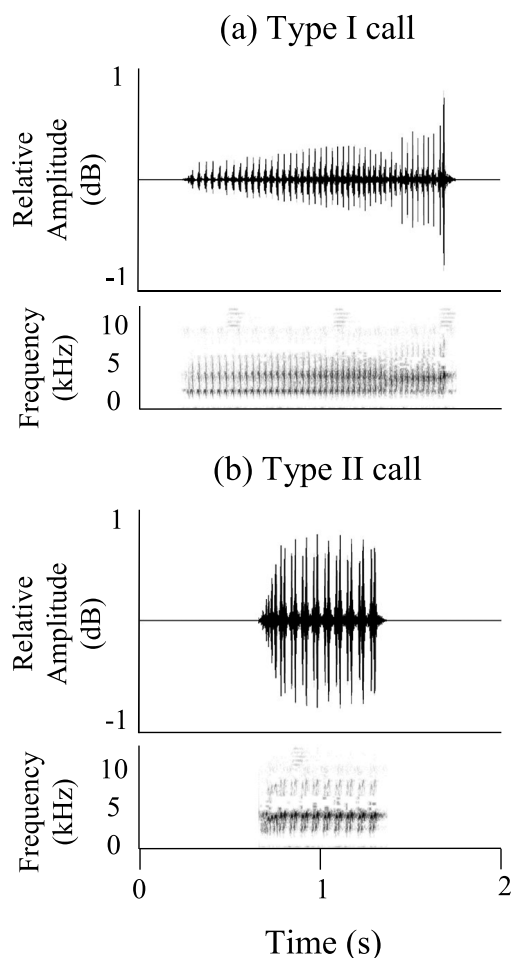


FIG. 1. Oscillograms (top) and spectrograms (bottom) of Type I (a) and Type II (b) mating calls.

or II, was broadcast to the focal frog. Only a single call was broadcast to the focal male and his first vocal response was recorded to assess call timing in response to each call type. Cases in which the focal male responded to the calls of neighboring frogs instead of the playbacks were not included in our analyses. All playbacks were haphazardly drawn from a library of 10 pre-recorded natural calls of each type, each recorded from different individual males. For the duration of this study, temperature ranged from 26.6–29.5°C, relative humidity from 82.4–97.4%, and wind speed from 0.0–4.5 m/s.

For Type I calls, male vocal behaviour was recorded using a Marantz Professional digital recorder (Model PMD660) and a Sennheiser microphone (Model ME66-K6) also placed 1 m from the focal frog ($n=27$) at ground level next to the speaker. These acoustic recordings were analyzed using CoolEdit2000 (Syntrillium Software). In contrast, for playbacks of Type II calls, timing of vocal responses could not be analyzed acoustically given the high degree of overlap and interference between the playback and the call produced by the focal male and neighboring conspecifics. Instead, we used a sound visualization method (Mizumoto et al., 2011). Specifically, we placed a small sound-to-light device next to a focal male frog in the chorus ($n=14$ focal males). A second sound-to-light device was placed next to the Pignose speaker 1 m from the frog. The sound-to-light devices contain a microphone and a light emitting diode (LED) which is activated by sound, thus the illumination visually represented sound production. The illumination of both devices, one stimulated by the playback and one stimulated by the frog's vocal response, was video-recorded (Sony HDR-XR550V, 59.94 fps). The videos were analyzed in MATLAB, following procedures established in Mizumoto et al. (2011). Given the number of frames-per-second at which the videos were recorded, the start of any sound indicated by the sound-to-light devices could be measured at a 16.68 ms resolution. Response time and degree of overlap between the acoustic playback and the focal male's call were measured and compared.

RESULTS AND DISCUSSION

Male *B. japonica* responded to playbacks of each call type suggesting that, as in many anurans, this experimental paradigm is an effective method to address vocal competition between males. For playbacks of Type I calls males responded with Type I calls, producing them at a relative delay to the playbacks, avoiding overlap and suggesting an alternating strategy, antiphonal calling. In general,

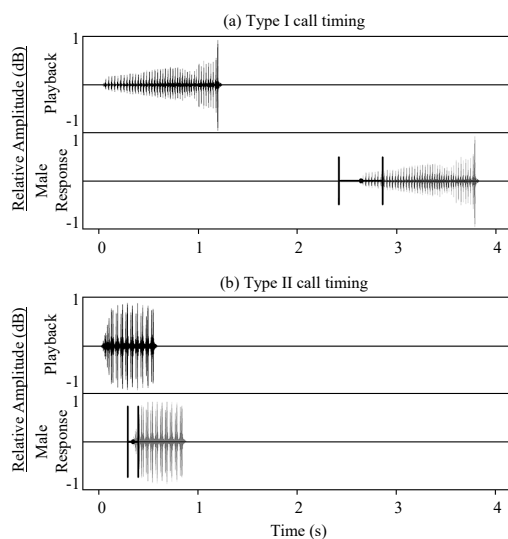


FIG. 2. Average timing of male responses to Type I (a) and Type II (b) call playbacks. Bars show standard error.

males called an average of 1.14 ± 0.22 s (\pm standard error) after the playback had ended (Fig. 2a), never overlapping with the playback. Similarly, male *B. japonica* responded to playbacks of Type II calls with Type II calls, but in this case, focal males synchronized their calls with the playbacks. Males produced Type II calls with an average latency of 0.35 ± 0.05 s, overlapping with the playback calls an average of $72.49 \pm 3.13\%$ (Fig. 2b). Thus, the playback experiments showed that males readily offset Type I calls and synchronize Type II calls with neighboring conspecifics to a high degree.

Within anuran species, the immediate timing of calls between males can be fluid, changing based on the acoustic environment or male-male interactions (Wells and Schwartz, 2007). In general, however, for a given species, call timing usually falls into a general pattern of either signal alternation or signal synchronization in which there is overlap between the calls or notes within calls (Wells and Schwartz, 2007). Male *B. japonica* provide a unique example of displaying two distinctly different call timing strategies,

antiphonal alternating calls and near-complete overlapped synchronized calls. Although the specific functions of these timing strategies are currently unknown for *B. japonica*, there are several non-mutually exclusive selective pressures that might have driven this divergence between the call types.

In high attendance choruses, numerous males calling in a bout produce an intense cacophony of chorus noise which females can use as a cue to detect and localize the chorus (Wells, 1977). This benefit is reduced when there are fewer males in the aggregation to produce such chorus sound to attract females. Previous studies on *B. japonica*, for example, found that for every 10 additional males in the chorus, the sound pressure level increased by about 3 dB SPL re. $20 \mu\text{P}$ at 1 m (decibel weighting not reported; Tang, 2009). Males in smaller choruses are thus expected to benefit from synchronized calling by increasing the peak amplitude of their combined calls through constructive interference. This “beacon effect” from synchronized calling has been previously studied in insect choruses (Shelly and Greenfield, 1991; Greenfield, 1994), and might allow male frogs in small choruses to increase the active space of their calls comparable to larger choruses. The benefits of synchrony may thus outweigh the costs when the chorus is small by increasing mate attraction to the chorus but reducing attraction to the individual. When the chorus is large, however, the sound of the chorus already serves as a “beacon”. We observed that *B. japonica* chorus size was highly variable from night to night over the period of this study, reaching over 200 calling males on nights following heavy rains (the largest observed chorus contained 355 males) and dropping below 20 males following multiple days without rain. While it has been reported that *B. japonica* calling effort generally decreases as chorus size decreases (Tang, 2009), how the relative use of each call type changes with chorus size is currently unknown. Furthermore, the assumption for this “beacon” hypothesis is that both call

types function to attracting mates. While there is evidence that both calls play a role in mate attraction (Tang, 2009; Wang et al., 2017), their exact social functions are also unknown. Empirical studies on *B. japonica* are needed to assess call type function and investigate the tradeoff between call alternation and synchrony in regards to chorus size in mate attraction.

In addition to tradeoffs in mate attraction, call timing may also be driven by nontarget receivers of mating signals, eavesdropping predators (Ryan et al., 1982). Calling *B. japonica* attract multiple species of frog-biting midges (*Corethrella* spp.) and mosquitoes (*Uranotaenia* spp.), which use frog calls as cues to localize male frogs and take blood meals (Toma et al., 2014). Frog-biting insects can impose costs on male frogs in the form of blood loss (Camp, 2006) and parasite infection (Johnson et al., 1993; Bernal and Pinto, 2016). Male *B. japonica* may synchronize their calls to reduce the ability of predators to localize individual signals, acoustically masking their calls with those of neighboring males (the eavesdropper avoidance hypothesis: Tuttle and Ryan, 1982). How call synchrony can reduce eavesdropper attraction while not also reducing female attraction is being currently investigated in other anuran species (Legett et al., 2019).

Finally, we observed that synchronized *B. japonica* Type II calls were produced sporadically and at low rates (0.61 ± 0.19 calls/min). This calling pattern is characteristic of choruses of other synchronizing species such as the neotropical pug-nosed treefrog (*S. sila*: Ryan, 1986) and the Kuvangu African running frog (*K. kuvangensis*: Grafe, 2003) suggesting similar selective pressures may have driven convergent evolution of calling strategies in these distantly related species. Overall, by displaying two distinct call timing strategies, *B. japonica* provide an ideal model for studying the costs and benefits of both call alternation and synchronization in anurans. Future studies investigating this species would provide insights into the function of signal

timing in anurans and, more broadly, how mating signals are shaped by social and environmental pressures.

ACKNOWLEDGMENTS

We thank the Tropical Biosphere Research Center of the University of the Ryukyus, Iriomote Station, for logistical support. We additionally thank C. Matsumoto and M. Matsumoto for their hospitality, advice on field sites, and knowledge of natural history. Finally, we appreciate the suggestions from two anonymous reviewers that improved the quality of the manuscript. This research was supported by an East Asia and Pacific Summer Institute Graduate Fellowship from the National Science Foundation and Japan Society for the Promotion of Science (award# 1515380). This research followed appropriate ethical and legal guidelines and regulations of the Japan Ministry of the Environment and was approved by Purdue University (IACUC Protocol #1504001224).

LITERATURE CITED

- BEE, M. A. AND MICHEYL, C. 2008. The cocktail party problem: what is it? How can it be solved? And why should animal behaviorists study it? *Journal of Comparative Psychology* 122: 235–251.
- BERNAL, X. E. AND PINTO, C. M. 2016. Sexual differences in prevalence of a new species of trypanosome infecting túngara frogs. *International Journal for Parasitology: Parasites and Wildlife* 5: 40–47.
- BRUMM, H. AND SLABBEKOORN, H. 2005. Acoustic communication in noise. *Advances in the Study of Behavior* 35: 151–209.
- CAMP, J. V. 2006. Host attraction and host selection in the family Corethrellidae (Wood and Borkent) (Diptera). Unpublished master's thesis. Georgia Southern University, Statesboro.
- CAPSHAW, G., FOSS-GRANT, A. P., HARTMANN, K., SEHUANES, J. F., AND MOSS, C. F. 2018. Timing of the advertisement call of the common tink frog (*Diasporus diastema*) shifts with the acoustic behaviour of local conspecifics. *Bioa-*

- coustics* 1–18.
- CLULOW, S., MAHONY, M., ELLIOTT, L., HUMFELD, S., AND GERHARDT, H. C. 2017. Near-synchronous calling in the hip-pocket frog *Assa darlingtoni*. *Bioacoustics* 26: 249–258.
- FARABAUGH, S. M. 1982. The ecological and social significance of duetting. *Acoustic Communication in Birds* 2: 85–124.
- GERHARDT, H. C. AND HUBER, F. 2002. *Acoustic communication in insects and anurans: common problems and diverse solutions*. University of Chicago Press, Chicago.
- GERHARDT, H. C. AND KLUMP, G. M. 1988. Masking of acoustic signals by the chorus background noise in the green tree frog: a limitation on mate choice. *Animal Behaviour* 36: 1247–1249.
- GRAFE, T. U. 1999. A function of synchronous chorusing and a novel female preference shift in an anuran. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266: 2331–2336.
- GRAFE, T. U. 2003. Synchronized interdigitated calling in the Kuvangu running frog, *Kassina kuvangensis*. *Animal Behaviour* 66: 127–136.
- GREENFIELD, M. D. 1994. Cooperation and conflict in the evolution of signal interactions. *Annual Review of Ecology and Systematics* 25: 97–126.
- IBÁÑEZ, R. 1993. Female phonotaxis and call overlap in the neotropical glassfrog *Centrolenella granulosa*. *Copeia* 1993: 846–850.
- JOHNSON, R. N., YOUNG, D. G., AND BUTLER, J. F. 1993. Trypanosome transmission by *Corethrella wirthi* (Diptera: Chaoboridae) to the green treefrog, *Hyla cinerea* (Anura: Hylidae). *Journal of Medical Entomology* 30: 918–921.
- LEGETT, H. D., PAGE, R. A., AND BERNAL, X. E. 2019. Synchronized mating signals in a communication network: the challenge of avoiding predators while attracting mates. *Proceedings of the Royal Society B* 286: 20191067.
- KURAMOTO, M. 1986. Call structures of the rhacophorid frogs from Taiwan. *Scientific report of the Laboratory for Amphibian Biology* 8: 45–68.
- MIZUMOTO, T., AIHARA, I., OTSUKA, T., TAKEDA, R., AIHARA, K., AND OKUNO, H. G. 2011. Sound imaging of nocturnal animal calls in their natural habitat. *Journal of Comparative Physiology A* 197: 915–921.
- RYAN, M. J. 1986. Synchronized calling in a treefrog (*Smilisca sila*). *Brain, Behavior and Evolution* 29: 196–206.
- RYAN, M. J., TUTTLE, M. D., AND RAND, A. S. 1982. Bat predation and sexual advertisement in a neotropical anuran. *The American Naturalist* 119: 136–139.
- SHELLY, T. E. AND GREENFIELD, M. D. 1991. Dominions and desert clickers (Orthoptera: Acrididae): influences of resources and male signaling on female settlement patterns. *Behavioral Ecology and Sociobiology* 28: 133–140.
- TANG, W. 2009. The chorus sound characteristics and phonotactic behavior of *Buergeria japonica*. Unpublished master's thesis. National Cheng Kung University, Tainan City.
- TOMA, T., MIYAGI, I., AND TAMASHIRO, M. 2014. Blood meal identification and feeding habits of *Uranotaenia* species collected in the Ryukyu Archipelago. *Journal of the American Mosquito Control Association* 30: 215–219.
- TUTTLE, M. D. AND RYAN, M. J. 1982. The role of synchronized calling, ambient light, and ambient noise, in anti-bat-predator behavior of a treefrog. *Behavioral Ecology and Sociobiology* 11: 125–131.
- WANG, Y. H., HSIAO, Y. W., LEE, K. H., TSENG, H. Y., LIN, Y. P., KOMAKI, S., AND LIN, S. M. 2017. Acoustic differentiation and behavioral response reveals cryptic species within *Buergeria* treefrogs (Anura, Rhacophoridae) from Taiwan. *PloS one* 12: e0184005.
- WELLS, K. D. 1977. The social behaviour of anuran amphibians. *Animal Behaviour* 25: 666–693.
- WELLS, K. D. AND SCHWARTZ, J. J. 1984. Vocal communication in a neotropical treefrog, *Hyla ebraccata*: advertisement calls. *Animal Behaviour* 32: 405–420.
- WELLS, K. D. AND SCHWARTZ, J. J. 2007. The behavioral ecology of anuran communication. p. 44–86. In: P. M. Narins, A. S. Feng, R. R. Fay, and A. N. Popper (eds.), *Hearing and sound communication in amphibians*. Springer, New York.
- WOLLERMAN, L. 1999. Acoustic interference limits call detection in a Neotropical frog *Hyla ebraccata*. *Animal behaviour* 57: 529–536.

Accepted: 6 January 2020