

Plasticity of Mating Calls in *Hyla japonica* (Amphibia: Hylidae)

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***Hyla japonica* males were observed to produce two distinctively different types of mating calls: advertisement call to attract conspecific females and encounter call to keep off potential competitor males. Whereas advertisement calls were organized in bouts of calls or notes, encounter calls were usually produced as separate calls. Encounter calls were much longer and had more pulses per call than advertisement calls. However, dominant frequencies or pitches of the two calls did not differ significantly. *Hyla japonica* males exhibited considerable plasticity in their calling behavior. They altered both qualitative and quantitative properties of their calls in response to other calling males. Sometimes, they even switched from producing advertisement calls to encounter calls. Advertisement calls produced by chorusing males were shorter in duration and thus more calls per bout than those produced by lone males. Males also produced much lower-pitched calls when calling together with other males. Considering that low pitch calls are often highly correlated with body size, it is possible that *H. japonica* males may try to generate deceptive calls to indicate the size greater than the actual.**

Social interactions between animals involve communication. Acoustic communication is the main mode of communication in most anuran amphibians. The significance of vocal signals have been extensively investigated as species-isolating mechanisms (Bogert, 1960; Blair, 1968; Salthe and Mecham, 1974; Littlejohn, 1977). More recently, however, much more attention has been paid on their possible functions in male-male competition and female choice (Littlejohn, 1977; Wells, 1977, 1988; Arak, 1983; Ryan, 1985; Andersson, 1994).

In general, two types of mating calls, advertisement calls and encounter calls, are produced by male anurans. Advertisement calls, also known as courtship or mating calls are produced by males to attract conspecific females, while encounter or aggressive calls are made in response to potential competitor males (Wells, 1977, 1988; Duellman and Treub, 1986). Advertisement calls and/or encounter calls have been found to play a role in maintaining inter-male distance (e.g. Awbrey, 1978; Whitney, 1980; Wilczynski and Brenowitz, 1988; Brenowitz and Rose, 1994; Rose and Brenowitz, 1997).

Although anurans have traditionally been thought of having rather invariant stereotyped acoustic signals, typical "prolonged breeders (sensu Wells, 1977)" such as most species of the genus *Hyla* are known to alter their calling behavior according to social contexts

(Wells, 1988; Wagner, 1989). In response to the calls of other males, calling males may alter the quantitative structure of the advertisement call (e.g. Wells and Schwartz, 1984a; Sullivan and Wagner, 1988) or switch from the advertisement call to the encounter call (Awbrey, 1978; Whitney, 1980; Wells and Schwartz, 1984b). Other anurans such as the Tungara frog, *Physalaemus pustulosus*, combine both advertisement and aggressive calls in one call (Drewry et al., 1982).

Despite that the structure and function of mating calls have been examined in detail for a number of species in *Hyla*, little has been studied in the Korean species. Earlier, Kuramoto (1980) analyzed vocal signals of *H. japonica* and *H. suweonensis* in Suwon, approximately 30 km south of Seoul, Korea. The calls recorded by Kuramoto were advertisement calls only and encounter calls were not mentioned.

In the following account, we report the result of a re-examination of the mating calls in *H. japonica*. We also investigated if *H. japonica* males alter their call structure in the presence of other calling males. Acoustic signals of the males calling alone and in choruses were recorded and their call properties were analyzed for comparison.

Materials and Methods

Preliminary recordings and observations were conducted on and near the campus of Seoul National University in Seoul, Namyangju in Kyonggi-do, and Kangchon in Kangwon-do during June and July, 1996. However,

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the data analyzed in this paper were all collected in the rice field in Pyongnae-dong, Namyangju-si, Kyonggi-do (37° 39' E, 127° 14' N) in 1997. We gathered information on the life history of *H. japonica* from March till September. We began recording acoustic signals as soon as males appeared in early May and continued until late July. A total of 35 males were marked for individual identification. We often heard and saw *Rana nigromaculata* and *Bufo bufo gargarizans* calling nearby.

Acoustic signals were recorded on a Sony TCD-D10 Pro II cassette tape recorder with an Audio-technica AT815b microphone and analyzed using Avisoft-Sonagraph Pro for Windows Version 2.71. Field observations and experiments were usually conducted between 1800 and 2400 h. We recorded acoustic signals of males when they called alone in early evening hours and those of chorusing males later in the evening.

Calls were classified into different types and analyzed with respect to call duration (measured in seconds), dominant frequency (kHz), the number of pulses per call, and the number of calls per bout, if it was organized in bouts. Calls within a bout were also compared in terms of amplitude (mV), duration (s), and dominant frequency (kHz). Since the number of calls per bout varies from call to call, we selected the first six calls for this comparison. In order to minimize the effect of variation among calls in a bout, we used the fourth call in a bout of advertisement call for comparisons to call properties. Call interval was measured in the interval between the fourth and fifth call.

To determine the responses of males to other calling males, we conducted playback experiments. Experimental acoustic stimuli were generated from a typical advertisement call recorded in May, 1997 at the field site. The call had the following properties: call duration-0.095 s, call interval-0.13 s, dominant frequency-2.98 kHz, pulse number-17, and number of calls in a bout-30. Calls of responding males were recorded in the field and analyzed in the laboratory.

Results

Natural history and mating behavior

Hyla japonica is widely distributed throughout South Korea. In Seoul and its vicinities in Kyonggi-do, *H. japonica* males began calling in early May but females did not appear until the start of June in 1996 and 1997. Mating activities continued until early July. Tadpoles were observed from mid-June to mid-July and the first adult in late June. Body length, measured as the snout-to-vent length, of males (mean \pm SD=3.62 \pm 0.26 cm; n=35) was significantly smaller (*t*-test, $P < 0.0001$) than that of females (4.17 \pm 0.16 cm; n=23), but its variance was greater in males (*F*-test, $P < 0.0132$).

Males usually began calling around 6 p.m. as the sun went down, but tended to begin calling earlier on cloudy or rainy days. Males often called alone in the early evening and formed choruses when additional males joined as the evening progressed. Calling sites of marked males did not change much from evening to evening.

When a female approached a calling male, the male stopped calling and began mounting the female. Amplexus occurred in a typical axillary position in which the male sat on the back of the female and held her by her armpits with his front legs. Soon after the male mounted the female firmly, she then began submerging in the rice field. With much of her body still under the water, she raised her rump barely above the water. She then moved her body side to side and released eggs. She kept switching her position in the water and continued to oviposit until all eggs were released.

Types of mating calls

Hyla japonica produced two different types of mating calls, i.e. the advertisement call and the encounter call (Fig. 1). The advertisement calls were organized in bouts of calls (Fig. 2), whereas the encounter calls tended to be in separate calls. The number of calls in a bout of the advertisement call (29.05 \pm 14.23) was highly variable (coefficient of variation (CV)=48.98%).

The two call types were also distinct in call duration, dominant frequency, and pulse number. Duration and pulse number of encounter calls (0.320 \pm 0.058 s) were longer (*t*-test, $P < 0.001$) than advertisement calls (0.097 \pm 0.011 s). Encounter calls (43.6 \pm 6.5) had significantly more pulses in a call (*t*-test, $P < 0.001$) than advertisement calls (15.7 \pm 2.2). However, dominant frequencies of encounter calls (2.66 \pm 0.21 kHz) and advertisement calls (2.97 \pm 0.20 kHz) did not differ significantly (*t*-test, $P > 0.05$). In both calls, duration (CV=11.12% for advertisement calls and 18.14% for encounter calls) and pulse number (14.01% for

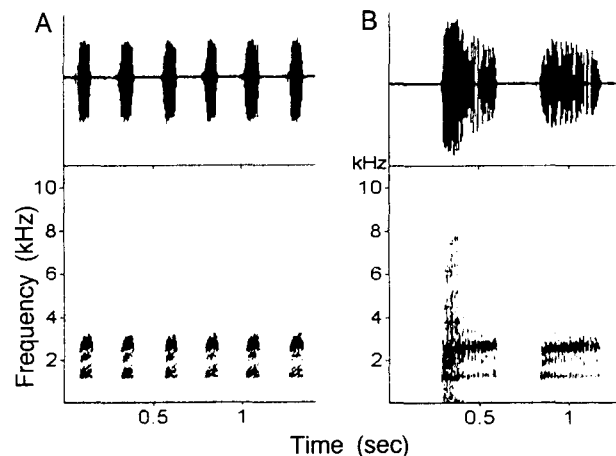


Fig. 1. Oscillograms (upper) and sonograms (lower) of advertisement call (A) and encounter call (B) of *Hyla japonica*.

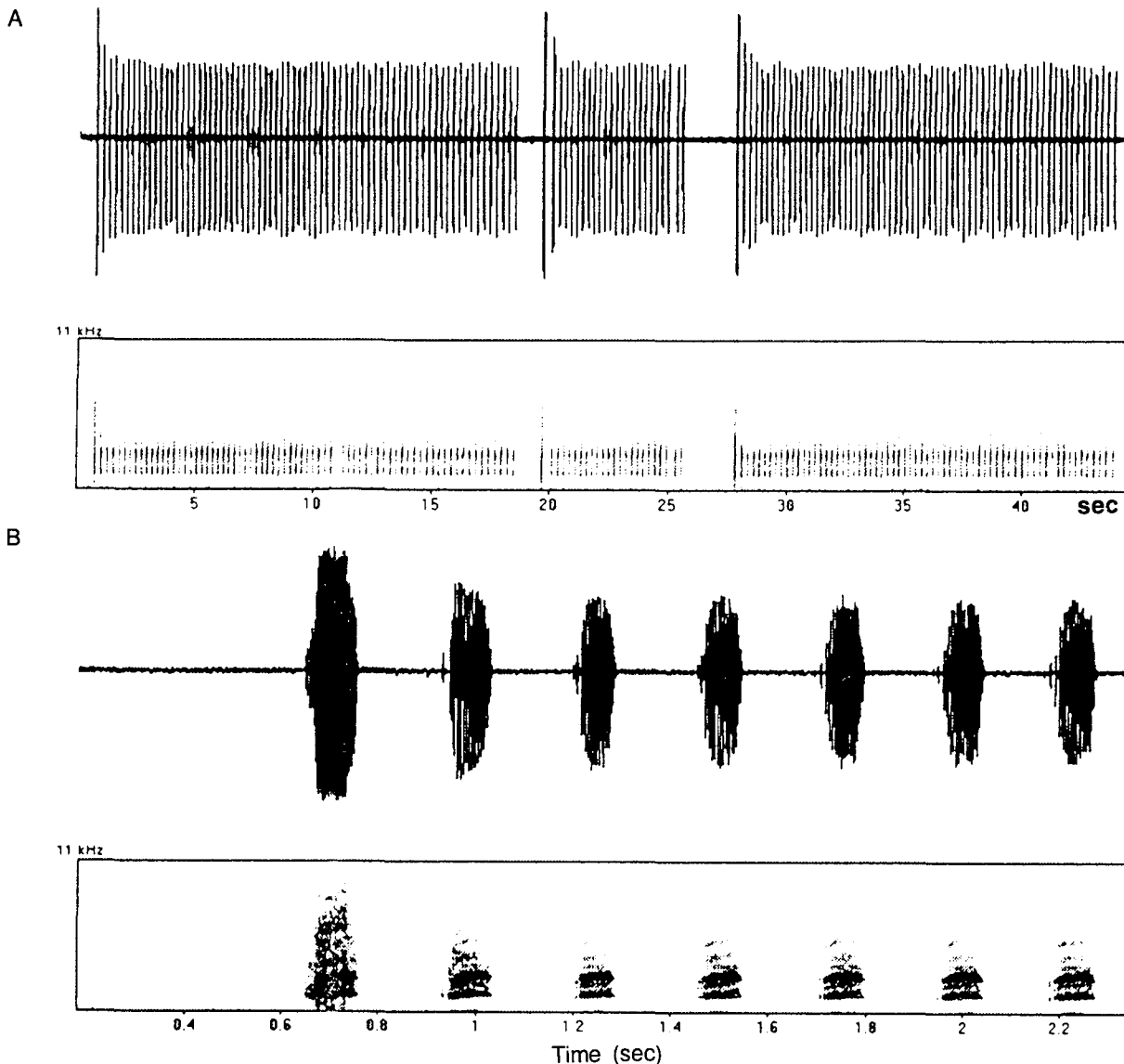


Fig. 2. Oscillograms (upper) and sonograms (lower) of advertisement calls of *Hyla japonica*. A, Three bouts of calls. B, The first seven calls of a bout.

advertisement calls and 14.91% for encounter calls) were highly variable while dominant frequencies (6.73% for advertisement calls and 7.89% for encounter calls) were relatively less variable.

Calls in a bout of advertisement call were not identical in terms of amplitude, duration, and frequency (Fig. 3). The first call had a greater amplitude and longer duration, followed by the second (two-way ANOVA, $P < 0.05$). Amplitudes of the third to sixth call did not differ from one another and was lower than the first and second call (two-way ANOVA, $P < 0.05$). The first and second call had lower dominant frequencies than the rest of the calls (two-way ANOVA, $P < 0.05$).

Plasticity in mating calls

Hyla japonica males modified their calls when there

were other calling males nearby. Compared to the advertisement calls they produced alone, the number of calls per bout increased considerably in the calls produced in choruses (Fig. 4). In the absence of other calling males, *H. japonica* males produced calls in bouts of 10-20 calls. In choruses, however, most calls had bouts of 20 to 40 calls. Males produced significantly shorter ($P < 0.001$ for the comparisons of means; $P < 0.05$ for standard deviations) calls with lower ($P < 0.05$ for means; $P < 0.05$ for standard deviations), dominant frequencies when calling in choruses than alone (Fig. 5). The means of the call intervals did not differ between the calls produced in choruses and those produced alone, but the calls in choruses were considerably more variable ($P < 0.001$) than those produced by lone males (Fig. 5). There were no significant differences in the number of pulses

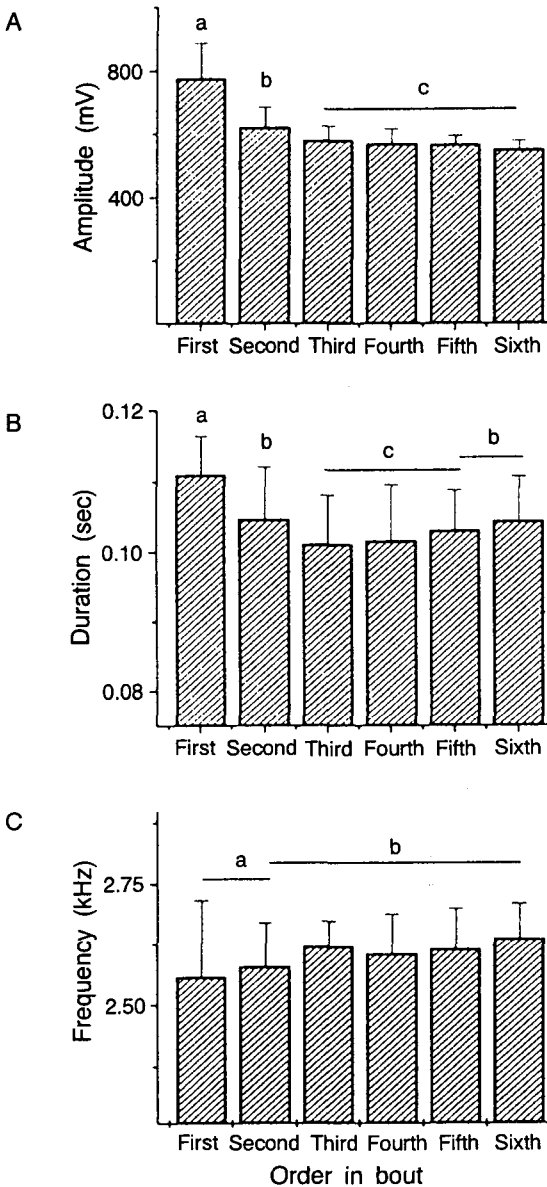


Fig. 3. Differences ($\bar{x} \pm SD$) in amplitude (A), duration (B), and dominant frequency (C) of advertisement calls of *Hyla japonica* in relation to the order of calls in a bout. Different alphabets indicate that their means are significantly different at $P=0.05$.

between the calls made by lone males and those by chorusing males (Fig. 5).

Hyla japonica males were observed to switch from the advertisement call to the encounter call when another male called nearby. In this study, however, we were not able to measure the threshold call amplitude that caused the switch. Males also produced encounter calls upon hearing advertisement calls from loudspeakers in playback experiments.

Discussion

The present study revealed that *Hyla japonica* produces

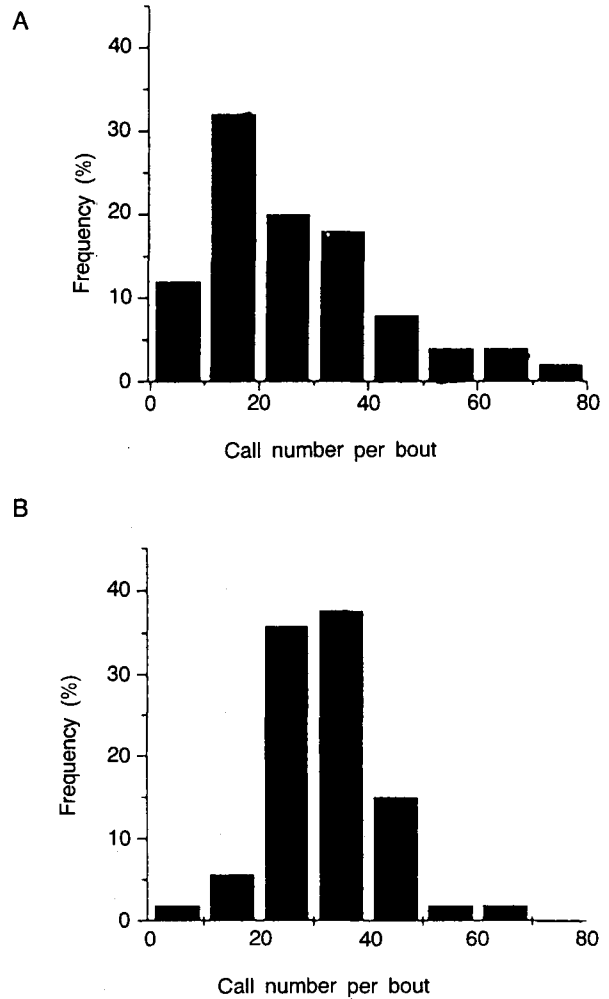


Fig. 4. Frequency distributions of the number of calls per bout when males call alone (A) and when in choruses (B).

two types of mating calls, advertisement call and encounter call. This result was not surprising, because all *Hyla* species whose calls have been analyzed in detail produce the advertisement or courtship call and one or more kinds of encounter or aggressive calls (Wells, 1977, 1988; Wells and Schwartz, 1984b). The differences in call properties between the advertisement call and encounter call of *H. japonica* are also largely in accord with those of other *Hyla* species. Encounter calls of *H. japonica* are significantly longer and have more pulses per call than advertisement calls. For example, *H. ebraccata* males in Panama also produce much longer encounter calls with higher pulse repetition rates than advertisement calls (Wells and Schwartz, 1984b).

As in other *Hyla*, the dominant frequency of the advertisement call did not differ from that of the encounter call in *H. japonica*. Dominant frequency or call pitch has been the subject of much study in anuran communication. In several species of frogs such as *Hyla chrysoscelis* (Morris and Yoon, 1989),

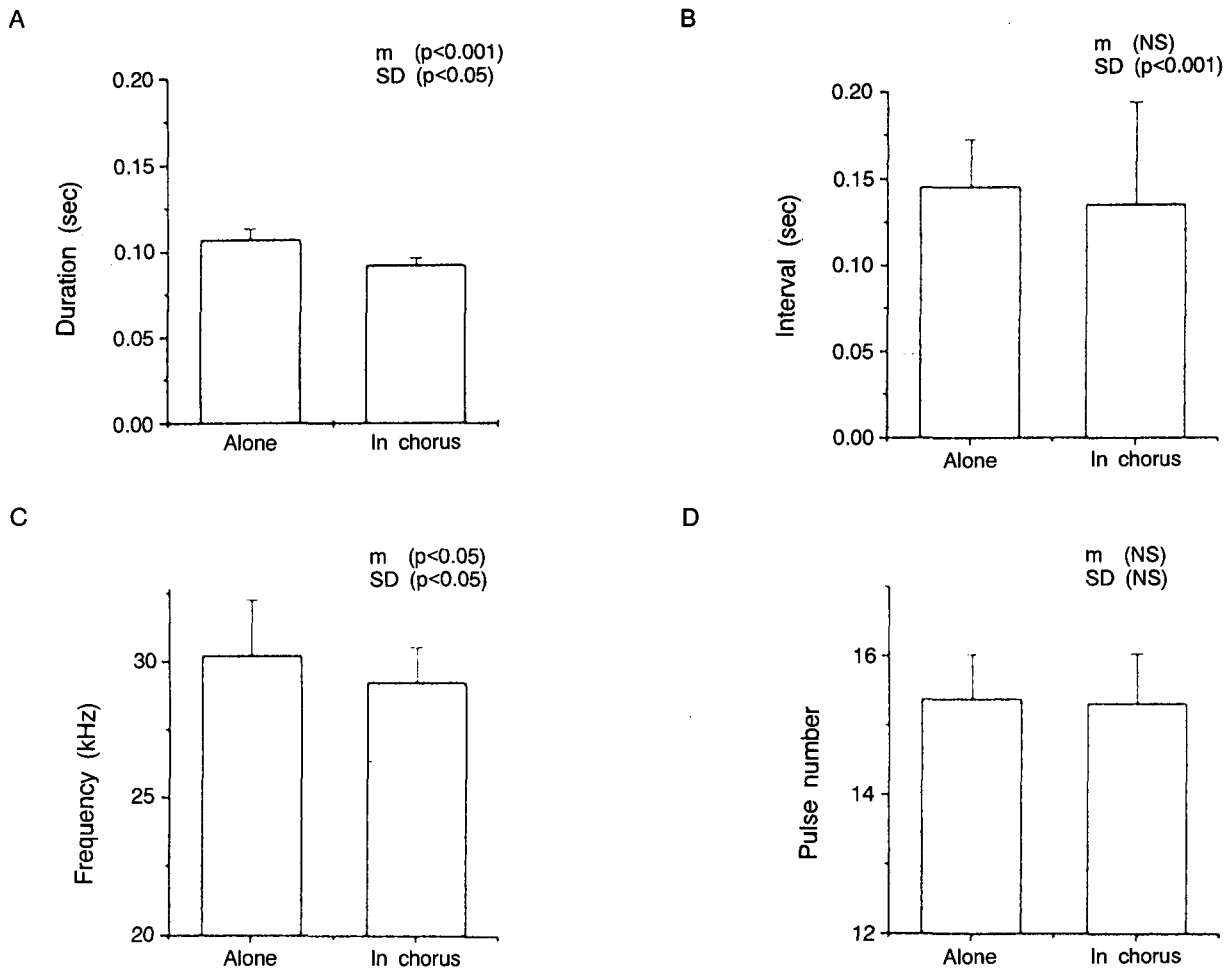


Fig. 5. Differences ($\bar{x} \pm SD$) in call duration (A), call interval (B), dominant frequency (C), and the number of calls per bout (D) between when males call alone and when in choruses. NS means that the difference is not significant at $P=0.05$.

Physalaemus pustulosus (Ryan, 1983, 1985), *Uperoleia rugosa* (Robertson, 1986) and *U. laevigata* (Robertson, 1990), females prefer low-pitched calls indicative of large males. Females may prefer large males, because large males can fertilize more eggs and thus yield higher reproductive success.

Body size is also important in the context of male-male competition (Andersson, 1994; Choe and Crespi, 1997). In many anurans, larger males tend to produce lower-pitched calls (Davies and Halliday, 1978; Ryan 1985; Gerhardt, 1982; Robertson 1986) and possess superior fighting abilities (Davies and Halliday, 1978). In the absence of actual fighting between males, males are more likely to retreat from low-pitched calls (Arak, 1983; Robertson 1986). Therefore, low dominant frequency may be adaptive in both advertisement and encounter call.

However, the role of male call pitch in female choice is by no means unanimous. Despite positive relationships between low dominant frequency of calls and male mating success found in some anurans, equally

numerous, if not more, negative or no relationships are also known in other species (e.g., Forester and Czarnowsky, 1985; Jacobson, 1985; Gerhardt et al., 1987). Relationship between male size and mating success is also debatable (Gerhardt et al., 1987). We learned in this study that females are much larger than males in *H. japonica*, but much more detailed investigations are needed to determine the functions of the two call types, and adaptive significance of body size and its relationship with various call properties.

Among various call properties, some are believed to be more static or conservative than others. Gerhardt (1991) identified dominant frequency as a static call property with coefficient of variation generally less than 4%. We found dominant frequencies of both advertisement and encounter calls in *H. japonica* to be 6-8%. Males lowered their dominant frequency when they called in choruses than when they called alone. Unlike most other anurans, males of at least two species of frogs, i.e. *Leptodactylus albilabris* (see Lopez et al., 1988) and *Acris crepitans blanchardi* (see Wagner,

1992), have previously been found to actively alter their dominant frequency. Wagner (1989, 1992) argued that males of *Acris crepitans blanchardi* not only assess the sizes of other calling males but also lower their dominant frequency to signal their fighting ability independent of size. In our study we found the number of pulses per call to be relatively invariant.

Gerhardt (1991) assessed dynamic call properties such as call rate to be much more variable with CV of 12% or more. Coefficients of variation for call duration and pulse number ranged from 11 to 18% in *H. japonica*. As mentioned above, dominant frequency, a static call property, did not vary much in the two call types of *H. japonica*.

Dominant frequency did vary within a bout of advertisement call in *H. japonica*. Typically the first two calls in a bout had lower pitches than the calls that followed them. The first call was also the loudest and longest among the calls in a bout. Wells (1988) reviewed cases in which the rate, duration, and complexity of calls change within a single bout. Such changes may require females to visit several males before initiating amplexus (Dyson et al., 1994). Starting a bout of calls with a longer, louder, and lower-pitched call is perhaps the males' attempt to distinguish himself from other calling males in a chorus.

Several studies of anuran communication have demonstrated that chorusing males exhibit considerable plasticity in their use of vocal signals (e.g. Wells, 1988; Schwartz, 1989; Brenowitz and Rose, 1994; Rose and Brenowitz, 1997). Upon hearing other males' calls, *H. japonica* males shortened call duration and added more calls to a bout of calling in addition to lowering dominant frequency. They even switched from producing advertisement calls to encounter calls. Modification of call repetition rate has been found in other *Hyla* species such as *H. crucifer* (Rosen and Lemon, 1974), *H. ebraccata* (Wells and Greer, 1981; Schwartz and Wells, 1983), and *H. phlebodes* (Schwartz and Wells, 1984). Switching from advertisement call to encounter call in response to either advertisement call or encounter call has also been observed in *H. regilla* (Whitney, 1980), *H. cinerea* (Perrill et al., 1982), *H. arborea savingnyi* (Brzoka et al., 1982), and *H. ebraccata* (Wells and Schwartz, 1984b).

We presented the first account on the characteristics of call properties in *H. japonica*. Further investigations using extensive playback tests will undoubtedly help uncover functions and adaptive values of various call properties. The data provided here are only preliminary, but will prove to be highly valuable in such investigations.

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