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# Territory Defense Strategy of the Wrinkled Frog, *Rana rugosa*

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**ABSTRACT:** The advertisement call of anurans functions to attract potential mates. The dominant frequency of an advertisement call is generally getting lower with increased snout-vent length (SVL) of the caller. *Rana rugosa* has an advertisement call with a particularly high frequency modulation. We conducted a playback experiment to verify the function of frequency modulation, and investigated the territorial behavior of the frog. The frog has five types of territory defense strategy. Strategy choice depended on the caller' s SVL. Small males became satellites or lowered the dominant frequency of their advertisement call, whereas large males actively defended their territory with encounter calls. In response to high frequency (1107 Hz) playback, the frogs lowered their advertisement call frequency, and lowered them further in response to the low frequency (1028 Hz) playback. In addition, the number of pulses in a call was increased in response to the playback. These results indicate that the frog avoids physical conflict with competitors by selecting a territory defense strategy suitable for the caller' s size, and by lowering its call frequency to disguise its SVL.

***Key words***: Call, *Rana rugosa*, Territory defense

## INTRODUCTION

The advertisement call of anurans presents information about the sex, location, reproductive state and quality of an individual, and functions to attract females and establish territories (Wells 1977). The advertisement call is thought to be used to select mates. Call elements vary with the caller' s size, age and vigor (Mauger 1989). By correlating with temperature, the advertisement call provides information about the caller' s quality and the environmental condition of its calling location. In general, the dominant frequency of the advertisement call is lower with increased snout-vent length (SVL), and the call is longer with warmer temperature (Wagner 1989a). Females choose their mates on the basis of the information transferred by the males' advertisement calls.

Territoriality has two major benefits: the first is acquiring and protecting needed resources, and the second is attracting a mate. However, defending a territory can be costly, especially if optimal resources are limited (Smith 1996). An effective territory defense strategy needs a low energy cost.

Sometimes, without any physical conflict, anurans can defend their territories with just calling behavior. The advertisement calls produced by one male probably inhibit calling by other nearby males (Whitney and Krebs 1975). The advertisement call has males spaced at some distance from their neighbors.

However, most anurans have a specialized 'encounter call' used in defending a caller' s territory, and the distance to neighbors or intruders seems to be the main factor in their converting from the advertisement call to the encounter call. In a certain distance to the neighbors, calling male could defense his territory by just increasing his repetition rate or the number of pulses in a call (Wagner 1989a, Wells 1989). By altering elements of the advertisement call, males avoid direct competition such as fighting with intruders (Sullivan 1985).

In a competition for restricted resources, such a fighting avoidance strategy is very meaningful. It allows frogs to save energy by avoiding costly fights with opponents they are unlikely to beat (Davies and Halliday 1978). Blanchard' s cricket frog (*Acris crepitans blanchardi*), for example, has a graded aggressive signal, and males decide their behavior - fight or jump away - according to the signal (Wagner 1989b).*Rana rugosa* inhabit northeast Asia. The call properties of this frog were studied extensively by No and Park (1992). No and Park categorized the frog' s call into four types: M type for advertisement (advertisement call); C and T type for territory defense (encounter call); and R type call for releasing from unwished amplexus (release call). No and Park also discussed the relation of breeding success with SVL. The dominant frequency of the advertisement call in *R. rugosa* is highly modulated and ranges from 658 Hz to 3107 Hz (No and Park 1992). We conducted an experiment to discover the function of the highly modulated advertisement call, and we conducted playback experiments to examine the relationship of territory

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defense strategy and individual characteristics. This study will be useful in understanding the social behavior and the concrete function of calls in *R. rugosa*.

## MATERIALS AND METHODS

Playback experiments using synthetic advertisement calls were conducted from May to June, in 1998 and 1999, at the ponds in Ok-cheon (lat. 36° 17′ 43″N, long. 127° 30′ 30″E) and Ka-duk (lat. 36° 34′ 38″N, long. 127° 30′ 32″E), Chungbuk.

Synthetic calls were constructed by a Kay CSL 4300B computerized speech lab. Two synthetic stimuli were emitted, with dominant frequencies of 1107 Hz (high frequency) and 1028 Hz (low frequency). These frequencies are within the natural range of variation for the population (No and Park 1992).

The two stimuli differed only in dominant frequency. Each synthetic call was 52 ms in duration and consisted of 11 pulses in a single call. Call groups of 20 calls were constructed with call rates within a call group of 1 call/s. The interval between call groups was 10 seconds. Although the pulse waveform of the synthetic calls differed slightly from that of natural calls, males responded to the synthetic calls in the same manner that they respond to the calls of real intruders.

A test male was chosen in the field and allowed to call for a 2 min pre-stimulus period. During this period, the male' s calls (natural call) were recorded with a DAT recorder (HHB PDR 1000) and condenser microphone (Sennheiser MKH816P48) within 30 cm of the calling male. Then, one of the two synthetic calls was emitted at a distance of 30 cm by a cassette recorder (Sony TCM-929). Calls were broadcast at 90 dB for 2 min stimulus periods. The vocal responses of the males were recorded throughout these periods. After about 2 min, when the vocal signal of the males had returned to the natural call, the other of the two synthetic calls was broadcast and the responses were recorded.

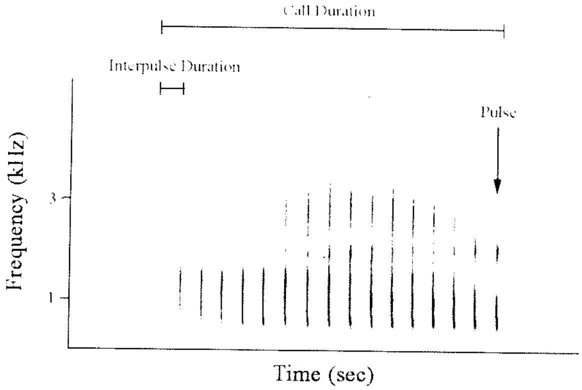


**Fig. 1**. Sonograph of typical advertisement call of *R. rugosa*.

Immediately after playback, we recorded the temperature of the calling spot with a digital thermometer (Delta Ohm HD8605). Then the male was captured and his SVL was measured to the nearest 0.01 mm with vernier calipers. Males were marked by toe clipping.

Dominant frequencies, call durations, inter-call duration, and the number of pulses of natural calls and response calls were analyzed with a CSL 4300B.

The correlation of the dominant frequency of the advertisement call with the SVL of callers was analyzed using a correlation test. The comparison of natural calls and response calls was analyzed by ANOVA.

## RESULTS

Two hundred and seventy-seven natural advertisement calls were recorded from 27 individuals. The duration of the natural calls was 47.77 ms (SD = 11.15), and inter-call duration was 55.15 ms (SD = 36.19). The natural calls contained 12.47 (SD = 2.42) pulses. The dominant frequency of natural calls was so modulated that the range was from 636 Hz to 2727 Hz, with a mean of 1408.19 Hz (SD = 610.72, Fig. 1). There was significant negative correlation between the dominant frequency of the natural call and SVL ($F = 37.252$, $p \leq 0.001$).

The behavioral responses to the broadcasted playback call fell into five distinctive types (Table 1), which were related to the SVL of the males. Large males responded with active agonistic behavior, making their encounter call, whereas small ones stopped calling, retreated, or lowered the dominant frequency of their advertisement calls ($F = 7.71$, $p \leq 0.05$, Table 1, Fig. 2). In other words, large males responded to the stimulus call more actively and aggressively than small ones.

*R. rugosa* changed not only their behavior but also the properties of their advertisement calls in response to the broadcasted call (Fig. 3). Males altered their natural call into a longer call with a lower dominant frequency. The dominant frequency of calls in response to the stimulus call was significantly lower than that of the natural call, and became even lower with lower stimulus call

Table 1. The behavioral responses of *R. rugosa* to the playback calls. The numbers in the brackets are the numbers of individuals

| Natural | Behavioral responses | | Individual size (cm) |
|---|---|---|---|
| | High frequency playback | Low frequency playback | |
| A | Satellite or Move away | | 4.08 ± 0.11 (4) |
| A | A | A | 4.11 ± 0.31 (3) |
| A | A, E | A | 4.56 ± 0.32 (3) |
| A | A, E | A, E | 4.52 ± 0.18 (9) |
| A | A | A, E | 4.92 (1) |

A: Advertisement call, E: Encounter call.

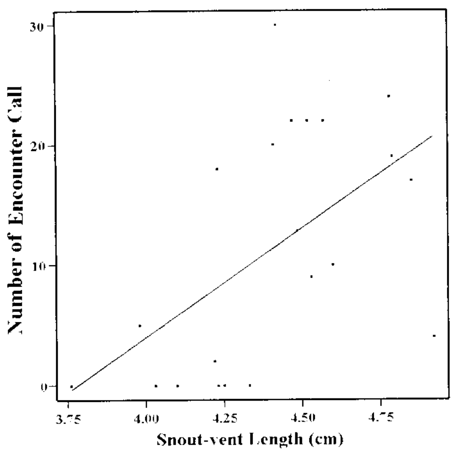


**Fig. 2.** The relationship between snout-vent length and number of encounter calls in response to the synthesized playback calls. Regression equation is $y = 12.853x - 48.898$ ($F = 7.71$, $p \leq 0.05$, $n = 20$).

frequency (Pearson' s correlation, $r = 0.298$, $p \leq 0.001$). There was a tendency for call duration to be longer, the number of pulses in a call to be greater, and inter-call duration to be shorter than for the natural call.

## DISCUSSION

Large male anurans have some advantages over small ones in two respects. One is in defending territories. In anurans, larger males often win wrestling contests over calling sites, territories, or females (Davies and Halliday 1978). Large male bullfrogs (*R. catesbeiana*), for example, usually defend the best quality territories where eggs develop rapidly and suffer the lowest rates of predation (Howard 1978). In Blanchard' s cricket frog, larger males win fights over calling sites (Wagner 1992).

The other is in mate choice. Females choose larger males as their mates by using the information about male snout-vent length transferred by acoustic signals (Morris 1989), although there is an optimal mating size of male and female (Davis and Halliday 1977).

From the results of this experiment, we suggest that *R. rugosa* have two territory defense strategies: (1) altering behavior, and

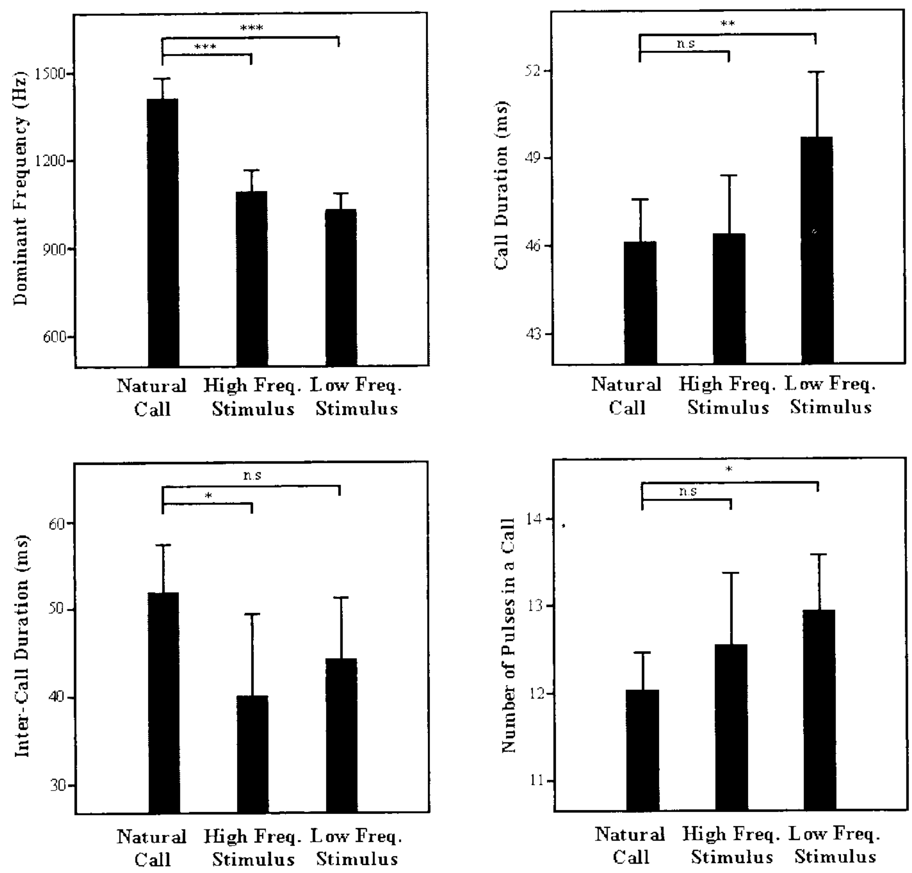


**Fig. 3.** Alteration of properties of call elements in response to the high frequency (1107 Hz) and low frequency (1028 Hz) synthesized calls (results of 521 calls from 19 individuals). * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; n.s, not significant.

(2) changing the properties of call elements. In this experiment, large calling males had a tendency to make encounter calls, the active territory defense strategy, whereas small ones tended to be satellites, to move away or to alter their advertisement calls in response to the playback. It is generally accepted that encounter calling behavior is an effective territory defense strategy (Wells 1978) in anurans. It has been shown experimentally that the encounter call inhibits calling by males in the vicinity and is often followed by the withdrawal of intruders (Fellers 1975, Pierce and Ralin 1972).

Robertson (1986) observed that males of an Australian frog (*Uperoleia rugosa*) can, on the basis of voice, assess differences in fighting ability between themselves and other individuals, and males of similar size are more likely to fight, whereas males retreat from opponents that are substantially larger. The results of this study indicated that small *R. rugosa* assessed the broadcasted advertisement call and responded by being a satellite or continuing an altered advertisement call, which is passive behavior in territoriality.

Altering the advertisement call could be a territory defense strategy. The advertisement call and the alteration of call elements are useful means of establishing distances between neighbors. In this experiment, *R. rugosa* altered call elements in response to the playback. Lower frequency seems to have special meaning in the context of mate choice and territory defense. Because the advertisement call of *R. rugosa* contains information about the caller' s SVL (in the significant negative correlation between SVL and dominant frequency), receivers such as neighbors or potential mates would perceive the size of a caller who lowers the frequency to be bigger than its actual size. Thus, lowered frequency seems to have the function of bluffing the caller' s SVL, and would have advantages in territory defense and female attraction.

Wagner (1989c) reported active lowering of the dominant frequency of advertisement calls in Blanchard' s cricket frog similar to that found in our study. Blanchard' s cricket frog assesses fighting ability by the dominant frequency of the call. Lowering the frequency functions to misrepresent size and fighting ability. In short, the advertisement call of *R. rugosa* contains information about the caller' s SVL. Listeners seem to assess the callers' fighting ability and decide their territory defense strategy according to this information. Therefore, we suggest that the dominant frequency of the intruder' s advertisement call is the major factor used by *R. rugosa* in selecting a territory defense strategy.

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