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Mating Call Structure and Variation of the Frog *Rana nigromaculata*

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참개구리(*Rana nigromaculata*)의 짝짓기 소리의 구조와 변이

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ABSTRACT

The structure and variation of the mating call in *Rana nigromaculata* was studied in a population at Da-rak, Chong-won, Chung-buk (36° 37′ latitude, 127° 21′ longitude) in Korea. The mating call consists of 3 to 8 pulse groups divided by clear silent intervals. Each pulse group is also composed of fine pulses. Temperature and body size affect the temporal and spectral characteristics of the mating call. Pulse, pulse group repetition rate and dominant frequency rise with increasing temperature, whereas pulse group repetition rate and dominant frequency decrease with increasing body size. A playback experiment was designed to establish the effect of a potential intruder on male calling. During the stimulus periods, resident males markedly decreased the pulse repetition rate, and increased the rate of pulse groups, dominant frequency, and the number of call groups. This results indicate that this species responds in a graded fashion when interacting with other individuals.

Key words: Mating call, *Rana nigromaculata*, Pulse group, Dominant frequency.

INTRODUCTION

The use of acoustic signals in anuran amphibians plays an important primary role in relation to both interspecific and intraspecific mate choice by females (Sullivan 1983, Robertson 1986a, Narins and Zelick 1988, Ryan 1990, Gerhardt 1991, Wagner and Sullivan 1995) and male-male competition (Davies and Halliday 1978, Ramer *et al.* 1983, Robertson 1986b, Wells 1988, Schwartz 1989, Wagner 1989 a,b). This is because these amphibians can distinguish between conspecifics and heterospecifics, and can discriminate among conspecifics by interacting through social communication systems that are based on significant call differences. Call discrimination experiments have revealed a few potential parameters such as call duration (Klump and Gerhardt 1987), call repetition rate (see Gerhardt 1988 for review), and call complexity (Wells and Schwartz 1984, Schwartz 1986, 1987).

Temperature and body size have been considered as the main factors that influence some important call parameters of the mating call (Gerhardt 1978, Sullivan 1984, Ryan 1985, Sullivan and Wagner 1988, No and Park 1992). In spite of such call variations, it has been reported that their mating calls possess species-specific characteristics and are used for species identification (Schneider *et al.* 1984, Gerhardt 1982). The differences in mating calls, serum proteins, and morphology of *Hyla japonica* and *H. suweonensis* in data collected in Suweon, Korea, led to the conclusion that these amphibians represent separate species (Kuramoto 1980, Yang *et al.* 1981). Furthermore, the comparative study of call types in the Genus *Hyla* in Korea showed that the A-type call belongs to *Hyla japonica* and the E-type call to *H. suweonensis* (Park *et al.* 1996). Therefore, the analysis of mating call provides important cues on the phylogenetic relationships of populations and species.

The main purposes of this study were to examine the natural structure and variation in the mating call of *Rana nigromaculata*. In order to achieve this goal, we have addressed the following: (1) call variation with temperature, (2) call variation with body size, (3) mating call variation in playback experiments. Third item was especially designed to examine how the presence of a nearby calling intruder influences mating call variation.

MATERIAL AND METHODS

Study area and general methods

We studied a population of *Rana nigromaculata* in May, 1997 at Da-rak, Chung-Won, Chung-buk (36° 37′ latitude, 127° 21′ longitude) in Korea. This population is located at a shallow seasonal pond bordered by narrow causeways. The mating call was recorded in the field with a Uher 4000 portable tape recorder, Portable Timecode DAT Recorder (PDR1000TC), and condenser microphone (type MKH 816 P48, AKG c1000s). After each recording, we measured the water temperatures (depth 3 to 5cm) adjacent to the calling males with a thermometer (HD 8605) and the snout-vent length to the nearest 0.1mm with vernier calipers. The calls was analyzed using a Kay electric sonagraph 5500. The following call parameters are measured: pulse group duration (ms), pulse repetition rate, call duration (ms), number of pulse groups per call, dominant frequency (Hz), and repetition rate of pulse groups (Fig. 1). Pulse repetition rate was calculated from the equation (N-1/pulse group dur-

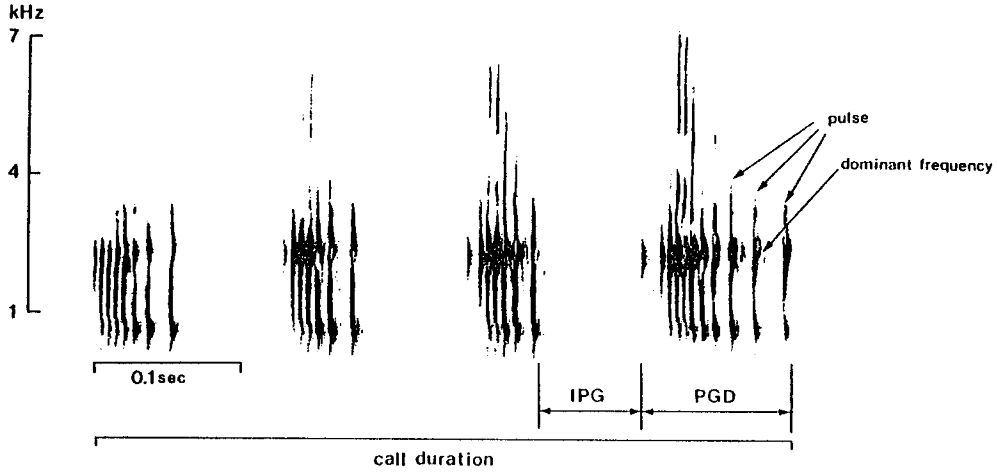

Fig. 1. Example of a mating call of *Rana nigromaculata* showing parameters used in analysis. Parameters measured are PGD (pulse group duration), number of pulses per pulse group, IPG (interval between pulse groups), pulse repetition rate, call duration, number of pulse groups per call, repetition rate of pulse groups, dominant frequency.

ation × 100; where N=the number of pulses).

Playback experiments

The experimental tape was constructed using a single mating call recorded from a single male from the study area. This call type had the following parameters: 4 pulse groups per call, call duration 34 ms, dominant frequency 1360 Hz, and inter-call intervals 3 s. We tested nine calling males of *R. nigromaculata* on 22 and 25 May 1997. Before each test was performed, for each male we recorded at least five calls from the isolated male. A male was considered isolated when no other males were calling within 5 m of this male's calling site. The stimulus tape was played for 2-minute periods from a Sony TCM 5000EV stereo cassette recorder placed approximately 1m from the calling male. During playback experiments, the response of the calling male was recorded with a Sony TCM 929 stereo cassette recorder and for closer calling males, a small Aiwa microphone fixed on long narrow rod(length 75 cm). The call intensity from the speaker varied from 83 to 87 dB at 50 cm, which was similar to the natural call intensity. Changes in the basic call parameters emitted during the non-stimulus period and stimulus period were compared, and the rate of the overlapping calls was investigated. All data were calculated using an SPSSWIN package.

RESULTS

Structure and variation of mating call

When this animal is isolated, one-group mating call is usually emitted. On the other hand, when an individual interacts with other individuals, more than two-group calls are emitted. The mating calls consist of 3 to 8 pulse groups($X=4.52\pm0.51$; N=28), which are separated by clear silent intervals. Each pulse group is also composed of fine pulses($X=8.60\pm1.46$; N=28)(Fig. 1).

As the water temperature increases from 15.7 to 21.1℃, the pulse group duration and the number of pulses per pulse group decrease, whereas the number of pulse groups per call increases(Table 1, Fig. 2~9). According to the regression calculations, the changes in the interval between pulse groups with temperature

Table 1. Relationship of mating call parameters with water temperature and body size. Results of the statistical calcultions. Singificance level: *, $P\leq0.05$; **, $P\leq0.01$; ***, $P\leq0.001$; n.s. = not significant

variable(y)	Regression equation	F-test
1. x=water temperature(N=20)		
Pulse group duration(ms)	Y=1351.54− 39.64x	197.8137***
Number of pulses per pulse group	Y= 10.16− 0.10x	6.0608*
Interval between pulse groups(ms)	−	n.s.
Pulse repetition rate	Y= 0.12+ 0.06x	50.83024***
Call duration(ms)	Y=5085.24− 56.91x	5.6656*
Number of pulse groups per call	Y= 2.19+ 0.14x	23.8687***
Repetition rate of pulse groups	Y= 0.01+ 0.004x	91.60424***
Dominant frequency(Hz)	Y= 766.27+ 44.84x	62.86***
2. x=body size(N=18)		
Pulse group duration(ms)	Y= 380.68+ 46.58x	15.1904***
Number of pulses per pulse group	Y= 12.96− 0.81x	36.8565***
Interval between pulse groups(ms)	Y= 546.41− 46.75x	22.5662***
Pulse repetition rate	Y= 2.24− 0.19x	54.55658***
Call duration(ms)	Y=2752.71+228.04x	7.7470**
Number of pulse groups per call	−	n.s.
Repetition rate of pulse groups	−	n.s.
Dominant frequency(Hz)	Y=3520.0 −340.06x	395.9495***

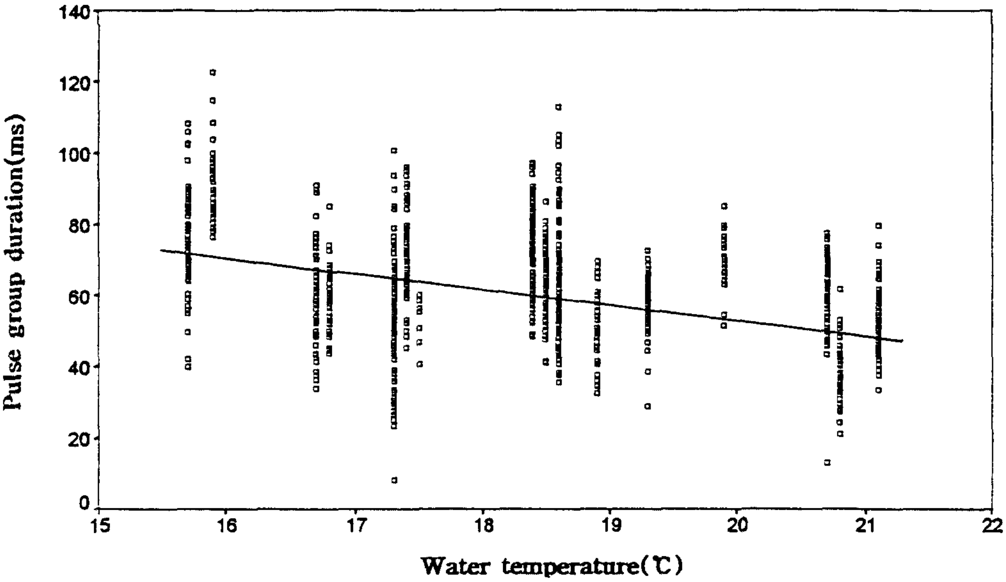

Fig. 2. The influence of water temperature on the pulse group duration.

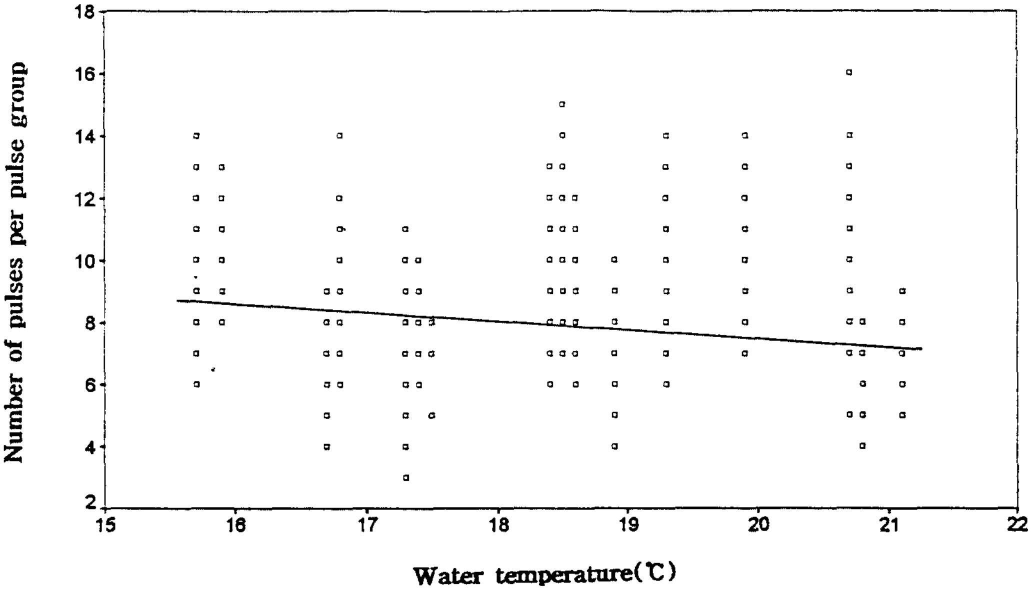

Fig. 3. The influence of water temperature on the number of pulses per pulse group.

leads to a decrease addition, the dominant frequency of the calls increases significantly with increasing temperature.

The increase of snout-vent length of the recorded males from 4.82 to 6.76 cm leads to a decrease in the number of pulses per pulse group, but an increase in the pulse group duration, which decreases the pulse repetition rate(Table 1, Fig. 10~17). The increase in the overall call duration mainly results from an increase in the interval pulse groups are not related to body size. The mating calls of small males

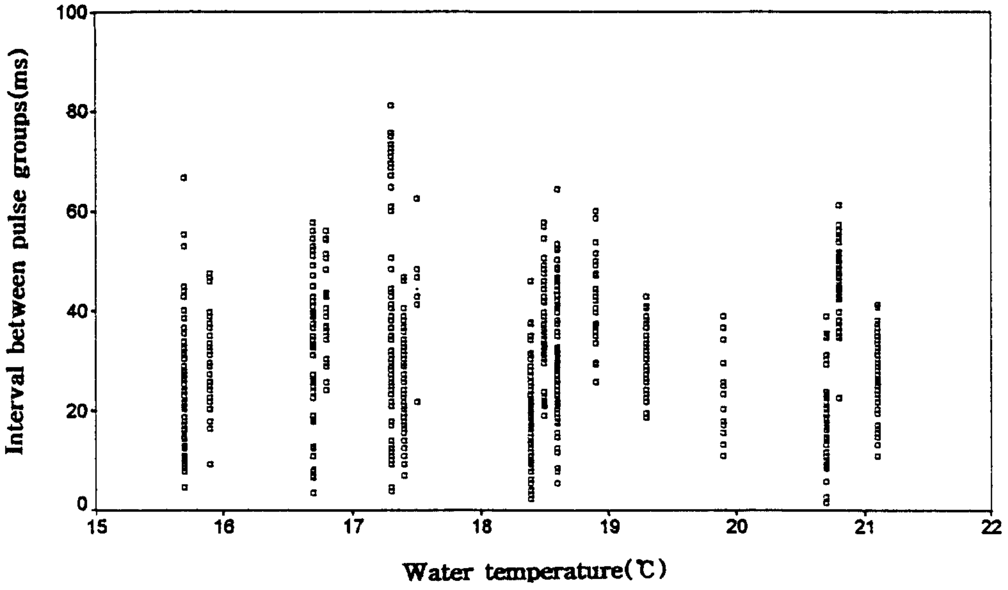

Fig. 4. The influence of water temperature on the interval between pulse groups.

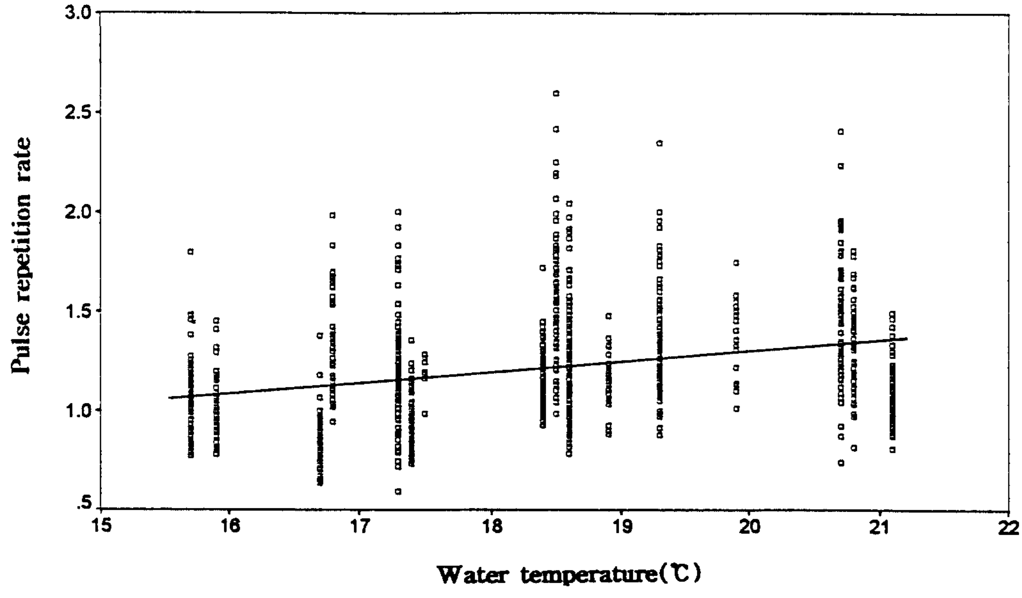

Fig. 5. The influence of water temperature on the pulse repetition rate.

show a tendency to produce a higher dominant frequency than those of the large males.

Playback experiment

The results of playback experiments are shown in Table 2. The pooled data from the mating calls of all nine frogs indicate that the interval between pulse groups is usually reduced to a greater extent and that the number of pulse groups per call is increased to a greater extent during the stimulus period than during non-stimulus period. This means that the re-

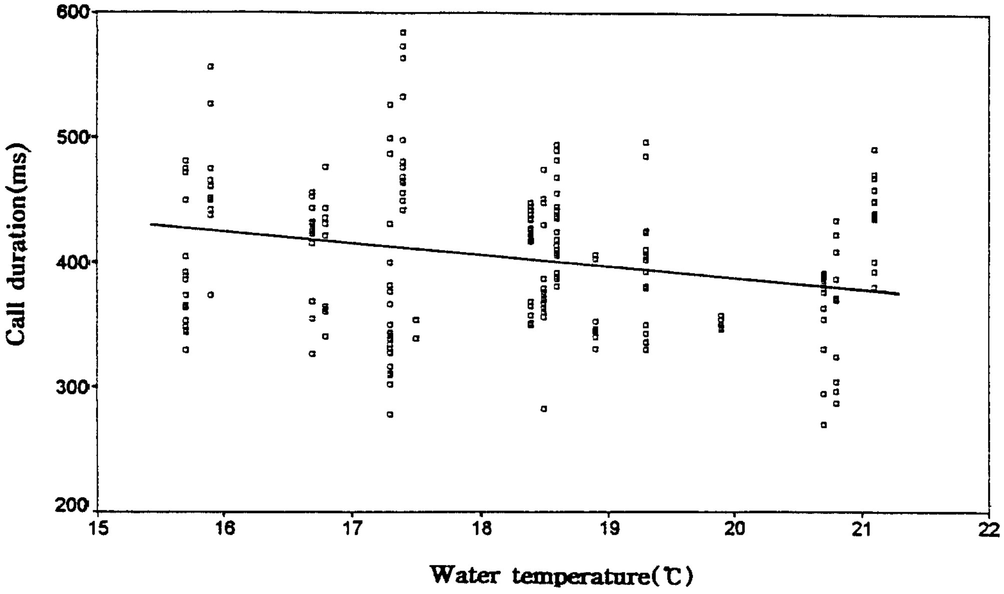

Fig. 6. The influence of water temperature on the call duration.

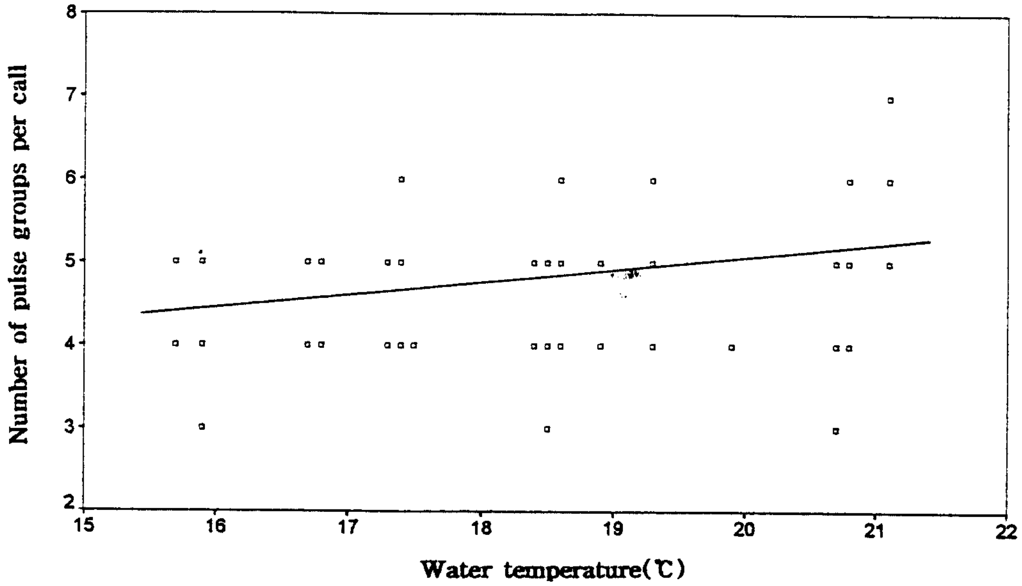

Fig. 7. The influence of water temperature on the number of pulse groups per call.

petition rate of pulse groups rises. However, the pulse group duration and the number of pulses per pulse group show insignificant differences. These consequences induce a constant call duration overall. When considering the changes in the group calls of the selected males, the males usually switch from one- to two- or more group calls during the playback experiment. Of the 158 response calls, 36.08% were onegroup calls, 44.94% were two-group calls, 12.66% were three-group calls, plus a few others. The males produce their calls immediately after hearing the stimulated call. In this respect, 27.85% of the calls

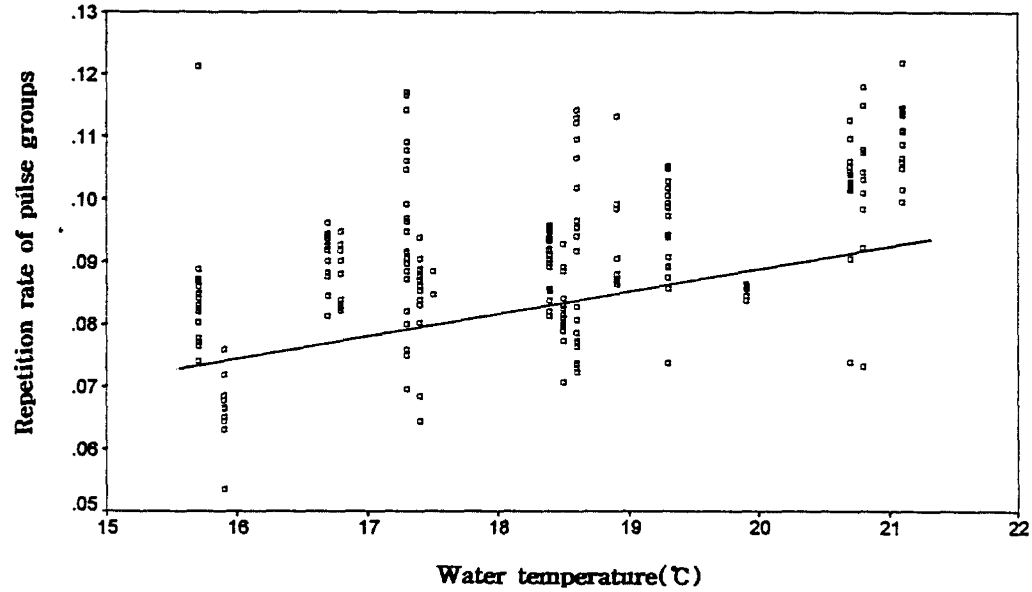

Fig. 8. The influence of water temperature on the repetition rate of pulse groups.

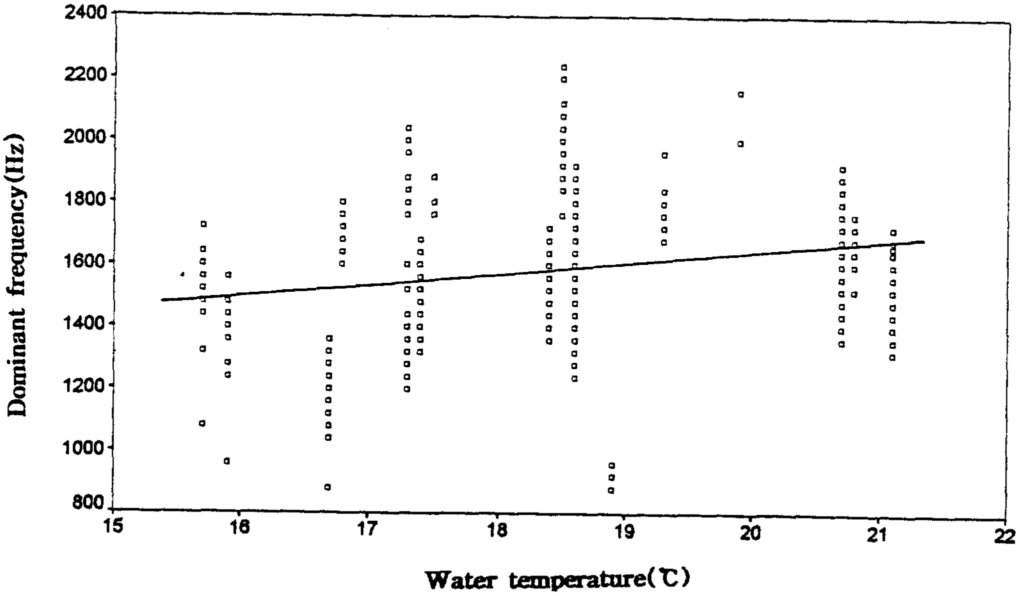

Fig. 9. The influence of water temperature on the dominant frequency.

given by the subject males overlapped with the playback calls. The dominant frequencies of the tested males increased significantly during the stimulus period.

DISCUSSION

Call features

Temperature and body size affect the temporal and spectral characteristics of the mating call of *R. nigromaculata*. It has been reported that temperature chiefly induces a decrease in the call duration and

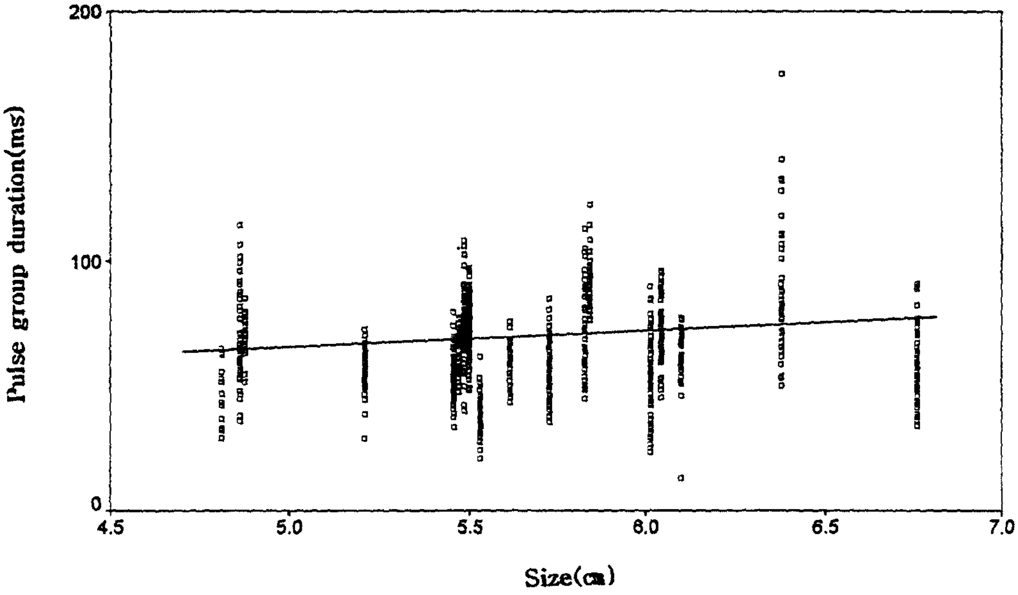

Fig. 10. The influence of body size on the pulse group duration.

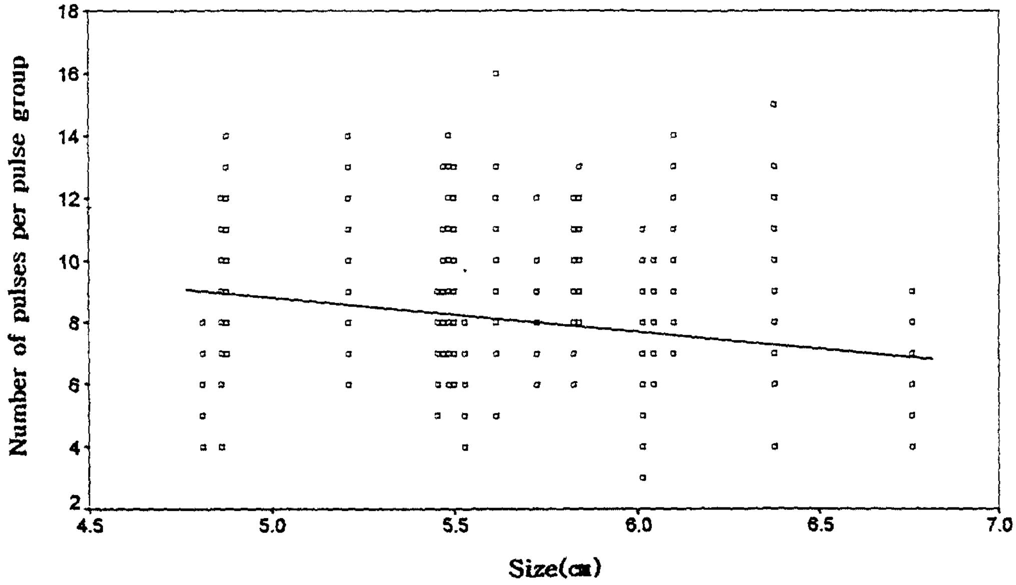

Fig. 11. The influence of body size on the number of pulses per pulse group.

the pulse group duration, and an increase in the pulse repetition rate and the number of pulse groups per call (Nevo and Schneider 1983, Wagner 1989c). These results are consistent with our research. According to the earlier research of Yang et al.(1988), it was shown that the differences in mating calls between *R. nigromaculata* and *R. plancyi* play an important role in the premating isolating mechanism. In addition, Schwartz (1987) showed that females in multi-species choruses could discriminate their conspecific males by a species-specific feature, the pulse rate. On the contrary, in our research body size infl-

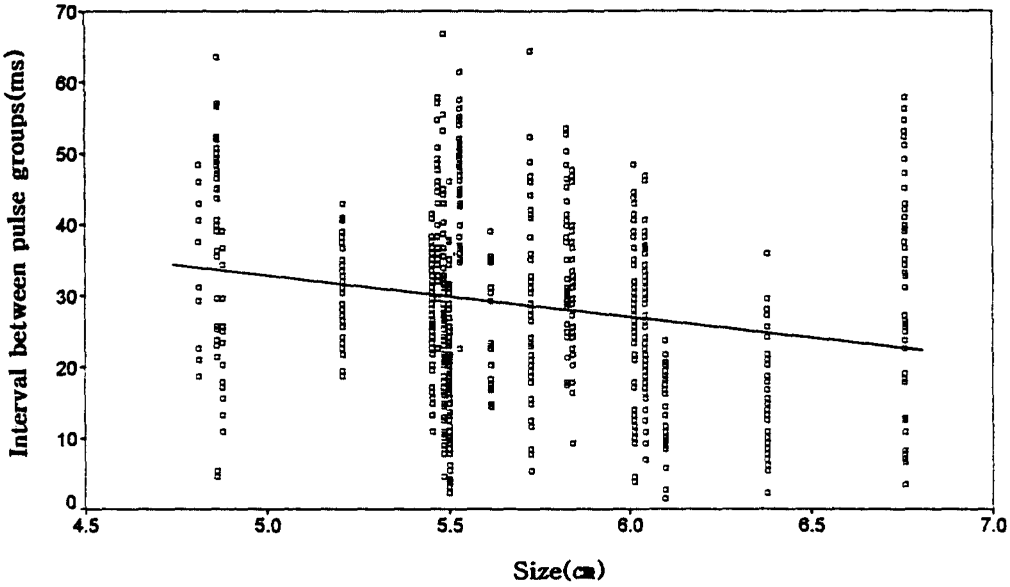

Fig. 12. The influence of body size on the interval between pulse groups.

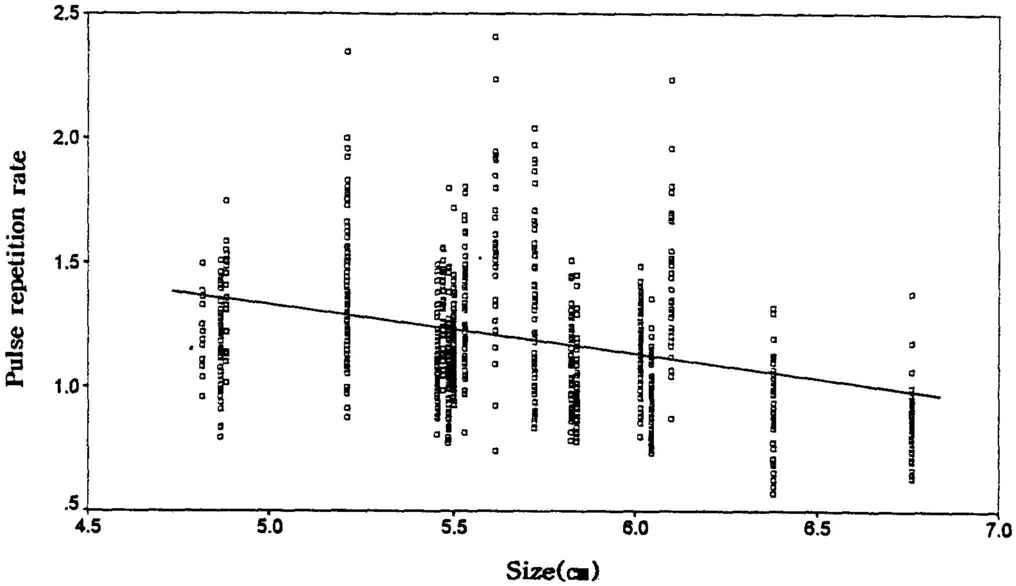

Fig. 13. The influence of body size on the pulse repetition rate.

uences these parameters inversely, except for the number of pulse groups per call. Another call parameter, dominant frequency, also shows obvious variations with body size. It has been stated that females prefer calls of a lower frequency which are produced by larger males (Ryan 1980, Mârquez 1995a), and that males assess the size of an opponent on the basis of the frequency differences of the calls(Arak 1983a, Robertson 1986b, Wagner 1989a, Wagner 1992). Gerhardt (1982), however, indicated that the calls of average size males are chosen by the gravid females more frequently than those of small and very

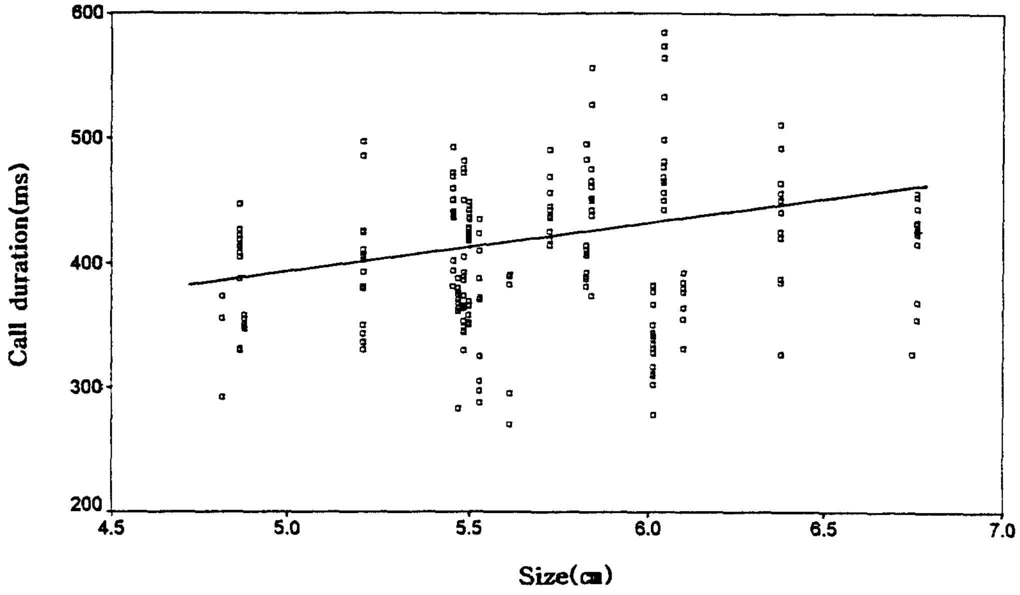

Fig. 14. The influence of body size on the call duration.

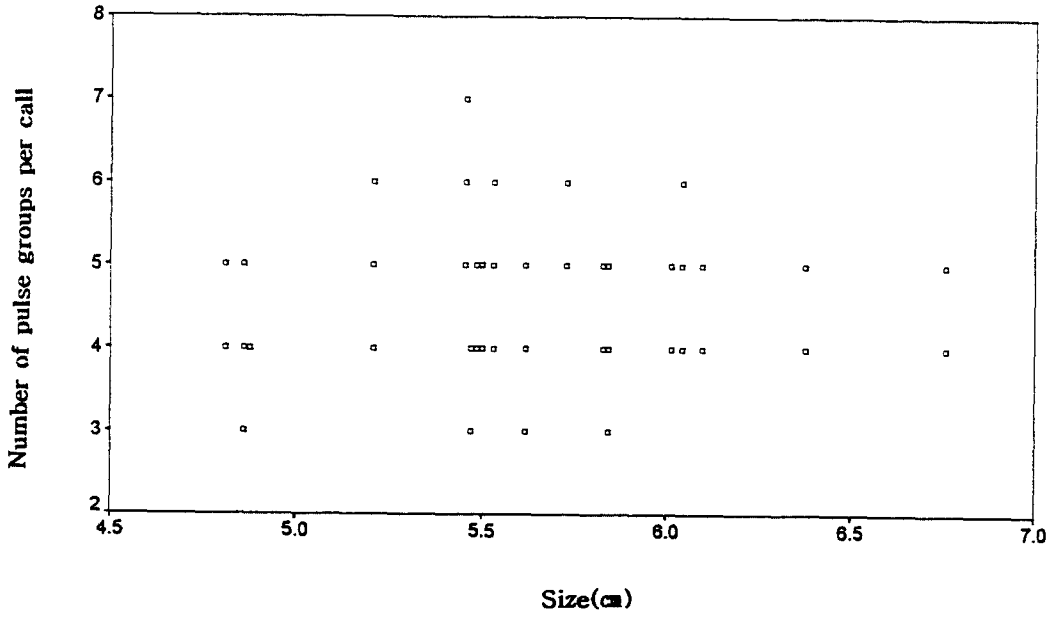

Fig. 15. The influence of body size on the number of pulse groups per call.

large males. In *R. rugosa*, more large males than small males were collected in amplexus with females during the breeding season(No and Park 1992). In this respect, our data seem to show a probability that size-related frequency differences are a main factor influencing female attraction and male-male competition.

Playback experiment

The results of research on *Hyla ebraccata* and *Pseudacris crucifer* showed that these species elevate

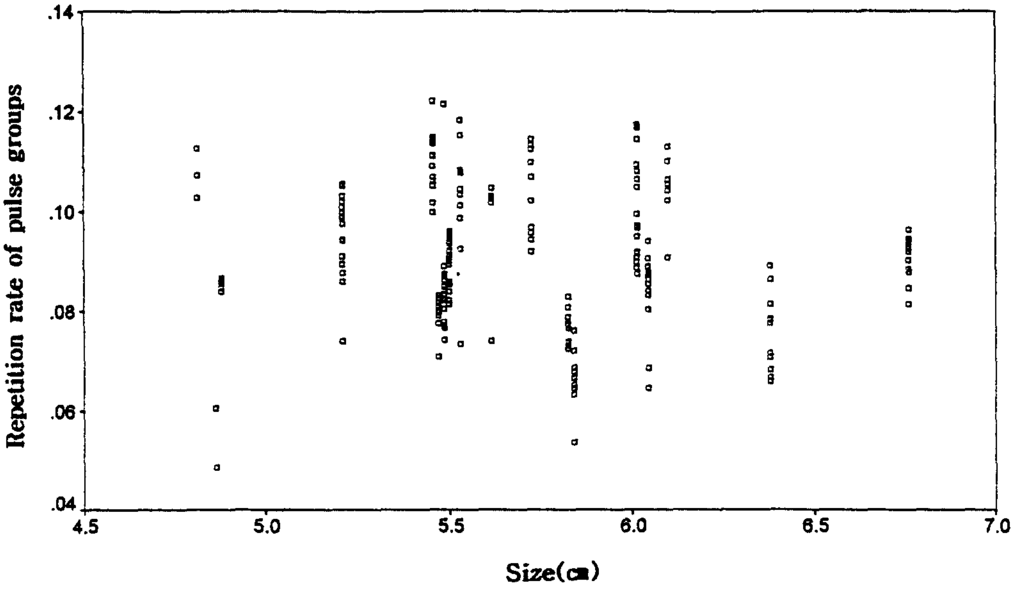

Fig. 16. The influence of body size on the repetition rate of pulse groups.

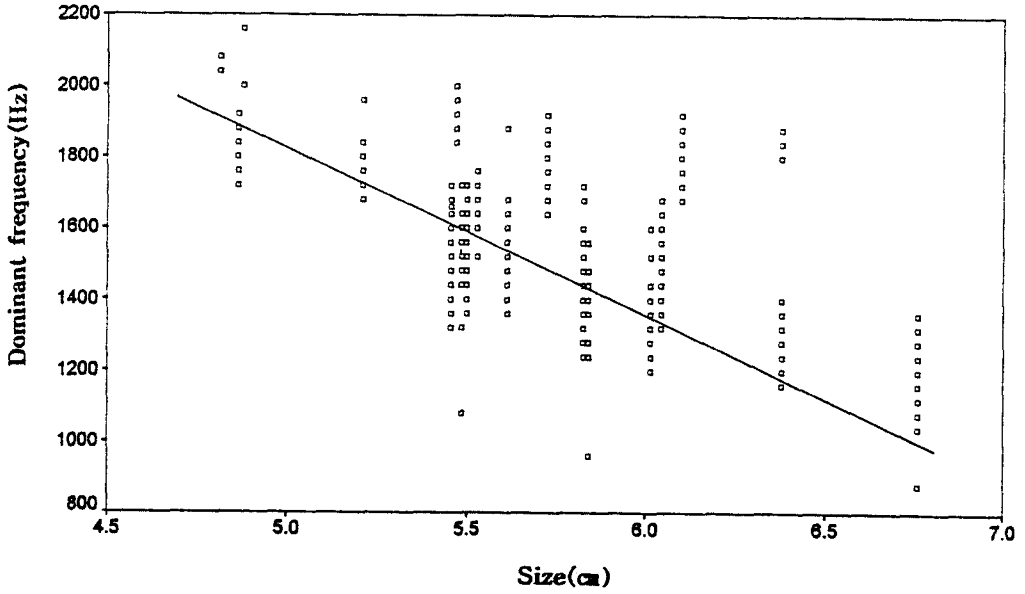

Fig. 17. The influence of body size on the dominant frequency.

their aggressive responses as a result of increases in the call duration of the playback which is perceived in a graded fashion (Wells 1928, Schwartz 1989). It has been proposed that the functional meaning of graded signals is to convey the signal's probability of escalating an agonistic encounter (Enquist 1985).

Brenowitz (1989) showed that male pacific treefrogs responded to an increasing amplitude of playbacks (87 to 99 dB) by producing fewer advertisement calls and replacing them with encounter calls; however, the total call rate stayed constant. Graded aggressive signals can thus reveal the motivational state of

Table 2. Comparision of call parameters emitted during the non-stimulus period and during the stimulus period by Wilcoxon matched-pairs signed-ranks test(significance level: *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$; n.s.=not significant)

Frog	Pulse group duration(ms)			Number of pulses per pulse group			Interval between pulse groups(ms)			Pulse repetition rate		
	Non-stimulus	Stimulus	p	Non-stimulus	Stimulus	p	Non-stimulus	Stimulus	p	Non-stimulus	Stimulus	p
1	53.55 ± 6.99	54.69 ±20.28	n.s.	7.38 ±1.06	7.50 ±2.78	n.s.	43.40 ±14.67	36.04 ± 7.78	n.s.	1.215 ±0.123	1.225 ±0.344	n.s.
2	50.96 ±23.10	46.40 ±20.99	n.s.	7.35 ±1.40	7.52 ±2.86	n.s.	62.78 ±16.08	66.48 ±11.38	n.s.	1.611 ±1.315	1.433 ±0.245	n.s.
3	58.67 ±12.69	60.84 ±12.85	n.s.	9.55 ±2.55	8.73 ±2.00	0.0274	45.10 ± 8.60	37.46 ± 7.45	0.0040	1.474 ±0.300	1.319 ±0.402	0.0036
4	52.70 ±10.47	50.84 ± 9.61	n.s.	9.45 ±1.18	8.18 ±0.96	0.0090	36.73 ± 6.06	22.81 ± 6.01	0.0010	1.638 ±0.268	1.429 ±0.146	0.0067
5	57.96 ± 8.80	59.04 ±11.65	n.s.	8.86 ±1.42	8.17 ±1.65	n.s.	46.75 ± 6.97	24.06 ±11.35	0.0001	1.377 ±0.278	1.226 ±0.204	0.0360
6	57.75 ± 9.09	56.55 ± 9.17	n.s.	8.95 ±1.69	8.00 ±1.80	0.0023	38.33 ± 8.08	23.39 ± 8.97	0.0000	1.386 ±0.250	1.240 ±0.242	0.0111
7	56.54 ± 9.16	56.04 ±10.73	n.s.	8.64 ±1.11	7.28 ±1.02	0.0024	36.75 ± 6.98	27.57 ± 9.17	0.0052	1.383 ±0.202	1.130 ±0.140	0.0001
8	64.61 ±12.11	62.38 ± 8.24	n.s.	12.10 ±1.30	12.20 ±1.91	n.s.	30.50 ± 7.02	30.56 ± 6.91	n.s.	1.753 ±0.240	1.818 ±0.362	n.s.
9	64.10 ±20.24	64.97 ±17.39	n.s.	9.03 ±1.57	9.18 ±1.99	n.s.	41.19 ± 7.05	27.33 ± 9.76	0.0000	1.320 ±0.313	1.227 ±0.226	n.s.
All frogs	57.42 ± 4.71	57.20 ± 6.37	n.s.	9.03 ±1.39	8.52 ±1.50	n.s.	42.32 ± 9.22	32.85 ±13.67	0.0209	1.452 ±0.490	1.315 ±0.311	0.0000

Table 2. Continued

Frog	Call duration(ms)			Number of puls group per call			Repetition rate of pulse groups			Dominant frequency(Hz)		
	Non-stimulus	Stimulus	p	Non-stimulus	Stimulus	p	Non-stimulus	Stimulus	p	Non-stimulus	Stimulus	p
1	346.50 ± 10.47	518.00 ± 18.81	n.s.	4.00 ±0.00	5.67 ±0.58	n.s.	0.083 ±0.006	0.090 ±0.011	n.s.	1800.00 ± 43.82	1700.00 ± 70.43	0.0277
2	369.46 ±211.19	334.06 ± 49.54	n.s.	4.60 ±0.55	3.60 ±0.55	n.s.	0.076 ±0.005	0.075 ±0.004	n.s.	1890.67 ± 77.78	1949.33 ± 57.50	0.0409
3	446.41 ± 33.67	519.09 ±148.83	n.s.	4.71 ±0.49	5.57 ±1.72	n.s.	0.083 ±0.007	0.086 ±0.011	n.s.	1832.50 ± 48.92	1922.50 ± 39.92	0.0004
4	292.72 ± 38.74	329.93 ± 39.19	n.s.	3.67 ±0.52	4.83 ±0.75	0.0431	0.088 ±0.008	0.114 ±0.011	0.0431	1633.33 ±111.63	2045.00 ±234.81	0.0022
5	362.65 ± 29.02	480.90 ±118.43	0.0117	3.89 ±0.33	5.78 ±1.30	0.0152	0.079 ±0.005	0.099 ±0.011	0.0077	1673.33 ± 39.41	1820.00 ± 96.28	0.0007
6	389.32 ± 52.75	557.55 ±198.50	0.0464	4.33 ±0.516	7.16 ±3.06	n.s.	0.086 ±0.003	0.099 ±0.006	n.s.	1720.00 ± 55.27	2000.00 ±147.71	0.0000
7	431.10 ± 18.81	507.18 ± 78.34	n.s.	5.00 ±0.00	6.20 ±0.45	0.0431	0.092 ±0.004	0.104 ±0.009	0.0464	2040.00 ±122.82	2000.00 ± 72.51	n.s.
8	451.38 ± 18.28	439.05 ± 5.72	n.s.	5.00 ±0.00	5.00 ±0.00	n.s.	0.090 ±0.002	0.091 ±0.001	n.s.	2066.67 ±103.92	2035.56 ± 76.01	n.s.
9	395.51 ± 28.29	410.15 ± 73.26	n.s.	4.13 ±0.35	4.63 ±0.91	n.s.	0.079 ±0.004	0.087 ±0.008	0.0500	1574.55 ± 86.30	1818.18 ± 51.73	0.0033
All frogs	406.99 ±67.27	467.87 ±92.25	n.s.	4.37 ±0.52	5.43 ±0.99	0.0300	0.085 ±0.007	0.094 ±0.012	0.0000	1807.06 ±180.43	1937.487 ±170.17	0.0000

individuals and are used to reveal, information about intention(Nelson 1984, Poole 1989, Capp and Searcy 1991, Hauser and Nelson 1991). The results of our playback experiments show the effect of a potential intruder in stimulating the subjects to produce a mating call in their territories. The experiments of Moon(1994) concerning territorial behavior in *R. nigromaculata* showed that the distance maintained between the males is usually more than 25 cm. In 20 % of 250 trials, in which other conspecifics invaded their territory, fighting behavior was induced, simultaneously producing changes in the mating call. In this way, the male of this species has a strong tendency to keep his territory. Analyses of the mating call in *R. nigromaculata* show that include a simple advertisement call and lacks a qualitatively distinct aggressive call type. However, overall males significantly decrease the pulse repetition rate, and increase the rate of pulse groups, dominant frequency, and the number of call groups during the stimulus periods (Table 2). Especially a mating call with more than two call groups can be observed easily in the natural situation when a individual interacts with other conspecifics. The consequence of these changes in the temporal and spectral characteristics of the mating call supports the proposal that this species responds in a graded fashion. It has not yet been elucidated as to why and to what extent alterations in the structure of the call itself occur according to the various situations. The main factor that influences the production of a graded call needs to be investigated. However, from the work of Wells and Schwartz(1984) we can infer that the reason for the production of a graded call is that it allows males to respond aggressively to other males while simultaneously retaining certain temporal elements in the call that are attractive to females.

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적요

충북 청원군 다락리(북위 37° 37′, 동경 127° 21′)에 서식하는 참개구리의 짝짓기 소리의 구조와 변이를 연구하였다. 참개구리의 짝짓기 소리는 3~8개의 pulse group들로 구성되어 있다. 각 pulse group은 또한 작은 pulse들로 이루어져 있다. 수온과 개구리의 몸크기는 짝짓기 소리의 temporal 그리고 spectral 특징에 영향을 미쳤다. 수온이 증가함에 따라 pulse, pulse group 빈도 그리고 dominant frequency는 증가했고, 반면에 몸의 크기가 커짐에 따라 pulse group 빈도와 dominant frequency는 감소하였다. 침입자가 짝짓기 소리에 어떠한 영향을 미치는지를 알아보기 위해 playback 실험을 하였다. 자극을 받은 기간 동안 실험 대상개체는 pulse repetition rate가 현저히 감소하였으며, pulse group의 빈도와 dominant frequency 그리고 call group의 수는 증가하였다. 이 결과는 참개구리가 다른 개체와 상호작용을 할 때 소리가 변한다는 사실을 보여준다.

LITERATURE CITED

Arak, A. 1983. Vocal interactions, call matching and territoriality in a Sri Lankan treefrog, *Philautus leucorbinus* (Rhacophoridae). Anim. Behav. 31: 292-302.

Brenowitz, E.A. 1989. Neighbor call amplitude influences aggressive behavior and intermale spacing in choruses of the Pacific treefrog. Ethology 83: 69-79.

Capp, M.S. and M.S. Searcy. 1991. Acoustical communication of aggressive intentions by territorial male bobolinks. Behav. Ecol. 2: 319-326.

Davies, N.B. and T.R. Halliday. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. Nature. 274: 683-685.

Enquist, M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. Anim. Behav. 33: 1152

-1161.

Gerhardt, H.C. 1978. Temperature coupling in the vocal communication system of the gray treefrog, *Hyla versicolor*. Science. 199: 992-994.

Gerhardt, H.C. 1982. Sound pattern recognition in some North American treefrogs (Anura: Hylidae): Implications for mate choice. Amer. Zool. 22: 581-595.

Gerhardt, H.C. 1988. Acoustic properties used in call recognition by frogs and toads. In: The Evolution of the Amphibian Auditory System.(Fritzsch, B., Ryan, M. J., Wilczynski, W., T.E. Hetherington and W. Walkowiak., eds.) John Wiley and Sons, New York, pp. 455-483.

Gerhardt, H.C. 1991. Female mate choice in treefrogs: static and dynamic acoustic criteria. Anim. Behav. 42: 615-636.

Hauser, M.D. and D.A. Nelson. 1991. 'Intentional' signaling in animal communication. Trends Ecol. Evol. 6: 186-189.

Klump, G.M. and H.C. Gerhardt. 1987. Use of non-arbitrary acoustic criteria in mate choice by female treefrogs. Nature. 326: 286-288.

Kuramoto, M. 1980. Mating Calls of Treefrogs(Genus *Hyla*) in the Far East, with Description of a NewSpecies from Korea. Copeia. 1980: 100-108.

Mărquez, R. 1995. Female choice in the midwife toads(*Alytes obstetricans* and *A. Cisternasii*). Behaviour. 132: 151-161.

Moon, K.Y. 1994. Acoustic Behaviour and Mating Call of *Rana nigromaculata* in Korea. Master's Thesis, Korea Nat. Univ. of Education.

Narins, P.M. and R. Zelick. 1988. The effects of noise on auditory processing and behaviour in amphibians. In: The Evolution of the Amphibian Auditory System.(Fritzsch, B., M.J. Ryan, W. Wilczynski, Hetherington, T.E. and W. Walkowiak, eds.)John Wiley and Sons, New York, pp. 511-536.

Nelson, D.A. 1984. Communication of intentions in agonistic contexts by the pigeon guillemot, Cepphus Columba. Behaviour 88: 145-189.

Nevo, E. and H. Schneider. 1983. Structure and variation of *Rana ridibunda* mating call in Israel (Amphibia: Anura). Israel J. Zool. 32: 45-60.

No, D.C. and S.R. Park. 1992. The Study of on the Acoustic Behaviour of Rana rugosa. The Korean J. of Behav. Biol. 1: 121-129.

Park, S.R., S.M. Cheon and S.Y. Yang. 1996. The classification of call types in Genus *Hyla* in habitats around South Korea. Korean J. Zool. 39: 207-214.

Poole, J.H. 1989. Announcing intent: the aggressive state of musth in African elephants. Anim. Behav. 37: 140-152.

Ramer, J.D., T.A. Jenssen and C.J. Hurst. 1983. Size-related variation in the advertisement call of *Rana clamitan*(Anura: Ranidae), and its effect on conspecific males. Copeia. 1983: 141-155.

Robertson, J.G.M. 1986b. Male territoriality, fighting and assessment of fighting ability in the Australian frog, *Uperoleia rugosa*. Anim. Behav. 34: 763-772.

Robertson, J.G.M. 1986a. Female choice, male strategies, and the role of vocalizations in the Australian frog, *Uperoleia rugosa*. Anim. Behav. 34: 773-784.

Ryan, M.J. 1980. Female mate choice in a neotropical frog. Science. 209: 523-525.

Ryan, M.J. 1985. The Tungara Frog: A study in Sexual Selecion and Communication. Univ. of Chicago Press, Chicago.

Ryan, M.J. 1990. Sexual selection, sensory systems and sensory exploitation. Oxford Surv. Evol. Biol. 7: 157-195.

Schneider, H., T.S. Sofianidou and P. Kyriakopoulou-Sklavounou. 1984. Bioacoustic and morphometric studies of water frogs(genus *Rana*) of Lake Ioannina in Greece, and description of a new species (Anura, Amphibia). J. Zool. Syst. Evolut.-forsch. 22: 349-366.

Schwartz, J.J. 1986. Male calling behavior and female choice in the neotropical treefrog *Hyla microcephala*. Ethology. 73: 116-127.

Schwartz, J.J. 1987. The importance of spectral and temporal properties in species and call recognition in a neotropical treefrog with a complex vocal repertoire. Anim. Behav. 35: 340-347.

Schwartz, J.J. 1989. Graded aggressive calls of the spring peeper, *Pseudacris crucifer*. Herpetologica 45: 172-181.

Sullivan, B.K. 1983. Sexual selection in Woodhouses's toad(*Bufo woodhousei*). II. Female choice. Anim. Behav. 31: 1011-1017.

Sullivan, B.K. 1984. Advertisement call variation and observations and on breeding behavior of *Bufo debilis* and *B. punctatus*. J. Herpetol. 18: 406-411.

Sullivan, B.K. and W.E.Jr. Wagner. 1988. Variation in advertisement and release calls, and social influences on calling behavior in the Gulf Coast toad (*Bufo valliceps*). Copeia 1988: 1014-1020.

Wagner, W.E.Jr. 1989a. Graded aggressive signals in Blanchard's cricket frog: vocal responses to opponent proximity and size. Anim. Behav. 38: 1025-1038.

Wagner, W.E.Jr. 1989b. Fighting, assessment, and frequency alteration in Blanchard's cricket frog. Behav. Ecol. Sociobiol. 25: 429-436.

Wagner, W.E.Jr. 1989c. Social correlates of variation in male calling behavior in Blanchard's cricket frog, *Acris crepitans blanchardi*. Ethology. 82: 27-45.

Wagner, W.E.Jr. 1992. Deceptive or honest signalling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. Anim. Behav. 44: 449-462.

Wagner, W.E.Jr. and B.K. Sullivan. 1995. Sexual selection in the gulf coast toad, *Bufo valliceps*: female choice based on variable characters. Anim. Behav. 49: 305-319.

Wells, K.D. and J.J. Schwartz. 1984. Vocal communication in a neotropical treefrog, *Hyla ebracata*: advertisement calls. Anim. Behav. 32: 405-420.

Wells, K.D. 1988. The effect of social interactions on anuran vocal behavior. In: The Evolution of the Amphibian Auditory system.(Fritzsch, B., Ryan, M.J., W. Wilczynski., Hetherington, T.E. and Walkowiak. W. eds). Wiley and Sons, New York. pp. 433-454.

Wells, K.D. 1989. Vocal communication in a neotropical treefrog, *Hyla ebraccata*: responses of males to graded aggressive calls. Copeia. 1989: 461-466.

Yang, S.Y., B.S. Park and H.J. Son. 1981. Species comparison of the genus *Hyla* in Korea. Bull. I.B.S., Inha Univ. 2: 75-83.

Yang, S.Y., C.H. Yu and B.S. Park. 1988. Natural hybridization and reproductive isolating mechanisms between two species of *Rana nigromaculata* and *Rana plancyi*(*Anura*). Korean J. Zool. 31: 1-10.

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