Interspecific Interactions between Two Japanese Pond Frogs, *Rana porosa brevipoda* and *Rana nigromaculata*

RYOHEI SHIMOYAMA

Abstract: Male social interactions between *Rana porosa brevipoda* and *Rana nigromaculata* were investigated. Males of *R. nigromaculata* were significantly larger and heavier than those of *R. porosa brevipoda*. Mixed-species choruses were formed by male *R. nigromaculata* joining the choruses of *R. porosa brevipoda*. In the mixed-species choruses, males of both species defended their own calling spaces against both conspecifics and heterospecifics. Most of the interspecific agonistic interactions were initiated by male *R. nigromaculata*, and most of the interactions were terminated by the victory of *R. nigromaculata*, probably due to its larger body size. Males of the two species emitted similar calls: advertisement calls with multiple notes and encounter calls with a single note. Advertisement calls of *R. nigromaculata* consisted of fewer notes and were lower in frequency than those of *R. porosa brevipoda*, although there was a considerable spectral overlap between the two species. Males of both species with SVL of approximately 65 mm emitted calls of similar dominant frequency. Playback experiments were performed to examine the response of the males to conspecific and heterospecific advertisement calls. Male *R. porosa brevipoda* tended to respond to only conspecific calls, whereas male *R. nigromaculata* tended to respond to both conspecific and heterospecific calls. This indicates that male *R. nigromaculata* do not distinguish heterospecific calls from conspecific ones. Heterospecific pairings and hybridization were observed within the mixed-species choruses. Two types of possible costs, energetic costs and hybridization, caused by the asymmetric interspecific interactions are discussed.

Key words: *Rana porosa brevipoda*; *Rana nigromaculata*; Vocal repertoire; Interspecific territoriality; Hybridization

Interspecific territoriality has been documented in a variety of animal taxa (e.g., Orians and Willson, 1964; Ebersole, 1977; Murray, 1981). Orians and Willson (1964) pointed out that natural selection should favor the divergence of preferred microhabitats between sympatric species with territoriality, and that interspecific territoriality may evolve if some common resource is contested. However, some investigators have considered that such interspecific aggressive encounters are caused by the misidentification of conspecifics and heterospecifics (Gochfeld, 1979; Murray, 1981). Among anurans, there are a number of intensive studies on intraspecific social behavior (see reviews by Wells, 1977; Ryan, 1985). However, little work has been done to document interspecific social interactions (see reviews in Given, 1990; Gerhardt and Schwartz, 1995).

The Japanese pond frogs *Rana porosa brevipoda* and *Rana nigromaculata* are closely related both phylogenetically and ecologically

(see Maeda and Matsui, 1989; Matsui, 1996 for review). Both species inhabit paddy fields, marshes and ponds of plains, and basins sympatrically (Maeda and Matsui, 1989). During the breeding season, males of both species form chorusing aggregations in shallow water, such as paddy fields, and establish "floating" territories which function as the sites for sexual advertisement but not for oviposition (Shimoyama, 1982, 1993). Shimoyama (1996) documented the similarity in temporal and spatial patterns of breeding activity between these frogs, which results in the formation of mixed-species choruses comprising males of both species. In the present paper, I first describe interspecific acoustic and agonistic interactions between males of the two species within the mixed-species choruses. I then examine the possible causes of such interspecific interactions by field experiments.

METHODS

Study area.—The study was done during the breeding seasons of the pond frogs in 1990,

1992–1993, 1995–1997 in Tatsuno (35° 56'N, 137° 58'E, 720 m above sea level), Nagano Prefecture, central Japan. A plot of paddy fields approximately 2.5 ha in area was selected for the study area. The paddy fields were filled with water approximately 5–10 cm deep from late April to early September, and young rice plants were planted in mid May. Footpaths and banks beside the paddy fields were partially covered with dense weeds and grasses. A more detailed description was given in Shimoyama (1996).

Observations.—Field surveys were made on 47 days in May–July 1990, five days in May 1992, six days in May 1993, eight days in May–July 1995, 18 days in May–June 1996, and six days in May–June 1997. I attempted to capture the pond frogs whenever possible with a net or by hand during the daytime of every visit. The snout-vent length (SVL) of the captured frogs was measured to the nearest 0.1 mm with a slide caliper and they were weighed to the nearest 0.05 g with an electric beam balance. Although all of the captured frogs were weighed in 1990, only a part of males were weighed in the other years. The frogs were marked individually by toe-clipping. A waist band with a numbered tag was also attached to each mature male. The frogs were then released at the sites of capture. The species was identified on the basis of the external characters of individual frogs (see Maeda and Matsui, 1989). Frogs with intermediate external characters, which were considered to be natural hybrids, were excluded from the later analyses.

Observations on male behavior were made usually between 0500–0700, when males of both species are most active (Shimoyama, 1996). When breeding activities were still intense after 0800, observations were also done between 0800–1000. The behavioral observations were done for a total of 265 hours. On every visit, I selected one or two mixed-species chorus and observed male and female behavior from nearby banks. Binoculars ($\times 7$) were used to identify individual markings. Spatial positions of individual males were recorded every five minutes, and social interactions between males were also recorded (the same method as Shimoyama, 1993). In the interspecific agonistic interactions, the males which initiated interactions were recorded. I defined the beginning of an agonistic interaction as the beginning of the approach to the opponent by a male. The winner and loser of each interaction were also recorded whenever they were clearly determined. I consi-

dered the male which first swam away as the loser, and the other as the winner. The analyses of interspecific interactions were made on the basis of the data obtained in these morning observations.

The sequence of formation of the mixed-species choruses was observed on a total of 14 nights (1700–2100) in May–June 1996 and 1997. I walked along footpaths within the study area once every hour and recorded positions and behavior of all mature pond frogs on a map. A flashlight and a headlight were used to ascertain individual markings.

Recording and analyses of vocalizations.—Vocalizations of 24 male *R. porosa brevipoda* and 13 male *R. nigromaculata* were recorded in 1996 and 1997. For each male, 3–5 advertisement calls and/or encounter calls (Shimoyama, 1993) were recorded using a minidisk recorder (Sony MZ-R3) with an external microphone (Sony ECM-717). Water temperature at the recording sites was $23.0 \pm 1.5^\circ\text{C}$. The recorded calls were analyzed using computer programs, Sound Edit or Sound Edit Pro (Macromedia Inc.), on a Macintosh computer. Mean values of acoustic characters for each male were used in the comparison of the advertisement calls between the two species.

Playback experiments.—Playback experiments were conducted between 1600 and 1800 on 9 days in June 1996 to examine the response of males to natural recordings of heterospecific and conspecific advertisement calls. The time of the experiments corresponded to the period of time just prior to the beginning of male chorusing activity. Responses of 30 marked males of each species to the playbacks were examined. The SVLs of these males are shown in Table 1. All of the 30 males of *R. porosa brevipoda* were smaller than the males of the same species whose calls were used in the playback experiments

TABLE 1. SVLs of males used in the playback experiments. Rpb: *Rana porosa brevipoda*; Rn: *R. nigromaculata*.

SVL (mm)	No. of males tested	
	Rpb	Rn
50.0–54.9	14	0
55.0–59.9	10	3
60.0–64.9	6	7
65.0–69.9	0	17
70.0–74.9	0	3

Rpb: mean = 56.1 mm (SE = 0.62)

Rn: mean = 65.7 mm (SE = 0.75)

(65.0 mm; see below). Similarly, all of the 30 males of *R. nigromaculata* were smaller than the males of the same species whose calls were used (75.2 mm; see below).

Acoustic properties of the stimuli used in the experiments were as follows. The advertisement call of *R. porosa brevipoda* was composed of six notes, lasted 0.58 s, and had a dominant frequency of 2.1 kHz. This call was emitted by a male of 65.0 mm SVL. The advertisement call of *R. nigromaculata* was composed of three notes, lasted 0.34 s, and had a dominant frequency of 0.5 kHz. This call was emitted by a

male of 75.2 mm SVL. Each stimulus tape consisted of 20 recordings of the same call at a rate of 20 calls/min. The stimuli were presented for 1 min at a distance of 1 m from the males using a cassette tape recorder (Sanyo U4-W46). Sound pressure levels of both stimuli were 85 dB. Heterospecific calls were presented first, and five minutes later, conspecific calls were presented as the control. Whether or not the males began calling in response to the stimuli during the playbacks was recorded. When a male began to call during the playbacks, I regarded the response as positive.

FIG. 1. Comparison of snout-vent length (a) and weight (b) between males of two species of pond frogs.

RESULTS

Comparison of male size.—Figure 1 compares frequency distributions of SVL and weight of males between *R. porosa brevipoda* and *R. nigromaculata* in 1990. SVL of male *R. porosa brevipoda* ranged from 40.3–64.9 mm with a mean of 56.1 mm (N=179, SE=0.43), whereas that of male *R. nigromaculata* ranged from 60.0–80.8 mm with a mean of 66.9 mm (N=84, SE=0.46). *Rana nigromaculata* were significantly larger than *R. porosa brevipoda* (Mann-Whitney U-test, $z=11.92$, $p=0.0001$), although their ranges overlapped each other. Similarly, *R. nigromaculata* (mean=22.3 g, SE=0.53) were significantly heavier than *R. porosa brevipoda* (mean=13.5 g, SE=0.30;

TABLE 2. Comparison of SVL between males of two species of pond frogs. Rpb: *Rana porosa brevipoda*; Rn: *R. nigromaculata*.

Year	Rpb			Rn			U-test
	N	Mean	SE	N	Mean	SE	
1992	15	56.7	1.34	2	70.1	1.35	$z=2.24$ $p=0.025$
1993	12	53.4	2.43	2	66.0	1.00	$z=2.19$ $p=0.029$
1995	10	56.7	1.10	4	66.1	1.62	$z=2.55$ $p=0.011$
1996	72	54.3	0.63	48	66.4	0.57	$z=8.86$ $p=0.0001$
1997	56	56.4	0.78	22	67.3	0.84	$z=6.31$ $p=0.0001$

FIG. 2. An example of the sequence of the formation of a mixed-species chorus (recorded on 7 June 1997). Closed circles: calling males of *R. porosa brevipoda*; Open triangles: calling males of *R. nigromaculata*. Open and shaded areas indicate paddy fields with water and vegetable fields without water, respectively.

$z=11.40$, $p=0.0001$). In the other years, *R. nigromaculata* were also larger than *R. porosa brevipoda* (Table 2).

Formation of the mixed-species choruses.—From late morning to the evening, males of both species stayed in the vegetation of the banks without calling (see Shimoyama, 1996). At dusk, some males of both species sporadically began to emit advertisement call in the water. There was a trend for male *R. porosa brevipoda* to begin calling earlier in the evening than male *R. nigromaculata*. Other males of *R. porosa brevipoda* and *R. nigromaculata* then assembled around the calling males of *R. porosa brevipoda* (Fig. 2). All of the 23 mixed-species choruses observed on the 14 nights were formed by male *R. nigromaculata* joining the choruses of *R. porosa brevipoda*. The sites of such mixed-species chorusing were not fixed, but were determined by the calling positions of the male *R. porosa brevipoda* which first began calling in the evening.

Interspecific interactions between males.—While making the mixed-species choruses, males of both species floated on the water surface, adopting a "high posture" (see Inoue, 1979; Shimoyama, 1993). Each male remained within an area of ca. 1.5–3 m² and actively swam within this area. Males emitted advertisement and encounter calls (see below). At the boundaries of the calling areas, aggressive interactions occurred both between conspecific males and between heterospecific males. A typical aggressive interaction of both species consisted of "approach", "jump attack", and "wrestling" (see also Inoue, 1979; Shimoyama, 1982, 1993).

In the interspecific aggressive encounters, larger males tended to initiate agonistic interactions more frequently than smaller males (Table 3). Agonistic interactions usually terminated when one or both frogs swam away, although the winners sometimes chased the losers. Losers stayed silently in a "low posture" (Inoue, 1979) for some minutes, and then resumed calling. Of a

total of 155 interspecific agonistic encounters, 116 (74.8%) were won by larger males, whereas only 11 (7.1%) were won by smaller males (Table 4). In the remaining 28 encounters, winners and losers could not be clearly determined, because both fighting males swam away simultaneously. *Rana nigromaculata* tended to initiate and win more interspecific aggressive encounters than *R. porosa brevipoda*, because of their larger body size. The calling spaces of individual males rarely overlapped both between heterospecifics or among conspecifics (Fig. 3). Such calling spaces were maintained within 2 hr of the observations, although males changed their calling positions every night.

Comparison of call structures.—Figure 4 shows sonagrams of advertisement and encounter calls of both species. The advertisement calls of both species are composed of multiple notes without frequency modulation or clear harmonics, whereas the encounter calls consist of a single note. However, the advertisement

TABLE 4. Winners of interspecific agonistic interactions with relation to relative body size. Rn: *Rana nigromaculata*; Rpb: *R. porosa brevipoda*.

Body size	Winner	
	Rn	Rpb
Rn > Rpb	100	4
Rn < Rpb	7	16

Fisher's exact test; $P < 0.001$

FIG. 3. An example of the distribution of calling spaces of males in a paddy field (0500–0700, 17 May 1992). Shaded polygons: calling spaces of *R. porosa brevipoda*; open polygons: calling spaces of *R. nigromaculata*.

TABLE 3. Males which initiated interspecific agonistic interactions with relation to relative body size. Rn: *Rana nigromaculata*; Rpb: *R. porosa brevipoda*.

Body size	Initiated by	
	Rn	Rpb
Rn > Rpb	111	14
Rn < Rpb	9	21

Fisher's exact test; $p < 0.001$

FIG. 4. Sonograms of the calls of two species of pond frogs. A: an advertisement call of *R. porosa brevipoda*; B: an encounter call of *R. porosa brevipoda*; C: an advertisement call of *R. nigromaculata*; D: an encounter call of *R. nigromaculata*.

calls of *R. nigromaculata* consist of fewer notes and have a lower dominant frequency than those of *R. porosa brevipoda* (Table 5). The calls of these two species show considerable spectral overlap, although the differences are still significant. The dominant frequency of the calls is negatively correlated with SVL in both species

(Fig. 5). Males of both species with an SVL of ca. 65 mm emit calls of a similar dominant frequency (Fig. 5).

Playback experiments.—The results of the playback experiments are shown in Table 6. In the trials with male *R. porosa brevipoda*, only one (3%) of the 30 males began to emit adver-

TABLE 5. Comparison of advertisement call variables between *Rana porosa brevipoda* (Rpb) and *R. nigromaculata* (Rn).

Variables	Rpb (N=24)	Rn (N=13)	U-test
SVL (mm)			
Mean	56.7	71.7	$z=4.95$
SE	1.11	1.20	$p=0.0001$
Range	45.0–65.0	65.0–81.0	
Duration (sec)			
Mean	0.61	0.41	$z=4.66$
SE	0.02	0.02	$p=0.0001$
Range	0.46–0.76	0.28–0.51	
N of notes/call			
Mean	6.5	3.9	$z=4.91$
SE	0.32	0.21	$p=0.0001$
Range	5.0–13.0	3.0–5.5	
Domi. freq. (kHz)			
Mean	2.25	0.91	$z=4.74$
SE	0.05	0.18	$p=0.0001$
Range	1.80–2.83	0.32–2.15	
N of notes/sec			
Mean	10.73	10.25	$z=2.51$
SE	0.43	1.06	$p=0.012$
Range	8.96–17.39	6.02–19.50

FIG. 5. Relationship between SVL and the dominant frequency of the advertisement calls. Regression equation for each species is: $Y = -0.35X + 4.234$ ($r^2 = 0.753$, $N = 24$, $p = 0.0001$) for *R. porosa brevipoda* and $Y = -0.108X + 8.635$ ($r^2 = 0.518$, $N = 13$, $p = 0.0055$) for *R. nigromaculata*. Each symbol shows the mean value for each male.

TABLE 6. Results of the playback experiments. Figures indicate the number of males. Rpb: *Rana porosa brevipoda*; Rn: *R. nigromaculata*.

Males tested	Stimulus				Chi-square
	Advertisement calls of Rpb		Advertisement calls of Rn		
	Response	No response	Response	No response	
Rpb	28	2	1	29	45.12 (p=0.0001)
Rn	26	4	28	2	0.185 (p=0.667)

tisement calls in response to the heterospecific calls, whereas 28 (93%) males responded to the conspecific calls. Thus the results of the experiments were quite different from those of the control.

In contrast, 26 (87%) of the 30 males of *R. nigromaculata* began to emit advertisement call in response to the heterospecific calls. The results of the experiments did not differ from those of the control. In summary, males of *R. porosa brevipoda* tended to respond to only conspecific calls, whereas males of *R. nigromaculata* responded to both conspecific and heterospecific calls.

Occurrence of heterospecific amplexus.—During the course of this study, I found a total of 62 conspecific pairs of *R. porosa brevipoda*, 30 conspecific pairs of *R. nigromaculata*, and 12

heterospecific pairs. Eleven (91.7%) of the 12 heterospecific pairs were composed of a male *R. nigromaculata* and a female *R. porosa brevipoda*. The mean SVL of male *R. nigromaculata* which formed heterospecific pairs was 58.4 mm ($SE = 2.03$). This value was smaller than the average size of males of this species (Fig. 1, Table 2). I observed a sequence of heterospecific pairing, from amplexus to deposition of eggs, for seven cases. In all of these seven cases, a male *R. nigromaculata* chased and clasped a female *R. porosa brevipoda* which was attracted to the mixed-species choruses. Although the spawning behavior of these two species differs (Maeda and Matsui, 1989), egg masses were normally deposited by the heterospecific pairs in the manner of the female species (*R. porosa brevipoda*). I ascertained that most of the

deposited eggs normally hatched within 10 days. Details of the conspecific and heterospecific pair formation will be reported elsewhere.

DISCUSSION

In my study site, mixed-species choruses comprised of males of both *R. porosa brevipoda* and *R. nigromaculata* were commonly observed. This seems to be very unusual among frogs because formation of similar mixed-species choruses has been reported only rarely. There are only a few known cases of anuran interspecific acoustic interactions: *Ranidella signifera* and *R. parinsignifera* (MacNally, 1979), three species of genus *Hyla* (Schwartz and Wells, 1983, 1984, 1985), the *Rana esculenta* complex (Blankenhorn, 1977), and *Rana clamitans* and *R. virgatipes* (Given, 1990). These studies of interspecific interaction pointed out the similarity of advertisement call structures and/or vocal repertoires between heterospecifics. In the *R. porosa-nigromaculata* community in the present study, males of these two species had similar vocal repertoires. They emitted advertisement calls with multiple notes and encounter calls with a single note. Although advertisement calls of *R. nigromaculata* consisted of fewer notes and were lower than those of *R. porosa brevipoda*, there was a considerable spectral overlap between them.

There were remarkable differences in the response rate to the heterospecific calls between the two species. Almost no males of *R. porosa brevipoda* responded to the heterospecific advertisement calls. This implies that males of *R. porosa brevipoda* are able to distinguish *R. nigromaculata* from conspecifics by auditory cues. On the contrary, most of the male *R. nigromaculata* responded to the advertisement calls of *R. porosa brevipoda*, suggesting that male *R. nigromaculata* did not distinguish advertisement calls of *R. porosa brevipoda* from conspecific calls. The mixed-species choruses were formed by male *R. nigromaculata* joining the choruses of *R. porosa brevipoda*. This joining phenomenon may be caused by the misidentification of conspecifics and heterospecifics by *R. nigromaculata*.

Males of *R. porosa brevipoda* and *R. nigromaculata* defended their calling spaces against both conspecific and heterospecific males with agonistic behavior. The defended calling spaces can be considered as interspecific "floating territories". Most of the interspecific aggressions were initiated by males with larger bodies, and the majority of the interactions were

terminated by the victory of the larger males. Thus, males with smaller bodies may incur energetic costs through such interspecific interactions. Because males of *R. porosa brevipoda* were smaller and lighter than those of *R. nigromaculata*, male *R. porosa brevipoda* were the losers in most of the interspecific interactions. Hence, there may be advantages for *R. porosa brevipoda* to distinguish heterospecific calls from conspecific calls to avoid interspecific interactions and reduce energetic costs. In contrast, for male *R. nigromaculata*, there may be less advantage in recognizing heterospecific calls. Because males of *R. nigromaculata* were larger and heavier than those of *R. porosa brevipoda*, they would be able to defeat heterospecifics with less energetic costs. This phenomenon is very similar to the case of the *Rana clamitans*-*Rana virgatipes* community (see Given, 1990).

There might be another type of cost for *R. nigromaculata* and *R. porosa brevipoda*. As shown by Shimoyama (1982, 1993), the choruses of both species are analogous to leks in which pairings occur. Therefore, most gravid females of both species visit the mixed-species choruses to mate with conspecific males. As males of both species frequently dash toward, and attempt to clasp, any frogs moving nearby (Shimoyama, 1989, 1993), the probability of mismatched amplexus would increase in the mixed-species choruses. I actually observed heterospecific spawning during the course of this study, in addition to noting the occurrence of frogs with intermediate external characters (i.e., presumed hybrids). The occurrence of natural hybridization at numerous localities where both species are syntopic (Nishioka et al., 1981, 1992) seems to be caused by the interspecific interactions mentioned above. Thus, hybridization may be another type of cost for the two species of the pond frogs.

ACKNOWLEDGMENTS.—I thank Toru Nakamura and the late Hiroaki Ueda for their helpful advice throughout this survey, and Mandy Dyson, Kinji Fukuyama, Tamotsu Kusano, and Masafumi Matsui for valuable comments on earlier versions of this paper. Thanks are also due to Takako Serizawa and Shoji Hamao for literature. This study was supported in part by a Grant-in-Aid (No. 09918012) from the Ministry of Education, Science and Culture, Japan.

LITERATURE CITED

- BLANKENHORN, H. J. 1977. Reproduction and mating behavior in *Rana lessonae*-*Rana esculenta* mixed populations. In: D. H. Taylor and S. I. Guttman (eds.), *The Reproductive Biology of Amphibians*.

- p. 389–410. Plenum Press, New York and London.
- EBERSOLE, J. P. 1977. The adaptive significance of interspecific territoriality in the reef fish *Eupomacentrus leucostictus*. *Ecology* 58: 914–920.
- GERHARDT, H. C. AND J. J. SCHWARTZ. 1995. Interspecific interactions in anuran courtship. In: H. Heatwole and B. K. Sullivan (eds.), *Amphibian Biology* Vol. 2. p. 603–632. Surrey Beatty & Sons, Chipping Norton.
- GIVEN, M. F. 1990. Spatial distribution and vocal interaction in *Rana clamitans* and *R. virgatipes*. *J. Herpetol.* 24: 377–382.
- GOCHFELD, M. 1979. Interspecific territoriality in red-breasted meadowlarks and a method for estimating the mutuality of their participation. *Behav. Ecol. Sociobiol.* 5: 253–260.
- INOUE, T. 1979. On the territorial behaviors of a Japanese pond frog, *Rana brevipoda*. *Jpn. J. Ecol.* 29: 149–161. (in Japanese, with English synopsis).
- MACNALLY, R. C. 1979. Social organization and interspecific interaction in two sympatric species of *Ranidella* (Anura). *Oecologia* 42: 293–306.
- MAEDA, N. AND M. MATSUI. 1989. Frogs and Toads of Japan. Bun-ichi Sogo Shuppan, Tokyo. 206 p. (in Japanese, with English abstract)
- MATSUI, M. 1996. Natural History of the Amphibia. Univ. of Tokyo Press, Tokyo. (in Japanese)
- MURRAY, B. G. 1981. The origins of adaptive interspecific territorialism. *Biol. Rev.* 56: 1–22.
- NISHIOKA, M., M. SUMIDA, AND H. OHTANI. 1992. Differentiation of 70 populations in the *Rana nigromaculata* group by the methods of electrophoretic analyses. *Sci. Rep. Lab. Amphibian Biol. Hiroshima Univ.* 11: 1–70.
- NISHIOKA, M., H. UEDA, AND M. SUMIDA. 1981. Genetic variation of five enzymes in Japanese pond frogs. *Sci. Rep. Lab. Amphibian Biol. Hiroshima Univ.* 5: 107–153.
- ORIAN, G. H. AND M. F. WILLSON. 1964. Interspecific territories of birds. *Ecology* 45: 736–745.
- RYAN, M. J. 1985. The Tungara Frog. Univ. of Chicago Press, Chicago.
- SCHWARTZ, J. J. AND K. D. WELLS. 1983. An experimental study of acoustic interference between two species of neotropical treefrogs. *Anim. Behav.* 31: 181–190.
- SCHWARTZ, J. J. AND K. D. WELLS. 1984. Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*. *Behav. Ecol. Sociobiol.* 14: 211–224.
- SCHWARTZ, J. J. AND K. D. WELLS. 1985. Intra- and interspecific vocal behavior of the neotropical treefrog *Hyla microcephala*. *Copeia* 1985: 27–38.
- SHIMOYAMA, R. 1982. Preliminary report on male territoriality in the pond frog, *Rana nigromaculata*, in the breeding season. *Jpn. J. Herpetol.* 9: 99–102.
- SHIMOYAMA, R. 1989. Why does hybridization occur between *Rana nigromaculata* and *R. porosa brevipoda*? *Jpn. J. Herpetol.* 13: 47 (abstract, in Japanese)
- SHIMOYAMA, R. 1993. Chorus organization and male mating behavior in the Japanese pond frog, *Rana porosa brevipoda*. *J. Ethol.* 11: 91–97.
- SHIMOYAMA, R. 1996. Sympatric and synchronous breeding by two pond frogs, *Rana porosa brevipoda* and *Rana nigromaculata*. *Jpn. J. Herpetol.* 16: 87–93.
- WELLS, K. D. 1977. The social behaviour of anuran amphibians. *Anim. Behav.* 25: 666–693.

Laboratory of Animal Ecology, Joetsu University of Education, 1 Yamayashiki, Joetsu, Niigata, 943 JAPAN; Present address: 2599-6 Yonezawa, Chino, Nagano, 391-0216 JAPAN.