

Reproductive Behavior of the Japanese Treefrog, *Rhacophorus arboreus* (Anura: Rhacophoridae)

Eiiti KASUYA¹⁾, Mariko HIROTA and Hideko SHIGEHARA

Laboratory of Biology, Faculty of Education, Niigata University, 2–8050 Ikarasi, Niigata City, 950–21 Japan

Abstract. Reproductive behavior of the foam-nesting treefrog, *Rhacophorus arboreus*, is described. Oviposition was made either by an amplexant pair (a female and an amplexant male) alone or by an amplexant pair and other males (joiners). The snout-vent length of males and females was negatively correlated with the date of the first appearance in the pond. The period of staying in the pond in males was longer than that in females. Physical body contacts of other males and encounter calls by amplexant males were frequently observed before oviposition with joiners. Snout-vent length of the female and an amplexant male were positively correlated. Encounter calls by amplexant males were likely to precede movements of females. There was no difference of snout-vent length between amplexant males and joiners. Females moved the hindlimbs more frequently than males during oviposition. Amplexant males made encounter calls more frequently in oviposition with joiners than oviposition without joiners. The patterns of transitions between acts of females and amplexant males were similar between oviposition with and without joiners. Females more frequently responded to amplexant males than joiners. Both the duration of a bout of the movements of hindlimbs of females and the interval between the bouts were longer in oviposition without joiners than that with joiners. The number of the movements per bout in oviposition without joiners was smaller than that with joiners. Encounter calls by amplexant males during oviposition tended to precede the hindlimb movements of females.

Key words: mating behavior, anuran, foam nest, *Rhacophorus arboreus*.

Introduction

Field studies on the mating behavior of frogs and toads (anuran amphibians) from the viewpoint of behavioral ecology revealed the male-male competition by physical and vocal means and the “parasitic” males that exploit the vocal activity of other males in a wide array of anuran species (reviewed by Arak 1983). In most anurans, oviposition and fertilization of eggs occur externally when a female and a male are in amplexus. In several foam-nesting rhacophorid treefrogs, however, a female and some males are engaged in oviposition and fertilization (hereafter the males other than amplexant ones are called joiners or joining males). The relationships among the males in these species have been considered as coopera-

tive by some authors (e.g. Coe 1967; Wilson 1975; but see Halliday and Verrell 1984; Kasuya et al. 1987; Kasuya 1992). Their reproductive behavior in the field has not been studied except for a small number of reports (e.g. Coe 1967, 1974; Kasuya et al. 1987; Jennions et al. 1992). Studies on behavioral ecology of the foam-nesting rhacophorids can provide interesting and critical information on the evolution of cooperation and competition in the male mating behavior of anuran amphibians.

In the present paper, we describe and analyze the mating and oviposition behavior and the relationship among adults of the Japanese treefrog, *Rhacophorus arboreus*. Though a test of “male cooperation hypothesis” on the adaptive significance of joining males during oviposition in this species was reported elsewhere (Kasuya et al. 1987), we refer to the adaptive significance of joiners in the present study since the joiner is a unique feature in several foam-nesting rhacophorids (Coe 1967; Kasuya et al. 1987; Fukuyama 1991; Kusano et al. 1991).

¹⁾ Present address: Department of Biology, Faculty of Science, Kyushu University, Fukuoka, 812–81 Japan. To whom reprint requests should be sent. E-mail: ekasuscb@mbox.nc.kyushu-u.ac.jp

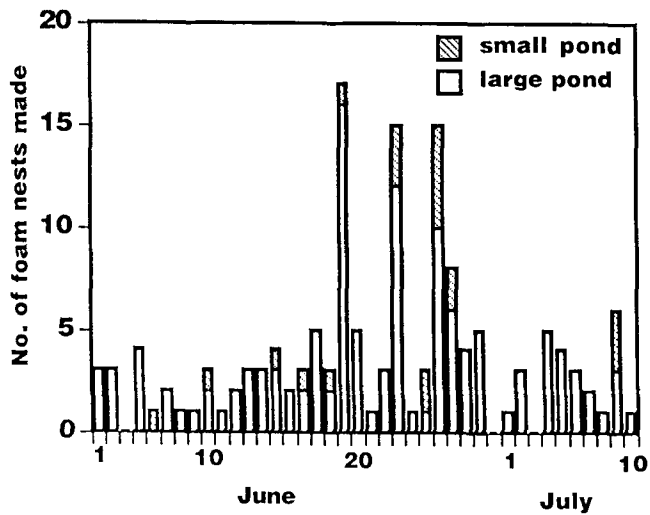


Fig. 1. Temporal change in the number of newly deposited foam nests. For an explanation of the large and small ponds, see Materials and methods.

Materials and methods

The study area was the 'Hyoutan' pond (Fig. 2) in Iwamuro, Niigata, Japan. The altitude of the pond is about 180 m. When the water level was low, the pond split into two parts: a large pond and a small pond. The observations were made from May to July, 1984. Frogs captured were marked with color-banded waist bands for later identification (Emlen 1968). We measured the snout-vent length (SVL or body size, hereafter) with a ruler to the nearest 0.1 mm and weighed each frog to the nearest 0.1 g. Observations in the night were performed with a

6 V battery lamp. This did not appear to disturb the behavior of frogs. We made the focal animal sampling (Martin and Bateson 1986) for females. Thus, behavior of solitary females and pairs in amplexus were recorded. Behavior of males that approached the observed females or pairs and that of joiners during oviposition were also recorded.

The vocalization of frogs was recorded with tape-recorder (Sony TC-D5M[®]) and microphone (Sony ECM-Z300[®]). This was analyzed with Kay 7800 Digital Sonagraph[®] at the Department of Zoology, Kyoto University and MacRecorder[®] Sound analyzing system in our laboratory. We follow the classification of vocalizations by Kasuya et al. (1992). The length and width of newly deposited foam nests were measured (Coe 1974) with a ruler to the nearest 1 mm. The product of length and width was used for the size measurement of a foam nest and called the 'size' of the foam nest.

Results

Temporal aspects of the breeding population in the pond

Figure 1 shows the temporal change in the number of newly deposited foam nests (eggs were oviposited into them). Oviposition began on June 1 and finished on July 10 in the 1984 reproductive season. There was a large variation in the number of foam nests made during one night. The total number of foam nests was 147. The spatial distribution of all the foam nests deposited is shown in Fig. 2. All the foam nests, except an unfertilized one, were deposited above the water (Fig. 2). The clusters

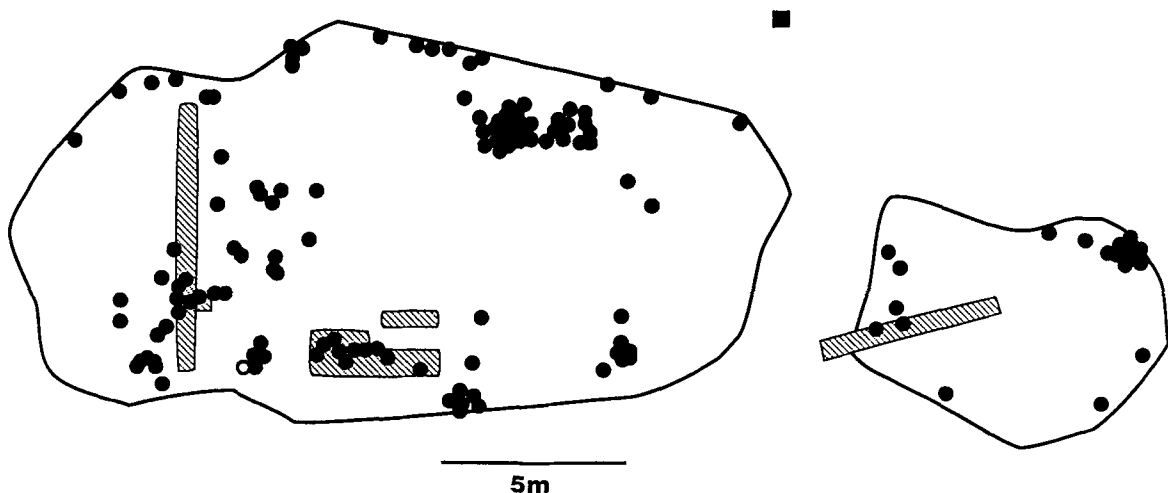


Fig. 2. The spatial distribution of all the foam nests deposited. Dot, foam nest; open circle, preyed foam nest; rectangle, unfertilized foam nest; hatched area, fallen tree.

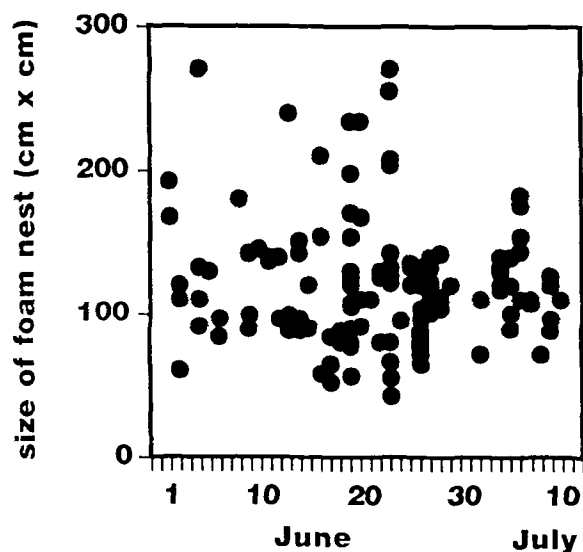


Fig. 3. The temporal change in the size of the foam nest. For an explanation of the size of the foam nest, see Materials and methods.

of foam nests were observed on twigs above the water and on the fallen trees floating on the water. Figure 3 shows the temporal change in the size of foam nests (the size of a foam nest is positively correlated with the number of eggs in the foam nest; Kasuya and Saito, unpublished). There was no significant correlation between the size of a foam nest and the date of oviposition ($r = -0.087$, $n = 132$, $P > 0.05$).

Figures 4 and 5 show the relationship between the date of the first discovery and the size of females and males (snout-vent length), respectively. There is a significant

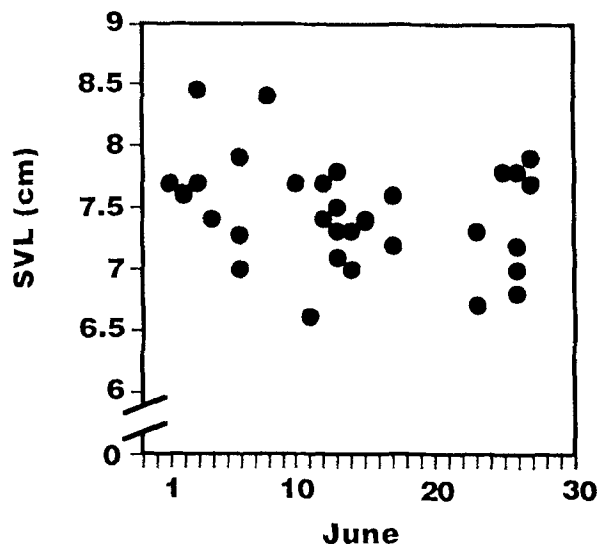


Fig. 4. The relationship between the date of the first discovery and the size of females (snout-vent length).

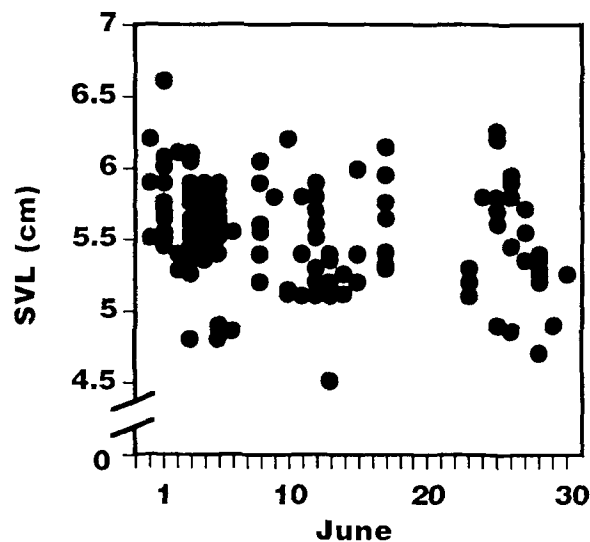


Fig. 5. The relationship between the date of the first discovery and the size of males (snout-vent length).

tendency that larger individuals were discovered earlier in both sexes (female: $r = -0.359$, $n = 36$, $P < 0.05$; male: $r = -0.25$, $n = 141$, $P < 0.05$). The size (SVL) of females was 7.44 ± 0.42 cm (mean \pm SD, hereafter, if not otherwise mentioned) ($n = 36$) and that of males 5.54 ± 0.35 cm ($n = 141$). The body weight was 33.4 ± 4.6 g in females before oviposition ($n = 13$), 18.2 ± 3.7 g in females after oviposition ($n = 20$) and 8.6 ± 1.5 g in males ($n = 137$). The breeding sex ratio (the sex ratio of individuals in and near the pond) was highly male-biased.

The duration from the first discovery to the last discovery of a given adult male was 4.3 ± 5.4 days ($n = 141$). The duration was 1.1 ± 0.2 days ($n = 36$) for females. It was only one day for most females and the longest was two days. No female was observed to make multiple foam nests (clutches). As we recorded the behavior of females or pairs in amplexus as mentioned above, this value for males is possibly an underestimate. The size distribution of females at the first discovery (Fig. 4) approximately shows that of females at the time because females stayed for one or two days. This was not the case for males (Fig. 5).

Sequence of mating behavior

In *R. arboreus*, mating and oviposition behavior usually proceeds as follows. First, a male catches a female in or near the pond. The pair in amplexus (the female and the amplexant male) moves to an oviposition site (often on the twigs of a tree). The female secretes fluid from which the foam nest is constructed and oviposits eggs into it. The amplexant male alone or the amplexant male and other males (joiners or joining males, hereafter) attend the

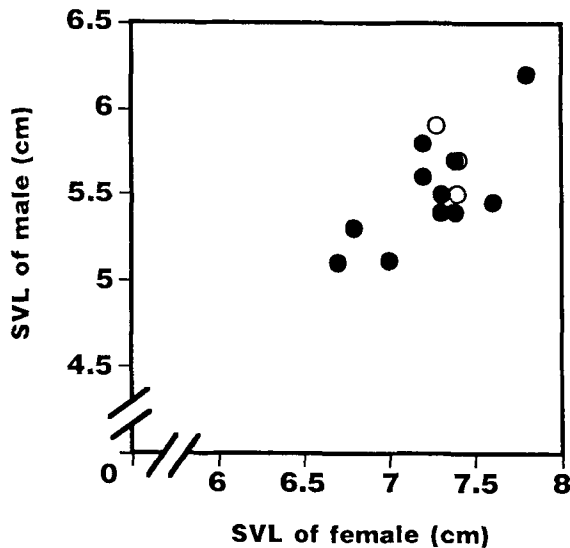


Fig. 6. The relationship between the size of females and males in amplexus (snout-vent length). Dot, pair that was observed in oviposition behavior; open circle, pair that was not observed in oviposition behavior.

ovipositing female and release sperm into the foam nest during oviposition. Oviposition is made by an amplexant pair or the pair and joining males. The former is called oviposition without joiners or a single male mating aggregation while the latter oviposition with joiners or multiple male mating aggregation, hereafter (following Kasuya et al. 1987). The female and males leave the constructed foam nest after oviposition. We present results on mating and oviposition behavior in the following two sections. We describe and analyze behavior before the start of oviposition in the first section while behavior during oviposition was dealt with in the second section.

In this section, we describe the behavior from the time when a male pairs up with a female (posture of amplexus) to the beginning of oviposition. Figure 6 shows the relationship between the size of the female and the male in amplexus. There was a significant positive correlation ($r=0.75$, $P<0.05$, $n=11$). We exclude the pairs in which oviposition was not observed from this data analysis (e.g. turn-over of the amplexant male).

Males in amplexus often made encounter calls (call type C in Kasuya et al. 1992) different from the ordinary advertisement call (call type A in Kasuya et al. 1992). The encounter call has only one note per call (Kasuya et al. 1992). Of 19 cases where we observed most of the behavior sequence, 4 cases resulted in oviposition without joiner (oviposition solely by the pair), 10 in oviposition with joiner (oviposition by the pair and joiner) and the composition of the mating aggregation was not recorded in 5 cases. In all of 6 cases where we recorded the calling

Table 1. Comparison of several male mating behaviors in behavior sequences of mating (from catching up with female by male to the beginning of oviposition).

	Behavior sequence resulting in oviposition	
	without joiners	with joiners
Physical body contacts by other males	2	51
Encounter calls by males in amplexus	0	45
Encounter calls by other males	0	7
Advertisement calls by other males	3	7

status of the amplexant male before amplexus, he called before he paired up with a female.

Table 1 shows the comparison of several behaviors between cases that resulted in oviposition without joiner and those with joiner. The pooled number of behavioral acts are shown. We compared occurrences of several behaviors under the null hypothesis that the number of a given kind of behavior per case is equal in both of the mating behavior sequences that resulted in oviposition with and without joiner. There are significant differences in the occurrence of physical body contact from other males ($\chi^2=15.96$, $P<0.001$, $df=1$) and encounter calls by male in amplexus ($\chi^2=18.00$, $P<0.001$, $df=1$). However, the differences were not significant in the occurrence of encounter calls by other males (binomial test, $P=0.095$) and advertisement calls by other males (binomial test, $P=0.266$).

Out of 7 encounter calls made by other males, 3 were preceded by encounter calls by males in amplexus and 2 were followed by encounter calls by males in amplexus. In 51 cases of the physical body contacts of other males in cases which resulted in oviposition with joiners, 10 were followed by an encounter call of a male in amplexus, 12 followed by the movement of a pair, 3 followed by the dropping of the pair into the water and 5 followed by the dropping of other males into the water. Two cases of physical body contact by other males in behavior sequences which resulted in oviposition without a joiner were followed by the movement of the pair. Out of 45 cases of encounter call by males in amplexus in those cases which resulted in oviposition with joiners, 33 were followed by the movement of the pair.

Figure 7 shows two cases of movement of pairs from the time when the male paired up with the female to the beginning of oviposition. These typical examples show that the pairs were frequently attacked by solitary males with physical body contacts, particularly before oviposition with joiners. Physical combat between males and turn-over of males in amplexus were observed.

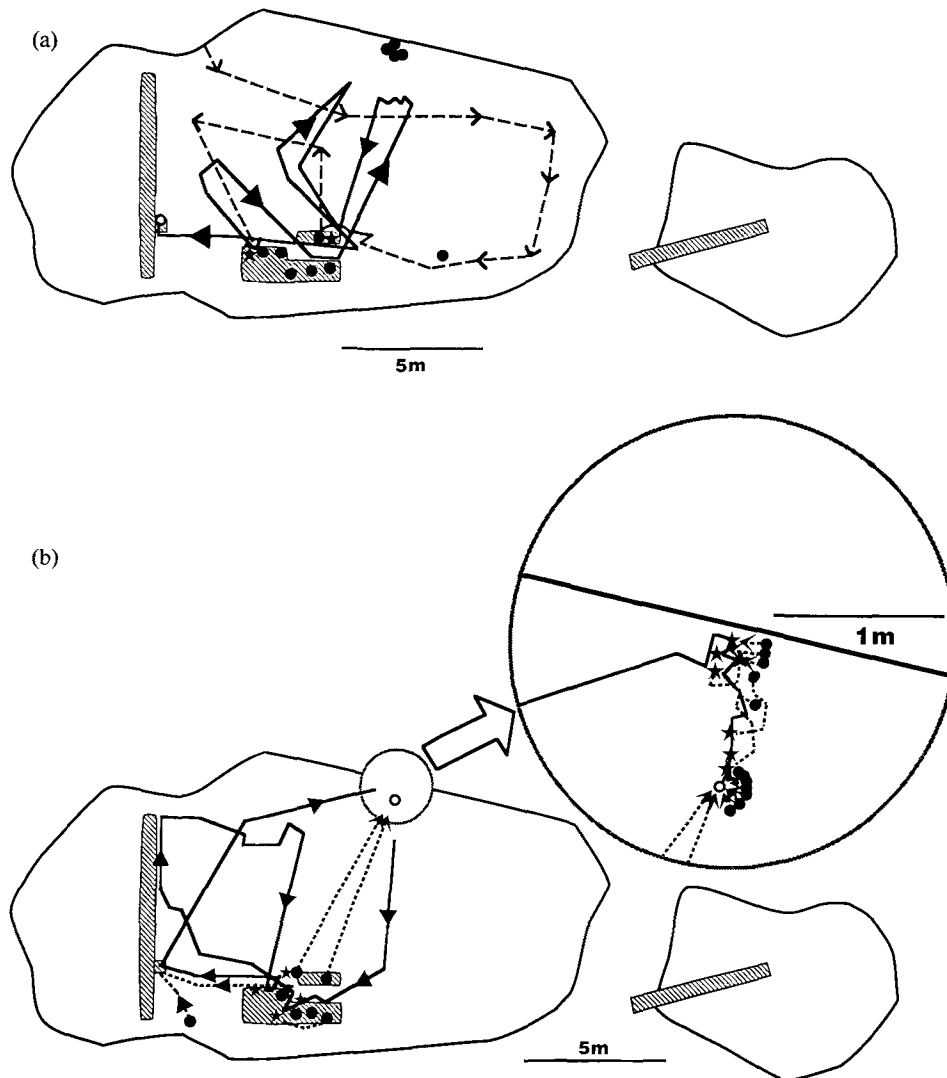


Fig. 7. Movement of pairs from the time when the male paired up with female to the beginning of oviposition. (a) oviposition without joiners; (b) oviposition with joiners. Solid line, itinerary of a pair; broken line, itinerary of a solitary female; dotted line, itinerary of a solitary male; dot, a male not in amplexus; open circle, oviposition site; and asterisk, physical attack by male.

Behavior sequence of oviposition

First, in this section, we describe the composition of mating aggregations. The maximum number of males in a mating aggregation was 3.46 ± 2.90 ($n = 14$). As a mating aggregation included one male in amplexus, the mean of the maximum number of joiners in a mating aggregation was 2.46. The correlation between the size of females and joiners in a mating aggregation was not significant ($r = -0.149$, $P > 0.05$). There was no significant difference between the size of the male in amplexus and joining males (Mann-Whitney U -test, $z = 0.004$, $P > 0.05$) and the correlation between them was not significant ($r = 0.145$, $P > 0.05$).

Table 2 shows the frequency of the movements of hind and forelimbs and that of encounter calls in mating aggregations with and without joiners. There were significant differences in frequencies of hindlimb movements between the female and the male in amplexus in mating aggregations without joiners ($\chi^2 = 409.2$, $P < 0.001$, $df = 1$), and those with joiners ($\chi^2 = 962.0$, $P < 0.001$, $df = 1$). The difference in the frequency of encounter calls by the amplexant male between single male mating aggregations and multiple male ones was significant ($\chi^2 = 32.04$, $P < 0.001$, $df = 1$).

Table 3 shows the inter-individual transition matrices in behavior sequences during oviposition. These matrices are based on inter-individual dyads. The explanation of

Table 3. (Continued)

(e) Joiner→female in multiple male aggregations

	Female					Total
	Bmh	Smh	Mb	Mfl	Nor	
Ab	0	0	0	0	62	62
Apa	0	0	0	0	22	22
Ja	0	0	0	0	53	53
Cn	0	0	0	0	66	66
Mva	1	0	0	1	38	40
Mfl	0	0	0	0	7	7
Bf	0	0	0	0	2	2
Sf	0	0	0	0	3	3
CAM	0	0	0	0	2	2
La	0	0	0	0	42	42

(f) Female→joiner in multiple male aggregations

	Joiner											Total
	Ab	Apa	Ja	Cn	Mva	Mfl	Bf	Sf	CAM	La	Nor	
Bmh	43	0	0	5	4	0	0	0	2	0	917	971
Smh	0	0	0	0	0	0	0	0	0	0	1090	1090
Mb	0	0	0	0	0	0	0	2	0	0	1	3
Mfl	0	0	0	0	0	0	0	0	0	0	1	1

(g) Joiner→male in amplexus in multiple male aggregations

	Male in amplexus								Total
	Ab	Cn	Mb	Mhl	Mfl	Pma	CAM	Nor	
Ab	8	0	0	0	0	0	0	54	62
Apa	0	3	0	0	0	0	0	19	22
Ja	0	16	0	0	0	0	0	35	51
Cn	0	12	0	0	0	0	0	39	51
Mva	0	10	0	0	0	0	0	2	37
Mfl	0	0	0	0	0	0	0	7	7
Bf	0	0	0	0	0	0	0	2	2
Sf	0	0	0	0	0	0	0	3	3
CAM	0	1	0	0	0	0	0	1	2
La	0	5	0	0	0	0	0	37	42

(h) Male in amplexus→joiner in multiple male aggregations

	Joiner											Total
	Ab	Apa	Ja	Cn	Mva	Mfl	Bf	Sf	CAM	La	Nor	
Ab	19	0	0	0	0	0	0	0	0	0	221	240
Cn	0	0	1	7	11	0	1	0	0	5	118	143
Mb	0	0	0	0	0	0	0	0	0	0	6	6
Mhl	0	0	0	0	0	0	0	0	0	0	3	3
Mfl	0	0	0	0	0	0	0	0	0	0	1	1
Pam	0	0	0	0	2	0	0	0	0	1	0	3
CAM	0	0	0	0	1	0	0	0	0	0	1	2

In contrast with the amplexant males, the interactions between females and joining males are one-sided ones. Females seldom responded to the behavior of joiners (Table 3 (e)). Joining males responded with Ab to Bmh by females, like the amplexant males (Table 3 (f)).

Interactions between amplexant and joining males include Ab→Ab and Cn→Cn or Cn→Mva (Table 3 (g) and (h)). The last two show that the encounter call (Cn) is also used in male-male interactions in mating aggregations.

The temporal features of swimming-like movements of female hindlimbs also show an aspect of relationship among frogs in mating aggregations. The duration of a bout in single male mating aggregations (12.6 ± 7.8 s) was significantly longer than that in multiple male mating aggregations (9.1 ± 7.1 s) (ANOVA by ranks, $z=7.85$, $P<0.001$, Meddis 1980, 1984). The interval between two consecutive bouts in single male mating aggregations (54.4 ± 40.4 s) was significantly longer than that in multiple male mating aggregations (38.7 ± 37.6 s) (ANOVA by ranks, $z=16.59$, $P<0.001$). The number of movements in a single bout during oviposition without joiner (5.76 ± 2.94) was significantly smaller than that with joiners (8.00 ± 3.64) (ANOVA of ranks, $z=3.20$, $P<0.01$).

Discussion

Rhacophorus arboreus in the present study was a prolonged breeder in the prolonged breeder/explosive breeder dichotomy (Wells 1977) on the ground of the duration of the reproductive period (40 days in the present study). In two major types of non-random mating in anurans (Arak 1983), size-assortative mating was observed in *R. arboreus* (Fig. 6). However, size dependent mating was not examined in a critical manner in the present study because our observations were made by focal animal sampling of females. As pointed out by Arak (1983), non-random mating does not mean the existence of mate choice by females, but this may be the consequence of alternative mechanisms, e.g. male-male competition. In the present study, size-assortative mating may be the consequence of the negative correlation of body size of males and females with the time of the first discovery (Figs. 4 and 5). Physical male-male competition, which is in the form of physical body contact between males and turnover of an amplexant male in the present study, was observed, but their contribution to the size-assortative mating was not evaluated quantitatively in this study.

The reproductive success of amplexant males with joiners would be lower than those without joiners because of fertilization of some portion of eggs by sperm of joiners. The observations that females did not make multiple foam nests and that females after oviposition

did not have residual eggs support this version. An interesting problem is what determines whether oviposition is performed with or without joiners. The comparisons of occurrences of physical body contacts and encounter calls in the behavior sequence of mating (from the time when a male catches up with a female to the beginning of oviposition) may be useful to answer this question. The comparisons suggest that whether oviposition is performed with or without joiners depends on the behavioral interactions between an amplexant male and other males before oviposition. Typical examples of trajectories of pairs (Fig. 7) also show that aggressive behavior by other males was observed frequently in cases that resulted in oviposition with joiners. Kato (1956) also noted similar behavior of males. A possible interpretation is that physical body contacts by other males or encounter calls by an amplexant male allow other males to locate the amplexant pair and to follow the pair. It thus results in oviposition with joiners. This is consistent with the version of Kasuya et al. (1987) that the joiners in *R. arboreus* are a special case of 'sneaky breeders' (Arak 1983; also see Fukuyama 1991).

The result in Table 1 suggests that encounter calls by amplexant males were made in response to approach or attack of other males. An analysis of behavioral transitions helps to clarify the situation where encounter calls are made. In 45 encounter calls by amplexant males before oviposition, 15 were preceded by the movement of the pairs, 11 preceded by physical body contacts by other males, 5 preceded by the movements of other males near the pairs and 2 preceded by encounter calls by other males. This transition supports the assertion that amplexant males make encounter calls in response to approach or attack of other males before oviposition. The result that 33 out of 45 encounter calls were followed by movement of the pair suggests that the function of encounter calls by males in amplexus before oviposition is to move the female in amplexus. This suggests that the encounter calls by amplexant males has a function to elicit the movement of females in amplexus in this species.

The result in Table 3 (g) suggests that encounter calls by males were used as a way of aggressive interaction among males during oviposition. Encounter calls by males in amplexus were frequently followed by Bmh (beginning a bout of the swimming-like movements of hindlimbs). This suggests that a function of encounter calls by amplexant males is to start the hindlimb movement of females in amplexus. Encounter calls were also made by joiners. In contrast with amplexant males, encounter calls by joiners seemed not to influence the behavior of females in amplexus (Table 3 (e)). Encounter calls by joiners were frequently followed by encounter calls by males in amplexus (Table 3 (g) and (h)). Kasuya et al. (1987) showed that oviposition with joiners did not result in larger foam nests than that without joiners. They also showed

that the duration of oviposition increased with the number of males in a mating aggregation. They presented a hypothesis that the mating aggregation in *R. arboreus* is a consequence of the selfish behavior of males rather than of cooperation among males. This hypothesis suggests that the behavior of males in mating aggregations is explained from the viewpoints of their reproductive success and sperm competition among them.

The comparisons of frequencies of the movements of hind and forelimbs between females and males (Table 2) show that females contributed to most of the limb movements while the contribution by males was small. This suggests that the construction of foam nests are almost made by females alone. This is consistent with the observation that the large number of males in mating aggregations did not contribute to the larger foam nests, but to the longer duration of oviposition (Kasuya et al. 1987). The comparisons of inter-individual transition matrices (Table 3) show that the patterns of transitions between acts of males in amplexus and those of females are similar between oviposition with and without joiners. These comparisons also show that most of the responses of females to those of joining males (99.3% = 297/299) were Nor's (no change in the behavior of females) (Table 3(e)). These are consistent with the observation that joiners do not positively contribute to the construction of foam nests.

The transition that Ab (bending abdomen) by males followed Bmh by females was common both in amplexant and joining males. This suggests that males release sperm when bending their abdomens during the swimming-like movements of female limbs. This may be a tactic to enhance reproductive success through sperm competition.

The comparisons of swimming-like behavior of females during oviposition show the differences in this behavior between oviposition with joiner and without joiner. In single male mating aggregations, the duration of a bout is longer, the interval of bouts is longer and the number of movements in a single bout is smaller, than in multiple male mating ones. These differences in behavior can be considered to cause the longer oviposition duration in mating aggregations with the larger number of males (Kasuya et al. 1987). Males are expected to compete with one another to enhance the probability of fertilization of eggs by their own sperm. This behavioral competition is predicted to be intense in mating aggregations with joiners while absent in those without joiners. The longer duration of oviposition in mating aggregations with more males may be a consequence that male behavior to compete with other males for fertilization of eggs interferes with female behavior for construction of foam nests.

The joiners in foam-nesting rhacophorid frogs has been considered a consequence of cooperative behavior by males (Coe 1967; Wilson 1975; Feng and Narins 1992) or

that of selfish behavior of males (Kasuya et al. 1987; Fukuyama 1991; Kasuya 1992; Jennions et al. 1992). Several hypotheses that assumed cooperation among males were falsified by Kasuya et al. (1987). It is useful to summarize the status of selfish and cooperation hypotheses in the light of the present study.

Movements of male limbs during oviposition were considered as evidence that supports the cooperation hypothesis (e.g. Coe 1967; Wilson 1975). Since some sub-hypotheses of the cooperation hypothesis were falsified, this is the only substantial evidence consistent with the cooperation hypothesis. Most of the data for the movements of limbs so far was not quantitative. In the present study, a small contribution by *R. arboreus* males is shown in a quantitative manner. Further, the movements of male limbs does not necessarily mean contribution by males to foam nest construction. They can be behaviors to facilitate the fertilization of eggs by their own sperm. Our observation showed that males made a unique abdomen-bending behavior just after the beginning of bouts of the movements of female limbs. This suggests that males synchronized their ejaculation to the oviposition of eggs by females into the foam. Other lines of evidence, for example, the large testes in *R. arboreus* shown by Kusano et al. (1991), also support the hypothesis that the mating aggregation in *R. arboreus* is a consequence of selfish behavior of males and that the joiners in *R. arboreus* are a special case of 'sneaky breeders'. At present, the cooperation hypothesis lacks substantial evidence.

Acknowledgements: We are grateful to K. Fukuyama, M. Kishimoto, T. Kusano, R. Shimoyama and M. Toda for discussion. Thanks are also due to members of our laboratory for technical assistance. This study was in part supported by Grant-in-Aid (No.59740320) from Monbusho.

References

- Arak, A. (1983) Male-male competition and mate choice in anuran amphibians. pp. 181–210. In P. Bateson (ed.) *Mate choice*. Cambridge University Press, Cambridge.
- Coe, M. J. (1967) Co-operation of three males in nest construction by *Chiromantis rufescens*. *Nature* **214**: 112–113.
- Coe, M. J. (1974) Observations on the ecology and breeding biology of the genus *Chiromantis*. *Journal of Zoology, London* **172**: 13–34.
- Emlen, S. T. (1968) A technique for marking anuran amphibians for behavioral studies. *Herpetologica* **24**: 172–173.
- Feng, A. S. and P. M. Narins (1992) Unusual mating behavior of Malaysian treefrogs, *Polypedates leucomystax*. *Naturwissenschaften* **78**: 362–365.
- Fukuyama, K. (1991) Spawning behaviour and male mating tactics of a foam-nesting treefrog, *Rhacophorus schlegelii*. *Animal Behaviour* **42**: 193–199.
- Halliday, T. R. and P. A. Verrell (1984) Sperm competition in amphibians. pp. 487–508. In R. L. Smith (ed.) *Sperm competition*

- and the evolution of animal mating systems*. Academic Press, Orlando, Florida.
- Jennions, M. D., P. R. Y. Backwell and N. I. Passmore (1992) Breeding behaviour of the African frog, *Chiromantis xerampelina*: multiple spawning and polyandry. *Animal Behaviour* **44**: 1091–1100.
- Kasuya, E. (1992) Unusual mating behavior of Malaysian treefrogs, *Polypedates leucomystax*. *Naturwissenschaften* **79**: 138. [a comment on Feng and Narins (1992)]
- Kasuya, E., H. Shigehara and M. Hirota (1987) Mating aggregation in the Japanese treefrog, *Rhacophorus arboreus*: a test of cooperation hypothesis. *Zoological Science* **4**: 693–697.
- Kasuya, E., T. Kumaki and T. Saito (1992) Vocal repertoire of the Japanese treefrog, *Rhacophorus arboreus*. *Zoological Science* **9**: 469–473.
- Kato, K. (1956) Ecological notes on the green frogs during the breeding season. 2. breeding habit and others. *Japanese Journal of Ecology* **6**: 57–61. (in Japanese with English summary)
- Kusano, T., M. Toda and K. Fukuyama (1991) Testes size and breeding systems in Japanese anurans with special reference to large testes in the treefrog, *Rhacophorus arboreus*. *Behavioral Ecology and Sociobiology* **29**: 27–32.
- Martin, P. and P. Bateson (1986) *Measuring behaviour*. Cambridge University Press, Cambridge.
- Meddis, R. (1980) Unified analysis of variance by ranks. *British Journal of Mathematical and Statistical Psychology* **33**: 84–98.
- Meddis, R. (1984) *Statistics using ranks*. Basil Blackwell, Oxford.
- Wells, K. R. (1977) The social behaviour of anuran amphibians. *Animal Behaviour* **25**: 666–693.
- Wilson, E. O. (1975) *Sociobiology*. The Belknap Press of Harvard University Press, Cambridge, Mass.

Received 15 June 1994; Accepted 10 April 1996