

Chorus Organization and Male Mating Behavior in the Japanese Pond Frog, *Rana porosa brevipoda*

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Abstract — Male mating behavior of a Japanese pond frog, *Rana porosa brevipoda*, was observed in an enclosed pond. Males organized chorus aggregation during the night. Within the chorus, most males defended “floating” territories. Territorial males exhibited 2 types of calls: advertisement and encounter. Mating occurred primarily in male territories with female initiation, while most spawning occurred outside of the territories. After spawning, males returned to their territories and resumed display behavior. The mating system of this frog is analogous to the typical lek system. Alternative male mating tactics, including satellite and ambush behavior, were also observed. Satellite and ambush males mated with females through forced clasping.

Recent studies of anuran mating systems revealed diversity of male mating behavior and mating systems both among and within species (see Wells 1977; Arak 1983). Wells (1977) divided anuran breeding patterns into 2 basic types. One is explosive breeding in which most breeding activities occur within a few weeks or less. The other is prolonged breeding in which breeding activities extend to a month or more. Wells also pointed out that active searching for gravid females is common in explosive breeders, whereas territorial or lek behavior is common in prolonged breeders.

In contrast with typical mating behavior, quite different mating behavioral patterns, termed alternative mating tactics, have been documented in numerous anurans, including both explosive and prolonged breeders (see Arak 1983, 1985 for reviews). For example, males of *Rana catesbeiana*, a typical prolonged breeder, adopt 3 alternative mating tactics that depend on body size. Large males in a population adopt territorial behavior, whereas small ones adopt satellite behavior and intermediate ones opportunism (Howard 1978). In some explosive breeders, quite different

forms of alternative mating tactics occur. In *Bufo bufo* and *Rana temporaria*, males adopt 2 behavioral patterns. Large males congregate around communal oviposition sites and attempt to dislodge paired males from females, while small males search for females (Arak 1983). Such alternative mating tactics have been considered to have an important role in mating system evolution (Waltz 1982).

Rana porosa brevipoda is a common Japanese pond frog with a prolonged breeding season. It inhabits boggy lowlands, and breeds from spring to early summer in still waters such as paddy fields and ponds. Females deposit 2 clutches per breeding season (Maeda & Matsui 1989). Inoue (1979) reported that some males of this frog exhibited territorial behavior in the breeding season whereas other males did not. However, there has hitherto been no description of the mating behavior or mating system of this frog. I made observations on male mating behavior of *R. porosa brevipoda* in an enclosure. The purpose of this paper is to describe male mating behavior and mating system of this frog.

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Materials and Methods

Study Pond and Frogs

This study was carried out between May and July 1989 in an enclosed shallow pond located in Shiojiri, Nagano Prefecture, Japan. This pond was an abandoned paddy field of an almost square form (ca. 10.5×10.5 m). The depth of the water was kept at 5-15 cm. The banks around the pond were 0.3-1.6 m in height above the water's surface. Water temperature varied from 14-32°C. There was little vegetation in the pond, but the banks were partially covered with weeds and grasses. Water depths and temperatures in the pond did not differ markedly from those of natural habitats. In order to record exact positions of the frogs, poles (ca. 40 cm ht.) were placed in the pool at 2 m intervals as reference points. The pond was enclosed with nets (1 m ht.) in order to prevent emigration. Because male *R. porosa brevipoda* tended to rest in the daytime on banks near calling sites, male behavior should not have been significantly influenced by this enclosure.

Thirteen males of *R. porosa brevipoda* captured in Tatsuno, located 15 km south of the study site, were introduced into the pond on 14 May. The breeding season of *R. porosa brevipoda* in Tatsuno extends from mid-May to early-July (Shimoyama unpublished). The number of the introduced males was determined based on the average density of males in Tatsuno. The size (snout-vent length) of these males ranged from 44.5-65.0 mm. All of these males had secondary sex characters, i.e. a pair of vocal sacs and thumb pads. Of the 13 males, 10 survived throughout the survey.

Introduction of females was made as follows. Because gravid females could not be identified, body fatness was used as an indicator, and fat females were introduced into the study pond at least once every 3 days throughout the observation period. On each introduction, 1 or 2 females were released to the banks more than 5 m from each calling male at the start of the observation. Snout-vent length of the females ranged from 54.0-72.5 mm. Of a total of 60 females introduced, 29 individuals were actually

gravid and deposited eggs. After spawning, females were removed within a day of the oviposition. Females which did not deposit eggs were also removed within a week from introduction.

All individuals were marked by toe-clipping. In addition, waist bands with a numbered tag were attached to all males and some females to identify individuals without capture. It was apparent that the waist bands did not affect breeding activities, at least for males.

Observations

Behavioral observations were made on 41 mornings between 29 May and 17 July 1989. Since males are most active in the early morning (Inoue 1979), regular observations were made during 04:00-10:30. Some additional observations were made during 16:00-20:30 for 3 nights and during 10:30-16:00 for 10 days. In subsequent descriptions, the hours between 18:00 and 08:00 of the next morning are defined as night.

Behavior of males was observed from a car parked beside the study site using binoculars ($\times 7$) and/or a night vision scope. The recording of male behavior was made through instantaneous sampling (Martin & Bateson 1986); spatial positions, posture (high or low), and behavior (i.e. calling, aggression, swimming, or sitting) of all males were recorded at 5 min intervals.

Advertisement calls (= "mating call" in Kuramoto 1977) and other types of calls of the males were recorded using a cassette tape recorder (Sanyo U4-W46[®]) with an external microphone (Sony ECM-21[®]). Water temperature at the recording was 23.5°C. The calls were analyzed by a sound spectrograph (Rion SG-09[®]) with both wide (300 Hz) and narrow (45 Hz) band filter.

Results

Chorus Organization by Males

Males in the study pond exhibited breeding

activities, i.e. calling and other sexual displays, between 29 May and 14 July. This period was somewhat later than that in the natural habitats of Tatsuno. Data for 4 nights with heavy rain-fall in which breeding activities did not occur are excluded in the later description. In the daytime, males sat silently in the vegetation or in pits on the bank. From dusk to the next morning, they actively called in the water. Individual males did not exhibit calling activity on all of the nights during the breeding season. Number of calling males on a given night changed from 1 to 10 (8.3-83.3% of individuals in the study pond).

Calling males did not call individually but tended to synchronize calling activities, organizing a chorus. A chorus aggregation was organized as follows. A male first swam into the water and began calling at dusk; then other males gradually assembled around the calling male and began exchanges of calls. Each night, a single chorus aggregation was organized in the study pond. Location of the chorus was not restricted to any particular site, but changed nightly. Similarly, location of each calling male also changed every night. Males continued calling activities until around 08:00, but gradually stopped calling and then moved to-

ward nearby banks. A few males sometimes continued calling activities until the afternoon.

Description of Male Behavior in the Chorus

Most males in the chorus aggregation called actively. They usually adopted high posture (Inoue 1979) and maintained 1-2 m of distance from each other with exchanges of vocalization and aggressive behavior, including approaching, jump attack, physical wrestling, and chase. These males exhibited 2 types of vocalization: an advertisement call and an encounter call (Fig. 1). The former consisted of 5-13 notes and the latter only 1 note. Advertisement calls were exhibited when males were calling alone and when they were approaching other males or females. Encounter calls were exhibited prior to or just after aggressive interactions with opponents.

These vocal and aggressive interactions produced regular spacing within the chorus; males occupied their own calling space. The fidelity of each calling male to a particular site was relatively weak, because their locations changed every night. In addition, males sometimes shifted their calling space within a few hours

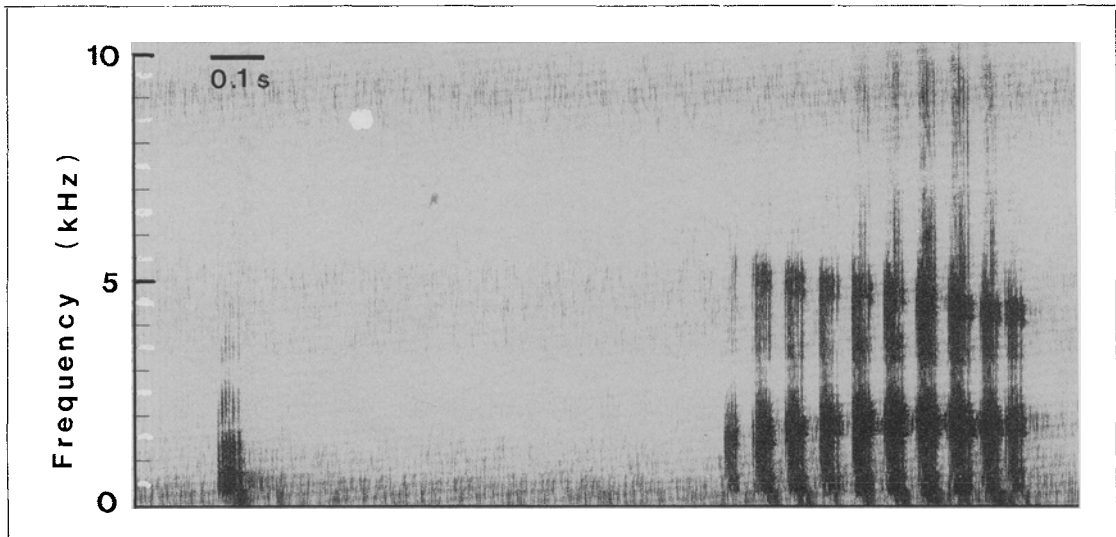


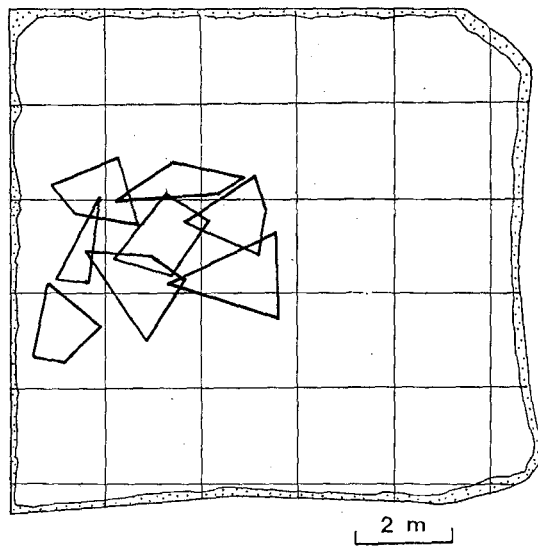
Fig. 1. Sonograms of an encounter call (left) and an advertisement call (right) analyzed with wide band filter.

(Fig. 2a, b). In such cases, nightly activity ranges of these males greatly overlapped (Fig. 2c). In any case, the male calling space occupied was not "typical" territory in the sense of long-term site attachment, but can be regarded as "floating" territory (Wilson 1975). I judged the male calling space occupied as territory as

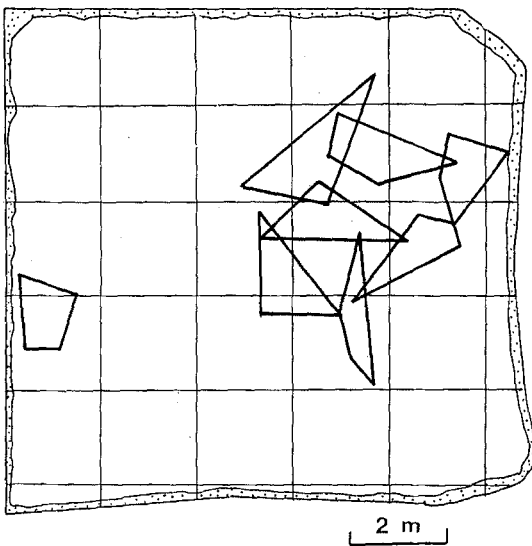
long as it hardly overlapped with others within any given time. I could not find any particular characteristic, such as vegetation, water depth, or water temperature, in the territories.

Some males in the chorus adopted low posture (Inoue 1979) for hours and sat silently near (usually < 1 m) territorial males. These males are referred to as satellite males. There was no significant difference in size (snout-vent length) between territorial and associated satellite males (Wilcoxon's signed-rank test, 2-tailed, $T = 5$, $P > 0.1$, $n = 7$). Of 7 territorial-satellite associations observed, 6 were maintained for only 1 night, but 1 was maintained for 3 successive nights. Satellite males attempted to clasp gravid females which were approaching territorial males, and 1 of them actually succeeded in mating, suggesting that satellite behavior is one of the male mating tactics. Satellite males rarely began advertisement calls when they were approaching gravid females, and never exhibited aggressive behavior nor encounter call.

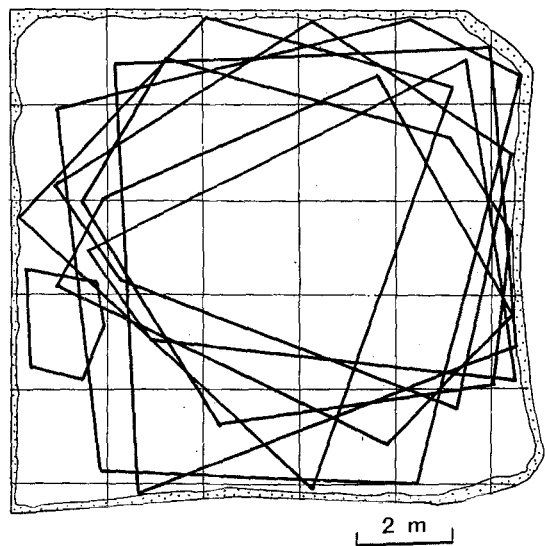
Of the 13 males, 7 males (53.8%) adopted only territorial behavior and 1 male (7.7%) did only satellite behavior, whereas 5 males



(a)



(b)



(c)

Fig. 2. Activity ranges of 8 calling males on 8 May, 1989. (a) 04:00-04:30; (b) 05:00-05:30; and (c) 04:00-10:00. Each polygon indicates the minimum activity range of each individual within a given time interval.

(38.5%) did both behavioral patterns on different nights. Switching between the 2 patterns within an observation night was not observed.

Ambush Behavior by Resting Males

As mentioned above, males did not appear in the choruses all of the nights. The resting males silently sat on the bank during the night as well as in the daytime. Nevertheless, these males were not necessarily passive. When other individuals appeared or moved nearby, some resting males suddenly began advertisement calls and attempted to clasp them.

Patterns of Pair Formation

Females usually sat silently on the banks both in the daytime and in the night. They visited male choruses only at the time of mating. Two major patterns of pair formation were observed. One was initiated by females. A female visits a male's territory and turns her back towards him for several seconds. The male then quickly clasps the female. Prior to mating by this pattern, 8 (36.4%) females visited 3 or more territories, 3 females (13.6%) visited 2 territories, and 11 females (50.0%) visited only 1 territory.

Another pattern was forced clasping by males, in which the male rushes at and clasps a female which moves nearby. Not only territorial males but also satellite and resting males exhibited forced clasping toward females. Forced clasping occurred with non-gravid as

well as gravid females, and thus only 35% of the amplexant "pairs" actually deposited eggs (Table 1). The frequency of progression to spawning from forced clasping pairs was significantly lower than that from pairs with the female initiation pattern (Chi-square = 20.71, $df = 1$, $P < 0.001$). In 2 pairs formed through forced clasping in which the males were much larger than the females, the females suffocated in the water and did not finish deposition of all of their clutches.

As shown in Table 1, sequence of pair formation differed significantly between territorial males and other behavioral males (Chi-square = 18.48, $df = 1$, $P < 0.001$). Most gravid females approached calling territorial males, and mated with them after female initiation. In other words, most of the successful matings were achieved by pairings of territorial males with females visiting males' territories.

Figure 3 shows an example of movement cycles of a gravid female from release to the finish

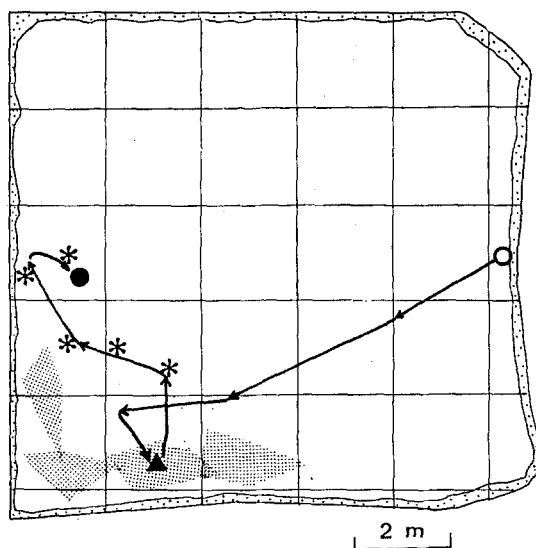


Table 1. Sequence of "pair" formation in relation to male behavioral pattern. Figures in parentheses show number of pairs which actually deposited eggs.

Male behavior	No. pairs formed through	
	Female initiation	Forced clasping
Territorial	22 (22)	8 (4)
Satellite	0	2 (1)
Ambush	0	10 (2)

Fig. 3. An example of the movement of a gravid female from release to the finish of spawning recorded at 05:20-09:35 on 1 June 1989. Open circle: the site of release; closed triangle: the site of mating; asterisk: the site where eggs were deposited; closed circle: the site where paired male and female were separated. Shaded areas show territories of four males determined by the minimum polygon.

ish of spawning. This female visited a territorial male and was clasped within his territory. The pair soon left this territory and began deposition of eggs more than 2 m away from the pairing point. They did not deposit eggs at 1 site, but repeated mutual movement and spawning. Likewise, other amplexant pairs also repeated mutual movements and egg deposition, and therefore egg clutches were partitioned into several small masses. The pairs tended to avoid the sites where egg masses of other females were already deposited for their oviposition sites. Of 26 ovipositions fertilized by territorial males, 21 (80.8%) were made outside of the territories of the paired males. In the remaining 5 cases, egg deposition sites were both within and outside of the paired males' territories.

After spawning, territorial males tended to return to their own territories and resumed display there, while satellite or ambush males moved toward banks. All of the females moved to the banks after spawning. The duration from the onset of amplexus to the finish of spawning was 0.9-3.0 h ($\bar{X} = 1.85$, $SD = 0.722$, $n = 14$). Neither males nor females displayed parental care after spawning.

Discussion

This study describes mating patterns of *R. porosa brevipoda* based on observations of an enclosed population. Males organized choruses in the night, and each male established small territories within the chorus aggregations. Males defended their territories with displays including high posture, 2 types of vocalization, and aggressive behavior. Territories were not maintained longer than a single night. Inoue (1979) noted similar territorial behavior in a natural population of this frog. He also showed an example of an assemblage of male territories in the paddy field (Inoue 1979: Fig. 8), although he did not discuss chorus organization. I therefore consider that male behavioral patterns in my study pond did not differ markedly from those in natural habitats. Because most gravid females visited male territories and mated with territorial males there, it is

probable that male territories functioned as the sites for sexual advertisement.

The important point in regard to the population's mating system is whether males defend resources used by females (Emlen & Oring 1977; Ryan 1985; Davies 1991). In *R. porosa brevipoda*, 21 of the 26 ovipositions (80.8%) fertilized by territorial males occurred outside of paired males' territories. A similar trend was also observed in a natural population of this frog inhabiting Tatsuno (Shimoyama unpublished). This indicates that male territories did not necessarily function as oviposition sites.

I believe that the mating system of *R. porosa brevipoda* is analogous to leks. Leaks have the following characteristics: (1) males aggregate and defend territories solely for mating; (2) females select their mates from among displaying males; and (3) females do not utilize any resources within the male's display area (e.g. Emlen 1976; Bradbury 1981). My observations are consistent with these characteristics of lek mating systems. It was likely that males did not defend any particular resources, but attempted to maintain their own calling space within chorus aggregations.

I believe that the lek mating system in *R. porosa brevipoda* has evolved with its relation to the environment of the breeding sites. The breeding sites of this species are shallow still waters. Water conditions such as depth and temperature can be very unstable, especially on sunny days during the breeding season, i.e. from late spring to summer. High temperature decreases oxygen in the water, which might influence embryo survival. Under such conditions, selective pressure would favor the dispersed deposition of eggs as actually observed. It is likely that male territory of this frog is not sufficient in area to utilize as an oviposition site. I suppose that other anurans which breed under similar conditions also have mating systems similar to leks. As found in many other anuran species (see Arak 1983, 1985), satellite males were observed in *R. porosa brevipoda*. It is widely recognized that satellite males are "sneaky" breeders which attempt to intercept females approaching calling males (Wells 1977; Arak 1983, 1985). In *R. porosa brevipoda*, satellite males also attempted to clasp females.

In my study, one of them actually intercepted gravid females. In addition to the satellites, resting males on the bank also attempted to clasp females, and some of them actually succeeded in mating. In contrast, territorial males mated with females through female initiation, while satellite and ambush males did so through forced clasping (Table 1). These results showed that both satellite and ambush behavior are alternative male mating tactics which require little exertion in comparison with territorial behavior.

Acknowledgements — I thank Professor Toru Nakamura for his kind advice throughout this survey. I also thank Drs. Tamotsu Kusano, Eiti Kasuya, Kinji Fukuyama and 2 anonymous referees for valuable comments on earlier drafts of the manuscript.

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(Received 26 December 1991; Accepted 31 May 1993)