Males compete for access to resources or females or to influence female mate choice in many animal species. Male competitive activities are accompanied by high-energy expenditure and increased risk of predator detection. We therefore hypothesized that information predicting female receptivity could affect male competition strategies in species in which such information is available to males. To test this hypothesis, male–male vocal competition was assessed in *Xenopus laevis*, a species in which females can produce receptive (rapping) and unreceptive (ticking) calls. Male vocalizations were recorded when 1) males called alone, 2) 2 paired males with similar body mass called competitively and established dominance, and 3) the paired males called when listening to playbacks of either rapping or ticking calls. On average, rapping but not ticking playbacks increased male calling and in many cases induced previously nondominant males to call more than their rivals. Moreover, males adopted either of 2 competitive strategies: an assertive strategy in which some individuals always called at a high rate and an opportunistic strategy in which some individuals only called at a high rate in the presence of receptive female call playbacks. Body mass and call rate were correlated only when males called alone or when rapping calls were played back. These results support the idea that male–male competition strategies can be influenced by information indicating that receptive females are present. **Key words:** female choice, male competitive strategy, vocal competition, *Xenopus laevis*. [Behav Ecol 23:307–312 (2012)]

**INTRODUCTION**

**M**ales compete directly for access to resources or females and indirectly for female mate choice in most animal species (Darwin 1871). It is well known that males from the same population use different competitive strategies (Andersson 1994). The literature is replete with examples of alternative reproductive phenotypes that are most readily interpreted as alternative tactics within a conditional strategy. For example, a common conditional reproductive strategy is the use of fighting or sneaking as alternative mating tactics that depend on body size or mass (reviewed by Gross 1996).

Male competitive activities are typically accompanied by high-energy expenditure and increased risk of predator detection. Nevertheless, competitive outcomes among males do not always lead to successful mating because female choice is often the final determinant of mating success (Cox and Leboeuf 1977; Contreras-Garduño et al. 2007). Thus, although males compete for access to females through establishing dominance, females have their own criteria for choosing mates in order to increase the fitness of offspring (Wiley and Poston 1996; Gerhardt and Huber 2002; Wells 2007) or minimize female mortality (Cordero and Eberhard 2003). Therefore, males might well be expected to adjust competitive strategies on the basis of signals produced by females indicating receptivity. Although some human and animal studies have reported that male reproductive behavior is affected by female responses (Montgomerie and Thornhill 1989; Semple 1998; Pawlowski et al. 2008; Cui et al. 2010; Frankenluis et al. 2010), adjustments of competitive strategy by males based on information predicting female responsiveness are not as yet well understood.

In the present study, the hypothesis that male competitive strategy can shift based on female responsiveness was tested in the African clawed frog, *Xenopus laevis*, a species that has proved to be a useful model for studying male–male competition and male–female interactions in previous studies (Tobias et al. 1998; Tobias et al. 2004). In *X. laevis*, males can produce 6 types of calls, the most prominent of which are advertisement and answer calls. Females can produce 2 call types, a sexually receptive rapping call (11–12 Hz click rate) that increases male vocal activity and an unreceptive ticking call (click rate of 4 Hz) that depresses male vocal activity (Tobias et al. 1998; Wang et al. 2010). A previous study (Tobias et al. 2004) showed that when 2 sexually active males are paired, each produces fewer advertisement calls than when calling alone, although the extent of call suppression usually differs so that one male asserts dominance, whereas the other plays a subordinate role. Because female calls indicate the presence or absence of receptive females, we predicted that some males would shift competitive strategies depending on whether they were exposed to female rapping (receptive) or ticking (unreceptive) calls.

To test the hypothesis, the effect of playbacks of female rapping and ticking calls were assessed on the vocal behavior of male pairs whose dominance relationships had previously been determined. The goal was to determine if male dominance relationships changed as a function of available information concerning female receptivity.
MATERIALS AND METHODS

Animal preparation

Adult *X. laevis* males purchased from Nasco (Fort Atkinson, WI) and bred in our lab were used. All animal procedures were carried out in accordance with the Animal Care and Use Committee of Chengdu Institute of Biology, the Chinese Academy of Sciences. Subjects were raised in aquaria 120 cm long, 50 cm wide, and 60 cm high with water depth approximately 20 cm (ca. 20 males in each tank) and were fed 3 times a week. The aquaria were placed in a room under controlled temperature conditions (20 ± 1°C) and maintained on a 12:12 light–dark cycle (lights on at 08:00 h). Two males with similar body mass were selected and used in each paired trial. Each animal was used exclusively in only one experimental trial. After being weighed and labeled by taking a photograph, the frogs were placed separately in 2 holding aquaria (80 × 50 × 60 cm) with the same water depth, photoperiod, and temperature as the home cage. Subjects were injected subcutaneously twice with human chorionic gonadotropin (hCG) 24 and 6 h before the experiment began (20:00 h); the first injection dosage was 0.2 ml (100 IU/0.1 ml) and the second was 0.15 ml (100 IU/0.1 ml), according to the protocol of Tobias et al. (2004).

Equipments and settings

Two kinds of aquarium were used for each experimental period: 2 aquaria (80 × 50 × 60 cm) for baseline recordings before pairing and 1 test aquarium (150 × 50 × 60 cm) for male–paired tests. The latter was divided equally into 3 sections (left, middle, and right) along the long dimension with 2 barriers separating the paired males at the left and right end sections. These barriers did not impede sound transmission. A Daravoc underwater speaker (frequency response: 0.1–10 kHz; Sun Pride Inc., Zhejiang, China) was placed in the middle section of the testing aquarium to play back natural female rapping and ticking calls, which had been recorded earlier. Both kinds of calls, each 10 s in duration, were played back repeatedly during the test sessions. Playback intensities were adjusted to be equivalent to those of natural calls as described in a previous paper (Wang et al. 2010). One lab-40 hydrophone (Lab-core System, Washington, DC) was installed under the water for each holding aquarium and 2 lab-40 hydrophones were installed at the left and right end sections of the large testing aquarium to record all calls produced by the 2 males. The hydrophones were connected to a digital recorder (Marantz PMD 660, 16 bit, 44.1 kHz). A computer-linked webcam was mounted above the testing aquarium to monitor the entire observational field. The temperature and photoperiod conditions were the same as for the home cage.

Experimental procedures

The experiment was conducted at 20:00 h and consisted of 3 conditions, which were carried out successively and are therefore referred to as stages: a prepaired stage, a paired stage, and a paired stage with female call playbacks. Each stage lasted 45 min. For the prepaired stage, 2 frogs of similar mass were acoustically isolated and recorded separately in the 2 holding aquaria for 45 min to determine baseline call production rates. The 2 males were then transferred randomly to the left or right sections of the testing aquaria and allowed to acclimatize to the aquarium for 15 min, after which calls for the paired stage were recorded for 45 min. Immediately, after recording the males during the paired stage, female rapping or ticking calls were presented and all male calls subsequently produced were recorded for an additional 45-min period. Fourteen pairs of males were used for the rapping call playback experiment and another 14 pairs of males were used for the ticking call playback experiment. The playbacks of rapping and ticking calls were conducted on different days with a random ordering.

Analysis and statistics

Call durations (i.e., total time spent calling in each timed session) for individual males in each experimental condition were measured using Adobe Audition 3.0 (Adobe Systems, San Jose, CA) software. Subsequent statistical analyses were accomplished using PASW version 18.0 software (SPSS Inc., Chicago, IL, USA). Data were examined for assumptions of normality and homogeneity of variance using Kolmogorov–Smirnov and Levene tests before any statistical analysis. Differences in mean values of call durations between males in each pair were compared by using paired *t*-tests. The repeated measures design in the general linear model was used to evaluate the differences of the total calling time among different session. Possible relationships between the call durations and the body mass were examined using Spearman’s correlation analysis. Values are expressed as mean ± standard deviation; *P* < 0.05 was considered statistically significant.

RESULTS

Rapping call playback alters competitive patterns

Total time spent producing advertisement calls by males was significantly reduced in the presence of another male (Figures 1 and 2). Moreover, when 2 males were paired, one male virtually always produced significantly more calls than the other (Figures 1 and 2). The former were referred to as dominant and the latter as subordinate males in the present study. In general, the call durations of both dominant and subordinate males decreased significantly when paired compared with the prepaired condition, whereas the playback of female rapping calls increased the vocalizations of both paired males (*F*$_{2,52}$ = 32.271, *P* < 0.01, Figure 1).

Although the total call durations of males in the dominant and the subordinate groups did not differ when calling alone (prepaired condition) (*t*$_{13}$ = 0.487, *P* > 0.05, Figure 1), total call durations differed between these groups when the males called in the paired stage (*t*$_{13}$ = 3.903, *P* < 0.01, Figure 1). Of particular importance is that the dominance pattern established by pairs was dramatically changed when the males were exposed to playbacks of female sexually receptive rapping calls. In such cases, the durations of advertisement calls of both dominant and subordinate males increased to nearly those of the prepaired condition and did not significantly differ between 2 groups (*t*$_{13}$ = 0.805, *P* > 0.05, Figure 1).

As can be seen in Figure 2, when exposed to female rapping calls, 12 of 14 dominants and 13 of 14 subordinates increased their call durations (*P* = 0.012 and *P* = 0.002, respectively, using the binomial test). As a result, 7 of 14 previous subordinates came to produce longer total call durations than their rivals who were previously dominant (Figure 2).

Ticking call playback did not affect male advertisement call production

As in the experiment with rapping call playbacks, total call durations for dominants and subordinates were not significantly different in the prepaired condition (*t*$_{13}$ = 1.183, *P* = 0.258), whereas call durations between dominants and subordinates differed very significantly in the paired condition (*t*$_{13}$ = 4.4943, *P* < 0.001). In contrast to the effect of rapping call
playbacks, ticking call playbacks did not significantly affect call durations for either dominant and subordinate males ($F_{2,52} = 55.933, P > 0.05$). Moreover, the call duration differences between dominants and subordinates were still significant ($t_{11} = 2.249, P = 0.043$, Figure 1) when males were exposed to female unreceptive ticking calls.

**Dynamic patterns of call production**

In view of the fact that call production increased when female rapping calls were played (Figure 1), call production by both dominants and subordinates was examined at 5-min interval in order to determine the detailed temporal relationships between call production and exposure to rapping calls. As can be seen in Figure 3, call production was fairly stable for both the dominant and the subordinate groups with only slight fluctuations during the paired stage. After rapping call playback, call production for both groups increased significantly immediately. Furthermore, call production for the subordinate group increased to the same level as that of the dominant group within 10 min ($t_{11} = 0.007, P = 0.995$) (Figure 3).

In addition to increasing call durations, playbacks of female rapping calls increased the occurrence of "simultaneous" call production by both the dominant and the subordinate males.

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**Figure 1**

Advertisement call durations for dominant and subordinate males in the prepaired, paired, and paired with playback conditions. Each bar represents the mean duration of advertisement call production in a 45-min recording period for each condition. Playbacks were female sexually receptive (rapping) call or female sexually unreceptive (ticking) call. Values with "**" differ significantly at $P < 0.05$, and "***" at $P < 0.01$ between vocally dominant and subordinate male groups.

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**Figure 2**

The amount of advertisement calling produced by: (A) dominant and (B) subordinate males during the prepaired, paired, and paired with rapping call playback conditions. Each male is represented by the same symbol; lines connect data points for the same individual. D1–D14 and S1–S14 represent the 14 dominant and subordinate males, respectively. Dominant and subordinate males labeled with the same number are paired males. $N = 14$ pairs.
compared with that of paired males without rapping call playback (14.4% vs. 0.7%, $r_{13} = -3.467, P = 0.004, n = 14$ pairs). Thirteen of 14 pairs exhibited such simultaneous call production during the calling session when rapping calls were played back, whereas only 2 of 14 pairs called simultaneously when female rapping calls were not played. Most simultaneous call production occurred during the first third of the paired condition with rapping calls.

**Relationships between body mass and call production**

There is no significant difference in mean body mass between the dominant and the subordinate groups in the present study ($t_{13} = -0.379, P = 0.711$). Nevertheless, in the prepaired condition, larger males produced more calls ($r = 0.419, P < 0.05, n = 28$, Figure 4A). However, when the males were paired without female rapping call playback, this positive correlation was not found ($r = 0.294, P > 0.05, n = 28$, Figure 4B). In contrast, a positive correlation was again observed when rapping calls were played back to the males ($r = 0.430, P < 0.05, n = 28$, Figure 4C).

Further support for the idea that competitive strategies are exhibited by males in this species is provided by separate analyses of the relationships between body mass and call production for the vocally dominant and subordinate groups across all 3 conditions. Results showed that there was no significant relationship between body mass and call production for the dominant group in all 3 conditions ($r = 0.190, P = 0.515; r = 0.487, P = 0.078; r = 0.279, P = 0.334$, for prepaired, paired, and playback rapping condition, respectively), whereas there was a significant positive correlation for the subordinate group in the prepaired and the rapping call playback conditions ($r = 0.701, P = 0.005; r = 0.409, P = 0.146; r = 0.648, P = 0.012$, for prepaired, paired, and playback rapping condition, respectively, $n = 14$).

**DISCUSSION**

The results of the present study reveal that vocal competitive patterns between paired males in *X. laevis* change when males hear playbacks of the calls of sexually receptive females but remain unchanged if males listen to playbacks of female unreceptive calls. These results indicate that the availability of information concerning female receptivity (i.e., female receptive or unreceptive call playbacks) can cause male–male competitive behaviors to change.

It is known that male behavior can change in the presence of females under some circumstances. For example, studies have reported that human males may become braver in the presence of females (Pawlowski et al. 2008; Frankenhuysen et al. 2010). Male Barbary macaques (*Macaca sylvanus*) reproductive behaviors have been shown to be enhanced by the copulation calls of females (Semple 1998). In some avian species, male–male competition has been shown to be incited by the loud calls or songs that advertise fertility in females (Montgomerie and Thornhill 1989). There are also several studies in fish reporting differences in male–male competition in the presence of females (Candolin 1997; Aspbury and Gabor 2004). In the Emei music frog (*Babina daunchina*), Cui et al. (2010) showed that a female call not only stimulates male–male physical contact and nest plundering but also increases the production rate of male aggressive calls and advertisement calls. Consistent with these results, we found that both the amount of calling and the occurrence of simultaneous calling in paired males increase when males listen to female receptive calls in *X. laevis*. These results indicate that the female receptive call can significantly incite male–male competition in this species.

Male competition based on dominance by itself does not necessarily lead to successful mating insofar as female choice is sometimes the final determinant (Cox and Leboeuf 1977; Contreras-Carduno et al. 2007). Males, in theory, might thus favor a different competitive strategy if females are present. Consistent with this hypothesis, we found that when female receptive calls are played back to males, half of subordinate individuals subsequently became vocally dominant supporting the idea that male competitive strategy changed when information concerning female receptivity was provided. This is also consistent with the fact that the female *X. laevis* produces 2 specific calls signaling either receptivity or a lack of sexual receptiveness, which would enhance the ability of males to discriminate the reproductive condition of females and adjust competitive strategy accordingly (Tobias et al. 1998; Wang et al. 2010).

It is important to note, however, that in the present study, some males were consistently observed to favor an assertive strategy regardless of whether receptive females were present or not insofar as calling changed little for these males in the presence of rapping call playbacks. It is possible that the adaptive value of such an assertive strategy is that it attracts female attention and also tends to suppress rivals and facilitate competition for territory regardless of female availability (Tobias et al. 2010). In contrast, the opportunistic strategy may be adaptive because individuals who do not compete for dominance when
receptive females are not available but behave competitively when information indicates that females are receptive allows such opportunistic males to optimize energy expenditure. Call production is associated with high-energy consumption, and call activity is correlated with body mass in many anurans (reviewed by Gerhardt 1994), thus, the trade-off between the assertive strategy and the opportunistic strategy might be expected to depend on the body mass of the individuals. In the present study, male call durations were found to be positively related to body mass in the prepaired condition. In the paired stage, however, such a correlation was not found (i.e., larger males did not produce longer calls in this condition). A logical reason for this is that some males adopt an opportunistic strategy independent of body mass and therefore exert less

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**Figure 4**

Relationships between body mass and call activity in the prepaired, paired, and prepaired with female sexually receptive call playback conditions. (A) A significant positive correlation between body size and call duration obtained during the prepaired stage. (B) No significant correlation was found when 2 males were paired. (C) A significant correlation was again observed when males listened to female sexually receptive rapping call playbacks.
energy in competing with rivals when receptive females are not available. When male pairs (with similar body mass) listened to playbacks of female rapping calls, however, a significant correlation between body mass and call durations was found (Figure 3). This suggests that adoption of an opportunistic strategy by some males is dependent mainly on the availability of receptive mate but not the male’s body mass.

Males have been shown to adopt conditional alternative strategies in many species including the use of fighting or sneaking as alternative mating tactics depending on body sizes or masses (reviewed by Gross 1996). However, this is not the case for X. laevis in which no significant correlation between body mass and adoption of a dominant or subordinate strategy was found and no correlation between body mass and call duration was observed in the paired competitive condition. These results support the idea that, in X. laevis, adoption of an assertive or opportunistic strategy is not determined by body mass but depends more on the presence of receptive females. Our results thus provide a new example of the conditional alternative strategy, which is typically defined as a reproductive tactic in which the decision to switch strategy is made on the basis of aspects of the male’s individual status (Gross 1996; Tomkins and Hazel 2007). Thus, the present study highlights the possibility that male reproductive strategy alternations can have different outcomes for males with the same body conditions.

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