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ORIGINAL PAPER

Vocal competition in male *Xenopus laevis* frogs

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Abstract Male *Xenopus laevis* frogs produce underwater advertisement calls that attract gravid females and suppress calling by male competitors. Here we explore whether groups of males establish vocal ranks and whether auditory cues alone suffice for vocal suppression. Tests of male–male pairs within assigned groups reveal linear vocal dominance relations, in which each male has a defined rank. Both the duration over which males interact, as well as the number of competitive opportunities, affect linearity. Linear dominance across the group is stable for about 2 weeks; rank is dynamic. Males engage in physical interactions (clasping) while paired but clasping and vocal rank are not correlated. Playbacks of advertisement calls suppress calling and calls from high- and low-ranking males are equally effective. Thus, auditory cues alone suffice to suppress vocal behavior. Playback intensities equivalent to a nearby male advertising effectively suppress calling while low-intensity playbacks are either ineffective or stimulate vocal behavior. *X. laevis* advertisement calls are biphasic, composed of alternating fast and slow click trills. Approximately half the males tested are more vocally suppressed by all slow than by all fast trills; thus, these males can distinguish between the two phases. The fully aquatic family Pipidae diverged from terrestrial ancestors approximately 170 mya. Vocal suppression in the *X. laevis* mating system may represent the translation of an ancient anuran social strategy to underwater life.

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Introduction

Vocal advertisement is the signature of male courtship in anurans. Advertisement calls function in female attraction and in male competition. While the role of advertisement calls in attracting females is ubiquitous and well documented, the role of calls in male–male competition differs across species (Gerhardt and Huber 2002). In some species the call of another male can affect call quality in the responding male. For example, males may shift from an advertisement to an aggressive call (Schwartz and Wells 1984; Given 1987; Rose and Brenowitz 1997), or change the timing of calls to avoid acoustic interference (Sullivan and Leek 1986; Grafe 2003). In many anurans, male calls affect the amount of advertisement calling and in the majority of these, males respond to neighbors or playbacks by increasing their vocal output (Gerhardt and Huber 2002; Wells and Schwartz 2007; Schwartz 1987). Vocal escalation, in which males attempt to out-signal competitors, occurs in both explosive (Bosch and Marquez 1996) and prolonged (Marguez et al. 2001; Wagner 1989a) breeders. The opposite effect, vocal suppression, is observed in satellite males that take up silent residence in a dominant frog's territory (Gerhardt and Huber 2002) but is uncommon outside the satellite situation (Harrison and Littlejohn 1985; Tobias et al. 2004).

In the wholly aquatic frog, *Xenopus laevis*, both sexes live together in the same pond year round. Sexual activity in males is maintained throughout the breeding season, approximately 6 months (Kalk 1960; Tobias et al. 2004); during this period, females are sexually active briefly and asynchronously. This difference in reproductive duration results in a highly skewed operational sex ratio in which many males are competing for the rare, sexually receptive female (Tobias et al. 1998). Since females oviposit even if not mated, the pressure on females to find a signaling male is immediate and intense. Females locate and swim towards advertising males (Picker 1983). Thus, a male that can vocally out-signal the competition has a presumptive reproductive advantage. Here, we examine male vocal behavior in response to playbacks and in male–male pairs to further explore vocal competition in *X. laevis*.

One out-signaling strategy used by male *X. laevis* is vocal suppression. When two males, each advertising for equivalent periods alone, are paired, one male is vocally suppressed; when the vocally dominant male is removed, the suppressed male resumes calling (Tobias et al. 2004).

Male–male social interactions are accompanied by clasping and vocal interactions involving a variety of calls: chirping, growling, answer, and advertisement calling. Male–male clasps consist of the clasping male placing his forearms around the inguinal fold of the clasped male, a behavior akin to amplexus observed in mating pairs. Vocal suppression occurs even when males are not allowed to clasp and only produce the advertisement call. However, adult *X. laevis* retain their lateral line system and could use this information, as well as olfaction and visual cues, to locate and detect another male. Given the prominence of vocal cues, however, it was possible that these alone suffice for vocal suppression and we explored this possibility using call playbacks.

No obvious acoustic features of the calls of isolated males predicted which male would dominate in a vocal competition. However, the calls of vocally high-ranking males might share more subtle features not expressed in the calls of low-ranking males. We tested this possibility using playbacks of calls from both classes of competitor. The ponds in which frogs are found in South Africa vary considerably in size and the calls of a distant male should be less intense than those of a close competitor. We thus also tested the idea that call intensity affects vocal competition using playbacks. Finally, the *X. laevis* advertisement call is biphasic, consisting of alternating short trains of rapid clicks and longer trains of slower clicks. We again used playbacks to determine whether each portion of the call is equally effective in vocal suppression.

That paired males can be vocally ranked, with one dominant and one subordinate, suggested that groups of males might also form ranked groups. Linear ranking across the group is achieved when A is dominant when paired with B, and B is dominant when paired with C, then A is dominant when paired with C (a transitive triad). An alternative ranking scheme is one in which some males call more than others, and thus out-signal more males, but there is no ordinal ranking. Since *X. laevis* males produce no visible body movement while calling, identification of the calling male in a group is difficult. The amount of calling by individual males in a pair can however be accurately measured using two hydrophones, one that records the vocal behavior of both males and a second, less sensitive, that only records calls in close proximity (Tobias et al. 2004). Thus, vocal rankings within a constructed group were examined by measuring the amount of calling in all pair-wise comparisons and then testing the probability of forming transitive triads. Having obtained evidence for ordinal rank, we went on to determine whether these are stable once formed and how time and number of competitions affect the formation and maintenance of rank.

Material and methods

Laboratory animal care

Adult, sexually mature, male and female *X. laevis* frogs were obtained from Xenopus I (Ann Arbor, MI, USA) or Nasco (Fort Atkins, WI, USA). Frogs were maintained in 43×21.5×19.5 cm (L,W, H) polycarbonate aquaria, five animals per tank, fed frog brittle daily, and the water changed once per week. The frog facility was illuminated with one 40 W aquarium light set on a 12:12, light–dark cycle. Temperature was maintained at 20°C.

Establishing and maintaining linear vocal ranks

Males used for vocal ranking experiments were arbitrarily assigned to a testing group for analyses but were housed separately for 3 days prior to pairing to prevent vocal interaction outside the test period. Within a group, each male was paired with one other male and the amount of time spent advertisement calling and the number of clasps made by each male were measured. Depending on the experiment, each pair met (was placed together) one, two, or three times. A color-coded thread sewn around a toe on the hind foot identified each male. Every male was injected with human chorionic gonadotropin (hCG, Sigma Corp., St. Louis, MO, USA) the day before the experiment began (100 IU) and on each subsequent day (50 IU) during the test period to equalize sexual receptivity. These are the established (Wetzel and Kelley 1983) doses for males in the range of body weights in this experiment (28–36 g). Males were maintained in the same low light conditions as those used during pairings (25 W red light bulb) and pairs were formed throughout the day and evening as required. Depending on the experiment, from three to 12 pairings might be recorded on a single day, and the start time varied accordingly. Males were selected randomly with regard to time of pairing.

To identify the calling male, two hydrophones were used. A small, relatively insensitive hydrophone (Knowles, Inc., Itasca, IL, USA; output sensitivity, −52 dB; re, 1 V/μPa; frequency sensitivity, 0.1–6 kHz) placed next to a male recorded only his vocalizations while a second hydrophone (High Tech, Inc., Gulfport, MI, USA; output sensitivity, −164.5 dB at 1 V/uPa, frequency sensitivity=0.015–10 kHz) recorded both males' calls. Comparing the recordings from the two hydrophones unequivocally identifies the calling male (procedure described in Tobias et al. 2004). Animals were paired in a 20 gal glass aquarium (58×30×41 cm (L,W,H); water depth 22 cm). On a given day, pairs from a group were randomly chosen, with the provision that no animal was tested more than twice in 1 day and all animals were tested the same number of times. Calling was recorded for 40 min (Marantz CDR300 digital recorder, Mahwah, NJ, USA). The number of clasps and the identity of the clasper were noted by the observer.

The number of animals in each group, the number of times each pair met, and the duration over which all pairs were examined is illustrated in Fig. 2 for all experiments. Five experiments tested linearity of vocal ranks over a short duration (5–10 days; Fig. 2 (A, B1, and B2)) while two experiments tested linearity of vocal ranks over a longer duration (23–24 days; Fig. 2 (C1, C2)). Two experiments tested the stability of linearity (Fig. 2 (B1, B2)). Two experiments tested the effect of number of competitions: one on stability of linear ranks (Fig. 2 (B1, B2)), the other on linear rank formation over a long duration (Fig. 2 (C1, C2)). We summed the amount of calling for pairs with multiple encounters over a given time block (Fig. 2 (A, B1 first block, and C2)) as this approximates dyadic encounters in natural ponds. When encounters were separated by a prolonged time period (Fig. 2 (B1, B2)), time spent calling was summed separately for the first and second set of encounters.

Linearity of rank was tested using the Mantel test (de Vries et al. 1993; de Vries 1998; MatMan, Noldus, Info. Tech., Wageningen, Netherlands). Two matrices, one for amount of time spent calling (Table 1) and the other for clasp number (not shown), were constructed for each group. The linearity score, which varies from 0 to 1, is based on Landau's linearity score h' (Landau 1951) and takes into account both tied and unknown relationships. To determine the statistical significance of the linearity, a sampling process using 10,000 randomizations is performed. A critical number of circular triads (for example cases in which A is dominant to B and B is dominant to C but A is not dominant to C) are allowed above which linearity is not significant; the number of circular triads is determined by the size of the matrix. Within matrices that were significantly linear, individual ranks were obtained by reordering the matrix to fit a linear hierarchy (a function of MatMan software which calculates the number and strength of circular triads for individuals; an example is shown in Table 2.). For matrices that were not significantly linear, we examined the correlation between the total amount of calling for a male and the number of times that male called more than other males he was paired with, using the Spearman correlation.

Playback and vocal suppression

General methods Playbacks were used to determine whether auditory cues are sufficient for vocal suppression, the effect of intensity on suppression and whether either phase of the biphasic advertisement call is more suppressive. For all three, 2 days prior to behavior testing, male frogs were isolated in 4-L plastic containers and injected with 0.2 ml (200 IU) hCG 1 day and again 6 h prior to testing to promote reproductive behaviors and increase vocal activity (Wetzel and Kelley 1983). The behavior testing room was illuminated with one 25-W red light bulb. The behavior tank is an inverse trapezoid, 97 cm^2 at the top and 85 cm^2 at the bottom and 68 cm high; water level to 49 cm. These dimensions, which are approximately one half the wavelength of the dominant frequency of the male advertisement call (~2 kHz), were used to reduce phase interference from sound reflected off the tank walls. The walls of the tank are constructed of a fiberglass sandwich filled with wood designed to absorb sound and reduce echoes. The tank is cushioned from vibration by a 3 cm thick layer of foam rubber on top of a 5.5 cm thick wood platform. Water in the recording tank was changed weekly and was kept at room temperature. Because males typically begin calling after dusk in the wild, experimental males were placed in the dimly lit behavior test room at least 30 min prior to testing.

As call intensity affects vocal responses (see below), playback volumes were normalized to a standard male's advertisement call recorded in the behavior tank. An advertising male was recorded in the behavior tank and the mean volume (dB) over 15 min was calculated using Goldwave software (v5.12, St. John's, Newfoundland, CA, USA). Stimuli were then matched to this volume by adding or subtracting volume from the playback using Goldwave software. The recording was band pass filtered around 0.9–5.0 kHz to reduce noise (the peak frequencies of the advertisement call are 1.7 and 2.1 kHz, well outside the filtered frequencies).

Playback onset was controlled using a computer (Dell Inspiron 9300, Round Rock, TX, USA) or CD recorder (Marantz PMD670; sampling frequency 44.1 kHz) connected to an amplifier (Realistic MPA30, Radio Shack, Fort Worth, TX, USA) which powered an underwater speaker (University Sound UW 30, Lubell Labs Inc., Columbus, OH, USA; frequency response 0.1–10.0 kHz). The speaker was placed on the floor of the tank in one

Table 1 Matrices indicating the amount of time-spent advertisement calling and rank for each male when paired with every other male in the group

Advertisement call matrix

	K	L	M	N	O	P	Q	S	T
K	*	0	13.1	91	0	16.3	505	14.5	26.4
L	437	*	0	94.5	0	127.1	44	0	7.5
M	118.6	0	*	40.4	0	301.8	14.3	19.5	34.9
N	124.7	0	0	*	5	68.4	60.9	12	27
O	286.7	0	0	188.3	*	110.6	0	29	306
P	172.3	0	14.6	139.5	0	*	0	15	171.7
Q	266	38.7	19.7	117.5	57.2	271	*	176.9	273.3
S	183.5	0	5.9	14	139	132	28.4	*	107.9
T	15.9	3.6	0	581	38.8	53.7	14.9	0	*
Total	1,604.7	42.3	40.2	1,175.2	240.0	1,064.6	162.5	252.4	928.3

Each cell represents the number of seconds the male indicated in the column called while paired with the male indicated in the row. Column totals are shown

corner, 9 cm from the sides and directed toward the center of the tank.

The animal was suspended in a basket; the distance from the speaker to the middle of the basket was 38 cm. Two hydrophones, one in front of the speaker and one in the basket with the test male were used so that the male's response could be distinguished from the playback stimuli. The basket hydrophone used to record the test male's vocal responses also recorded playbacks; no distortion of playbacks was detected at the position of the male. The basket hydrophone (High Tech, Inc.) was connected to a digital recorder (Marantz, PMD670). Except as noted, the amount of time spent calling before, during, and after playback was measured.

Because we wished to measure the relative, not absolute, amount of calling in response to playback compared to no playback, and because the amount of time spent calling varies between males, values were normalized for each animal by calculating the % of time spent calling in each experimental situation [time calling in one test period (i.e., before, during or after)/male's total time calling]; this is referred to as the "normalized amount of calling" throughout the paper. The normalized amount of calling was calculated and data were tested for the normality of the distribution using the Kolmogorov–Smirnov and D'Agostino and Pearson omnibus normality tests. If data were normally distributed, a repeated-measures ANOVA was used to determine if there was a significant difference in the normalized amount of calling across conditions. ANOVA here and elsewhere were followed by a Tukey HSD post-hoc test comparing between all groups. In some playback experiments, a suppression index [the amount of calling, (before-during)/before, playback] was also calculated to determine how much less the animal called during a stimulus compared with no stimulus (i.e., before). An unpaired *t* test was used to determine whether this difference was significant.

The effect of playbacks on vocal suppression Two playback paradigms were used: in one, a single male's call was broadcast to six test males and in the other, six male's calls were broadcast to six test males. In both experiments, the test male heard only one male's calls and none of the males tested had prior experience with the broadcast call nor had they ever been housed with the male that produced the broadcast call. The calls used for playbacks were originally recorded from males paired with other males (from the

Table 2 Matrices indicating the amount of time spent advertisement calling and rank for each male when paired with every other male in the group

Reorder matrix to fit linear hierarchy

	L	Q	M	S	O	P	K	T	N
L	*	44	0	0	0	127.1	437	7.5	94.5
Q	38.7	*	19.7	176.9	57.2	271	266	273.3	117.5
M	0	14.3	*	19.5	0	301.8	118.6	34.9	40.4
S	0	28.4	5.9	*	139	132	183.5	107.9	14
O	0	0	0	29	*	110.6	286.7	306	188.3
P	0	0	14.6	15	0	*	172.3	1,717.7	139.5
K	0	505	13.1	14.5	0	16.3	*	26.4	91
T	3.6	14.9	0	0	38.8	53.7	15.9	*	581
N	0	60.9	0	12	5	68.4	124.7	27	*

The matrix is reordered to indicate rank, from lowest to highest rank, for each individual. This group is illustrated in Fig. 2 (B), bottom left ranking experiment). In the first paradigm, the playback broadcast was recorded from a single high-ranking caller and lasted 25 min. Advertisement calls from test males were recorded for 25 min before and during the playback; no post-test recording was made. Males were prescreened for advertisement calling by pairing with a female.

In the second paradigm, the calls used in playbacks were originally recorded from three high and three low-ranking callers. All of the natural amplitude fluctuations and variability in song quality were maintained in the broadcast calls; all of the calls from a single animal were looped into 15 min with silent pauses ranging from 3.6–13.2 s (these pauses mimic those recorded from a singing male and were randomly inserted between bouts to form a 15-min stimulus). To create the 15-min broadcast from vocally low-ranking males (with little calling), the same brief bout of calling was looped more times than calling from vocally high-ranking males. The same overall call time and pauses are present in all playbacks. Advertisement calls from the test male were recorded for 15 min before, during, and after the playback. The volumes of all playbacks as well as the test male's volume were analyzed after the experiment to insure that the playback volume did not exceed the frog's.

Biphasic calls and vocal suppression X. laevis advertisement calls consist of a short, fast, intensity-modulated trill followed by a longer, slower, unmodulated trill (for simplicity, hereafter referred to as "fast" and "slow" trills, respectively). To determine whether the fast or slow trills are more effective suppressors, we examined the amount of time spent calling by test males during broadcasts of all fast or all slow trill stimuli. A recording from one high-ranking male was looped into a 15-min recording (as described above). This recording was manipulated using Goldwave software by muting either all fast trills or all slow trills. Differences in duration, rate, and intensity modulation within each trill are thus maintained. All stimuli were amplitude adjusted to the same mean volume (as above). There were no pauses between broadcasts.

Robust callers were identified by listening to the test male in the tank for 15 min; only males who called for at least 3 min were tested. Each test male ($N=11$) heard broadcasts of all three call types, control (both trills), all fast, and all slow, for 15 min each in random order without replacement. All males were recorded for 15 min after the stimuli to ensure they had not stopped calling due to exhaustion or inattention. Six of the 11 males were also recorded for 15 min before the playback. Data were normally distributed and a repeated-measures ANOVA was thus used to determine if there was a significant difference in the normalized amount of calling to the three stimuli. A suppression index was not calculated as the time, and exposure to other stimuli, differed between experiments, depending on stimulus order.

Playback intensity and vocal suppression The effect of playback intensity on vocal suppression was measured in eight males. In a preliminary study, using four broadcast intensities each differing by 6 dB, males did not distinguish between the two intermediate values and we thus adopted a three-intensity paradigm, each differing by 11 dB. The highest intensity was equivalent to a male calling (see "General Methods"); the lowest intensity was 21 dB below this value (this intensity did not suppress calling in the preliminary experiment). The intermediate intensity was 10 dB higher than the least intense calls. As different exemplars have the same effect on vocal responses (shown in the experiment "effect of playbacks on vocal suppression" above) and since using different exemplars for different intensities would add a second variable to the experiment, we modified intensity of a single exemplar and used this for the playback to all test males.

Intensity varies during an individual advertisement call and during natural bouts of calling. To insure that the intensity was more uniform within a test stimulus, the natural volume changes were attenuated so that the maximum difference between the least and most intense portions of the stimulus was 7 dB. This result was achieved by adding or subtracting volume from very low- and high-intensity bouts, respectively. Each intensity playback was broadcast for 15 min and each male was exposed to all three volumes chosen randomly without replacement. There was no pause between presentations of different intensity stimuli. Only males that called for 100 s prior to stimulation were used. Advertisement calling was recorded for 15 min before stimulation, during the three stimuli, and after stimulation.

The amount of time spent calling in response to each stimulus was determined and normalized across animals as described above. Data were normally distributed and a repeated-measures ANOVA was used to determine if there was a significant difference in the normalized amount of calling to the three stimuli. A suppression index was not calculated as the time, and exposure to other stimuli, differed between experiments, depending on stimulus order.

Results

Establishing linear vocal rankings

Previous work showed that paired males sort into dominant and subordinate callers (Tobias et al. 2004). Here we ask whether groups of males establish linear ranks in which the highest-ranking male calls more than all others and the second-ranking male calls more than all others except the first, etc. While males are paired, they are quiescent or swim; only quiescent males advertise. Males that come into close contact will clasp; clasps are brief and may be made alternately by both males (Fig. 1). During clasps, the clasped male growls and the clasping male chirps (described in Tobias et al. 2004); although growls are typically sufficient to elicit release, males may also kick and struggle. Males usually swim away from one another following a clasp.

Males within an assigned group were tested in pairs. The amount and timing of vocal and clasping activity for each male in a pair is illustrated for two such pairs (Fig. 1). In the first example, the vocally subordinate male called only once and briefly, about 10 min into the recording. This male clasped the vocally dominant male eight times and was clasped nine times (Fig. 1, top). Clasping did not depend on continued vocal signaling. In the second example, both males called frequently throughout the recording. The male that called less clasped the other male twice and was clasped four times (Fig. 1, bottom). In general, male advertisement calls rarely overlap (not shown) and either male may advertise at any time during the 40-min recording session.

We constructed matrices containing the total amount of time spent advertisement calling by each male within a pair (see sample matrix: Table 1). In this matrix, when male K was paired with male L, male K called for 437 s (column K, row L) and male L called for 0 s (column L, row K). The matrix, containing the results of all pairings for a group, was then used to determine whether a significant linear ranking was formed. If so, the matrix was reordered to determine the rank of each individual (Table 2). Rank is determined by the probability that a male will call more than any other male below him in rank; rank does not necessarily reflect total amount of calling although the strongest callers hold the highest ranks. Thus, male K advertises the most but male N has the highest rank.

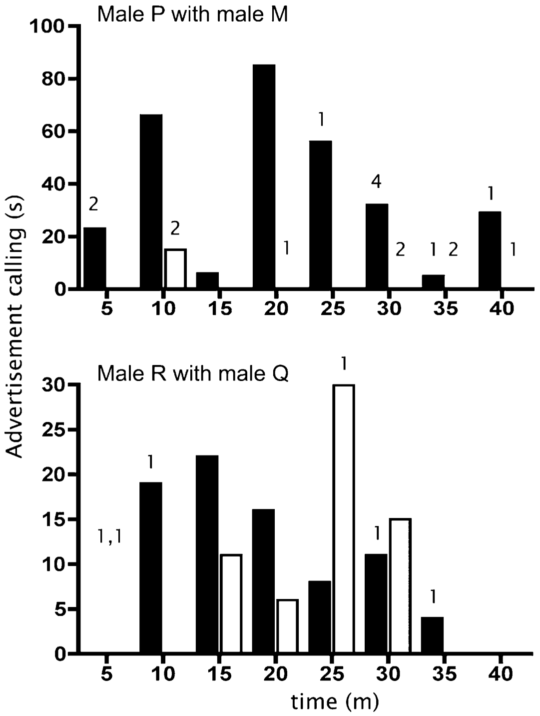

Fig. 1 The amount and timing of advertisement calling and clasps made by each male while paired. *Top* vocally dominant male P (*solid bars*) calls throughout the experiment while the vocally subordinate male M (*open bars*) calls only once. The number of clasps (*indicated above bars*) made by each male is similar for the two males. *Bottom* two vocally similar males, R (*solid bars*) and Q (*open bars*) call during most of the recording session and rarely clasp

The results of all ranking experiments are illustrated (Fig. 2). In five experiments, seven to nine males were paired in all possible combinations over a brief (5 to 9 day) period (Fig. 2 (A, B1, and B2, left and right)). Males formed a linear vocal hierarchy in four out of five experiments (see exception below) and linearity was achieved whether pairs met once or twice (h'=0.87, df=21, p=0.004, Fig. 2 (A); h'=0.83, df=21, p=0.006, Fig. 2 (B1), left; h'=0.71, df=20.16, p=0.007, Fig. 2 (B2), left). To test for stability, all pairs in two of these groups were re-tested 18 and 28 days after the initial ranking was established (Fig. 2 (B), right). Pairs tested 18 days later again could be ranked linearly (h'=0.93, df=23.33, p=0.01; Fig. 2 (B1), right) while pairs tested 28 days later could not (h'=0.48, df=20.16, p=0.157; Fig. 2 (B2), right; this experiment accounts for the one trial in which linear ranking was not achieved when the group was tested over a brief period). Changes in rank were more dramatic over longer durations (Table 3). Two of the highest-ranking males and one of the lowest-ranking males retained their ranks over 18 days (Table 3 (18 days between test 1 and test 2)) while no male maintained his rank over 28 days (Table 3 (28 days between test 1 and test 2)). In addition, the extent of rank changes (the rank change values) is smaller over 18 than 28 days (Table 3). We conclude that ranks are not stable indefinitely; vocal rank is dynamic changing in frequency and magnitude with time.

The loss of linearity over 28 days in the previous experiment could have resulted from the lack of competitive opportunities during this time due either to the 28 days in which no competitions occurred (males were singly housed during this period) or because the number of interactions was less in this group (pairs represented in Fig. 2 (B1) met twice while pairs represented in Fig. 2 (B2) met once). To examine the first possibility, we tested two groups of animals over a longer period (23 or 24 days) and neither group was significantly linear (h'=0.35, df=20, p=0.25; h'=0.55, df=20.16, p=0.058; Fig. 2 (C1, C2, respectively)) again affirming that duration plays a role in linear rank. The number of times pairs meet may also play a role. Both the stability experiments (Fig. 2 (B)) and the long duration experiment (Fig. 2 (C)), include one group in which pairs met only once and another in which pairs met multiple times.

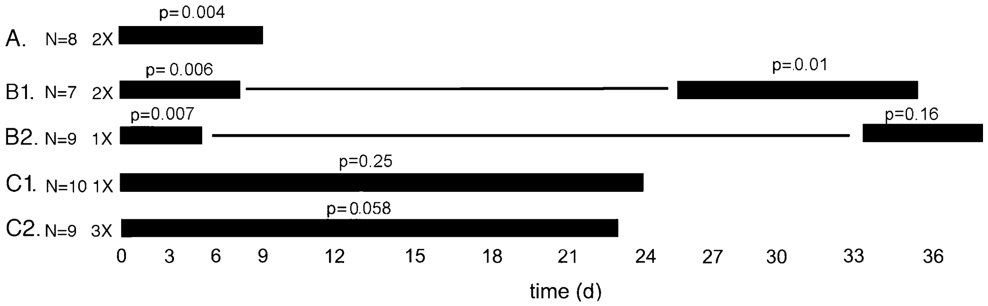

Fig. 2 Establishing a linear vocal hierarchy. The duration over which pairs of frogs within a group were tested (*bar length*), the number of times each pair met ("*X*"), the number of individuals in the group ("*N*") are shown to the *left of each bar*; the probability of rejecting the null-hypothesis (that frogs do not form a linear hierarchy) is shown *above each bar*. (*A*, *B*) Groups tested over a brief (<2 weeks) period, (*B*) examines hierarchy stability. The same group is tested initially and at a later date. *Lines* represent the time during which animals are individually housed between the first and second test periods. (*C*) Groups tested over a longer (>3 weeks) period. (*B*, *C*) Examines effect of the number of competitions

Groups with more competitive opportunities either maintained linearity (as in the stability experiment; Fig. 2 (B1)) or came closer to achieving linearity (as in the long duration experiment; Fig. 2 (C2)). Thus, the number of competitive opportunities may increase the chance of forming linear ranks but does not overcome the limitations imposed by a long period of time between encounters.

We next examined whether some other type of vocal ranking system operates in the three groups of animals that did not establish linear ranks using our statistical criteria. One alternative is that these animals sort into vocal groups (i.e., strong, intermediate, and weak callers represent nominal ranks) but there is no defined, or ordinal, rank for individual males within a group as there is in a linear ranking. For example, A, B, and C may all be strong callers when compared to the rest of the group, but A may sometimes be dominant to B and sometimes subordinate (this would not support a linear ranking but would support a system in which some males are stronger callers than others). Ranks cannot be determined simply by examining the total amount of time each male calls since a male could produce all of his calls when paired with only one or a few other males. Nominal ranking would, however, be supported if the total amount of time spent calling were correlated with the number of times a male called more than the male he was paired with. We thus measured the total amount of advertisement calling for every male in a group and compared that value to the total number of times that male called more than any other male he was paired with ("wins", Fig. 3). For the three groups that did not form linear rankings, the amount of time spent calling and number of wins are strongly and positively correlated (r=0.94, n=9, p=0.0002; r=0.75, n=10, p=0.0117; r=0.82, n=9, p=0.0073; Fig. 3a, b, and c respectively).

Table 3 Changes in rank over time

Test 1	Test 2	Rank change
18 days between test 1 and test 2		
B	B	0
C	C	0
D	A	−2
H	E	−3
E	D	1
F	F	0
A	H	4
28 days between test 1 and test 2		
N	T	−4
T	P	1
K	Q	−1
P	K	2
O	N	−4
S	L	−1
M	S	−1
Q	M	5
L	O	3

In contrast to observations on vocal rank, clasping ranks were rare. In only one experiment (Fig. 2 (A), clasping data not shown) was there evidence for linear clasping ranks (h'=0.9, df=20, p=0.003) and in this experiment calling and clasping were correlated (r=0.65, t_8=3.72, p=0.0005). In one other experiment (Fig. 2 (B), top right) clasping and advertisement calling were correlated but males did not rank linearly for clasping. Thus, the prevalence of clasping does not reliably accompany vocal status.

Together, these experiments show that *X. laevis* frogs can establish linear vocal ranks. For linearity, the duration over which all pairs in the group interact is a critical determinant although the number of interactions also plays a role. Linear rankings are formed even when pairs met only once, but were never formed when pairings occurred over long durations (>18 days). Vocal rank is dynamic, changing more with time. When ranks are not linear, males

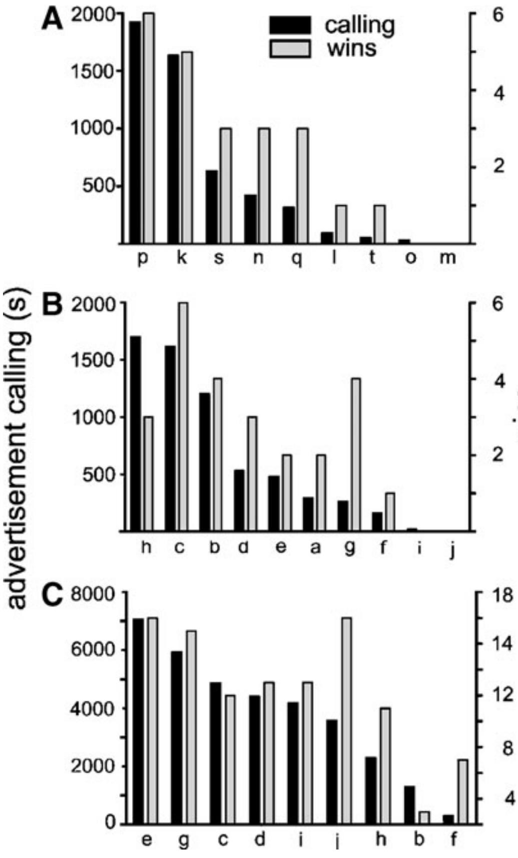

Fig. 3 Vocal status in groups that do not form linear hierarchies. Each graph represents one experiment shown in Fig. 2 in which a linear hierarchy was not established. Each graph shows the total amount of time spent calling (*left y-axis*) for each male (*x-axis*) and the number of times he called more than any other male with which he was paired ("wins"; *right y-axis*). Individuals are identified by *letters*; however, since each graph represents one group, the same letter in different graphs represents different animals. **a** Group shown in Fig. 2 (B2), right. **b** group shown in Fig. 2 (C1), **c** group shown in Fig. 2 (C2). For **c**, the amount of time spent calling is summed over the three trials

maintain a system in which robust callers out-signal competitors. Clasping and vocal behavior were correlated in only two out of seven experiments, suggesting that physical interactions are not reliable predictors of vocal status.

The effect of advertisement call playbacks on vocal behavior

To determine if auditory cues alone are sufficient for vocal suppression, the amount of advertisement calling produced by males before, during, and after playbacks of advertisement calling was measured (Fig. 4). In the first experiment, advertisement calls from one male were broadcast to six males for 25 min (Fig. 4a). The amount of advertisement calling was markedly lower during (13±17 s, mean ± SD) than before (290±210 s) playback. Three of the six males did not call at all during playback. The suppression index (see "Material and methods") was 97±1.7, equivalent to values obtained when two males interact (97±5; Tobias et al. 2004). In the second experiment, advertisement calls from six males were broadcast; three from the highest-ranking males and three from the lowest-ranking males from one ranking experiment (shown in Fig. 2 (B), bottom). The normalized amount of calling was significantly different before, during, and after playback ($F_{2,5}$=37.84, p=0.001; Fig. 4b). Males called significantly less during (4.7±6.2%) than before (49.8±9.2%) or after (45.4±8.5%, p=0.001) playback but there was no difference in the normalized amount of calling before and after the broadcast (p=0.62). The suppression index during playback was 89.5±13.3%. The normalized amount of calling by males was not significantly different for broadcast calls from vocally high-ranking (5.2±8.9%) vs. vocally low-ranking callers (4.3±4.2%; unpaired t test, t_4=0.14, p=0.89). We conclude that auditory stimuli are sufficient for vocal suppression. Equivalent suppression is observed whether the playback is from one or six call exemplars and a difference in the suppression

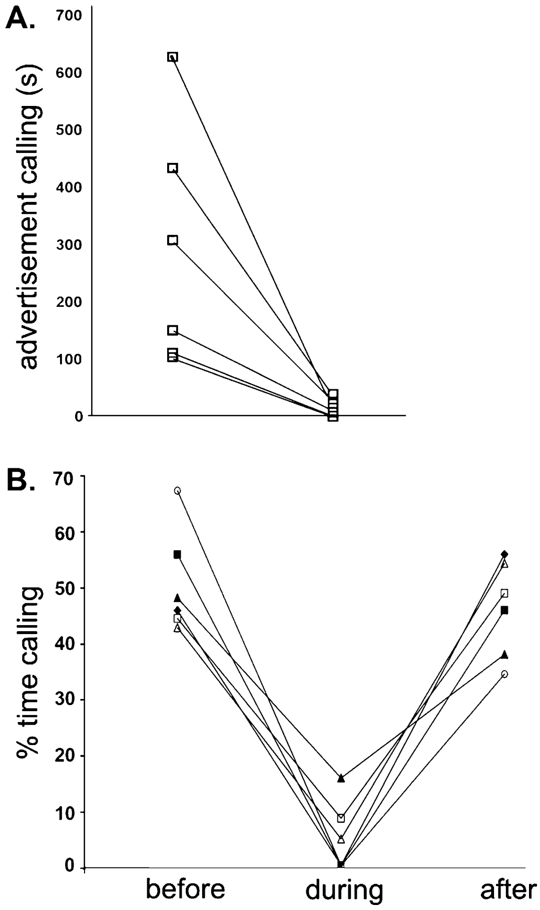

Fig. 4 Auditory cues alone are sufficient for male vocal suppression. **a** The amount of advertisement calling produced by males before and during playbacks of advertisement calls from a single male is shown. **b** The normalized amount of calling in response to advertisement calls from three highest-ranking (*filled symbols*) and three lowest-ranking (*open symbols*) males before, during, and after playbacks is shown

produced by broadcast calls of high- vs. low-ranking males was not detected.

The *X. laevis* advertisement call consists of alternating fast (17 ms inter-click interval), short (250 ms duration) intensity modulated, and slow (30 ms inter-click interval), long (750 ms duration) unmodulated trills (Fig. 5a). To determine whether the fast or slow trill portions are better at suppressing male vocal behavior, we examined the amount of time spent calling in 11 males during broadcasts of all fast, all slow or biphasic (control) calls. Over all, there was a significant difference in the normalized amount of calling to all slow (23.0±19.5%; mean ± SD), all fast (56.7±20.3%), and control (20.4±15.1%) calls ($F_{2,10}$=8.84, p=0.0018). The normalized amount of calling was significantly less during broadcasts of all slow or control than all fast calls (p=0.001 and 0.002, respectively) but there was no difference in the normalized amount of calling between all slow and control calls (p=0.551). However, an examination of how individual males behaved in response to the three playbacks (Fig. 5b) indicates that males could be divided into two groups based on their ability to discriminate between the stimuli. In one group (Fig. 5b, left), there is a significant difference in the normalized amount of calling across the three stimuli ($F_{2,4}$=15.86, p=0.0016) but the normalized amount of calling was significantly higher (i.e., the effect was less suppressive) in response to all fast trills (72.1±20.6%; n=5, p=0.002 vs. control; p=0.001 vs. all slow) and there was no difference in the normalized amount of calling between control (24.6±18.6%) and all slow trills (3.3±3.7%, p=0.134). In the second group (Fig. 5b, right), there is also a significant difference in the normalized amount of calling across the three stimuli ($F_{2,5}$=10.91, p=0.0031) but in contrast to the preceding group, the normalized amount of calling was less in response to control (16.8±12%) than either all slow (39.4±6.2%, n=6, p=0.001) or all fast (43.8±6.9%, p=0.001) calls. Thus, some males discriminate between all fast and all slow trill calls while some discriminate between biphasic (control) and monophasic calls. There is no difference in the normalized amount of calling to control calls between the groups (unpaired *t* test, t_9=0.84, p=0.42) and the normalized amount of calling is significantly greater to all fast than to control calls in both groups. The difference between the two groups cannot be accounted for by differences in the stimulus itself, as all animals heard the same calls. We considered the possibility that stronger callers might be less suppressed by any vocal stimulus, for example they might attempt to out-signal all callers. However, there is no significant correlation between the amount of calling before compared with the all fast (Spearman correlation, r=−0.49, n=6, p=0.36) or all slow stimuli (r=0.09, p=0.92) suggesting that the difference between the groups is not accounted for by overall calling strength. Fast and slow trills differ in rate as well as in duration and intensity modulation and any or all of these characters may aid in discrimination; these experiments do not determine which feature is salient for discrimination.

We next determined whether the intensity of advertisement call playback influences vocal behavior. There was a significant effect of sound intensity on the normalized

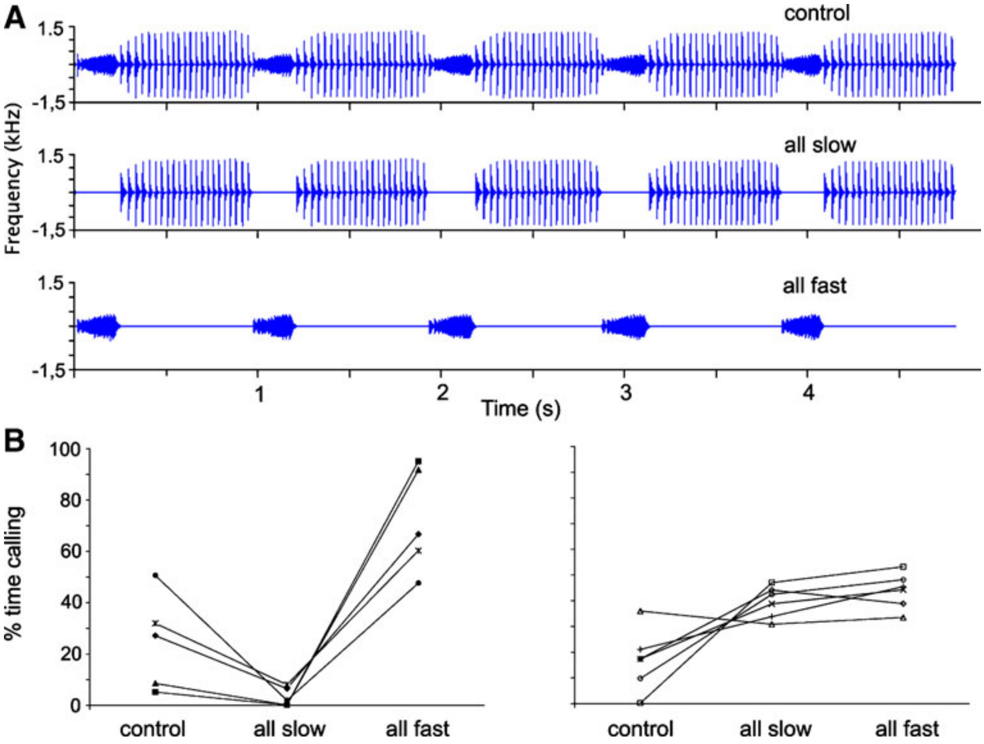

Fig. 5 Advertisement calling in response to all fast, all slow, and control trills. **a** Sample oscillographs (amplitude vs time) of the control (biphasic; *top*), all slow trill (*middle*), and all fast trill (*bottom*). **b** The normalized amount of calling in response to the three stimuli is shown. *Lines* connect data from the same animal. Data from males that discriminate (*left*) and do not discriminate (*right*) between all fast and all slow trills are shown separately

amount of advertisement calling ($F_{2,7}$=10.16, p=0.0019; Fig. 6a). Animals called significantly less in response to the call intensity equivalent to an advertising male (high; 10.8± 18.8%, t_8=4.3, p=0.001) and intermediate (24.8±16.4%, t= 3.2, p=0.002) intensity playbacks than to the low-intensity playbacks (64.4±24.4%). There was no significant difference in the amount of advertisement calling in response to intermediate and high-intensity playbacks (t=1.1, p=0.365). Thus, males discriminate between high and low, but not between high and intermediate intensities.

Examination of the vocal behavior of individual's show that seven of eight males called progressively less as playback intensity increased; one male called more in response to the high than to the low-intensity playback (filled diamond symbol, Fig. 6b). Five of the eight males called more during the least intense playback than before the playback suggesting that low-intensity calling may actually stimulate advertising. Thus playback intensities equivalent to that of a nearby male advertising are effectively suppressive while playbacks of low-intensity calls are not suppressive.

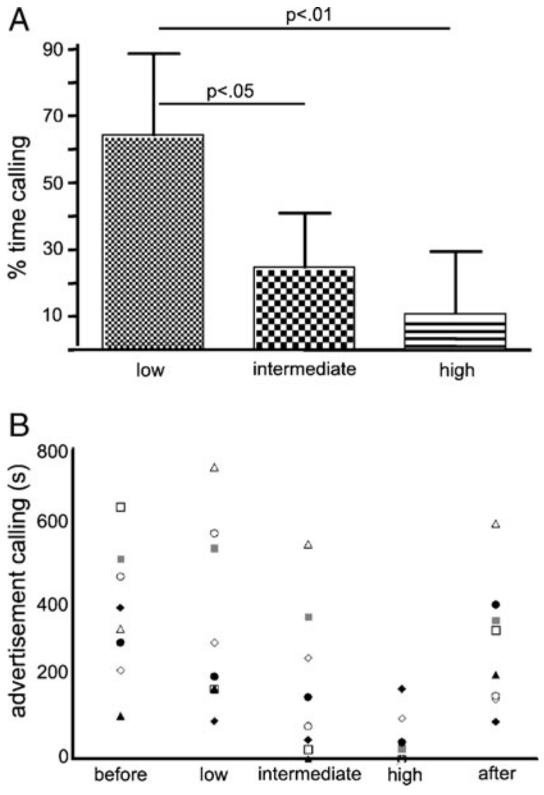

Fig. 6 The effect of sound intensity on advertisement calling. **a** The normalized amount of advertising in response to each intensity playback is shown (mean ± SD). Significance levels are indicated between *bars*. **b** The amount of time spent calling produced by each male (indicated by a *symbol*) before, during each of the three stimuli, and after playback. Note that only one male, indicated by a *filled diamond*, calls more to high, than to intermediate or low-intensity stimuli

Discussion

In South Africa, *X. laevis* call underwater and there are no visual signals, such as the inflation of a vocal sac, that accompany calling. Thus, calling males cannot be identified by observation. The lack of obvious individual vocal signatures—and the ability of males to move freely within the pond and call from different sites—have made it difficult to determine whether calling by a male reflects a vocal hierarchy and, if so, how this hierarchy is established. Because the identity of a calling male can be readily determined for pairs of males in the laboratory we started with this approach and have shown that even males that are robust callers can be suppressed when paired with another male (Tobias et al. 2004). Here we extend our observations on pairs to a larger group of males and determine linear vocal rankings within groups.

The study of hierarchies relies on two approaches to sampling social interactions. In the first, all dyadic interactions are measured for a focal place and time; social interactions of the pairs outside of the dyad are not monitored systematically (e.g., Clark and Faulkes 1997, 1998; Frank 1986). In the second, experimenter-constructed small groups are observed for longer periods, sometimes continuously (Schwartz et al. 2002; Martin and Moore 2007; Czoty et al. 2009). The advantage of the experimental approach used here (dyad observations drawn from a constructed group) is the ability to manipulate some of the variables that could affect vocal dominance such as the number of encounters and the time course over which encounters occur. The limitation of this approach is that the interactions between members of a pair that take place within a larger social context, and would occur in nature, are not included. The small number of studies that have examined isolated pairs versus pairs with more extended contact with conspecifics have concluded that social context can blunt or even reverse the rankings assigned from isolated pairs (Chase et al. 2003; Graham and Herberholz 2009). In the small tanks we used, males cannot escape vocal domination as they can, for example, in nature by swimming to a shallow portion of the pond where calls are attenuated (Elepfandt 1996). Whether the rankings obtained by observing pairs in the laboratory translate into those in natural ponds awaits advances in technology that permit identification of vocalizing individuals underwater.

When all possible pairs within an arbitrarily constructed group are tested over brief periods (~2 weeks), each individual occupies a defined rank. Rank is not determined by total vocal output, but rather by the probability that a given male will call more than all those beneath him in rank. Linear ranks are stable over brief (~2 week) periods but not longer. Rank is dynamic: the frequency and magnitude of rank changes increases with time. In the absence of linear ranks, we can sort males into non-linear systems by status (i.e., strong vs weak callers); rank is nominal not ordinal. As in nature, any experimentally constructed group of males will include both robust and weak callers; these experiments do not distinguish between an inherently poor caller and a suppressed caller, differences which could reflect a male's physiological condition and contribute to his rank. If so, the data from these experiments suggest that naturally occurring groups may maintain rankings for brief periods; the dominant caller could shift over time. For example, males call very little while in amplexus, which lasts throughout the night, and thus vocally dominant males might forfeit this position during mating.

Across taxa, dominance relations between males are influenced by physical interactions (Alcock 1979). In this study we examined both clasping and calling in pairs of males from groups. Males do not form linear clasping rankings and clasping is typically not correlated with calling rank. Since clasping is not a predictor of vocal status and playbacks of advertisement calls are as effective as actual physical encounters between individuals (Tobias et al. 2004), rank in *X. laevis* appears to rely entirely on acoustic signals.

The role of individual recognition in establishing social hierarchies may depend on whether the social structure involved is stable or fluid. Social hierarchies reflect the competition for limited resources: food, shelter or access to mates. High rank can be attained by aggression, or bequeathed by inheritance. Regardless, aggression is typically used to maintain position in a social hierarchy or to move up the hierarchy. Recognition of rank can stabilize the social order, decreasing energetic demands and injuries incurred during fights. In stable social groups where members are resident for long periods and are often related, recognition of an individuals' rank is essential. For example, rank in male hyenas is determined by time of entry into a clan; males queue in order of immigration (Frank 1986). Males are not aggressive, and ranks are maintained through individual recognition. Similarly, naked mole rats live in stable colonies with strict social hierarchies in which access to reproduction is determined by weight although naked mole rats also use antiphonal calls to signal identity (Yoshida and Okanoya 2009).

The role of individual recognition in more fluid social hierarchies, in which members are transient and unrelated, is less clear. Crayfish for example obtain preferred shelters by evicting subordinate dwellers (Martin and Moore 2007). Information on the outcome of previous contests is available to conspecifics but does not signal individual identity (Moore and Bergman 2005). Lizards remember agonistic partners, although memory is short, 1 to 3 days (Korzan et al. 2007) and recognition does not rely on eyespot size, a dominance marker. Vocal recognition of familiar vs. unfamiliar individuals has been shown in bullfrogs (Bee and Gerhardt 2002) where males are territorial and recognition is required to distinguish intruders. Thus the absence of recognition does not preclude the ability to form social hierarchies. Our experiments do not address the issue of individual recognition in the establishment of vocal dominance in *X. laevis*. The studies described above, however, suggest that in fluid social systems, like *X. laevis*, recognition may not be required.

We found no evidence that advertisement calls from high-ranking males are better suppressors than calls from low-ranking males suggesting that vocal rank is not conveyed by an acoustic signature. In our experiments, the duration and intensity of calling was equivalent in all playbacks and the amount of calling in a playback was generally higher than that of the test male. Thus, though a single advertisement call may not include dominance information, calling first, louder or for a longer duration could convey dominance. An *X. laevis* male might profit by trying to out-signal a higher ranking male if that male's singing ability changes with time and we show here that rank is dynamic. The breeding season is long in *X. laevis* (approximately 6 months, Tobias et al. 2004) providing ample time for rank changes. Vocally dominant males may have a physiological advantage over lower ranking males and ranks may change as physical attributes change.

In this paper, we extend our initial observation that in male pairs one male is vocally suppressed (Tobias et al. 2004), to determine whether auditory cues alone are sufficient for vocal suppression, the effect of sound intensity on suppression and whether either phase of the biphasic advertisement call is a more effective suppressor. In addition to clasps, paired males receive sensory information conveyed by lateral line, visual, and olfactory nerves which might contribute to suppression. Male–male competition could require combined visual/auditory information as in *Allobates femoralis* where the sight of the vocal sacs combined with calling increases male aggression (Narins et al. 2003). However, we found that the suppression produced by playbacks, broadcast at intensities equivalent to those of a calling male, is similar to the suppression observed in male–male pairs (Tobias et al. 2004) and conclude that auditory cues alone suffice.

Biphasic calls can function to simultaneously but separately signal males and females. In *Eleutherodactylu*s *coqui*, a species in which notes alternate in pitch, the "co" note alone is as effective in eliciting a male response as the entire advertisement call while the "qui" note alone is as effective in attracting females (Narins and Capranica 1976). In *Geocrinia victoriana*, in which the phases vary in rate, males respond to the introductory note while females are attracted to the second, repeated note phase (Littlejohn and Harrison 1985). Females might use the intensity modulation of fast trills to aid localization as has been shown in the king penguin (Aubin and Jouventin 2002) and males might use slow calls to signal to each other. However, that some *X. laevis* males are not suppressed by all slow trills, argues against the biphasic advertisement call of *X. laevis* being partitioned into separate signaling channels for the sexes.

Playback experiments reveal that vocal suppression in *X. laevis* is affected by call intensity: calls that mimic the intensity of an advertising male and even those that are considerably lower in intensity (−11 dB) are suppressive. Very low-intensity calls (−22 dB below that of an advertising male) are not suppressive. Because of reliable decreases in sound intensity with distance (Bradbury and Vehrencamp 1998), intensity can be used as a proxy for distance in terrestrial frogs. A loud call most probably emanates from a nearby male and could be a prelude to a physical struggle for dominance. Although *X. laevis* males in the laboratory are hearing playbacks under near field conditions, in which the low frequencies of their calls can have larger effects on sound pressure, males do distinguish between different intensities and the relation between distance and sound intensity may still be relevant. In contrast to *X. laevis*, in many terrestrial frogs increasing call intensity excites calling in other frogs (Given 1987; Grafe 2003; Rose and Brenowitz 1997; Schwartz and Wells 1984). Differences in the role of sound intensity between terrestrial frogs and *Xenopus* could reflect two influences: the diminished fall off in intensity with distance in water and the relative unimportance of physical proximity in animals where the effective vocal space is paramount. Acoustic territories might be quite large in *X. laevis*, the number of calling males depending on call amplitude and size of the pond.

All vocalizing male frogs must distinguish themselves both from environmental noise as well as from each other. Terrestrial frogs use a number of methods to accomplish this task, including increased amplitude (Lopez et al. 1988), altered spectral components (Given 2009), call rate (Gerhardt et al. 2000), number of pulses per call (Jehle and Arak 1998), call duration (Benedix and Narins 1999), or some combination thereof (Wells and Taigen 1986). In *Hyla versicolor*, the extent to which males adjust call parameters to avoid overlap is proportional to chorus size (Schwartz et al. 2002). As noted above, in many terrestrial frogs increasing call intensity excites calling. Vocal suppression would be disadvantageous in these chorusing species because it would work against the advantage of simultaneous advertisement calling in attracting distant females to the pond. This feature is not necessary in *X. laevis*, because both sexes are resident year round. *X. laevis* males may have a simpler strategy for distinguishing themselves: simply out-signaling their competitors. Support for this strategy comes from our playback experiments. Playbacks are nearly continuous advertisement calling and are not responsive to the test male; all playbacks thus out-signal the test male and all playbacks suppress calling.

What accounts for the persistence, especially in the absence of physical combat, of vocal suppression in *X. laevis*? Vocal suppression in native ponds could help females locate calling males. Female *X. laevis* locate males by sound (Picker 1983) and thus can only find acoustically distinct callers. This condition is better met when only one or a few males advertise. Vocally suppressed males could maintain reproductive opportunities by themselves locating the advertising male and clasping females en route to him. In the laboratory, removal of the vocally dominant male restores calling in the subordinate (Tobias et al. 2004). In the wild, the suppressed male could resume advertising when the signaling male is silenced (e.g., during amplexus). Furthermore, vocal ranks change over time suggesting that dominance relations formed at the onset of the breeding season are not likely to persist.

Whether vocal suppression in *X. laevis* is considered an unusual reproductive strategy for anurans depends largely on whether it is a variant of the satellite male strategy. In terrestrial frogs, it is common for calling, territorial males to be accompanied by silent satellites (Gerhardt and Huber 2002). Satellite males have typically been rebuffed in physical encounters with the resident male and avoid further combat by not calling and often assuming a subservient posture (Wells and Schwartz 2007). Although satellites are vocally suppressed, advertisement calling or playbacks excite rather than suppress non-satellite neighbors (Perrill and Magier 1988; Gatz 1981; Fellers 1979; Wagner 1989b; Wells and Taigen 1986). Thus, vocal suppression outside of a satellite situation is uncommon; one example is in *Geocrinia laevis* (Harrison and Littlejohn 1985). Vocally low-ranking male *X. laevis* males do not avoid contact with vocally higher ranking males when paired (for example, the vocally subordinate male illustrated in Fig. 1a clasps the vocally dominant male repeatedly). Furthermore, distinctive agonistic calls, common in terrestrial frogs, are not used in establishing vocal dominance in *X. laevis*. These differences distinguish vocal suppression in *X. laevis* from the satellite strategy of terrestrial frogs. For species that call underwater, all males within the acoustic territory of a calling male, a space likely to be larger in water than in air, could be considered satellites.

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