



Vocal communication between male *Xenopus laevis*

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This study focuses on the role of male–male vocal communication in the reproductive repertoire of the South African clawed frog, *Xenopus laevis*. Six male and two female call types were recorded from native ponds in the environs of Cape Town, South Africa. These include all call types previously recorded in the laboratory as well as one previously unidentified male call: chirping. The amount of calling and the number of call types increased as the breeding season progressed. Laboratory recordings indicated that all six male call types were directed to males; three of these were directed to both sexes and three were directed exclusively to males. Both female call types were directed exclusively to males. The predominant call type, in both field and laboratory recordings, was the male advertisement call. Sexual state affected male vocal behaviour. Male pairs in which at least one male was sexually active (gonadotropin injected) produced all call types, whereas pairs of uninjected males rarely called. Some call types were strongly associated with a specific behaviour and others were not. Clasped males always growled and clasping males typically produced amplexant calls or chirps; males not engaged in clasping most frequently advertised. The amount of advertising produced by one male was profoundly affected by the presence of another male. Pairing two sexually active males resulted in suppression of advertisement calling in one; suppression was released when males were isolated after pairing. Vocal dominance was achieved even in the absence of physical contact (clasping). We suggest that *X. laevis* males gain a reproductive advantage by competing for advertisement privileges and by vocally suppressing neighbouring males.

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Vocal communication is a hallmark of reproduction in anurans (Gerhardt & Huber 2002). In most frogs, male advertising is instrumental in acquiring a mate. Calling increases the male's access to females either directly, through attraction, or indirectly, via competition with other males. Understanding the role of vocal communication in the reproductive strategy of a species thus requires examination of both inter- and intrasexual signals. Although vocal behaviours accompany male competition in many vertebrates (e.g. cowbirds, *Molothrus ater*, Dufty 1986; squirrel monkeys, *Saimiri sciureus*, Barclay et al. 1991; fallow bucks, *Dama dama*, McElligott et al. 1999), calling alone usually does not suffice to establish social dominance. In anurans, however, male–male vocal communication directly determines intermale spacing, territory defence and chorusing (reviewed in Wells 1977, 1988). Here, we examine intrasexual communication in a fully aquatic species, the South African clawed frog,

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Xenopus laevis, an anuran with a particularly rich vocal repertoire.

Xenopus laevis is native to sub-Saharan Africa (Tinsley et al. 1996). The best-studied vocal behaviour in this species is the male advertisement call used to attract gravid females (Picker 1983; Tobias et al. 1998). Less studied, but potentially important for male–male competition, are the vocal behaviours produced and received by males. Here, we used field recordings to characterize male call types produced during the breeding season (Kalk 1960). Because *X. laevis* cannot be observed in the turbid ponds that are its preferred habitat, we could not use field recordings to determine the sex, sexual state or behaviour of the signaller, nor could we determine the sex of individuals that responded to vocal signals. Laboratory experiments with male–male or male–female pairs allowed us to identify which call types are used during inter- and intrasexual communication. In the laboratory, we were also able to identify calls produced by each individual and thus correlate call type with other behaviours.

The amount of calling by males depends on sexual state; sexually active males advertise but castrated males do not (Wetzel & Kelley 1983). Sexual state can also affect which type of vocalization is produced; for example, sexually

receptive females rap, whereas unreceptive females tick (Tobias et al. 1998). In this study, we manipulated sexual state by gonadotropin injection and compared the calls produced by pairs of gonadotropin-injected and uninjected males.

The vocal behaviour of the signaller can affect the vocal behaviour of the receiver. Thus, female rapping increases male calling, whereas ticking suppresses male calling (Tobias et al. 1998). Here, we show that advertising males profoundly affect the vocal behaviour of male neighbours. When we paired two sexually active males, both of whom were advertising in isolation, one male was vocally suppressed while the other continued to advertise. Although males clasp one another while establishing a vocal hierarchy, physical contact between males is not required for vocal suppression. We suggest that male *X. laevis* use suppression to establish vocal dominance and thus increase the probability of attracting a sexually receptive female.

METHODS

Field Recordings

At the beginning of June 1997, we placed bone-baited funnel traps (Picker 1983) in a number of ponds in the vicinity of Cape Town, South Africa. One pond, containing sexually mature adults of both sexes (males with nuptial pads, females with swollen cloacae), was chosen for monitoring. Using a hydrophone, we recorded from this pond on 20 nights from 20 June to 20 August. No calling was recorded before 20 June (from this or two other ponds recorded on three nights), suggesting that this date marked the onset of the breeding season. The selected pond was ovoid ($\sim 15 \times 44$ m), with a mud bottom covered with decayed vegetable matter. On most nights, we placed a single hydrophone 0.6 m from the shore and suspended it 0.4 m deep just above the pond floor. Although we typically began each 45-min recording session at 1930 hours, we also recorded calling as early as 1500 hours and as late as 0030 hours.

On some nights, more than one male called simultaneously. However, it was not possible, either by ear or by examining the spectrograms of recorded calls, to identify individual callers and thus to determine how many males were calling or whether the callers in one tape segment differed from those in another tape segment. We attempted to identify individual callers by using two hydrophones placed at varying distances (6–17 m) from one another; in all cases, recordings from the two hydrophones were sufficiently similar to preclude caller identification. We were thus unable to use this approach to determine the number of male callers and no attempt was made here to distinguish between single and multiple callers in field recordings. These experiments did, however, indicate that the single hydrophone effectively recorded frogs at distances up to 17 m.

All vocalizations were recorded using a Cornell Bioacoustics hydrophone (output sensitivity: -163 dB at 1 V/ μ Pa) and analysed using Canary software (Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A.: [http://](http://www.canarycom.com)

www.canarycom.com). Each recording was 45 min long. We determined the total amount of time that each call type was produced each night. In recordings that contained noise or echoes at 60 Hz, we filtered out frequencies below (0.5 kHz) and above (2.5 kHz) the dominant frequencies of a click using Canary software.

Xenopus laevis calls consist of click trains (trills) with distinctive acoustic features. Clicks are brief and noisy bursts of sound that contain frequencies between 0.5 and 2.5 kHz. Distinct spectral and temporal features of each call can be used to identify call types (Wetzel & Kelley 1983; Watson & Kelley 1992; Tobias et al. 1998). Briefly, the seven previously identified call types can be characterized as follows. Advertisement calls consist of alternating fast (19-ms interclick intervals) and slow (38-ms interclick intervals) trills; the fast trill can be intensity modulated (i.e. there is a progressive increase in click volume). Answer calls are similar to advertisement calls, but the fast trill is lengthened, the slow trill is shortened and the intensity modulation of the fast trill is more pronounced. Growling is a brief (typically <1 s), fast (10-ms interclick interval) trill. Amplectant calls are short trills (2–3 clicks/trill) with an intertrill interval of about 1 s; amplectant calls are of low intensity. Male and female ticking is a slow (~ 230 -ms interclick interval), monotonous call with no intensity modulation. Female rapping is similar but has a faster click rate (80-ms interclick interval). Male and female call types are distinguished by frequency spectra of clicks. The peak frequency of clicks in male advertisement calls, answer calls and ticking is 1.7–2.3 kHz, whereas the frequency spectra of amplectant calls and growls reveal a third, lower peak at about 1 kHz. The peak frequency for female ticking and rapping is 1.2 kHz.

Laboratory Recordings and Observations

Animals

Animals were obtained from *Xenopus I* (Ann Arbor, Michigan, U.S.A.) and housed singly in polycarbonate tanks at 20 °C. Frogs were fed frog brittle (Nasco, Ft Atkinson, Wisconsin, U.S.A.) three times per week and maintained on a 12:12 h light:dark cycle. Males to be paired were selected for similar body size; individuals were recognized by colour and body markings.

Recordings

We used a glass aquarium (60 \times 15 \times 30.5 cm, L \times W \times H; water depth = 23 cm; 20 °C) fitted with a stationary tank hydrophone as a recording chamber. To determine which male was calling during a vocal interaction, we also used a miniature waterproof microphone (-52 dB, 0.1–6 kHz; Knowles, Inc., Itasca, Illinois, U.S.A.) attached to a thin rod (hereafter 'wand hydrophone') to preferentially record the calls produced by one of the males. Because calibration measurements revealed an 8.9-dB drop in intensity between 3 and 12 mm from the sound source, we placed the wand hydrophone as close as possible to the larynx of the male to be recorded (the larynx is immediately dorsal and anterior to the heart).

Vocal behaviours in frog pairs

Field recordings indicated that some male call types not previously associated with male–female interactions were produced during the breeding season. To explore the effect of sex on vocal repertoire, we recorded vocalizations produced by same-sex and opposite-sex pairs during 45-min encounters. For some observations, we manipulated the sexual state of one or both members of the pair by gonadotropin injection, a treatment known to increase clasping and calling in males (Kelley & Pfaff 1976; Wetzel & Kelley 1983). Subjects received two injections of 0.2–0.5 ml (100 IU/0.1 ml) of human chorionic gonadotropin (hCG; Sigma, St Louis, Missouri), usually 24 h and 6–8 h before observation. Before the start of each observation (1 h before lights out), we placed both members of the pair in a dimly lit room and began observations 30 min later. We recorded vocalizations from nine pairs in which one member of the pair (male: M; female: F) was injected (+) or not injected (–) with hCG ($N = 3 M^+F^-$, $3 M^+M^-$, $1 F^+F^+$, $2 F^-F^-$ pairs).

To explore the effect of sexual state on vocal repertoire, we used the same paradigm as above. We recorded vocalizations during 45-min interactions between 13 male pairs ($N = 5 M^+M^+$, $5 M^+M^-$, $3 M^-M^-$ pairs).

To determine whether call types are associated with particular male behaviours, we observed 15 pairs of males ($N = 9 M^+M^+$, $6 M^+M^-$ pairs) and recorded the vocalizations produced by each male during a 45-min encounter using two hydrophones (see above). Clasping is the predominant interaction between pairs of males and can be directed towards the leg, the side of the body or the head of another male, but is most often directed towards the inguinal region, as is the case for clasps directed at females (Kelley 1982). We noted the call type produced by each male when clasped and when clasping, and when males were not engaged in clasping (i.e. 'separate'). During a clasp, a male may make the same call repeatedly; in this experiment, we counted only one of each vocalization type/clasp. For pairs not in physical contact (separate), we measured the duration of each call type.

To determine whether males excite or suppress vocal behaviours in other males, we observed 21 male pairs ($N = 13 M^+M^+$ pairs, $N = 8 M^+M^-$ pairs) and recorded their vocalizations before, during and after they were placed together in a tank. Before pairing, we placed each male in a recording chamber, allowed the male 20 min to adapt, and recorded all vocalizations produced for 45 min; males that vocalized less than 90 s during this pretest period were not paired. We then placed a second male into the tank and simultaneously recorded vocalizations produced by both males for 45 min. There was no effect of home tank on amount of calling. In some cases, we then removed either the dominant or the subordinate male and measured the amount of advertisement calling made by the remaining male for an additional 45 min.

To determine whether clasping is required for vocal suppression, we obtained recordings from nine M^+M^+ pairs in which males were separated by a barrier. The barrier divided the tank into two equal compartments and prevented all physical contact (touching, clasping)

between males. The barrier consisted of two metal frames, each covered with neoprene mesh (0.6-cm openings), separated by 3 cm. Injection, housing and recording paradigms were all as described above. Calls from individuals were distinguished using two hydrophones.

Statistical analysis

Dominance in *X. laevis* is based on an ordinal scale, not an interval scale, because a male that advertises for 100 s is not necessarily twice as dominant as a male that advertises for 50 s. To determine whether the data on calling duration were normally distributed, we used the Kolmogorov–Smirnov test; the null hypothesis (no difference between the actual and ideal data) was rejected at the 0.0002 level. Thus, we used nonparametric statistics. To compare the vocal behaviour of dominant and subordinate males, we used the Mann–Whitney *U* test (for unpaired comparisons). To compare changes in male vocal behaviour across experimental conditions, we used the Wilcoxon matched-paired signed-ranks test. To compare the amount of suppression between dominant and subordinate callers, before and during pairing, we normalized the amount of calling to the pre-pairing values by calculating: (amount of calling before pairing) – (amount of calling during pairing)/(amount of calling before pairing). We then used a Mann–Whitney *U* test to compare suppression indices of dominant and subordinate males. We omitted two values, one from a dominant male and one from a subordinate male, in which calling increased during pairing.

We measured the temporal features of two call types, chirping and amplexant calling, neither of which had been analysed previously. We calculated a group mean \pm SD from the means of four individuals (each individual mean contained 6–12 values) for each measurement. For chirping, we measured the intertrill interval and the number of clicks within a trill; for amplexant calling, we measured intertrill interval, number of clicks and interclick interval.

RESULTS

Call Types Recorded in the Field

In field recordings, we identified eight call types using spectral and temporal characteristics (Fig. 1); these included the seven call types previously identified from laboratory recordings (see Methods) and a novel call type, chirping (Fig. 1a). Spectra of clicks from each call (insets, Fig. 1) revealed characteristic male and female frequencies. The fundamental frequency of the component clicks in chirping was about 1.8 kHz, similar to the power spectra for other male call types: advertisement, answer and male ticking. Chirping consists of short (five click) trills with a mean \pm SD intertrill interval of 239 ± 88 ms. The clicks within a trill are so rapid that each click overlaps the one preceding it, preventing a reliable determination of the interclick interval. The amplexant call (Fig. 1d) was recorded only rarely, perhaps because it is a low-intensity call whose detection requires close proximity to the hydrophone. Female rapping was also recorded in the field; one example

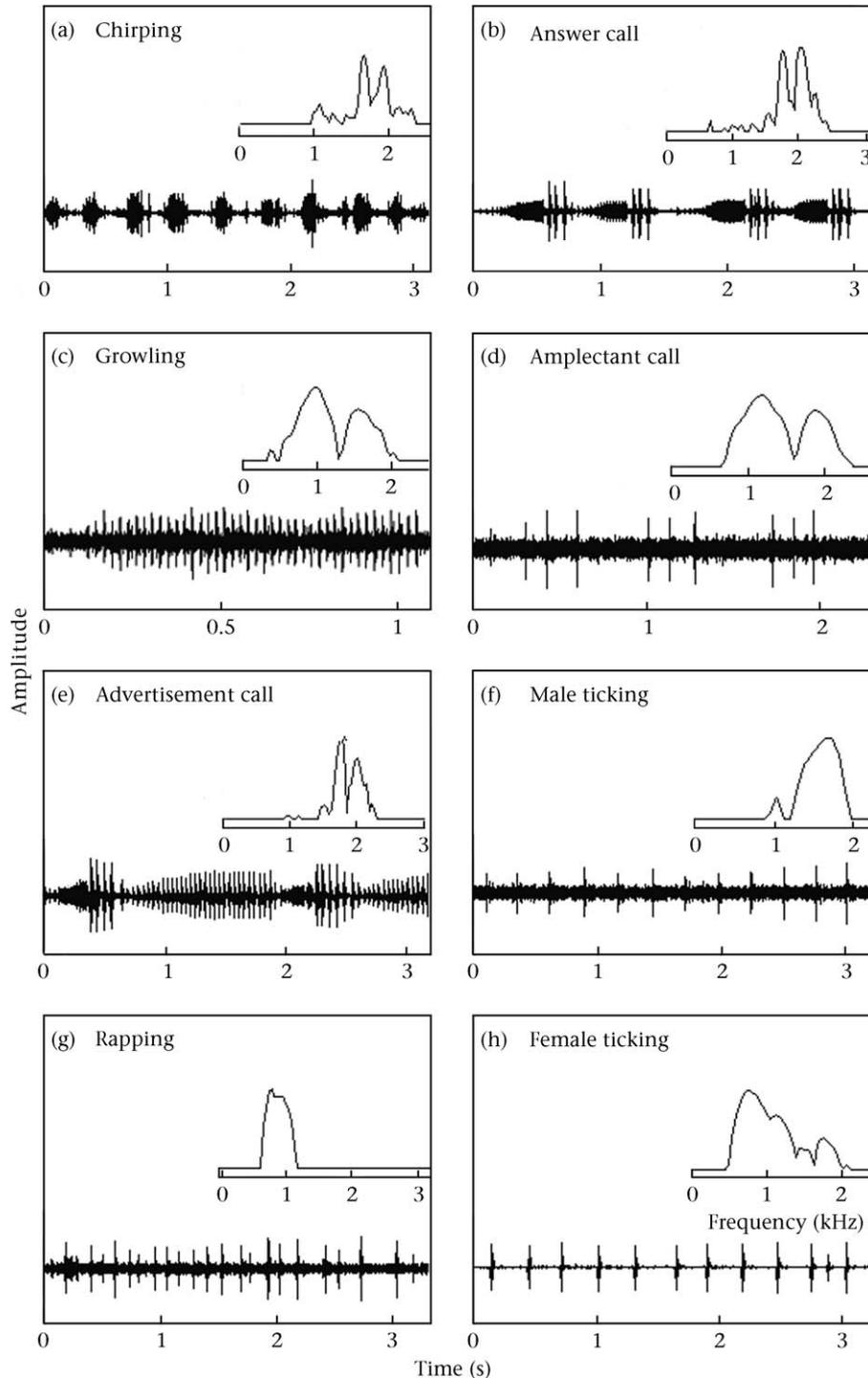


Figure 1. Male and female call types recorded in the field. Each call type is illustrated by an oscillogram indicating amplitude versus time and a sound spectrum (inset) indicating amplitude versus frequency. The amplitude scales are omitted because sound intensity was not comparable between recordings. Frequencies outside the dominant frequencies for clicks, below 0.5 and above 2.5 kHz, were filtered out.

recorded during a male–female vocal exchange is shown (Fig. 1g). Robust male advertisement calling immediately preceded the sample of rapping illustrated; this female may thus have been responding to the male's call.

To determine how male calling changed across the breeding season, we measured the amount of time each call type was produced during the 45-min recording (Fig. 2).

Four of the six male vocalizations were examined. We excluded male ticking, because it could not reliably be distinguished from female ticking in field recordings, and we excluded the amplectant call, because it was so rarely recorded in the field. The amount of calling for all call types increased after mid-July. Advertisement calling was the most frequent vocalization both in terms of the total

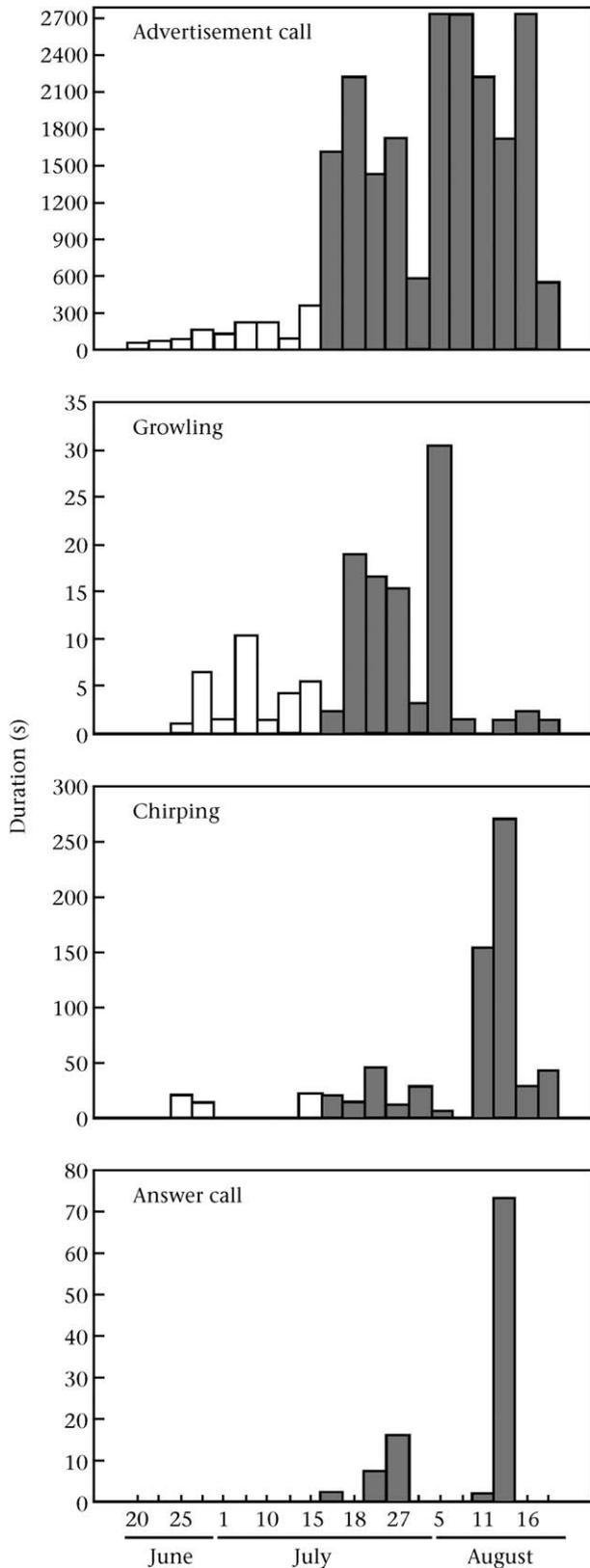


Figure 2. The duration of male advertisement calling, growling, chirping and answer calling on various nights during the recording season. Each bar represents the duration of calling in a 45-min recording period. There was an abrupt increase in advertisement call duration on 16 July that was maintained for most of the recording

amount of calling (note scale on Y-axis compared with other call types) and the fact that it was recorded on every night (Fig. 2). On some nights, advertisement calling was recorded continuously during the 45-min recording period. Although advertisement calling predominated, it was accompanied by at least one other male call type on most nights. The time that males spent producing other call types was relatively brief. Growling was recorded on most nights, whereas chirping and answer calling were recorded less frequently. Thus, males produced a variety of call types during the breeding season and calling intensified as the breeding season progressed.

Call Types Produced in the Laboratory

Males in M^+M^- pairs produced all six male call types (Fig. 3a), whereas those in M^+F^- pairs produced only three male call types (advertisement, answer and amplexant calls; Fig. 3b). Thus, calls previously associated with male-female communication (advertisement, answer and amplexant calls) were also recorded from male-male pairs. The remaining male calls (growling, chirping and ticking) were produced exclusively during male-male interactions. No male calls were used exclusively to communicate with females. Females did not vocalize when they were paired with other females, whether they were injected with hCG or not injected (data not shown). In previous studies, females produced both rapping and ticking when paired with males (Wetzel & Kelley 1983; Tobias et al. 1998). Thus, males vocalized to either sex, but females vocalized only to males.

Male vocal behaviour was markedly affected by sexual state. Males in M^+M^+ and M^+M^- pairs produced more call types than males in M^-M^- pairs (Fig. 4). However, not all pairs within an injection paradigm produced the same calls. Two of five M^+M^- pairs produced amplexant calls, whereas zero of five M^+M^+ pairs did so. Although none of the M^+M^+ pairs produced amplexant calls during these tests, they did produce amplexant calls during subsequent tests (see Fig. 8). Because we did not distinguish which male was producing each call type during these recordings, we could not determine whether this variability was due to sexual state or a partner effect.

Vocal Suppression

When two males were paired, one male advertised significantly more than the other (mean \pm SD = 302 ± 251 versus 22 ± 31 s; Mann-Whitney U test: $U = 6.5$, $N_1 = N_2 = 13$ pairs, $P < 0.0001$; Fig. 5a). We refer to these males as the vocally dominant and the vocally subordinate male, respectively. There was no significant difference in the amount of advertisement calling produced by these males before pairing (Fig. 5b); males that became dominant callers during pairing advertised for

period (■). Note that the Y-axis scale differs for each call type. Advertisement calls were most frequent and had the longest durations.

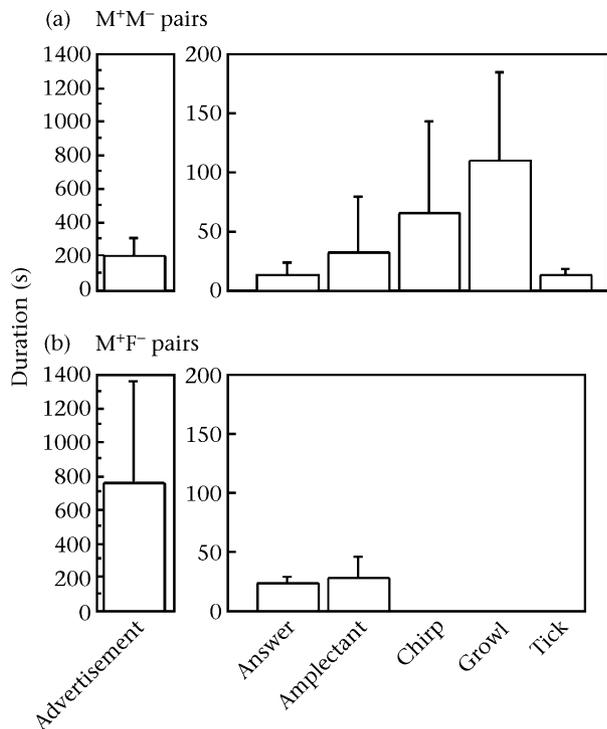


Figure 3. The type and mean \pm SD duration of calls produced by pairs of males and/or females that were injected (M^+ , F^+) and not injected (M^- , F^-) with human chorionic gonadotropin: (a) M^+M^- pairs, $N=5$ and (b) M^+F^- pairs, $N=5$. Because advertisement calls have such long durations, they are separated, with a different Y-axis scale, from the other call types. Males produced male-directed calls but no female-directed calls. No vocalizations were produced by female–female pairs.

1053 ± 799 s and males that became subordinate callers during pairing advertised for 623 ± 726 s ($U = 54$, $P = 0.12$). Because the dominant caller could not be predicted by the amount of calling before pairing, dominance was the result of the interaction between the two males.

Because clasping could accompany vocal dominance, we compared the number of clasps made by both members of the pair. The average \pm SD number of clasps made by the dominant caller (11.3 ± 5.7) significantly exceeded the number made by the subordinate caller (4.8 ± 3.7 ; $U = 21.5$, $N_1 = N_2 = 12$, $P = 0.004$). Thus, dominance in clasping accompanied dominance in calling.

The amount of advertisement calling was reduced in both males during pairing and returned to pre-pairing levels after removal of the other male (Fig. 5c, d). Dominant callers advertised significantly more before pairing than during pairing (Wilcoxon matched-pairs signed-ranks test: $T = -2.76$, $N = 13$, $P = 0.006$; Fig. 5c) as did subordinate callers ($T = -3.11$, $P = 0.002$; Fig. 5d). When the decrease in time spent calling was compared, the mean \pm SD suppression index was greater for subordinate males (97 ± 5) than for dominant males (64 ± 27 ; Mann–Whitney U test: $U = 5$, $N_1 = N_2 = 11$, $P = 0.0003$). Thus, subordinate callers were more suppressed by the presence of another male than were dominant callers. There was no

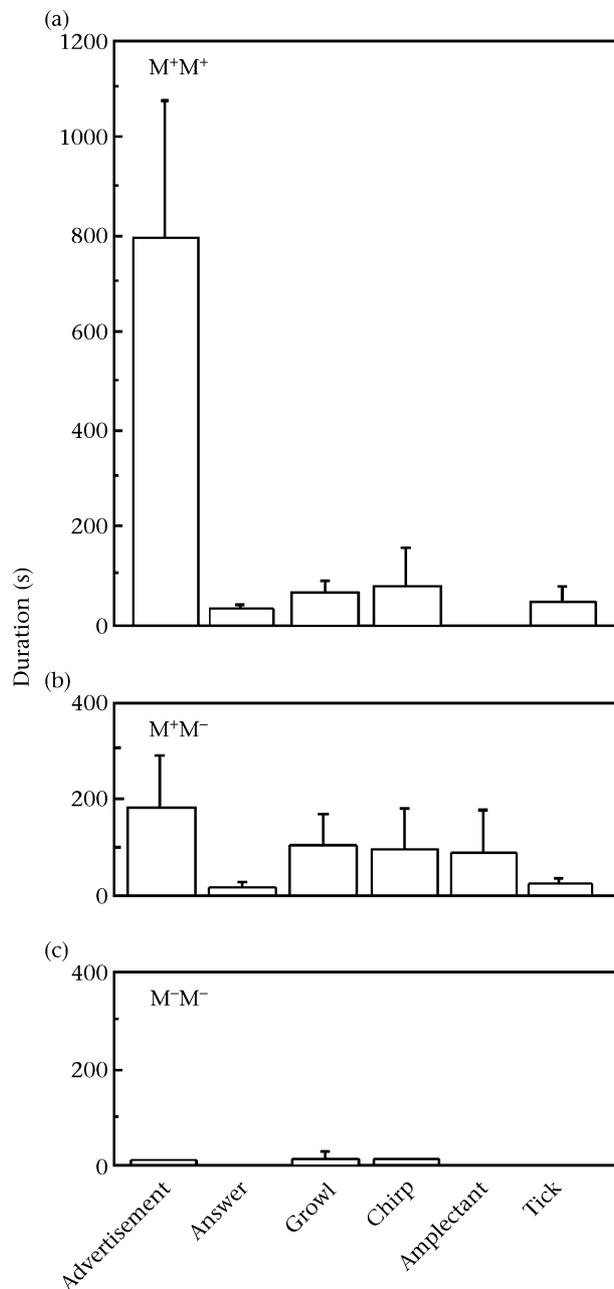


Figure 4. The effect of gonadotropin stimulation on male vocal behaviour: (a) M^+M^+ ($N=5$ pairs); (b) M^+M^- ($N=5$ pairs); (c) M^-M^- ($N=3$ pairs). Each bar represents the mean \pm SD duration for the call type indicated on the X axis.

significant difference in the mean \pm SD amount of advertisement calling before and after pairing in dominant males after removing the subordinate male (post-pairing = 1776 ± 1084 s; Wilcoxon matched-pairs signed-ranks test: $T = -1.85$, $N = 4$; $P = 0.07$; Fig. 5c) or in subordinate males after removing the dominant male (post-pairing = 885 ± 722 s, $T = -1.26$, $N = 8$; $P = 0.21$; Fig. 5d).

We also examined the duration of advertisement calling and number of clasps in eight M^+M^- pairs. Uninjected males rarely advertised, either while separated or paired;

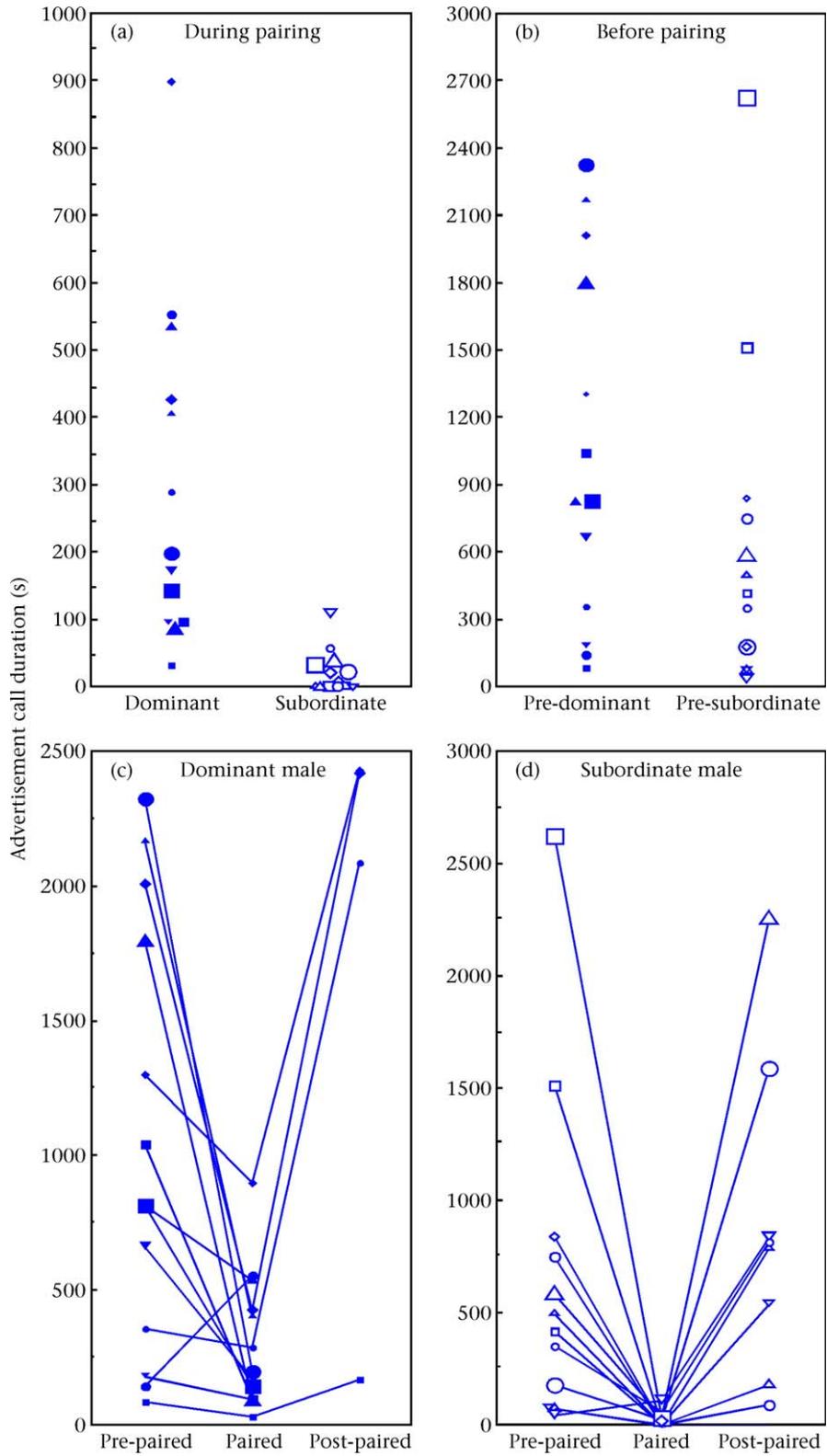


Figure 5. The amount of advertisement calling produced by: (a) dominant and subordinate callers during pairing; (b) pre-dominant and pre-subordinate callers before pairing; and (c) dominant and (d) subordinate males before (pre-paired), during (paired) and after (post-paired) pairing. Open and closed symbols represent pairs in (a) and (b). Each male is represented by the same symbol in (a)–(d). Lines connect points for the same individual in (c)–(d). $N=13$ M⁺M⁺ pairs.

only one male called, for 12 s, while separated. Uninjected males also rarely clasped; the total number of clasp attempts made by uninjected males was two. Thus, the hCG-injected male was dominant, both with respect to the amount of advertisement calling and the number of clasping attempts. As with M^+M^+ pairs, the dominant caller advertised significantly more before (722 ± 638 s) than during (126 ± 130 s) pairing (Wilcoxon matched-pairs signed-ranks test: $T = -2.52$, $N = 8$, $P = 0.02$). Thus, advertisement calling was suppressed by the close proximity of another male, regardless of the other male's sexual state.

The Role of Physical Contact in Vocal Suppression

When males were paired but separated by a barrier that prevented physical contact, one male advertised significantly more than the other (357 ± 262 versus 23 ± 42 s; Mann–Whitney U test: $U = 2.0$, $N_1 = N_2 = 9$, $P = 0.0007$; Fig. 6a). The dominant male advertised more, on average, before pairing (mean \pm SD = 693 ± 522 s) than the subordinate male (412 ± 584 s; $U = 17.0$, $P = 0.04$; Fig. 6b). The mean amount of advertisement calling did not differ before and during pairing for dominant males (Wilcoxon matched-pairs signed-ranks test: $T = -1.24$, $N = 9$, $P = 0.21$; Fig. 6c), although most (6/9) dominant males advertised less during pairing. In subordinate males, the amount of advertisement calling was significantly less during pairing than before pairing ($T = -2.67$, $N = 9$, $P = 0.008$; Fig. 6d). Thus, vocal suppression was achieved in the absence of physical contact.

In the absence of physical contact, few calls other than the advertisement call were made. Answer calling was produced by two dominant males (18 s total duration) and chirping was produced by one dominant (12 s) and two subordinate (23 s) males. Males that were allowed to interact physically produced more call types, suggesting that physical contact stimulates male vocal behaviours. Because vocal dominance was established in the absence of other call types, advertisement calling alone may be sufficient for producing vocal suppression.

The Relation Between Behaviour and Call Type

All male frogs swam around the tank, surfaced for air or remained quiescent on the tank bottom. When two males, at least one of which was hCG injected, came into contact, one male clasped the other. In contrast, clasping was observed in only one M^-M^- pair. Simultaneous or alternating vocalizations were produced by the clasped and clasping males during contact. In one vocal exchange recorded during a clasp, the clasping male produced advertisement calls while the clasped male growled (Fig. 7a). Chirping was a common part of vocal exchanges recorded during clasps (Fig. 7b); the clasping male chirped and the clasped male growled. When males were paired but not in physical contact (i.e. 'separate'), both males called, but not simultaneously.

To determine whether specific call types were associated with the three identified behaviours (clasping, clasped and

separate), we identified vocalizations made by each male in nine M^+M^+ pairs. Some calls were highly context specific (Fig. 8); clasping males rarely growled and clasped males never produced the advertisement, answer or amplexant calls. Because subordinate callers clasped less frequently, most calls made by clasping males were made by the dominant caller and most calls made by clasped males were made by the subordinate caller. All call types were produced when males were separate. Advertisement calling was most frequently produced when the male was not engaged in physical contact. While separate, dominant males produced more amplexant and answer calls than did subordinate males.

We also examined the association between vocal and physical behaviours in M^+M^- pairs (data not shown). The results were similar to those of M^+M^+ pairs in that growling was produced predominantly by clasped males and chirping was produced predominantly by clasping males. In these tests, the M^- male only growled or chirped and only when clasped; this result differs from that of subordinate M^+ males in the previous experiment, which produced the same call types as the dominant caller, only less frequently. Again, advertisement calling was most frequent in the separate condition.

Together, these experiments indicate that the type and amount of vocal behaviour depend on three factors: sexual state, vocal status and behavioural context. For example, growling was produced by a clasped male regardless of hCG injection or dominance, whereas the advertisement call was only produced by hCG-injected males. Although advertisement calling requires that the male be sexually active (i.e. hCG injected), the amount of advertisement calling depends on his position in the vocal hierarchy.

DISCUSSION

Male-directed calls are common among vocal vertebrates; they are used to defend territories, maintain intermale spacing and can avert physical combat (reviewed in Bradbury & Vehrencamp 1998; Gerhardt & Huber 2002). However, male-directed vocal signals are also costly: they can attract predators, be energetically expensive and some are unattractive, even repulsive, to females. Time spent in aggressive signalling is also time lost advertising. Thus, males must find ways of maximizing the benefits while minimizing the costs of vocal signals. Anurans have evolved a variety of strategies to deal with trade-offs between advertisement and aggressive signals. Below, we discuss which strategies could be used by *X. laevis*.

One strategy is temporal partitioning of call types. In some species, males are the first to arrive at a breeding site. For example, during the early part of the evening, *Hyla cinerea* males compete for calling sites and produce aggressive calls during this time. Once calling sites are established, males almost exclusively produce advertisement calls that serve to attract females to the pond and subsequently to individual callers (Garton & Brandon 1975). In *X. laevis*, males and females reside in the same ponds, and temporal partitioning by males is not possible.

Another method is plastic accommodation. Here, males have a graded response to a neighbour's calls, allowing brief

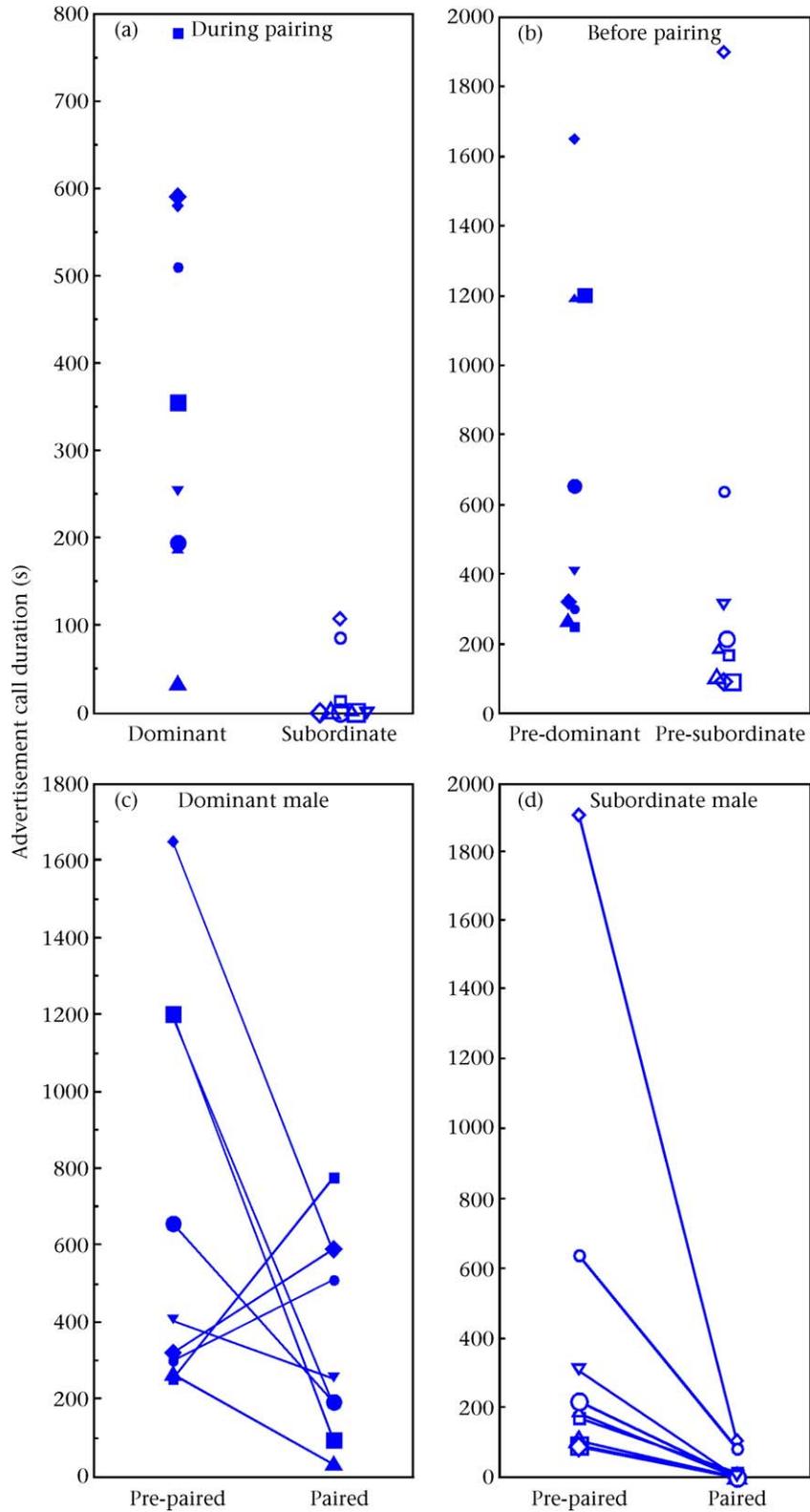


Figure 6. Vocal suppression in the absence of physical contact. The amount of advertisement calling produced by M⁺M⁺ pairs when males were separated by a barrier (N=9). All categories and definitions as in Fig. 5.

displays of aggressive vocal signals and long displays of advertisement signals. Thus, in *H. regilla*, males exposed to playbacks of calls at intensities slightly above their threshold for producing aggressive calls accommodate (return to

advertising) within 15 s; males have been observed to accommodate at distances as close as 20 cm (Rose & Brenowitz 1997). The authors suggested that accommodation is an adaptation to ever changing chorus density,

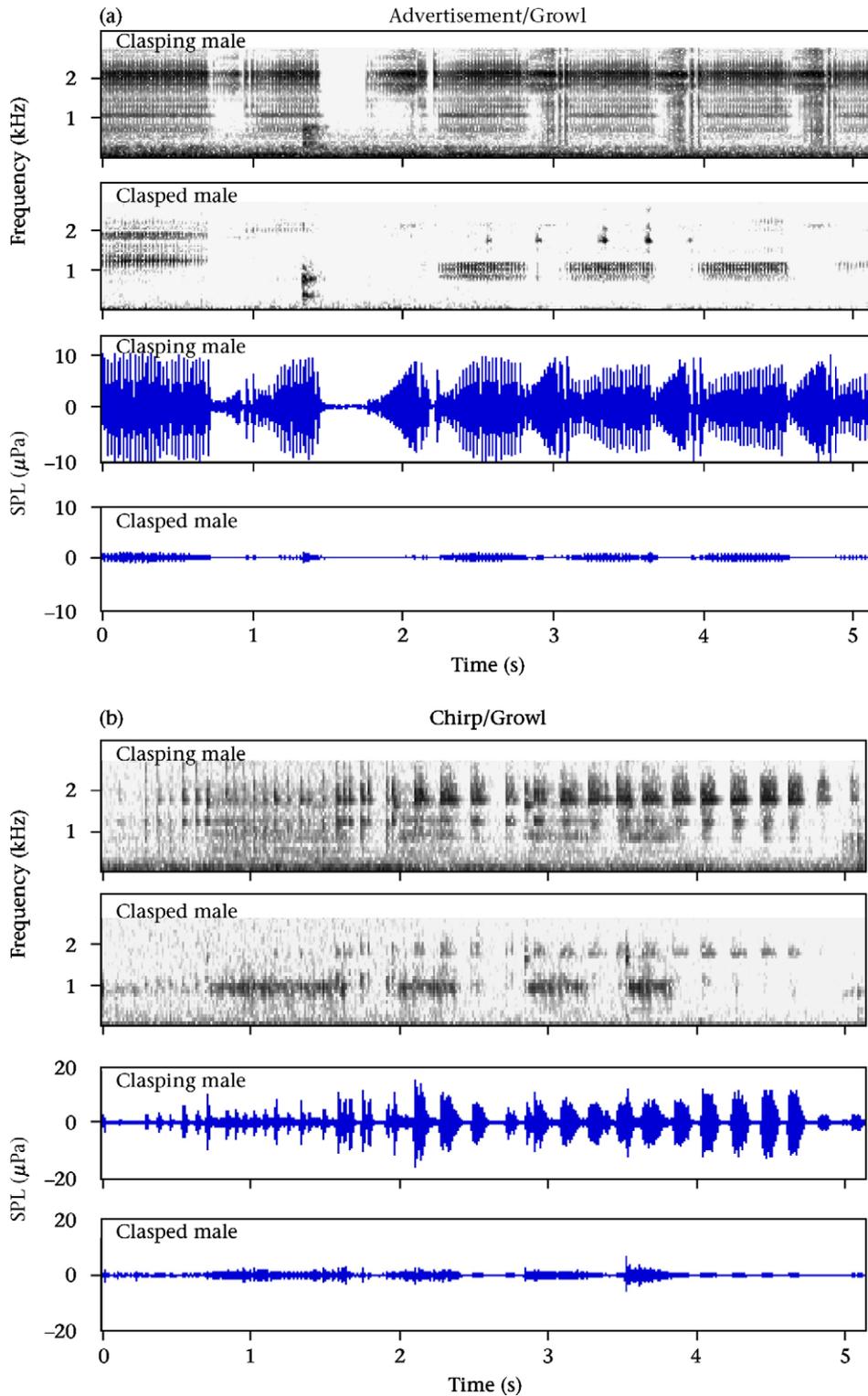


Figure 7. Simultaneous recordings of calls produced by two males during clasping in which the clasped male growled and the clasping male produced (a) advertisement calls and (b) chirps. Spectrographs (upper two traces) and oscillographs (bottom two traces) were from recordings obtained using a tank hydrophone (clasping male) and a wand hydrophone (clasped male). Frequencies below 0.5 and above 2.5 kHz were filtered out. SPL: Sound pressure level.

which is re-established nightly. In contrast, *X. laevis* males do not appear to accommodate to a neighbour's call, at least not over the 45-min recording periods used in this study.

Male signals can also be partitioned into two phases, with one part directed towards males and the other directed towards females. This strategy is adopted by *Eleutherodactylus coqui*; the 'co' note alone elicits male

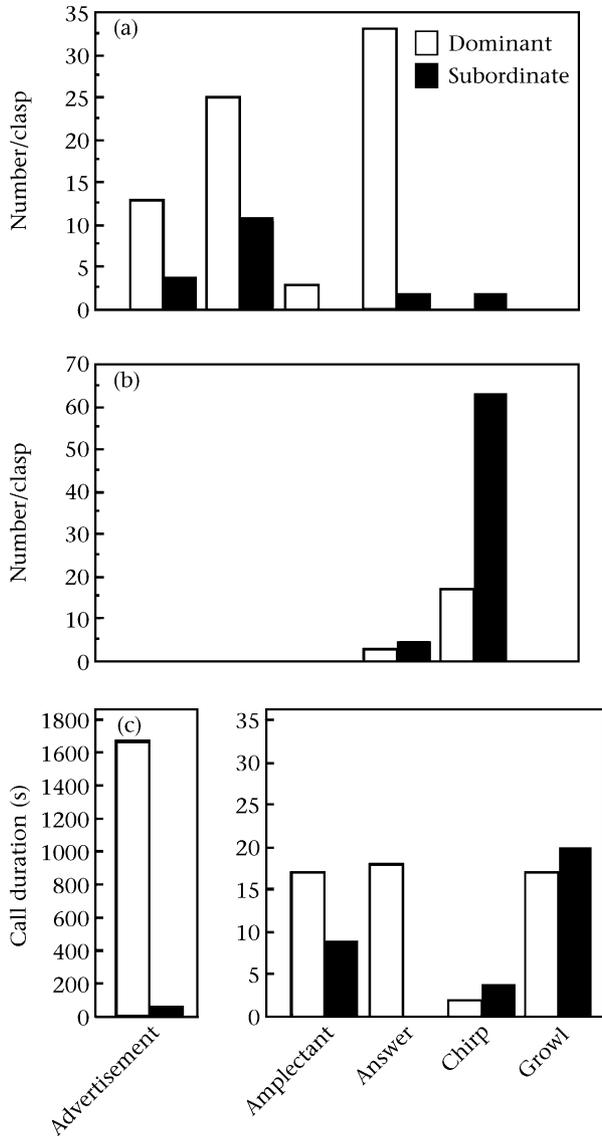


Figure 8. The relation between call type and behaviour. The number of times per clasp that each call type was produced by a male while (a) clasp is present or (b) being clasp is absent, and the duration of each call type produced by males while (c) separate. These data are from 9 of the 13 M⁺M⁺ pairs shown in Fig. 5.

responses and the 'qui' note is attractive to females (Narins & Capranica 1978). *Geocrinia victoriana* also uses a biphasic advertisement call in which males respond aggressively to the long introductory note and females are attracted to the short repeated notes that follow (Littlejohn & Harrison 1985). Because the *X. laevis* advertisement call is biphasic (a rapid trill followed by a slower, longer trill), the two portions of this single call might also be perceived differently by males and females. This possibility seems unlikely because answer calls, which consist almost exclusively of rapid trills, are directed towards, and responded to by, both sexes (Tobias et al. 1998; this study). Whether the slow trill phase of the advertisement call elicits different responses in males and females remains to be determined.

A variant of this strategy is a single call (the advertisement call) that is perceived by females as attractive and by males as aggressive. The advertisement call of male *X. laevis* attracts gravid females (Picker 1983; Tobias et al. 1998) and thus functions as an intersexual attraction signal. Can the advertisement call also be considered an intrasexual aggressive signal? In some anurans, aggressive calls are readily identified because they accompany physical fights between males (e.g. McDiarmid & Adler 1974; Davies & Halliday 1978). Male *X. laevis* do not box or bite; clasp, however, is accompanied by struggling and could be considered a form of the wrestling behaviour observed in other genera (Wells 1977; Duellman & Trueb 1986). The clasp male produces chirping, amplectant and advertisement calling, each of which might serve as an aggressive call. However, when clasp is prevented, male advertisement calling still results in vocal suppression, suggesting that this signal by itself may serve an agonistic function.

One form of male–male competition is for the signaller to distinguish himself from competitors; vocal suppression is a particularly powerful example of this tactic. Vocal suppression allows males to attract females while silencing neighbouring males. In terrestrial anurans, vocal suppression often occurs in species that use satellite tactics. Satellite males associate with a calling male in anticipation either of intercepting females en route to the caller or of taking over a calling site vacated by the caller. This tactic is particularly common among chorusing frogs under high-density conditions where intermale spacing between callers is not possible. For example, in *Bufo cognatus*, the incidence of satellite males is density dependent (Garton & Brandon 1975). Satellite males (and females) are attracted to males that produce longer call bouts and the number of satellites associated with a calling male is also proportional to bout length. The satellite tactic can be unstable; switching between satellite and caller is observed in most species. The choice, to sing or be silent, may be driven by energetic constraints; being silent conserves energy while still providing mating opportunities.

An alternative strategy for the loser in a signalling competition is vocal distancing. In *H. versicolor*, for example, aggressive interactions result in the loser either leaving or remaining in the dominant male's territory but not calling; remaining silent or leaving are equally probable reactions (Fellers 1979). The small aquaria we used to observe male–male interactions in *X. laevis* did not provide an opportunity for the subordinate male to distance himself from the dominant male and it remains to be determined whether, in actual ponds, males flee, adopt a satellite strategy or take turns calling sequentially. In the laboratory, individual males can call continuously for several hours. Although the energetic costs of calling in *X. laevis* have not been determined, this observation suggests that the issue may not be paramount for signalling strategy.

Because aggressive calls frequently accompany other agonistic displays, as well as actual fighting, the importance of acoustic signals by themselves in the establishment of the victorious male is often unclear. In cowbirds, muting largely prevents a bird from attaining a high

dominance rank; after rank is established, however, muting has no effect on dominance (Dufty 1986). In *X. laevis*, advertisement calling can establish vocal dominance in pairs of males; whether calling is required to maintain dominance and the role of calling in the reproductive success of individuals are open questions.

What are the boundaries of vocal suppression? Sound intensity decreases 150–200 times less with distance in water than in air; loss is also relatively greater for higher-frequency than for lower-frequency signals (Bradbury & Vehrencamp 1998). The intensity of the 1–2-kHz (low frequency) signals of *X. laevis* calls may thus decrease very little in small ponds (although water depth and obstacles also influence sound attenuation). In a small pond, the acoustic boundary for suppression could be the entire pond. In very large or acoustically unfavourable ponds, *X. laevis* males could use acoustic suppression as a spacing device as in other anurans. If so, below a threshold value for acoustic attenuation, the number of simultaneously calling males should increase as pond size increases. If vocal suppression reflects acoustic features of the underwater habitat, we might also expect it to occur in other aquatic anurans, particularly other species of *Xenopus*. The only other species that has been examined extensively is *X. borealis*. Yager (1992) paired hCG-injected males and observed male–male clasping, as in *X. laevis*. Three call types, advertisement, approach and agonistic, were recorded; the agonistic call was usually given by the clasping male (determined in muting experiments). Yager also observed that one male continued to produce the advertisement call while the other was silent and that the suppressed male resumed calling when isolated. No relation between male size and vocal dominance was noted. Thus, vocal suppression could be widespread within the Xenopodinae. Whether this characteristic reflects only a shared phylogeny or is instead promoted by physical constraints imposed by underwater signalling remains to be tested in other groups of anurans.

Although *X. laevis* mate over a prolonged breeding season (July–December), periods of female receptivity are brief (<24 h in laboratory-reared, gonadotropin-injected females; Wu et al. 2001) and asynchronous (Kalk 1960). When a female becomes receptive, she shows little preference for individuals and instead swims towards any advertising male (Tobias et al. 1998). The scarcity of receptive females, and their attraction to any calling male, creates a strong pressure for a male to be the only advertiser, or one of a few advertisers, on a given night. These conditions favour the development of robust competition between males for mating opportunities. By swimming towards the advertising male, females are selecting the male that is both vocally dominant and dominant in clasping encounters with other males. Because female attraction and success in male competition can be achieved with one call type, the advertisement call, male *X. laevis* could maintain a reproductive advantage simply by advertising incessantly. Therefore, we propose that male *X. laevis* compete for the right to advertise by establishing a vocal hierarchy in which subordinate males rarely advertise.

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