



Females whisper briefly during sex: context- and sex-specific differences in sounds made by croaking gouramis

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Croaking gouramis, *Trichopsis vittata* (family Osphronemidae), possess enhanced pectoral fin muscles and tendons, enabling the fish to generate series of short or long broadband bursts while beating the fins. Agonistic disputes over territories result in lateral displays during which both sexes produce croaking sounds. During mating, a female approaches a male's nest at the water surface and emits purring sounds in a vertical, head-up position. This behaviour is followed by spawning bouts. I investigated whether aggressive and prespawning sounds differ in acoustic characteristics and whether they might convey different information. Agonistic sounds of both sexes lasted longer than the females' prespawning sounds, consisting of four or five bursts/sound compared to 2.4 bursts in purring sounds, and included a smaller percentage of short bursts. Sound pressure levels were higher in agonistic than in prespawning sounds. The dominant frequency of male agonistic signals was lower than that of female prespawning sounds. Both sexes produced long, high-intensity croaking sounds during agonistic disputes; these probably help them assess the fighting ability of opponents. On the other hand, only females emitted short, low-intensity purring sounds, which probably initiate and coordinate spawning behaviour. The low sound level and short duration of prespawning sounds indicate that they function as mating displays at very short distances; this probably reduces the chance of attracting competitors or predators. The croaking gourami is the only fish species in which females are known to initiate spawning acoustically.

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Representatives of several dozen fish families produce sounds during agonistic behaviour, courtship and spawning (Myrberg 1981; Ladich 1997; reviewed in Ladich 2004; Ladich & Myrberg 2006; Myrberg & Lugli 2006). In all but a few studies, sound production has been described in males. Furthermore, descriptions of some female sounds, for example during reproduction in the blacktail and yellow shiners (genus *Cyprinella*) by Delco (1960), have been regarded as erroneous and therefore attributed to males (Myrberg & Lugli 2006). This striking difference in the number of reports of sound production between males and females is due either to females producing less sound because of differences in life history between the sexes or to a male-biased or territory-biased research approach.

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Sound-generating mechanisms are usually sexually dimorphic in most fish species (Ladich & Fine 2006). In the oyster toadfish, *Opsanus tau* (family Batrachoididae), males have about 47% more fibres per swim bladder muscle than females, resulting in larger sonic muscles in males (Fine et al. 1990). A similar trend has been observed in the closely related midshipman, *Porichthys notatus* (Brantley et al. 1993a). Sexually dimorphic sonic muscles have also been described in unrelated families such as in the Atlantic croaker, *Micropogonias undulatus* (family Sciaenidae; Hill et al. 1987), the striped cusk-eel, *Ophidion marginatum* (family Ophidiidae; Courtenay 1971), and the haddock, *Melanogrammus aeglefinus* (family Gadidae; Templeman & Hodder 1958). In the croaking gourami, *Trichopsis vittata* (family Osphronemidae), pectoral sonic organs are about one-third smaller in females (Kratochvil 1985). Sex-specific differences have also been found in several other traits such as in the fine structure of sonic muscles, in vocal pathways and in the differential effects of

hormones on sonic muscles (Bass & Marchaterre 1989; Bass & Baker 1990; Brantley et al. 1993b).

Despite our knowledge of structural and physiological differences in sound-generating mechanisms in fish, there have been few descriptions of sex-specific differences in acoustic behaviour and sound characteristics. Female sounds are either briefly mentioned or totally ignored. Clearly, as in many other vertebrates, sound production in fish is more pronounced in males, which often advertise and defend nest sites and care for offspring. Despite these general differences in life history, it is assumed that both sexes produce sounds when defending resources such as food or feeding sites. Several authors have described sound production by females during aggressive encounters, for example in cod (Brawn 1961), toadfish (Gray & Winn 1961; Winn 1967; Brantley & Bass 1994), sculpins (Ladich 1989), sunfish (Ballantyne & Colgan 1978), cichlids (Myrberg et al. 1965), gobiids (Ladich & Kratochvil 1989) and gouramis (Marshall 1966; Brittinger 1991; Schleizer 1992). In the European river bullhead, *Cottus gobio*, both sexes defend territories year round and aggressive calling depends mainly on size and not sex. Large females are as successful in defending territories as males are and produce more sounds than smaller males (Ladich 1990). After spawning, in species with biparental care, both parents defend eggs or fry against conspecifics or heterospecifics. In *Archocentrus centrarchus*, attacks by females on males are often accompanied by low-frequency growls (Schwarz 1980). Parmentier et al. (2005) mentioned that it is likely that female clownfish, *Amphiprion akallopisos*, defend their sea anemones by producing sounds, while males remain stationary within the anemone's tentacles.

While sex-specific differences in agonistic sounds are probably minor, major differences exist in the reproductive context. Only males seem to advertise breeding sites acoustically, for example in toadfish (Winn 1967; Ibara et al. 1983), pomacentrids (Myrberg et al. 1986) and mormyrids (Crawford et al. 1997). In addition to mate attraction to nest sites, males of numerous species are known to produce sounds during courtship and spawning (reviewed in Myrberg & Lugli 2006). This is particularly well described in gobiids (Lugli et al. 1997) and damselfish (Kenyon 1994; Lobel & Mann 1995) and is well known in other groups such as drums (Connaughton & Taylor 1996), cyprinids (Stout 1963), catfish (Prusinzsky & Ladich 1998) and cichlids (Amorim et al. 2003; Amorim 2006).

Sounds made by female fish during mating have been mentioned in only a single species, the croaking gourami, *T. vittata*. Both sexes produce croaking sounds during agonistic displays, but only females generate sounds during courtship and spawning, termed purring sounds (Marshall 1966). This general observation has been confirmed by Brittinger (1991), but differences in sound characteristics between sexes and contexts are unclear because different sound characteristics have been analysed, sound intensity measurements are lacking, there is a lack of statistical analysis in the older papers, and results are contradictory.

I investigated sex- and context-specific sounds of *T. vittata* by measuring and including sound characteristics that have not been dealt with before (sound pressure levels, fine structure of bursts) and that might help to elucidate

the functional significance of acoustic signals. The sounds are built up of trains of bursts, which are produced by the pectoral fins beating alternately (Kratochvil 1978). I hypothesized that agonistic sounds (croaks) and courtship sounds (purr) differ in their sound structure because they address different receivers. Agonistic signals should be exaggerated to help assess the fighting ability of territorial intruders and thus to keep them away (Ladich 1998), whereas courtship sounds should be less conspicuous to keep the reproductive act private (Krebs & Dawkins 1984; Bradbury & Vehrencamp 1998).

METHODS

Study Animals

I used 10 males (1.11–1.52 g body weight; 37–44 mm standard length) and 15 females (agonistic experiments: 0.95–1.57 g; 37–42 mm; reproductive experiments: 0.97–1.49 g, 36–41 mm), obtained from local pet suppliers. They were kept in 100-litre community tanks (70 × 35–40 cm and 40 cm high) at 25 ± 1°C and a 12:12 h light:dark cycle was maintained. Tank bottoms were covered with sand, and halved flowerpots were provided as hiding places. Fish were fed primarily live food (*Chaoborus* larvae, *Tubifex* worms) and occasionally food flakes (Tetramin) four or five times a week. Sexing of fish was based on the presence or absence of the whitish ovary, which was visible against bright light. After the experiments, the fish were returned to the community tanks.

Behaviour and Sound Recordings

Before the experiments, fish were isolated for at least 1 week in tanks (25 × 30 cm and 35 cm high), similarly equipped as the holding tanks, to reduce dominance experience. Afterwards, I introduced two fish (either two males, two females or a male and a female) into the left and right halves of the test tanks (50 × 30 cm and 35 cm high), which were divided by a white plastic grid. The walls of the aquarium were lined on the inside, except for the front glass to allow video recordings, with air-filled packing wrap to reduce resonance and reflection. To facilitate the building of floating bubble nests, I added natural and artificial (silk) floating plants. Some males started to build nests immediately, others after several days. Test tanks were placed on a table that rested on a vibration-isolated concrete plate. The entire set-up was enclosed in a walk-in sound-proof room, which was constructed as a Faraday's cage.

I recorded acoustic signals and behaviour on HiFi videotapes by using a hydrophone (Brüel & Kjær 8106, sensitivity –172.5 dB re 1 V/μPa) that was placed close to the back wall in the centre of the aquarium and a video camera (Sony CCD-VX1E), positioned behind a curtain. Both the hydrophone and the video camera were connected to a HiFi S-VHS video cassette recorder (JVC HRD 4700 EG). HiFi audio and S-video signals were both stored synchronously on videotapes. The hydrophone was fed by a microphone

power supply (Brüel & Kjær 2804), which was connected to the aquarium water via a grounding cable.

Recordings were made after the fish had been in the tanks for 1 day for agonistic tests and several days for reproductive tests. To start a recording I removed the plastic grid, which separated both parts of the test tank, allowing the two fish to interact with each other.

Sound Pressure Level Measurements

I measured the sound pressure levels (SPLs, RMS Fast, broadband A weighting) with a hydrophone (Brüel & Kjær 1801, sensitivity -184 dB re 1 V/ μ Pa) and the microphone power supply (Brüel & Kjær 2804) connected to a sound level metre (Brüel & Kjær Mediator 2238). The equipment was calibrated with the hydrophone calibrator (Brüel & Kjær 4229). All dB values were measured relative to 1 μ Pa.

Because of the varying distances of the fish to the hydrophone, I divided the test tank into 50 sectors by using a grid applied to the front glass of the aquarium (grid size 5×5 cm), and I noted the sector in which a croaking or purring sound was produced. To compensate for different distances between the hydrophone and the fish I calculated a correction factor (Ladich et al. 1992). One typical fish sound was played back at a constant SPL from a small loudspeaker (Fuji 7G06, 8 Ohm, 0.8 W) in each of the 50 sectors and I noted the SPL. The relative SPL differences between the sector nearest to the hydrophone (10 cm away) and all 50 sectors were calculated and added to the SPL values measured while the fish produced sounds in a particular sector. Thus, I could determine a distance-independent absolute SPL value for each sound emission.

Sound Analysis

To analyse the sounds recorded I used Cool Edit 2000 (Syntrillium Software Corporation, Phoenix, AZ, U.S.A.) and S_TOOLS-STX 3.7.4 (Acoustics Research Institute, Austrian Academy of Sciences, Vienna, Austria). All sounds were digitized using a sampling rate of 16 kHz.

I determined the following acoustic variables for each male, female and context: (1) total number of bursts per croaking or purring sound; (2) number of short (single-pulsed) and long (double-pulsed) bursts and percentage of short bursts within a sound; (3) burst period defined by the time interval between the onset of two successive bursts; (4) the dominant frequency of sounds for one individual, determined by copying all bursts in one file and calculating the cepstrum-smoothed power spectrum of this entire file (set-up chosen in STX 3.7.4: bandwidth 1 Hz, number of coefficients 15–50, overlap 50%, Blackman–Harris window; Noll 1967).

Statistical Analysis

I recorded the aggressive sounds of 10 males and 10 females and the spawning sounds of 10 females. While

agonistic behaviour could be elicited regularly during staged contests, half of the females did not show any reproductive behaviour. Therefore, I had to use 20 females to obtain purring sounds from a total of 10 females.

I analysed 10–15 sounds per fish and context. I first calculated means and standard errors of sound characteristics (total number of bursts, number of short and long bursts within a croak and purr, percentage of short bursts, burst period, dominant frequency and SPL) for each individual ($N = 10$, except SPLs of purring sounds, $N = 7$). A total of 2346 bursts were used for analyses. I then used individual means for calculating the context- and sex-specific differences in sound characteristics by one-way analysis of variance (ANOVA). Differences between sexes and behavioural contexts were calculated with a Bonferroni post hoc test.

Ethical Note

Agonistic interactions between croaking gouramis consist of two stages: a lateral display phase followed by a frontal display phase (Ladich 1998). Lateral displays consist of visual and acoustic displays without any physical contact between opponents. As my intention was to record sounds in various contexts (the influence of displays on the outcome of contests was investigated in Ladich 1998), agonistic interactions were stopped as soon as enough sounds were recorded. Fights were not allowed to proceed to the frontal display phase where biting might occur. In addition, I interrupted pairings between females and males when agonistic interactions instead of reproductive behaviour took place. I terminated any unwanted aggressive behaviour by reinserting the white plastic grid between individuals.

RESULTS

Sound Production Behaviour

Agonistic interactions between two males or two females (or a male and a female) started after the fish detected the territory intruder. They approached each other, began to spread their unpaired fins and circled vigorously head to tail. This behaviour was generally accompanied by rapid pectoral fin beating and the generation of croaking sounds (Fig. 1a). Opponents usually produced sounds alternately. The individual producing the sounds could be recognized by the shaking of its body during intense pectoral fin beating and sound generation. In addition, sounds could also be assigned to a particular individual by small differences in acoustic characteristics. No obvious differences between the sexes were evident in the lateral displaying behaviour. During lateral displaying, fish did not physically come into contact with each other. Bouts of lateral displaying regularly ended when the fish swam to the surface for air breathing.

Pairing a male and female could end in either agonistic behaviour as described above or mating behaviour. The mating behaviour in *T. vittata* may be subdivided into

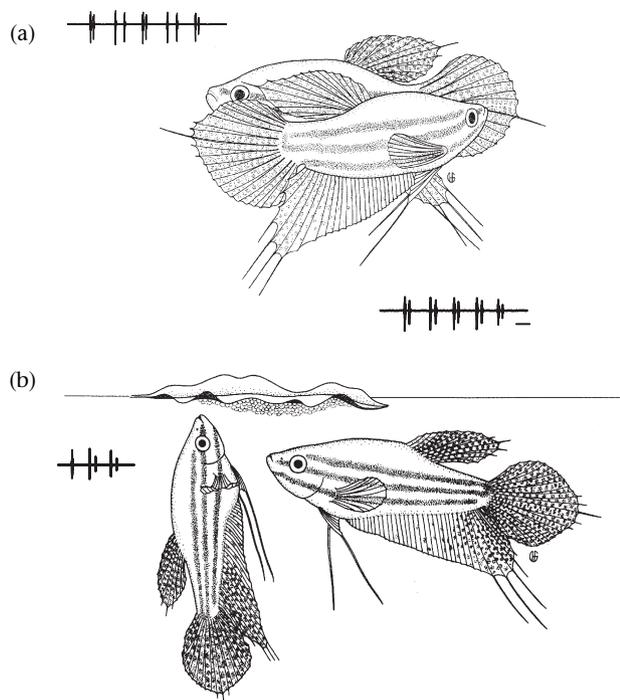


Figure 1. (a) Lateral displays of two sound-producing males. Inserts show oscillograms of croaking sounds produced by both opponents alternately. Both sounds are built up of five double-pulsed long bursts. Scale bar 25 ms. From Ladich (2004). (b) Mating behaviour of croaking gouramis. The female is on the left side in a vertical head-up position. The male is on the right in a horizontal position beneath his bubble nest under floating leaves. The insert shows an oscillogram of a female's purring sounds. Drawings by H. C. Grillitsch.

three stages, early mating, late or prespawning and spawning behaviour. In the early stages of mating behaviour males followed a female and displayed laterally, sometimes producing croaking sounds. The subsequent behaviour of the females determined whether males responded with ongoing agonistic behaviour or female-following behaviour. In cases where the female did not flee or respond aggressively to the male but swam slowly in front of him, the male followed the female. If he took up a position under a nest or at a planted nest site at the water surface, the female adopted an oblique or vertical head-up position (Fig. 1b). In this upright position she was never attacked. She then began undulating her body while beating her pectoral fins rapidly, thereby producing a purring sound. During this courtship behaviour, the male hovered horizontally under his nest (Fig. 1b). This was followed by spawning behaviour, during which the male wrapped his body tightly around the female, turning her on her back. At this moment, eggs were released; these were picked up by the male and spat into his bubble nest. After a spawning bout, females took up the head-up posture and produced sounds again. After several spawning bouts females purred less often and spawning could take place without purring. Because purring sounds were always uttered immediately before a spawning bout, I call them 'prespawning sounds'.

Description of Sounds and Temporal Patterns

Sounds of croaking gouramis were built up of series of broadband bursts, each one produced by one pectoral fin (Fig. 2a, b). The number as well as the percentages of burst types within a sound differed significantly between behavioural contexts.

The number of bursts in male and female agonistic sounds was approximately twice the number recorded in female prespawning sounds (Fig. 3a). No sex-specific difference was found in croaking sounds. Croaking sounds in both sexes consisted primarily of long double-pulsed bursts (approximately 90%), whereas this percentage was significantly lower in purring sounds, in which approximately one-third of the bursts were short and single-pulsed (Fig. 3b). This higher percentage (37.5%) was not due to more short bursts, which did not differ between the sexes and contexts (ANOVA: $F_{2,27} = 1.66$, $P = 0.21$), but to more long double-pulsed bursts in croaking sounds ($F_{2,27} = 27.10$, $P < 0.001$).

The time between the onset of two consecutive bursts within a sound differed significantly (Fig. 3c). The burst period in female agonistic sounds was 5 ms longer than in female prespawning sounds, whereas burst periods in male sounds did not differ from those in females (Fig. 3c).

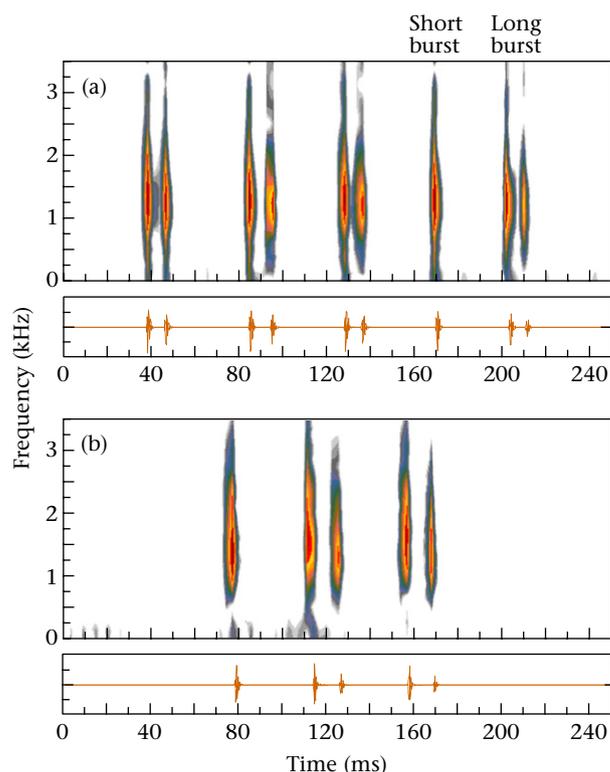


Figure 2. Examples of sonograms and oscillograms (below) of (a) a croaking sound and (b) purring sounds. A short and a long burst are indicated. (a) The croaking sound consists of four long double-pulsed bursts and one short single-pulsed burst. (b) The purring sound consists of one short single-pulsed burst and two long double-pulsed bursts. Sampling frequency 16 kHz, filter bandwidth 180 Hz, 50% overlap, Blackman–Harris window.

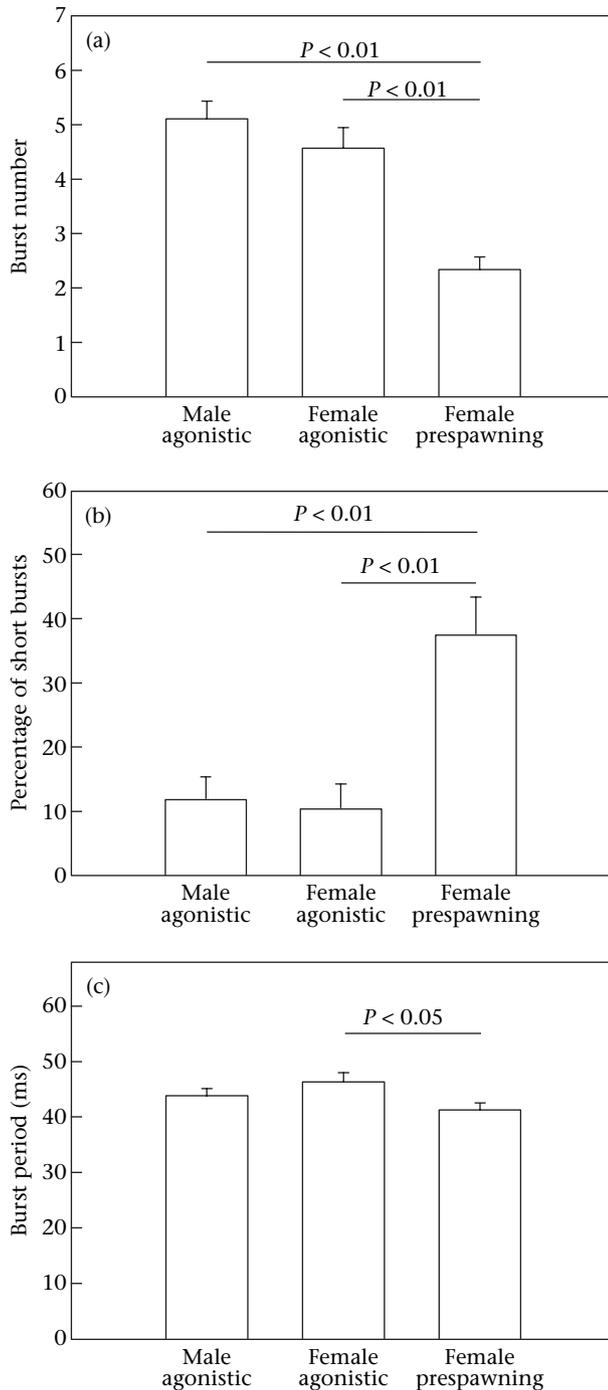


Figure 3. Mean + SE (a) number of bursts, (b) percentage of short single-pulsed bursts and (c) burst period per male and female agonistic sounds and female prespawning sounds (ANOVA: number of burst: $F_{2,27} = 20.43$, $P < 0.001$; Bonferroni post hoc test: $P < 0.01$; % short single-pulsed bursts: $F_{2,27} = 11.51$, $P < 0.001$; Bonferroni post hoc test: $P < 0.01$; burst period: $F_{2,27} = 3.99$, $P < 0.05$; Bonferroni post hoc test: $P < 0.05$).

Dominant Frequency and Sound Pressure Level

Croaking gouramis produced broadband pulsed sounds with the main energy concentrated between 1 and 2 kHz

(Fig. 4). The mean dominant frequency was significantly lower in male croaking sounds than in female prespawning sounds but did not differ between female sound types (Fig. 5a).

The sound intensity was sex and context dependent. Male croaking sounds were loudest, whereas the female purring sounds had the lowest SPL (Fig. 5b). Female agonistic croaking sounds were twice as loud as their prespawning sounds (5.9-dB difference).

The differences between groups in SPLs and dominant frequencies of sounds were not due to differences in morphological characteristics. Neither body weight nor standard length differed between groups (ANOVA: weight: $F_{2,27} = 1.83$, $P = 0.18$; standard length: $F_{2,27} = 0.81$, $P = 0.46$). Dominant frequency was negatively correlated with male weight (Pearson correlation: $r_8 = 0.69$, $P < 0.05$), but not with female weight or standard length of either sex.

DISCUSSION

Sound-producing Behaviour

Croaking gouramis showed clear, context-specific differences in sound production behaviour. Differences in agonistic behaviour were small, and the sexes could not be recognized based on their fighting or sound production behaviour. This was true for male–male, female–female and female–male agonistic interactions. Occasionally, females defeated males during territorial disputes. In contrast, sex-specific differences in mating behaviour were pronounced. Purring sounds were produced only by females in the prespawning stage. No sound production in a head-up posture was ever observed in males, although males occasionally take up this posture to gulp air from the surface and to build their floating bubble nests (see also Richter 1988).

Agonistic Croaking Sounds

Male croaking gouramis produce on average 3.7–5.0 bursts and females 3.9–4.0 bursts per croak (Marshall

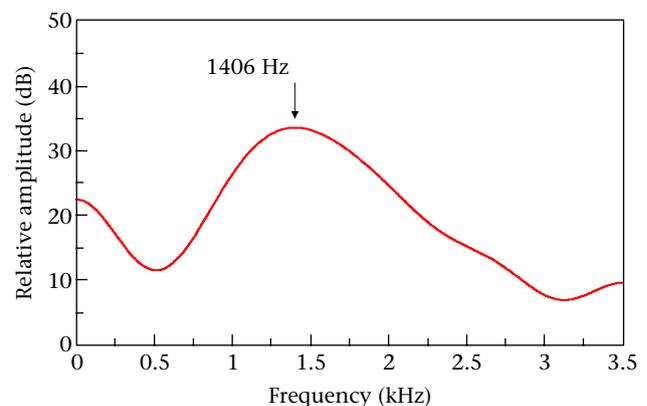


Figure 4. Cepstrum-smoothed power spectrum of all bursts that a female produced in an agonistic context. The dominant frequency is indicated. Sampling frequency 16 kHz, filter bandwidth 1 Hz, 50% overlap, number of coefficients 25, Blackman–Harris window.

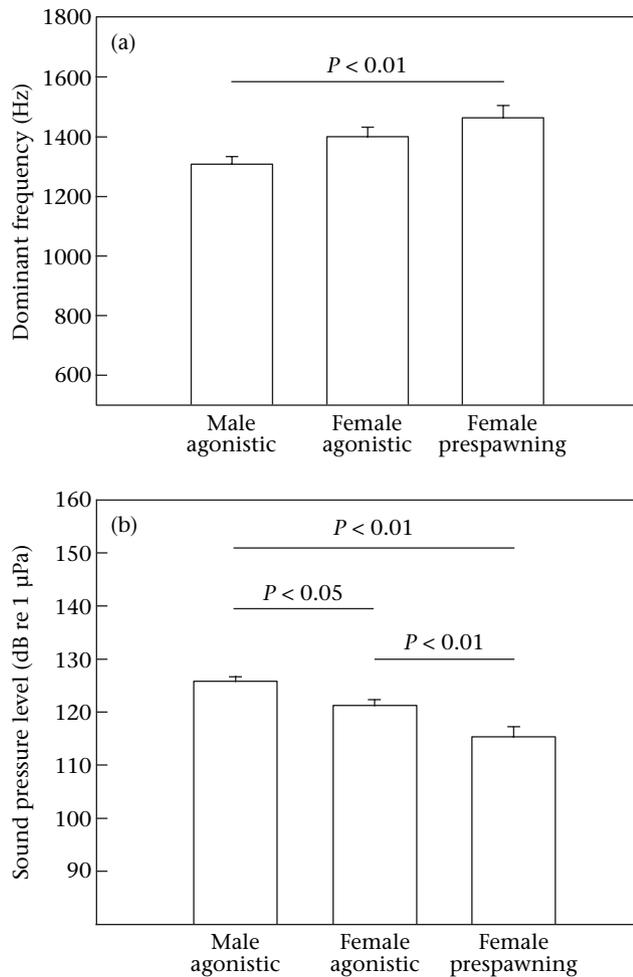


Figure 5. Mean \pm SE (a) dominant frequency and (b) sound pressure level of male and female agonistic sounds and female prespawning sound (dominant frequency: ANOVA: $F_{2,27} = 6.31$, $P < 0.01$; Bonferroni post hoc test: $P < 0.01$; sound pressure level: $F_{2,24} = 18.03$, $P < 0.001$; Bonferroni post hoc test: $P < 0.01$).

1966; Brittinger 1991; Schleinzer 1992; this study). None of these studies found any significant difference in mean burst number between the sexes (although Marshall 1966 did not test this statistically). Marshall (1966) measured burst duration and found out that it averages 22.5 ms in males and 15.5 ms in females. However, burst duration is difficult to measure because the end of short acoustic signals (transients, pulses) is obscured by resonance and reflection. I used a more robust parameter, number of pulses within bursts. I found no difference in the percentages of short single-pulsed and long double-pulsed bursts, or in the burst period, the time between the onset of two consecutive bursts, between male and female croaks. Although this sound variable was not analysed in previous studies it can be calculated by adding burst duration and the interval between bursts. In Marshall's (1966) and Brittinger's (1991) studies, burst periods seemed to be approximately 10% longer in males than females, whereas in my study, where males and females of similar size were studied, no such difference was found in agonistic sounds.

Marshall (1966) reported the midpoint frequency of maximum energy of all sounds in croaking gouramis to be between 0.6 and 2.6 kHz. Neither Brittinger (1991) nor I found significant sex-related differences in dominant frequencies of croaking sounds. This is understandable particularly in the current study, where similar-sized fish were studied. In general, when analysing the main (peak, dominant) frequencies of short-pulsed bursts, the size of the animal producing the sound has to be considered.

Dominant frequency has frequently been shown to be negatively correlated with standard length or body mass, for example in gouramis (Marshall 1966; in males of all three species of croaking gouramis: Ladich et al. 1992), in damselfish (Myrberg et al. 1993) and in mormyrids (Crawford et al. 1997). I found a negative correlation only between male weight and dominant frequencies but not for female weight or for standard length. This may reflect the difficulty in measuring the dominant frequency of broadband pulsed bursts and the fact that fish were of similar size, in contrast to previous studies, complicating the detection of subtle differences in dominant frequency.

No previous study has measured SPLs. My study clearly shows that males produced louder sounds than females during agonistic interactions. This may be explained by sexual dimorphism in sound-generating structures. Males have larger sound-generating muscles and thus might be able to produce higher tensions on enhanced pectoral fin tendons (Kratochvil 1985). This results in louder pulses when these stretched tendons are plucked during pectoral fin beating.

In summary, only minor or no differences existed between the sexes in the duration, temporal patterns and dominant frequency of acoustic signal production during agonistic interactions; an exception was sound intensity, which is probably the result of sexual dimorphism.

Agonistic versus Prespawning Sounds

Croaking gouramis are apparently the only fish species in which females are known to produce sounds during courtship. These sounds are heard only when females take up a particular vertical posture close to the water surface. How pronounced are the differences between these prespawning sounds and agonistic sounds? In the present study they differed from agonistic sounds in duration, structure of bursts and intensity. The number of bursts within a purring sound averaged 2.4, which was approximately half the number in croaking sounds. This result is in good agreement with Marshall's (1966) result (mean: 2.3 bursts) but not with Brittinger's (1991) data (mean: 4.0 bursts). Brittinger's high value might be caused by false classification of sounds.

The fine structure of bursts reveals clear differences between the contexts during which they are produced. Prespawning sounds consisted of a much higher percentage of short bursts than croaking sounds did, which had more long double-pulsed bursts. The number of short bursts did not differ between the sexes and contexts. The

higher number of short bursts consequently means a shorter mean burst duration in purring sounds. This conclusion is clearly not supported by Marshall's (1966) results, which showed similar burst durations but based on a much smaller sample size ($N = 5$). Burst periods are most likely to be shorter in purring than in agonistic sounds in females (Brittinger 1991; this study). Dominant frequencies are lower in male agonistic sounds than in female purring sounds. This may reflect the (not significantly) higher weight in males (mean: 1.3 g; females agonistic: 1.2 g; females prespawning: 1.1 g). Besides burst number, the most conspicuous difference between croaking and purring sounds is that purring sounds were approximately 6 dB lower in sound pressure than female croaking sounds. Thus, prespawning sounds were only half as loud as agonistic sounds. This could mean that females do not contract the relevant muscles fully when generating purring sounds or that the maximum tension of enhanced pectoral fin tendons is reached only in longer sounds.

In summary, female purring sounds were much shorter than agonistic sounds because of fewer bursts, a higher percentage of short bursts and a shorter burst period. This and the lower SPL clearly differentiate these courtship sounds from agonistic sounds.

Context-specific Differences in Fish Sounds

Quantitative analyses of context-specific sound types are rare, although numerous researchers have mentioned that fish produce different sounds during agonistic behaviour and courtship. In particular no descriptions of sex-specific differences in courtship sounds are available. Female fish are apparently always mute during courtship with the exception of *T. vittata*.

Male fish are able to produce up to five different sound types, although the classification of types has often been subjective and, in most species, differences have not been proven statistically. Perhaps the best-studied example for context-specific sound differentiation is the Caribbean pomacentrid *Stegastes partitus*, which produces intense single-pulsed pops during aggressive interactions in both sexes (Myrberg 1972; Ladich & Myrberg 2006). The chirp and long chirp are comparable to the pop in intensity (no SPLs were given), but the growl and grunt have a far lower level. This intensity difference is probably because the former two are used to advertise the territory and attract females, and the latter two are produced when a spawning partner is at the nest and acoustic interception by neighbouring competitive males has to be precluded (Kenyon 1994).

The weakly electric mormyrid fish *Pollimyrus adspersus* produces hoots and pops during aggression in both sexes. When a gravid female visits a male's territory, the male produces moans as well as grunts and growls when she leaves (Crawford 1997). The grunt is the most intense sound produced (no SPLs were given) and obviously used for territory advertisement in general because it is also used during disputes with neighbouring territory owners. In codfish the differentiation between agonistic

and reproductive signals is even less pronounced. The cod, *Gadus morhua* and the related haddock, *Melanogrammus aeglefinus*, produce sounds during courtship that do not differ from agonistic sounds (Brawn 1961; Hawkins & Amorim 2000; Amorim 2006).

While, in the majority of species investigated, male reproductive sound production declines as courtship proceeds and stops during oviposition, several gobiids show the opposite behaviour. In the freshwater goby *Knipowitschia punctatissima* the male is silent when courting outside the nest, but pulse trains are emitted as soon as females enter the nest and for the entire duration of spawning (Lugli et al. 1997). In this species, sounds cannot serve in mate attraction but may synchronize gamete release (Myrberg & Lugli 2006).

What could be the reason for the absence of sound production by female fish (except croaking gouramis) during courtship rituals? Most benthic fish live singly and, because eggs are usually deposited in a male's nest, females have to be attracted to the nest (Myrberg & Lugli 2006). Because females are the ones to be attracted, there is no reason for them to call, particularly in a predator-rich environment. On the other hand, males have to advertise their territory or nest site and attract partners. This, however, does not explain why females do not produce low-intensity courtship or prespawning calls at the nest site. One explanation for the difference between croaking gouramis and most other species might be that *T. vittata* seems to be monogamous. Although females are expelled from the nest vicinity after spawning they may defend the nest site against conspecifics and occasionally pick up fry to bring them back to the nest (personal observation).

Functional Significance of Sound Production

Differences between croaking and purring sounds in *T. vittata* indicate that sounds address different receivers and that different information is communicated. Krebs & Dawkins (1984) argued that two kinds of evolutionary processes, manipulation (mutual exploitation) and cooperation, give rise to different kinds of signals. The first coevolutionary process will lead to exaggeration of signals, paralleled by resistance of the receiver to manipulation. Following the design rules of Bradbury & Vehrencamp (1998), acoustic signals should evolve to become louder and longer in duration. These design rules are realized in loud and long agonistic signals in croaking gouramis. They may function in assessing the fighting ability of the territory owner and subsequently help to chase off invaders (Ladich 1998). In contrast, if there is a benefit from receiving the signal, then less conspicuous signals of lower amplitude should arise from this cooperative process. To minimize costs, such as those that arise when predators are attracted or when time or energy is wasted, the signals should become 'conspiratorial whispers' (Krebs & Dawkins 1984). Courtship signals fall into this category and are typically designed for short-range communication. Purring sounds of female gouramis have a low SPL and short duration and may be regarded

as a typical cooperative signal, most likely designed to help synchronize the spawning activity. Differences in the design of signals produced in agonistic and reproductive contexts in *T. vittatus* are similar to those found in the unrelated damselfish *S. partitus*.

Faint prespawning or spawning sounds that do not serve to attract females to nest sites (but are more likely to synchronize gamete release) probably occur more often in females than in males. More sensitive recording devices may help in looking for and finding such female sounds in other species.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.anbehav.2006.04.014](https://doi.org/10.1016/j.anbehav.2006.04.014).

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