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Both sexes produce sounds in vocal fish species: testing the hypothesis in the pygmy gourami (labyrinth fishes)

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ABSTRACT

In vocal fish species, males possess larger sound-generating organs and signal acoustically with pronounced sex-specific differences. Sound production is known in two out of three species of croaking gouramis (*Trichopsis vittata* and *T. schalleri*). The present study investigates sex-specific differences in sonic organs, vocalizing behaviour and sounds emitted in the third species, the pygmy gourami, *T. pumila*, in order to test the hypothesis that females are able to vocalize despite their less-developed sonic organs, and despite contradictory reports. Croaking gouramis stretch and pluck two enhanced (sonic) pectoral fin tendons during alternate fin beating, resulting in a series of double-pulsed bursts, termed croaking sound. We measured the diameter of the first and second sonic tendon and showed that male tendons were twice as large as in similar-sized females. We also determined the duration of dyadic contests, visual displays, number of sounds and buttings. Sexes differ in all sound characteristics but in no behavioural variable. Male sounds consisted of twice as many bursts, a higher percentage of double-pulsed bursts and a higher burst period. Additionally, male sounds had a lower dominant frequency and a higher sound level. In summary, female pygmy gouramis possessed sonic organs and vocalized in most dyadic contests. The sexual dimorphism in sonic tendons is clearly reflected in sex-specific differences in sound characteristics, but not in agonistic behaviour, supporting the hypothesis that females are vocal.

KEY WORDS: Anabantiformes, Pectoral sound-generating mechanism, Dyadic contests, Dominant frequency, Sound pressure level

INTRODUCTION

Since Aristotle (350 B.C.), we have known that numerous fish are able to produce sounds. Sound production has now been described in numerous fish taxa in different behavioural contexts such as agonistic behaviour, courtship and when handled (see reviews by Fine et al., 1977; Myrberg, 1981; Amorim, 2006; Ladich and Myrberg, 2006; Myrberg and Lugli, 2006). In parallel, our knowledge on sound-generating structures (also called mechanisms or apparatus or sonic organs) is rapidly increasing (Schneider, 1967; Tavolga, 1971; Ladich and Fine, 2006; Ladich and Bass, 2011; Fine and Parmentier, 2015).

Sonic organs in fish are larger in males than in females (Ladich, 2015). This sexual dimorphism is found in mechanisms involving

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the swim bladder such as swim bladder drumming muscles in toadfishes (Batrachoididae: Fine et al., 1990; Bass, 1992; Brantley et al., 1993; Modesto and Canário, 2003), cods (Gadidae: Templeman and Hodder, 1958; Rowe and Hutchings, 2004; Casaretto et al., 2016), cusk-eels (Ophidiidae: Courtenay, 1971; Kéver et al., 2012; Fine et al., 2018) and croakers (Sciaenidae: Fish and Mowbray, 1970; Hill et al., 1987; Ueng et al., 2007). The sexual dimorphism may even increase during the spawning season when swim bladder drumming muscles hypertrophy in males (Connaughton et al., 2000). Sex-specific differences in pectoral sonic mechanisms are known in callichthyid armoured catfishes (Callichthyidae: Pruzsinszky and Ladich, 1998; Hadjiaghai and Ladich, 2015) and labyrinth fishes or gouramis (Osphronemidae). The osphronemid genus *Trichopsis* (three species) evolved a unique pectoral sound-generating mechanism consisting of enlarged pectoral fin muscles, which stretch two enhanced (sonic) fin tendons and snap them over a specialized process of pectoral fin rays, resulting in pulse emission. Sex-specific differences vary considerably within the genus *Trichopsis*, resulting in the notion that females of the smallest species may not be vocal (Kratochvil, 1978, 1980). Interestingly, only females in some representatives of the family Sciaenidae lack sound-producing structures (drumming muscles), but not females in any other fish taxon investigated (Hill et al., 1987; Connaughton et al., 2000).

Male fish often signal acoustically when defending their territories and nest sites, and when courting females (Myrberg, 1981; Ladich and Myrberg, 2006; Myrberg and Lugli, 2006). Males are therefore typically more vocal than females. Nevertheless, investigations in several species revealed that both sexes vocalize during agonistic interactions. This includes cichlids (Cichlidae: Myrberg et al., 1965; Schwarz, 1980; Simões et al., 2008), sculpins (Cottidae: Ladich, 1989), cods (Gadidae: Hawkins and Rasmussen, 1978), pearlfish (Carapidae: Lagardère et al., 2005), damselfish (Pomacentridae: Mann and Lobel, 1998) and gouramis (Ladich, 2007). Only few studies, however, have compared sounds emitted by both sexes under the same standardised conditions. These studies found only small sex-specific differences in sound characteristics of agonistic (or courtship) sounds (Ladich, 2015). Male sounds might differ in temporal properties from female sounds (Lagardère et al., 2005; Ueng et al., 2007; Simões et al., 2008; Colleye et al., 2009) or they might utter different types of sounds (Hadjiaghai and Ladich, 2015). In some species, differences in spectral properties and sound pressure levels were described (dominant frequency: Hadjiaghai and Ladich, 2015; sound pressure level: Ladich, 2007), which reflect differences in sonic organ size. Other studies, however, did not find any sex-specific differences in sound characteristics (Tellechea et al., 2011; Oliveira et al., 2014; Fine and Waybright, 2015).

Within the osphronemid genus *Trichopsis*, sex-specific differences in sound production during dyadic contests have been analysed in detail in the croaking gourami, *T. vittata*, and the

threestripe gourami, *T. schalleri* (Ladich, 2007; Ladich and Schleinzer, 2020), revealing more differences in the latter species. Marshall (1966), without presenting any data, claimed that females in the third species, the pygmy gourami, *T. pumila* (Arnold 1936), produce agonistic sounds similar to those of congenerics. Kratochvil (1980) contradicts this report in his anatomical work, assuming that females are unable to vocalize owing to their less-developed sonic mechanism.

The present study was designed to test the hypothesis that both sexes in vocal fish species produce sounds during agonistic interactions and to disprove the notion that female pygmy gouramis are mute. Sexual dimorphism in sound-generating structure will affect sound characteristics, but not the ability to produce sounds or the vocalizing behaviour. Sonic organ anatomy, dyadic contests and sound properties are analysed in both sexes and subsequently compared in order to test the hypothesis.

MATERIALS AND METHODS
Study species
Seventeen male [body mass (M_b)=0.3–0.61 g] and 20 female (M_b=0.33–0.63 g) pygmy gourami, *T. pumila*, obtained from a local pet supplier, were used for dyadic contests. Agonistic sounds of 12 males and 13 females were analysed. The remaining fish did not produce sounds during dyadic contests.

Fish were kept in two community tanks (110×55×30 cm) equipped with sand, plants and flower pots as hiding places under a 12 h:12 h light:dark cycle. Water was maintained by external filters and the temperature was kept constant at 25±1°C. Fish were primarily fed food flakes five times a week (Tetramin). Sexing of fish was based on the presence of the whitish ovary in females visible against bright light.

Anatomy
The left side of 21 males (M_b=0.28–0.59 g) (Fig. 1) and 13 females (M_b=0.21–0.8 g), previously fixed in 70% ethanol, was dissected. The rays of the left pectoral fin were turned cranially and fixed by a clip (Fig. 1). Then the skin on the base of the fin was carefully removed to render visible the enhanced sonic tendons (ETs). To increase the visibility of the tendons, they were stained with Methylene Blue (Merck, Darmstadt, Germany). The diameters of the first and the second enhanced tendon (ET1, ET2) were measured using a digital microscope system (Leica DMS 1000, Leica Microsystems, Vienna, Austria).

Fish used in anatomical measurements are not identical to those used in the behavioural investigations.

Behaviour and sound recordings
The test tank (50×30×27 cm) was placed on a vibration-isolated table in a walk-in semi-anechoic room constructed as a Faraday cage. The bottom of the tank was covered with sand and contained two half flowerpots. The light:dark cycle and the water temperature were identical to those of the community tanks. The walls inside the test tank, except for the front glass, were lined with acoustically absorbent material. Agonistic behaviour and sounds were recorded using a hydrophone (Brüel & Kjær 8101, Naerum, Denmark; sensitivity −186 dB re. 1 V μPa^{-1}) connected to a microphone power supply (Brüel & Kjær 2804), which was connected to the XLR microphone input of a 4-K video camera (Panasonic HC-X1000, Kadoma, Japan). The entire setup was positioned behind a curtain so that the experimenter could not be seen by the animals. Recordings were controlled via the camera display and a video monitor (Sony PVM 4000, Tokyo, Japan).
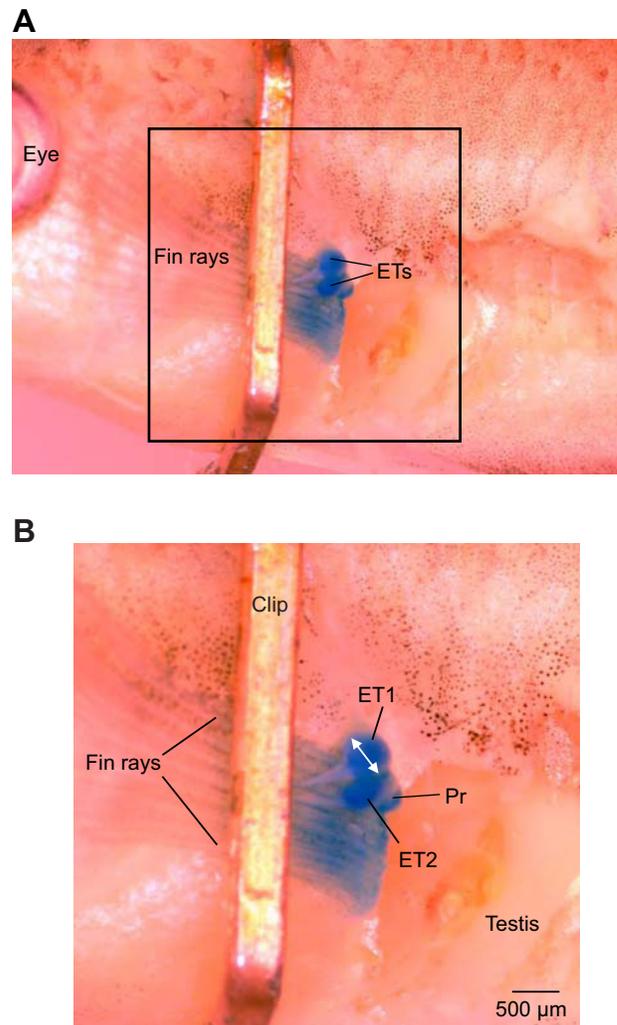
Fig. 1. Views of the left pectoral fin of a male pygmy gourami. Anterior is to the left. Tendons have been stained with Methylene Blue. (A) An overview of the cranial part of the fish for orientation purposes. Pectoral fin rays are turned cranially and fixed by a clip to render visible the enhanced sonic tendon (ETs). The black rectangle in A is enlarged in B. (B) The first and second enhanced tendons (ET1, ET2) are visible. The measurement of the tendon diameter is illustrated by a white double-headed arrow. Pr, enhanced basal process of the second fin ray. During vocalization, sonic tendons are stretched and snapped over this process, producing a double-pulsed burst.

Prior to experiments, two fish of the same sex were isolated for 5 days under conditions similar to community tanks to reduce dominance effects. After the isolation period, both fish were introduced to the test tank and isolated for another day by a plastic plate, which separated the left and right halves of the tank.

Sound pressure level measurements
Sound pressure levels (SPL LAFmax, broadband A frequency weighting, RMS Fast time weighting) were recorded using a sound level meter (Brüel & Kjær 2250) connected to the second output of the microphone power supply. The equipment was calibrated with the hydrophone calibrator (Brüel & Kjær 4229). All dB values were referenced to 1 μPa.

Because of the differing distance between the fish and the hydrophone, the test tank was divided into 50 sectors (5×5 cm) by a grid applied to the front glass of the aquarium, and the sector in which fish produced agonistic sounds was noted (see fig. 2 in

Ladich and Schleinzer, 2020). To compensate for different distances between the hydrophone and the croaking fish, a correction factor was calculated (Ladich, 2007). For this correction factor, a typical pygmy gourami croak was played back at a constant level from a small loudspeaker (Fuji 7G06) in the centre of each of the 50 sectors and the SPL noted. The SPL differences between the sector nearest to the hydrophone (10 cm away) and all other sectors were calculated and added to the SPL values measured when the fish produced sounds in a particular sector. This distance-dependent correction yielded comparable absolute SPLs for each sound produced.

Behavioural analysis
Behaviour was analysed using Sony Vegas Pro 13.0 (Sony Creative Software Inc., Middleton, WI, USA).

The following four variables were determined. (1) Contest duration: the time between the onset of the first and the end of the last agonistic behaviour including breaks, e.g. for air-breathing. The end of a contest was defined as the moment when one fish gave up and fled, and the other clearly emerged as winner. (2) Lateral display duration: lateral displays (LD) consisted of erecting unpaired fins, head-to-tail circling and sound production. Such fight sequences were interrupted by air-breathing. LD duration constitutes the sum of the duration of all LD sequences excluding breaks. (3) Number of sounds: constitutes the number of croaking sounds produced by both fish during a dyadic contest. Sounds produced after the contest ended, i.e. by the winner only, were not included. (4) Number of buttings: buttings are thrusts of the head to the body of the other fish. The number constitutes all buttings of one opponent towards the other during one contest.

Sound analysis
Sounds were rendered (44.1 kHz, 16 bit) to WAV format using Sony Vegas Pro 13.0 and subsequently analysed using Cool Edit 2000 (Syntrillium Software Corporation, Phoenix, AZ, USA) and S_TOOLS-STX 3.7.8 (Acoustics Research Institute, Austrian Academy of Sciences, Vienna, Austria).

The following four sound characteristics were determined for each individual (Fig. 2). (1) Number of bursts: the total number of double-pulsed and single-pulsed bursts per croaking sound.
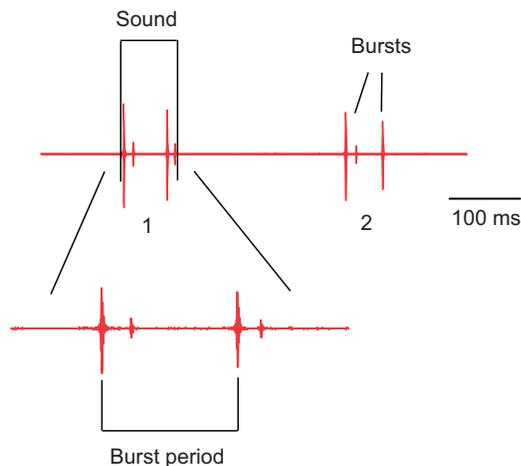
Fig. 2. Oscillogram of two male croaking sounds consisting of two bursts each and an expansion of the second sound, illustrating the sound characteristics analysed. The first croaking sound consists of two double-pulsed bursts and the second of a double-pulsed burst and a single-pulsed burst.

(2) Percentage of short bursts within a sound. (3) Burst period: the time between the maximum peaks of two successive bursts within a sound. (4) Dominant frequency: the frequency of highest spectral level in a cepstrum-smoothed power spectrum (Ladich, 2007; Ladich and Schleinzer, 2020) (STX settings: bandwidth 5 Hz, overlap 75%, number of coefficients: 30–200, Hanning window). Frequencies were not analysed above 3.5 kHz to avoid the resonance frequencies of our small tank, which were above this frequency according to Akamatsu et al. (2002).

Statistical analysis
In order to obtain a minimum number of dyadic contests per sex, some fish were used twice (females: $n=8$; males: $n=1$), but two individual fish were never paired twice. Fourteen female–female contests and nine male–male contests were analysed. Only sounds recorded in the first contest of an individual were used for sound analyses. Up to 18 sounds were analysed for each female and up to 17 sounds for each male. Means of each sound characteristic (number of bursts, percentage of short bursts, burst period, dominant frequency and SPL) were calculated for each individual and used for further analyses.

Variables of both sexes were tested for normality using a Shapiro–Wilk test. When data were normally distributed, an independent-samples t-test (in all other cases Mann–Whitney U-test) was chosen to calculate differences between sexes. Burst period was normally distributed for both sexes, but given the small number of samples in females, a non-parametric test was applied to compare sexes. A paired-sample t-test was used to compare ET diameters within sexes. Relationships between body mass and sound characteristics were calculated using a Pearson's correlation coefficient, because all data were normally distributed. It was not possible to correlate tendon size and sound characteristics, because different fish were used for both analyses.

All statistical tests were run using IBM SPSS Statistics Version 26. The significance level was set at $P\leq0.05$.

Ethical considerations
Agonistic behaviour in pygmy gouramis consisted of visual and acoustic signalling and butting behaviour. The latter included physical contact between opponents, but injuries were never observed in this study. All applicable national and institutional guidelines for the care and use of animals were followed (permit numbers BMWF-66.006/0038-II/3b/2013 and BMWFW-66.006/0011-WF/II/3b/2014).

RESULTS
Anatomy
Twenty out of 21 males and 10 out of 13 females possessed two enhanced sonic tendons, the remaining individuals only one (Fig. 1, Table 1). The diameter of the first (ET1) and the second enhanced tendon (ET2) was on average twice as large in males as in females (independent-samples t-test; ET1: $t=6.155$, d.f.=28, $P<0.001$; ET2: $t=5.926$, d.f.=28, $P<0.001$) (Fig. 3). Within both sexes, the diameter of ET1 was approximately 1.5 times larger than that of ET2 (paired-sample t-test; females: $t=3.351$, d.f.=9, $P<0.01$; males: $t=12.405$, d.f.=19, $P<0.01$) (Fig. 3). The ratio between ET1 and ET2 diameters was similar in both sexes (U-test, $U=89$, $N=30$, $P=0.628$).

Dyadic contests
Agonistic behaviour started shortly after removal of the plastic aquarium divider when one fish detected the other visually. They approached each other and started lateral displaying, which

Table 1. Mean **b**ody **mass**, diameter of the first and of the second enhanced tendon (ET1 and ET2), and the ratio between ET1 and ET2 of female and male pygmy gouramis

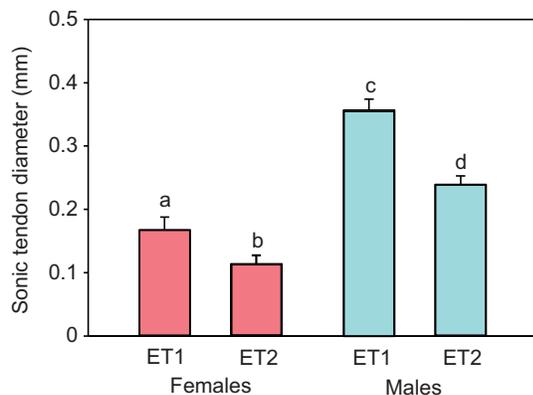| Variable	Females	Males
Body mass (g)	0.43±0.06 (0.21–0.78; 10)	0.42±0.02 (0.28–0.59; 20)
ET1 (mm)	0.17±0.02 (0.11–0.30; 10)	0.35±0.02 (0.19–0.52; 20)
ET2 (mm)	0.11±0.01 (0.06–0.20; 10)	0.24±0.01 (0.12–0.34; 20)
Ratio ET1/ET2	1.54±0.15 (1.04–2.73; 10)	1.50±0.04 (1.17–1.92; 20)

Values are means±s.e.m. (range; number of animals measured).
Males and females did not differ in body mass (independent-samples t-test: $t=-0.047$, d.f.=13.37, $P=0.963$). Thus, the sex-specific difference in ET diameters was not due to differences in mass.

consisted of spreading of unpaired fins, head-to-tail circling and sound production. Croaking sounds were produced by rapid pectoral fin beating, which resulted in shaking of the fish's body. Initially, contests consisted primarily of lateral displaying, which gradually decreased while the number of buttings increased. As soon as butting behaviour started, fish stopped producing acoustical signals. Butting behaviour was observed in 20 out of 23 contests.

No sex-specific differences were observed in agonistic behaviour (Table 2). Dyadic contests lasted for approximately 8 min and did not differ between sexes either in total duration (U-test: $U=60.5$, $N=23$, $P=0.877$) or in duration of lateral displays (t-test: $t=0.234$, d.f.=21, $P=0.818$). Furthermore, males did not vocalize more than females (U-test: $U=48.5$, $N=23$, $P=0.369$) nor did sexes differ in the number of buttings (U-test: $U=78$, $N=23$, $P=0.369$).

Sound characteristics and differences between sexes
Croaking sounds of *T. pumila* were built up of one to four bursts, which were either double-pulsed or single-pulsed (Figs 2, 4). All sound characteristics differed between sexes (Table 3). Male croaking sounds consisted of approximately twice as many bursts as female sounds, which were built up of one or two bursts (U-test: $U=12$, $N=25$, $P<0.001$; Fig. 5A). Approximately 20% of male bursts were single-pulsed, whereas the percentage was more than four times higher in females (U-test: $U=141$, $N=25$, $P<0.001$; Fig. 5B). The burst period was longer in male than in female sounds (U-test: $U=3$, $N=14$, $P<0.05$; Fig. 5C). Male sounds were significantly lower in dominant frequency (independent-samples t-test: $t=-4.959$, d.f.=23, $P<0.001$; Fig. 5D) and had a significantly

Table 2. Mea**n** **c**ontest duration, lateral display duration, number of sounds and number of buttings in female–female and male–male contests

Variable	Females	Males
Contest duration (s)	484±135 (21–1608; 14)	493±172 (21–1710; 9)
Lateral display duration (s)	89.3±12.9 (11–165; 14)	95.3±25.5 (10–204; 9)
Sound number (n)	5.8±1.75 (0–24; 14)	9.7±3.45 (0–28; 9)
Butting number (n)	24.1±10.15 (1–141; 14)	13.7±6.16 (0–55; 9)

Values are means±s.e.m. (range; number of animals measured).

higher sound pressure level (LAF) than female sounds (independent-samples t-test: $t=7.152$, d.f.=23, $P<0.001$; Fig. 5E).

Vocalizing males and females did not differ in body mass (independent-samples t-test: $t=1.045$, d.f.=23, $P=0.307$). Thus, differences in sound characteristics were not due to any difference in size.
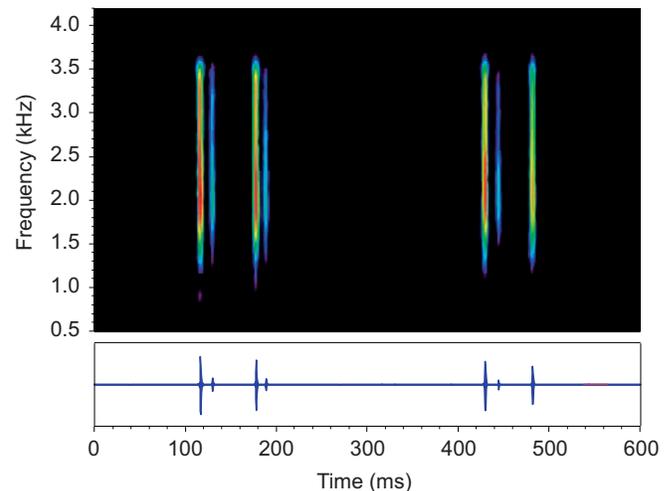
Sound characteristics and body size
In males, body mass was negatively correlated with dominant frequency ($r=-0.505$, $N=12$, $P<0.05$, one-tailed; Fig. 6A) and positively correlated with SPL ($r=0.544$, $N=12$, $P<0.05$, one-tailed; Fig. 6B). Neither dominant frequency ($r=0.111$, $N=13$, $P=0.359$, one-tailed) nor SPL ($r=0.387$, $N=13$, $P=0.095$, one-tailed) was correlated with body mass in females. Burst period did not correlate with body mass in either sex (males: $r=-0.258$, $N=11$, $P=0.443$; females: $r=0.498$, $N=3$, $P=0.498$).

DISCUSSION
Sound production within the labyrinth fish genus *Trichopsis* has been described in both sexes of *T. vittata* and *T. schalleri* (Ladich, 2007; Ladich and Schleinzer, 2020), but remained questionable in females of the smallest species *T. pumila* owing to contradictory reports (Marshall, 1966; Kratochvil, 1980). The present study provides evidence that most female pygmy gouramis possess sound-producing structures that enable them to vocalize during agonistic interactions, similar to males, supporting the hypothesis that female fish are vocal.

Sex-specific differences in sonic organs
The pygmy gourami is the first vocal osphronemid in which sex-specific differences in sonic structures have been measured and

Fig. 3. Mean (+s.e.m.) diameter of the first and second enhanced tendon (ET1, ET2) of female and male pygmy gouramis. Different letters above bars indicate significant differences in sonic tendon diameters within sexes (ET1 versus ET2) and between sexes (female ET1 versus male ET1; female ET2 versus male ET2). (females: $N=10$; males: $N=20$).

Fig. 4. Sonagram (above) and waveform (below) of two croaking sound produced by a male pygmy gourami. For details see Fig. 2. Sampling frequency 44.1 kHz, filter bandwidth 100 Hz, 75% overlap, Hanning window.

Table 3. Mean body mass, number of bursts, percentage of short bursts within a sound, burst period, dominant frequency and sound pressure level (LAF) of female and male *T. pumila*

Variable	Females	Males
Body weight (g)	0.45±0.02 (0.33–0.55; 13)	0.48±0.02 (0.30–0.61; 12)
Burst number	1.12±0.06 (1–1.7; 13)	2.12±0.19 (1–3; 12)
Percentage of short bursts (%)	93.62±4.51 (47.1–100; 13)	21.25±10.78 (0–100; 12)
Burst period (ms)	44.88±0.33 (44–45; 3)	54.96±1.71 (42.4–61.9; 11)
Dominant frequency (Hz)	2283±31 (2080–2412; 13)	2089±23 (1954–2234; 12)
Sound pressure level (dB re 1 µPa)	98.8±1.3 (91.9–107.6; 13)	113.5±1.6 (100.4–121.7; 12)

Values are means±s.e.m. (range; number of animals measured).

compared statistically. Sonic tendons are twice as large in males as in females, whereas no difference was recorded between sexes in size ratios between the first and second enhanced tendon. In *T. vittata*, sex-specific differences were only qualitatively described. Kratochvil (1985) estimated that sonic organs are approximately one-third smaller in females than in males based on dissections. A sexual dimorphism was also postulated for the third species, *T. schalleri*, although anatomical data are lacking (Ladich and Schleinzer, 2020).

Sonic organs are larger in males than females in most vocal fish taxa; rarely does one sex possess additional structures or do females lack any sound-generating structures. In cusk-eels (Ophidiidae), only males may possess a swim bladder ossification (rocker bone) (Courtenay, 1971; Kéver et al., 2012). In the majority of taxa

possessing sonic organs, quantitative differences were reported, such as in several toadfish species (oyster toadfish, *Opsanus tau*: Fine, 1975; Fine et al., 1990; Lusitanian toadfish, *Halobatrachus didactylus*: Modesto and Canário, 2003; plainfin midshipman, *Porichthys notatus*: Brantley et al., 1993; Brantley and Bass, 1994) and cods (haddock, *Melangrammus aeglefinus*: Templeman and Hodder, 1958; Casaretto et al., 2016). Within sciaenids (drums or croakers), many species possess sexually dimorphic swim bladder muscles such as the Atlantic croaker, *Micropogonias undulates*, or the Japanese meagre, *Argyrosomus japonicus* (Hill et al., 1987; Ueng et al., 2007), whereas in some species such as in the squeteague, *Cynoscion regalis*, and silver perch, *Bairdiella chrysoura* (Fish and Mowbray, 1970), females have no swim bladder muscles. It is entirely unexplained why females of only a
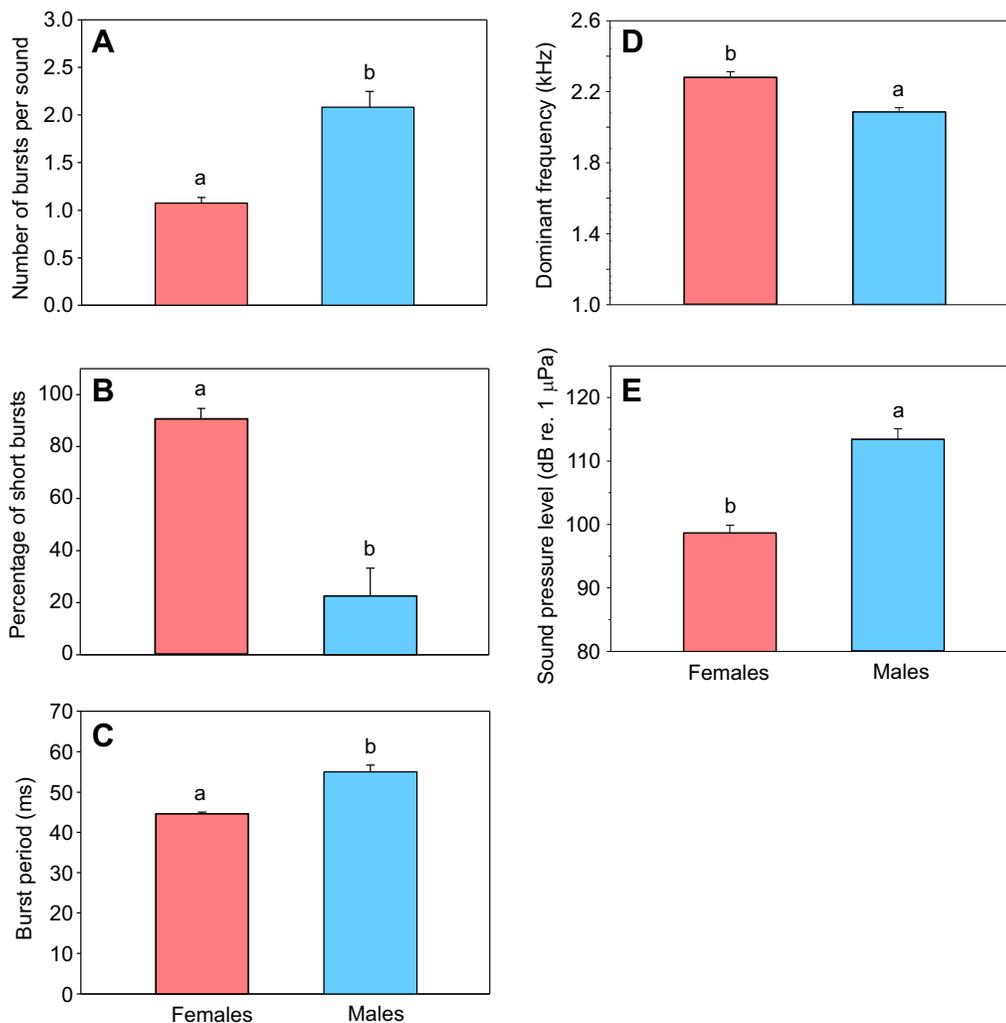
Fig. 5. Mean (+s.e.m.) characteristics of agonistic sound produced by female (*N*=13) and male (*N*=12) pygmy gouramis. (A) Number of bursts, (B) percentage of short bursts, (C) burst period (females: *N*=3; males: *N*=11), (D) dominant frequency and (E) sound pressure level. Different letters above bars indicate significant differences between sexes.
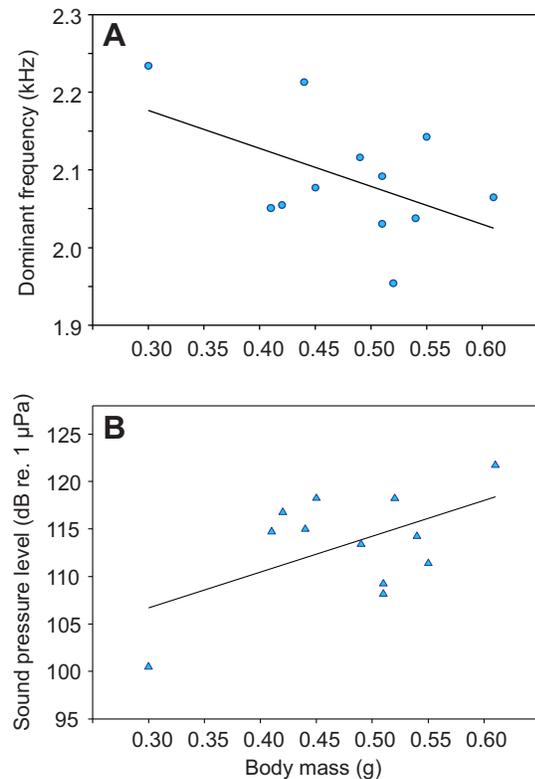
Fig. 6. Relationship between body mass and sound characteristics in male pygmy gouramis. Regression equations: (A) Dominant frequency=2.323–body mass×0.488. (B) Sound pressure level=95.4+body mass×37.7. (*N*=12).

few species within a single teleost family did not develop sonic structures when males did. Except for sciaenids, females possess sonic organs in all other teleost taxa when males are vocal. The present study demonstrates that pygmy gouramis are no exception to this rule. Females possess sonic structures that enable them to generate sounds.

Sex-specific differences in agonistic behaviour

Sounds are typically produced by both sexes during agonistic interactions, including stress or disturbance situations when fish are hand-held. This enables intersexual comparisons under similar circumstances. In the majority of vocal fish species, only males vocalize during reproductive behaviour, making comparisons between sexes difficult. Only in seahorses do males and females produce click sounds during courtship (Oliveira et al., 2014).

Sound production during male–male and female–female dyadic contests have been described in representatives of numerous fish families, but mostly without detailed behavioural analysis. The current detailed study revealed no differences between sexes in the pygmy gourami with regard to intensity of agonistic encounters and the amount of visual and acoustic signalling, thus in agreement with the hypothesis that both sexes are vocal in all representatives of the genus *Trichopsis*. No sex-specific differences were mentioned either by Marshall (1966) or Ladich (2007) in the congeneric *T. vittata*. Among gadids, various sounds were produced by male and female Atlantic cod, *Gadus morhua*, and *M. aeglefinus* outside the breeding season during aggressive and defensive behaviour (Brawn, 1961; Hawkins and Rasmussen, 1978). Among toadfishes (Batrachoididae), both sexes of *O. tau* are known to emit grunts during agonistic behaviour (Gray and Winn, 1961; Maruska and

Mensinger, 2009). In the family Cottidae, male and female bullhead, *Cottus gobio*, produced two types of sounds during threat displays with no obvious difference between sexes in vocalizing behaviour (Ladich, 1989, 1990). Among cichlids, both sexes of the jewelfish, *Hemichromis bimaculatus*, and the flier cichlid, *Archocentrus centrachus*, vocalized before attacking an intruder or when behaving aggressively towards each other (Myrberg et al., 1965; Schwarz, 1980).

Differences between sexes in agonistic behaviour have been reported only in the callichthyid catfish *Megalechis thoracata* (Hadjiaghai and Ladich, 2015). While males uttered thumps during threatening displays and barks mostly during approaching and swimming, females, in contrast, emitted crackles mainly during chasing behaviour.

Specific differences in vocalizing behaviour can be investigated only in fish eliciting a certain level of aggressiveness in both sexes, which is particularly the case in territorial species. While staged contests were possible in all representatives of the genus *Trichopsis*, because both sexes behave aggressively towards intruders, this approach is impossible in non-territorial species such as representatives of the callichthyid genus *Corydoras* (Pruzsinszky and Ladich, 1998). Hand-held experimental conditions may be the only way to study differences in sound production between sexes under standardised conditions in several species. Bosher et al. (2006) argue that disturbance calls may function in deterring predators and should thus be equally useful for both sexes.

Sex-specific differences in sound characteristics

In the pygmy gourami, all sound properties differed between males and similar-sized females. Male sounds were longer in duration (higher number of double-pulsed bursts, longer burst period), lower in dominant frequency and higher in SPL. Four out of five acoustic differences can be explained by the fact that female sonic organs are considerably less developed than in males. Male sonic tendons are apparently stretched more intensely by larger pectoral fin muscles, which then results in higher SPLs when pulled over the bony process of the second fin ray (Kratochvil, 1980). Furthermore, stretching of larger sonic tendons by larger muscles will more often result in the production of a sound pulse and subsequently the emission of double-pulsed bursts than in females, which emit more single-pulsed bursts. The smaller percentage of double-pulsed bursts in females can, in addition, be explained by a small or even entirely lacking second enhanced tendon. Larger sonic mechanisms in males may take somewhat longer to be beaten, which could explain the longer burst period, namely the time between beating both pectoral fins alternately. Finally, larger sonic tendons in males help explain why the dominant frequency was lower than in females. This parallels guitar strings, where a thicker string of the same length has a lower fundamental frequency.

The large number of differences in sound characteristics in the pygmy gourami contrasts with the small number in *T. vittata*, the largest species within the genus *Trichopsis*, where sexes differ only in SPL (Ladich, 2007). Moreover, the difference in SPL is considerably smaller in *T. vittata* than in the pygmy gourami (4 dB versus 14 dB). This may reflect the weaker sexual dimorphism in *T. vittata* versus the pygmy gourami (Kratochvil, 1980, 1985). Interestingly, the third species *T. schalleri* takes up an intermediate position in body size and in number of acoustic differences (Ladich and Schleinzer, 2020), indicating that the so far undescribed sexual dimorphism in the sound-generating mechanism in *T. schalleri* is stronger than in *T. vittata*, but weaker than in the pygmy gourami.

In general, only a few studies recorded sounds in males and females in the same behavioural context, allowing a context-independent comparison between sexes. In all other studies, in particular when the behavioural contexts differ or are unknown, no such comparison will be possible. For example, agonistic and courtship sounds of female *T. vittata* differ in four out of five sound characteristics, whereas they differ in only one acoustic variable from male agonistic sounds (SPL; Ladich, 2007). A recent study in *M. aeglefinus* revealed that female sounds differ in three sound properties from males', but making a comparison between sexes is difficult because sounds were emitted in different behavioural contexts (Casaretto et al., 2016). Differences in agonistic sounds in the skunk clownfish, *Amphiprion akallopisos*, are mainly due to differences in body size between sexes: females were larger than males (Colleye et al., 2009). Ueng et al. (2007) found sex-specific differences in pre-spawning advertisement calls in the sciaenid *A. japonicus* in single-sex groups, but the behavioural observations were insufficiently detailed to support the notion that sounds were recorded in the same context in both sexes. A 'tight relationship between morphology of the sonic apparatus and sound characteristics' was stated by Kéver et al. (2012) for the cusk-eel *Ophidion rochei*. The lack of behavioural observations precludes determining whether sounds were produced in the same behavioural contexts and whether differences in sound properties are entirely based on differences between sexes.

Vocalizations were seldom unequivocally recorded in the same context in both sexes, such as dyadic contests, courtship or distress (disturbance) situations. Differences in sound properties were reported in all representatives of the genus *Trichopsis* (see above discussion) and by Simões et al. (2008) in the cichlid zebra mbuna, *Maylandia zebra*, in which sexes differed in two out of three sound characteristics. Interestingly, distress (disturbance) sounds emitted under hand-held conditions tended to be more similar between sexes than sounds emitted during dyadic contests despite sexual dimorphism of sonic organs (toadfish, *O. tau*: Fine and Waybright, 2015; black drum, *Pogonias cromis*: Tellechea et al., 2011) Similarly, low-frequency growling sounds produced by the longsnout seahorse, *Hippocampus reidi*, when hand-held did not differ between sexes (Oliveira et al., 2014), although clicks emitted during courtship differed somewhat: male clicks were louder than females' (12 dB), but similar in duration and dominant frequency. This difference between behavioural contexts indicates that researchers should, wherever possible, record sounds during social interactions when comparing sexes.

Correlations between sound characteristics and size

In general, the dominant frequency of pulsed sounds is negatively correlated with body size in fish and may convey reliable information about the fighting ability of opponents or fitness of mates (Myrberg et al., 1986; Ladich, 1998). A negative relationship between dominant frequency and body mass was found in both sexes of *T. vittata* and *T. schalleri* as well as in male *T. pumila* (Ladich et al., 1992; Ladich and Maiditsch, 2018; Ladich and Schleinzer, 2020). The lack of such a relationship in female pygmy gourami could be due to the small size range tested here or to their small sonic organs. Perhaps for similar reasons, no such relationship was found between click sounds and size in seahorses (Oliveira et al., 2014). A negative relationship between size and main sound frequencies is known in representatives of several bony fish families such as pomacentrids (bicolor damselfish, *Stegastes partitus*: Myrberg et al., 1993; Hawaiian dascyllus, *Dascyllus albisella*: Lobel and Mann, 1995; clownfish *A. akallopisos*: Colleye et al.,

2009), sciaenids (*P. cromis*: Tellechea et al., 2011; *C. regalis*: Connaughton et al., 2000; whitemouth croaker, *Micropogonias furnieri*: Tellechea et al., 2010) and catfish (peppered corydoras, *Corydoras paleatus*: Pruzsinsky and Ladich, 1998). Such a correlation is typically lacking in species producing drumming sounds, because their fundamental frequency is based on the contraction rate of drumming muscles, which is primarily controlled by central pattern generators and thus ambient temperature (Bass et al., 2015; Fine and Waybright, 2015; Ladich, 2018).

Relationships between body size and SPL were less often described in fish. Within the genus *Trichopsis*, positive correlations were found in male pygmy gouramis and female *T. schalleri*, but not in adult *T. vittata* (Ladich et al., 1992; Ladich and Schleinzer, 2020; Ladich and Maiditsch, 2018). Beyond *T. vittata*, in the mochokid catfish *Synodontis schoutedeni* and in the toadfish *H. didactylus*, SPL increases during ontogeny (Henglmüller and Ladich, 1999; Vasconcelos and Ladich, 2008; Lechner et al., 2010). Moreover, SPL increased with size in the sciaenid *C. regalis* as well as in the toadfish *O. tau* up to 200 g before levelling off (Connaughton et al., 2000; Fine and Waybright, 2015).

Temporal properties such as pulse duration or pulse periods typically increase with body size. The lack of a relationship between burst period and mass in the present study is in contrast to a prior study showing a significant correlation in male pygmy gourami (Ladich et al., 1992). Interestingly, no correlation was found in other species or sex except in female *T. schalleri* (Ladich and Schleinzer, 2020). Positive correlations were occasionally observed between pulse duration or interval and size, for example in the clownfish *A. akallopisos* (Colleye et al., 2009).

Conclusions

The osphronemid genus *Trichopsis* represents the first fish genus in which sex-specific differences in sound production have been analysed in the same behavioural context in all representatives. The present study clearly demonstrates that despite considerable differences in the size of female versus male sonic organs, females are vocal in all representatives of this genus. This observation supports the hypothesis that both sexes in sound-producing fish are able to vocalize, independent of the sexual dimorphism of sonic organs (but see exception in sciaenids). The functional significance of female acoustic signalling is less well understood, partly because researchers focus more on male sound production during territory maintenance and courtship. Nevertheless, females may vocalize similarly to males when defending resources (territories, nest sites) or occasionally during spawning.

Data availability
Data are available from the University of Vienna Phaidra repository: http://phaidra.univie.ac.at/o:1080518

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