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Sound Characteristics and Outcome of Contests in Male Croaking Gouramis (Teleostei)

Friedrich Ladich

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Abstract

A correlative study using similar-sized males of the croaking gourami *Trichopsis vittata* was carried out to investigate whether sound characteristics influenced winning and if relative fighting ability was assessed by acoustic signals. Pair-wise contests between males were decided using lateral displays (LD) and vocalization in 26 cases, whereas 66 fights escalated to the frontal display (FD) phase. Physical fighting (mouth wrestling) and injuries were rarely observed in this species. Winners were generally larger than their opponents, and this effect was more pronounced in non-escalated than in escalated contests. Sounds of fight winners had a higher sound pressure level and also a lower dominant frequency. Neither number of acoustic signals nor duration of lateral and frontal displays were predictors of contest outcome. Acoustic measures were highly correlated to body weight. These results indicate that traits correlated with RHP (such as sound pressure level and dominant frequency) were predictors of the outcome, while traits not correlated with size (such as number and duration of displays) did not influence winning. In accordance with the main prediction of assessment models, the contest duration (cost) increased with the decrease in asymmetry of body length as well as sound pressure level. No such relationships were found for weight and dominant frequencies in LD- and FD-contests.

The present study indicates that morphological and sound characteristics influence winning in fish. Moreover, the results suggest that croaking gouramis settle conflicts without damaging combats by assessing asymmetries in different components of RHP such as body weight and length, which may reliably be signalled by acoustic and visual assessment signals.

Friedrich Ladich, Institute of Zoology, Althanstraße 14, 1090 Vienna, Austria. E-mail: friedrich.-ladich@univie.ac.at

Introduction

Animals competing for a resource often resolve conflicts without escalated fighting, thus avoiding inflicting serious injuries or death. This is achieved through the use of assessment strategies, whereby the opponents gain information about their fighting ability through assessment signals (Maynard Smith & Price 1973; Parker & Rubenstein 1981; Enquist & Leimar 1990; Hack 1997).

Sounds are often emitted during agonistic encounters in different animal groups (Clutton-Brock et al. 1979; Arak 1983; Ladich 1990, 1997a; Greenfield &

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Minckley 1993). However, evidence is sparse that certain acoustic features of calls influence winning and contribute to the assessment of a rival's fighting ability. Assessment of opponent's size based on call dominant frequency is known in frogs and toads (Davies & Halliday 1978; Robertson 1986; Wagner 1989). In red deer, roaring rate is used in assessing fighting ability of opponents (Clutten-Brock & Albon 1979).

Vocalization during agonistic behaviour is widespread in fishes. A recent survey listed representatives of 40 families of bony fishes, although this number is likely to be much higher (Ladich 1997a). Data on the functional significance of calling during agonistic behaviour are sparse in fish and apparently no species decides contests by sounds alone. This might be explained by the predominance of short-range calls in fishes, which are regularly accompanied by visual displays and perhaps tactile stimuli (Fine et al. 1977; Ladich 1989, 1997a; Myrberg 1981). Correlative studies showed that opponents were more effectively repelled when sounds were uttered (Valinsky & Rigley 1981; Schuster 1986; Ladich et al. 1992b). Responses to playbacks of sounds in the absence of other cues were observed in courtship calls (Ibara et al. 1983; Myrberg et al. 1986) but not in aggressive sounds. If mirror images or fish in neighbouring tanks were presented (Schwarz 1974; Stout 1975; Jeppesen 1981), playbacks resulted in changes in the duration of lateral displays. In none of these cases is it known whether sound characteristics influence the behaviour of conspecifics. The ability to differentiate between different numbers of sounds and different sound frequencies and intensities has been demonstrated for a few species using behavioural (Stout 1975; Myrberg & Riggio 1985; Myrberg et al. 1986) or classical conditioning experiments (for a review see Fay 1988).

In a previous study it was shown that soniferous male croaking gouramis *Trichopsis vittata* won more contests than muted individuals, provided that contestants were closely matched for size (Ladich et al. 1992b). If the winner was, on average, 120% the weight of its opponent, size was the only factor determining the outcome of the encounters.

A correlative investigation was conducted because *T. vittata* did not react to sound playbacks. My approach was to create symmetrical contests with regard to sex and residency and to analyse: (1) to what extent morphological, acoustic and behavioural variables influence fighting success; (2) if the acoustic traits are related to morphological measures and thus to the 'resource holding potential' (RHP sensu Maynard Smith & Parker 1976); and (3) if fish use size measures and sound characteristics to assess the opponent's fighting ability. Assessment models predict that decreased asymmetry between opponents in RHP, assuming equal motivation to win, results in more costly contests (Enquist & Leimar 1983; Enquist et al. 1990). One measure for the costs of fighting is the duration of agonistic actions (Enquist et al. 1990). Therefore, asymmetries in various components of the RHP were correlated to contest durations.

Because the intention was to study the significance of sound characteristics, fish had to be closely matched in size and only fights in which both contestants vocalized were analysed.

Materials and Methods

One-hundred and eighty-four male *T. vittata* purchased from local aquarium shops or reared in the laboratory were used during this study. They were initially kept in several 100–250 l community tanks. Contestants were always taken from different community tanks. After 6 d of isolation in a 20 l tank, two fish were chosen and placed in either half of a 50 × 27 × 30 cm test aquarium divided by an opaque plastic partition. All tanks contained a sand substrate 2–3 cm deep, plants and a flower pot half. The temperature was kept at 28°C and a 12 h/12 h light/dark cycle was maintained. Fish were fed daily on *Tubifex* worms and *Daphnia*. They were between 42.7 mm and 63.3 mm in total body length and weighed between 0.67 and 1.8 g when tested.

The test was started by removing the plastic partition in the test aquarium. All filming took place from behind a curtain, so that the operator could not be seen by the animals. Fish were measured and weighed after a fight.

Acoustic and Video Equipment

Sound production was monitored with a Brüel & Kjaer 8101 hydrophone and 2804 power supply and was recorded on a HiFi-S-VHS VCR (JVC HRD 4700 EG). The hydrophone was placed in the middle of the rear wall of the test tank. Behaviour was filmed using a Sony CCD V800 video camera recorder and recorded in parallel on the S-VHS VCR. Thus, HiFi-audio, S-VHS video signals and time code were stored synchronously on videotapes.

Test aquaria were lined with acoustically absorbent material (closed-cell foam) to reduce resonances and reflections.

Acoustic Analysis

The number of croaks and dominant frequency were determined using S-Tools, the Integrated Workstation for Acoustics, Speech and Signal processing, developed by the Austrian Academy of Sciences, Department of Sound Research, Vienna.

Number of croaks

Croaks consisted of a series of double pulses generated by the pectoral fins (Kratochvil 1978; Ladich et al. 1992a). The sound-producing individual could easily be recognized by rapid pectoral fin beating and by individual waveform characteristics such as small differences in pulse periods.

Dominant frequency

Sampling frequency was always 16 kHz. Dominant frequencies of calls were measured using cepstrum-smoothed spectra (Noll 1967). Power spectra were calculated using fast Fourier transform (FFT). The highest peak of the smoothed curve is a better representation of the energy distribution than the highest peak energy of the power spectra. The main frequency of calls was concentrated between

1000 and 1800 Hz. Frequencies above 4 kHz were not analysed because they are thought to be outside the hearing range of *T. vittata* (Ladich & Yan 1998). Tank-specific resonance frequencies above 4 kHz were also avoided by this method. Measurements were made on the first 6–8 calls of each fish and means were calculated.

Sound pressure level

Sound pressure level (SPL) was measured in decibels (dB) from the audio level meter of the HiFi-VCR. Thus, no absolute sound pressure measurements were possible and only a relative difference between opponents was calculated. Because fish circled during vocalization and the distance to the hydrophone was continuously changing, only SPLs of croaks of opponents following each other within 1–2 s were used.

Those vocalizations at the beginning of a fighting bout were usually taken. SPLs from up to 12 calls of each fish were measured and the means calculated separately for each fish.

Behavioural Analysis

Agonistic encounters between male *T. vittata* consist of several behavioural elements, occurring in two phases: lateral display phase and frontal display phase. Fights which were decided during the lateral display phase are termed lateral display (LD) contests or non-escalated contests. Fights ending during the frontal display phase are termed escalated or frontal display (FD) contests. The frontal display phase usually followed the former and was seldom interrupted by lateral displays.

Lateral display phase

Fish typically assumed a head-to-tail position during lateral display. Unpaired fins (dorsal, caudal and anal) were extended fully and fish usually circled around one another and vocalized. At very short distances, dorsal and anal fins were bent slightly toward the opponent. Undulations of the body and fins sometimes changed into tail-beating. Total lateral display time was measured.

Frontal display phase

Fish protruded their mouths toward each other and usually pivoted ≈ 45° around the longitudinal axis. The tails of both gouramis were usually bent to one side, with the tail of one fish extending in the opposite direction from the tail of the other. FD was frequently interrupted by mouth bites. Because bites were very short it was not possible to determine which male was the aggressor. Frontal display was always performed simultaneously by both contestants and therefore no statistical difference was calculated.

Duration of contests

Contest duration constituted the sum of the durations of the lateral and frontal displays (and mouth locking) including short breaks pausing for airbreathing.

Statistics and Asymmetries

Total body length was strongly correlated to body mass ($r = 0.55$, $p < 0.001$, $n = 92$) and standard length ($r = 0.60$, $p < 0.001$, $n = 92$). Total body length appeared to be the most relevant measure of size for visually assessing the opponent's fighting ability because it also included unpaired fins which were always erected during lateral display. Furthermore there was no physical contact between contestants in LD-contests and contact was limited to short mouth bites in FD-contests. Body weight was also analysed because it was thought to have a greater influence on sound variables such as dominant frequency and SPL.

Differences between winners and losers were tested using the Wilcoxon matched pairs signed-ranks test. The relationships between asymmetries in acoustic and other variables (morphological traits, contest duration) were calculated using Spearman's correlation coefficient, because acoustic variables revealed departures from normality. Asymmetry for continuously distributed characters was calculated as the relative difference between opponents (intrapair difference/mean value for pair).

Results

Course of the Fight

Removing the barrier between fish almost immediately caused one or both of the fish to approach the other, both with spread unpaired fins (= lateral displaying), and to start circling. As soon as fish were close to each other in an antiparallel position (1–3 cm) they beat their pectoral fins rapidly; this generally resulted in the production of sound. Twenty-six fights were decided during lateral displaying and 66 escalated to, and were decided during the frontal display phase. Mouth locking and bites into parts of the body other than the mouth were rarely observed.

Contests were organized in bouts, after which the fish usually swam to the surface for airbreathing. Bouts averaged 15 s (range 2–45 s, $n = 50$) in LD-contests and 10 s (range: 1–35 s, $n = 50$) in FD-contests. FD-bouts usually ended with a short lunge by one fish and mouth bites. Lateral displays were performed simultaneously by both contestants in all 92 fights; in 20 of these, small differences in duration were observed. Frontal displays were even better synchronized: no differences in duration were found here (see next section).

Mean duration of the displaying phase in LD-contests was 161 ± 24.7 s ($\pm$ SE, $\tilde{x} = 131$ s, $n = 26$), while total contest duration (including breaks) was 570 ± 99 s ($\tilde{x} = 415$ s, $n = 26$). Mean duration of the displaying phase in FD-contests was 684 ± 64 s ($\tilde{x} = 544$ s, $n = 66$), while total contest duration (including breaks) was 1368 ± 129 s ($\tilde{x} = 1066$ s, $n = 66$). The lateral display time (time to the first FD-bout) took almost half of the total time in escalated contests ($\tilde{x} = 47.5 \pm 3.7\%$, n = 66). Contests which ended during lateral displaying were significantly shorter than FD-contests (Mann–Whitney U-test, $U = 415$, $n_{LD} = 26$, $n_{FD} = 66$, $p < 0.001$).

Acoustic signals were always emitted alternately and in a similar number by both contestants (see next section). Sounds of both contestants were, on average, produced during 6.5% of the lateral display time.

Giving up, i.e. the end of the fight, was signalled by the loser moving toward the surface and away from the opponent, folding its fins and exhibiting three or four dark horizontal bars.

Determinants of Fighting Success

Based on a previous study which showed that vocalization affects fighting success in similar-sized rivals (Ladich et al. 1992b), I tested the hypothesis that certain sound characteristics influence the overall outcome of contests. In fact, in addition to body size, lower dominant frequency and higher sound pressure levels were also associated with winning (Table 1). Winners were from 87% to 136% the length of their opponents, with a mean of 104%. The relative dominant frequency ranged from 80% to 110% ($\bar{x} = 97\%$) and the SPL difference between winners and losers ranged from −3.6 to 5.8 dB ($\bar{x} = 2.07$) (Table 1). The number of sounds and duration of lateral displaying did not differ significantly between winners and losers.

Relationship between size and acoustic measures

Acoustical variables were related to morphological variables in order to test if they are reliable indicators of RHP. Asymmetries in two acoustic variables were significantly correlated with asymmetries in size measures (Table 2).

Comparison between non-escalated (LD) and escalated contests (FD)

Two out of three acoustic traits were predictors of winning in non-escalated and escalated contests (Table 1): dominant frequency and SPL. Asymmetries in these two traits were related to each other in LD-contests ($r_s = -0.49$, $p < 0.05$, $n = 26$). In escalated FD-contests no relationship was found between SPL and dominant frequency. Furthermore, in FD-contests (n = 19) in which winners were smaller, none of the acoustic asymmetries were predictors of winning (number of winners/losers: dominant frequency = 8/11, SPL = 9/10; number of sounds = 10/9). These data suggest that sounds are of more importance in non-escalated contests.

The other traits such as number of sounds and duration of lateral displays did not differ between LD- and FD-contests. Mean differences in size measures were significantly larger in non-escalated than escalated interactions (Mann–Whitney U-test: total body length, $U = 458$, $p < 0.001$; body weight, $U = 527$, $p < 0.01$). Similarly, differences in degree of asymmetries between LD- and FD-winners existed for dominant frequencies ($U = 529$, $p < 0.01$) but not for SPL ($U = 829$, NS) (see also Table 1 for absolute differences and sample sizes).

Table 1: Mean values of variables investigated. Values were calculated for all contests (n = 92) as well as for lateral display (LD) contests (n = 26) and frontal display (FD) contests (n = 66) separately; SPL = sound pressure level

Variable	Winners Mean	Winners SE	Losers Mean	Losers SE	Z[1]
All contests					
Weight (g)	1.18	0.022	1.05	0.016	5.22***
Body length (mm)	54.82	0.37	52.78	0.37	4.75***
Dominant frequency (Hz)	1431	11.32	1473	11.16	4.39***
SPL (dB)	14.40	0.62	12.33	0.66	5.79***
No. of sounds	47.76	3.35	46.27	3.44	0.98
Lateral Displays (s)	248.35	22.09	245.83	22.22	0.15
LD-contests					
Weight (g)	1.26	0.035	1.02	0.028	4.41***
Body length (mm)	56.30	0.59	52.10	0.92	3.62***
Dominant frequency (Hz)	1412	24.13	1497	26.56	4.15***
SPL (dB)	15.20	1.07	12.50	1.46	3.54***
No. of sounds	33.96	4.65	33.04	4.80	0.20
Lateral Displays (s)	160.00	24.78	163.10	24.11	0.94
FD-contests					
Weight (g)	1.16	0.030	1.06	0.020	3.16**
Body length (mm)	54.24	0.44	53.04	0.36	3.03**
Dominant frequency (Hz)	1438	12.60	1464	11.47	2.43*
SPL (dB)	12.95	0.94	11.15	0.97	4.26***
No. of sounds	53.20	4.12	51.49	4.26	1.00
Lateral Displays (s)	283.20	28.12	278.40	28.60	0.70

[1]: Wilcoxon matched-pairs signed-ranks test; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 2: Correlations between asymmetries in size measure and acoustic variables. Spearman's coefficients of ranks correlation were given for all contests (n = 92) as well as for lateral display (LD) contests (n = 26) and frontal display (FD) contests (n = 66)

	Dominant frequency All contests r_s	Dominant frequency LD-contests r_s	Dominant frequency FD-contests r_s	Sound pressure level All contests r_s	Sound pressure level LD-contests r_s	Sound pressure level FD-contests r_s
Body weight	−0.62***	−0.52**	−0.60***	0.37**	0.63***	0.30*
Body length	−0.38***	−0.14	−0.35**	0.23*	0.28	0.23

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Assessment

In order to demonstrate that opponents do in fact assess their fighting ability, asymmetries in morphological and acoustic traits were related to the duration of the contest. Contest duration decreased significantly with increasing asymmetry in body length (Fig. 1). Furthermore, there was a negative relationship between contest duration and SPL (Fig. 2). However, contest duration was not correlated to asymmetry in body weight (LD: $r_s = -0.28$, ns, $n = 26$; FD: $r_s = -0.01$, ns, $n = 66$) or in dominant frequency (LD: $r_s = 0.21$, ns, $n = 26$; FD: $r_s = -0.03$, ns, $n = 66$). These data indicated that neither weight nor dominant frequency was used to assess the fighting ability of rivals.

Traits thought to be used for assessing fighting ability — body length and SPL — were not correlated with each other (LD: $r_s = 0.28$, $p = 0.16$, $n = 26$; FD: $r_s = 0.23$, $p = 0.064$, $n = 66$).

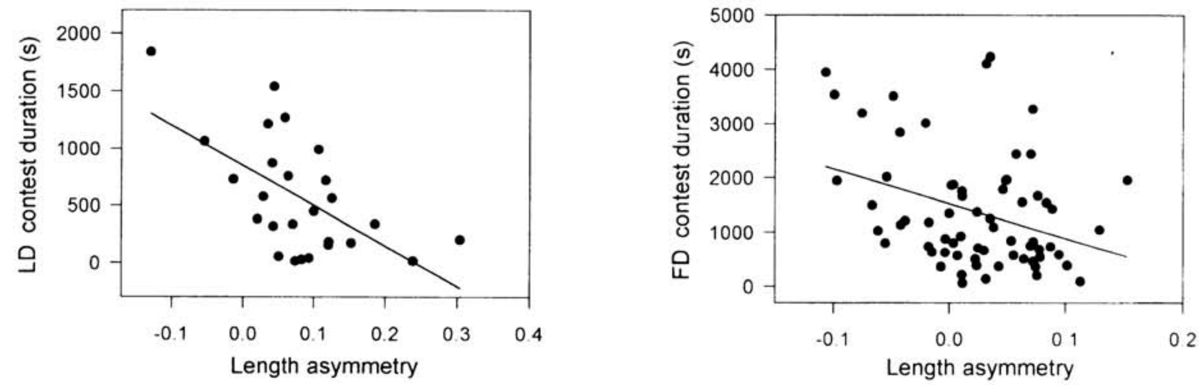

Fig. 1: Lateral display (LD) and frontal display (FD) contest duration as a function of the asymmetry between opponents in body length ((winner's − loser's length)/mean length). Regression equations: LD-contests, $Y = 851 - 3520X$, $r = 0.60$, $p < 0.001$, $n = 26$; FD-contests, $Y = 1519 - 6394X$, $r = 0.34$, $p < 0.01$, $n = 65$

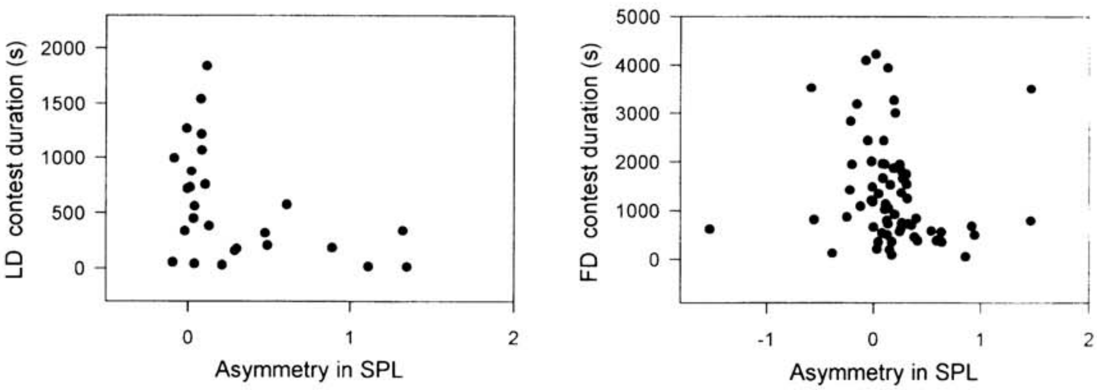

Fig. 2: Lateral display (LD) and frontal display (FD) contest duration as a function of the asymmetry between both opponents in their sound pressure level (SPL) ((winner's − loser's SPL)/mean (SPL). LD-contests: $r_s = -0.44$, $p < 0.05$, $n = 26$. FD-contests: $r_s = -0.30$, $p < 0.05$, $n = 66$

Discussion

Predictors of Winning

The present study demonstrates that the outcome of contests between male croaking gouramis is related to differences in morphological and acoustic traits. Body size measures were correlated with fighting success, suggesting their major contribution to fighting ability. This is in agreement with the importance of size in other fishes such as cichlids (Barlow et al. 1986; Beeching 1992), poeciliids (Kodric-Brown 1993) and in other animal groups, including mammals (Clutton-Brock et al. 1979) and insects (Hack 1997). Overall body length probably reflects a visually perceived component of RHP. Consistent differences in sound characteristics between winners and losers indicate that components of RHP were also signalled by sounds. Asymmetries in dominant frequencies and SPL were correlated with the outcome of contests, which indicates that the acoustic structure of sounds affects winning. Not surprisingly, dominant frequency and, to a lesser degree, SPL are better correlated to body weight than body length; this indicates that these sound characteristics are connected to body mass and to the volume of resonating structures such as airbladders (Myrberg et al. 1993; Ladich 1997b; Ladich & Yan 1998).

In contrast to the acoustic structure of sounds and morphological measures, the number of acoustic signals and duration of behavioural displays did not influence winning. The lack of a connection between the amount of signalling and the outcome of interactions on one side and between morphological features and the amount of signalling on the other suggest that the latter are not 'costly' traits and not reliable indicators of RHP (Maynard Smith & Harper 1988). In other animal taxa such as frogs or red deer the amount of calling is decisive for the outcome of contests (Clutton-Brock & Albon 1979). However, the difference in the amount of calling (number of sounds or calling rates) differs widely between these groups. While the percentage of time spent vocalizing is about 3% for one croaking gourami in LD-contests and much less in contests proceeding to the FD-phase, red deer stags call for hours and thus advertise honestly their resource-holding power.

The similar amount of displaying in contesting croaking gouramis agrees with theoretical studies which concluded that contestants should conceal their intention to escalate and that it should therefore not be possible to predict the winner by observing the course of a fight (Maynard Smith 1974, 1982). Several studies have demonstrated that predicting the winner in symmetrical contests was not possible (Simpson 1968) or only possible in the last stage of a fight (Jakobson et al. 1979; Turner & Huntingford 1986).

Are acoustic asymmetries more 'predictive' of the winner in those contests not resolved by size asymmetry? This was not the case in croaking gouramis. A comparison between non-escalated and escalated fights revealed that the number of acoustic traits which predicted winning decreased when size asymmetry decreased and contests escalated. In LD-contests, dominant frequency and SPL influenced the outcome, while in FD-contests the dominant frequency was not a predictor of winning. Dominant frequency and SPL were not correlated to each other in these combats. Furthermore in FD-contests in which the smaller fish won, no sound characteristic predicted the winner.

Are absolute differences in morphological and acoustic traits large enough to be assessable? Barlow et al. (1986) reported that Midas cichlid weight did forecast winners, who averaged only 2% heavier than their opponents. Turner & Huntingford (1986) showed that in contests between male Mozambique mouthbrooders the larger fish won more often, even when standard length differed by as little as 1 mm. In the present study, size clearly was a predictor of winning in both non-escalated and escalated contests, and mean size differences of 7% and 2%, respectively, were distinguished.

Sound intensity and frequency discrimination abilities have not yet been tested in croaking gouramis. A recent investigation in *T. vittata* (and other anabantoid species) demonstrated that these fish are hearing specialists that possess greatest auditory sensitivity at about 1500 Hz, which corresponds to the dominant frequencies of sounds (Ladich & Yan 1998). Otophysans such as cyprinids — non-related hearing specialists — are able to discriminate SPL differences of 1–2 dB (Fay 1988). Therefore, it seems likely that croaking gouramis are able to detect differences in sound intensity in LD- and FD-contests (2.7 and 1.7 dB, respectively). The best frequency discrimination ability is between 3% and 4% for the optimal hearing range in otophysans (Dijkgraaf & Verheijen 1950; Fay 1970) and about 8% for hearing generalists (Enger 1981). Croaking gouramis are therefore probably able to discriminate differences in dominant frequencies in LD-contests (mean difference between winners and losers: 6%). However, it is unlikely that they are able to differentiate between frequencies in FD-contests, where the mean difference is 1.8%.

Assessment of Fighting Ability

The preceding section demonstrated a correlation between fighting success and several potential components of RHP, such as total length and sound quality. According to the assessment models (Enquist et al. 1990) a decrease in asymmetry in RHP between opponents results in more costly contests. Based on the presented data, asymmetries in two of these components, body length and SPL, were assessed by contesting gouramis to resolve conflicts. Moreover, the lack of a correlation between body length and SPL in both non-escalated and escalated contests indicates that each might, to some extent, independently influence male fighting ability.

How are different asymmetries assessed? Croaking gouramis may visually assess relative body length. This probably occurs during lateral displaying, when fish appear to demonstrate or enhance their apparent size by spreading unpaired fins. Additional assessment may take place through the acoustic traits (i.e. SPL) of sounds, which provides information linked more to weight, a second component of the body size. Different modalities of ‘assessment signals’ (Maynard Smith & Harper 1988) thus provide reliable information about body size and subsequently fighting ability without assessing strength by physical contact, such as mouth locking or mouth wrestling, between rivals. Injuries were rarely observed. Obviously, *T. vittata* assess their opponent mainly by visual and acoustic signals (and perhaps lateral line stimuli), unlike other fish such as the Midas cichlid, which quickly escalate to the damaging phase (Barlow et al. 1986; see also the following section). The present study shows that contests were longer when asymmetries in these 'assessment signals' were small. These contests tended to escalate beyond the stage in which visual and acoustic stimuli predominated. These interactions might have been decided by additional components of RHP such as endurance (asymmetries in energy expenditure; Hack 1997).

This is the first study demonstrating that the outcome of contests in fish is influenced by sound characteristics related to size. The correlation between the opponents' asymmetry in two of these characters (length and SPL) and the duration (= costs) of contests indicates that relative fighting ability is assessed by rivals utilizing visual and acoustic signals to resolve conflicts.

Comparison between Croaking Gouramis and Other Labyrinth Fishes

Do differences in vocal behaviour between labyrinth fishes result in different strategies to assess the fighting ability of opponents? Within labyrinth fishes (anabantoids), only representatives of the genus *Trichopsis* possess a well-developed pectoral sound-producing mechanism and regularly vocalize during agonistic interactions. Representatives of other genera such as *Colisa*, *Macropodus* and *Betta* vocalize only occasionally or are not known to produce sounds; none possess a specialized sonic mechanism (Frey & Miller 1977; Kratochvil 1985; Schuster 1986; Bischof 1996). Although a quantitative comparative analysis is lacking, a qualitative comparison between agonistic behavioural elements utilized during contests indicate that physical fighting occurs more frequently in these last genera. In contrast, in croaking gouramis, one-quarter of the contests were decided during lateral display, and even in escalated contests physical contact was limited to short mouth bites and seldom involved mouth locking. Mouth wrestling for assessing the strength of opponents was lacking. However, bites into various body regions are common in other species such as *Colisa lalia* (Vaquette 1996) and frequently results in mouth wrestling in *Macropodus opercularis* (Bischof 1996), *Betta splendens* (Simpson 1968) or biting sessions and fin tugging in *Trichogaster trichopterus* (Frey & Miller 1977). Therefore it is assumed that *Trichopsis* utilizes a second type of 'assessment' signal in addition to visual signals. Croaking gouramis may gain information about certain components of the opponent's fighting ability (which are connected to body weight) without escalated fighting. Visual signals also appear to be more elaborate in *Macropodus*, *Betta* and *Trichogaster* than in *Trichopsis*. While all species exhibit lateral displays during contests, the former genera also spread opercula and gill membranes during frontal displaying. In summary, in contrast to other labyrinth fishes, it is suggested that *Trichopsis* exploits the acoustic channel for reliable assessment of the RHP of an opponent. Sound production may well reduce assessment of RHP by damaging combat.

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