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Diversity in Agonistic Behavior of Croaking Gouramis (*Trichopsis vittata, T. schalleri,* and *T. pumila*; Anabantoidei) and the Paradise Fish (*Macropodus opercularis;* Anabantoidei)

Claudia Bischof

Institute of Zoology, University of Vienna, Wien, Austria

Agonistic encounters of all three species of the vocalizing genus *Trichopsis* were observed in order to compare species-specific fighting strategies and the specific investment in acoustics. Additionally, these encounters were compared to agonistic encounters of *Macropodus opercularis* which was considered to be mute. The aim of this comparison was to investigate if mute fishes stress visual or tactile displays. Within the genus *Trichopsis*, significant differences among the three species were found in qualitative and quantitative analysis of displays. Frontal display occurred only in *Trichopsis vittata,* whereas a strong tail-beating while vocalizing was only observed in *Trichopsis pumila.* Fight duration and the number of sounds and circlings were highest in *Trichopsis schalleri.* The largest relative distances between circling opponents occurred in *T. pumila,* the smallest species. Also, the number of attacks was lowest in *T. pumila.* Fighting assessment seemed to be different in each species. For the first time, sound production has been reported for *Macropodus opercularis* (infrequently and with extreme low sound pressure levels), but much more investment in visual and tactile displays has been demonstrated. Lowering the branchiostegal membrane and spreading the opercula occurred only in *M. opercularis* and was never observed in any of the *Trichopsis* species. The number of attacks was higher in *Macropodus* than in any *Trichopsis* species. The relative distance between *Macropodus* opponents while circling was closest compared to the three *Trichopsis* species. Visual and contact displays are reduced in extensively vocalizing fish species, like *Trichopsis* sp., compared to mute or seldom vocalizing species, like *Macropodus.*

Key words: agonistic behavior, acoustics, attack, communication, threatening displays, vocalization

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Address reprint requests to Claudia Bischof, Institute of Zoology, University of Vienna, Althanstrasse 14, A-1090 Wien, Austria.

INTRODUCTION

In many osteichthyan species, ritualized behavior patterns among conspecifics enable the assessment of fighting abilities [Enquist et al., 1988, 1990]. Some species show visual and contact displays while others also vocalize during agonistic encounters [Myrberg, 1981; Ladich, 1991]. Physical features of sounds allow the assessment of the caller's body size or discrimination of conspecifics [Gerald, 1970; Spanier, 1979] and sound production can also influence the outcome of dyadic conflicts [Ladich et al., 1992b].

The anabantoid genus *Trichopsis* consists of three species (*T. vittata, T. pumila,* and *T. schalleri*) and is characterized by a unique sonic organ derived from its pectoral fins [Kratochvil, 1978]. Distinct croaks accompany visual displays in all three species during aggressive and reproductive behavior [Marshall, 1966; Brittinger, 1991]. An analysis of the physical structure of sounds emitted during agonistic encounters revealed species-specific differences in temporal parameters as well as in main frequency and sound pressure levels: Sound pressure levels were highest in *T. pumila,* the smallest species; *T. schalleri* produced sounds with the highest number of pulses, and *T. vittata* was the only species to utter croaks in series [Ladich et al., 1992a].

These findings raise some important questions concerning the species-specific investment in visual, acoustic, or tactile displays during agonistic encounters. It is examined in this study if each (visual, contact, or acoustic display) represents a different strategy in an encounter. Thus, fishes with much investment in sound production, for example, are supposed to show less visual displays and vice versa.

In contrast to *Trichopsis,* the paradise fish *Macropodus opercularis*—a closely related anabantoid fish—is considered mute [Kratochvil, 1978, 1985]. This allows the use of *Macropodus* as an ideal control for the hypothesis suggested above and leads to the assumption that agonistic encounters of paradise fish will comprise more visual and contact displays than those of the croaking gouramis.

MATERIALS AND METHODS

The genus *Trichopsis* (Belontiidae, Anabantoidei; Teleostei) consists of three species (*T. vittata, T. schalleri,* and *T. pumila*) living in shallow waters in Southeast Asia. Thirty males of each species (*T. vittata:* 0.68–2.58 g, *T. schalleri*: 0.21–1.36 g, *T. pumila*: 0.17–0.39 g) and 34 male paradise fish, *M. opercularis* (1.59–3.86 g) were used in this study. Fishes were kept in 50 l–300 l community tanks at a temperature of 28°C; a 12 hr:12 hr light:dark cycle was maintained. Fishes were purchased from local aquariums and reared in the laboratory for this study.

Two conspecific males were first separated in a small test tank (50 x 27 x 30 cm) by a nontransparent plastic sheet. After 2 days, the sheet was removed and the following agonistic encounters were monitored. Sounds were recorded using a Brüel and Kjaer 8101 hydrophone and a Brüel and Kjaer 2804 power supply. Differences in body mass between opponents were limited (<30%) to avoid influences of mass asymmetries between the opponents on the outcome of the dyadic conflict. The paired contestants were always taken from different tanks to reduce previous experience. Each fish was used only once.

Analysis of sounds was made using digital sound analysis equipment (Sound-Tools).

Behavior Patterns

Lateral display. The opponents stand in a head-to-tail or head-to-head position and spread their unpaired fins.

Circling. This feature is part of the lateral display pattern. Both individuals swim fast in small circles with erect fins.

Sound production. Sounds are normally produced during lateral display and interrupt circling. Sound production is accompanied by a rapid movement of the pectoral fins and therefore by a vibration of the whole body. Vocalization consists of distinct elements (croaks), which are built up by a series of short pulses. Croak lengths are species specific.

Frontal display. For *Trichopsis*, the opponents face each other with opened mouths at close distance. For *Macropodus*, the gill covers are spread away from the body, and the fish faces its opponent or stands in a head-to-head position. The branchiostegal membrane is lowered.

Attacks (bites). Accelerated approach between opponents including body contact. Attacks are aimed to fins and flanks (*Trichopsis*) as well as head and gill covers (*Macropodus*).

Mouth wresting. The opponents bite for some seconds in each other's mouth (mouth biting) and additionally push each other forward or backward.

Total fight duration. This is the period from the beginning of the first to the end of the last aggressive behavior pattern including time for air breathing and pausing. Encounters of *T. schalleri* were stopped after a maximum time of 120 min, encounters of *M. opercularis* after a maximum of 90 min (in order to avoid serious injuries). Neither encounters of *T. vittata* nor of *T. pumila* had to be interrupted.

Statistics

Distributions of data were evaluated with the Kolmogoroff-Smirnov test (all data were normally distributed). Displays were compared between species by means of analysis of variance (ANOVA) and Student's *t* test. The influence of body mass differences on displays and fight duration was tested with Spearman correlations, that on the outcome of encounters with Wilcoxon tests.

RESULTS

Description of the Agonistic Encounters

T. vittata. On visual contact, the fishes reacted to the presence of an opponent by changing their body coloration. Sometimes, the head, flanks, and fins darkened, mostly, two or three dark stripes in the flanks and the head appeared normally. A few seconds later, they usually approached each other and started with lateral display (including circling and sound production) in a head-to-tail position. This behavior pattern lasted 5–20 min, then the fishes changed from lateral to frontal display (in 12 of 15 fights, this feature comprised more than 50% of the fight duration). Alternatively, the fishes changed to direct contact displays (attacks). In frontal display, the opponents faced each other with opened mouths at a close distance, their tails bent in a right angle. This display was interrupted by air breathing, attacking, or mouth wrestling. When frontal display occurred, it was always the last aggressive behavior pattern to be observed.

T. schalleri. In agonistic encounters of male *T. schalleri,* neither changing the body coloration nor frontal display or mouth wrestling occurred. After removing the separating sheet, the opponents started with lateral display (and circling) which was accompanied by sound production, which sometimes lasted for more than 2 hr. Attacks were observed in each fight—either at the end of encounters or between lateral display periods.

T. pumila. Similar to *T. schalleri, T. pumila* individuals started immediately after removing the sheet with circling and sound production. The rivals stood in a unique head-up or head-down position while vocalizing that was accompanied by intense tail beating (= lateral undulating movements of the tail). In 10 of 15 encounters, the last lateral display complex was already observed after 5 min of an encounter and was followed by attacking behavior. Frontal display and mouth wrestling never occurred.

Comparison Between *Trichopsis* Species

Fight duration. The length of the agonistic encounters was significantly different among species (ANOVA, $F = 21.32$, $df = 2, 42$, $P < .001$); fight duration of *T. schalleri* was much longer than that of *T. vittata* and *T. pumila* (Table I).

Lateral display. Aggressive behavior of all three species included lateral display. The number of circlings was positively correlated with the number of sounds ($r = .89$,

TABLE I. Comparison of Fight Duration and Displays Between Species Considering the Total Length of Their Encounters (*t* tests) and Mean (± s.e.) of Fight Duration and Agonistic Displays of *T. vittata* (*T.V.*), *T. pumila* (*T.p.*), *T. schalleri* (*T.sch.*), and *M. opercularis* (*M. opercul.*) (Total Fight Duration)[†1]

Display species	*t*	*P*	Mean	S.E.
Fight duration				
T.v./T.p.	0.65	n.s.	24	5.3
T.v./T.sch.	–5.03	***	18	6.4
T.sch./T.p.	4.81	***	99	14.5
M. opercul.			67[a,b]	16.4
Number of circlings				
T.v./T.p.	1.66	n.s.	18.4	5.5
T.v./T.sch.	–2.47	*	7.7	3.1
T.sch./T.p.	2.85	**	95	12.4
M. opercul.			48[a,b,c]	6.8
Number of sounds				
T.v./T.p.	3.71	***	24.3	4.3
T.v./T.sch.	–2.04	*	6.6	1.8
T.sch./T.p.	3.89	***	46.9	7.8
M. opercul.			Not calculated	Not calculated
Relative circling distance				
T.v./T.p.	–5.33	***	72	3.6
T.v./T.sch.	–2.01	n.s.	175	23.8
T.sch./T.p.	–4.23	***	86	6.0
M. opercul.			50[a,b,c]	2.0
Number of attacks				
T.v./T.p.	–0.79	n.s.	11	4.7
T.v./T.sch.	–1.78	n.s.	6.2	3.8
T.sch./T.p.	2.20	*	33.9	11.8
M. opercul.			82[a,b,c]	20.1

[†]a = significantly different to *T. vittata*; b = significantly different to *T. pumila*; c = significantly different to *T. schalleri* (*t* tests, $P < 0.05$).

[1]*$P < .05$; **$P < 0.01$; ***$P < 0.001$ (t test).

$P < .001$). Considering the total length of all fights, the number of sounds significantly differed among species (ANOVA, df = 2, 87, F = 9.706, $P < .001$). The number of circlings and number of sounds were highest in *T. schalleri* and lowest in *T. pumila*, whereas the relative circling distance (distance between species in percent of the standard length) was highest in *T. pumila* and not different between *T. vittata* and *T. schalleri* (Table I). Temporal analyses revealed characteristic differences in the number of sounds during the course of a fight (ANOVA, df = 2, 87; min 0–10: F = 16.9; min 10–20: F = 9.1; min 20–30: F = 14.8; $P < .001$; Table II). The number of sounds was generally highest in the first 10 min of fights when *T. vittata* produced nearly as many sounds as *T. schalleri;* both differ significantly from *T. pumila*, which vocalized least. In the following 10 min (between min 10 and 20), the number of sounds decreased rapidly in all three species, but still remained at a high level in *T. schalleri* even after 20 min. While most individuals of *T. vittata* and *T. pumila* had stopped fighting after 30 min, *T. schalleri* still continued (Fig. 1).

Attacks. Attacks occurred in all three species, but injuries were never observed in this study. The number of attacks per fight was highest in *T. schalleri* and lowest in *T. pumila* (Table I).

Weight Asymmetries

Body mass differences did not influence the number of displays or the fight duration (tested with Spearman correlations) in any of the fish species or the outcome of the agonistic encounters (win-lose) (Wilcoxon tests; *T. vittata:* Z = .289, n.s.; *T. schalleri:* Z = .809, n.s.; *T. pumila:* Z = –.354, n.s.). For *M. opercularis*, the outcome of many fights was still not decided when the encounters were interrupted.

M. opercularis

After removing the separating sheet, both fishes immediately darkened (from orange/red to blue/black) or, at least, dark blue stripes at the flanks of the body appeared. When the competitors approached, they spread their opercula and occasionally lowered their branchiostegal membrane. Additionally, the unpaired fins were spread. Circling with erect fins has been a major feature of the agonistic encounters of two male paradise fishes. The distance (relative to their standard length) between the opponents while circling was very close (Table I). Frequently, body vibrations due to accelerated fin beating were observed. In 6 of 17 encounters the accelerated fin beating was accompa-

TABLE II. Number of Sounds Within the First 30 Min (divided in 10-min classes) of agonistic encounters in *T. vittata, T. pumila*, and *T. schalleri**

Time	Species	*t*	*P*
Min 0–10	*T. vittata/T. pumila*	2.52	<.05
	T. vittata/T. schalleri	0.09	n.s.
	T. schalleri/T. pumila	2.45	<.05
Min 10–20	*T. vittata/T. pumila*	1.31	n.s.
	T. vittata/T. schalleri	–0.93	n.s.
	T. schalleri/T. pumila	2.19	<.05
Min 20–30	*T. vittata/T. pumila*	1.66	n.s.
	T. vittata/T. schalleri	–2.51	<.05
	T. schalleri/T. pumila	3.07	<.01

*Significant differences between species were analyzed with *t* tests.

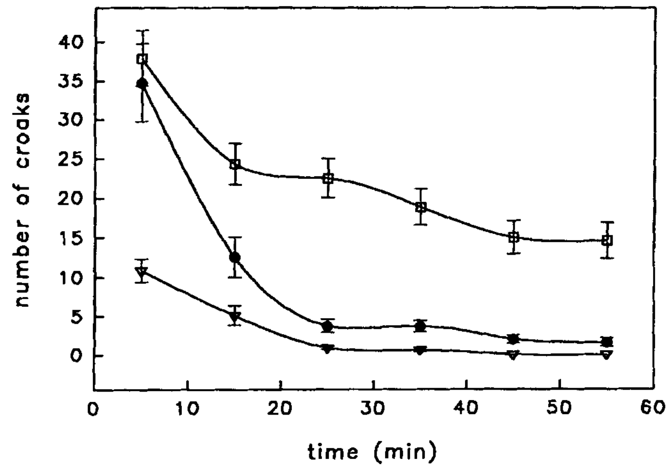

Fig. 1. Vocalization within agonistic encounters (in 10-min time units) of *T. vittata* (▽), *T. schalleri* (□), and *T. pumila* (●).

nied by sounds; all together, 49 sounds were recorded. The sound pressure levels were extremely low (the sounds could only be heard when being amplified), but their temporal characteristics are similar to those of *Trichopsis*. The mean pulse period is 72 (±10.9) ms, a sound consists of six to seven pulses. The encounters consisted of numerous attacks (exceeding those of any *Trichopsis* species, Table I). The aim of the attacks was usually the head (very often the eyes or the opercula), sometimes the flanks. Frequently, mouth biting occurred (the opponents bite in each other's mouth and push each other).

Differences in the characteristics of single features between *Macropodus* and the *Trichopsis* species are demonstrated in Table I.

DISCUSSION

Acoustic threatening was described for several fish families, like gobiidae [Ladich and Kratochvil, 1989], cottidae [Ladich, 1990], cichlidae [Myrberg et al., 1965; Schwarz, 1974], pomacentridae [Myrberg, 1972], and belontiidae [Ladich et al., 1992a,b]. For some teleost fishes, species-specific differences were analyzed [sunfish: Gerald, 1970; damselfish: Spanier, 1979; Albrecht, 1989; labyrinth fish: Ladich et al., 1992a]. In genus *Trichopsis*, interspecific differences were found for sound pressure levels (*T. pumila* vocalizes loudest) and for dominant frequencies, which depend on the body mass of the fish; frequency is highest in *T. pumila* and lowest in *T. vittata*. In *T. schalleri*, the number and period of pulses within a croak are significantly higher than in both other species [Ladich et al., 1992a]. Accordingly, it was of great interest to find out if species-specific differences are restricted to acoustics or if they can also be observed in other behavior patterns of agonistic encounters.

For the comparison of agonistic behavior, it was necessary to keep differences in body mass between opponents small. In previous studies on agonistic behavior in fishes, it was shown that weight asymmetries play an important role for outcome and duration of encounters as well as for the frequency of different behavior patterns [Enquist and

Jakobson, 1986; Enquist et al., 1988, 1990; Beeching, 1992]. The results of the present study suggest that the weight asymmetries of maximum 30% did not influence the outcome of encounters.

Generally, this study demonstrated that agonistic encounters of male *T. vittata*, *T. pumila*, and *T. schalleri* comprised several different threatening displays, such as visual, acoustic, and contact displays. Furthermore, it was shown that not only physical parameters of sounds but also visual and tactile agonistic features, as well as the investment in acoustics, revealed characteristic differences among the three *Trichopsis* species. Whereas in *T. vittata* and *T. pumila* the outcome of encounters was decided after a few minutes of fighting, the duration of encounters between *T. schalleri* males was significantly longer and provided more lateral display (more circlings and more sounds). *T. schalleri* did not only produce the highest number of sounds (this study), but also the longest croaks of all species. The croak length was the product of the mean number of double pulses, the double pulse period being 142 ms for *T. vittata*, 316 *Macropodus* for *T. pumila*, and 473 ms for *T. schalleri* [Ladich et al., 1992a]. Consequently, the total number of pulses emitted in agonistic encounters was highest in *T. schalleri* (mean number of pulses per fight: *T. schalleri*, 394; *T. vittata*, 114; *T. pumila*, 45). Interestingly, despite the fact that *T. schalleri* is smaller than *T. vittata*, there are no differences in sound pressure levels [Ladich et al., 1992a]. While *T. pumila*, the smallest species, produced the least number of sounds, the amplitude is highest [Ladich et al., 1992a]. Additionally, croaking was accompanied by strong vibrations of body and tail (tail beating), suggesting that in *T. pumila* the intensity of sounds, rather than the number of sounds, was more important for assessing the rival. Sound pressure levels for the genus *Trichopsis* can be found in the literature (*T. vittata*, 117.1 dB; *T. schalleri*, 118.3 dB; *T. pumila*, 126.5 dB, all re 1 μPa [Ladich et al., 1992a]; however, they were not measured in the present study because of the varying distance of the combatants to the hydrophone. Though circling distance was longest in *T. pumila*, this will probably not diminish the effect of sound pressure or tail beating. Both displays occur at close distance between opponents. Males of *T. vittata* produced less sounds than *T. schalleri* and vocalized at lower sound pressure levels than *T. pumila*. Within the genus *Trichopsis*, only in encounters of *T. vittata* are lateral displays usually followed by a frontal display phase. From these results it can be assumed that fighting strategies are species specific in the genus *Trichopsis*. In *T. vittata*, optical cues seem to play a major role. In *T. schalleri*, acoustics—above all quantity—is peculiar. *T. pumila* neither stresses optical nor acoustic displays, but is by far the loudest and the only species showing tail beating.

M. opercularis generally shows similar behavioral patterns as the *Trichopsis* species, enabling a comprehensive comparison among the genera. The paradise fish was, until now, considered to be mute. As this species does not exhibit any morphological modifications for sound production, it was assumed that vocalization is not developed in the paradise fish [Kratochvil, 1978, 1985]. However, in the present study, vocalization of *M. opercularis* was reported for the first time: temporal characteristics and structure of the sounds are similar to those of the *Trichopsis* species and vocalization co-occurred with rapid movements of the pectoral fins. This suggests that the mechanism of sound production could be the same or at least very similar to the vocalization apparatus of *Trichopsis*. Nevertheless, the sound pressure levels were very low (they could not be heard by the human ear if not amplified).

However, optical cues seemed to play a more important role than acoustic cues in agonistic encounters of *M. opercularis*. High investment in visual displays was also demonstrated by comparison with the *Trichopsis* species. For example, changes of the body coloration involved the entire body of *M. opercularis,* whereas in *T. vittata*, only dark stripes appeared in very aggressive opponents and neither contrahents of *T. schalleri* nor of *T. pumila* changed their coloration during encounters. Two of the most abundant threatening displays of *M. opercularis* (spreading the opercula, lowering the branchiostegal membrane) were never observed in any of the *Trichopsis* species. Additionally, contact displays were distinct: by far most attacks were observed in encounters of *M. opercularis* and the relative distance between two threatening fishes was closer in the paradise fish than in the gouramis. Consequently, body vibrations accelerated fin beating, or other features inducing water movements may be received more intensively by the opponent.

These results suggest that species with less developed vocalizing mechanisms rely more on visual or contact displays. This hypothesis is further confirmed by investigations on the mute genus *Betta,* where the latter displays, as well as spreading the opercula, lowering the branchiostegal membrane, mouth protrusion, mouth biting, and mouth wrestling (which are also typical features in the agonistic behavior pattern of *Macropodus*) occur frequently [personal observation; Forselius, 1957; Simpson, 1968; Kühme, 1961].

The theory that vocalization reduces visual and tactile displays (and vice versa) could not have been verified with certainty in this study within the genus *Trichopsis*. Contradictorily, *T. schalleri* shows the highest number of sounds but also the most attacks. On the other hand, in encounters of *T. schalleri* no distinct optical displays can be observed, whereas the less croaking species, *T. vittata*, stresses optical cues. However, as discussed above, within this vocalizing genus it seemed very likely that not only the number of sounds, but also the quality (sound pressure levels, frequency, tail beating, and water pushing while vocalizing) are of importance in deciding the outcome of agonistic encounters. Alternatively, it might be assumed that *T. schalleri* is merely more aggressive than the other investigated species, thus displaying several aggressive behavior patterns in a more intense manner. A possible reason for this higher aggressive level, however, remains to be studied.

In summary, analyses of aggressive behavior revealed species-specific investment in different agonistic displays in *T. vittata*, *T. pumila*, and *T. schalleri*, as well as differences between the genera *Macropodus* and *Trichopsis*. While mute or rarely vocalizing fish species use a lot of visual and contact displays for threatening and fighting assessment, some of these displays are obviously reduced in species with frequent sound production.

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