Development of agonistic behaviour and vocalization in croaking gouramis

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The development of agonistic behaviour and vocalization in the croaking gourami Trichogaster willani was studied from hatching to sexual maturity (4 months of age). Initial interactions started when fry were 11 days old and consisted of approach and flight in a feeding context. More complex threat patterns appeared during dyadic encounters as fish grew older. Lateral display (spreading of median fins in a lateral position) first occurred during the third week, circling shortly afterwards and pectoral fin beating when fish were 7 weeks old. Rapid pectoral fin beating was first accompanied by sound emission at 8 weeks. Initially, croaking sounds were built up mainly of a series of single pulses, each one produced by one pectoral fin. Later, single pulses gave way to double pulses. Furthermore, pulse period and number of pulses increased, while the dominant frequency of croaks decreased significantly with age. After vocalization was established, frontal display, mouth biting and retreat behaviour occurred at the age of 10 weeks. Initially, young exhibited vertical bars which gave way to dots and horizontal bars at 8 weeks when fish started to vocalize. The order of appearance of behavioural patterns during ontogeny corresponds to the order of appearance in fights between adults. This is the first study demonstrating that the ontogenetic development of social signalling comprises characteristic changes in behaviour, vocalization and coloration in a teleost fish.

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Key words: sound characteristics; acoustic behaviour; coloration; ontogeny; fish.

INTRODUCTION

The ontogenetic development of vocalization has been studied frequently in birds and mammals (e.g. Kroodsma, 1996). Vocalization often starts on the first day after hatching or birth. Sound characteristics change with the growth of the animals and the sound repertoire often increases until maturation (Würdinger, 1970; Hohmann, 1991). Changes in sound features depend on an increase in the size of sound-producing structures or on improved co-ordination of vocal tract movements (Podos et al., 1995).

Data on sound production of juvenile poikilothermic vertebrates, however, are sparse. Contact calls were described in young American alligators (Hunt & Watanabe, 1982) and in Andean frogs (Penna & Veloso, 1987). Young of a few fish species are known to produce sounds during agonistic interactions and in distress situations. Immature skunk loaches Botia horae (Smith 1965) emit clicking sounds when defending their territories (Valinsky & Rigley, 1981). Juvenile tigerperch Terepon jambua (Forsskål 1775) utter drumming sounds and juvenile mormyrids, Gnathonemus petersi (Günther, 1862), clicking sounds.

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(Schneider, 1964; Rigley & Marshall, 1973). In all these species, however, the ontogenetic development of vocalization and agonistic behaviour was not investigated.

The development of social and agonistic behaviour has been studied in representatives of several fish families such as salmonids (Dill, 1977; Cole & Noakes, 1980; Ryer & Olla, 1991), poeciliids (Dwyer & Beulig, 1991), cichlids (Ohm, 1964; Myrberg, 1965; Bergmann, 1971; Williams, 1972), centrarchids (Brown & Colgan, 1985) and belontiids (Davis & Kassel, 1975; Tooker & Miller, 1980; Miklosi et al., 1992). Agonistic behaviour could be observed first as early as a few days after birth in Poecilia (Dwyer & Beulig, 1991), but in most species it starts at the age of 3–4 weeks, for example in Salmo (Wright & Huntingford, 1993), Pterophyllum (Bergmann, 1971) and Trichogaster (Tooker & Miller, 1980). The repertoire of agonistic behavioural patterns is, in most species investigated, fully developed at the age of 4 months. This period was marked by increasingly complex behaviour as well as by a replacement of overtly aggressive acts (e.g. biting) by ritualized displays (lateral display) (Ohm, 1964; Wyman & Ward, 1973; Cole & Noakes, 1980). These changes in behavioural patterns were paralleled by changes in body coloration, for example, in Etropus (Wyman & Ward, 1973) and Haplochromis (Fernald & Hirata, 1979).

The aim of the present study was to describe the ontogenetic development of sound production in the croaking gourami Trichopsis vittata (Cuvier, 1831) from hatching to sexual maturity at 4 months of age. Trichopsis vittata was chosen because adults regularly produce high-intensity, pulsed sounds during agonistic encounters in both sexes (Marshall, 1966; Ladich et al., 1992a, b) and intersexual differences in the sound-producing mechanism and sound characteristics are minor (Kraothchil, 1978; Schleinzer, 1992). The investigation of vocalization ontogeny involved determining the onset and the development of all agonistic behavioural patterns, the start of sound production, and the change in sound characteristics. Finally, the development of coloration is described.

**MATERIALS AND METHODS**

**ANIMAL REARING**

The stock of adult T. vittata was purchased from local aquarium shops. Prior to spawning, eight breeding pairs were transferred each to a separate 40-l aquarium. The bottom was covered with sand and the tank was planted with Anubias, Valesneria and floating Riccia as a spawning substratum. The temperature was maintained at 28°C, with a 12L : 12D cycle. Water was neither filtered nor aerated throughout the study.

Breeding pairs were removed from the tanks 1 week after spawning when parental care ended. The young stayed in the breeding tanks for 3 weeks (except for the first group). Afterwards they were separated into two groups (c. 50 fish each) and transferred to 70-l aquaria. Young were fed twice daily with live zooplankton or brine shrimp nauplii ad libitum to about 1 month of age. Later they were fed Cyclops, Daphnia and Tubifex ad libitum.

**EXPERIMENTAL SET-UP**

A group of five young was observed from hatching to 26 days of age. They were kept in a 1.5-l aquarium until day 26; observations were made 10 min before and after feeding. Sixty-six dyadic agonistic encounters were investigated from day 27 until day 132. Three interactions between two young of the same brood were recorded every 5 days. We
did not pair different-sized fish because previous studies (Ladich et al., 1992a) showed that this results in short fights and the full repertoire, the main topic of this study, would not have been exhibited. Members of a pairing were taken from different aquaria and transferred into observation tanks, where they were isolated from each other by a non-transparent plastic sheet for 2 days. The test was started by removing the plastic partition and encounters were recorded for 15 min or until one fish retreated. Observation tanks measured 20 × 10 × 10 cm for fish smaller than 2.5 cm and 20 × 14 × 14 cm for larger fish. After tests, both fish were put together into a new holding tank and were not used for at least 2 weeks. Some animals were used twice but were never paired with the same opponent. Fish were measured after the tests. No sexing was possible during the experimental period.

BEHAVIOUR AND SOUND RECORDING

All experiments were monitored with a video camera (Canon EX1) and video signals were recorded simultaneously with acoustic signals by an S-VHS HiFi VCR (JVC HR-S4700). The acoustic equipment consisted of a hydrophone (Bruel & Kjaer 8101, voltage sensitivity—184 db re 1V/µPa) and a battery power supply (B & K 2804) to reduce electromagnetic background noise. Using this equipment, sound pulses could be detected even if their peak-to-peak amplitude was smaller than the background noise. The hydrophone was placed in the middle of the tank with the maximum distance from the fish being 10 cm. Filming took place behind a curtain so that the operator could not be seen by the animals. All experiments were conducted in a sound-proof chamber.

BEHAVIOURAL ANALYSIS


Approach consisted of movement of one fish in the direction of the other, with unpaired fins adducted or slightly erected.

Chase and flight were recorded when a fish followed a fleeing individual.

Lateral display was regarded as the full extension of the dorsal, caudal and anal fins in a parallel, antiparallel or T-position. Fish in antiparallel position often moved in a circular pattern (=circling). If lateral display was interrupted by folding fins it was qualified as a new behavioural sequence. Lateral display and circling, at close distance, were accompanied regularly by rapid pectoral fin beating. Rapid pectoral fin beating resulted frequently in sound production. The vocalizing fish could be distinguished from its opponent by the rapid pectoral fin beating, which resulted in whole body vibrations.

Frontal display consisted of fish protruding their mouths towards each other and usually pivoting about 90° around the longitudinal axis with a lateral curving of the body in a sigmoid posture. 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. Frontal display was interrupted frequently by a lunge of one fish in which the mouth of the opponent was bitten (mouth biting).

Retreat (appeasement) was defined as an inclined position of the fish, in which all fins were abducted and movements generally reduced.

Agonistic behaviour duration (AD) constituted the sum of the duration of agonistic behavioural sequences or bouts excluding breaks for airbreathing.

Total contest duration (TD) was the period from the first agonistic behaviour until one fish retreated.

The age of the first young exhibiting a particular behavioural pattern either within the first 26 days or afterwards during the dyadic encounters (d), the number (n), the mean duration of behavioural patterns (sequences) and the total duration (s) per fight were determined.

ACOUSTICAL ANALYSES

Adult T. vitata generate sounds by enlarged pectoral fin tendons, which snap over basal elevations of fin rays like guitar strings (Kratochvil, 1978). In adults, double pulses
are usually produced by one fin due to two enhanced tendons; single pulses are rare. Thus the term single or double pulse always refers to one pectoral fin. During rapid alternating pectoral fin beating, series of broad-band double pulses termed sounds or croaks are emitted in adults.

Measurements of the following variables of up to five sounds were averaged per individual depending on the number of sounds emitted during an encounter. Sounds were analysed using S-Tools, the Integrated Workstation for Acoustics, Speech and Signal processing, developed by the Research Laboratory of Acoustics at the Austrian Academy of Science. Sampling frequency of all sound recordings was 16 kHz.

The following acoustical variables were measured (Fig. 1):

The number of single and double pulses within a croak was determined.

The pulse period was defined as the period between the onset of pulses produced by different pectoral fins. This could either be single pulses or, in the majority of cases, double pulses.

The dominant frequency of sounds was measured using cepstrum-smoothed power spectra. Power spectra was calculated using fast Fourier transform (FFT). The highest peak of the smoothed curve gives a better representation of the energy distribution than the highest peak energy of the power spectra (Noll, 1967).

Sound amplitude measurements were not carried out because peak-to-peak amplitude of earliest sounds made by juveniles were smaller than the background noise [see Fig. 5(b)]. Furthermore, the distance between fish and hydrophone varied during fighting and thus SPL measurements would not have been comparable.

**STATISTICAL ANALYSIS**

Data were analysed using SPSS (SPSS Inc.). The following behavioural patterns were subjected to statistical analysis: approach, lateral display, lateral display and sound production, frontal display. Mouth biting ended 98% of frontal display sequences and
thus was not calculated separately. On the other hand, flight, chase and retreat behaviour were seldomly observed during fights and were therefore not analysed statistically.

The number and duration of approach behaviour were determined individually and then averaged per fight. Behavioural patterns shown by both opponents, lateral display, lateral displays/sound production and frontal display, were determined per agonistic encounter. The number, mean and total duration of each behavioural pattern were determined.

Analyses of data distributions revealed departures from normality for behavioural, but not for acoustical variables.

RESULTS

ANIMAL GROWTH

Standard length was correlated highly with age ($r=0.86$, $n=66$, $P<0.001$) (Fig. 2). The average growth rate between day 27 and 132 was $0.19$ mm day$^{-1}$.

BEHAVIOURAL DEVELOPMENT WITHIN THE FIRST 26 DAYS

*Trichopsis vittata* fry started free-swimming on the second and third day after hatching. They moved slowly near their bubble nest or under floating plants. On the third or fourth day, they began feeding on *Artemia* nauplii, which were approached quickly and chased. No social behaviour was observed when fish encountered one another during the first 10 days.

Approach and flight were the first behavioural patterns to appear (day 11) (Fig. 3). Lateral display in T-position was recorded initially on day 18.

DEVELOPMENT OF AGONISTIC BEHAVIOUR FROM DAY 27 TO 4 MONTHS OF AGE

The frequency of approaches per fight ($r_s=0.196$, $n=66$, NS) and the mean duration did not vary with age ($r_s=0.065$, $n=66$, NS). Chases were observed for the first time on day 27 (Fig. 3).

Lateral displays changed qualitatively and quantitatively during the observation period. During the first dyadic encounters on day 27, lateral display
started out with slow movements and young fish displayed laterally in T-position or in parallel position. With increasing age, antiparallel postures and circling dominated. Furthermore, the speed of circling increased. The number of lateral display sequences per fight remained unchanged until day 82. It did, however, increase fourfold between days 82–132 (total correlation between number fight$^{-1}$ and age: $r_S=0.34$, $n=66$, $P<0.01$). The mean duration of lateral display sequences was not correlated with age ($r_S=-0.01$, $n=66$, NS) [Fig. 4(a)]. The total duration of lateral displays per fight increased with age ($r_S=0.29$, $n=66$, $P<0.05$). Rapid pectoral fin beating during lateral display was observed on consecutive experimental days from day 52 to day 92 and afterwards sporadically. Pectoral fin beating was first accompanied by sound production on day 57 (Fig. 3). From day 72 to day 87, sounds were recorded during at least one out of every three agonistic interactions. Afterwards, sounds were produced in the course of all fights. There was a 10-fold increase in the mean number of lateral display sequences which included sound production from day 62 to day 107 ($r_S=0.80$, $P<0.001$). The mean (and total) duration of these sequences was correlated positively with age (mean duration: $r_S=0.70$, $P<0.001$) [Fig. 4(a)].

Frontal display and mouth biting appeared at the age of 72 days (Fig. 3). They were observed at least in one out of three contests starting with day 102. Frontal display did not change qualitatively during the period studied. Its frequency per fight increased significantly with age ($r_S=0.65$, $n=66$, $P<0.001$). There was a fourfold increase in the mean duration of the frontal display sequences from its first appearance until the end of the experimental period (mean duration: $r_S=0.62$, $n=66$, $P<0.001$) [Fig. 4(b)]. Retreat behaviour occurred first on day 72 and at least once per trial day when fish were 107 days old. The performance of retreat remained unchanged throughout the experimental period.

The agonistic behaviour duration (AD) and total fight duration (TD) increased throughout the experiment, especially at the end of the third month.
Fig. 4. Development of mean duration (± s.e.) of single sequence of (a) lateral display, lateral display with sound production and (b) frontal display (n=12 for the first, second and third age group, n=15 for the fourth and fifth group; n=number of dyadic tests).

(Fig. 5). Both were correlated significantly with age (AD: $r_S=0.65$; TD: $r_S=0.60$; both: $n=66$, $P<0.001$).

DEVELOPMENT OF SOUND PRODUCTION

The mean number of single pulses within a sound uttered in an agonistic encounter decreased from 3–2 to 0–3 with increasing age ($r= -0.36$, $n=67$, $P<0.01$), whereas mean number of double pulses increases from 0 to 7–2 ($r=0.55$, $n=63$, $P<0.001$) [Figs 6 and 7(a)]. The pulse period increased significantly ($r=0.30$, $n=63$, $P<0.05$) [Fig. 7(b)]. Therefore, the total duration of sounds, the product of the pulse period and the number of pulses, became larger. The dominant frequency of sounds was correlated negatively with age ($r= -0.55$, $n=67$, $P<0.01$) (Fig. 8). It decreased from about 3.5 kHz in the youngest fish to about 1.5 kHz in the oldest fish investigated.
DEVELOPMENT OF COLORATION

Juvenile colour patterns changed over the 132 days of observation. Only a horizontal eye-bar, reaching from the mouth to the operculum, was present in all stages. From hatching until 4 weeks of age, the young exhibit several interrupted vertical bars on the trunk [Fig. 9(a)]. In the following days these bars gave way to single dots on the trunk and bases of unpaired fins. At 7 weeks, a difference in the body coloration of winners and losers was observed. Generally, winners were paler [Fig. 9(c)]. When fish were 8 weeks old, horizontal bars appeared clearly for the first time [Fig. 9(c)]. At this age, body coloration changed in the course of the contest. Horizontal stripes were exhibited especially during lateral display and unpaired fins were darkly coloured. During frontal displaying, horizontal stripes appeared mainly on the head and faded on the trunk, while unpaired fins kept their dark patterns [Fig. 9(d)]. After 12 weeks, no further changes were observed.

DISCUSSION

DEVELOPMENT OF VOCALIZATION

Sound production in T. vittata appeared first at the age of 8 weeks and occurred regularly from week 10 on. Thus, vocalization starts parallel to the development of lateral display and prior to other agonistic behavioural elements such as frontal display and mouth biting. This order of appearance is similar to that in the course of a fight between adult fish (Marshall, 1966; Ladich et al., 1992b). Individual differences in the first appearance of vocalization might be due to differences in the development of sound-generating structures and/or differences in the motivation to emit acoustic signals during an aggressive interaction. Agonistic encounters between individuals younger than 10 weeks are generally shorter and less aggressive than later on.
The character of sounds changed widely during ontogeny, probably due to the development of the sound-generating structures and, more importantly, to larger body size. Croaks consisted initially of single pulses, which indicates that each fin had only one enlarged tendon. Later, sounds are built up mostly of series of double pulses, which demonstrates that both pectoral tendons and thus the sound-producing mechanisms and pectoral fin-movements were fully developed. In adult fish cutting of one enlarged pectoral fin tendon always resulted in disappearance of one pulse (Kratochvil, 1978; Ladich et al., 1992b). The increase in the number of double pulses per croak probably reflects the more intense aggressive encounters, which is reflected in longer lateral display sequences as well as total fight durations. The increase in the pulse period and number of
Fig. 7. Correlation between age (x) and (a) the number of double pulses (y) and (b) the double pulse period \( \gamma_p \). Regression equations: \( y = 0.048x - 1.80, P < 0.01 \); \( \gamma_p = 0.08x + 22.27, P < 0.05 \).

Pulses results necessarily in a longer sound duration as the fish grow. In adult *T. vittata* both pulse period and number of pulses were no longer correlated to body size (Ladich et al., 1992a). Longer courtship calls in heavier fish were described in the damselfish *Dascyllus albisella* (Lobel & Mann, 1995).

Decreasing dominant sound frequencies with increasing body size is a general phenomenon in animals, and is based largely on resonance. Such a correlation is known in several adult fishes that produce pulsed sounds, including catfishes (Ladich, 1997b), damselfish (Myrberg et al., 1993; Lobel & Mann, 1995), and mormyrids (Crawford et al., 1997). This negative relationship between size and dominant frequencies of sounds was observed in adults of all three species of croaking gouramis *T. vittata*, *T. schalleri* (Ladiges, 1962) and *T. pumila* (Arnold, 1936) (Marshall, 1966; Ladich et al., 1992a). A size dependency of frequencies of calls has also been reported for other groups such as scarobins, theraponids and cichlids (Schneider, 1964; Myrberg et al., 1965; Bayoumi, 1970). Decreasing
main frequencies are also known in other vertebrates such as adult frogs (Davies & Halliday, 1978; Ryan, 1985). This is in accordance with our data because age is highly correlated with body size in our investigation ($r=0.87$). However, a decrease in frequency during development has, to our knowledge, been described only in higher vertebrates such as birds. Würdinger (1970) showed that in the greylag goose the dominant frequency of sounds is correlated negatively to the size of the tympaniform membranes.

The frequency changes during the ontogeny of croaking gouramis is probably based on the growth of the suprabranchial chamber (SBC), an airbreathing cavity dorsally of the gills in all labyrinth fishes. The SBC is suggested to be the main resonating structure in gouramis. Calculations of the resonance frequencies using Minnaert’s formula in adult $T$. vittata and $Colisa lalia$ (Hamilton-Buchanan) yielded frequencies close to the main energy of sounds (Schuster, 1989; Ladich & Yan, 1998). The large variation in dominant frequencies and other sounds is caused mainly by the differences in growth rates among juveniles.

DEVELOPMENT OF AGONISTIC BEHAVIOUR

Sound production seems to be a fixed element of the agonistic behavioural repertoire in juvenile and adult croaking gouramis. Vocalizations in juveniles is also known from representatives of other families such as cobitids, cichlids and tigerperches (Schneider, 1964; Lanzing, 1974; Valinsky & Rigley, 1981). We assume that the young of many fish species, in which adults vocalize, produce sounds. Currently, representatives of about 40 families of bony fishes are known to vocalize during aggressive behaviour (for a review see Ladich, 1997a). However, studies investigating the ontogeny of behaviour in vocal species have tended to neglect this signalling system. Myrberg et al. (1965) described sound production in an aggressive context in the adult cichlids $Cichlasoma nigrofasciatum$ ( Günther) and $Pterophyllum scalare$ (Cuvier & Valenciennes), but ontogenetic studies did not record sounds in juveniles (Bergmann, 1971;
Fig. 9. Development of coloration from 4 weeks of age until maturity. See text for details. Scale bars in all stages=5 mm. (d) Two young are shown during frontal display. (e) A winner is chasing the fleeing loser. Note the difference in body coloration.
Williams, 1972). The ontogenetic study on the anabantoids *Macropodus opercularis* (L.) (Davis & Kassel, 1975) did not mention sounds either, although adult fish vocalize occasionally (Kratochvil, 1985). This might either be explained by the absence of sounds in young, or by different experimental set-ups, and/or a true lack of appropriate equipment and recording conditions.

The order of the appearance of behaviour patterns in an agonistic context in croaking gouramis is similar to those of other family members such as the paradise fish *M. opercularis* (Davis & Kassel, 1975) and the blue gourami *Trichogaster trichopterus* (Pallas, 1770) (Tooker & Miller, 1980). Approach, flight and chase appear in the second or third week after hatching, while threatening displays as lateral display occur later (fourth to sixth week). Frontal display, mouth biting and retreat behaviour are the last behavioural patterns to appear. A similar order can be found in members of other families such as cichlids (Fraley & Fernald, 1982). This sequence followed that observed in individual encounters between two mature fish in all belontiids investigated (Davis & Kassel, 1975; Tooker & Miller, 1980; present study). Obviously, this is not a general characteristic in fishes. Barlow (1962) stated that the order of appearance of agonistic behaviours during ontogeny in the nandid *Badis badis* (Hamilton-Buchanan, 1822) is not the same as seen in well-developed fights between adults.

During ontogeny, lateral display in *T. vittata* develops from a spreading of the unpaired fins while in a simple lateral orientation to a facing fish (T-position), to a parallel orientation of both opponents, and finally to fish aligned antiparallelly, creating a circular movement. Furthermore, it includes rapid pectoral fin beating at the age of 6–7 weeks. From the eighth week on, lateral display and pectoral fin beating was increasingly accompanied by sound production. Frontal display differs to some degree in various Belontiidae. Contrary to that noted in croaking gouramis, it consists mainly of abduction of opercula in the paradise fish, and is obviously absent in the blue gourami (Davis & Kassel, 1975; Tooker & Miller, 1980). Retreat behaviour occurs simultaneously with frontal display and mouth biting at the age of 10 weeks in croaking gouramis, but earlier (seventh week) in the blue gourami (Tooker & Miller, 1980). Frontal display does not develop over the course of several weeks like lateral display; rather fish exhibit the ‘adult’ behavioural patterns from the onset.

The agonistic behavioural repertoire is fully developed at the age of 4 months, similarly to the blue gourami and several cichlids such as *Aequidens latifrons* (Gill, 1858), *A. portalegrensis* (Hensel, 1870) and *Cyprinodon variegatus* (Lacépède, 1803) (Ohm, 1964; Tooker & Miller, 1980; Dwyer & Beulig, 1991).

The increase in the duration and number of threat display sequences in the croaking gouramis led to longer fights over the period studied. The pronounced increase at the end of the third month is attributed mainly to the appearance of frontal display.

**DEVELOPMENT OF BODY COLORATION**

Fish exhibited characteristic changes in coloration, except for a horizontal eye bar, which was a constant marking throughout the observation period. Vertical bars were present on the flanks for the first four weeks and horizontal bars appeared as early as 8 weeks of age in losers of encounters. By this time, fish
start with rapid pectoral fin beating and sound production. Fully developed horizontal stripes appeared during lateral display at 10 weeks. Additionally, fish changed their coloration according to the outcome of aggressive interactions. Such a parallel appearance of behavioural motor and colour patterns was also observed in *Etroplus maculatus* (Bloch) (Wyman & Ward, 1973) and *Haplochromis burtoni* Günther (Fernald & Hirata, 1979) and is suggested for centrarchids (Brown & Colgan, 1985).

In summary, these data demonstrate that signalling in young croaking gouramis progresses from simple to complex patterns as additional behavioural elements and signal modalities are included. Our present study is the first one demonstrating that ontogenetic development of social signalling comprises characteristic changes in behaviour, vocalization and coloration in a teleost fish, the croaking gourami *T. vittata*.

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