Reprint

COMMUNICATION IN FISHES

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24

Intra- and Interspecific Electrocommunication among Sympatric Mormyrids in the Upper Zambezi River

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ABSTRACT

We have studied intra- and interspecific communication in a free-ranging group of three species of mormyrid fish in large 'naturally' equipped aquaria. The three species, *Cyphomyrus discorhynchus, Petrocephalus catostoma,* and *Hippopotamyrus szaboi,* had been sampled together from the Upper Zambezi River, Namibia, at the same time and place. They differed characteristically in territoriality, circadian activity, social behaviour, and intra- and interspecific agonistic behaviour. Rather stable hierarchies within and between the species were observed for over two years. The concurrent EOD activity of up to five fish was analyzed and unambiguously attributed to these five individuals. EOD activity was correlated with their overt, nocturnal behaviour. Members of the three species responded differentially to trespassing members of the other two species, probably based on the differences in EOD waveforms. Certain inter-discharge interval (IDI) patterns—preceding or accompanying agonistic behaviours such as aggression or threat displays—appeared to be similar for all species and 'understood' beyond species boundaries. We report evidence for intraspecific as well as interspecific cooperation. Members of the social, non-aggressive species *C. discorhynchus* seemed to 'invite' solitary *H. szaboi,* which were dominant over all other individuals of different species to join their group for protection during communal foraging.

Key Words: Electric organ discharge; Inter-discharge intervals; Territoriality; Schooling; Hierarchy; Aggression; Threat; Social behaviour; *Cyphomyrus discorhynchus; Petrocephalus catostoma; Hippopotamyrus szaboi.*

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1. INTRODUCTION

Weakly electric Mormyridae represent the largest fish family endemic to African freshwaters with at least 188 species (Gosse, 1984). This number corresponds to a total of freshwater fish species of 190 found in all of Europe. Whereas the Central Congo basin alone holds at least 75 mormyrid species, the adjacent, southern Zambezi region holds 10 species, and the relatively species-rich Upper Zambezi River system only seven species (Skelton, 2001). While these numbers are likely to increase slowly with better knowledge of differentiation between allopatric populations (already observed in a few instances, see below), they reflect strong contrasts between ichthyological provinces.

We chose the Upper Zambezi region for its relatively low and still-manageable species abundance to study species differences and adaptive specializations in ecology and behaviour. In spite of considerable advances over the years by a number of field studies (such as Moller et al., 1979; Hopkins, 1981; Friedman et al., 1996; Crawford et al., 1997; Kramer, 1997), our knowledge of the life history and ecology of mormyrids has remained limited and its study difficult and elusive. What was known about mormyrids appeared in the popular and scientific literature as 'they live in turbid waters, eat small invertebrates, such as insect larvae, and are active at night'.

We wanted to find answers to questions such as: (1) what is the diversity of ecological niches held by sympatric species, and in what ways do these niches differ; (2) is there evidence for interspecific communication, cooperation or predator pressure affecting the evolution of their communication system and the differentiation of sympatric populations; and (3) do sympatric mormyrids exhibit differences in the use of and competition for territories such as breeding and day-time resting places? All these questions are best studied in the field; however, technical and logistical difficulties have prevented this for the major part.

Here we report observations made in large, up to 3000-l aquaria, mimicking naturalistic conditions as closely as possible. We have observed several specimens belonging to three mormyrid species collected from the same location on the Upper Zambezi River on the same day. Skelton (2001) provides some basic information on the biology and ecology on two of them; little is published on the third, an only recently described species (Kramer et al., 2004). Some of our data were reported earlier in a shorter form (Scheffel and Kramer, 2000).

2. METHODS

2.1 Animals and Handling

All fish were sampled from the same location on the Upper Zambezi River at Katima Mulilo, East Caprivi, Namibia, approx. 17°29′30″S, 24°16′18″E, on

9 August 1994, and reached our laboratory within two days. Following Skelton (1993, 2001) there were 12 specimens of churchill, *Petrocephalus catostoma* (Günther, 1866), 7 specimens of the Zambezi parrotfish, *Cyphomyrus discorhynchus* (Peters, 1852), and 7 specimens of slender stonebasher, recently described as the new species, *Hippopotamyrus szaboi* (Kramer et al., 2004), that is distinct from its sibling species, *H. ansorgii* (Boulenger, 1905). In the laboratory, an initial L:D cycle of 12:12 h was changed to 14:10 h, simulating the Namibian summer period. Water temperature and conductivity were 25 ± 0.5°C and 100–200 µS/cm. To keep the water conductivity constant, part of the aquarium water was exchanged for deionized water about every two weeks.

2.2 Electric Organ Discharge Waveform

We recorded the electric organ discharge (EOD) waveforms from individual specimens kept in separate tanks (150- up to 300-l), water conductivity and temperature, 100 ± 2 µS/cm and 25 ± 0.2°C). We waited at least two days before recording in order to exclude any effect on the discharge waveform due to conductivity changes (see Bell et al., 1976; Bratton and Kramer, 1988; Kramer and Kuhn, 1993). Taking advantage of the churchills' constant day-time territories and hiding places, we were able to record their EODs in the communal tank.

EODs were differentially recorded with carbon electrodes placed, respectively, near the head and tail of a resting test fish using a digital oscilloscope (Tektronix TDS 420; bandwidth 100 MHz, vertical resolution 12 bit) from which data were transferred to computer for storage and analysis. We normalized the head-positive first peak of an EOD to the same amplitude of 1, and subsequently determined phase durations, amplitude ratios and phase areas using customized routines programmed with a signal analysis package, Famos v 3.1 (IMC, Berlin).

2.3 Behaviour and Electrocommunication

We maintained three stable populations to study behavioural strategies and electrocommunication, and several less permanent populations in order to study certain points (as specified in Results). The *H. szaboi* were intolerant of each other and had to be separated. In a 3000-l tank we kept eight *P. catostoma*, two *C. discorhynchus* and one *H. szaboi* together for more than 1.5 years. We kept four *P. catostoma* in a 720-l tank but, after one year, replaced one of them with a *H. szaboi*, and introduced one *C. discorhynchus* after another one and a half years. In a 600-l tank, we kept a group of four *C. discorhynchus* and added one *P. catostoma* after one year.

In our 3000-l (3 × 1 × 1 m^3) observation tank, we imitated rocky shore areas and sand banks planted with dense swamp shrubs with submersed roots and water plants, offering many hiding places (Fig. 24.1A). A waterfall and periodically timed rain created water turbulence and currents. The fish's nocturnal behaviour was observed and taped using an infrared-sensitive video camera and infrared illumination. The other two tanks were similarly equipped but without sandbanks and rainfall.

EODs were recorded with at least two pairs of carbon electrodes connected to separate differential amplifiers for each pair, and separately stored on the two audio-tracks of video tape (Fig. 24.1B), or the tracks of a synchronized six-channel instrumentation recorder (Racal Store Plus VL). We digitized selected audio sequences off-line for disk storage, using a four-channel transputer system (Hydra Light with H109-ADC; Kinzinger Systeme GmbH, Rastatt; Fig. 24.1C). Customized routines programmed with the software package DIGIS v 3.43 (GfS mbH, Aachen) displayed EOD representations on a computer screen, allowing for visual discrimination between fish by comparison of waveforms and amplitudes. Sorted and synchronized EOD recordings are shown as Inter-Discharge Interval (IDI) sequences for each fish for defined social interactions (Fig. 24.1D).

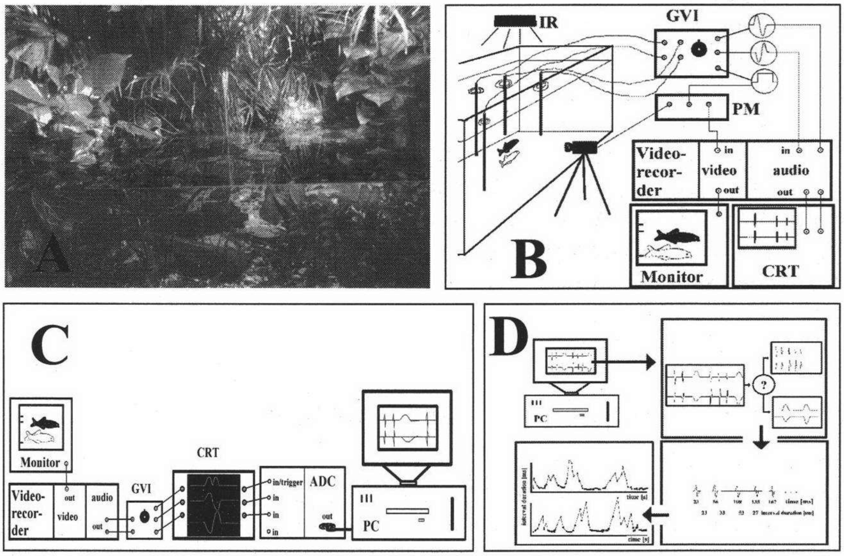

Fig. 24.1: Analysis of behaviour and electrocommunication in freely swimming nocturnal mormyrids. (A) Partial view of an observation and recording tank. (B) Apparatus for recording overt behaviour and EODs. The behaviour was videotaped using an infrared-sensitive camera under infrared illumination (IR), while the EODs were measured by pairs of carbon electrodes, connected to separate differential amplifiers (GVI), and stored on the audio tracks of video tape. (C) Selected EOD sequences were digitized by a transputer system comprising an ADC and stored in a computer disk. (D) EODs from different fish were identified using small differences in EOD waveform, as well as polarity and amplitude cues. Such identified EOD sequences served for sequential IDI diagram construction.

3. RESULTS

3.1 EOD Waveforms

EOD waveforms differed characteristically between species (Fig. 24.2A; in agreement with Kramer 1996, his Fig. 5.4). The EOD of *H. szaboi* lasted the longest and was monopolar. Its head-positive pulse of 1.3 ms average duration was followed by a long and weak head-negative post-potential (Fig. 24.2B).

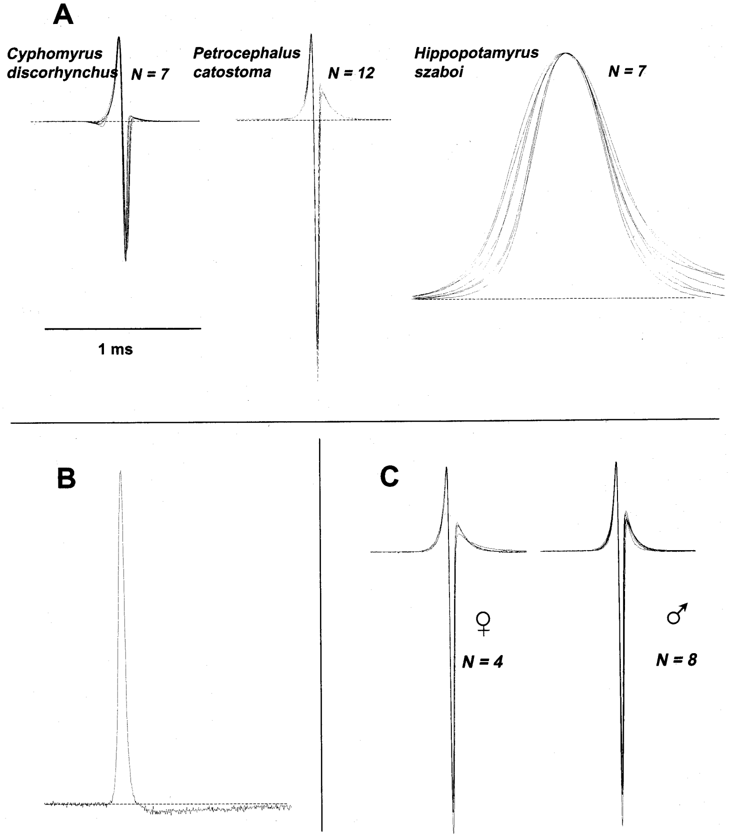

Fig. 24.2: Species-specific EOD waveforms and its individual variation for the three sympatric species of mormyrids used in the present study. (A) Individual EOD waveforms of all fish superimposed, separately for each species (*N*, number of individuals). Ordinate (not shown): linear voltage, with head-positivity upwards; dashed baseline = zero Volt; time bar identical for all. (B) Single EOD pulse of a *H. szaboi* at low temporal resolution shows a long postpotential phase. (C) Cryptic sex difference in *P. catostoma*: the second positive peak in male EODs (normalized to same first positive peak amplitude) tends to be stronger than in females of the same size.

C. discorhynchus followed a more typical bipolar mormyrid pattern (no net current) with a head-positive main phase followed by a strong head-negative second phase lasting, on average, 0.19 ms (disregarding weak pre- and post-potentials). *P. catostoma* also emits a bipolar EOD with three phases composed of a short and strong head-negative main phase preceded and followed, respectively, by a positive phase of much weaker amplitude (P1 and P2) lasting about 0.4 ms in total duration.

Some waveform parameters of *P. catostoma* (such as the N-amplitude, the P2 amplitude and phase durations) changed within two and a half years of observation (for a detailed discussion on the dependency of waveform parameters on standard length, see Kramer, 1997). In *P. catostoma,* first sexual maturity was estimated for fish measuring from about 5.2 cm SL on (or 40% maximum size for that species; Kramer, 1997). At the end of our study, all specimens exceeded a standard length of 9 cm, and the shape of the anal fin base revealed their sex (straight line in females, kinked in males; see also Moller et al., 2004).

For better comparison between the sexes, the waveforms of *P. catostoma* EODs are superimposed for males ($N = 8$) and females ($N = 4$) separately in Fig. 24.2C. The P2 amplitude in male EODs was stronger than in females of the same size, corroborated by studies that surveyed more specimens (Kramer, 1997; Kramer and Van der Bank, 2000). For our analyses, small differences between individual fishes' EODs served to identify the sender even when interacting freely with conspecifics in large aquaria, and also to establish IDI patterns during social encounters.

3.2 Behaviour

Clear species differences in behaviour and characteristic interspecific response patterns between the coexisting species have been summarized in Fig. 24.3A.

3.2.1 P. catostoma

Both sexes of *P. catostoma* occupied small mosaic-like territories that fish patrolled by day and night. Once established, the territories of *P. catostoma* remained constant within discrete borders for prolonged periods of time. In rocky areas, these borders also extended vertically, and the hiding places of neighbours were sometimes stacked on top of each other (Fig. 24.4). Whether or not a territorial *P. catostoma* attacked an intruder depended very much on the intruder species. As shown in Fig. 24.3B, trespassing conspecifics were never tolerated and always attacked, whereas trespassing *H. szaboi* were never attacked and always avoided. Trespassing schools or single fish of *C. discorhynchus* were attacked at an intermediate rate, but they were avoided when a *H. szaboi* was a member of the group. *P. catostoma* when hungry with no food present spontaneously formed schools at nightfall (Fig. 24.3C).

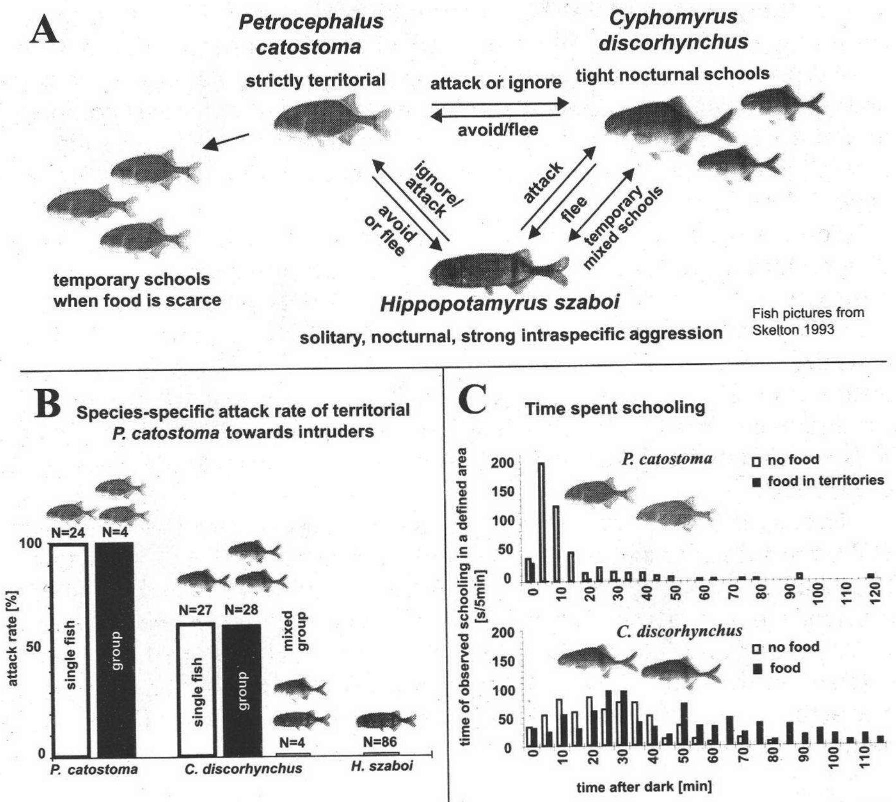

Fig. 24.3: (A) Summary of species-specific behaviour and interspecific relationships. (B) The frequency of attacks on intruders of different species in a territorial *P. catostoma*. Any fish approaching the territory holder closer than two fish lengths was tallied an intruder. The bar graph shows the percentage of attacks on an intruder (relative to all intrusions by a member of that species), sampled over the beginning of three nights (total sampling time: 90 min); white bars: attacks on single fish; black bars: attacks on groups. (C) Schooling behaviour in *P. catostoma* and *C. discorhynchus* in a mixed species group of 8 *P. catostoma*, 2 *C. discorhynchus*, and 1 *H. szaboi*. We observed the middle sector of 1 m^2 bottom area in a 3000-l tank for the first two hours of a night. Ordinate: total time of schooling/successive 5-min observation intervals (in s); abscissa: time from dark (min). White bars: time spent schooling in a night without food in the tank. Black bars: same as white bars, but with plenty of food available (following night). Schools were defined as 'at least two fish within 2 fish-lengths swimming into the same direction without any aggression'.

3.2.2 *C. discorhynchus*

Cyphomyrus discorhynchus were only active at night and would not leave their daytime hiding places even at the slightest shimmer of light (for example, from the oscilloscope screen, even when facing away from the aquarium). Often members of a group swam quickly through open water in a single file

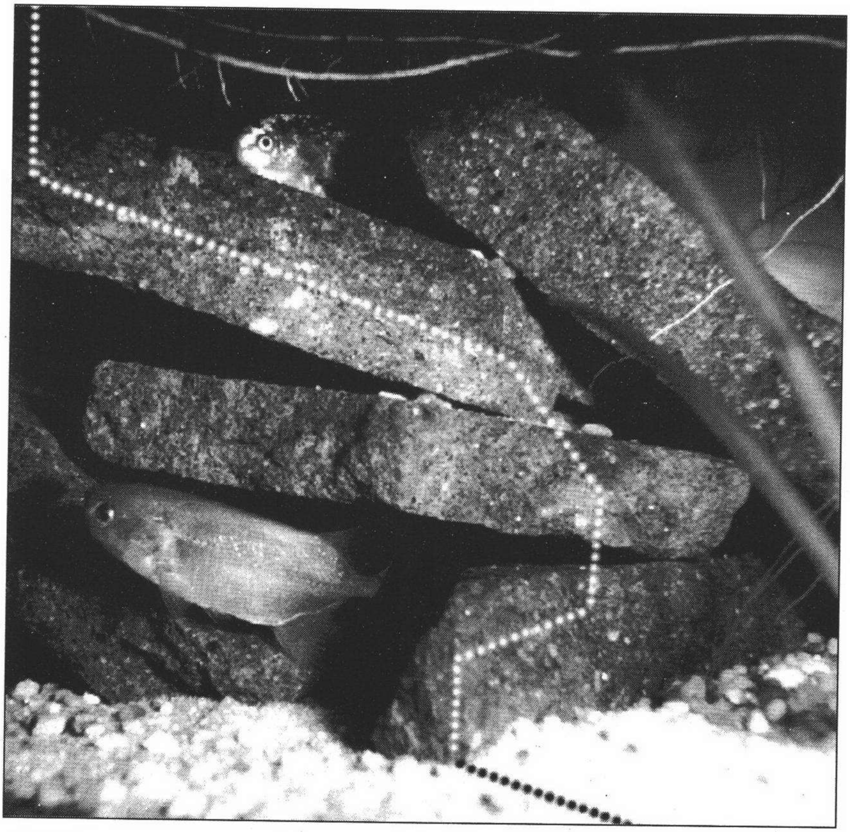

Fig. 24.4: The territorial border (dotted line) between these two *P. catostoma* remained constant for more than 2 years.

to gather as a tight foraging school at another place ('single file swimming', Moller, 1976). Gathering or group movement was often initiated by the whole group swimming fast on a circular path. Schooling behaviour occurred regardless of whether food was present or not (Fig. 24.3C).

Mixed shoaling between solitary *H. szaboi* and *C. discorhynchus* was regularly observed. Either *H. szaboi* joined a moving *C. discorhynchus* group or was followed by a *C. discorhynchus* group swimming in a single file. Sometimes a group of *C. discorhynchus* circled around a stationary *H. szaboi* in mid-water, apparently 'inviting' *H. szaboi* to join their group (see Fig. 24.8C), termed *schooling invitation*. Regardless of whether a group of *C. discorhynchus* consisted of 2, 4, or 6 members, they invited solitary *H. szaboi* to join.

3.2.3 H. szaboi

Hippopotamyrus szaboi were totally inactive during the day when they usually rested in dark and narrow rocky niches. At night, they roamed about the entire aquarium and usually ignored all other fish, including the territorial *P. catostoma*. However, even in our largest aquarium with a bottom area of 3 m^2, *H. szaboi* did not tolerate a single conspecific that, if present, was attacked viciously.

3.3 Electrocommunication in Social Encounters

3.3.1 Inter-Discharge-Interval (IDI) Patterns

We found clear species- and context-specific IDI patterns that accompanied defined interactions in social behaviour.

3.3.1.1 *P. catostoma*

Patrolling their territories, *P. catostoma* discharged highly variable IDI of about 40 to 100 ms, interspersed by one or a few shorter IDIs of about 20 ms (Fig. 24.5A). When threatened by an intruding *H. szaboi*, *P. catostoma* changed to a series of regular short IDI of about 20 ms (Fig. 24.5B,C). A non-electric, larger fish (goldfish), placed into the tank just before lights went off, evoked a similar discharge pattern (Fig. 24.5D). Territorial neighbours joined in these regular IDI patterns (Fig. 24.6A).

Territorial *P. catostoma* that visited a neighbour's territory at night did so while stopping their discharge for prolonged periods of time ('social silence'; Moller et al., 1989). To return home, trespassers often made a detour around a conspecific's territory. On arrival in their own territory, 'exploring' *P. catostoma* resumed discharging (Fig. 24.6B).

3.3.1.2 *C. discorhynchus*

While foraging together, a pair of *C. discorhynchus* discharged synchronized short IDIs of 20–50 ms as revealed by the presence of a high percentage of Preferred Latencies of about 11 ms (Fig. 24.7A, B; for Preferred Latencies, also termed echo responses, see Bauer and Kramer, 1974; Bell et al., 1974; reviews Kramer, 1990, 1996). When attacked, *C. discorhynchus* often ceased discharging for about 200–300 ms; these short discharge breaks sometimes occurred synchronized in both, apparently flight-motivated *C. discorhynchus* simultaneously. One of these instances is shown in Fig. 24.7A, where both *C. discorhynchus* stopped discharging for about 0.3 s when attacked by one of the two *P. catostoma* present (coded orange and red). *H. szaboi* passing by in the background was not involved but may have triggered the regular 3-s IDI pattern in the *P. catostoma* (red) shown on the left in Fig. 24.7A.

When swimming in mid-water, the leading *C. discorhynchus* in a pair discharged in characteristic, long sequences of regular, short IDIs of about 20 ms, the duration of which slowly increased, but became shorter again when the swimming direction changed. The following fish discharged less regularly and at a lower rate, but joined in the more regular pattern when following a change in swimming direction (Fig. 24.8B, D).

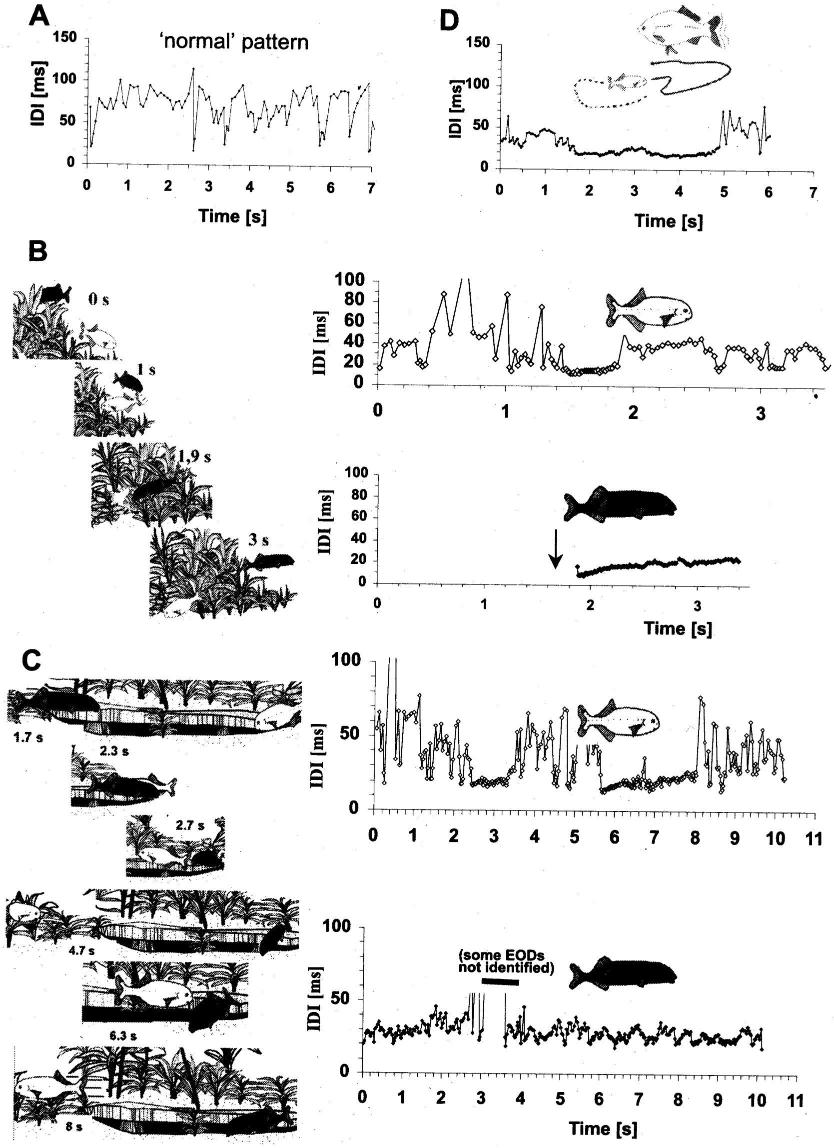

Fig. 24.5: Interspecific relationships for *P. catostoma* at night. (A) IDI pattern over a period of time of a *P. catostoma* while patrolling its territory. Each IDI (in ms) is plotted individually over time (s). (B) Sequence of regular, short IDIs in a *P. catostoma* (white) during escape manoeuvres evoked by an attacking *H. szaboi* (black). Note *H. szaboi's* HD display beginning just 0.2 s after attack onset (arrow). (C) When passing by a non-attacking *H. szaboi* intruding into its territory, a *P. catostoma* displays sequences of regular, short IDIs (2 instances shown). (D) Similar regular IDI pattern evoked by the presence of a non-electric, big goldfish introduced into the aquarium a few minutes before dark that was slowly swimming about the aquarium.

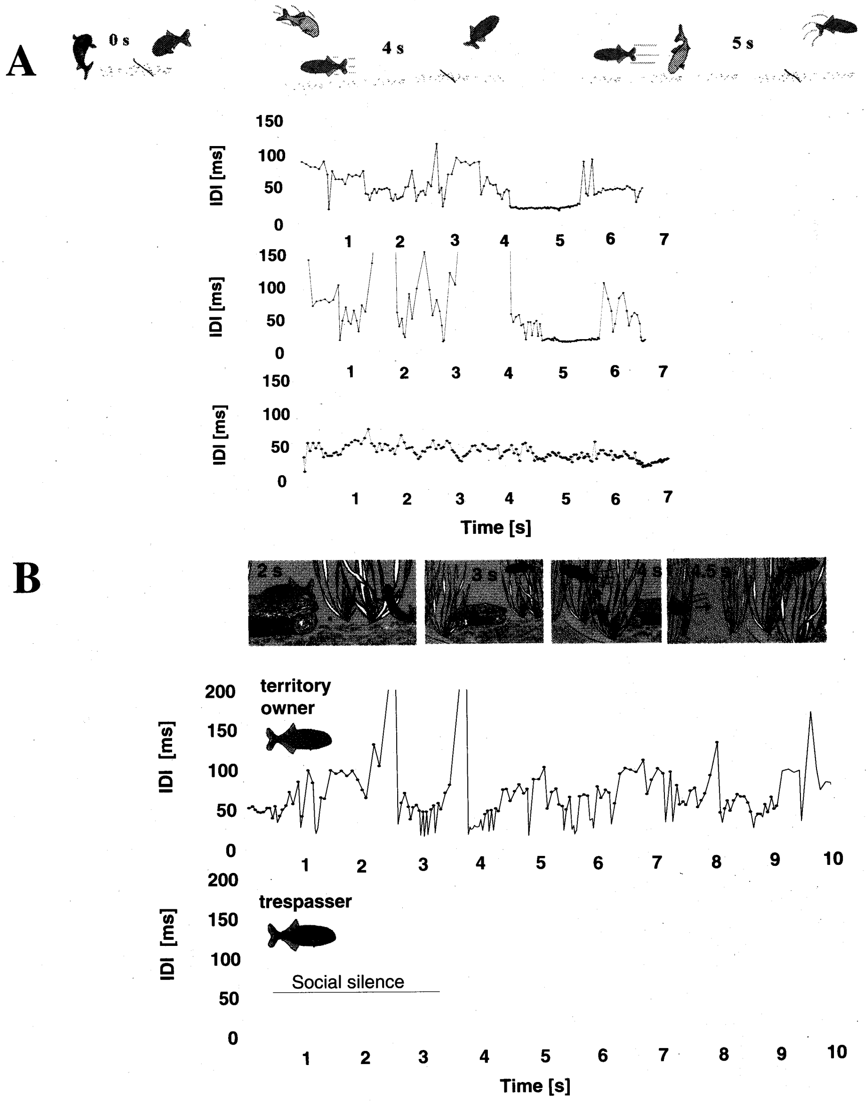

Fig. 24.6: Social interactions and IDI patterns in *Petrocephalus catostoma* (diagrams as in Fig. 24.5). (A) IDI pattern for two territory-holding *P. catostoma* patrolling (without interaction) at their common territory boundary (line), both giving regular sequences of short IDI when threatened by a trespassing *H. szaboi* (yellow). (B) A *P. catostoma* (red) trespassing its neighbour's (blue) territory turns off its EOD ('social silence') and only resumes discharging when back in its own territory. Note how the electrically 'silent' trespasser curves around the territory-owner. On arrival in its own territory, short reciprocal sham attacks occur.

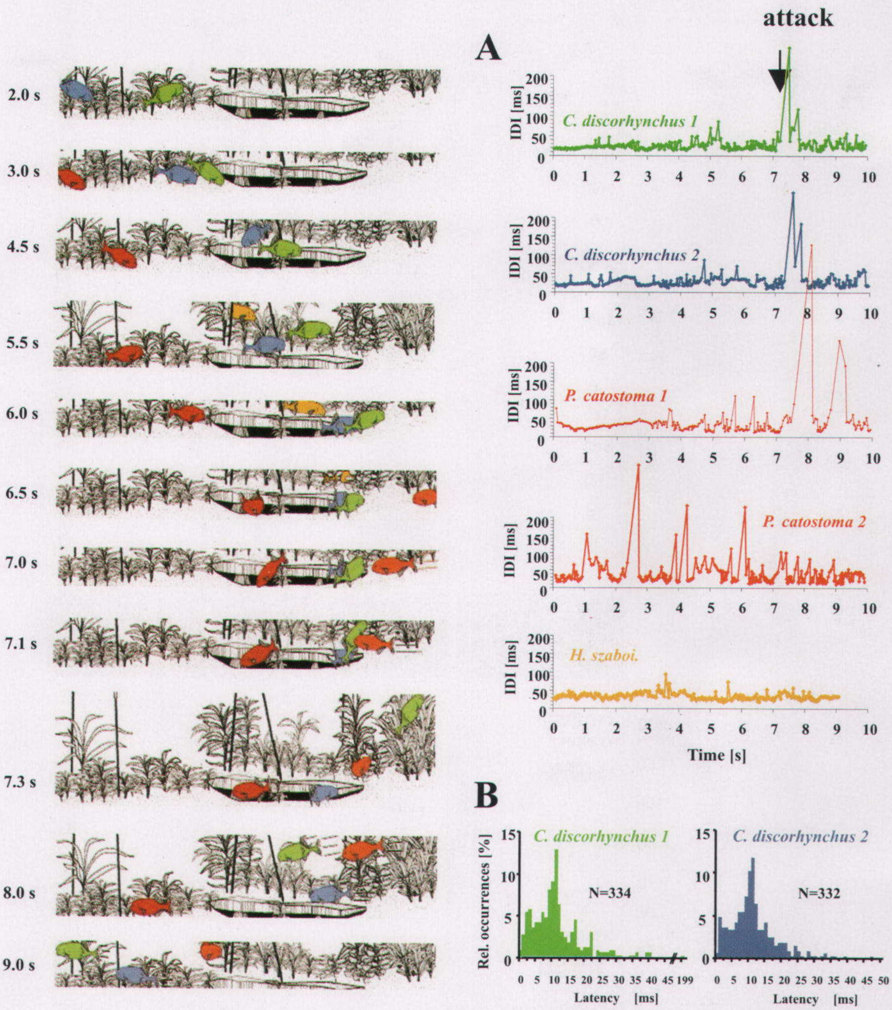

Fig. 24.7: IDI patterns in a pair of *C. discorhynchus* (blue and green) in the presence of 2 *P. catostoma* (orange, territory holder; red, its neighbour) and a *H. szaboi* (yellow). (A) Note the simultaneous discharge breaks in both *C. discorhynchus* when attacked by *P. catostoma* no. 2 (orange). (B) High proportion of mutual Preferred Latencies displayed by the *C. discorhynchus* pair, shown as histograms (ordinate: relative occurrences (%), abscissa: inter-individual response time (latency) between EODs (ms).

When a *H. szaboi* joined a pair of *C. discorhynchus* displaying 'schooling invitation', we observed characteristic IDI-patterns in both species. *C. discorhynchus* displayed sequences (of variable length) of regular, short IDI of about 20 ms that slowly became longer, resembling the IDI pattern seen in the leading fish of a pair of *C. discorhynchus* (Fig. 24.8C, D).

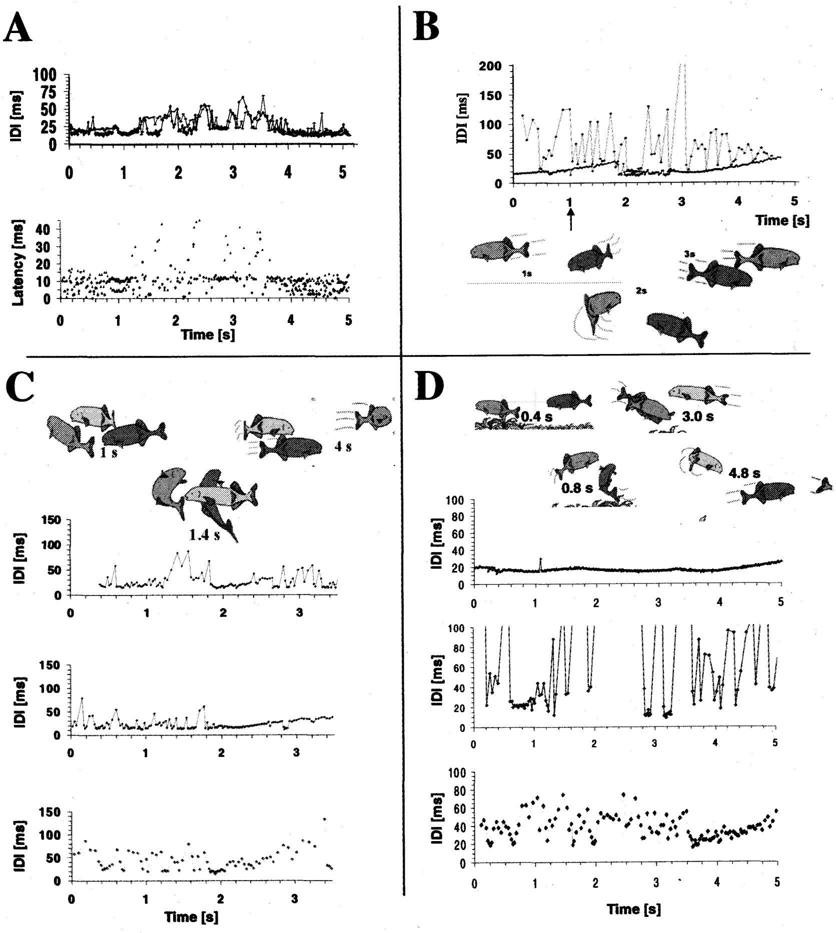

Fig. 24.8: IDI patterns of schooling *C. discorhynchus* (ordinates and abscissae, see Fig. 24.5). (A) IDI pattern shown by a close pair of *C. discorhynchus* foraging near the bottom. Individuals harmonized their IDI patterns (upper panel) by discharging in Preferred Latencies (lower panel; note high density of points around 11 ms). Latency is the time between the discharges of two individuals. (B) IDI pattern in a pair of *C. discorhynchus* swimming fast in mid-water. Note the characteristic pattern composed of regular short IDI, displayed by the leading fish, whereas the following one discharged in longer, irregular IDI but joined the regular pattern of short IDI for a fast, close turn-around. (C, D) Joint schooling in *C. discorhynchus* and *H. szaboi*. (C) A pair of *C. discorhynchus* (green and blue) circled around a single *H. szaboi* (yellow) and then resumed swimming further on with the *H. szaboi* following. During this episode, one or both *C. discorhynchus* displayed interval patterns else only seen intraspecifically in leading fish. When joining, *H. szaboi* changed from mostly irregular IDI to regular short ones, the duration of which gradually increased while becoming more irregular again. (D) IDI patterns in a pair of two fast-swimming *C. discorhynchus* and a *H. szaboi* eventually joining. Note the highly regular pattern of short IDIs displayed by the leading *C. discorhynchus* individual and the IDI pattern change in *H. szaboi* when joining (at about 3.4 s).

3.3.1.3 *H. szaboi*

Hippopotamyrus szaboi usually discharged irregular IDIs lasting from 20 to 50 ms while swimming and foraging (Figs. 24.7A, 24.9A). When joining a *C. discorhynchus* group, *H. szaboi* changed to regular, short IDIs of about 20 ms that gradually increased and became more irregular (Fig. 24.8C, D). Whenever *H. szaboi* attacked another fish, irrespective of species, an initial discharge break was followed by a stereotyped high-frequency burst of IDIs, as short as 8 ms, that slowly increased in duration (HD or high discharge rate display; Figs. 24.5B, 24.9B). When confronting a conspecific (which was introduced for only a short time and stayed under surveillance to avoid serious injury), *H. szaboi* showed typical threat displays, such as antiparallel display and short attacks. Both fish would display many short HDs alternating with discharge breaks, the HDs resembling those displayed while attacking, but, unlike later stages of the fight (see below), there was no strict temporal association between HDs and overt attacks (Fig. 24.9C). When a fish became dominant, it continued to display HDs with initial discharge breaks that, under these conditions, coincided with its attack behaviour. The submissive fish discharged in regular short IDIs displaying HDs (lacking the initial discharge breaks), which exactly coincided with its escape from the attacker (Fig. 24.9D).

4. DISCUSSION

EOD waveforms showed little variation between individuals and were species-specific, which was in agreement with field recordings (Kramer, 1996). The difference in EOD waveform duration that characterizes our three species agrees with a hypothesis stating that brief EODs are typical of social species (Hopkins and Bass, 1981). Short EODs would reduce the probability of jamming their electric signals in dense schools. This hypothesis, however, does not seem to be generally applicable. The large and apparently non-social *Mormyrops* species of West and southern Africa do generate brief EODs (Kramer, pers. obs.). Likewise, the three-species complex of *H. ansorgi/szaboi* in the Upper Zambezi system differs widely in EOD pulse duration, in spite of no known differences in ecology or spacing (Kramer et al., 2004 report on a third species for the Kwando River, a Zambezi tributary). Bulldog males, from the Upper Zambezi, when sexually mature, appear to be social and emit long-duration EODs, which are up to 11x the average duration of female EODs (Kramer, 1997).

The species-specific EOD waveforms and the specific behavioural relationships observed between species point to an important role of the EOD waveforms in discrimination between species. EOD discrimination based on a time-measuring mechanism for EODs essentially resembling single-cycle square-wave pulses of different duration was suggested by Hopkins (1986) for *a B. brachyistius* species complex. Inter- and intraspecific discrimination between more complex EODs (Graff and Kramer, 1992), even when of almost

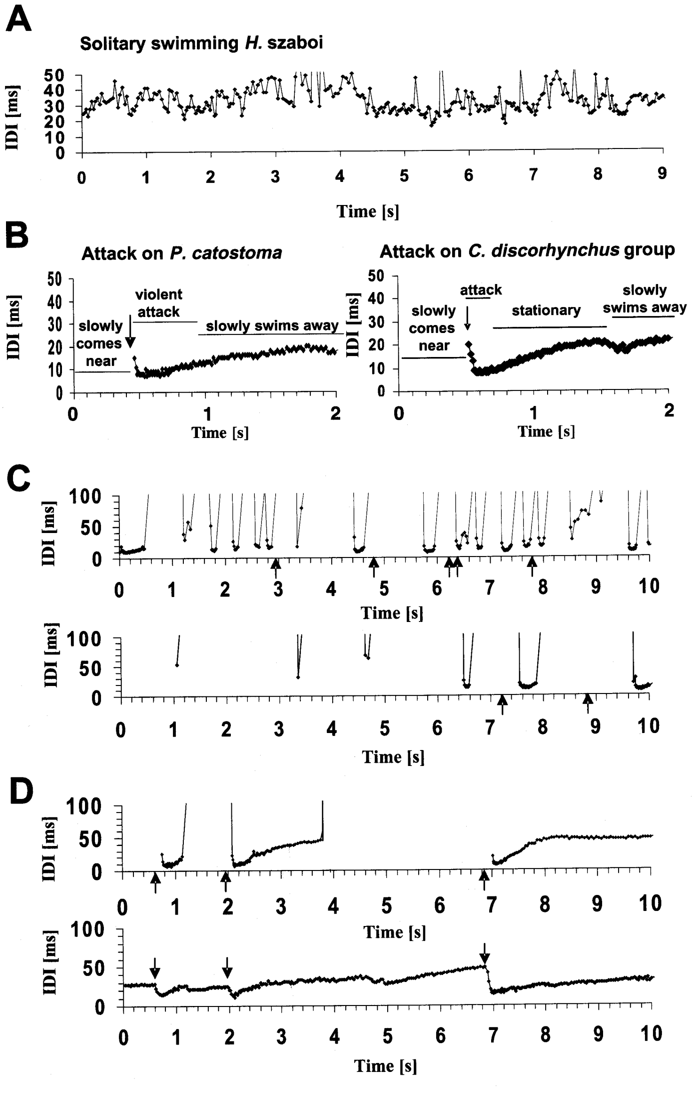

Fig. 24.9: IDI patterns in *H. szaboi.* (A) Pattern of irregular IDI observed in a swimming fish when not interacting with other fish. (B) Stereotyped HD displays accompanying *H. szaboi*'s attacks on a *P. catostoma* and a *C. discorhynchus.* (C) Intraspecific fight and threatening behaviour between two *H. szaboi* that were unfamiliar to each other. The fish showed mutual antiparallel displays and short attacks (arrows below abscissae denote who attacked when). Note that the HD discharge bursts did not coincide with the exact times of attacking. (D) When one fish had become clearly dominant, both attacks (arrows up) and escape behaviour (arrows down) coincided precisely with discharge bursts (HD) for both fish. The dominant fish announced an imminent attack by a discharge break, followed by an HD display, whereas the submissive fish, when attacked, increased its discharge rate to series of regular short intervals without any breaks.

identical waveform differing on a microsecond-scale, and of identical Fourier amplitude spectrum or not, was demonstrated in *Pollimyrus adspersus* (Paintner and Kramer, 2003). The EOD waveform differences between the species studied in the present chapter are far beyond the discrimination limen as determined in *Pollimyrus adspersus*, and allow individual discrimination between conspecifics.

From an electrosensory point of view it is, therefore, not surprising when a territorial *P. catostoma* decides to chase away an intruding *C. discorhynchus* but to shy away from attacking a *H. szaboi*. The monopolar *H. szaboi* EOD is detected by predatory catfish (Hanika and Kramer, 2000) and, because of its large DC component, can, therefore, also efficiently stimulate the ampullary electroreceptor organs of mormyrids, in addition to the knollenorgans (for receptor organ responses to *Gnathonemus petersii's* EODs, see Bell, 1986). Simultaneous afference by two electrosensory channels (rather than just the Knollenorgan pathway as in *G. petersii*; Bell, 1986) might render *H. szaboi's*, EOD particularly conspicuous and easily distinguishable from that of most other species, and similar (except for their strength) to the monopolar, strong EOD of the electric catfish *Malapterurus electricus*. It appears safe to assume that this predator's EODs evoke alarm in any mormyrid community (on electric catfish ethology, see Bauer, 1968; Rankin and Moller, 1986, 1992).

The clear context-specific IDI patterns appear to signal imminent behavioural actions to conspecifics and even to other sympatric species. The importance of context-specific IDI patterns in intra- and also interspecific interactions has already been demonstrated in other mormyrid species (Kramer and Kuhn, 1993; Kramer and Lücker, 1990).

The observation of regularized IDI patterns of threatened *P. catostoma*, in which neighbours may join in, gives reason to believe that these patterns may function as an early warning system—maybe ritualized from probing motor acts (probing motor acts, see Toerring and Belbenoit, 1979). By reciprocating their altruism, *P. catostoma* individuals could keep low the success of nocturnal predators within their neighbourhood. Reciprocal alarm signals between individually known neighbours ('dear enemies') pay off when the territorial borders are stable, resulting in less effort for territorial defence (Smith, 1986; Hanika and Kramer, 2005). 'Dear enemies' are potential schooling partners for *P. catostoma* when food in their territories gets scarce. Trespassing neighbours avoid being attacked by the territory owner by turning off their EOD.

Closely associated *C. discorhynchus* pairs synchronized their IDI patterns by Preferred Latencies ('echo response'). Of course, many Preferred Latencies are likely to reduce temporal overlap (jamming) of EODs within a school, but synchronization of EODs could also be an important factor to facilitate coordination and school cohesion. In a normally schooling species, *Marcusenius cyprinoides*, schooling behaviour was absent in fish whose electric organ had been surgically 'silenced' (Moller, 1976). The regular, high-frequency IDI patterns of a leading *C. discorhynchus* in a swimming school may function as a beacon to other fish to follow, but could also play a communicative role, e.g. as a startle response alarming conspecifics, or even as an invitation signal to *H. szaboi* to join their group. An advantage of mixed schooling for *C. discorhynchus* might result from a reduced risk of being chased away by territorial *P. catostoma*, whereas the non-social *H. szaboi* might gain by joining a heterospecific school of *C. discorhynchus* reducing predation risk by dilution (attack abatement; Turner and Pitcher, 1986). In the Upper Zambezi, nocturnal electroreceptive predators for mormyrids are, for example, *Schilbe* and *Clarias* catfish (Merron, 1993; Winemiller and Kelso-Winemiller, 1996) that can detect the spectral low-frequency components of bipolar long-duration EODs, or of monopolar waveform (Hanika and Kramer, 2000).

Discharge cessations render a fish 'electrically invisible', which appears advantageous for both attack and escape. The prevalence of short discharge cessations in agonistic contexts, observed in the present study in both intra- and interspecific interactions, seems to betray a communication function such as in threatening. For example, the high frequency bursts emitted by *H. szaboi* that start with a discharge break and accompany attacks are an obvious aggressive warning signal for every mormyrid around, e.g. when signalling to a *C. discorhynchus* school an 'unwillingness' to join. In agonistic conflict situations with unfamiliar conspecifics, repeated cascades of HDs occurred that did not coincide precisely with attack movements. This suggested a ritualized form of threatening behaviour resulting from a conflict in intraspecific communication. Similar burst cascades correlated with threat behaviour are known from other mormyrids (such as *Marcusenius senegalensis*, Scheffel and Kramer, 1997; *M. macrolepidotus*, Werneyer and Kramer, 2002, 2005; *Gnathonemus petersii*, Kramer, 1976).

Our observations have provided good evidence for the importance of inter-discharge interval (IDI) codes, in addition to details of the EOD waveform, in intra- as well as interspecific communication in mormyrid fish. The present study has shown a tiny glimpse of the complexity that characterizes mormyrid intra- and interspecific ecoethology. There are two prerequisites to significant advances in the biology of mormyrids: (1) improving the current, often unsatisfactory state of systematics by critical comparisons of allo- and sympatric populations; and (2) field observations to test some of our hypotheses, and to learn more about what life is like among some of the most fascinating creatures on earth.

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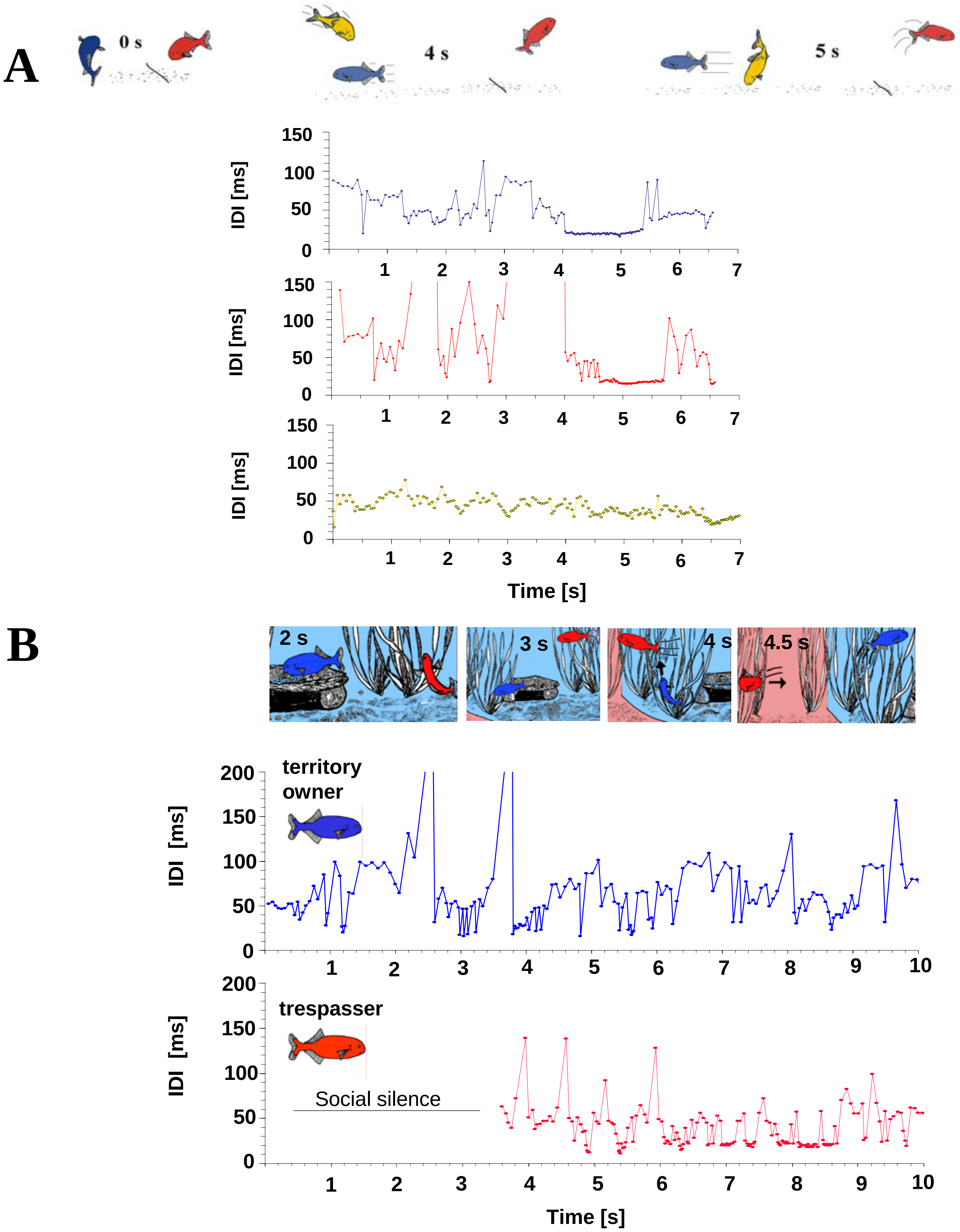

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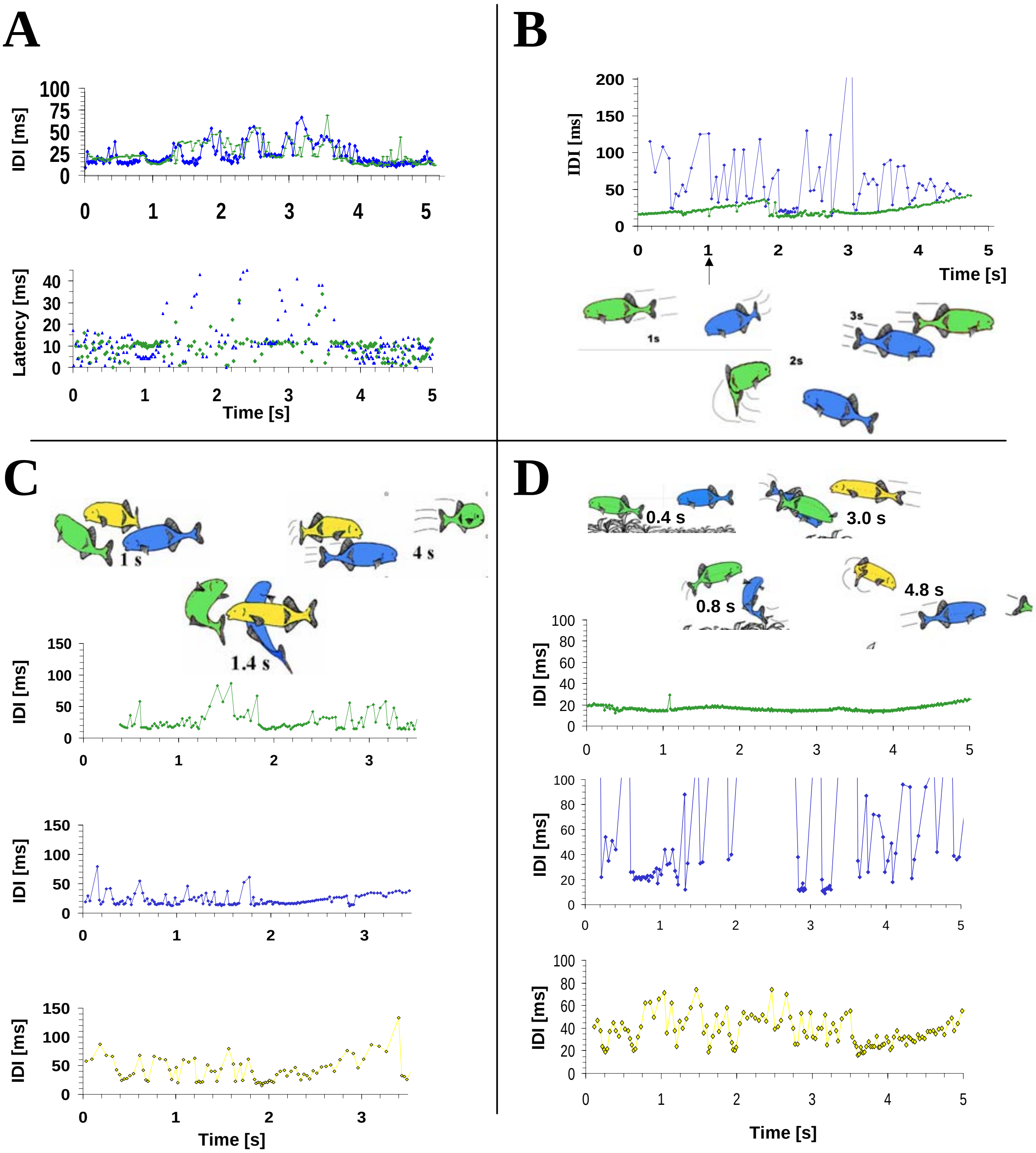

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