SHORT COMMUNICATION

Electric Signals in the Social Behavior of Sympatric Elephantfish (Mormyridae, Teleostei) from the Upper Zambezi River

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Abstract Electrocommunication in mormyrid fish from African freshwaters is a challenging research field in neuroethology (Turner et al. 1999). However, virtually nothing is known about electrocommunication within natural mormyrid populations involving sympatric, syntopic species. Here we report on the nocturnal activities and electrocommunication among three syntopic species in a spacious laboratory setting resembling the natural one. *Petrocephalus catostoma*, *Cyphomyrus discorhynchus*, and *Hippopotamyrus* sp. nov. differ characteristically in their behavior, such as in territorial defense, schooling, and joining members of other species during foraging. Comparing social encounters within and between species, the first evidence for interspecific electrocommunication among syntopic species was found.

Electric organs and electroreceptors enable mormyrids to communicate using weak electric signals that are brief pulses of species-specific waveform displayed at variable, situation-dependent rate (reviews: Kramer 1990, 1996; Moller 1995). The interplay between overt behavior and electrocommunication in pairs of fish of West African mormyrid species has been examined in various laboratory studies (Bell et al. 1974; Bratton and Kramer 1989; Kramer and Bauer 1976). The small amount of data on behavior from the field, based on electric organ discharge (EOD) recordings in situ or using captive fish, allow only limited conclusions to be drawn (Crawford et al. 1997; Friedman and Hopkins 1996; Hopkins and Bass 1981; Kramer 1997; Moller et al. 1979). The present investigation offers a detailed view on the interplay of social behavior and communication among three syntopic (same place) species and provides information on the function of electrocommunication in natural mormyrid populations.

We have studied undisturbed groups of mormyrids living in large aquaria (700–3000 l) for several years (no transfer of individuals between tanks during our study). The aquaria were well equipped with dense submerged plants, shrubs, roots, rocks, and gravel in an effort to simulate the river bank region where the animals live. The nocturnal behavior was videotaped under infrared lighting, and the electric discharges were recorded by at least two pairs of carbon electrodes, which were connected to differential amplifiers, and the output separately stored on the audio tracks of the videotape, or the tracks of a synchronized instrumentation recorder (Racal Store Plus). For selected sequences the discharges were digitized by a three-channel transputer system (sampling rate, up to 100 kHz per channel) and stored on computer disk. Scrolling through records allowed discrimination between EODs by comparing waveforms, amplitudes, and polarity. The times of discharge occurrences were visualized as interdischarge interval (IDI) diagrams for each of up to five interacting fish (in previous work up to three fish; Scheffel and Kramer 1997).

The EODs of *P. catostoma* are short, triphasic waveforms of about 0.3 ms duration, those of *C. discorhynchus* short-biphasic of about 0.2 ms duration, and the EODs of *Hippopotamyrus* sp. nov. long-monophasic waveforms with durations greater than 1 ms (Fig. 1A; as already observed in Kramer 1996). (*Hippopotamyrus* sp. nov. is an as yet undescribed sibling species of *H. ansorgii*; Van der Bank and Kramer 1996).

All three mormyrid species coexisted in the same large communal tanks (bottom area, 1.2–3 m^2, about 40 cm water depth; water conductivity and temperature, 100–200 μS/cm and $25 \pm 0.5°$ C) that simulated the river bank biotope (Fig. 1B). Light control was either L:D 12:12 h or, in a few instances, 14:10 h in these subtropical species. Each species was repre-

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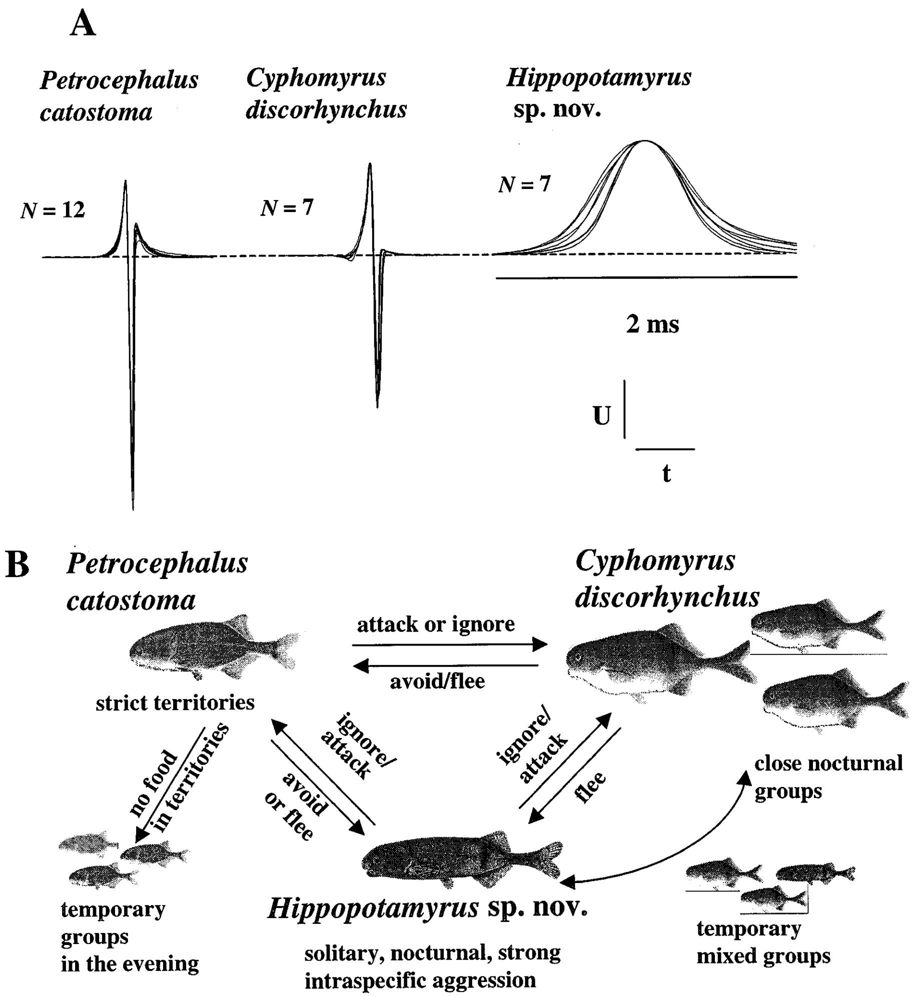

Fig. 1A,B. Overview over EOD waveforms and species-specific behavioral strategies of the three coexisting species. A) Individual EOD waveforms of all investigated animals superimposed, separately for each species. *N* Number of individuals investigated; *ordinate* (not shown) linear voltage; *dashed baseline* 0 V; *up* head-positive; *abscissa* time. B) Behavioral strategies and reciprocal actions. The territorial species *Petrocephalus catostoma* defends mosaiclike territories against conspecifics but avoids solitary *Hippopotamyrus* sp. nov. Nocturnal schooling *Cyphomyrus discorhynchus* usually avoid other mormyrids but temporarily form mixed species groups with solitary *Hippopotamyrus* (fish pictures from Skelton 1993)

sented by between one and eight members. Standard length was greater than 40% of the maximum species size except in *C. discorhynchus* where only two individuals exceeded this limit. (Sexual maturity occurs at about 40% of the maximum species size in several natural populations of mormyrid species; review: Kramer 1997.) Both sexes of *P. catostoma* ($n=3$ or $n=8$ in different tanks) occupied small territories with discrete borders that were stable within the whole observation period of 2–3 years (size, 1/4–1/2 m^2). Fish patrolled their territories (also by daylight) and defended them against *C. discorhynchus* ($n=1$, 2, 4, or 6 in different tanks), and especially against conspecifics. Intruding *Hippopotamyrus* ($n=1$) were never attacked, but were avoided. When there was no food available in their own territories, individual *P. catostoma* formed temporary groups ($n=2$–6) by joining their territorial neighbors at the beginning of the night to search for food in surrounding areas. These groups never existed for periods longer than a few seconds up to several minutes, and fish soon returned to their territories. *C. discorhynchus* was a social species at night for all observed group sizes ($n=2$, 4, 6) and occasionally formed temporary mixed groups with the solitary *Hippopotamyrus* in their tank. The presence of a *Hippopotamyrus* in a group prevented territorial *P. catostoma* from attacking these mixed groups. *Hippopotamyrus* was highly aggressive against conspecifics (and it was not therefore possible to keep more than a single specimen in a tank with bottom area of 3 m^2), but usually *Hippopotamyrus* ignored the presence of the other two species. During the day all our *Hippopotamyrus* ($n=7$) rested individually in one preferred hiding place in their respective tank – mainly dark niches in rocks – which was often the same for several months. During the night they continuously patrolled the whole tank.

Territorial *P. catostoma* which were threatened by intruders such that they did not dare to counterattack (e.g., an *Hippopotamyrus* or a large, nonelectric fish), changed their discharge activity from normal

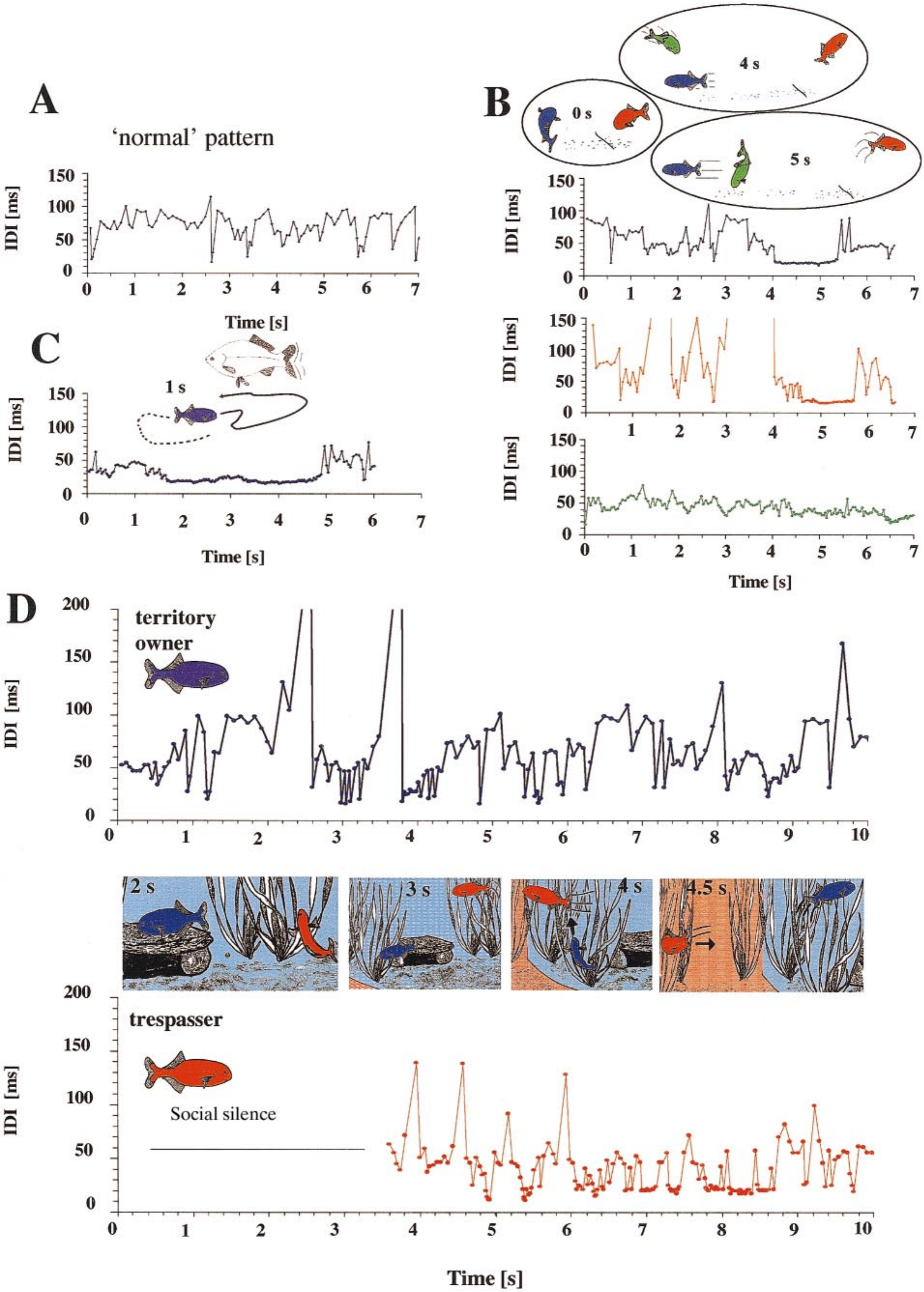
A
'normal' pattern
IDI [ms]
Time [s]
B
0 s
4 s
5 s
IDI [ms]
Time [s]
C
1 s
IDI [ms]
Time [s]
D
territory owner
IDI [ms]
2 s
3 s
4 s
4.5 s
trespasser
Social silence
IDI [ms]
Time [s]

Fig. 2A–D. Interdischarge interval (IDI) patterns in *P. catostoma* over time. *Ordinates* successive IDI (ms); *abscissas* time (s). A) IDI pattern when patrolling the territory without interaction. B) IDI patterns of a territorial *P. catostoma* (*blue*) and its territory neighbor (*red*; image at 0 s) when both were avoiding an intruding (not attacking) *Hippopotamyrus* (*green*) at 4 s and 5 s. *Short slanted line in each image* the same territory border on gravel (*dots*). C) Similar response of a *P. catostoma* to a large, nonelectric fish (goldfish) trespassing a territory. D) "Social silence" when trespassing a conspecific's territory: interval pattern of a *P. catostoma* (*red*) returning into its own territory by swimming through the territory of a neighbor (*blue*). The trespasser curves around the territory-owner while suppressing its own EOD activity. On arrival in its own territory it resumes discharging and short reciprocal sham attacks occur

irregular interpulse interval patterns with rare short intervals (Fig. 2A) to regular series of short intervals around 20 ms (Fig. 2B, C). With little delay, near *P. catostoma* neighbors joined in this regular pattern (Fig. 2B). During short visits to neighboring territories, long discharge breaks of trespassing (electrically "hiding"?) *P. catostoma* were observed while they made a detour around a *P. catostoma* territory owner. Such discharge breaks in mormyrids resemble a behavior called "social silence" observed under experimental conditions (Moller et al. 1989). Arriving in their own territory, "exploratory" *P. catostoma* resumed discharging (Fig. 2D).

Pairs of *C. discorhynchus* ($n=2$, showing the same behavior as in bigger groups) tended to harmonize their discharge patterns among each other by discharging at the same rate, and with "preferred latencies" of around 11 ms (Fig. 3A; preferred latencies, review: Kramer 1990). When swimming in midwater the leading fish discharged in characteristic, regular patterns of short intervals, the duration of which slowly increased (Fig. 3B). Similar IDI patterns occurred when an *Hippopotamyrus* had joined (Fig. 3C). By circling around a *Hippopotamyrus*, one or more *C. discorhynchus* seemed to "invite" *Hippopotamyrus* to join their group. *C. discorhynchus* that showed threatening postures in (rare) conflicts with a territorial *P. catostoma* discharged in a regular pattern of two short and one long interval that alternated with a series of constant short intervals (Fig. 3D).

Hippopotamyrus usually discharged in irregular intervals between 20 ms and 50 ms, and all observed attacks were accompanied by high-frequency discharge bursts of intervals as short as 8 ms (Fig. 3D). When joining mixed groups *Hippopotamyrus* discharged in regular short interval patterns that gradually decreased in pulse rate and became more irregular (Fig. 3C).

Context-specific discharge interval patterns indicate an important role for electrocommunication in social behavior – even in interspecific interactions (Kramer and Kuhn 1994; Kramer and Lücker 1990). The signal function of various interval patterns has been shown in playback experiments with *Gnathonemus petersii* (Kramer 1979; Teyssèdre and Serrier 1986). The present observations support the hypothesis of interspecific communication, as shown by context-dependent responses, cooperation and sharing of resources within a mixed-species population. Assuming that *Hippopotamyrus* also tends to show solitary behavior in its natural environment, then the strict association of interval patterns displayed with overt behavior probably gives cues to members of the other coexisting species, i.e., interspecific communication. (All three species detect play-back EODs of the other two species at natural intensities; Scheffel and Kramer, unpublished). This helps to avoid useless conflicts, save energy, and reduce injury, but it also provides the possibility for cooperation in mixed-species schools, for example, in a group of *C. discorhynchus* with a single *Hippopotamyrus* characteristic discharge patterns occur in both species. An advantage of mixed schooling for *C. discorhynchus* is surely to reduce the number of attacks from territorial *P. catostoma*, whereas the single *Hippopotamyrus* in nature probably gains from attack abatement (Turner and Pitcher 1986) which reduces predation risk by dilution. Nocturnal predators for mormyrids are, e.g., catfish of the genera *Clarias* and *Schilbe* (Hanika and Kramer 1999; Merron 1993; Skelton 1993; Winemiller and Kelso-Winemiller 1996).

For territorial *P. catostoma* a reciprocal early warning system seems to exist. Stable relationships between territorial neighbors are also known for many songbirds and have been shown in captive individuals of the weakly electric, South American knifefish *Gymnotus carapo* on the basis of their individual-specific EODs (McGregor and Westby 1992); trained mormyrids distinguish the small, interindividual differences in EOD waveform of conspecifics (Graff and Kramer 1992). According to Smith (1986), reciprocal alarm signals between individually known neighbors ("dear enemies") pay off when their territorial borders are stable, meaning less effort for territorial defense. Another obvious advantage of constant neighbor relationships in *P. catostoma* is the presence of potential schooling partners when food is scarce.

Our results show contrasting species-specific behavioral strategies among coexisting mormyrid species, especially regarding schooling, territoriality, and social behavior. The observed strategies and the clear

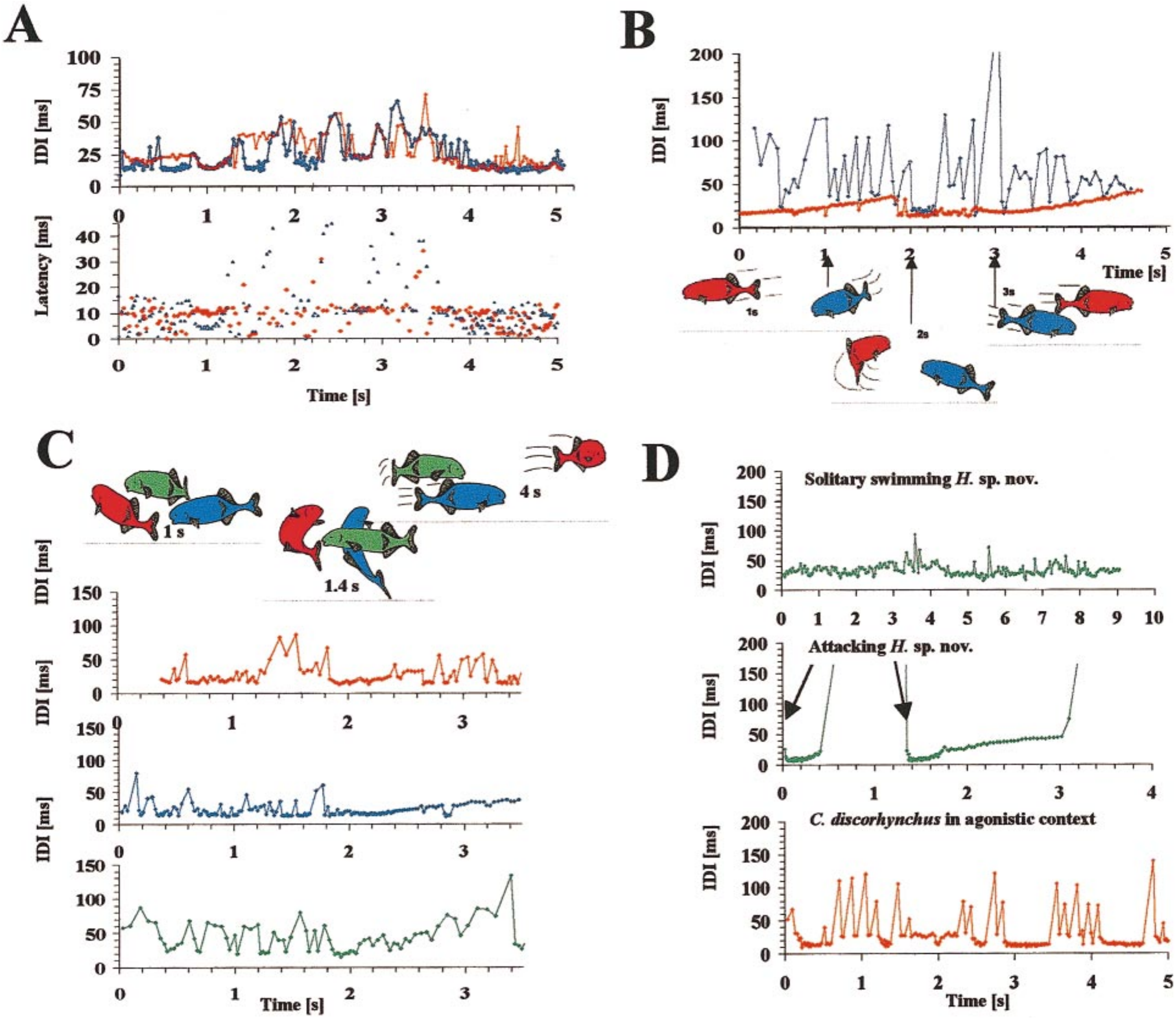

Fig. 3A–D. IDI patterns of *C. discorhynchus* when schooling (*ordinates* and *abscissas*, as in Fig. 2). A) Close pair of *C. discorhynchus* foraging near the bottom. Individuals harmonize their IDI patterns (*above*) by discharging in preferred latencies (*below*; note high density of points around 11 ms). Latency is the time between the discharges of two individuals. B) Discharge pattern in a fast-swimming pair of *C. discorhynchus* in midwater. Note the characteristic regular pattern of the leading fish, whereas the following one discharges in longer, irregular intervals but joins the regular pattern for a fast, close turnaround. C) Mixed schooling of *C. discorhynchus* and *Hippopotamyrus*: a pair of *C. discorhynchus* circle around a single *Hippopotamyrus* (*green*) and swims further on with the *Hippopotamyrus* following. During this episode *C. discorhynchus* displayed interval patterns that resemble the pattern of a leading *C. discorhynchus*. The joining *Hippopotamyrus* changed from mostly irregular intervals to regular short ones, the duration of which gradually increased while becoming more irregular again. D) IDI patterns that are not involved in schooling behavior

hierarchy between the species are correlated with characteristic IDI patterns of EODs that suggest interspecific communication.

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