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The ecology, discharge diversity and predatory behaviour of gymnotiforme electric fish in the coastal streams of French Guiana

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Summary. 1. A survey of the species distribution, discharge characteristics, ecology and behaviour of South American Gymnotiforme electric fish was carried out during two field trips to sites in the vicinity of Kourou, French Guiana, in 1983 and 1985. 2. Measurements of water conditions, collected over a twelve month period, highlight the strong ecological pressure on species exploiting the rapidly fluctuating and often temporary coastal streams. Adaptation of the reproductive cycle to the rainy seasons is particularly marked and the possible *zeitgebers* are considered. Given the almost invariant water conductivity, its suggested use as an environmental trigger is rejected in favour of acoustic or mechanical cues. 3. The two main study areas were inhabited principally by pulse gymnotoids of the genera *Gymnotus* and *Hypopomus*. A new *Hypopomus* species was discovered as well as specimens of *G. pantherinus*, previously undescribed in French Guiana. Larvae of *H. beebei* were found prior to the start of the 1985 rainy season. Developmental data for this species are presented which support the view that, as in other weakly electric gymnotoids, a primitive larval electric organ probably precedes the adult structure. The larval discharge also strongly resembles that of the adult electric eel, lending weight to published theories of an *Electrophorus*-like ancestor to the weakly electric fish. 4. The predatory behaviour of the strongly electric eel was recorded in detail. The field results indicated that this species preyed on weakly electric fish whose responses to the foraging eel are also reported. The probable use of electrical cues by hunting eels was further investigated in a laboratory experiment in which predatory responses were compared in the presence of non-electric and electric live prey, and models mimicking electric prey. It is concluded that electrical cues are probably of paramount importance in the eel's normal prey capture behaviour.

Introduction

Behavioural studies on the South American weakly electric fish have been continuing now for over two decades. The work has been advancing on several fronts, notably in electrolocation and its preservation by the Jamming Avoidance Response, the role of the electric organ discharge (EOD) in the communication of agonistic and courtship messages and, more recently, on the mechanisms employed in the extraction of species, sex and age-specific information from the pulse waveform. For reviews see: Bullock (1982), Heiligenberg (1977), Heiligenberg and Bastian (1984), Westby (1981, 1984).

Unfortunately there has been little fieldwork carried out on these fish to the extent that we are still surprisingly ignorant of species distributions and abundance and, in particular, practically nothing is known of normal social interactions in the natural environment, including intra- and interspecific communication and predator-prey relationships. Early field studies by Lissman (1961), Lissman and Schwassmann (1965) and Steinbach (1970) did attempt to answer these questions and provided some basic information about diurnal movements and distribution of species. A major obstacle to detailed field analysis is the fish's nocturnal behaviour. They also occupy habitats which present many difficulties for the field worker. For these reasons the bulk of work has consisted of the collection and identification of the different species and behavioural field studies limited to EOD recordings and observations in local aquaria, e.g. Hopkins (1974a), Hopkins and Heiligenberg (1978), Kramer et al. (1981). Other field work has been concerned with the collection of specimens of different sex and maturity for the investigation of physiological properties of the electric organ and control of sex-specific EODs by steroid hormones (e.g. Hagedorn and Carr 1985). A notable exception is Hopkins' (1972, 1974b) work on *Sternopygus* in which field playback experiments were used to investigate the significance of the EOD frequency sex-difference first described in this species.

While a considerable amount is known about species distributions in small study areas for the African Mormyriforme group of weakly electric fish, see Hopkins (1980, 1981) and Moller et al. (1979), there is no comparable data on the South American Gymnotiformes. The present paper is an attempt to rectify this imbalance by describing the results of two field trips to the Kourou region of French Guiana in 1983 and 1985. The principal aim of the trips was to test a new theory of waveform recognition in pulse-type gymnotids – the 'scan-sampling' hypothesis (Westby 1984; Hopkins and Westby 1986). These results will be presented elsewhere but I report here data on the species identified and recorded, their distribution and ecology and some findings on predator-prey interactions with a recent supplementary laboratory study.

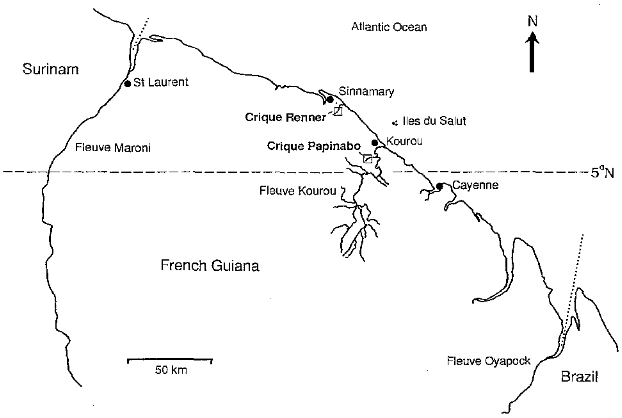

Fig. 1. The position of the two main study areas, the Papinabo and Renner 'creeks'. These streams are situated at the edge of the tropical rainforest, flowing out onto the coastal savannah and mangrove. Note that the Renner runs directly into the ocean whereas the Papinabo first enters the major river system of the Kourou

Methods

Study areas

The work reported here was carried out over two field trips in 1983 (15 June to 1 July) and 1985 (7 April to 1 May), with additional data collected in August 1986. The studies were based at the Institut National de la Recherche Agronomique (INRA) Hydrobiology labs at Kourou, French Guiana (5°10′ N, 52°40′ W). Freshwater streams and rivers of varying ecology were sampled at up to 30 km inland. A coastal savannah strip of 10 to 15 km width separates the Atlantic Ocean from the rain forest. Most of the data was collected at two intensively studied locations. The Papinabo Creek (5°6′ N, 52°41′ W), a minor tributary of the Kourou River (Fig. 1), was selected as the principal study area in 1983. Although the Papinabo runs through dense rain forest, it has the advantages of easy access from the road to the pumping station at La Douane on the Kourou and, most important, was used for regular census of fish populations by the INRA laboratory. In 1985 I was unfortunately obliged to shift my main site to the Renner Creek (5°18′ N, 52°51′ W) following the destruction of the Papinabo to make way for a banana plantation. The Renner, situated closer to the coast, was studied at the edge of the rain forest as it emerged onto the savannah to flow through mangrove to the ocean, SE of Sinnamary (Fig. 1). A number of other sites were sampled in both years, notably two further tributaries of the Kourou, the Passoura Creek (5°9′ N, 52°40′ W) and the Parforce Creek (5°3′ N, 52°42′ W). Banks and inlets of the Sinnamary river were sampled from a boat in the region of Combi (5°22′ N, 52°57′ W) while the contrasting habitat of the flooded savannah (*Prispris*) was studied at Corossony (5°26′ N, 53°2′ W). In all cases the freshwater sytems studied were beyond the range of tidal effects.

The two creek study areas, Papinabo and Renner, shared similar water characteristics. The water was clear, acidic (pH range 5.2 to 5.8) and of very low conductivity (20 to 30 $\mu S.cm^{-1}$). Water temperature was in the range 26 to 29° C for air temperatures around 30° C. Away from the rain forest shade (which reduced incident light levels to 20 lux), water temperature rose above that of the air, to 34° C on the flooded savannah. Rivers in the forest were filled with deep (up to 50 cm) leaf litter, dead branches and fallen trees with occasional clearings revealing a sandy substrate, although the banks were usually heavily undercut mud, bound with tree roots. Water depth varied between a few cm and 1.5 m and was generally very slow running (about 10 $cm.s^{-1}$). Aquatic vegetation was sparse in the forest with occasional lily beds where light could penetrate. In clearings and on the savannah the water was filled with dense *Cabomba* sp.

Measurements of water conditions in the Papinabo for more than a year prior to my first visit were kindly made available to me by Rojas-Beltràn (personal communication) and I present the data for the 12 months commencing May 1982 in Figs. 2 and 3. The average annual rainfall in Kourou is 3.1 m with the major Rainy Season in May and a Dry Season lasting from mid-October to the end of December. Fig. 2 shows how the Papinabo water depth followed closely, with a drainage lag of about one month. It should be noted that the figure of 750 mm for April 1983 is unusually high and early for the Rainy Season peak which official statistics indicate more commonly occurs in May/June. In fact we have to go back to March 1972 to find a higher monthly rainfall (850 mm). The river is generally dry for two months although again there are marked variations from year to year. Figure 3 shows that both water temperature and conductivity vary only very slightly

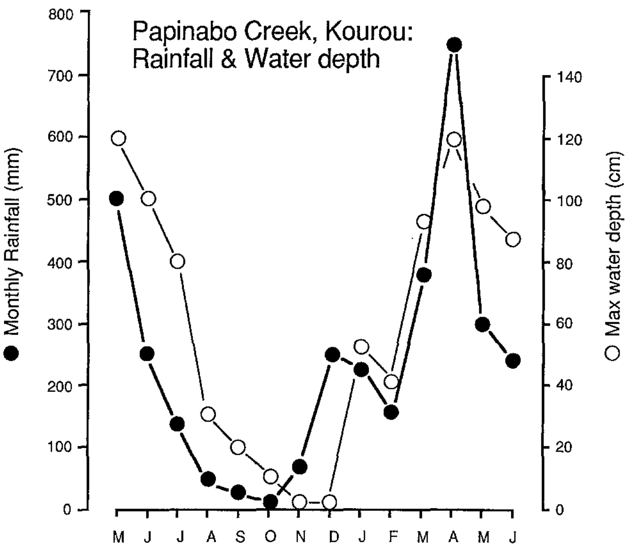

Fig. 2. Rainfall and water depth data in the Papinabo creek, Kourou for a 13 month period in 1982/83. A minor rainy season in January and February is normally followed by a relatively dry period before the major rainy season commences in late April. Water depth follows the rainfall closely with a drainage lag of approximately one month for most of the year

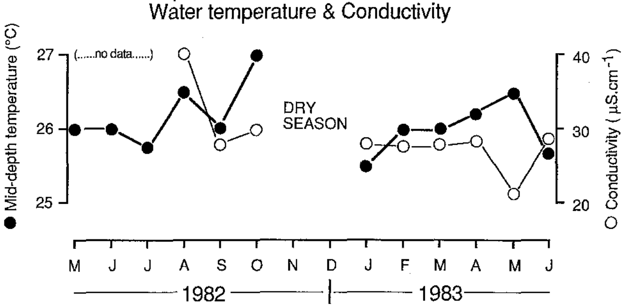

Fig. 3. Available data for water temperature and conductivity in the Papinabo shows remarkable consistency. Temperature fluctuating over a 1.5° C range and conductivity very low at around 30 µS.cm^{-1}

throughout the year. pH was more or less constant for 1982/83 at 5.6.

Gymnotiforme fish are well known to breed at the start of the major rainy season (see Kirschbaum 1984) and it was for this reason that the field trips were undertaken at this period. Adults in breeding state migrate from the main rivers up the streams to spawn in time to take advantage of the improved conditions. The Papinabo Gymnotiformes sampled with Rotenone poisoning over the 12 month period from May 1982 represent 14.6% of the fish found (25% of the biomass) compared to 13.5% (20.5%) for Siluriformes, 7.9% (19.9%) for Cichlids and 63.2% (34.3%) for Characins. Only 0.8% (0.3%) of the fish species belonged to other groups (see Rojas-Beltràn 1986 for details). It is interesting to note that *Gymnotus carapo* alone accounts for 5.3% (133 specimens) of the fish recovered in the 12 month period and nearly 20% of the total biomass of 11 kg.

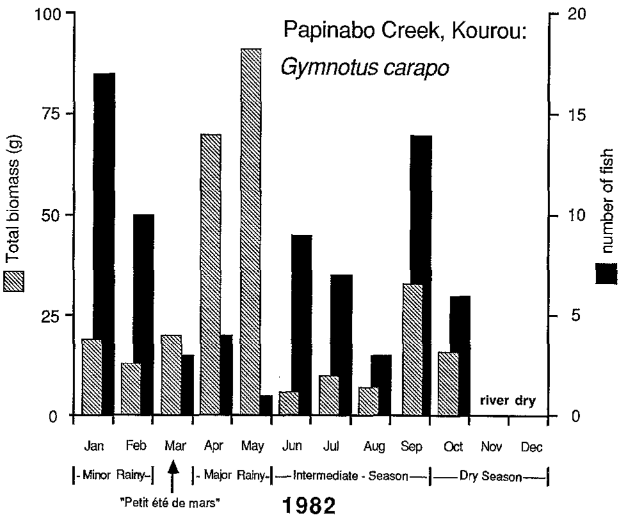

Fig. 4. Numbers and total wet weight of *Gymnotus carapo* sampled monthly in the 100 m stretch of the Papinabo study area in 1982. Note the striking variations caused by mature adults migrating into the area to breed in April and May

Figure 4 clearly shows that while the total mass of *G. carapo* increases dramatically at the start of the rainy season this is due to a relatively small number of large adults appearing for the first time after their migration. As the adults depart in June the population is composed primarily of juveniles.

Classification, fish collection and EOD recording techniques

The taxonomy of the Gymnotiformes is highly confused [see Hopkins and Heiligenberg (1978) for the specific problems of the *Hypopomus* genus]. A useful recent key to the identification of French Guianan species has appeared (Le Bail et al. 1984), but is incomplete in many respects. Kirschbaum (personal communication) is currently undertaking a complete reexamination of the group and it seems that *Eigenmannia* and *Hypopomus* in particular will soon be reorganised. Here we follow the *H. beebei* identification of Hopkins and Heiligenberg (1978), but not their classification of *H. brevirostris* and *H. artedi*. These two species should now be interchanged (see Hopkins and Westby 1986). The commonest *Eigenmannia* species has been traditionally identified (e.g. by Kirschbaum 1979 and others prior to 1983) as *E. virescens* (as it is here), but this, in all probability, is *E. lineata* according to current thinking (see Kirschbaum 1984). Hopkins and Heiligenberg (1978) also discuss the problems of the *Eigenmannia* genus. A *Gymnotus* species new to French Guiana, *G. pantherinus* (see below) was identified with information kindly provided by F. Kirschbaum.

Fish populations were estimated by poisoning sections of stream. The Papinabo and Renner were sampled following all work in the areas in 1983 and an inlet of the Sinnamary in 1985. The technique employed was first to completely block downstream escape with a fine seine net. Then a solution of 100 g of 100% Rotenone powder and 200 ml of liquid detergent in 5 l of river water was made up. The detergent ensured dispersion of the poison as it was distributed over the full width of the river about 100 m upstream from the barrage. Two assistants waded downstream following the Rotenone cloud chasing the fish towards the net. The effect of the poison was extremely variable depending principally on the size of the fish and their location in the river. As the poison took effect the fish rose to the surface. Small characins and the more fragile gymnotoids, such as *Eigenmannia* sp., were often killed outright but the larger cichlids and most bottom dwelling species of gymnotoid and silurid surfaced much later and almost invariably survived in uncontaminated water. This method was obviously highly destructive and was only used where the species data of wider interest could also be collected.

Usually electric fish were located with an electronic fish finder. This consisted of a tripole probe with silver wire electrodes at 110 mm spacing mounted on the end of a 2 m rod. The electrode output was differentially amplified at gains of up to 10000 and monitored via an audio stage through headphones. The fish finder was worn on the experimenter's belt and was also equipped with variable band-pass and notch filters for the removal of both natural (meteorological electrostatic) and man-made (50 Hz) electrical noise. This latter source was a particular problem since the 50 Hz fields emanating from even distant power transmission lines suffered only minimal attenuation in the very low conductivity stream water. A miniature (5 cm screen) oscilloscope (Thandar SC-110A) was also worn by the experimenter. Most gymnotoid species could then be identified from the audio monitor and/or the waveform observed on the oscilloscope. Once detected, fish were captured in a large hoop net (Ø 0.7 m) for identification and transport to the lab in Kourou for electrical recording.

Laboratory measurements were made in stream water transported with the fish at a standard temperature of 27° C. A small (12 cm × 40 cm) glass aquarium was used for recording. Each end was fitted with 12 cm × 12 cm carbon plate recording electrodes. In many cases EODs were also recorded in situ using either a Nagra IV–SJ open reel recorder at 37 $\mathrm{cm.s^{-1}}$ or a Marantz 640 high fidelity portable cassette deck. These machines were mainly used for long term sampling of interpulse intervals (IPIs) and interactions between fish using stereo recording. In these cases electrodes were installed close to fish resting in their daytime hiding places and signals differentially amplified to suitable levels for the recorders. Pulse waveform was monitored using either a Scopex 'Voyager' LCD digital oscilloscope or a Hitachi V209 analogue instrument. Due to the frequency response limitations of conventional recorders, pulse waveforms were captured either in the field or lab with a specially constructed microprocessor-controlled digital transient recorder. This 'Pulse Logger' (Helpware: Sheffield) digitised incoming fish pulses to 8 bits at 1 MHz storing the data in a 4 Kbyte circular buffer. Oscilloscope monitoring enabled 'pre-triggered' pulses to be observed after D/A conversion in the manner of a digital oscilloscope. An integral digital cassette deck could be used to store the waveforms for later analysis. A second function of the Pulse Logger enabled IPI samples to taken. The IPIs were measured to 1 µs accuracy and 24 bit range. They could also be stored on digital cassette and displayed on the scope monitor. A third function of the device was to act as a stimulator. Pre-digitised waveforms and IPI lists could be read into the Pulse Logger's memory. A trigger signal started the device in replay mode, generating a high fidelity mimic fish output of variable amplitude which could be played back through a model.

On return from South America the EODs and IPIs could be read from the digital cassettes into the Pulse Logger and then along a serial line into a host microcomputer (Research Machines 380Z) for disc storage and further analysis. EOD waveforms were scaled to constant peak-to-peak amplitudes, Fast Fourier Transforms computed and power spectra and input waveforms plotted using a Juki 6100 Daisywheel printer in graphics mode.

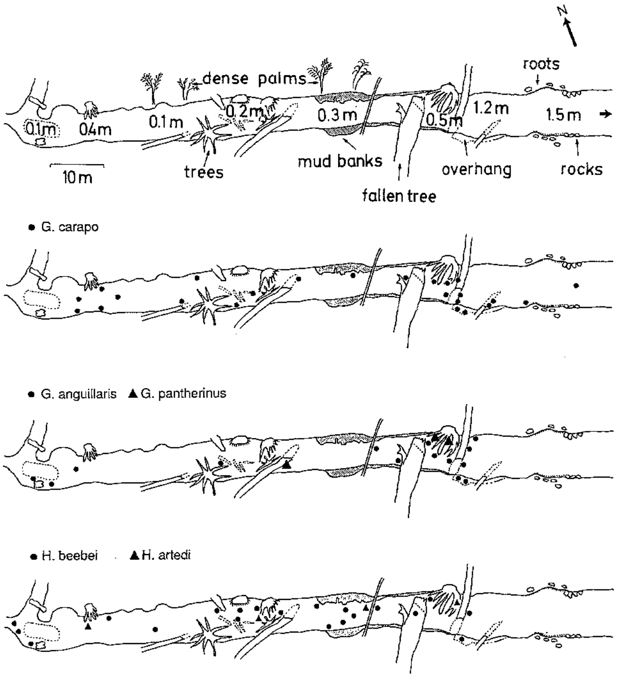

Fig. 5. Papinabo Creek: Ecological conditions and distribution of species located electrically in the area. Not marked is the single non-resident *Electrophorus electricus* which entered the area only late in the day. For all other species the *symbols* represent the location of an individual's day time hiding place

Results

Distribution of gymnotoids in the Papinabo and Renner creeks

Figure 5 shows the distribution of gymnotoid species in the Papinabo study area. A detailed census of this 100 m upper stretch of the stream was carried out between 20 and 23/6/1983. The upper map shows the gross features of the area. The river was overhung with dense rain forest vegetation: principally various palms (*Astrocaryum vulgare* and *A. paramaca*) and *Pterocarpus officinalis* with its characteristic buttress roots – where they entered the water these formed a favourite hiding place for the fish. For most of the stream the water was less than 1 m deep and these shallow areas were clearly preferred by all electric fish. Only three species were found in significant numbers, *Gymnotus carapo*, *G. anguillaris* and *Hypopomus beebei*. Figure 5 shows their somewhat different habitat preferences. All were well spaced out, never occurring closer than 1 m to the nearest conspecific neighbour. *G. carapo* showed preference for refuges in roots, sunken logs and holes under the banks. They were more rarely found buried in leaf litter. The closely related *G. anguillaris* preferred very similar sites, although their total population was lower ($n=14$ compared to 24 for *G. carapo*). Several times both *Gymnotus* species were found in very close association – being commonly netted simultaneously. A third, much rarer *Gymnotus* species, *G. pantherinus* – previously undescribed in the Guianas – was found in sunken log hiding places, similar to those occupied by the other members of the genus. Note the very strong preference in all of these fish for the point where the stream bed drops from 0.5 to 1.2 m caused by a natural barrage. This was presumably an ideal feeding area. *H. beebei* ($n=20$) and the less common *H. artedi* ($n=3$: filled triangles) showed a marked presence in open water, preferring to be buried in leaf litter rather than hiding in roots or bank holes. No other weakly electric fish species were found in the area. On several occasions throughout the two weeks a single specimen of the strongly electric eel (*Electrophorus electricus*) was observed and recorded. Its predatory behaviour will be described below. The fish was clearly not resident in the 100 m area and migrated in from the deeper downstream regions towards the end of the day. It was the only electric species to be seen swimming in open water in daylight.

The Renner creek flows directly into the Atlantic. The study area itself, on the forest margin, was beyond any noticeable tidal effects. Figure 6 shows the distribution of gymnotoids in the study area. It comprised a 40 m stretch of very slow running water (approx 2 cm.s^{-1}) with thinner tree cover than the Papinabo. This meant that very deep (up to 1 m) beds of leaf litter had built up in areas where the flow was exceptionally low, such as the river edges and upstream from natural obstructions such as fallen trees. Clear sandbanks were however exposed in the centre of the river (Fig. 6: upper diagram). As in the Papinabo the two principal species were *G. carapo* and *H. beebei.* Both were found buried in leaf litter and hiding under roots and sunken branches. The census and mapping were carried out at the start of the principal rainy season on 22/4/1985, two months earlier than the Papinabo study in 1983. In contrast with the Papinabo, most of the specimens were therefore adult and the majority caught were in breeding condition. There were, however, some juveniles well hidden and close together (small filled symbols in Fig. 6 *Gymnotus* map). Judging by their size (40 to 70 mm – see below) they were probably spawned during the first (minor) Rainy Season in January that year. *G. anguillaris*, was far less common than in the Papinabo. Only three specimens were recorded in the area. Again members of the *Hypopomus* genus were abundant. Total numbers detected for the two principal genera were 38 and 25 for *Gymnotus* and *Hypopomus* respectively. This is a ratio of 1.5:1 which compares well with the ratio of 1.7:1 for the Papinabo two years earlier.

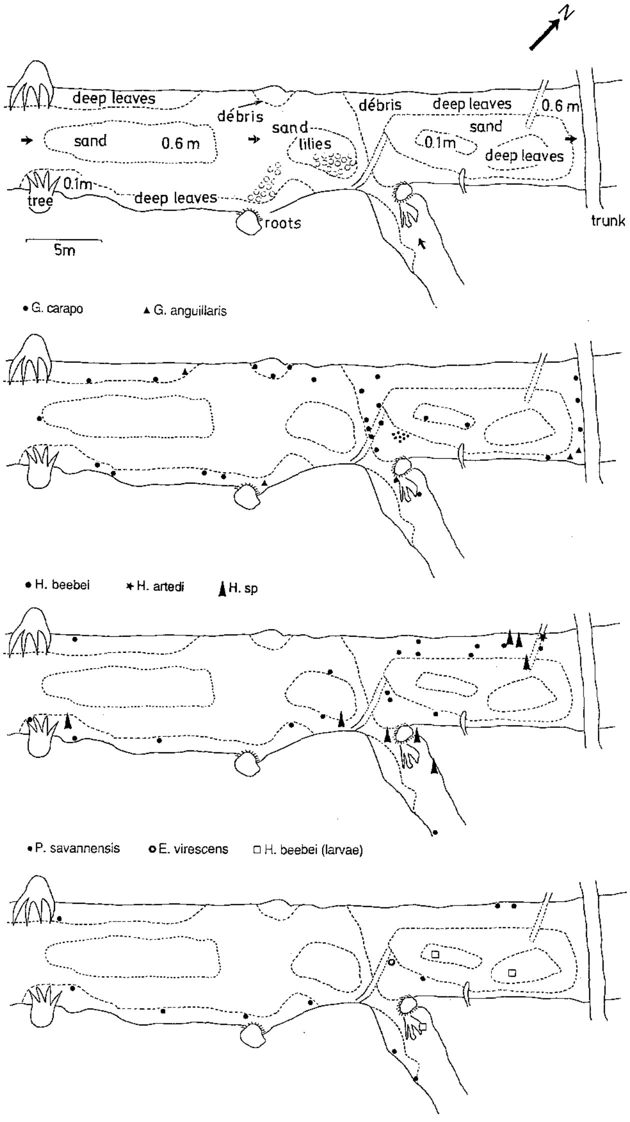

Fig. 6. Renner Creek: Ecological conditions and distribution of species as in Fig. 5

The lower two maps in Fig. 6 illustrate the major differences with the Papinabo. Firstly while *H. artedi* was still represented with just one specimen, seven examples of an undescribed species of *Hypopomus* were also discovered. This same species has also been found by Hopkins in other streams on an independent visit to French Guiana in 1985.

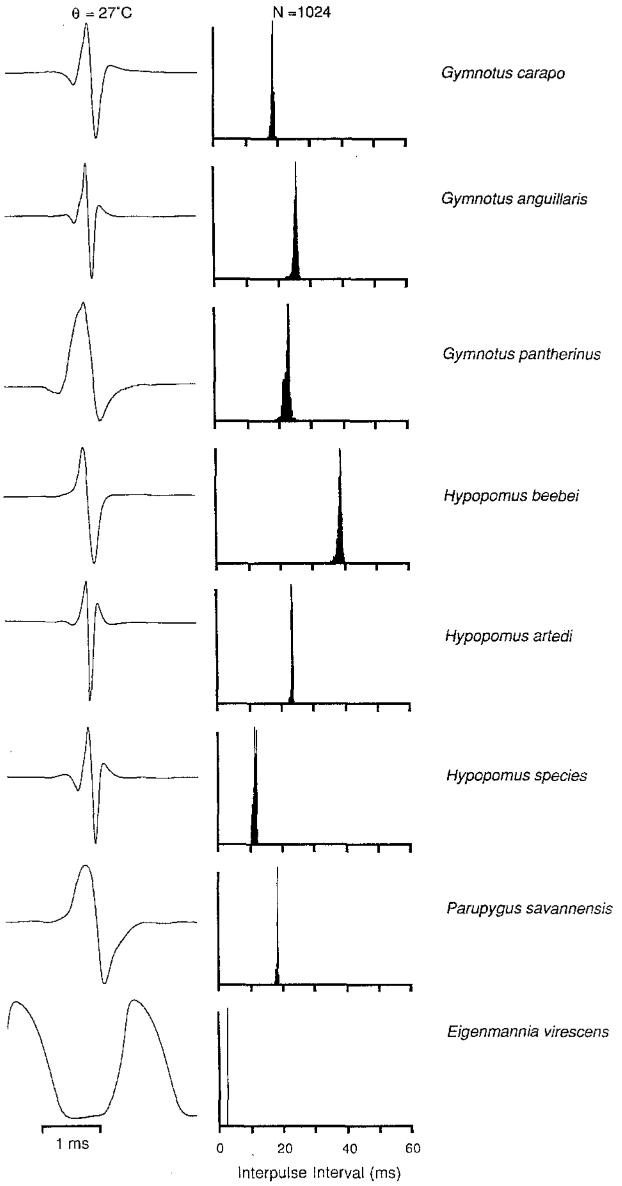

Fig. 7. Electric organ discharges (EODs) and interpulse interval (IPI) histograms for the weakly electric species found in the two study areas. Discharges were recorded under standard conditions from fish transported to the laboratory in Kourou. Waveforms were digitised at 1 MHz, scaled to constant peak-to-peak amplitude, and are presented with head-positivity upwards. IPIs were measured digitally to 1 μs accuracy in real time. Bin width is 0.25 ms. 1024 EODs were sampled from each fish at rest. *Histograms* are scaled to constant height for comparison of dispersion

We have described its characteristics elsewhere (Hopkins and Westby 1986). Secondly, two species not recorded in the Papinabo were present. *Parupygus savannensis* were found well spaced out and buried very deep in the leaf litter. A solitary *Eigenmannia virescens* was present in the most popular part of the stream where it could always be found over a period of 3 weeks.

Probably the most interesting finding in the Renner study area was the discovery of 'crêches' of larval *Hypopomus beebei.* Two groups, estimated as comprising about 15 individuals were clustered together under leaf litter and a third was buried deep inside a piece of rotting wood (Fig. 6). It was possible to remove all of the last group (22 specimens) and record their discharges under optimal conditions (Fig. 8). The larvae of 6 to 8 mm total length were electrically active. Based on data from previous studies on the development of the EOD (Kirschbaum and Westby 1975; Westby and Kirschbaum 1977), they were estimated to be no more than 10 days of age – or one week from hatching.

Other habitats

The Papinabo and Renner creeks share rather similar ecological characteristics. They are shallow, slow running and have relatively constant temperature of 26° to 28° C. Light levels are low and hiding places are restricted to dêbris from broken branches, roots and leaf litter. Open habitats, in contrast, unless very fast flowing, are generally filled with dense vegetation – affording abundant hiding places for midwater species such as the glass knifefish (*E. virescens*). Indeed this species was found in large numbers in several of the rivers sampled, in particular the Renner itself as it crossed open savannah. More than 100 specimens were caught in a 4 m stretch of the Renner by sweeping a hoop net through the dense beds of *Cabomba* sp. The genera *Gymnotus* and *Hypopomus* were also represented in these open habitats but only in very small numbers, apparently preferring the shallower water. The results were similar for the Passoura and Parforce creeks. The flooded savannah examined at Corrosony offered a different type of open habitat. Here the water was practically stagnant and covered an area about 400 m in diameter. The water level was mostly less than 25 cm and very warm – mid depth temperatures up to 36° C were recorded. The vegetation consisted mostly of grasses and reeds with some floating plants, such as *Ceratopteris thalictroides* and various lily species. Here, as in the open rivers, the principal gymnotoid species was *E. virescens* which spent the day hiding in the plants often hovering just below the surface in trailing roots. Small numbers of juveniles only of *G. carapo* and *H. beebei* were found predominantly in plants at mid depth. No other species were detected. The only

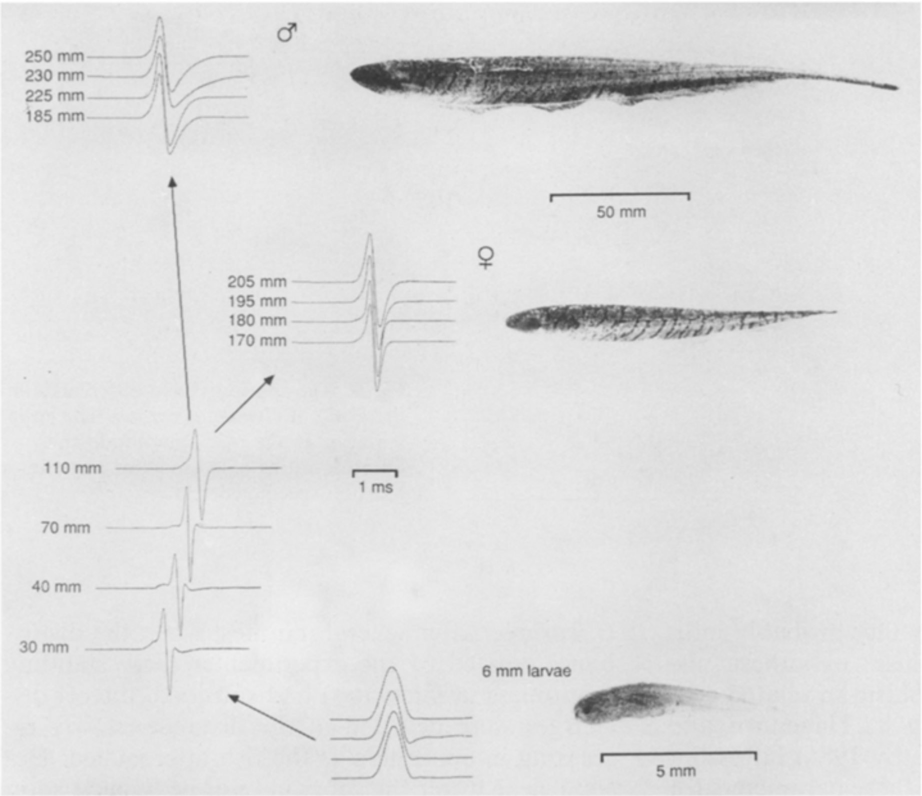

Fig. 8. Sex and age differences in the EODs of *Hypopomus beebei* from the Renner creek. The larger males possess a characteristic naked tail filament and their pulses have consistently longer duration head-negative phases. The female EOD is symmetrical. Larvae have a head-positive discharge, quite different from the adult. EODs of juveniles illustrate the developmental changes as the biphasic adult EOD, superimposed on the larval pulse gradually increases in amplitude

major river habitat sampled in detail was the Sinnamary near the village of Combi about 20 km upstream from the estuary. Here an additional species, *Sternopygus macrurus*, was found following a Rotenone census of a small inlet. Sampling of the river Maroni 250 km upstream and several small streams in the vicinity of Abanasounga on the Surinamese border yielded no new species. *H. beebei*, *G. carapo* and *G. anguillaris* were all abundant and several *E. electricus* were also present.

Species, sex and age-specific EOD characteristics

Figure 7 shows the field sampled EOD waveforms and IPI distributions for the eight weakly electric species found in the two study areas. The marked species-specificity of the waveforms could be reliably used in the field for identification purposes. For the majority of these fish within-species variation for the adult population was small and showed no obvious relationship to size, sex or location (for full data on EOD durations and IPI ranges see Hopkins and Westby 1986). However, in two species interesting intra-specific variation was noted. In *H. beebei* clear sex differences were discovered. The fish were sexed using the dimorphic tail filament characteristic of other members of this genus (Hagedorn 1986; Hopkins and Westby 1986). Males have a long naked tail filament in contrast to the short, pointed structure of females. In common with *H. occidentalis* (Hagedorn and Carr 1985), male *H. beebei* were found to possess longer head-negative than head-positive phases to their EODs (i.e. low P/N ratios), whereas the female EODs were almost symmetrical (Fig. 8). The larvae (see above) produced quite different discharges which were monophasic head positive. The mean IPI was 14.78 ms, range 12.98 to 17.64 ms for $n=10$ (based on pulse logger samples of 1024 EODs per fish). These discharge rates are at least double those of the adults which gave a mean IPI for males of 36.31 ms (range 28.65 to 46.49 ms: $n=15$) and for females a mean IPI of 43.41 ms (range 37.1 to 53.7 ms: $n=20$). The morphological sex and age differences have now been confirmed by a breeding success with *H. beebei* in this laboratory (Westby, unpublished).

In *G. carapo*, unlike *H. beebei*, we were unable to identify any morphological sex differences, but adult EODs showed variation in the ratio of the amplitudes of the n_1 and n_2 phases. The possibility of a sexual dimorphism in this feature was considered. The variation was large with n_1/n_2 ratios varying between 0.64 and 1.5 (open symbols), but

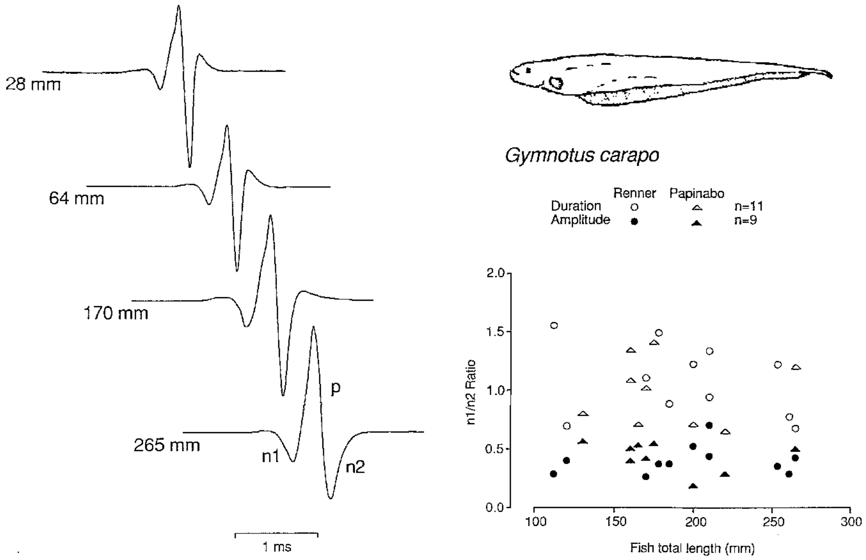

Fig. 9. Age and individual differences in the EOD of *Gymnotus carapo*. The large variation in the n_1/n_2 amplitude and duration ratios failed to show any size or location specific correlation

seemed unrelated to size. This fact probably mitigates against the sex dimorphism hypothesis, assuming the strong size dimorphism in related genera such as *Hypopomus* (Fig. 8; Hagedorn and Carr 1985; Hopkins and Westby 1986) holds out for *Gymnotus*. Figure 9 shows these parameters for 20 adult specimens, 11 from the Renner site and 9 from the Papinabo. There is no evidence for local characteristics or 'dialects' in the two populations, or any link between size and these measures. The figure shows (left) the EODs from four individuals of different size from the Renner site. In marked contrast to adults, juveniles possess p and n_2 phases of similar amplitude. Note also the final overshoot not seen in adults.

Predator-prey Interactions in the field

As described above, a single specimen of the predatory gymnotiforme, *Electrophorus electricus*, was recorded on several occasions in the Papinabo study area. The fish usually appeared in late afternoon, cruising in open water, a behaviour never seen in weakly electric species. This was a large male, measuring 1.8 m, with the characteristic bright red colouration on the underside of the head and belly. Prey capture behaviour in the field has not previously been described for this species so I was fortunate in being able to record a complete sequence involving predation on the weakly electric *G. carapo*. Electrodes had been established under a section of overhanging bank approximately 20 m from the downstream limit of the study area (marked *overhang* on Fig. 5). The electrodes had been positioned to record a pair of interacting *G. carapo*. After several minutes, when the disturbance created by the experimenter (now standing motionless in midwater) had subsided, the eel discharges were detected in the distance, slowly increasing in amplitude as the fish approached. Despite clear water the eel could not be seen. It soon became evident that it was approaching in the upstream direction under the overhang. From this point onwards a complete record was made, lasting $8^1/_2$ min in which all the discharges of the *E. electricus* and the closest *G. carapo* could be accurately timed following later analysis in the lab.

Figure 10 summarises the results. In the lower part of the figure is the IPI histogram for the electric eel for the whole of this period. Its shape as we will see in the next section is typical of that for a hunting individual. Strong discharges from the main organ can be reliably identified from their elevated emission frequency and appear as a unique sub-distribution. The high amplitude of even the 'weak' eel discharges at the electrodes meant that the two fish's EODs could be perfectly separated with a window discriminator. The lower repetition frequency of the majority of the eel EODs allowed the construction of a sequential time plot in which all the discharge intervals could be visualised. The mean discharge interval of the *G. carapo* was 19.58 ms, while the burst of eel pulses had a mean IPI of 158 ms. For clarity the main record represents the discharges of the two fish schematically as horizontal lines at different levels on a graph depicting the eel as a thick line and the *G. carapo* as a thin line. Tick marks on the abscissa are at one second intervals. The sequence starts just before the first recorded burst of eel pulses.

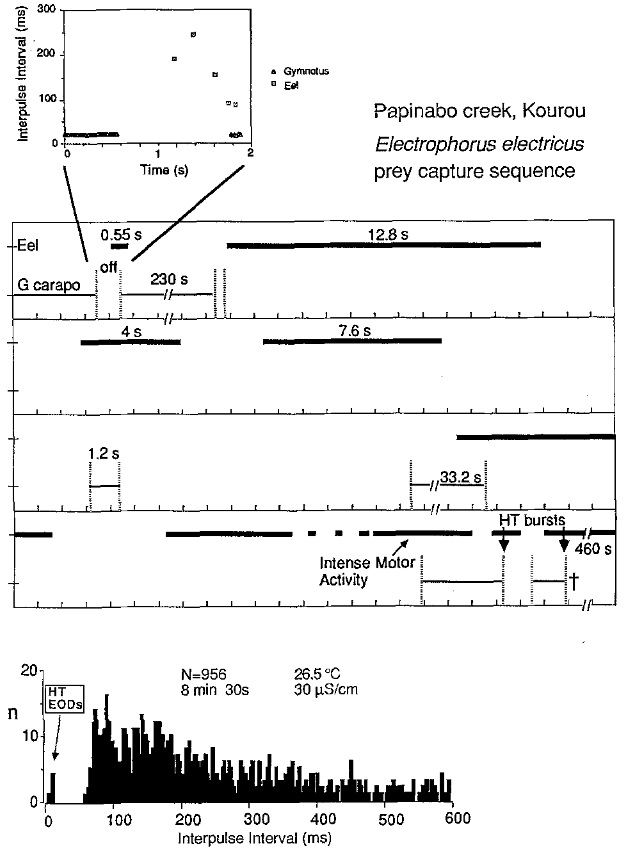

Fig. 10. Analysis of electrical behaviour of *Gymnotus carapo* and *Electrophorus electricus* during hunting and prey capture by the electric eel. The sequence lasts 8 min 30 s. Tick marks are at 1 s intervals. The *thin horizontal line* represents the presence of *G. carapo* EODs, while the *thick line* shows the eel discharges. The inset (*top*) shows a 2-s portion of the raw interval data from the original recording. High tension (*HT*) prey capture EODs from the eel are shown as *arrows*. The *histogram at the bottom* shows the IPI distribution of eel pulses over the whole recording period. Further details are in the text

Note that the *G. carapo* responds with an 'off' or discharge cessation about 600 ms *before* the eel discharges. No obvious change to firing rate occurred following reinstatement of the *G. carapo*'s discharge which then continued uninterrupted for a further 230 s. At this point an off of 300 ms preceded a long burst of low voltage EODs from the eel which, as could be judged from the recorded amplitude, had further approached. The *G. carapo* remained silent for 45 s during which time another two bursts of eel EODs were recorded. A brief burst of *G. carapo* pulses were emitted following 10 s of silence from the eel, then, after another delay a longer continuous period of discharge lasting 33.2 s, the eel recommenced discharging. This silenced the *G. carapo* within 2 s. There then followed several bursts from the eel (bottom line) ending in intense motor activity with a great deal of splashing and turbulence evident from the area of the recording electrodes. The *G. carapo* turned back on again briefly twice but was instantly silenced each time by a short high voltage discharge from the eel (arrows). All activity stopped following the second burst of HT EODs at which point, it is assumed, the *G. carapo* was eaten. Recording continued for another 460 s. During this time the eel discharged *continuously* at low frequency (IPIs >250 ms contributing to the long low-frequency tail of the IPI distribution) finally swimming away into open water. No further evidence of the *G. carapo* was recorded.

Predator-prey interactions in the laboratory

The above results clearly suggest that *E. electricus* preys, at least in part, on weakly electric species. To investigate this further, a laboratory experiment was designed to determine the rôle of interspecies electric communication in prey detection. A single specimen of *E. electricus*, 105 cm in length was housed in a 700 l aquarium (150 x 70 x 70 cm) well furnished with hiding places, plants and rocks. EODs were recorded from two pairs of orthogonally positioned carbon electrodes, the outputs of which were differentially amplified and summed. Motor behaviour was video recorded concurrently with the amplified EODs on the sound track. Experiments were carried out during three hours preceding the start of the dark period of the 12:12 light dark cycle. Although principally nocturnal *E. electricus* commences active foraging in the late afternoon and dusk as we observed in the field.

We set out to compare motor and electrical responses of the eel to three different 'prey' stimuli concealed in an electrically transparent, plastic mesh cage (180 x 120 x 70 mm). These were a live goldfish (80 mm length), a live specimen of *G. carapo* (140 mm length) and a 140 mm dipole electrode emitting a sequence of EODs, recorded from the same *G. carapo* and played back at the same amplitude. A fourth condition was an empty cage used as a control. The cage, appropriately set up for one of the above conditions was presented to the eel following a standardised procedure. The eel spent most of the final 3 h period of the day hovering near the surface of the tank at the position where it was normally given its daily feed of goldfish. With the eel in this position the cage was lowered on a thread to the bottom of the tank amid a large clump of plants. The cage was left in this position for 6 min during which time a full video and EOD record of the eel's behaviour was made. Twenty presentation trials were made in

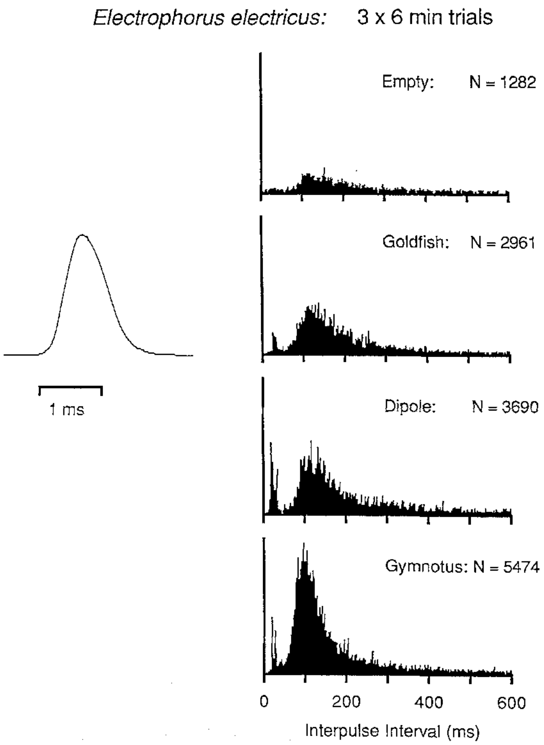

Fig. 11. Laboratory study of prey capture behaviour in the electric eel. A single low voltage (Sach's organ) pulse is shown on the *left*. The IPI distributions show the accumulated discharge intervals from three 6 min presentation trials in each of the four experimental conditions. Note the contrasting form of these distributions and, in particular, the high frequency strong EODs from the main organ which occurred in the presence of live prey or a prey EOD mimic

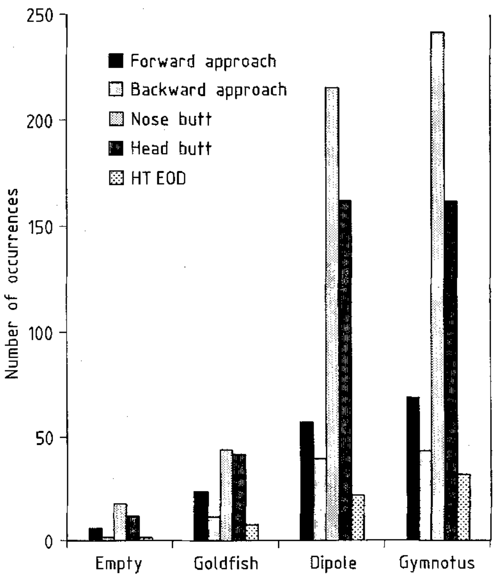

Fig. 12. Behaviour of *Electrophorus* in the four experimental conditions. The data are for twenty 6-min trials. Note the powerful influence of an electrically active live prey or mimic. See text for full details

each condition with no more than two, separated by 1 h minimum, on 1 day. Trials and conditions were presented in counterbalanced fashion to eliminate order effects. The eel's response to the cage in each condition was determined by detailed behavioural analysis of the videotapes. EOD responses were characterised by computer time interval histogram analysis.

The results of this study are summarised in Figs. 11 and 12 and Table 1. The high voltage, prey capture discharges were identified by the high frequency emission which accompanies them. It is known that the selection of low (Sach's) or high voltage (Main) organs is determined by the EOD command signal frequency (Albe-Fessard and Chagas 1954; Bauer 1979). Thus high discharge frequencies of 400–500 Hz are *exclusively* associated with the high voltage discharge. The small amplitude EODs used for electrolocation, and possibly communication (Bullock 1969; Cox 1938), are generated at very low frequencies in resting fish, often as low as 1 EOD/min. When rising to gulp air and swimming, the frequency is around 10 Hz rising to approximately 25 Hz with intense activity. High voltage EODs are therefore readily identified as a twenty-fold increase in the discharge rate of a fast moving fish. IPI histograms of *E. electricus* (Fig. 11) show marked bimodality when high voltage discharges occur. The figure presents the accumulated IPIs of 3 trials from each of the four experimental conditions. Complete records of all the IPIs generated in the 1st, 10th and 20th trials were combined to produce the histograms in Fig. 11. It is clear from visual inspection that the four conditions generated radically different distributions. Table 1 shows that pairwise statistical comparison of the distributions, using the Kolmogorov-Smirnov two sample test (Siegel 1956) yielded significant differences at $P<0.001$ in every case (2-tailed). Overall mean frequency varied from 1.19 Hz in the control condition (Empty) to 5.07 Hz in the live *Gymnotus* condition. The increase in mean discharge rate over the conditions is largely a result of increased motor activity but the most striking feature is the variation in proportion of high voltage EODs. These were further compared by looking at all 20 trials and comparing, across the conditions, the number within which at least one high voltage EOD occurred. The data were 2, 5, 13 and 17 for the Empty, Goldfish, Dipole and Gymnotus conditions respectively. $\chi 2$ analysis of the 4×2 contingency table showed a significant difference across conditions at $P<0.001$ ($\chi 2=29.11$ $df=3$). Pairwise $\chi 2$ analysis of these data (Table 1) shows the powerful effect

Table 1. Pairwise statistical comparison of the IPI histograms shown in Fig. 11. The D statistic of the Kolmogorov-Smirnov two sample test (2-tailed) yields a significant difference in every case at $p<0.001$. The χ^2 values are for a comparison of the frequency of occurrence of High Tension (HT) EODs over all trials ($df=1$). Comparison of Gymnotus or Dipole with the other conditions reveals the dramatic effect of an electric prey or mimic

		Empty		Goldfish		Dipole
Goldfish	IPI hist	$D=0.126$ ***				
	HT EOD	$\chi2=1.56$ ns				
Dipole	IPI hist	$D=0.089$ ***	IPI hist	$D=0.074$ ***		
	HT EOD	$\chi2=12.9$ ***	HT EOD	$\chi2=6.46$ *		
Gymnotus	IPI hist	$D=0.185$ ***	IPI hist	$D=0.201$ ***	IPI hist	$D=0.178$ ***
	HT EOD	$\chi2=22.6$ ***	HT EOD	$\chi2=22.6$ ***	HT EOD	$\chi2=2.13$ ns

Significance levels: * $P<0.05$; ** $P<0.01$; *** $P<0.001$

of electrical activity from the cage on the occurrence of high voltage EODs.

Figure 12 presents the behavioural data for all 80 trials analysed by 4 channel event recorder from the video recordings. Behaviours directed towards the prey were categorised into Forward and Backward Approaches and Nose and Head Butts. Nose Butts are medium intensity thrusting or prodding with the nose while Head Butts are powerful swipes with the side of the head. The terminology is the same as that used for the aggressive behaviour of *G. carapo* (Westby 1975). For this analysis all high voltage EODs were also counted. They were identified, as described above, by high frequency (>400 Hz) discharge bursts. The video recordings allowed us to check the reliability of this procedure by comparing the audio record of the EODs with the characteristic jolting of the fish's body as it discharged the main organ. The massive increase in approaches and attacks when the cage produced either real or recorded *G. carapo* EODs is evident from the bar graph. The goldfish elicited only about one quarter as many attacks. The occurrence of high voltage discharges (Table 1, Figs. 11 and 12) is significantly associated with the presence of electric prey.

Discussion

Ecological conditions

The data collected from the field work in 1983, and the measurements made by workers at the INRA lab in Kourou, allow us to build up a detailed picture of the aquatic conditions for electric fish in the Papinabo creek over a 12 month period. The extreme annual rainfall cycle in the region (Fig. 2) leads to abrupt changes in water depth from an average 1.2 m in April to zero in the dry season in November and December. Clearly the fish will require behaviour patterns appropriate for the effective exploitation of such a habitat. The census data from the INRA archives presented in Fig. 4 reflects the response of the fish to the water conditions. The figure shows the now well-documented breeding response of electric fish to the first rains in December. Hopkins (1974b) reported the presence of adult *Sternopygus macrurus* in the Rupununi district of Guyana with ripe gonads prior to the onset of the main rains. Juveniles, several weeks old, were also found at the start of the rainy season. Similarly, this data for *G. carapo*, indicates a large number of juveniles in January and February. The onset of the major rainy season in April/May sees the influx of large sexually mature individuals from the deep water of the main river system, following which there is a further increase in the number of larvae with the proportion of juveniles increasing later in this intermediate season. In anticipation of the dry season the numbers decrease and Rojas-Beltràn's (1986) data indicate a massive fall in the total number of fish of all species.

The reproductive response to the onset of the rainy season raises important questions about the environmental factors controlling gonad development. This problem has been studied in detail by Kirschbaum (1975, 1979) who showed that gonadal recrudescence and successful reproduction of *E. virescens* could be repeatedly provoked by a systematic imitation of the Rainy Season. Continuous decrease in water conductivity appeared a vital factor, with increasing water level and imitation falling rain contributing to its effectiveness. Increasing conductivity alone was effective in causing gonad regression. Similar results have been obtained in the laboratory with *Apteronotus leptorhynchus* and *S. macrurus* (Kirschbaum 1984). Kirschbaum's assumption about the importance of conductivity as a triggering factor is based on data from the Amazon basin where soil conditions and water chemistry are known to be quite different (Planquette, personal communication). Studies in Manaos, Brazil indicate a conductivity increase at the start of the rainy season as salts are washed from the soil. From then on further rainfall causes a steady decline in conductivity which then rises again in the dry season (Kirschbaum 1979). Measurements made in French Guiana over more than 12 months (Fig. 3) present a contrasting picture. Conductivity remains very low and remarkably constant irrespective of rainfall, rarely rising above 40 $\mu S.cm^{-1}$. We must therefore conclude that, in these areas at least, factors other than conductivity trigger spawning behaviour. The most obvious candidate would be water level but this, as Fig. 2 shows, follows with a drainage lag of nearly a month in the critical part of the season. The mechanical and/or auditory stimulation of falling rain is a *zeitgeber* which should be considered, indeed the South American catfish *Calichthys*, common in the Guianas, is known to start nest-building after acoustic rainfall-like stimulation (Hoedeman 1952). It is perhaps more likely that the appearance of many small fish in January is due to the fact that the sudden expansion of rich feeding grounds following the dry season triggers adults in the lower reaches into spawning at a time when the newly emerging shallow, predator free habitats are appearing upstream. In the absence of conductivity cues, it is possible that the Guianan populations are triggered into gonadal recrudescence simply by the rapid appearance of suitable food supplies and spawning areas at the start of the minor rainy season in December. The onset of the major rainy season would be signalled by the torrential rains of March/April.

Species distribution and discharge characteristics

The distribution of gymnotids in the study areas was determined by the two methods of electrical detection with the fish-finder and Rotenone poisoning, the technique used for routine census purposes by the INRA laboratory. The two techniques were compared on the last day of field work in 1983 and the detailed results are presented by Rojas-Beltràn (1986). An electrical census was carried out, followed by an immediate poisoning of the 100 m Papinabo study area. The agreement was within 5% for the majority of species. The detailed maps are shown in Figs. 5 and 6. The near complete lack of wave species such *Eigenmannia* and *Apteronotus* was particularly striking. *Eigenmannia* was found in the lower reaches of both of the streams studied but only where they emerged onto open savannah. Here there were high densities of fish hiding by day in dense clumps of plants such as *Cabomba*. Just two genera of pulse species, *Gymnotus* and *Hypopomus*, made up the large majority of electric species found in the study areas. In common with the observations of Lissmann (1961) and Hopkins and Heiligenberg (1978) in Brazil, Guyana and Surinam, the pulse gymnotids were found well spaced out during the day, usually 2 to 10 m apart. They showed strong site attachment and the same individuals could be found day after day occupying the same bank or sunken-log hiding place despite emerging at dusk to undertake foraging trips of several tens of metres. The greatest concentrations of fish were to be found where sunken dèbris and tree roots offered the best hiding places, this was particularly the case in the Renner creek where the lower density tree canopy gave increased light levels. The principal species were always found in close association. Apart from the discovery of *G. pantherinus* and a new *Hypopomus* species in the Papinabo (see Hopkins and Westby 1986), the presence of *H. beebei* larvae in the Renner creek was particularly interesting. Their monophasic EODs strongly resemble the larval EODs of *Eigenmannia* (Kirschbaum and Westby 1975) and as we pointed out these 1 to 2 ms duration pulses also resemble those of the electric eel, *Electrophorus electricus*. Lissmann (1958) argued that weakly electric fish originated with a low frequency, pulse-type ancestor. Its EODs were probably little different from the muscle action potentials at the muscular origin of the electric organ. Hopkins and Heiligenberg (1978) develop this evolutionary scenario and suggest that the primitive EOD resembled *E. electricus*. Morphological evidence from the *Electrophorus*-like primitive larval electric organ of *Eigenmannia* (Kirschbaum 1977) supports this view and the striking similarity of the *Hypopomus* larval pulses to the adult *Electrophorus* EOD (c.f. Figs. 8 and 11) provides still further evidence.

Although the larval electric organs of *Hypopomus* have yet to be studied, the EOD development data (Fig. 8) give some indication of the course of the replacement of the larval by the adult discharge EOD. The only electric fish for which complete developmental data are available is the mormyrid *Pollimyrus isidori* (Westby and Kirschbaum 1977, 1978). Here the larval and adult electric organs (and their EODs) coexist for about 40 days before the larval structure degenerates. In the gymnotoids studied so far (Kirschbaum 1984) the same pattern of organ replacement occurs. The waveform development through the juvenile stages in *H. beebei* is consistent with the adult biphasic EOD riding on top of the larval pulse, triggered close to its peak. A comparison of the EODs from individuals of 30 to 110 mm length with the larval discharge reveals the diminishing contribution of the larval EOD seen as an initial head-positive wave with final overshoot. This slow phase has the same duration (approximately 1 ms) as the head-positive larval EOD (Fig. 8).

Predatory behaviour of the electric eel, Electrophorus electricus

As far as can be ascertained, there are no published field studies of the prey-capture behaviour of the electric eel. Stomach content analyses are poorly documented, but it is known that the eel's principal food source is small fish (Ellis 1913). The observations on *E. electricus* in the Papinabo creek described above provide evidence that the electric eel preys on weakly electric gymnotids. The unusual manner in which the eel was foraging, maintaining electrical silence for long periods, suggests that it was using a strategy of stealth to locate electric prey. The eel would presumably have no trouble using its tuberous electroreceptors (Hagiwara et al. 1965) to target weakly electric gymnotids. Bullock (1969) working on captive eels in large outdoor tanks determined the optimum playback IPI for attraction to artificial pulses. Interestingly, this was not at a value typical of *E. electricus* but was found to be 10 ms. Stimuli delivered at this interval attracted eels, even when delivered at very low intensity. Ten milliseconds is an EOD interval never seen in the *Electrophorus* weak EOD even during violent activity. The strong EOD (see Bauer 1979; and above) is emitted at much shorter intervals, predominantly 2–5 ms. The optimal attraction IPI of 10 ms found by Bullock corresponds to the IPI 'gap' in the typical eel interval histogram (e.g. Fig. 11) and is therefore much closer to the IPIs of potential swimming prey such as *Hypopomus* and *Gymnotus* than to those of conspecifics.

The response of *G. carapo* to the approach of a hunting eel, summarised in Fig. 10, is especially interesting. Discharge arrests on detecting the approaching predator appear to be attempts to 'hide' electrically and, when the eel is close, long periods of electrical silence are observed. This 'off' response is known to be associated with submissive behaviour in intra-specific social behaviour (Black-Cleworth 1970; Westby 1975; Westby and Box 1970) and playback experiments (Westby 1974) have shown that discharge arrests inhibit attacks from dominant individuals. Such arrests would be most effective if the eel hunts principally using passive electrolocation. The difficulties encountered with such field observations meant that detailed study had to be left for the laboratory. The results showed the striking difference that an electrically active prey or model had on detection by the eel. While the presence of an EOD was paramount, non-electric prey were still very effectively located compared to the control condition (Fig. 12). Here the eel could be using active electrolocation and/or employing passive detection of the prey's bioelectric potentials, using the highly sensitive ampullary DC receptors (Kalmijn 1974). Bauer (1968) has shown that the strongly electric African catfish, *Malapterurus electricus*, responds to low intensity DC dipole fields. Similarly Belbenoit et al's (1979) field study of *M. electricus* in the Swashi river, Nigeria, shows that this species preys principally on genera such as *Tilapia* and the characoid *Alestes*. Perhaps *M. electricus* preys principally on these non-electric species because, unlike *E. electricus*, it lacks the tuberous electroreceptors necessary for the detection of electric prey?

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