Nesting and Paternal Care in the Weakly Electric Fish *Gymnotus* (Gymnotiformes: Gymnotidae) with Descriptions of Larval and Adult Electric Organ Discharges of Two Species

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We describe nesting and paternal care in two species of the weakly electric fish, *Gymnotus*: *Gymnotus carapo* from savanna swamps on the Caribbean island of Trinidad; and *Gymnotus mamiraua* from whitewater floodplains of the Amazon Basin. In both species, single adult males guard eggs and juveniles. Male *G. carapo* excavate depressions in the substrate or nest in the roots of aquatic macrophytes. Male *G. mamiraua* form nests exclusively in the root mass of floating meadows of macrophytes. Twelve nests of *G. mamiraua* were encountered, containing juveniles up to a maximum total length (TL) of 67 mm and estimated maximum age of 8–12 weeks. Two of these nests exhibit a bimodal size distribution, implying more than one spawning event. Juveniles remain close to the male during the day and disperse little more than 1 m away at night. Larval *G. carapo* and *G. mamiraua* (approximately 15–20 mm TL) generate a characteristic Electric Organ Discharge (EOD) with a dominant positive phase followed by a very weak negative phase. The Peak Power Frequency of the larval EOD is in the range 0.015–0.04 kHz. It is possible that the EODs of larvae may be sensed by animals with ampullary electroreceptors, including the male as well as predatory catfishes. Larval *G. carapo* and *G. mamiraua* generate EODs at a low repetition rate compared to adults and with no increase at night. This low rate reduces the probability of coincident pulses and may mitigate sensory jamming between nestlings in crowded nests. The repetition rate, and the waveform and spectral features of the EODs from 40 mm TL specimens of *G. mamiraua*, resemble those of mature adults.

MALE parental care and nesting are common in fish (Blumer, 1979; Baylis, 1981; Gross and Sargent, 1985) but until recently were unknown in the Neotropical gymnotiform electric fish. Assunção and Schwassmann (1995) reported both phenomena in the strongly electric eel *Electrophorus electricus* (Gymnotidae) from field studies in the Eastern Amazon. Kirschbaum and Wieczorek (2002) described male mouth brooding in a captive colony of the weakly electric *Gymnotus carapo* (Gymnotidae). Kirschbaum and Schugardt (2002) reported egg guarding in male *Sternopygus macrurus* (Sternopygidae) but no subsequent care of the hatched fry. Westby (1988) reported a small aggregation ("crèche") of juvenile *Brachyhypopomus beebei* (Hypopomidae) in Surinam but no parental care was implicated.

Parental care is unknown in other weakly electrical gymnotiform species that have been studied in the wild or successfully captive bred. These include *Apteronotus leptorhynchus* (Kirschbaum and Schugardt, 2002), *Brachyhypopomus brevirostris* (Kirschbaum and Schugardt, 2002), *Brachyhypopomus occidentalis* (Hagedorn, 1986), *Brachyhypopomus pinnicaudatus* (Franchina, 1997), *Eigenmannia virescens* (Hopkins, 1974;

Hagedorn and Heiligenberg, 1985; Kirschbaum and Schugardt, 2002), and *Rhamphichthys* sp. (Kirschbaum and Schugardt, 2002). Two species of the unrelated weakly electric mormyriform fishes from Africa are also known to undertake nesting and paternal care: *Pollimyrus isidori* (Mormyridae; Hopkins, 1986, Bratton and Kramer, 1989), and *Gymnarchus niloticus* (Gymnarchidae; Budgett, 1901, Hopkins, 1986).

Gymnotus is the most widely distributed and species-rich gymnotiform genus, with 28 valid species distributed from Southern Mexico to the Pampas of Argentina (Albert and Crampton, 2003). Ecological studies of *Gymnotus* have been concerned primarily with habitat preferences (Crampton, 1998a,b), electric signal diversity (Crampton, 1996a; Crampton and Albert, 2003, 2005), feeding habits (Teixeira, 1989), and reproductive seasonality (Barbieri and Barbieri, 1983; Barbieri and Barbieri, 1984, 1985). The nonreproductive behavior of *Gymnotus* is well known from laboratory-based ethological studies on one species identified as *G. carapo* (Black-Cleworth, 1970; Valone, 1970; Westby, 1975). *Gymnotus* is noted for its aggressive electric signaling between males and the establishment of dominance relationships, but

nothing is known of territoriality, courtship, mating, or spawning behavior in the wild.

The EODs of larval and young juvenile *Gymnotus* have not previously been documented. The age and size at which *Gymnotus* begins to generate electric organ discharges (EODs) is also unknown. In gymnotiforms for which data are available (e.g., *B. pinnicaudatus*, *Eigenmannia electricus*, *S. macrurus*, *Eigenmannia* sp., *A. leptorhynchus*), this occurs between seven and 12 days when the larvae are from 8–12 mm long (Kirschbaum, 1995, Franchina, 1997). The onset of electrogenesis corresponds to the time at which exogenous feeding begins (Kirschbaum, 1995).

Here we report field observations of nesting and paternal care in two species, *G. carapo* and *Gymnotus mamiraua*, present descriptions of the juvenile and adult EODs, and speculate on the role and function of electric signals in nesting. The nesting behavior of these two species is similar but in each case adapted to specific ecological circumstances, which we describe in detail.
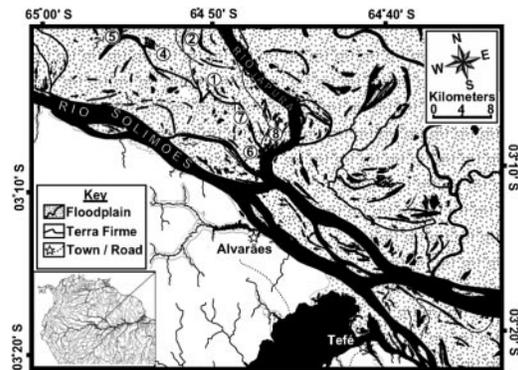

Fig. 1. Map of Tefé area in the lowland Amazon Basin of Brazil. Localities at which nests of *Gymnotus mamiraua* were encountered are numbered 1–8 (see Table 1). Areas exposed to an annual flood regime are stippled. White areas are Tertiary terra firme peneplain. The terrain to the north of the Rio Solimões is Quaternary whitewater floodplain (várzea). Base map traced from 1999 1:150:000 Landsat TM5 images. Flood extent plotted from June 1995 NASDA JERS-1 images.

MATERIALS AND METHODS

We present observations of nesting in two species of *Gymnotus*, each under different ecological circumstances. To do so, we combine observations from fieldwork conducted in the Aripo Savanna of the Caribbean island of Trinidad (CDH, July 1969) and in whitewater floodplains of the lowland Brazilian Amazon Basin near Tefé, Brazil (Fig. 1; WGRC, 1993–1999). Observations in the Amazon basin formed part of a long-term (1993–2002), multihabitat, quantitative sampling program (Crampton, 1996a,b) aimed at elucidating patterns of species and electric signal evolution in gymnotiforms (Crampton 1998a,b; Crampton and Albert, 2005).

Specimens were localized with an Electric-Fish Locator (EFL) consisting of dipole electrodes mounted on a submersible pole and connected to an amplifier and monitoring device. Direct observations of *Gymnotus* were possible in Trinidad. In the Amazon floodplain, low water transparency and thick plant cover prohibited the visual observation of nests. Instead, evidence for nesting in the Amazon floodplain was accumulated slowly from surveys with an EFL and from random quantitative netting.

WGRC amplified EODs from EFL electrodes using a custom-built AC-coupled wide-band differential preamplifier (frequency response of ± 3 dB from 0.2 Hz to 110 kHz) and monitored with an oscilloscope (Thurlby-Thandar SC-110A) and earphones. The amplified signals were recorded onto the left stereo channel of digital audio tape (DAT) at an *fs* of 48 kHz using a Sony TC-D3 or D7 DAT recorder. The location and depth of single fish or aggregations of juveniles were estimated by orientating the electrodes toward electrical sources, and a synchronized running voice commentary was recorded onto the right stereo track of the DAT tape. Fishes were then captured with a dipnet (46 cm diameter, 3 mm mesh). The field recordings were analyzed later using bioacoustic software (Avisoft SASLab). Electric fish in floating meadows wedge themselves into the root mass when disturbed, and it was usually possible to recover recalcitrant fishes. Some juveniles were undoubtedly dislodged during the netting of nests and fell into the water column under the meadows (depth 3–7 m). Netting continued until no electrical signals were detectable within a radius of 2 m from a nest site.

Quantitative sampling without the use of an EFL involved either dip-netting (same net as above) or seine-netting (30 × 4 m with 4 mm mesh). Seine nets encircle large areas (6–18 m²) of floating meadows, but the wider mesh reduces the capture efficiency for small juveniles. Mesh penetration experiments were conducted by placing live *G. mamiraua* into a dipnet or part of a seine net panel placed in a tank of water. The net was then repeatedly lifted out of the water to allow fishes narrower than the mesh to pass through. The seine net and dipnet were 100% effective in catching *G. mamiraua* larger

than 45 mm and 15 mm, respectively. In the field, many fishes smaller than the threshold for mesh penetration were captured by becoming trapped on the surface of vegetation in the net.

Body lengths for *Gymnotus* were measured with calipers and are reported here as TL to the nearest millimeter. Some *Gymnotus* exhibited signs of damage to the caudal appendage and/or subsequent regeneration. In each damaged specimen, the percentage lost (before any subsequent regeneration) of the estimated original TL was estimated (to nearest 5%) from head length by reference to regressions of head length and TL from intact specimens (see Albert and Fink, 1996). Total lengths of all damaged specimens are reported as estimated undamaged length to reconstruct size distributions. Sexual maturity and sex can be assessed reliably in *Gymnotus* only by dissection. The testes of mature males are pinkish-white and smooth in surface texture. The ovaries of gravid females are packed with eggs, which are yellow when mature. Sexually mature females and males are defined here as specimens with fully enlarged eggs or with enlarged testes such that eggs or sperm exit the urinogenital orifice when slight pressure is applied to the flanks. Juveniles cannot be sexed reliably.

A large type series of specimens of *G. mamiraua* from the region of this study is available (Albert and Crampton, 2001). Specimens of *G. carapo* from Trinidad in 1969 were unfortunately not vouchered. However, only one gymnotiform species occurs in Trinidad, and this is unquestionably *G. carapo* (Albert and Crampton, 2003).

To record single EOD waveforms, specimens of *Gymnotus* were restrained in a narrow mesh cage in an aquarium with electrodes placed equidistant from their tail and head and in line with the long-axis of their bodies. WGRC used the amplifier and oscilloscope described above and digitized single EODs at an fs of 50–150 kHz using an analog-digital signal acquisition board at a resolution of eight bits and with a time-base resolution of better than 0.01% (Amplicon PC99 with bipolar input module). EODs captured by CDH were amplified with an AC-coupled differential amplifier and recorded on magnetic tape with a Uher 4400 recorder and digitized at a later date (fs = 50–100 kHz). The original recordings made by CDH in 1969 were noisier than those possible with modern equipment but preserved all the important temporal and spectral features of EOD waveforms. The total duration of EODs was measured with the beginning and ends taken at a 1% threshold of the normalized peak-to-peak amplitude using custom-written software. Spectral analysis of EODs was undertaken by computing 2048-point Fast Fourier Transforms. All EODs are plotted with head positivity upward and we adopt the following terminology for EOD components. Phases of alternating polarity separated by zero-crossovers are labelled P0 through P3 in chronological order, where P1 is always the dominant positive component.

We measured EOD repetition rates from digitized tape recordings of signals by calculating interpulse intervals (IPIs) with custom-written software in MATLAB. Repetition rates (in Hz) represent the reciprocal of the average IPI during 1-min recordings. Diel activity rhythms were characterized from specimens recorded at hourly intervals in large water tanks stocked with aquatic vegetation and exposed to a shaded natural photoperiod.

RESULTS

Description of the study sites and assemblages of Gymnotus.—Trinidad: *Gymnotus carapo* is the only gymnotiform in a freshwater fish fauna of some 70 species (Price, 1955; Boeseman, 1960). It is common in rain-forest streams of the Northern Range of hills (approximately 10°45′N,61°15′W) and also occurs in shallow waterbodies of lowland grasslands such as the Aripo Savanna (approximately 10°36′N,61°12′W).

Brazil: The Quaternary whitewater floodplain or várzea of the Central Amazon basin of Brazil, where *G. mamiraua* occurs (Fig. 1) is a mosaic of lakes, channels and seasonally flooded forests, the structure and water quality of which are described by Crampton (1998a,b, 1999), Henderson et al. (1998), and Henderson and Crampton (1997). The Amazon River near Tefé (Fig. 1) has an annual flood regime with an amplitude of 8–16 m (Ayres, 1993). Floating meadows of grasses and other macrophytes cover large areas of water surface, and their dense root mats support productive and diverse assemblages of fishes (Henderson and Crampton, 1997; Crampton, 1999; Petry et al., 2003). Várzea meadows in the vicinity of Tefé region host a syntopic assemblage of eight species of *Gymnotus*, all of which are able to tolerate the long periods of anoxia that typify várzeas by employing a modified gas bladder as an accessory air breathing structure (Liem et al., 1984; Crampton, 1998a).

Field observations of nesting.—*Gymnotus carapo*: Observations of nesting were made in a shallow (approximately 10 cm) blackwater drainage ditch on the Aripo Savanna. Two nests were lo-
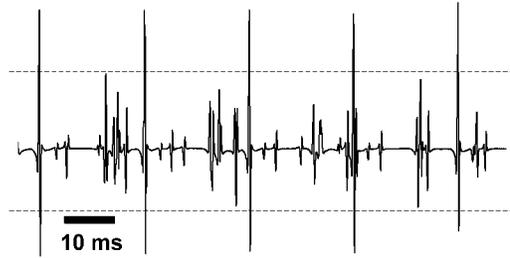
Fig. 2. Field recording from a *Gymnotus mamiraua* nest (nest 6, Table 1) in a floating meadow of the várzea floodplain. Voltage and time are displayed on the vertical and horizontal axes, respectively. The recording was made at night when the nestlings are maximally dispersed. The EODs of the single male (EOD peaks exceeds dotted lines) and many juveniles (EOD peaks do not exceed dotted lines) are in most cases coincidental. Variation in EOD amplitude is due to variation in distance from the recording electrode as well as relative voltages.

cated with an EFL. Both were located under a large pile of branches, palm fronds, and leaves; and both were guarded by a single adult male (180–335 mm, 10–98 gm). Both males lay in a circular depression about 15 cm in diameter and 5 cm in depth that appeared to have been excavated into the silt and sand substrate. Each depression also contained a dense aggregation of several hundred larval fishes ranging in size from 10–21 mm. Most of the larvae were clustered within 30 cm of the adult, but some were spread out in leaf litter up to 2 m away. All the larvae were generating EODs, creating a contin-

uous discharge "hash" on the EFL loudspeaker. One of the males lay on its side over the top of a depression with its anal fin expanded horizontally in a guarding posture. In spite of extensive removal of vegetation and disturbance near the site, both males remained on the nest tenaciously. Adult females were not found in the vicinity of the nests.

Larval aggregations of *G. carapo* similar to those reported above were observed by P. Stoddard (pers. comm.) in creeks of the Venezuelan Llanos. One dense aggregation of larval *G. carapo* about 20 mm in size was found in interstices of a gravel and mud stream bed. A second aggregation of larval *G. carapo*, ranging in size from 20–30 mm was located inside the floating root mass of a water hyacinth, *Eichornia crassipes*, at the edge of a stream. At both sites, the larvae were all discharging weak EODs and a single (uncaptured) adult specimen was detected nearby.

Gymnotus mamiraua: Twelve nests of *G. mamiraua* were found in floating meadows. Seven of these nests were detected with an EFL from a conspicuous cacophony of pulsed EODs generated from fish in very close proximity (Fig. 2). A further five nests were found during routine quantitative dipnetting or seine netting (Table 1). Each nest consisted of an aggregation of small juveniles (13–67 mm) hidden within the dense roots of floating macrophytes. Six of the 12 nests were attended by a single adult male, but adult females were never present near nests. None of the sites showed any traces of foam or

TABLE 1. NESTS OF *Gymnotus mamiraua* IN FLOATING MEADOWS OF THE AMAZON FLOODPLAIN. Method: EFL = electric-fish locator; Dip = dipnet. L = locality (see Fig. 1). S = nest substrate: C = *Cyperus* sp., E = *Eichornia crassipes*, P = *Paspalum repens*, R = *Reussia* sp. Adult: No. = number (M = male). Juveniles: No. = number; SD = standard deviation; % (Damage) = percentage of juveniles in nest with damage to caudal appendage; mean = mean damage to caudal appendage as % of TL.

| | | | | | Adult | | Juveniles | | | | | | |
| | | | | | | | | TL | | | Damage | | |
Nest	Method	L	Date	S	No.	TL	No.	Min	Max	Mean	SD	%	Mean
1	EFL and Dip	1	18.06.93	P	1 M	230	27	31.2	43.4	37.7	1.98	3.7	0.19
2	Dip	2	16.09.93	R	0	—	13	28.0	31.9	30.7	0.94	0	0
3	Dip	1	07.04.94	P	1 M	270	44	28.0	35.1	30.7	2.17	0	0
4	EFL and Dip	3	23.05.94	E	1 M	265	19	30.0	35.0	33.9	1.29	0	0
5	Dip	4	29.05.94	C	0	—	86	13.0	19.9	16.7	1.58	0	0
6	EFL and Dip	5	17.04.97	E	1 M	226	31	31.8	53.2	43.1	6.10	5.4	0.3
7	EFL and Dip	5	18.04.97	E	1 M	224	45	34.1	55.1	43.4	7.11	2.2	0.1
8	EFL and Dip	6	17.05.97	E	0	—	35	41.4	53.4	48.1	2.85	5.7	0.3
9	EFL and Dip	5	26.04.97	E	0	—	20	43.5	55.7	49.0	3.83	0	0
10	EFL and Dip	6	07.05.97	E	0	—	12	54.0	67.0	59.5	4.46	59	7.5
11	Seine	8	04.06.98	E	0	—	35	40.0	59.0	48.7	4.75	17	1.6
12	Seine	3	05.06.98	E	1 M	260		31.0	55.2	42.5	8.05	21	1.4
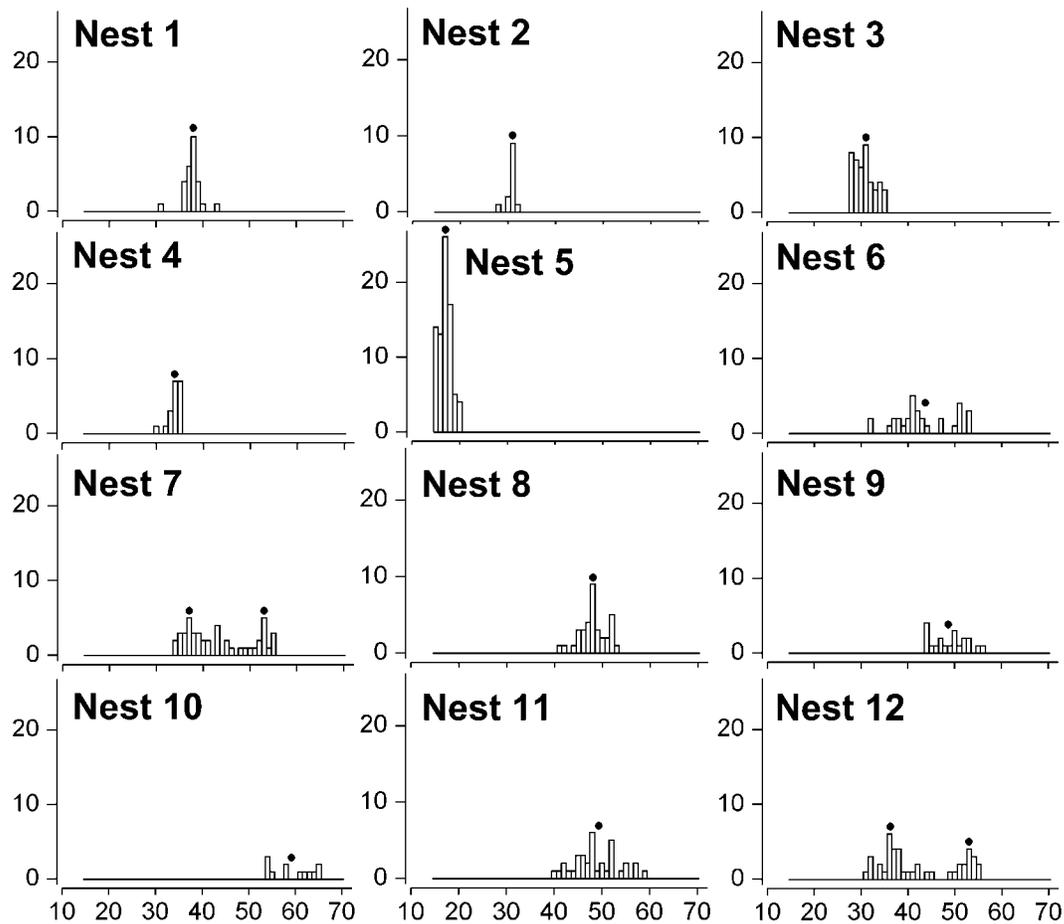
Fig. 3. Histograms of size distribution of juvenile *Gymnotus mamiraua* in 12 nests from floating meadows of the Amazon floodplain. Total length (mm) is displayed on the x-axis and frequency of occurrence on the y-axis. Single dots indicate mean where data fit a normal distribution. Double dots indicate modes of a bimodal distribution.

bubbles. The nests were all encountered during the high water period when *G. mamiraua* breeds. Summary data on each nest site are presented in Table 1, and histograms of the size distribution of juveniles are presented in Figure 3.

At each nest detected with an EFL, the EODs emanated from single dense clump of roots from 10–20 cm wide and 30–40 cm deep. Some EODs were detected (with submerged electrodes) up to around 30 cm from the clump, very few beyond 50 cm, and none beyond 1 m. The size distribution of juveniles in 10 of the 12 nests (Fig. 3) fits a normal distribution (Kolmogorov-Smirnov normality test with 95% confidence). The two exceptions, nests 7 and 12, exhibit a clear bimodal distribution of juvenile size classes, suggesting the occurrence of more than one cohort (i.e., juveniles from more than one spawning event).

Observations of a single nest.—The full-time attendance of a guardian male *G. mamiraua* was confirmed by monitoring Nest 6 (see Table 1). This nest was visited and recorded with EFL electrodes for 30–45 min at 1400, 2000, and 2400 h on the day it was discovered (at 1030 h), at 0800, 1400, 2000, and 2400 h on the next day, and at 0800 h on the third day. The water hyacinth root mass in which the nest was located was marked with a flag and on each occasion approached quietly in a canoe. During daylight hours, the juveniles were mostly concentrated within a single root mass with the male apparently in their midst. No more than half a dozen juveniles appeared to be spread out to about 50 cm away from the nest and none any further. At night, the juveniles dispersed to 1 m, and exceptionally 1.5 m, away from the same root mass although most appeared to be no further than

0.5 m away. No aggressive electrical behavior such as transient increases in EOD repetition rate were recorded from the guardian male although on several occasions a lack of finesse with the handling of the electrodes prompted rapid increases in the repetition rate of the EOD from around 30–50 Hz to 100–120 Hz. The guardian male changed position many times during each nocturnal monitoring period but during the day remained motionless. The site was netted at 1000 h on the third day, and the male was captured along with 31 juveniles (Table 1).

Aquarium observations.—Live specimens of *G. mamiraua* from Nest 6 were transferred from the field to a large aquarium filled with water from the capture locality and stocked with water hyacinths. On the first night, the adult male and juveniles did not congregate, perhaps because of the stress of transit. However, on the second day, more than half of the juveniles were lodged into the same root mass as the male, and the remaining juveniles were within 50 cm. Observations with red light (which does not disturb normal nocturnal behavior) on the second night showed that the juveniles were moving around constantly but remained for the most part in one side of the tank near the male. Most of the juveniles occasionally rose to the surface to gulp air, even though dissolved oxygen levels exceeded 5 mg/liter. The male changed positions relatively infrequently, but no shepherding behavior was observed. This pattern was repeated on the third and fourth nights, and the observations terminated at the end of the fourth night.

Observations from quantitative sampling.—Seine-net samples of 10,860 m² of floating meadows sampled between 1996 and 1998 revealed a mean density of approximately 8.5 specimens of *G. mamiraua* per 100 m² of meadow (not including nests). Solitary juvenile *G. mamiraua* in the 60–90 mm size range were commonly encountered outside nests during the high water season and exhibited a scattered, nonaggregated distribution. In contrast, very few specimens smaller than 60 mm and none smaller than 45 mm were encountered outside nests. Adult females and males (larger than 150 mm) were common and also exhibited a nonaggregated distribution. Breeding occurs during the rising and high-water period from February to August, and the proportion of mature specimens declines as water levels drop (generally September to November). Some populations continue to breed in isolated várzea lakes until as late as De-

cember. The eggs in fully developed ovaries of female *G. mamiraua* occur in three or four distinct size classes (pers. obs.). This implies partial-spawning through the breeding season as has been documented in *G. carapo* (Barbieri and Barbieri, 1985).

Notes on damage to juvenile caudal appendage.—*Gymnotus*, like other gymnotiform fishes, are able to regenerate the entire postcoelomic portion of the body as a routine part of their natural history (Ellis, 1913). The caudal appendages of many specimens of *Gymnotus* exhibit damage, and subsequent regeneration, sustained from predators or intraspecific aggression (Albert and Crampton, 2003). Only 2.7% (9/331) of nestling *G. mamiraua* in the size range 13–50 mm exhibited damage to the caudal appendage, and the extent of damage never exceeded 5% of the TL. In contrast, 29.8% (29/97) of nestlings in the size range 50–67 mm exhibited damage ranging in extent from 5–20% of the TL. The proportion of damaged juveniles and average percent damage were highest in nest 10, which contains the largest juveniles (Table 1).

Electric organ discharges.—*Gymnotus carapo*: EODs of larval *G. carapo* from Trinidad (12–21 mm) have a dominant positive phase followed by a weak negative phase and a total duration of around 3 msec (Fig. 4B). The Peak Power Frequency (PPF) of the Fourier Power Spectrum of these EODs ranges from 0.02–0.04 kHz. Sexually mature male and female specimens of *G. carapo* (larger than 250 mm) generate an EOD consisting of four phases (P0,P1,P2,P3; Fig. 4D), a total duration of approximately 2 msec and a Peak-Power Frequency of approximately 1.4 kHz. No sexual differences in EOD waveform or repetition rate were observed. From nests of *G. carapo* observed in the Venezuelan Llanos, P. Stoddard (pers. comm.) noted that specimens around 20 mm long generated approximately monophasic EODs, whereas specimens around 30 mm had already undergone a transition to approximately biphasic EODs (P1 + P2).

The resting daytime EOD repetition rate of four larval *G. carapo* from Trinidad (sizes 12, 12, 14, and 21 mm) averaged 26, 27, 14, and 18 Hz, respectively (Fig. 4A). Surveys in the early night showed that the EOD repetition rate does not increase substantially and remains in the range 15–35 Hz for all larvae (see also Hopkins, 1977). Adult EOD repetition rate is typically in the range 35–45 Hz by day and 55–65 Hz at night (Fig. 4C).
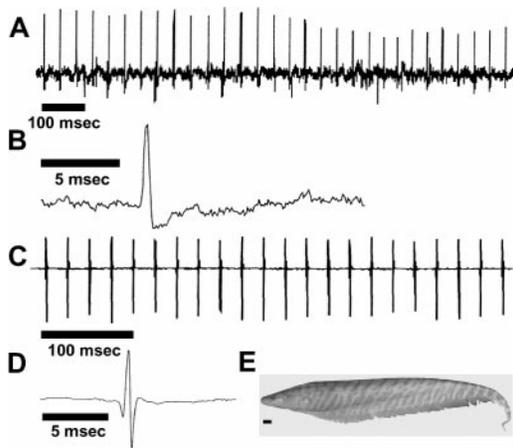
Fig. 4. Field recording of larval (A,B) and adult (C,D) EODs of *Gymnotus carapo* from Trinidad. Sequences of EODs (A,C) and single EODs (B,D) are plotted with head positivity upwards and the time base expanded for the single EOD. Fluctuation in the peak-to-peak amplitude of the sequences of EODs are caused by movement of the fish relative to the recording electrode. The noisy background in (A) and (B) is an artifact of magnetic tape recording. (E) Photograph of adult *G. carapo* from nearby Venezuela (UF 77334). *Gymnotus carapo* from Trinidad are indistinguishable in pigmentation, meristics and morphometrics from populations in Venezuela and the Guyana Shield (Albert and Crampton, 2003).

Electric organ discharges.—*Gymnotus mamiraua*: Developmental transitions in the EOD waveform of *G. mamiraua* are illustrated in Figure 5. The juvenile EOD undergoes a radical transformation from a predominantly monophasic shape (P1 + small P2) at 20 mm TL to a triphasic shape (P0,P1,P2) in the size range 30–32 mm. The EODs of specimens in the 50–56 mm size range are indistinguishable from those of sexually mature adults, with four phases (P0,P1,P2,P3). Nest 7 (Table 1, Fig. 6) contained two size classes of nestlings within the size range 34.1–55.1 mm. Here, there is a positive correlations between PPF and size, with the larger size class having significantly higher PPFs than the smaller one (two-tailed two-sample t-test, $t = -4.53$, df $= 15$, $P = <0.001$).

The PPF range of specimens in the size range 80–100 mm has risen to 1.547–1.828 kHz, which is higher than juveniles in the size range 19–56 mm (0.015–1.547 kHz) and also higher than sexually mature adults (1.219–1.594 kHz). There is no significant difference between the EOD PPF of sexually mature females (1.266–1.547 kHz, $N = 10$, mean 1.406, SD 0.075 msec) and mature males (1.219–1.594 kHz, $N = 10$, mean 1.397, SD 0.039).

Diel patterns in the EOD repetition rate of *G. mamiraua* are presented in Figure 7. Larval specimens (15–20 mm) have a low repetition rate with no increase during the night. Juveniles in the size range 32–50 mm and adults generate EODs at a higher rate, and with higher and more variable EOD repetition rates during the night when foraging occurs.

DISCUSSION

Phylogenetic considerations.—Parental care is known in only three genera of gymnotiform fishes: *Electrophorus*, *Gymnotus*, and *Sternopygus*. In both *Electrophorus* and *Gymnotus*, females lay discrete balls or disks of eggs and males guard the eggs and hatchling juveniles in nests. Mouth brooding has been observed in *G. carapo* but not in *E. electricus* (Kirschbaum and Wieczorek, 2002). Although *Gymnotus* and *Electrophorus* differ considerably in the design of their electrogenic systems, they share many synapomorphies and have recently been united within the most basal gymnotiform family, Gymnotidae (Albert, 2001). In *Sternopygus*, females lay eggs singly and males fertilize and guards the eggs but abandon the hatchlings (Kirschbaum and Schugardt, 2002; F. Kirschbaum pers. comm.).

Egg guarding and nesting is known in many families of catfishes (Siluriformes), the sister group to the Gymnotiformes. Parental care is largely undocumented among extant basal groups of siluriforms (e.g., Diplomystidae, Cetopsidae; de Pinna, 1998) and sporadically documented in derived groups (Breder and Rosen, 1966; Ferraris, 1991).

Function of nesting and paternal care.—The aggressive behavior of male *Gymnotus* is well known (Black-Cleworth, 1970; Westby, 1975) and undoubtedly plays a strong role in protecting eggs and nestling young from the many predatory fishes and invertebrates of Neotropical freshwaters. Parental care is common in many families of Neotropical fishes, including Osteoglossidae, Erythrinidae, Lebiasinidae, Aspredinidae, Callichthyidae, Doradidae, Loricariidae, Cyprinodontidae, Synbranchidae, Cichlidae, and Lepidosirenidae (Breder and Rosen, 1966; Crampton, 1999). Parental care is especially common in hypoxic habitats of the Neotropics where juvenile fishes are faced with exceptionally severe conditions for growth (Machado-Allison, 1990; Hostache and Mol, 1998; Crampton, 1999).

Several Amazonian floodplain fishes produce floating foam nests, which provide oxygen for eggs and larvae that rest near the surface (Hos-
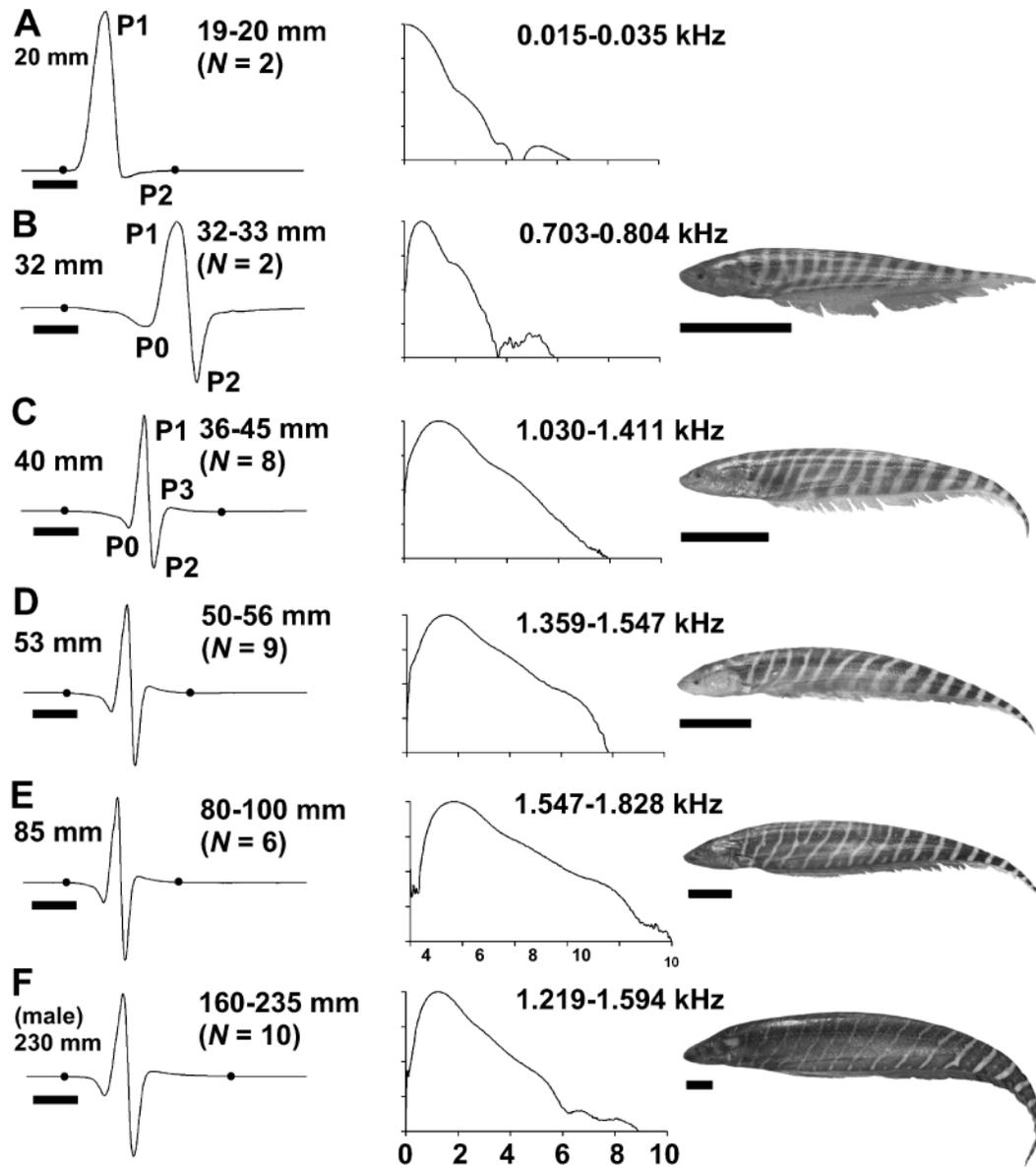
Fig. 5. Developmental changes in the EOD waveform of *Gymnotus mamiraua*. Left row illustrates EOD plotted with head positivity upward and component phases labeled P0 through P3, where P1 is the dominant positive component. Scale bar = 1 msec. Size of recorded specimen to upper left (below letter). Size range with similar EOD shape/duration annotated in upper right corner for *N* recorded specimens. Right column shows Power Spectrum computed by a 2048 point Fast Fourier Transform with frequency (kHz) on x-axis, amplitude in dB on y-axis (maximum 0dB, minimum −20dB), and Peak Power Frequency (PPF) scaled to 0dB. PPF ranges are annotated in upper right corner. Scale bar for photographs = 10 mm. Photograph not available for 20 mm specimen. Waveforms in this series are from specimens from more than one locality.

tache and Mol, 1998; Crampton, 1999). We found no evidence for the production of foam in nests of *Gymnotus*, nor was this observed in Kirschbaum and Wieczorek's (2002) study of captive *G. carapo*. Rafts of foam are, however, made by *E. electricus* in the early stages of its nests (Assunção and Schwassmann, 1995).

Kirschbaum and Wieczorek's (2002) observations of spawning and early paternal care in captive *G. carapo* throw some light on what may
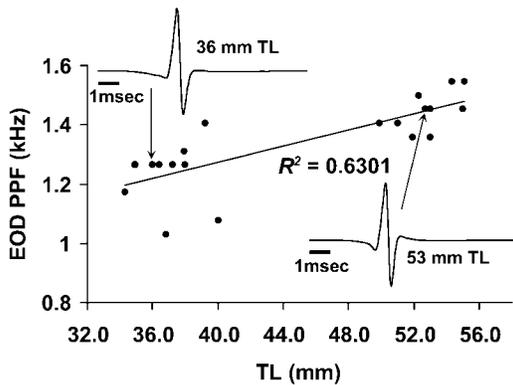
Fig. 6. EOD Peak Power Frequency as a function of body length in *Gymnotus mamiraua* nestlings from a single nest. EODs were recorded from only 20 of the 45 juveniles in Nest 7 (see Table 1). The 10 datapoints to the left refer to specimens from the cohort in this nest composed of smaller juveniles (see Fig. 3). Datapoints to the right are from the cohort composed of larger specimens. EODs plotted with head positivity upwards. Scale bar = 1 msec.

happen in the earlier stages of paternal care in other species of *Gymnotus*. They observed a large male mouth-brooding up to 250 larvae, all approximately 15 mm long and already capable of exogenous feeding. They also reported an apparent shepherding behavior in which a specimen of "*Gymnotus carapo,* despite the many disturbances, swam slowly in the aquarium, just above the bottom and tried to pick something up from the bottom. We could only conclude that it was trying to put lost young fish back into its mouth" (Kirschbaum and Wieczorek, 2002: 101–104). Mouth brooding is known from several Amazonian floodplain fishes including *Arapaima gigas, Osteoglossum bicirrhosum,* and several cichlids (Breder and Rosen, 1966; Crampton, 1999).

Adaptation of nesting to habitat.—Intraspecific variability of substrate selection is documented here for *G. carapo.* This is the most widely distributed species of *Gymnotus* and occurs in a variety of habitats, including streams, swamps and floodplains (Albert and Crampton, 2003). This species has so far been documented to form nests only on the bottom of shallow water bodies where it forms a depression in which eggs and larvae are guarded. *Gymnotus mamiraua* is confined to várzea floodplains of the Central Amazon where during the high water period the benthos of lakes and flooded forests is deeply inundated (2–12 m), anoxic, and almost devoid of life (Crampton, 1998a). Oxygen levels are generally much higher during the low water
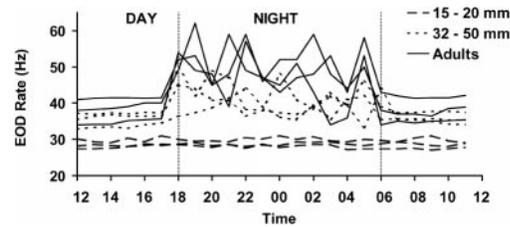

Fig. 7. Diel patterns of EOD repetition rate in three size classes of *Gymnotus mamiraua.* Time on the horizontal scale begins at 1200 h and ends at 1100 h on the following day. Note that small juveniles have a lower repetition rate with no appreciable increase from day to night.

season, and the bottom substrate of shallow lake edges offer suitable areas for nesting. Nonetheless, the extraordinary concentrations of predators in whitewater floodplains during the low water have apparently led many floodplain fishes to breed only during the rising and high water seasons when predator densities decline considerably (Crampton, 1999). *Gymnotus mamiraua* has adapted nesting behavior to the conditions of deep and anoxic floodwaters during the high water season by forming nests only in floating rafts of macrophytes. These meadows form a dense nesting substrate that is located near the water surface, allowing the adult and juveniles to reach the surface and breath air relatively easily. The meadows are also rich in plankton and small invertebrates, which sustain juvenile fishes. Male *G. mamiraua* select large and dense clumps of roots as nesting sites, a behavior that appears to mirror the selection of a covered area of substrate in *G. carapo.* However, unlike in *G. carapo,* which modifies the nesting site by excavating a shallow depression, *G. mamiraua* does not modify the root clump by adding bubbles or debris. The thin white bands of juvenile and adult *G. mamiraua* are well camouflaged by the roots of aquatic plants, especially the dense feathery root masses of water hyacinths. The cryptic effect of the pigmentation of this species is enhanced by a common tendency to spend the day wedged vertically upright in the rootmass. Nesting in floating meadows nonetheless also has disadvantages. Meadows are prone to disintegrating and drifting with winds and currents (Henderson et al., 1998). Moreover, as the waters of the várzea drop rapidly toward their ebb the concentration of predators increases dramatically, and large areas of floating meadow become grounded or swept into adjacent rivers (Crampton, 1999).

Spawning and the role of females.—Our observations of nests in *G. carapo* and *G. mamiraua,* and

Kirschbaum and Wieczorek's (2002) study of captive *G. carapo* implicate only males in parental care. An expected feature of male egg guarding in fish with external fertilization is that males will fertilize several clutches of eggs laid by one or more visiting females (Ridley, 1978; Clutton-Brock, 1991). The presence of more than one size class of juveniles in two of the nests of *G. mamiraua* (Fig. 3) and the presence of multiple size classes of eggs in the ovaries of *G. mamiraua* supports these expectations for this species. *Gymnotus carapo* also has multiple size classes of eggs (Barbieri and Barbieri, 1985).

Dispersal from nests.—The maximum observed size of a nestling *G. mamiraua* was 67 mm. The abundance of specimens larger than 60 mm outside nests, combined with the paucity of specimens smaller than 60 mm outside nests, and the complete absence of specimens smaller than 45 mm outside nests indicates that dispersal occurs when the juveniles reach around 50–70 mm. Extrapolating from growth data for *G. carapo* presented by Kirschbaum and Wieczorek (2002), *G. mamiraua* is expected to reach 60 mm no earlier than 11–12 weeks after hatching.

The high proportion of nestling juveniles larger than 50 mm with substantially damaged caudal appendages, and the known tail-nipping behavior of juvenile *Gymnotus* suggest that filial aggression could be a cue for the disbandment of nests. Damage to the caudal appendage might alternatively or additionally be inflicted by visual predators, such as piranhas, and may increase as larger juveniles venture further away from the nest and also provide a larger visual target. Dispersal from nests may also be forced by the disintegration and grounding of floating meadows and the increase in predator density as the waters of the várzea recede. These events may also reduce the survivorship of clutches that hatch later in the breeding season.

Role of electric signals in nesting.—The production of EODs by both the parent and nestling juveniles raises the possibility that electric signals could serve to maintain the cohesion of nestlings and maintain the proximity of nestlings to the adult. Visual and olfactory components of the central and peripheral nervous system are relatively reduced in *Gymnotus* in comparison with outgroups (Albert, 2001). Moreover, visual cues are unlikely to be important in a nocturnally active fish.

The almost monophasic EOD waveform of larval *Gymnotus* reduces the EOD PPF to close to 0 Hz (direct current), in principle allowing the guardian males to employ ampullary electroreceptors to detect and shepherd their young. Ampullary electroreceptors are stimulated by low-frequency electrical fields (around 0–60 Hz; Bennett, 1971; Szabo et al., 1972; Bastian, 1990) and have been implicated in gymnotiforms for detecting the low-frequency bioelectric fields of prey items such as small invertebrates (Bastian, 1976, 1990). The ampullary electroreceptors of *Gymnotus* reach their greatest density on the dorsal surface of the head (Albert, 2001).

Larval *Gymnotus* must also be conspicuous to predatory catfishes and other gymnotiform fishes, all of which possess ampullary electroreceptors. That larvae apparently broadcast their presence and location suggests that electroreceptive predators are either relatively unimportant or that the parental location function must be important enough to outweigh the disadvantages of attracting potential predators.

Larval nestling *G. carapo* and *G. mamiraua* (12–20 mm) differ from the guardian male on the basis of two EOD parameters: Peak-Power Frequency (PPF) (Figs. 4, 5) and repetition rate (Figs 4, 7). Both of these differences may influence the amount of sensory jamming, an impairment of electrolocating ability caused by coincident pulses of EODs with similar power spectra produced by two or more fishes whose tuberous electroreceptors are tuned to approximately the same frequency range (Heiligenberg et al., 1978).

The EODs of larval *G. carapo* and *G. mamiraua* (approximately 12–25 mm) are characterized by very low PPFs (0.015–0.04 kHz) relative to the adult male EOD (around 1.4 kHz in *G. carapo* and 1.219–1.594 kHz in *G. mamiraua*). This disparity should render the guardian males of nests immune to sensory jamming from the many (up to several hundred) EODs generated by its young nestlings. Juvenile *G. mamiraua* have nonoverlapping EOD PPFs with respect to adult male until they reach the size range 36–45 mm (Fig. 5C). Therefore, adults are potentially sensitive to jamming by juveniles larger than 36 mm. Extrapolating from growth curves for captive *G. carapo* (Kirschbaum and Wieczorek, 2002), 36 mm specimens are approximately 5–7 weeks old. Relatively few juveniles survive to this size and age in comparison with the hundreds of recently hatched larvae reported in nests of *G. carapo* from Trinidad and the 250 or so larvae that were mouthbrooded by a captive *G. carapo* (Kirschbaum and Wieczorek, 2002). In *G. mamiraua*, up to only 45 specimens per nest were recovered from nests with juveniles in the 34–67 mm size range (vs a minimum of 96 in

specimens 13–20 mm). The smaller number of nestlings must result in a lower probability of repeatedly coincidental EODs both between juveniles and between the juveniles and the guardian male. Nonetheless, the male and all the nestling juveniles probably suffer some degree of degradation of electrolocation performance throughout the latter stages of nesting. The extended nesting behavior in *Gymnotus* implies that the disadvantages of sensory jamming are outweighed by the benefits of increased survival of the older juveniles.

The immunity of nesting males to jamming from young larvae may not be a feature that has evolved for this function per se but rather a fortuitous consequence of the transition of EOD shape and PPF during the growth of the electric organ. In *Gymnotus,* the adult electric organ develops from a portion of the hypaxial musculature extending along the ventral margin of the hypaxial musculature (Kirschbaum, 1977). This contrasts with the families Apteronotidae and Sternopygidae in which a hypaxial larval electric organ is replaced during development by an adult electric organ not derived from hypaxial musculature (Albert, 2001). This ontogeny means that the transition in *Gymnotus* from a dominantly monophasic EOD (Figs. 4B, 5A) to a four-phase EOD (Fig. 5C) is related to the rapid growth and internal differentiation of the electric organ and not the replacement of a larval electric organ with an adult organ.

The EOD repetition rate of juvenile *G. carapo* and *G. mamiraua* in the size range 12–20 mm (Figs. 4, 7) is substantially lower than that of the adult and of larger juveniles in the size range 32–50 mm (Figs. 4, 7) and is also characterized by the absence of an increase in the repetition rate between day and night. The low and constant EOD repetition of larval *Gymnotus* may have evolved to reduce coincidental pulses between themselves. There are unlikely to be the same kind of developmental constraints on evolutionary transitions in EOD repetition rate as there are on the waveform shape and spectral properties of EODs. For instance, in at least one species of pulse-generating gymnotiform, *Brachyhypopomus brevirostris,* the larvae generate EODs at a substantially higher rate (around 30–40 Hz during activity) than the adults (15–25 Hz during activity; pers. obs.).

Acknowledgments

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