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Court and spark: electric signals in the courtship and mating of gymnotoid fish

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Abstract. By mimicking tropical rainy season conditions in aquaria, we stimulated two species of gymnotoid electric fish, *Eigenmannia virescens* and *Apteronotus leptorhynchus*, to spawn in captivity. Their courtship activity, breeding behaviour and electric social communication were monitored in several groups over 2 years. Groups of both species established dominance hierarchies correlated with electric organ discharge frequency, aggressiveness and size. Spawning was preceded by several nights of courtship during which the male modulated its electric organ discharge to produce 'chirps'. Continual bouts of chirping lasted for hours on evenings prior to spawning. These electrical signals play a significant role in courtship and spawning, as gravid *E. virescens* females could be stimulated to spawn by playing back into the tank a tape recording of male courtship chirps. In both species the chirp involves a slight increase in frequency followed by a cessation of the dominant frequency. This suggests a common mode of signal production in these two different genera of fish. Chirps are short and abrupt during aggressive encounters, but assume a softer and more raspy quality during courtship.

In his pioneering field studies on electrical communication in gymnotoid fish, Hopkins (1972, 1974a,b) described a variety of ways in which courting animals modulate their otherwise monotonic, nearly sinusoidal electric organ discharges (EOD). Since these animals are nocturnal and sometimes live in waters with poor visibility, Hopkins chose to observe gravid animals in small aquaria and under dim light in order to correlate their electrical signals with their physical activity. He corroborated Black-Cleworth's (1970) findings on captive *Gymnotus carapo* that certain EOD modulations are context-specific and indicate motivational states. Since Hopkins's animals had been taken from their natural habitat and presumably were not well adapted to their confined aquarium environment, it is conceivable that the full spectrum of agonistic and courting activity was not expressed. What was needed was a stable breeding colony in a spacious aquarium, where individual animals could be observed continually, under conditions similar to their natural environment.

The first successful breeding experiments on captive electric fish were conducted by Kirschbaum (1975). By providing three typical environmental conditions of the tropical rainy season, i.e. repeated sprinkling of water on the surface of the aquarium, a slow rise of the water level, and a gradual increase in electrical resistivity (due to steady dilution of electrolytes), he induced captive animals to become gravid over the course of 8–12 weeks and eventually to spawn. Kirschbaum, however, did not monitor the electrical activity of his animals, and therefore did not learn to what extent electrical communication might play a role in the reproductive behaviour of captive animals.

Since this is the first instance of electric communication being observed in the context of reproductive behaviour in captivity, we will start out with a general description of the behaviour and life history of *Eigenmannia virescens* and *Apteronotus leptorhynchus*. Our study is based upon a total of approximately 600 hours of observations of 12 groups of 3–9 animals courting and spawning in the laboratory, and also upon a few field observations of *E. virescens* in lakes near Fernando de Apure in Venezuela and of *A. leptorhynchus* in small streams in Panama.

The animals in our laboratory displayed the full range of electrical signals previously recorded from undisturbed animals courting in their natural habitat (Hopkins 1974a,b). Most importantly, we could show by playback experiments that specific courting signals facilitate successful reproduction in these animals.

METHODS

Ten groups of *E. virescens* and two groups of *A. leptorhynchus* were kept in large glass or clear acrylic 200–800-litre aquaria at 26–28°C. These

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animals were purchased from tropical fish importers. Animals were induced to spawn following the methods of Kirschbaum (1975, 1979). Each day deionized water was added to the aquaria so that the water level rose by 1–5 cm. When the water reached the top of the aquarium the level was lowered by approximately 50%. Clock-controlled pumps sprinkled water on the surface of the aquaria for 3 h every 6 h. The regular addition of deionized water raised the resistivity of the aquarium water from approximately 1 kOhm.cm to 50–100 kOhm.cm in the course of 8 to 12 weeks. The animals were kept in temperature-controlled rooms and at a clock-controlled 12-h-light–12-h-dark cycle.

The aquaria had several pairs of electrodes connected to a switch box and an audioamplifier, so that discrete areas of a tank could be monitored as the fish moved about. During instances of very active courtship, the EODs of the fish were recorded on audiotape with a Hewlett-Packard 3964A instrumentation recorder at 1·19 cm/s. Eight-minute segments could be simultaneously recorded digitally on a magnetic disc for subsequent Fourier analysis.

Signals were played back into the tanks through pairs of electrodes. We used either pure tones generated by a sine wave generator or tape recordings of nocturnal courting activity.

The animals were fed daily on chopped tubificid worms. They became gravid on this high-protein diet, but unless they were placed in the rain regime, spawning did not occur. After initiation of the rain regime, animals spawned as long as the rain regime was maintained, which varied from 10 weeks to over 6 months. First-generation animals spawned more readily and regularly than their wild-caught parents, as was also observed by Kirschbaum (1975).

Red lights were positioned over all tanks, and the animals quickly became accustomed to this night-time illumination. The low light level permitted clear nocturnal viewing of their behaviour. Many behavioural sequences were videotaped with a Panasonic black-and-white video camera fitted with a light-sensitive Novicon tube. Animals could be recognized individually on the basis of morphological features and EOD frequencies, which changed only gradually over time.

Long sequences of audiotaped activity (8 min–12 h) were analysed in Carl Hopkins's laboratory at Cornell University on a Federal Scientific Ubiquitous Spectrum Analyzer model UA-7B. The spectra were displayed on an oscilloscope and recorded with a Grass Instruments camera. Short segments of electrical activity (< 8 min) were digitally recorded on our PDP-11/40 computer, at a sampling rate of 2·5 kHz and with a 12-bit accuracy. Successive records of 1024 sampling points (bins) were 'windowed' with a Gaussian function with its mean in bin 512 and with a standard deviation of 128 bins. These weighted time functions were Fourier-transformed, and the peaks of the resulting power spectra were displayed on the ordinate of the oscilloscope, with time on the abscissa. The frequency resolution was 2·5 Hz, and the bandwidth was 1250 Hz (see example in Fig. 5 below). Thus it was not possible to examine the higher harmonics of the EOD of *A. leptorhynchus*.

Since the temporal resolution of the spectrograms was of the order of 0·1 s and could not be enhanced further without an intolerable loss in frequency resolution, we analysed the timing of the EOD zero crossings of individual animals in order to show the structure of signals of short duration. For this purpose, segments of recordings were chosen in which a given animal's signals were minimally contaminated by those of its neighbours. The intervals between successive EOD zero crossings in the positive direction were measured in μs by on-line computation and could be displayed on an oscilloscope, synchronously with the ongoing EOD. The inverse of these intervals represents the instantaneous fundamental EOD frequency (see examples in Figs 7, 9 below).

RESULTS

Observations on Breeding and Behaviour

Eigenmannia virescens

As confirmed by our own observations in the field, *E. virescens* lives in gregarious social groups associated with floating vegetation. In the laboratory, we provided them with surface plants, such as *Ceratopteris sp.* and *Eichhornia crassipes.*

As the simulated rainy season progressed, females became gravid, and yolky eggs could be seen through their translucent body wall. Males outgrew females in total length, and their developing testes could be seen as white bands shining through the underside of the belly.

Owing to their larger size, males have a more powerful EOD than females and, when converted to audio signals, the faint signals of females are often, for the human ear, drowned out by the powerful EOD of a nearby male. They can, however, be retrieved by Fourier analysis. Both males and females establish a dominance hierarchy based on size and EOD frequency. Usually, the largest male has the lowest frequency and is the most dominant male, and the largest female has the highest frequency and is the most territorial female. Smaller, more aggressive animals may, however, usurp the dominant role. As a first indication of territorial activity, larger males begin to interrupt their EOD, as described by Hopkins (1974b). The audioamplified pattern of such interruptions has the quality of 'chirps', and this word will hence be used to denote this signal.

In a community of several males, only one of the larger individuals chirps routinely, sometimes only a few times per minute, at other times as often as several times per second. Series of chirps are produced as the male suddenly approaches another male and stops just short of colliding with him. A male approached in this sudden manner often withdraws, while the dominant male may slowly pursue him, still chirping.

In almost all instances, a tank will be dominated by a single male which routinely patrols the whole area of the tank and chirps at challengers. In only one of the 10 groups and only for a period of a few days, however, a second male did not cease chirping in the dominant male's presence, and, after long duels of chirping, a long mouth fight ensued. During such mouth fighting, the two males locked their jaws and chirped, pushing each other again and again. These encounters also included lateral fighting, head butting and sidling as described by Hopkins (1974b). A clear dominance decision was not reached between these two males for several nights. The combatants would separate briefly, then meet again and resume fighting after a short pause. Two additional males and all five females in this group never participated in these fights.

In the momentary absence of the dominant, patrolling male, a submissive male may court a female. He will usually cease chirping the moment the dominant male reappears at the scene. The submissive male will also soon cease chirping in response to playbacks of the low-frequency signal of the dominant male. This suggests that the submissive male may be able to recognize the dominant male on the basis of his EOD frequency alone.

In contrast to territorial males, which regularly patrol a large area, single females tend to settle in an area of the aquarium within a dense thicket of floating plants. During courtship, a female will select a plant and defend it against other females. A stationary female will push, and sometimes even chase other females away from her site, though she will tolerate the presence of males. She normally assumes a vertical, head-up 'submissive' posture while hovering in her plant. The dominant male frequently visits such a territorial female and will hover under her while producing long series of chirps (Fig. 1). He may gently push the female or even show intentions of chasing her away. A gravid female, however, will tolerate such approaches and often withdraws her flank from an attack by rolling over to her side. In response to such low-intensity attacks and while trying to move away as little as possible, the female will repeatedly and smoothly raise the frequency of her EOD by a few to several Hz over a period of tens of seconds (see Figs 5a, 6b below). The dominant male will pursue the territorial female gently, but he will violently chase away other females from her site. The territorial female may join in such attacks, sometimes chirping herself.

As the night of spawning draws near, the male spends longer periods of time at the side of the female and chirps incessantly, at a rate of 2–5 brief interruptions per second. Whereas he chirps at male rivals in a very abrupt manner, his long series of chirps to a female gradually assume a softer and more raspy quality, as individual interruptions are often only partial (see example in Fig. 8 below). Both male and female repeatedly rub their bodies through the root hairs, thus cleaning them of sediments and perhaps depositing a layer of mucus to help the eggs stick to the roots. When the female moves away from her site, the male may suddenly dive under her while briefly raising his EOD frequency to produce a 'howl' in the audio-transduced signal (see example in Fig. 5b below). With a few swift manoeuvres, he ushers the female back into her plants. As the bouts of male chirping become more protracted, the female begins to stick her head vertically into the root hairs. A small contraction of her body indicates the deposition of eggs, which she expels through the cloacal aperture under her chin. The male alternately sticks his head into the same or nearby sites and apparently fertilizes the eggs at this moment; no sperm is visible in the water.

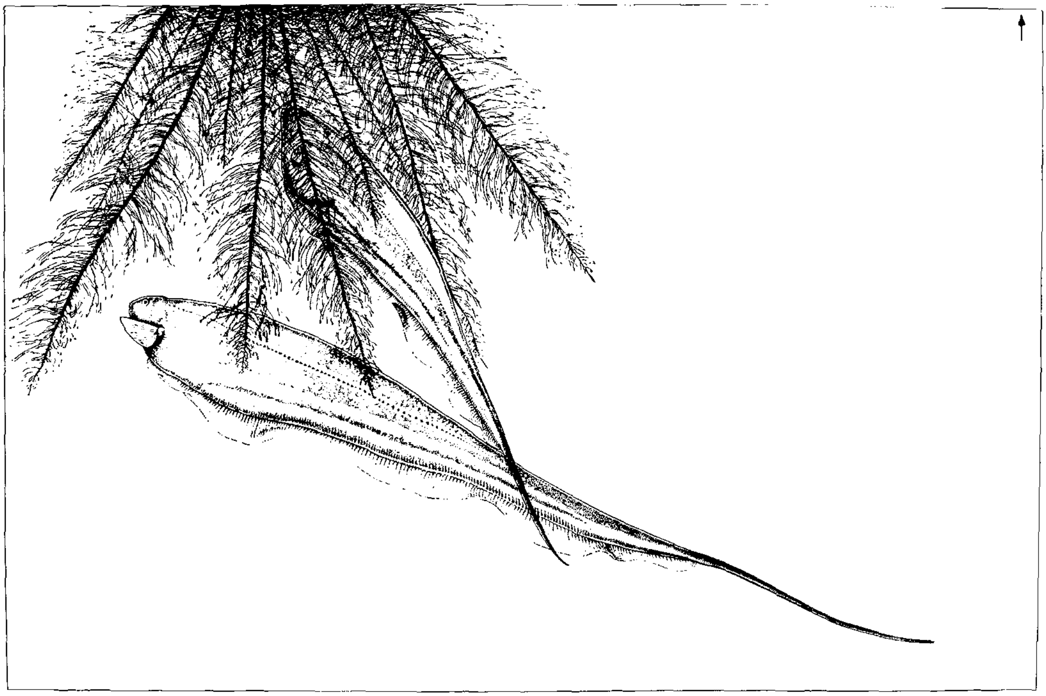

Figure 1. A typical courtship posture of a male (lower) and a female (upper) *Eigenmannia virescens*. The female hangs vertically in the root hairs while the male hovers below chirping.

While the territorial female is spawning, other females try to sneak into her plants, sometimes turning off their EOD as they approach. The male drives away all subordinate females, thus forcing them to spawn on the periphery. Such eggs normally remain unfertilized.

A pair may spawn well over 100 eggs in one night, and may spawn again 4–7 days later. The eggs are sticky and remain in the plants for 3 days. Larvae hatch from the eggs on the third day and eventually fall wriggling out of the floating plants onto the bottom of the aquarium. We observed no form of parental care but rather saw the adult fish feed on larvae which lay on the ground. Dense leaf litter may protect them from this fate in their natural habitats. As already reported by Kirschbaum (1979), the larvae begin to swim on the seventh to eighth day after spawning and, within another 2 days, their electric organ becomes active. Animals become sexually mature within their first year.

Apteronotus leptorhynchus

Courtship and spawning in this species was observed for 6 weeks in one group (two males, five females), and frequencies were recorded in another group (two males and three females).

As confirmed by our own field observations, *A. leptorhynchus* lives in loosely associated groups in rocky environments or along river banks. In the laboratory, a dominance relationship was observed between the two males: the dominant male was the largest, had the highest frequency, and participated in all the spawnings. No clear-cut dominance among the females was observed, as the dominant male tended to spawn at about 2-day intervals, with a different female each time.

A. leptorhynchus tend to be bottom dwellers, so we provided them with broken clay pots, which permitted viewing of the animals' nightly behaviour. Much as in the case of *E. virescens*, spawning in *A. leptorhynchus* is accompanied by long bouts of chirping by the dominant male, which may last all night. At sunset, the female approached the hiding place of the dominant male. The pair swam under cover side by side while the male chirped. Soon the female pushed her nose under an object, rolled on her side and began chirping. The short

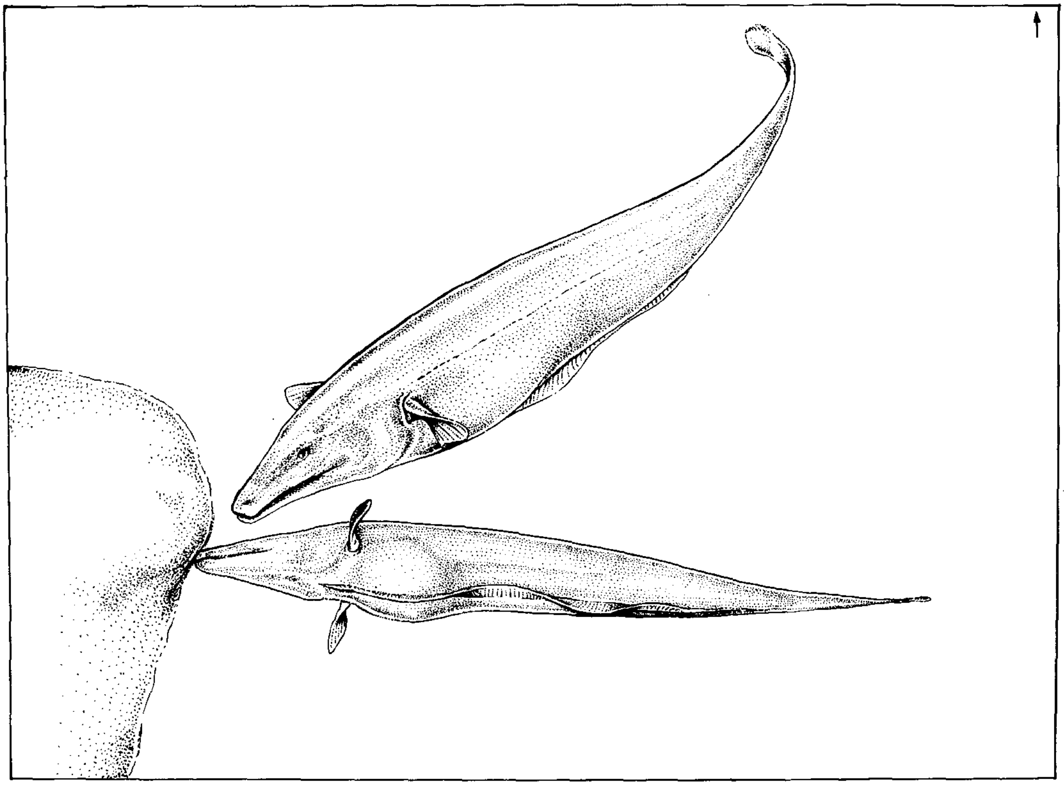

Figure 2. A typical courtship and spawning posture of a male (upper) and a female (lower) *Apteronotus leptorhynchus*.

chirps of the female elicited an approach by the male, and he hovered over her while she contracted her side and tried to squeeze out a single egg (Fig. 2). This process could take several minutes, as an egg is quite large (1–2 mm). A female spawned from 5 to 30 eggs in an evening depending upon her size. The egg was ejected into the water column from the force of the female's contraction, and the male presumably fertilized the egg as it left the cloacal opening. The eggs are heavy and sticky and may fall into cracks or leaf debris in the wild. No form of parental care was observed. We confirmed Kirschbaum's (1983) observation that animals hatch after 2–3 days and begin emitting an electric discharge 8 days after spawning.

Sexually Dimorphic Characters

In both gymnotoid species, mature males are larger than mature females (males 20–30 cm; females 10–20 cm), and have thicker tails (probably due to their more powerful electric organ, the main portion of which is located in the tail). The *E. virescens* male is also characterized by a small indentation in the ventral contour of the body at the beginning of the anal fin. The *A. leptorhynchus* male has an elongated nose.

EOD frequencies show sex-specific differences in both species. Although individual EOD frequencies may fluctuate considerably over the course of days (see Fig. 4), a sex-specific difference emerges clearly towards the time of spawning: *E. virescens* males tend to have the lowest frequency in the tank, while the dominant female, which does most of the spawning, has the highest frequency. Figure 3a shows the EOD frequencies of animals at the time of spawning in tanks that were monitored during the spawning period (approximately 1 to 2 months). In two tanks which were observed throughout the spawning period, the dominant male only courted and fertilized the eggs of the highest-frequency female, although other females spawned eggs. Most significantly, a female may raise her frequency by tens of Hz before becoming

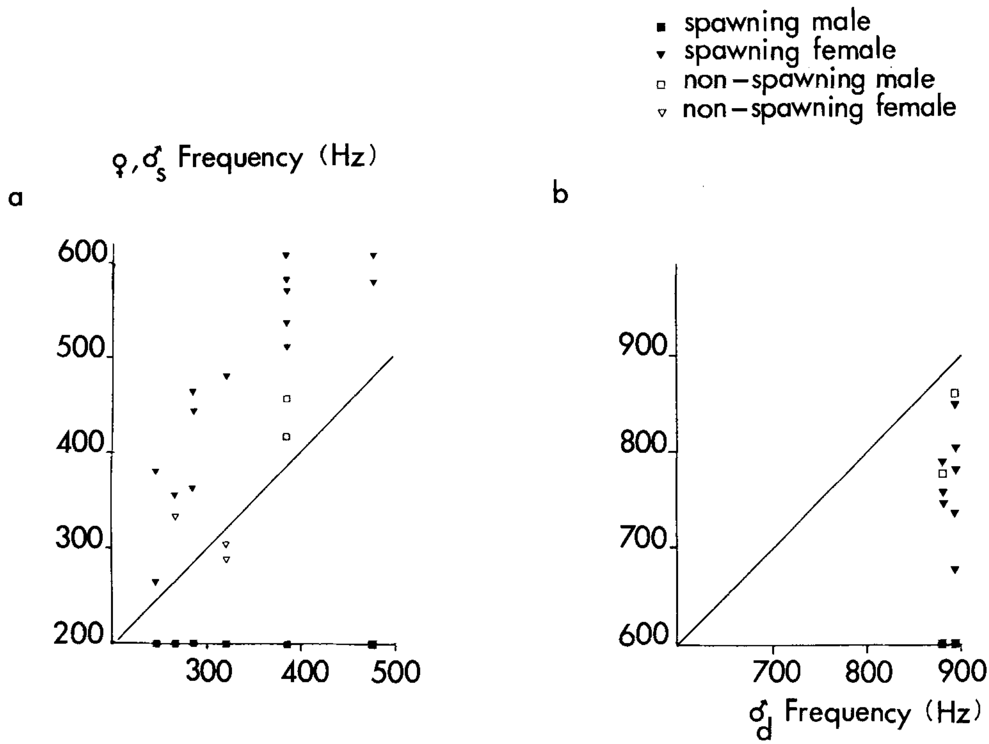

Figure 3. EOD frequencies reflect a dominance hierarchy: the frequencies of dominant, spawning males are shown on the abscissa, with the frequencies of the other animals in the same group plotted on the ordinate in a line above the dominant male's symbol. a: *Eigenmannia virescens*; b: *Apteronotus leptorhynchus*.

ready to spawn (Fig. 4). Females never spawned while their frequency, in rare instances, happened to be even lower than that of the dominant male.

In contrast to *E. virescens*, the EOD frequency of the breeding male *A. leptorhynchus* is higher than that of the female, as was also reported by Kirschbaum (1983). In both spawning groups, the dominant male had the highest frequency (Fig. 3b). The data for our groups agree with the data of 25 additional animals from Kirschbaum's laboratory (personal communication).

Since we did not wish to stress the animals and thus possibly inhibit spawning by handling, we did not measure the peak-to-peak voltage of the signals in every group. From our measurements in one group of *E. virescens* and our qualitative observations with an audioamplifier in all other groups, however, the dominant male appears to have the signal of largest amplitude, regardless of his size. Further, the amplitude of his signal seems to increase at night such that he drowns out even more the EODs of other animals in the tank, especially those of females.

EOD Modulations in the Context of Reproductive Behaviour

As already reported by Hopkins (1974b), wave-type electric fish modulate their EODs in a context-specific manner. These modulations include changes in frequency and amplitude as well as interruptions of the EOD cycle. Examples of such signals are shown in Figs 5 and 7–9, with a summary of all signal forms in Fig. 6.

Frequency modulations (FMs)

Four types of frequency modulation were observed in *E. virescens* during courtship. The first type, 'long rise', is characterized by a rapid increase in frequency, followed by a slow return to the base line (see the 520-Hz female's signal in Fig. 5a and the schematic representation in Fig. 6b). These

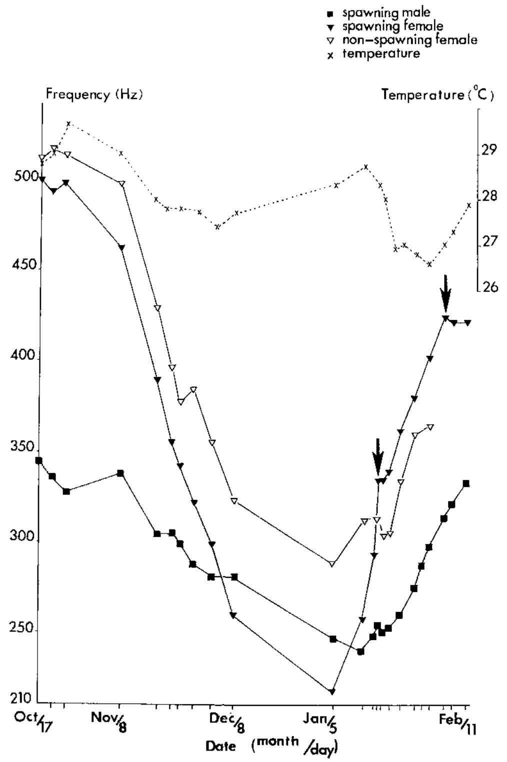

Figure 4. Record of the individual EOD frequencies of *E. virescens* in a rain regime. The abscissa is a linear time scale with marks on dates when frequency measurements were taken. All frequencies have been corrected to 27°C with an assumed Q_{10} of 1·5. The temperature in the tank varied by 3°C in a non-systematic fashion (dashed lines) (26·6–29·7°C) over the study period. Arrows indicate nights of spawning.

relatively small (2·5–40-Hz) but sustained (several to tens of seconds) rises in EOD frequency have been interpreted as 'submissive' signals in *E. virescens* (Hopkins 1974b). Frequency rises are commonly observed in courting females in response to mild aggression by a male.

A second type of frequency modulation, 'short rise', is a rapid up–down modulation lasting 1–2 s, as displayed by a male and a female *E. virescens* in Fig. 5c. This signal is commonly produced by a male on the night of spawning, often before a rapid swimming movement. Such rapid rises then often lead to an interruption of the EOD (see responses of male in Fig. 5b).

A third type of frequency modulation, displayed rarely by *E. virescens* males, is a quick drop in frequency, followed by a slow return to the base line (see schematic representation in Fig. 6d). The significance of this signal is unknown. A fourth and equally uncommon signal is a small frequency modulation or 'warble' around the mean frequency (see Fig. 6e). Male *E. virescens* occasionally produce such warbles following female chirps.

Three forms of FM have been observed in *A. leptorhynchus*: long and short rises similar to those seen in *E. virescens*, and a very brief rise which has the acoustical quality of a chirp (see Fig. 6). The latter signal was first described as a 'ping' by Larimer & MacDonald (1968). Bullock (1969) then demonstrated that such pings were a smooth, brief increase in EOD frequency, covering a period of approximately 25 EOD cycles, and he renamed these signals 'chirps'. *A. leptorhynchus* frequently produces chirps in response to any sinusoidal signal of a frequency similar to that of its own EOD, and long sequences of chirps commonly accompany aggressive encounters. In the context of courting, the duration of chirps may increase by up to tenfold. As the chirps become longer, the EOD amplitude decreases at the peak of the frequency rise (Fig. 7a). For still longer chirps, the fundamental cycle of the EOD will collapse altogether so that the EOD cycle is interrupted (Fig. 7b,c).

EOD interruptions

In *A. leptorhynchus*, EOD interruptions are a consequence of a sudden and strong rise in EOD frequency. While the fundamental EOD cycle is halted, a faint signal with harmonically unrelated higher frequencies persists (Figs 6a, 7). The fundamental EOD cycle then recovers with a downward frequency sweep back to the base line. Brief, uninterrupted frequency rises and long interruptions form the ends of a continuum, with longer interruptions occurring more frequently during vigorous courting, and short interruptions and uninterrupted rises characterizing aggressive encounters. All signals have the acoustic quality of chirps. The long courting chirps, however, are characterized by more dramatic FMs (see Fig. 7).

EOD interruptions in *E. virescens* were interpreted as aggressive signals by Hopkins (1974b). Aggressive encounters are characterized by sudden and mostly complete interruptions of the EOD cycle (Fig. 8a), whereas interruptions during long periods of courting tend to be incomplete and thus sound more raspy (Fig. 8b). Initially incomplete interruptions may lead to a prolonged and total cessation of the EOD cycle (Fig. 8c). All forms of

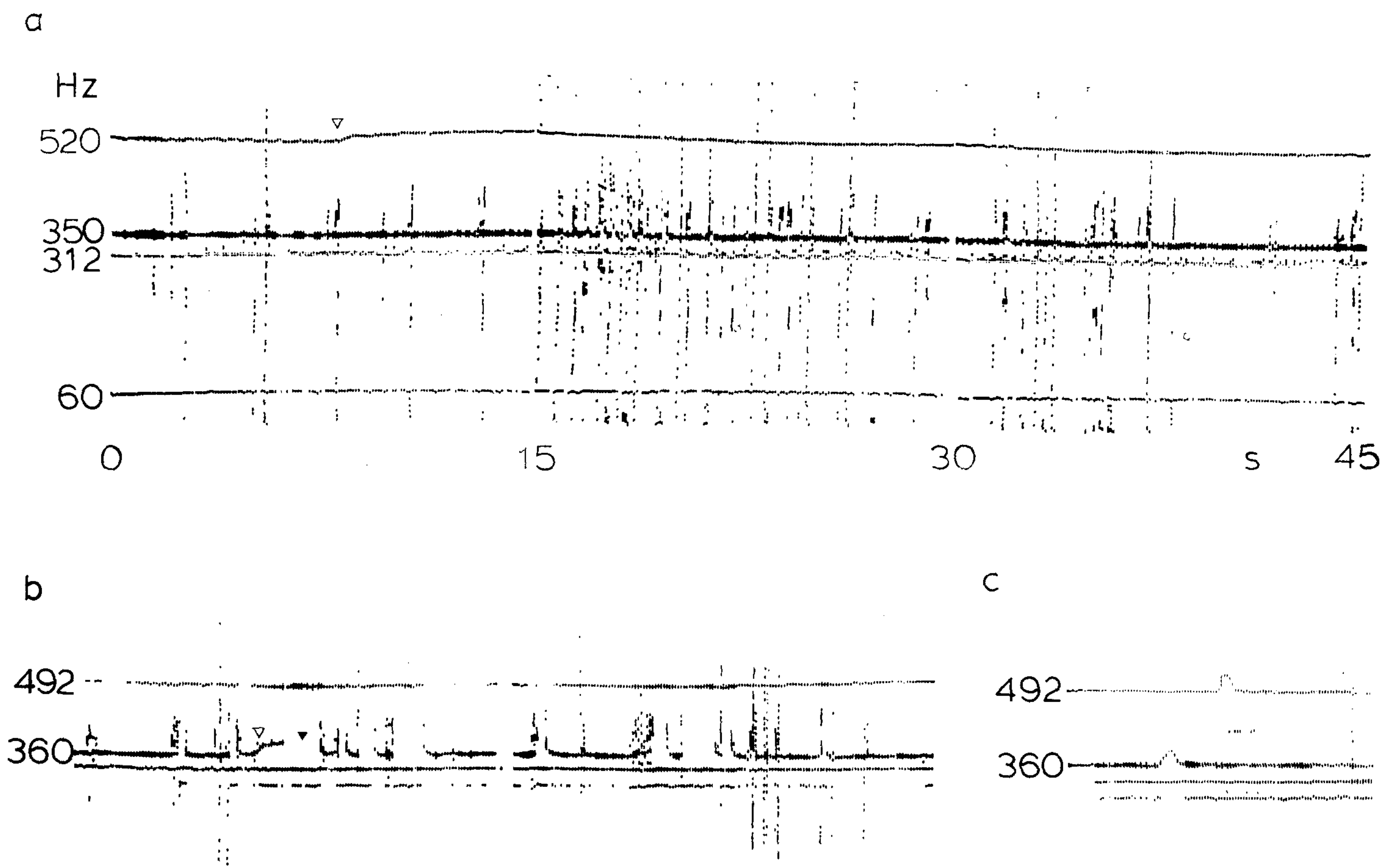

Figure 5. Spectrograms of courting signals in *E. virescens*. The abscissae show time in seconds, on the same scale for all parts of the figure. The ordinates show frequencies of local peaks of power spectra (linear scale). See Methods for details of analysis. (a) A 45-s recording of the EOD of a male (350 Hz) and two females (312 and 520 Hz). The 60-Hz signal is due to line-frequency hum. Note the sustained frequency rise by the 520-Hz female (open triangle) at approximately 7 s from the beginning. The male produces long sequences of interruptions, and each interruption causes a temporary spread of energy in the power spectrum (points scattered along the vertical axis). (b) A 30-s recording of the EOD of a male (360 Hz) and three females. Note the short frequency rises by the male (open triangle) followed by long interruptions (filled triangle). Such interruptions are characterized by sharp boundaries in the spectrogram and can thus be distinguished from gradual cessations of the signal due to the animal's departure from the electrode. (c) A short frequency rise by a male (360 Hz) followed by a short frequency rise by a female (492 Hz).

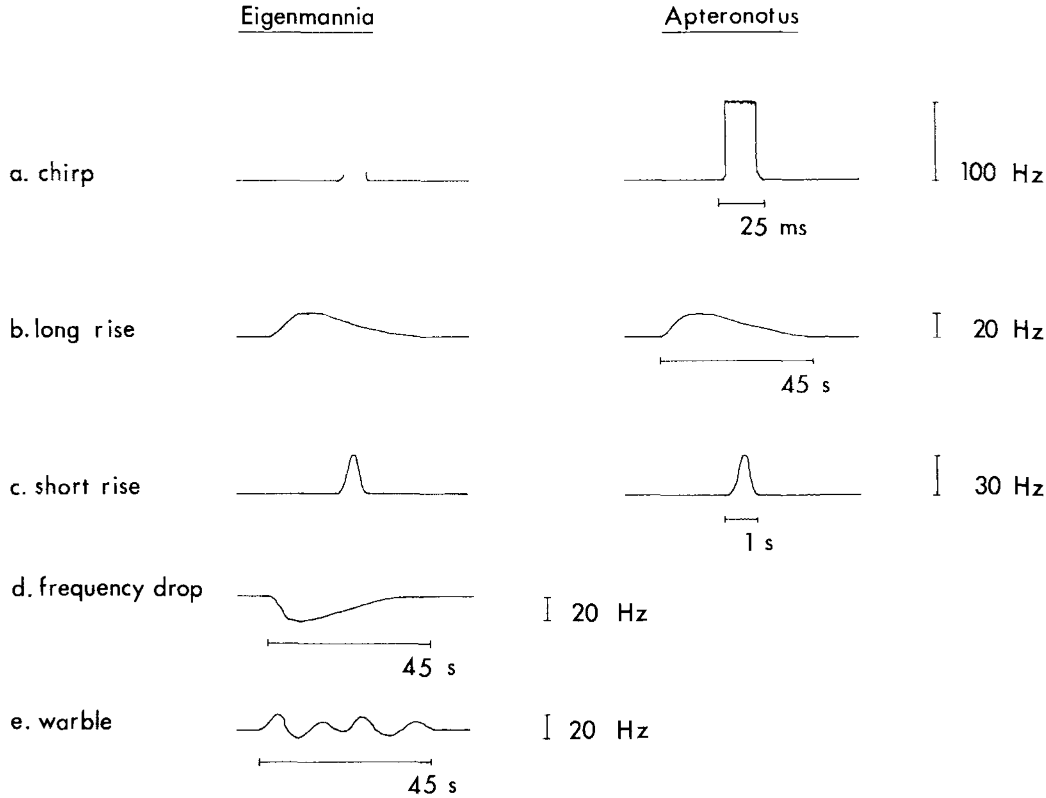

Figure 6. A schematic representation of the signals used in courtship in *Eigenmannia virescens* and *Apteronotus leptorhynchus*. The abscissa displays time, the ordinate frequency, with individual scales for each row of signals.

interruptions have the acoustic quality of chirps, with the sudden chirps in aggressive encounters sounding sharper and almost shot-like, and the chirps during courting sounding softer and more raspy. Interruptions in *E. virescens* follow a small, sudden rise in EOD frequency, less distinct than in the case of *A. leptorhynchus*. The EOD recovers after longer interruptions with a frequency shift down to the base line (see Figs 5b, 9). This suggests similarities in the underlying neural mechanisms of EOD interruptions in these two genera.

Long-term silencing of the EOD

In rare instances, an animal may stop its EOD for unusually long periods of time. A submissive female that for several nights was subject to aggressive butting and chasing by the dominant male gradually reduced the amplitude of her signal. As the attacks continued this animal was wounded. Finally, she turned off her EOD entirely and hung, electrically 'silent', in a head-up posture in the plants. During the day, when attacks did not occur, she resumed her normal EOD. After she was transferred to another tank, with a less aggressive male, she maintained her EODs throughout the night.

On at least 10 occasions we observed a female of lower rank approaching the spawning site of the dominant female with her EOD turned off. As her EOD activity resumed she was discovered by the resident female and chased away.

Silencing of the EOD appears to be an effective way of hiding from other fish. This strategy is very common in mormyrids and in *Gymnarchus niloticus* (Bell et al. 1974; Bullock et al. 1975; Heiligenberg 1975, 1976). We do not know why *E. virescens* makes use of this strategy so rarely.

Responses to Signals during Courtship

A female will only begin to spawn after a male has chirped at her site almost uninterruptedly for at

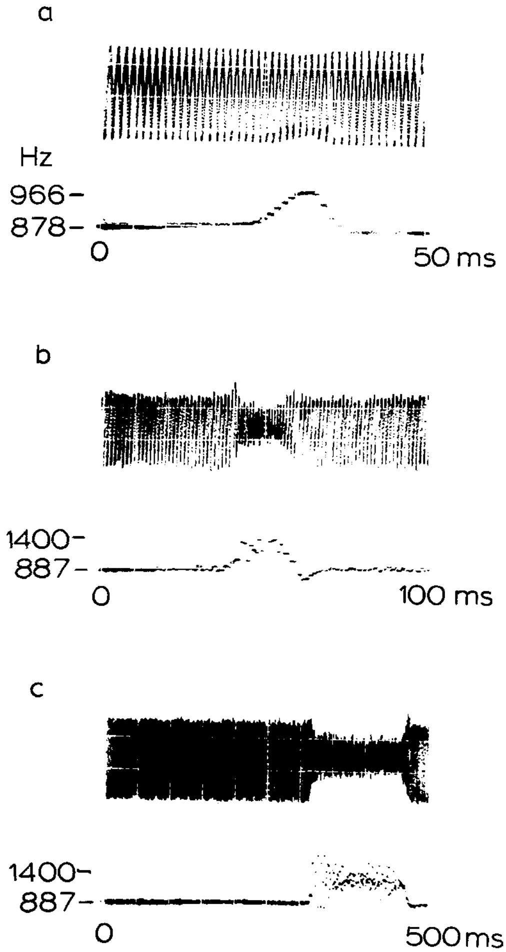

Figure 7. Modulations in instantaneous frequency characterize chirps in *A. leptorhynchus*. Instantaneous frequency, the inverse of the current interval between positive zero crossings of successive EOD cycles, is plotted underneath the recordings of the EOD. The corresponding frequency scale is given in Hz. (a) A chirp of short duration; (b) and (c) increasingly longer chirps: these are characterized by a steeper and higher rise in instantaneous frequency and by an interruption of the fundamental EOD cycle. A weak signal of higher frequency appears for the period of the interruption.

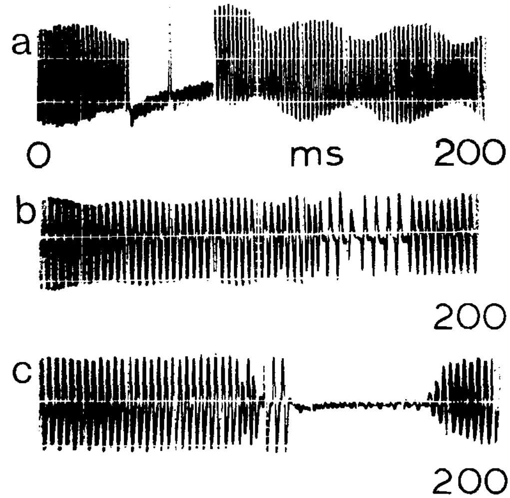

Figure 8. Discharge interruptions in a male *E. virescens*. (a) A sudden, almost complete interruption; the modulation of the record is due to interference with the EOD of a distant neighbour with a similar frequency. (b) An incomplete interruption, with approximately every other EOD cycle missing. (c) A long and complete interruption following an initially incomplete interruption.

least one hour. If a male repeatedly leaves her site in order to patrol the aquarium in search of rivals, spawning will not occur. The importance of being exposed to a male's chirping becomes evident from the fact that gravid female *E. virescens* will spawn in the vicinity of electrodes through which a recording of a courting male is played back. In a group with one male and eight females, a tape recording of the courting male released spawning in the females in three out of four cases. Most of the eggs which were spawned, however, remained unfertilized, suggesting that the male did not participate in much of the courtship. After the removal of the male on the evening before the last playback experiment, the females still spawned in the vicinity of the playback electrodes; most of the eggs, however, were small and appeared to be released prematurely. In no other instance did we observe spawning in the absence of a male.

Although the long rises produced by *E. virescens* females have been interpreted as submissive signals (Hopkins 1974b), they may play an additional role in courtship. During the early morning, when the intensity of male chirping is waning, females produce a series of long rises which stimulate the male to chirp (compare the rates of chirping before and after the long rise in Fig. 5a). On two nights of spawning, the female produced 53 long rises during the early morning hours: 37 of these were followed by bouts of male chirping. In a tank with two females and one male, both females were removed and their frequencies were replaced with sine waves played through electrodes. The male produced no chirps in response to the constant frequencies of the sine-wave generators, but as soon as the frequen-

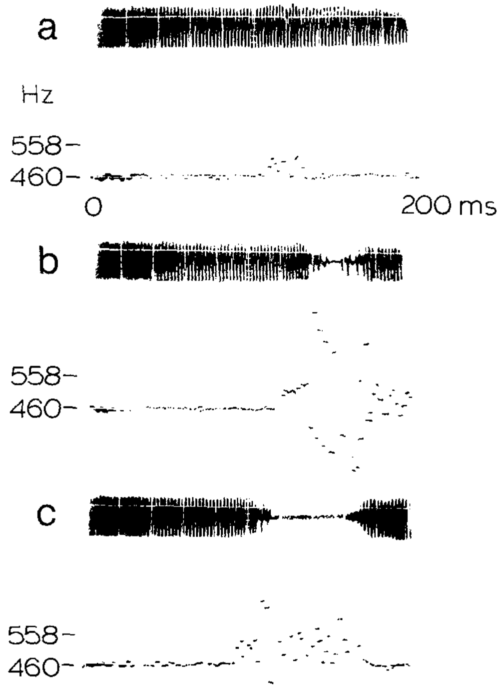

Figure 9. Chirps in *E. virescens* are characterized by modulations in instantaneous frequency which are less regular than in those of *A. leptorhynchus*. The presentation is of the same kind as in Fig. 7. A subthreshold elevation in instantaneous frequency in (a) fails to interrupt the EOD cycle.

cies were modulated from 1 to 10 Hz, in the manner of a long rise, the male began chirping.

During bouts of male chirping, female *A. leptorhynchus* roll onto their side ready to spawn an egg. While on their side, females produce chirps. In 141 observations of female bouts of chirping, the female was positioned on her side in 122 instances. The chirping of the female may act as an alerting signal for the male so that he can position himself to fertilize the egg before it is ejected into the water column. *E. virescens* females may also chirp while they are laying eggs; as in *A. leptorhynchus*, this chirping may direct the male to the appropriate part of the plant.

DISCUSSION

Observations in our largest aquarium ($2{\cdot}4 \times 0{\cdot}6 \times 0{\cdot}6$ m) suggest that large dominant males of *E. virescens* occupy and defend territories which may accommodate more than one female. Even with a 1:1 sex ratio, only one specific male chirped regularly and over long periods of time. Commonly, this dominant male would visit two or three stationary females in a row and chirp to each of them. Our aquarium observations, however, can only suggest that *E. virescens* follows the pattern of a harem-forming species, and field studies are needed to test this assumption.

With the beginning of dusk, the dominant male's EOD drowns out the EODs of other animals in the tank even more than during the day. This suggests that the EOD amplitude of the male is modulated in a diel cycle. Daily amplitude modulations were measured in individuals of the related, pulse-type species, *Hypopomus occidentalis*, with chronically implanted electrodes (Hagedorn, in preparation). Such daily modulations of amplitude may play a role in the establishment of dominance.

As first suggested by Hopkins (1974b), chirps, i.e. sudden interruptions of an otherwise continual, nearly sinusoidal EOD pattern, contain low-spectral frequencies and should thus drive ampullary or low-frequency electroreceptors. This can indeed be demonstrated by recording from single primary ampullary afferents while exposing the animal to electronically simulated chirps of a supposed neighbour (Heiligenberg, unpublished). It is possible that the driving of the ampullary receptors of a female being courted by a male initiates a series of physiological responses which lead to the act of spawning.

Schleidt (1973) and Heiligenberg (1977) suggested that the repeated broadcasting of a stereotyped social signal exerts a tonic and motivational effect upon the receiver. The extended bouts of chirping by the male may bring about physiological readiness of a female to spawn, much as male dewlap displays in *Anolis* lizards (Crews 1975) and male bow-cooing in ring doves, *Streptopelia* (Lehrman 1965) are conducive to ovulation.

Before spawning, *E. virescens* and *A. leptorhynchus* may change their frequencies by tens of Hz in the course of one month (Fig. 4), in spite of the fact that an individual's pacemaker frequency can be very stable over thousands of successive EOD cycles (Bullock et al. 1975). This change in frequency in breeding fish suggests a labile mechanism for controlling the pacemaker frequency, as well as receptor tuning. Studies on another gymnotoid fish, *Sternopygus dariensis*, have implicated steroid hormones in the control of pacemaker frequency and plasticity in receptor tuning (Meyer 1983; Zakon & Meyer 1983).

Since the EODs of wave-type electric fish provide individual frequency tags, these animals are ideally suited for behavioural field studies. Large arrays of electrodes could be spread out over a natural habitat during the breeding season and, by fast Fourier analysis executed on a small portable computer, the whereabouts of undisturbed individuals could be monitored on the basis of their individual frequencies. The movement and distribution of specific animals, as well as their electrical communication and responses to playback signals, could thus be recorded continually. Using programmable signal generators, playback experiments can be designed to test hypotheses concerning frequency and dominance structures and individual recognition under natural conditions.

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