Carl D. Hopkins

Electric Communication in Fish

Certain species of fish produce electric signals that are used for identification, aggregation, and dispersal

Communication is a process by which the behavior of one individual affects the behavior of another. It is not merely a series of responses to stimuli, but rather a relationship that is set up by the transmission of a stimulus and the evocation of a response (Cherry 1961; Altmann 1967). Yet we do not think of a predator's responses to the actions of its prey as communication; we restrict our view to those relationships in which the transmission of the stimulus and the elicitation of a response are mutually beneficial, in the evolutionary sense, to both participants. As observers of animals, we depend heavily upon changes in the recipient's behavior—shown either by a specific response or by a change in the probability of different behaviors—as an indication of the presence of communication.

Animals respond to many channels of stimuli: light, sound, touch, and chemicals are the most widespread and best known for purposes of communication. The use of the electrical modality is known for only a few species of aquatic animals; it is well developed in several divergent groups of freshwater fishes from South America and Africa and may be developed in several species of marine elasmobranchs. In spite of its rarity, the study of this relatively unexplored mode of communication may give us some feeling for the evolution of communication systems in general, including possible relationships between an animal's ecology and its social behavior and between its physiology and the choice of a modality of communication.

Figure 1. *Gymnarchus niloticus* is a well-known electric fish found in many rivers in West Africa. (Photo courtesy of H. W. Lissmann.)

Two principal groups of freshwater fishes have well-developed communication systems using electrical stimuli—the gymnotid fishes of South America and the mormyriform fishes of Africa. The Gymnotoidei are a characoid-related sub-

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field of cognition experiment more actively with human imagery, we finally seem to be on the threshold of a period when inner experiences can be understood more scientifically as a basis for psychotherapeutic practice. Methods as diverse as hypnosis, transference-analysis, *le rêve éveillé* of Frétigny and Virel, psychodrama, gestalt therapy, covert sensitization, and vicarious modeling can all be seen as special approaches to the training of increased sensitivity to one's ongoing stream of thought and to control over such awareness.

The experience of undertaking a program of research on daydreaming has been exhilarating. It is increasingly clear that psychology or, more broadly, the behavioral sciences possess the technology and methodological sophistication for even greater clarity in studying what seem to be such ephemeral phenomena. We have psychometric tools, models for examining attention during ongoing processing, and scales and rating methods for describing make-believe play in children. None are as fully developed as they can be. Still, they offer methods of approach through research to the ongoing inner flow of thought which we so value as a part of our private selves but which we have overlooked when devising scientific theories of human behavior.

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order of Cypriniformes consisting of four closely related families (Greenwood et al. 1966), represented by 60 to 80 species, including the well-known electric eel. The Mormyriformes (superorder Osteoglossomorpha) have also evolved current-generating abilities. There may be up to 200 species of mormyrids (fam. Mormyridae) and one species of *Gymnarchus* (fam. Gymnarchidae) making up this group. Other electric fishes such as the electric catfish (Malaptururidae), the electric rays (Torpedinidae), the electric skates (Rajidae), and the stargazers (Uranoscopidae) may also use electrical stimuli for communication, but these species have received little attention. (For general reviews dealing with electric fish, see Lissmann 1958, 1963; Bennett 1971a and b; Bullock 1973.)

Sending and receiving signals

Electric communication requires special physiological "hardware" for both the production and the reception of electric signals. Electric currents are generated in organs that are similar in structure to either muscle tissue (Bennett 1971a) or nerve tissue (Waxman et al. 1972; Couceiro and de Almeida 1961). Muscle-derived electric organs are the most common type. Large multinucleated cells or electrocytes (Bennett 1971a) which lack contractile elements are organized into long columns in the tail region to make up the electric organ of most gymnotids and mormyrids. Each electrocyte is innervated by a separate spinal electromotor neuron. A synapse, which appears to be acetylcholine-mediated, forms the link between the neurons and the electrically excitable cells of the electric organ.

Neurally derived electric organs are found only in the gymnotid family Apteronotidae (Sternarchidae). In members of this group, a large bundle of myelinated nerve fibers emerges from the spinal cord and runs along the side of the fish into its tail to form the electric organ. There are no intervening synapses.

During the synchronous discharge of all the electrocytes of the electric organ, the potentials generated across the membranes of individual

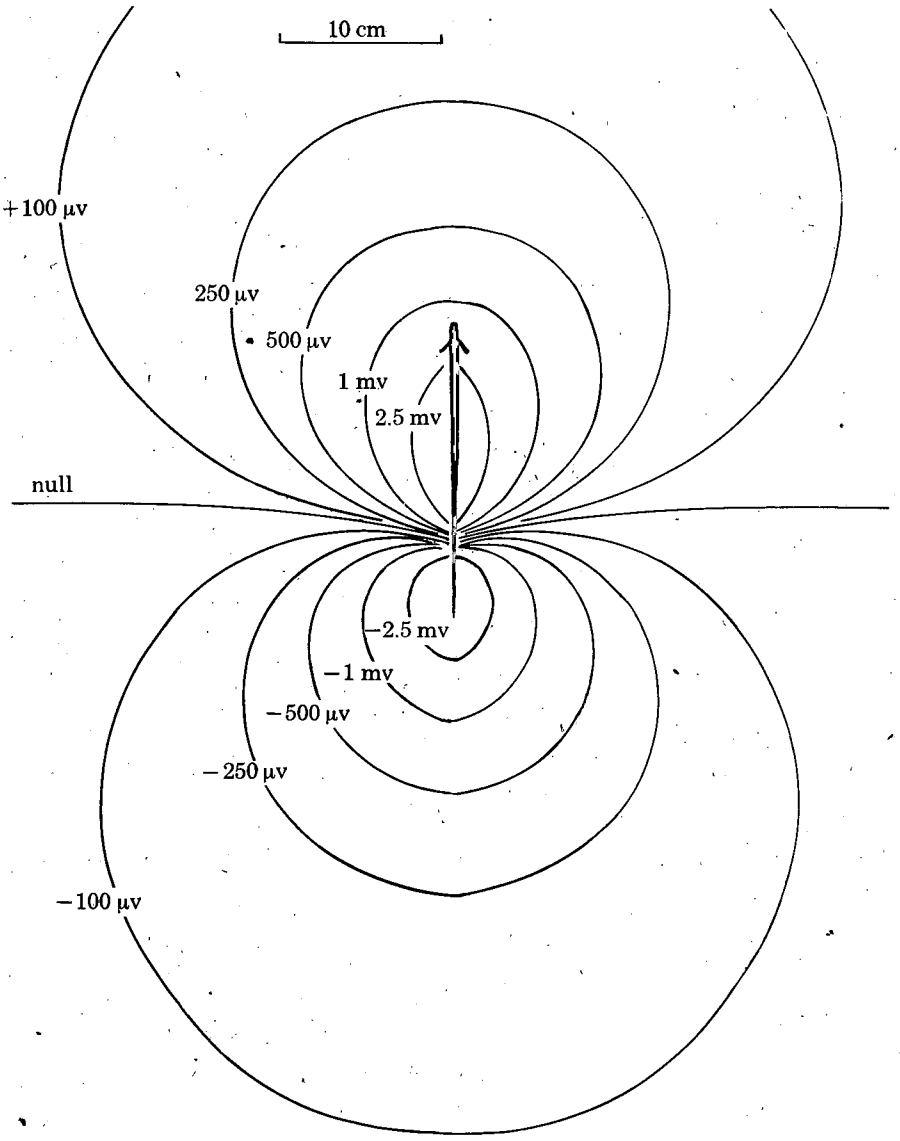


Figure 2. Electric signals spread out in all directions, but their range is restricted. Here lines of peak-to-peak equipotential surround an *Eigenmannia virescens* 18.6 cm long. The values indicate potential referred to a distant circular electrode. Measurements were made in water 1 m deep (conductivity = 2.6×10^{-2} mho/m). (Data courtesy of E. I. Knudsen.)

electrocytes summate to produce a relatively large voltage. In some electric fish current generated in this manner is sufficient to shock prey or predators. However, the discharge of most species—only a fraction of a volt during the peak of the discharge—is employed in the detection of objects and in communication.

Electric signals are perceived as current flowing through specialized electroreceptor organs embedded in the fish's skin. Although electroreceptors almost certainly evolved separately in the Mormyriformes (Africa) and in the Gymnotoidei (South America), there is remarkable similarity in receptor morphology between the two groups. Both groups have two general classes of electroreceptors—ampullary and tuberous (see review in Bennett 1971b; Bullock 1973). All known ampullary electroreceptors respond to low-frequency electrical stimuli (less than 50 Hz) with modulations in the discharge frequency. All tuberous electroreceptors adapt rapidly to sustained electric currents through the receptor and respond best to higher-frequency stimuli (greater than 50 Hz).

The weak electric signals emitted by an electric fish can be detected with two metal or carbon electrodes placed in the water near the fish. The signal is amplified with an ordinary high-gain audio amplifier and passed through a loudspeaker or audio monitor. Amplified signals can be recorded on magnetic tape for analysis on an oscilloscope, a sound spectrograph, or computer.

Both laboratory and field studies have contributed to our knowledge of electric communication. Whereas laboratory studies have concentrated on the role of electric signals in agonistic behavior—maintaining territories or dominance relationships—field studies have explored other uses, such as in reproductive behavior. Early suggestions about the possible role of electric discharges in social communication resulted from Lissmann's (1958) field work on the Black Volta River in northern Ghana and subsequent behavioral experiments in the laboratory using *Gymnarchus niloticus* (Fig. 1). Gymnotids and mormyrids are nocturnal, and thus most studies have been conducted at night or in a darkened laboratory. The views on the evolution of electric communication presented here have benefited from field experience in Guyana, South America.

The communication medium

Electric currents generated by one fish's electric organ are picked up by the electroreceptors of another individual. It is important at this point to understand some of the peculiarities of current flow in water that endow this sensory modality with special properties when it is used for communication.

Electric signals are conducted very rapidly in water. Conduction velocity is determined by the conductivity of the medium and the frequency of the signal (see Liebermann 1962). For freshwater (conductivity $=, 5 \times 10^{-3}$ mho/m) and the low frequencies used by most electric fish (1 kHz), the conduction velocity is about 1.4×10^6 m/s. In seawater, where the conductivity is as high as 4 mho/m, the velocity may be only 6×10^4 m/s. Nevertheless, for biological systems, conduction times resulting from velocities such as these may be considered instantaneous, and in this respect the electrical modality resembles the visual.

Noninstantaneous conduction times play an important role in other communication modalities. With sound, for example, differences in the time of arrival at the two ears are important for spatial localization of sound sources (Marler 1959).

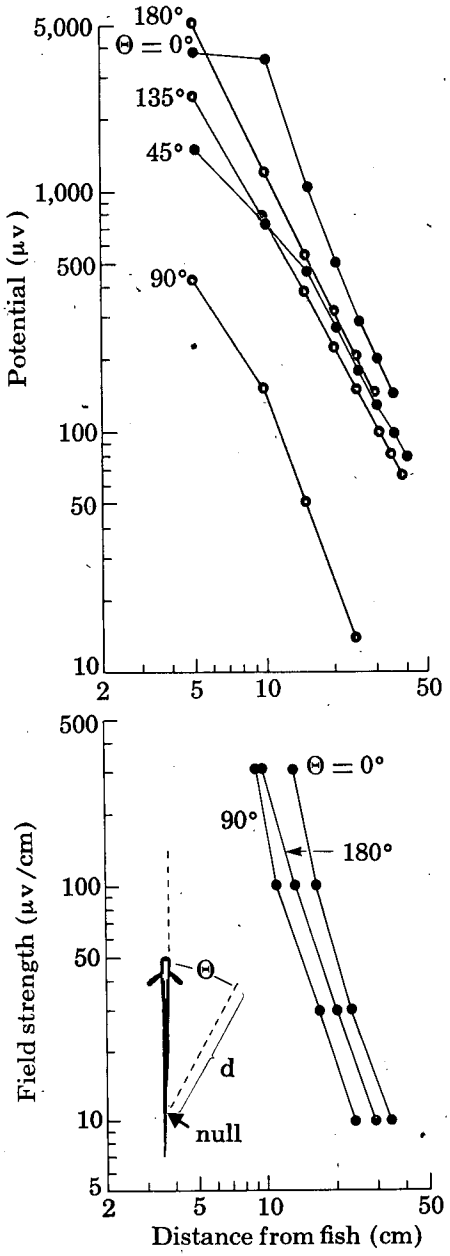


Figure 3. *Top:* The peak-to-peak potential falls off according to the inverse square of distance from the null of the fish for various angles; colored lines represent negative values. *Bottom:* The amplitude of the electric field strength falls off according to the inverse cube of the distance. Measures are of the same *Eigenmannia* as in Fig. 2. (Data courtesy of E. I. Knudsen.)

Although electric fish cannot rely upon differences in arrival times for signal localization, they apparently are capable of directional reception, as indicated by right-left discrimination tasks using sinusoidal stimuli with two species of gymnotids (Knudsen, pers. comm.). The instantaneous conduction time of the electrical modality contrasts strongly with the chemical modality, in which signals are transmitted very slowly, especially in water.

Electric signals are transmitted from the electric organ as an approximately dipole-shaped field (Fig. 2) that is broadcast in all directions (Hockett 1960), much like the loud territorial calls given by many species of birds or primates. Attempts to focus the signal by bending the body one way or another probably do not result in a significant narrowing of the beam of communication.

The distance of transmission of electric signals is short—probably on the order of 1 to 10 meters. Estimates of the maximum distance of communication vary. Using measurements of equipotential lines and of conditioned response thresholds, Granath and his co-workers (1968) estimated the maximum distance of signal reception at 3 m for *Apteronotus* (*Sternarchus*) *albifrons*. Using a similar approach, Knudsen (pers. comm.) estimates the threshold field strength of *Eigenmannia virescens* to occur at between 25 cm and 200 cm, depending upon the size of the individual sending the signal, the angular orientation of the sender with respect to the recipient, the electrical conductivity of the water, and the presence of nonconducting surfaces near the signaler that might compress the field. In the mormyrid *Gnathonemus petersii*, consistent behavioral responses were elicited by the presence of a discharging conspecific at a maximum distance of 30 cm (Moller and Bauer 1973; Russell, Myers, and Bell 1974).

Communication distances are short because of the severe attenuation of electric fields around a dipole source (Fig. 3): the electric potential surrounding a perfect dipole falls off according to the inverse square of the distance. The electric field, which is the driving force for the electric current, falls off according to the inverse cube of distance. In shallow water, electric signals may extend farther horizontally because the rate of attenuation is reduced owing to vertical compression by the nonconducting surface and bottom.

Electric signals are capable of crooked-line transmission and in this feature are similar to both sound and chemical signals. Rocks, stumps, or vegetation may alter the shape of a fish's electric field but do not change the temporal character-

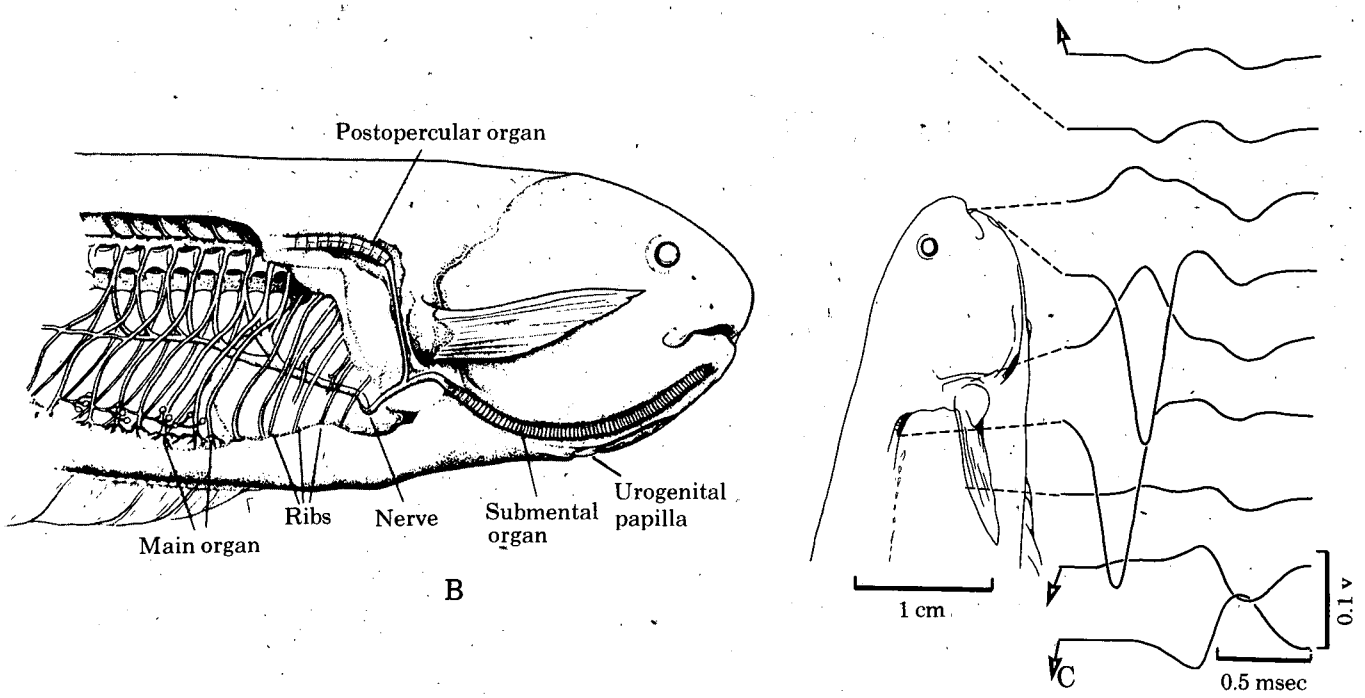


Figure 4. Certain species of electric fish show adaptations for modifying the shape of the electric field. *Steatogenes elegans* is one such example. It possesses accessory electric organs that alter the more typical shape of the field produced by the tail organ. (A) The dissected view of the rostral electric organs of *Steatogenes* shows the postopercular organ, the submental organ, and the nerve that innervates them. (B) The oscilloscope tracings of monopolarly recorded potentials show how the electric field is distorted—especially near the head. Colored lines indicate the recording sites of the various traces; the three traces with arrows were recorded 2.5 cm rostral to the snout, 4.5 cm caudal to the snout, and near the tip of the tail. The greatest change in the electric field occurs near the operculum and near the urogenital papilla. (From Bennett 1971a, with permission.)

istics of its emission. Suspended particulate matter, a common impediment to visual communication in tropical freshwater rivers and streams, does not affect electric current flow.

Electrical emissions have rapid fade-out; once the signal is discontinued, it does not linger as do chemicals or visual marks. Because transmission of electric signals is instantaneous and fade-out rapid, this modality seems well adapted for sending quickly fluctuating messages. Communication signals that accompany fighting behavior, for example, tend to reflect each participant's rapid changes in agressive motivation (Marler and Hamilton 1966) and demand a channel with instantaneous conduction and rapid fade-out.

The electric channel of communication is contaminated by noise, not only from other nearby electric fish but also from nonbiological sources, including lightning. Lightning discharges are especially common in South America and Africa and are often of sufficient amplitude to be detected by electric fish (Hopkins 1973).

Electric organs and electroreceptors are not specialized for communication in the sense discussed by Altmann (1967) and Hockett (1960): they are also employed in the detection of objects (Lissmann 1958; Lissmann and Machin 1958). Because natural selection has operated upon electric organs and receptors for both functions, we find some compromises in their shared design, a major one being that electrical emissions potentially conspicuous to predators are necessarily generated continuously so that the object-sensing system can function.

One final distinctive feature of the electrical modality is that electric fish use their own energy to produce signals rather than, as with most visual signaling mechanisms, depending upon an external source of energy such as sunlight. In addition to permitting signaling at night, this characteristic allows the fish to generate a signal of sufficient strength to overcome background noise.

Signal diversity

If electric communication is to serve multiple functions in the social behavior of electric fish, there must be a diversity of signals, signs, or displays that elicit different responses from the recipient. Electric signals *are* diverse, and yet it is possible to classify the diversity according to one or more parameters. The most important parameters appear to be the shape of the electric field, the waveform of the electric discharge, the discharge frequency, timing patterns between signals from sender and receiver, frequency modulations, and cessations of the discharge.

The shape of the electric field of most gymnotids and mormyrids resembles a slightly modified dipole (see Fig. 2). Variations of this basic shape may be due to changes in the position of the electric organs within the body of the fish; such changes occur in several species of gymnotids that possess accessory electric organs in addition to the more typical ones found in the tail. The best example is *Steatogenes elegans*, which has two columns of electrocytes lying in grooves on either side of the anteriorally positioned genital papilla, as shown in Figure 4A. These organs create a slight negative phase to the discharge in the head region (Fig. 4B; also see Bennett 1971a). The significance of accessory organs is unknown; however, Bennett has suggested that they might increase the

acuity of the fish's ability to sense objects. Species differences in the structure and activity of these organs might also be important in specific identification of the signaler at a range of several centimeters.

Temporal characteristics of the electric discharge appear to be an important dimension of diversity. The diversity of discharge waveforms is shown in the oscilloscope traces in Figure 5 for ten of the most common sympatric species of gymnotids in my study area in Moco-moco Creek, Guyana. Two general classes of discharge waveforms are apparent immediately—tones and pulses. With tone discharges (also termed wave discharges), each impulse has a long duration compared to the interval between impulses. With pulse discharges, the impulse is brief compared to the interval. All adults of a given species seem to have similar waveforms. Pulse discharges recur among the mormyriform fishes in Africa (Fig. 6); *Gymnarchus niloticus* is the only known species with a tone discharge.

Two sources of selection pressure are likely to affect the evolution of discharge waveform. First, the signaler may be recognized by some characteristic of its waveform—its shape, duration, amplitude, or spatial features. Second, as Bennett (1971a) points out, the discharge may have evolved multiple phases that have little or no energy in the low-frequency or dc range so that the electric organ discharge does not stimulate low-frequency (ampullary) electroreceptors, which are now known to be utilized in the detection of prey, and possibly predators (Kalmijn 1971; Bullock 1973; Roth 1972). Multiple-phasic discharges may not jam a fish's own low-frequency electroreceptors and, in addition, they may not attract potential predators such as catfish, which have low-frequency (ampullary) but not high-frequency (tuberous) electroreceptors. From the wide overlap in the discharge waveforms among the gymnotids (even those that occur sympatrically, Fig. 5) and among the mormyrids (Fig. 6), it would appear that species distinctiveness is, in many cases, not important.

In contrast, the wide range of discharge frequencies among the gymnotids suggests that there is some selective advantage to difference in frequency of interpulse interval. Table 1 shows the frequency ranges for twelve species of gymnotids in Moco-moco Creek. The tone fish maintain a stable discharge frequency both day and night, whereas the pulse fish have somewhat higher frequencies at night, when they are active. In some cases, overlap in discharge frequency may not result in confusion as to the identity of the signaler. For example, *Sternopygus macrurus* is distinctive because it is the only species in the high middle-frequency range that has a tone discharge. Overlap that occurs when two species are inactive (day) may not occur when they are active. Thus, although *Gymnorhamphichthys hypostomus* and *Hypopomus artedi* have similar frequencies during the day, they differ at night, thereby avoiding confusion. In addition, species with similar frequencies at night, such as *Gymnorhamphichthys hypostomus* and *Rhamphichthys rostratus,* may never share the same habitat (Hopkins, diss.).

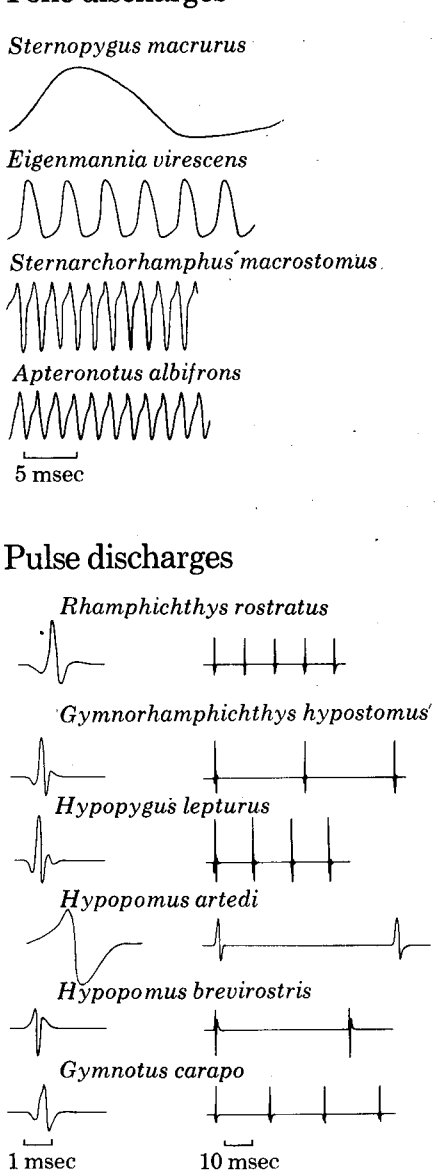


Figure 5. The waveform of the electric discharge is another parameter of signal diversity. These oscilloscope tracings are from the ten most common species of gymnotids in Moco-moco Creek, Guyana. The positive electrode is located near the head, the negative electrode near the tail. A positive signal is deflected upward.

Little is known about the discharge frequencies of mormyrids that share the same habitat, although several species have received considerable attention in laboratory studies. In general the mormyrids vary tremendously in their discharge frequencies from moment to moment; thus identifiable frequency bands may have less importance to mormyrids than to gymnotids. Instead, frequency modulations and timing patterns may play a more important role in signal identification.

We should not overlook the possibility that electric fish might use timing relationships between their own discharge and that of another individual as a means of communicating, in a manner analogous to the flash-answer system that has evolved in many species of fireflies (Lloyd 1966, 1971). It is interesting that the mormyrid *Gnathonemus petersii* responds to artificial electrical pulses or to the discharge of a conspecific with a characteristic "echo" pulse delivered after a delay of 12 to 14 msec (Russell, Myers, and Bell 1974). As yet, there is no measure of the species specificity of this echo response.

All known species of electric fish are capable of modulating the frequency of their electric discharge. In those species that have been studied, modulations result from depolarization of the large, electronically coupled cells in the pacemaker nucleus of the medulla (Bennett et al. 1967; Szabo and Enger 1964). The modifications are often rather stereotyped and have been given names such as chirp, SID (Sudden Increase in frequency followed by a Decrease to the resting frequency), ping, rise, burst, rasp, and so on. The sound spectro-

grams in Figure 7 compare frequency modulations of several species of electric fish. Some of the records were obtained during aquarium observations of fighting behavior, some from field observations of male courtship during the breeding season, while others were chance field observations, in which the context of the display is unknown.

The similarity in the time course of the frequency modulations is striking: generally they take the form of a sudden increase in frequency followed by a slow, and generally exponential, decrease back to the resting frequency. There are exceptions to this general pattern: *Hypopomus brevirostris* produces a rasp discharge during aggressive displays in which the normal discharge frequency of 50 to 60 impulses per second is suddenly elevated to over 400 per second for approximately 40 to 50 msec (Fig. 7F). *Gymnarchus niloticus* produces frequency modulations in which a decrease in frequency is followed eventually by an increase back to the resting frequency (Fig. 7H). It is especially interesting that the mormyrids in Africa also produce frequency modulations fundamentally the same as those produced by the gymnotids in South America. Moller and Bauer (1973) and Bell, Myers, and Russell (1974) have shown that sudden increases in frequency are followed by decreases to the resting frequency and that these SID patterns alternate with periods of high discharge frequency or with cessations in the discharge when two individuals are interacting aggressively.

The final known pattern in the diversity of electric signals, which occurs in all known electric fish except those in the family Apteronotidae, consists of a complete cessation of the discharge for a variable period. Figure 8 shows both field and laboratory records for several species.

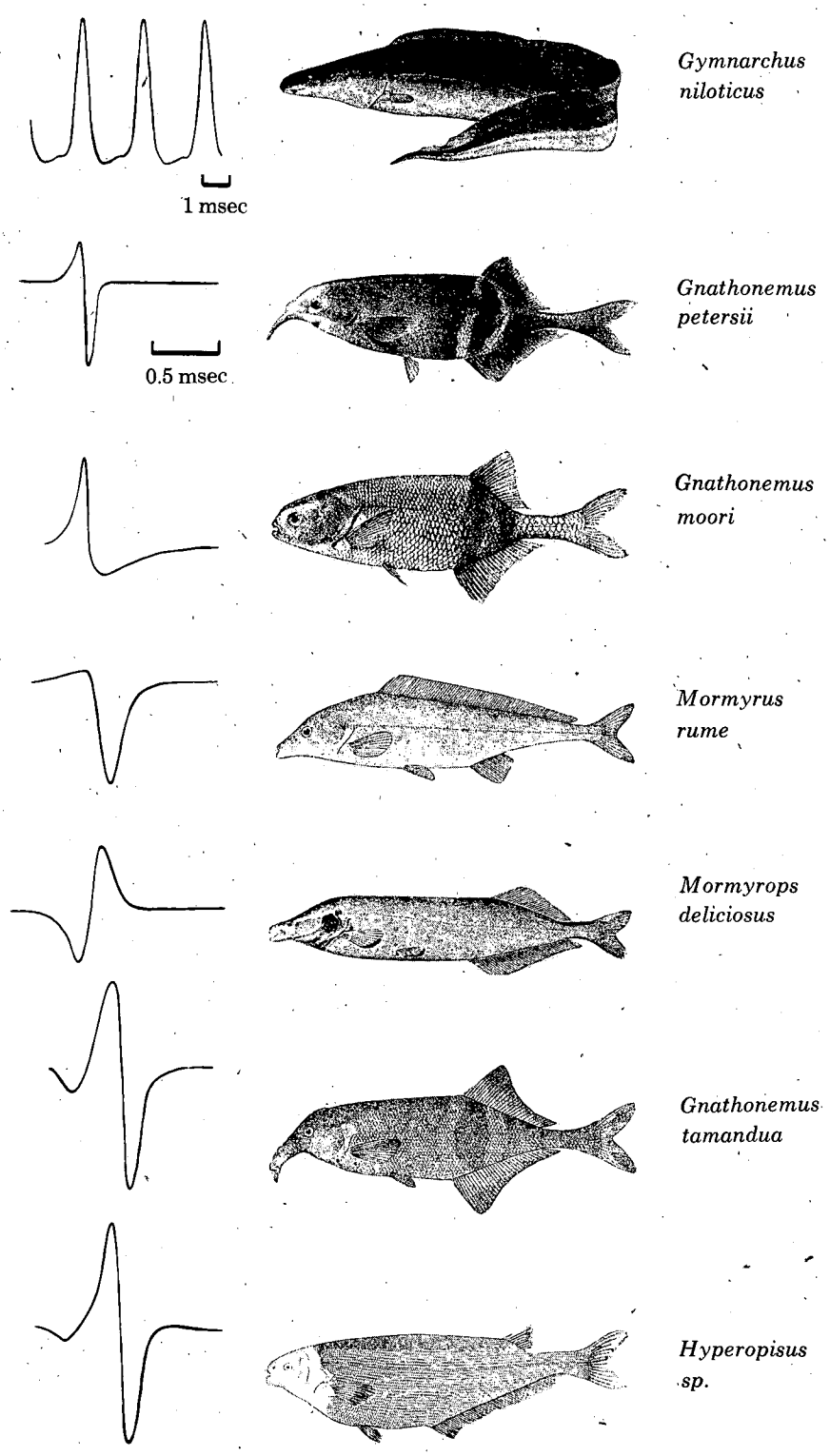


Figure 6. Oscilloscope tracings show discharge waveforms of various mormyriform fishes. *Gymnarchus niloticus* is the only African electric fish with a tone discharge. (Waveforms are from Bennett 1971a; fish photographs from Boulenger 1909, Daget 1954, and Poll 1956, with permission.)

Functions of electric communication

What are the functions of all these electric signals? How did the diversity, which exists not only in the variations in the discharge (frequency modulations, cessations) but also in the characteristics of the resting discharge (waveform, frequency, shape), come about through natural selection?

Identification. Some electrical displays serve to identify the species, sex, or age class of the signaler (Smith 1968). Species recognition is particularly critical during the breeding season, when loss of gametes through attempted hybridization lowers an individual's reproductive success. It may also be important at other times, especially when individuals of the same species form protective social groups or when intraspecific aggression aids in dispersal over the available habitat. The electric signals used in object sensing, since they

are emitted continuously, seem well adapted to this role.

Eigenmannia virescens, one of the common gymnotids encountered in Guyana, uses the resting frequency of its electric discharge for species recognition. The range for the species, in my study area in Mocomoco Creek, was between 250 and 600 Hz (at 25°C), but each individual is remarkably stable in its own frequency—variations amounted to less than 0.3 percent during 10-minute sampling periods (Bullock 1969). None of the other thirteen species in this area had frequencies that overlapped with *Eigenmannia* (see Table 1). Species recognition is expressed in aggressive behavior and in sexual behavior. *Eigenmannia* are mildly aggressive toward conspecifics, and when one *Eigenmannia* meets another on its nightly excursions in the shallow creek, it gives electrical threat displays. No displays are given when another species, such as *Sternopygus,* is encountered, but *Eigenmannia* will fight vigorously if two are placed together in a tank. During the breeding season, males give courtship displays (long sequences of discharge interruptions delivered at a rate of 2 to 3 per second) when they are in the presence of a conspecific (see Fig. 8C).

Tests conducted during the nonbreeding season showed that aggressive behavior in captive *Eigenmannia* is elicited primarily by electrical stimuli within the frequency range characteristic of the species. When tape recordings of various species of gymnotids were played through electrodes placed on a gymnotid-shaped plexiglass model, *Eigenmannia* gave the most attacks, threats, and discharge interruptions in response to recordings of conspecifics. The least effective electrical stimulus was a recording of a pulse-discharging species, *Gymnorhamphichthys hypostomus.* Sinusoidal stimuli were also very effective in eliciting aggressive responses when the frequency was 250–700 Hz (Fig. 9).

During the breeding season, *Eigenmannia* respond to signals resembling another *Eigenmannia* with discharge interruptions delivered at a high rate, a normal form of courtship display for this species. The maximum response to sinusoidal stimuli was achieved using 500 Hz stimuli (Fig. 10). Males pay little attention to sinusoidal stimuli outside the species range.

Another common species in Mocomoco Creek, *Sternopygus macrurus,* also uses electrical cues for species recognition. Its frequency range (50 to 150 Hz) is unique among the four species of tone fish found in this area, and courtship displays are elicited from males only by stimuli in the appropriate range. *Sternopygus* is particularly interesting because its resting discharge also serves to identify the sex of the signaler. As males and females reach sexual maturity, their discharge frequencies appear to change: males adopt lower frequencies than females (see Fig. 11), with no evidence of overlap.

As with many tropical species of fish, the reproductive season coincides with the beginning of the rainy season, the period with the most food and space. Just prior to the breeding season, I noted that large, reproductively mature male *Sternopygus,* recognizable from the very low frequency of their discharge, were found hiding in deeply undercut banks, in holes in submerged trees, and under large rocks, even during the night, when it was more typical for *Sternopygus* to swim in the creek to feed. In several cases, 5 to 6 males were clumped together within 3 to 5 square meters. At night, as *Sternopygus* that were thought to be female passed near a male's hiding place, the male produced a series of dramatic modifications in his discharge frequency. Spectrograms of some of the modulations are shown in Figure 12. *Sternopygus* males seemed to recognize the discharge frequency of the female and produced a type of courtship song in response to it.

Table 1. Discharge frequencies of gymnotid fish from Moco-moco Creek, Guyana. All species may be categorized as pulse (P) or tone (T) according to the waveform of the discharge.

	Day	*Night*
Low-frequency species (all P discharge)		
Electrophorus electricus	1–5 Hz	2–10 Hz
Hypopomus artedi	5–10 Hz	10–30 Hz
Gymnorhamphichthys hypostomus	5–10 Hz	(see high-middle frequency)
Low middle-frequency species (all P discharge)		
Hypopygus lepturus	30–40 Hz	40–50 Hz
Hypopomus brevirostris	20–30 Hz	25–60 Hz
Gymnotus carapo	40–50 Hz	50–60 Hz
Gymnotus anguillaris	30–40 Hz	35–50 Hz
High middle-frequency species (P and T discharge, as noted)		
Rhamphichthys rostratus (P)	80–90 Hz	80–90 Hz
Sternopygus macrurus (T)	55–150 Hz	55–150 Hz
Gymnorhamphichthys hypostomus (P)	(see low-frequency)	70–90 Hz
High-frequency species (all T discharge)		
Eigenmannia virescens	250–600 Hz	250–600 Hz
Apteronotus albifrons	750–1,250 Hz	750–1,250 Hz
Sternarchorhamphus macrostomus	750–1,000 Hz	750–1,000 Hz

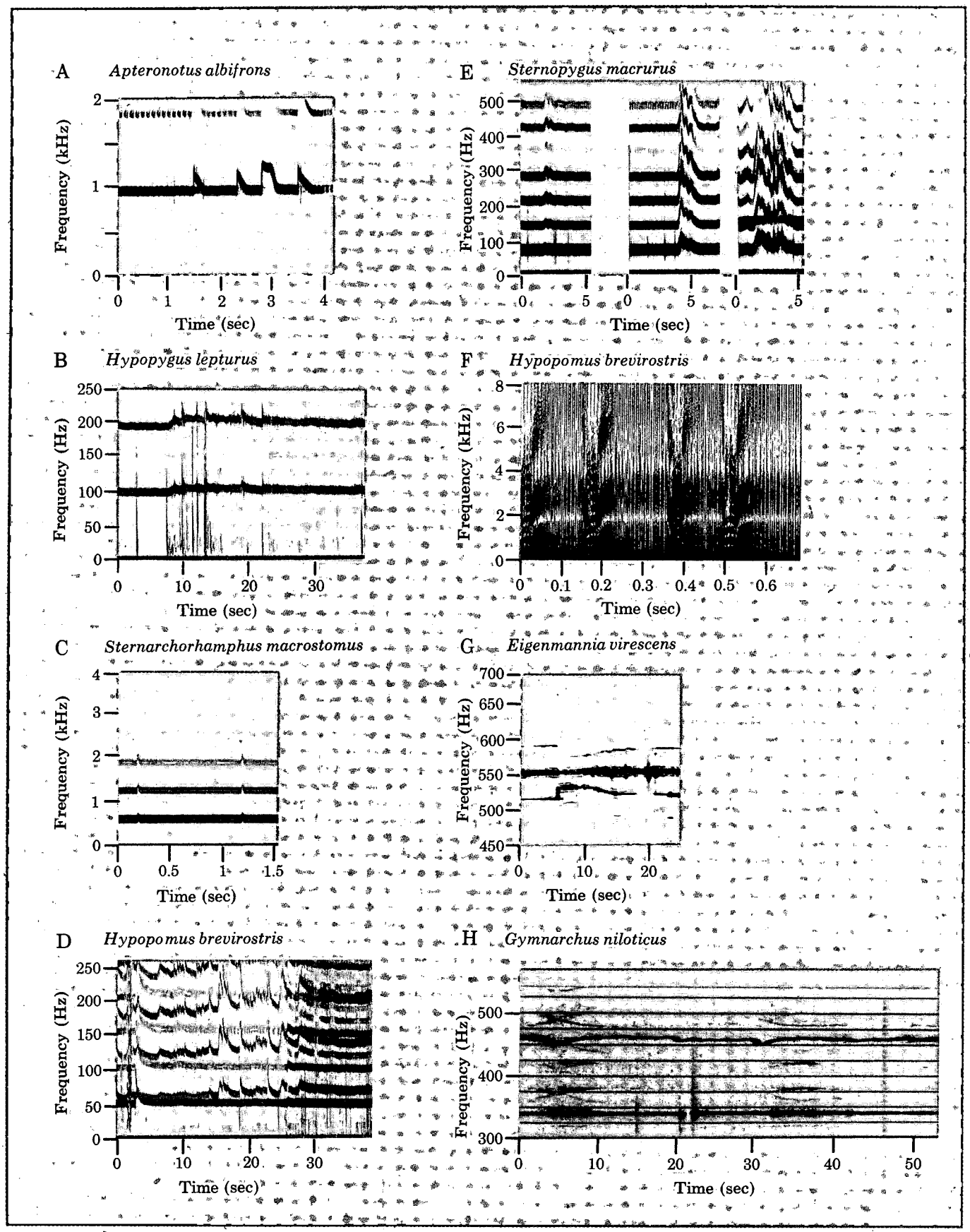


Figure 7. All known electric fish are capable of producing frequency modulations in their discharges, thereby adding an important dimension to signal diversity. (A) "Chirp" displays given by *Apteronotus albifrons*. The band at 900 Hz is the fundamental frequency of the discharge; the band at 1,800 Hz is the second harmonic. (B) Slight frequency modulations in *Hypopygus lepturus*. (C) "Chirps" produced by *Sternarchorhamphus macrostomus*. (D) Sequences of SID displays produced by *Hypopomus brevirostris*. Two fish are present; the fundamental frequencies are indicated by the two lowest frequency bands, at 50 Hz and 60–70 Hz. (E) "Rises" produced by a male *Sternopygus macrurus*. (F) "Rasp" discharges from *Hypopomus brevirostris* are used as an aggressive threat display. In this spectrogram, a major time expansion compared to D, individual pulses from the two fish are seen as vertical lines. The high-frequency rasp display is seen as a series of horizontal bands. (G) "Long rise" by *Eigenmannia virescens;* two fish are present. (H) Frequency modulations consist of *decreases* in the resting frequency in *Gymnarchus niloticus*. Two fish are present.

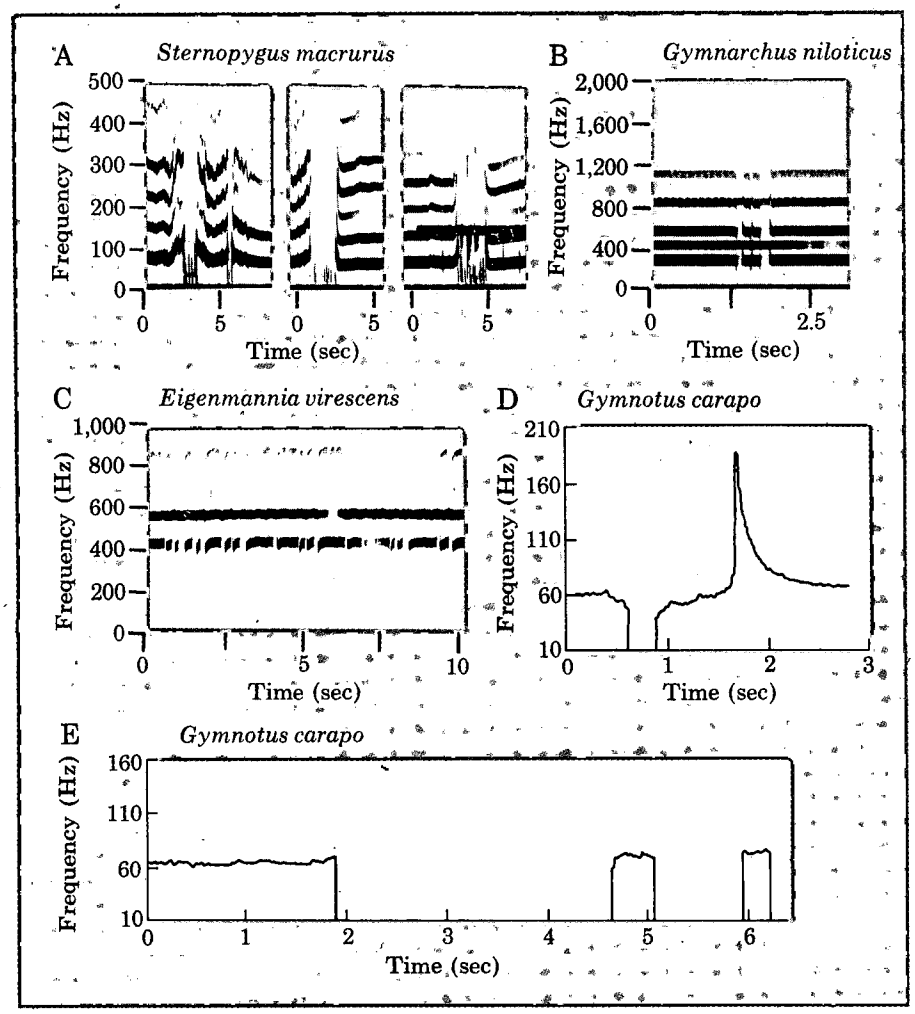


Figure 8. Discharge cessations are an important parameter of signal diversity. Brief cessations are used as courtship displays by *Sternopygus macrurus* (A) and *Eigenmannia* (C) and as aggressive threat displays by *Gymnarchus niloticus* (B) and *Gymnotus carapo* (D). Cessations of longer duration are used by *Gymnotus* (E) and *Gymnarchus niloticus* (not shown) as an indicator of submission. (D and E are from Black-Cleworth 1970, with permission.)

I tested whether the frequency of the stimulus was important in eliciting "song" by delivering stimuli from a sine-wave generator into the water near the hiding places of several large male *Sternopygus*. Sine waves with frequencies typical for females (130–141 Hz) evoked variations in the male's discharge that consisted of both rises (Fig. 7E) and interruptions (Fig. 8A). Although sine waves that corresponded in frequency to a female *Sternopygus* evoked responses, those matched to another male *Sternopygus*, an *Eigenmannia*, or an *Apteronotus* did not (see Fig. 12).

Signals that identify the age class of the signaler have not been studied extensively. Black-Cleworth (1970) suggested that in *Gymnotus carapo* the amplitude of the discharge could reflect the size, and consequently the age class, of the signaler. (Brown and Coates, 1952, found a nearly linear relationship between size and discharge voltage in *Electrophorus electricus*.) Gymnotids have never bred in captivity, and thus there has been no systematic study of newly hatched fish, but I observed in Trinidad that larval and postlarval *Gymnotus* 6 to 25 mm long discharged at a rate of 15 to 35 pulses per second, which then gradually increased to the adult frequency of 40 to 60 pulses per second. Similarly, in Guyana, *Hypopomus brevirostris* juveniles less than 20 mm long discharged at high frequencies (up to 90 per second), whereas adults discharged at 30 to 40 per second.

Although the frequency of juvenile *Apteronotus albifrons* is exactly the same as adults, juveniles have monophasic discharges that change gradually into the adult, biphasic type (shown in Fig. 5) by the time the juveniles are 50 mm long. Some age-specific changes in signaling properties may merely reflect stages in the development of the electric organ rather than an age-typical social signal. Further work is needed to test the responsiveness of adults to signals emitted by different age classes.

Aggregation. Some electrical displays function as distance-reducing signals, much like display postures described for gulls (Tinbergen 1959) or vocal aggregating signals of primates (Marler 1968). The sequences of rises and interruptions given by a *Sternopygus* in the presence of a female certainly appear to belong to this category. Their function is to attract a female to the male's hiding place so that further courtship activities can take place.

In an early study of electric communication, Bullock (1969) found that electric eels will congregate around a discharging eel in a net, around electrodes carrying artificial electrical pulses, or around electrodes carrying electrical emissions from an aroused eel in another tank. Since high-frequency discharges are normally emitted during feeding, these aggregations may be in response to a signal indicating the presence of food (Bullock 1969; Black-Cleworth 1970).

During fighting behavior, a subordinate animal may give displays that indicate a clear lack of aggressiveness on his part. These displays appear to play a role in permitting an aggregation to persist or, in Marler's terms (1968), in helping to maintain proximity. Black-Cleworth has found, for example, that subordinate *Gymnotus* will frequently give a discharge arrest—a cessation of 1.5 seconds to 3 minutes—during agonistic encounters. A statistical analysis of sequences of events showed that arrests were commonly elicited from a subordinate fish by the approach of a dominant one. Once the arrest had been given, the dominant showed a reduced tendency to attack or chase the subordinate when compared to its tendency to attack following other electrical displays.

Arrests, therefore, appear to function as an aggression-reducing or appeasement signal—one that helps maintain proximity. Similar dis-

Figure 9. Responses of *Eigenmannia virescens* to sine-wave stimuli of various frequencies. Responses of 5 fish to tests conducted during the nonbreeding season include discharge interruptions, attacks, approaches, and retreats. The ordinate represents the median number of responses during the 2-minute stimulus for the 5 fish tested. (From Hopkins, in press.)

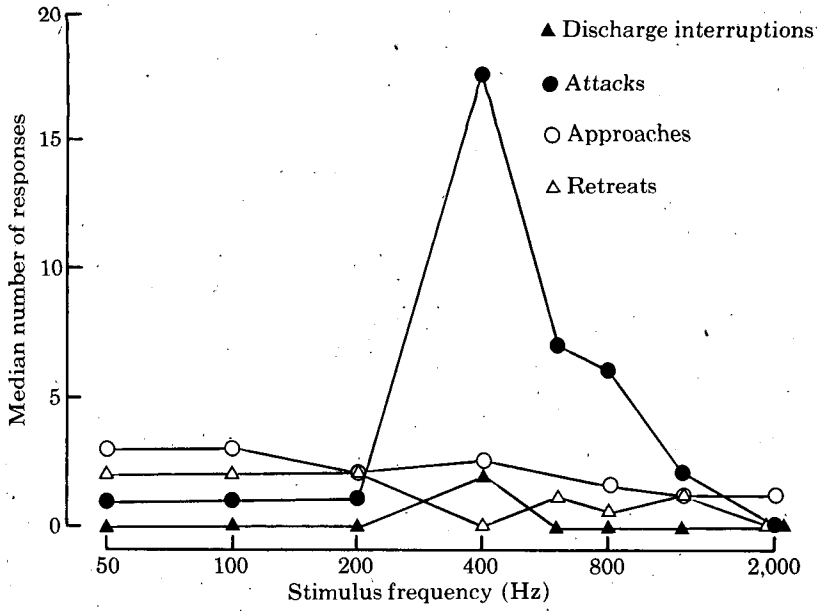
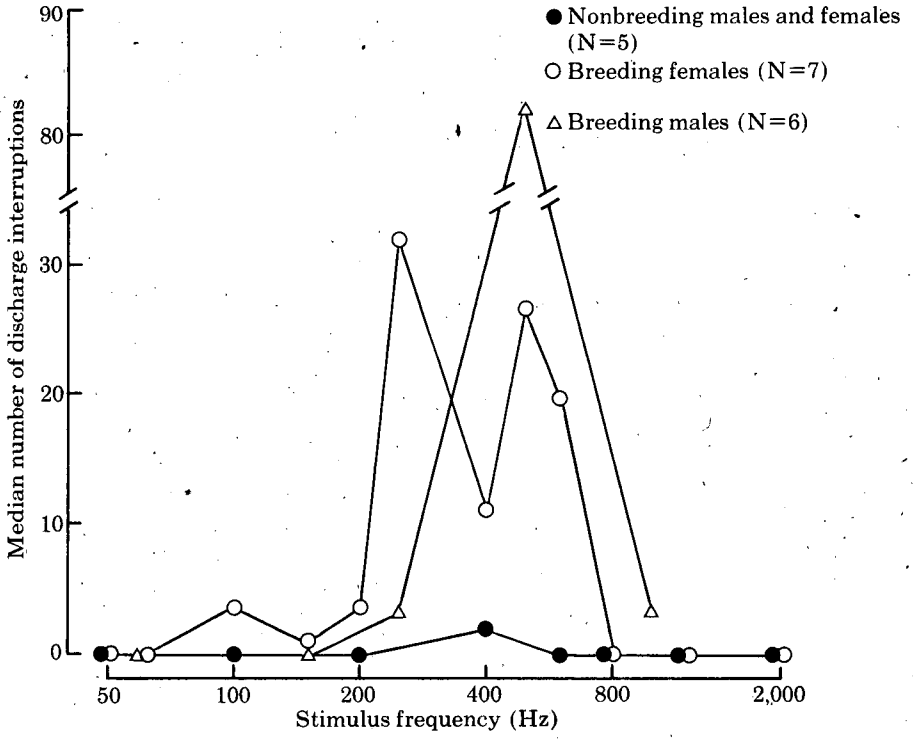


Figure 10. The number of discharge interruptions given by *Eigenmannia virescens* in response to sine-wave stimuli. (From Hopkins, in press.)



plays have evolved in the Mormyriform *Gymnarchus niloticus*. During discharge cessations for periods of up to 20 minutes by subordinate individuals, there is a reduced rate of attack by the dominant (Hopkins, unpub.). Long cessations are also given by subordinate *Gnathonemus petersii* during fighting behavior, and the function seems to be the same as in *Gymnotus* and *Gymnarchus*. Subordinates generally have a low rate of firing when in the presence of a dominant individual (Bell, Myers, and Russell 1974).

Silencing the electric organ seems well suited as a display used for appeasement or aggression reduction, because it renders the fish inconspicuous electrically. Especially in species such as *Gymnotus* and *Gymnarchus*, which are intolerant of conspecifics and will react aggressively toward a wide variety of electrical stimuli resembling their own discharge (Lissmann 1958; Black-Cleworth 1970), silencing may have evolved as an appeasement signal because it is the antithesis of an attack-eliciting stimulus (Darwin 1872). Other species produce submissive displays of an entirely different nature. *Eigenmannia virescens* in subordinate roles produce prolonged increases in frequency followed by a slow decrease to the resting frequency. These long rises (see Fig. 7G) are often given while the subordinate fish is retreating from the dominant's attacks, approaches, or threats. Long rises are typically 5 to 40 seconds in duration and consist of a 5 to 20 Hz elevation in frequency.

Long rises in *Eigenmannia* resemble, to a certain extent, the slow, subtle frequency changes elicited by electrical stimuli near the fish's own discharge frequency (Watanabe and Takeda 1963), a response adapted to avoid "jamming" of the object-sensing capabilities (Bullock, Hamstra, and Sheich 1972; Heiligenberg 1973). Whenever two fish with similar frequencies meet, they must perform this "jamming-avoidance response" if they are to approach close to one another without serious deterioration of their object-sensing abilities. Under these circumstances one may say that the subtle frequency change permits aggregation. It is easy to see how such a jamming-avoidance response could have become ritualized as a display allowing individuals to approach without aggression.

Dispersal. Another important function of electric signals is to increase or maintain the distance between the sender and the receiver (Tinbergen 1959; Marler 1968). Threat displays fall into this category, and a variety of electrical displays have been discovered that are used for threat. For example, it was possible to make nighttime observations of freshly captured *Eigenmannia* by placing them in pairs in an aquarium under dim red illumination. A statistical analysis of their behavior revealed that dominant individuals (the member of the pair that made the greatest number of attacks during a standard watch and also won competitions for daytime hiding

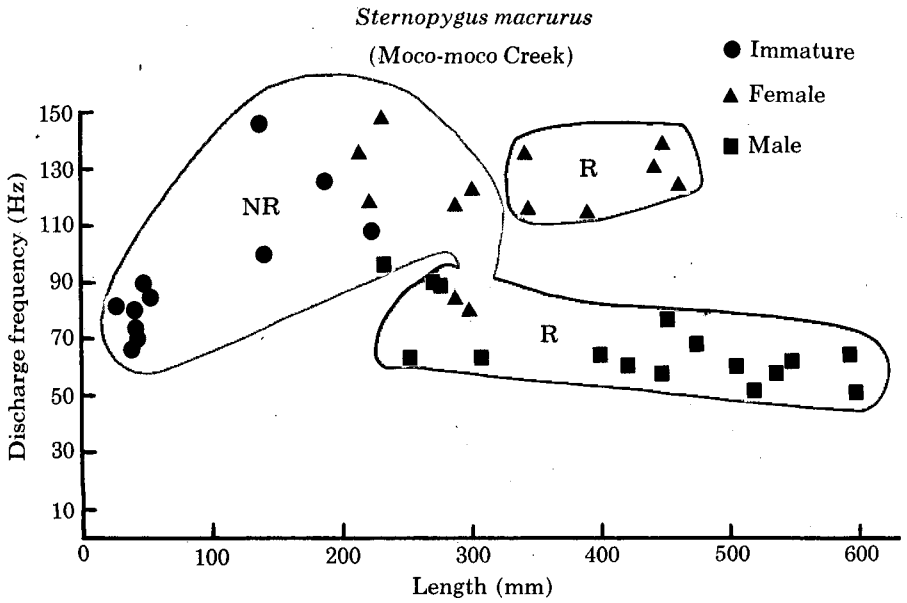


Figure 11. Discharge frequencies (in water 25°C) of male, female, and immature *Sternopygus macrurus* are plotted against the length of the fish. Fish in reproductive condition (R) are distinguished from those in nonreproductive condition (NR). The sex of small immature fish could not be determined in the field.

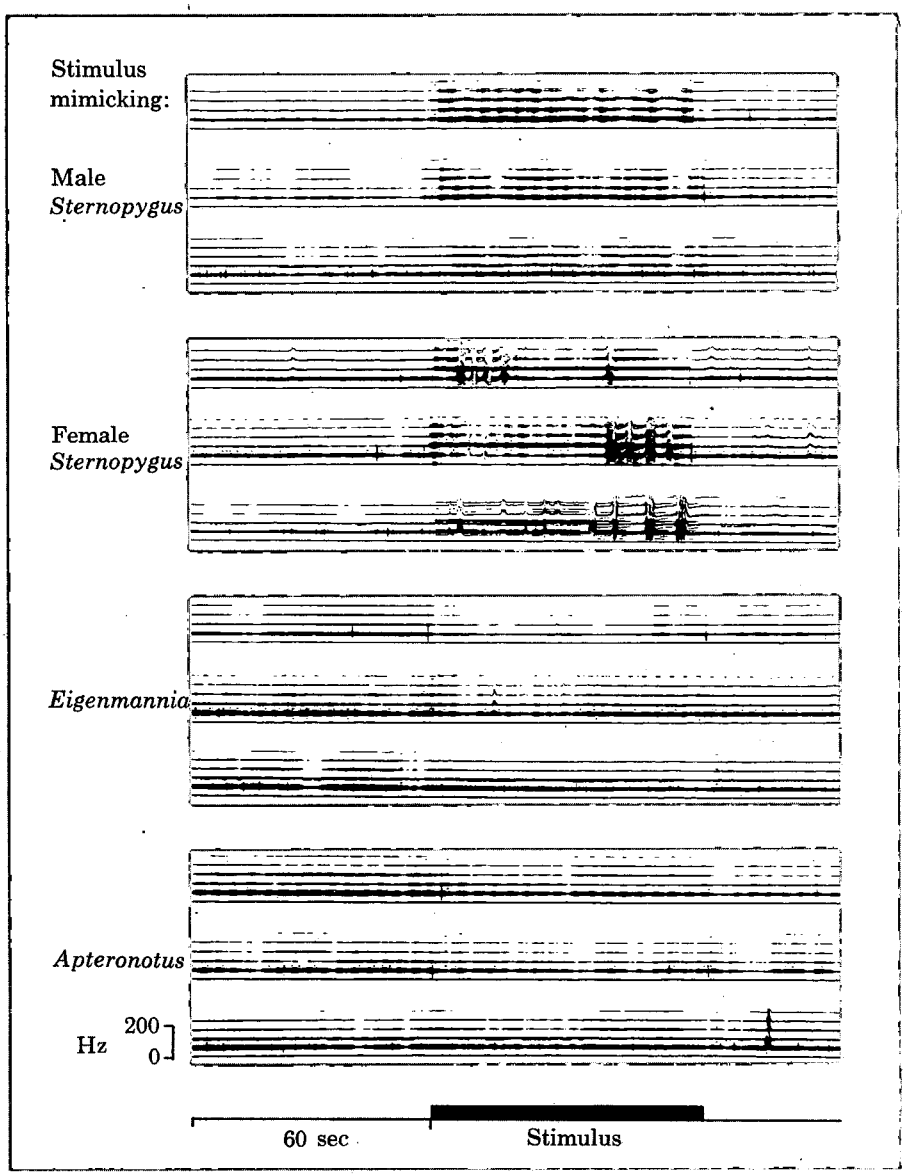


Figure 12. Sound spectrograms indicate that a male *Sternopygus macrurus* responds to sinusoidal waves imitating a female of its own species but hardly reacts at all to stimuli imitating conspecific males or fish of other species. Fish imitated are listed at left, and 3 trials are shown for each. The scale applies to all 12 trials.

places) gave many more 0.01 to 0.1 second discharge interruptions (see Fig. 8C) than subordinate fish.

A temporal analysis showed that the discharge interruptions came at the same time as attacks (butts to the opponent's side, or chases) or threatening actions (rapid darts directed at the opponent), but rarely during retreats from the opponent. Further, in an analysis of the behavior of recipients of electrical displays, it was shown that retreat was likely to follow a bout of discharge interruptions by an opponent but attack or approach was not (Hopkins, in press). Thus, discharge interruptions were shown to act as a threat display in that they resulted in the retreat of the recipient. It is interesting to note that in field situations discharge interruptions are detected much more frequently at night, when *Eigenmannia* are dispersed over the available habitat, than during the day, when they clump in hiding places; thus the discharge interruptions may play a role in dispersal.

In a remarkable case of convergent evolution, the African fish *Gymnarchus niloticus,* which morphologists believe evolved independently from *Eigenmannia* and its relatives, has an electric discharge nearly identical to *Eigenmannia*'s with regard to frequency, waveform, and polarity (compare Figs. 5 and 6). *Gymnarchus* and *Eigenmannia* produce almost identical discharge interruptions (see Fig. 8B and C) that serve as effective threat displays, as shown by a statistical analysis of electrical and motor actions of conspecific pairs of fish held in laboratory tanks (Hopkins, unpub.). Convergence in the physical forms of a communication signal used as a display raises many interesting questions as to the adaptive significance of the particular signal.

Another type of distance-increasing or -maintaining threat display consists of modulations in discharge frequency. In a laboratory study of *Gymnotus carapo,* Black-Cleworth (1970) found a significant correlation between SID displays and aggressive actions such as attacks and chases. She also found that if she placed electrodes inside a hiding place, an introduced *Gymnotus* showed a reduced tendency to enter

and spent less time inside when the electrodes were emitting artificial SID displays than when they emitted unmodulated pulses.

SID displays are associated with threat in numerous pulse species, including *Hypopomus beebei, H. brevirostris,* and *H. artedi,* as well as numerous mormyrids. The rasp discharge is merely an exaggeration of a similar phenomenon. Tone fish also use SID displays for threat.

Both SID and brief cessations act as effective social signals because they conspicuously contrast with the fish's normal discharge activity. Of course, an interruption cannot persist for long without its loss as a conspicuous contrasting feature. Although the evolution of these threat displays is still uncertain, Black-Cleworth has suggested that SID in *Gymnotus*—also given while attacking prey—may be a ritualized feeding display. Much further work is needed before we will be able to understand the evolution of social signaling among electric fish.

In summary, certain South American and African fishes capable of producing and sensing electric discharges have evolved an unusual modality of communication—electric signaling. Signals are broadcast in all directions within what appears to be a limited range. Nevertheless, owing to instantaneous conduction and rapid fade-out, this modality seems well adapted for transmitting messages quickly. Electric signals show a great deal of diversity, which can be classified according to one or more parameters, including the shape of the field, waveform, frequency, timing, frequency modulations, and cessations. In addition to helping to increase, decrease, or maintain the distance between signaler and receiver, electric communication seems to play an important role in species, sex, and age-class recognition.

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Wolf Häfele

A Systems Approach to Energy

Handling large amounts of energy in a way that is safe, clean, cheap, and efficient is a more serious long-range problem than producing an adequate fuel supply

In the past, the demand for energy was the primary driving force in the development of energy technology and the evolution of an energy economy. Other considerations were secondary, and it was therefore possible to deal only with gross parameters in the energy field, such as the increase in the demand for electrical energy, which doubled every 10 years. Now the situation has changed. In the short range, the supply of certain fuels cannot easily meet demand, and ecological and other constraints can no longer be ignored. The need for more detailed evaluations of parameters and their components leads to the mathematical modeling of energy supply and demand.

There are three aspects of modeling: sensing, optimization, and forecast. The sensing or assessment aspect could serve several purposes. First, the creation of models enables us to view the energy problem more comprehensively and to test the effects of various policies and regulations. Environmental and economic options may be most susceptible to modeling techniques, but it may also be possible to approach the complex problems of technology assessment in this way, evaluating the priorities for research and development. Further, the relation of energy conservation to a limited-growth or no-growth economy could be studied.

The goals of optimization are obvious: the best and most timely distribution of fuel supply, the most efficient interfuel substitution, and the most effective provision of capital. Although until recently optimization was determined by economic considerations, we must now take into account multiple objectives, environmental and social as well as economic.

The third function of modeling, forecast, is of special interest as it relates to the problems of energy systems. A typical example of an energy demand and supply model was presented at a recent M.I.T. conference on energy modeling, by Schweizer, Love, and Chiles of the Westinghouse Corporation (*1*), based on demand and its growth for various types of fuel in various regions and market sectors. The demand model is combined with a model of various partial elasticities, to serve as an input for a linear programming allocation algorithm. The same is done for a model of supply, its growth, and the elasticities involved. The linear programming algorithm then allocates demand growths to supply growths for a given objective function. The result is an energy strategy for meeting the demand growth with related price changes. Such an approach implies certain fuel interchangeabilities, which leads to problems of energy conversion and the related models for that. New technologies must be considered, but so must models for proposed energy policies. The overall model can help to assess priorities for technological research and development, to evaluate the consequences of considering objectives other than minimum price, and to assess the impact of specific policies.

The process of designing and playing with such a model can give us a better understanding of the reality to which the model is applied. Of particular importance is the identification of various levels of the system and the degree of interrelation among them (*2*). Of course, mathematical models are of value only if the necessary input data are available. Evaluations for the asymptotic solution of the energy problem require global considerations. The type of data required must be identified and the degree of aggregation of raw data made compatible. And although the required economic data may be available, of equal importance are pollution, thermal waste heat, and sociological data—data related to more general objectives.

Since in the discussion to follow we will be dealing with large amounts of energy, it will be useful to introduce the unit Q = 10^{18} Btu. The equivalent of Q in several units is given in Table 1. World consumption of energy in 1970 was roughly ¼ Q/year. In the year 2050, it could be 6 Q/year (see Table 2), or a factor of 25 larger than the 1970 value. The figure of 10^{10} for population growth by 2050 is an unsophisticat-

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