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PATTERNS OF ELECTRICAL COMMUNICATION AMONG GYMNOTOID FISH

A thesis submitted to the Faculty of The Rockefeller University
in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

by

aug 21
Carl D. Hopkins, A.B.

Approved for publication.

Rita Mark

Professor.

June, 1972

The Rockefeller University

New York, New York

PREFACE

This study was made possible through the kind cooperation and hospitality of the Ministry of Agriculture and Natural Resources in Guyana, who provided official support during my two year study. I am deeply indebted to the people and the government of Guyana for allowing me this opportunity to do research in their country. During each visit to the Rupununi, Geoffrey Lomas and his family helped me get established in a study site. In Trinidad I was a guest at the William Beebe Tropical Research Station, owned and operated by the New York Zoological Society.

During this study I was assisted in some of the field work by Elliot Olton, David Singh, and Emerich Roth. I thank them for their capable assistance and excellent work. Jose and Susan Torre-Bueno from the Rockefeller University joined me in 1970. Jose helped greatly in some of the more difficult field work during the peak of the rainy season, and Susan did a study of meteorological and hydrological conditions in Moco-moco and kept accurate records of experimental work. Jose worked out many techniques for studying Eigenmannia in aquaria which I later used to great advantage. My sister, Dolly, spent her 1970 summer vacation in Guyana. I am grateful to her for her assistance as well as company. Peter Marler and R. Haven Wiley gave me invaluable assistance and advice during visits to Guyana in 1970 and 1971.

Most of the rather specialized equipment used in the field was the design of Mike Rosetto of the Rockefeller University Electronics Shop.

Throughout my studies I have benefited from the friendships and guidance of many people at Rockefeller University. I am especially grateful to Dr. Peter Marler who has given me expert advice and encouragement throughout this project. I have also benefited from many discussions with other people at Rockefeller, including Drs. Donald Griffin, Thomas Struhsaker, Floyd Ratliff, Clarence Connelly, Bertil Hille, Fernando Nottebohm, Roger Payne, Jack Bradbury, Bruce Knight, and especially, R. Haven Wiley.

I am grateful for the opportunities to discuss this work with Michael V.L. Bennett, Theodore Bullock, Rosemary McConnell, Hans Lissmann, and Tyson Roberts.

My wife, Kathy Hopkins, assisted in every phase of the field work and preparation of the manuscript. I thank Kathy for her help.

SUMMARY

This paper presents the results of a twelve-month field study of the behavior and ecology of gymnotid fish from the Rupununi District of Guyana, South America, and from Trinidad, W.I. There are 13 species of gymnotids in the Rupununi District, of which six to eight species occur frequently in the main study area in Moco-moco Creek. All species produce electrical discharges which are presumably used for object location and for electrical communication.

Gymnotids are active at night and inactive during the day. Some species tend to specialize on the types of daytime hiding places selected, while others generalize. Eigenmannia virescens and Sternopygus macrurus select a wide range of hiding places, but Sternopygus individuals are randomly dispersed whereas Eigenmannia tend to clump together. The breeding season of most gymnotids starts with a migration into a quiet, flooded swamp, immediately after the first flood at the beginning of the rainy season. Inspection of gonadal condition and plots of the growth rates of gymnotid larvae show that most species delay breeding until the onset of the rains. Sternopygus is an exception in that it begins breeding in the main creek before the beginning of the rains.

Both Eigenmannia and Sternopygus produce electric discharges that differ from all other species of gymnotids from Moco-moco Creek. Among the fish with tone discharges, Sternopygus produces the one with lowest frequency (50 to 150 Hz) and Eigenmannia produces the one with next lowest (250 to 600 Hz). Each species produces an appropriate species-specific response when presented with an electric sine wave stimulus of the appropriate frequency.

Sternopygus exhibits a sexual difference in the resting frequency of its normal discharge. Reproductive males discharge at 55 to 70 Hz whereas females discharge at 100 to 140 Hz. This frequency difference has communicative significance. Males, showing site-attachment during the breeding season, respond to playback of sine waves of frequencies within the female range with transient frequency increases and discharge

cessations. Males do not respond to playback of sine waves of frequencies corresponding to the other males nor to other species of tone fish from the Rupununi. Further evidence indicates that variations in the discharge of males may function in the courtship of this species.

Although there is a statistical difference in the discharge frequency between male and female Eigenmannia, the overlap is extensive. Males discharge at 250 to 600 Hz whereas females discharge at 340 to 560 Hz.

The agonistic behavior of Eigenmannia was observed in aquaria in the field, and was described in terms of the component actions, both electrical and motor. Aside from the normal discharge, electrical actions included Rises and Interruptions. Rises that lasted longer than 2 seconds (Long Rises) were given by subordinate fish, while they were retreating from attacks from their opponent. Some Rises were given spontaneously, and they tended to elicit attacks from the dominant fish. Long Rises act as a submissive display in Eigenmannia. Interruptions were given by dominant fish. They were given in bouts of varying numbers depending on differences in the likelihood of attack. Interruptions cause the opponent to retreat, and are thus classed as a threat display.

During playback experiments with Eigenmannia, Attacks and Interruptions were given in response to playback of Eigenmannia-like sine waves, and of tape-recorded signals from Eigenmannia. Playback of non-Eigenmannia-like frequencies, or of other species from Moco-moco Creek, were ineffective.

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I. INTRODUCTION

Communication between organisms implies some adaptive exchange of information between a participating sender and receiver which alters the behavior of the receiver. Communication systems play a central role in the organization of animal social systems.

Communication signals help to orient behavior. Many signals aid in increasing, decreasing, or maintaining the distances between the signaler and the receiver (Marler, 1968). Communication signals also serve the function of identification (Morris, 1946; Marler, 1961). The song of the male chaffinch, for example, conveys information about the species, the sex, the individual, the motivation, and the environment of the singer (Marler, 1956; 1961). The responses of male and female chaffinches to this song will, of course, be quite different.

Many modalities of communication are available to animals. The uses of visual, auditory, and chemical modalities are well known (Sebeok, 1968). Remarkably little is known about communication using the electrical modality, even though the capabilities for producing and sensing electrical signals by fish has been known for over 20 years (Lissmann, 1951). This paper is concerned with communication using the electrical modality.

The abilities to both produce, and receive electrical signals has been well studied for two large groups of fresh water fish: the Mormyriiformes and the Gymnotoidei (review in Bennett, 1971a,b). The African Mormyriiformes (Osteoglossomorpha) are a large order of fishes that includes two families, the Mormyridae, and the Gymnarchidae. The South American Gymnotoidei (Ostariophysi) are a primitive sub-order of characoid-related fishes including four families, Gymnotidae, Electrophoridae, Apteronotidae, and Rhamphichthyidae. This classification scheme follows that proposed by Greenwood et. al. (1966).

Electrical communication has been suggested for these two groups of fishes. Møhrhous (1957) proposed that the electric discharges of mormyrids function in maintaining territorial boundaries much as the song of birds. It has long been recognized that many species of electric fish have species-

specific discharges (Lissmann, 1958; Coates, Altamirano, & Grundfest, 1954; Hagiwara and Morita, 1963; Steinbach, 1970). Several studies have shown that well defined variations in the discharge frequency of some electric fish occur during social interactions. Möhres (1957) showed that when an individual Gnathonemus was introduced into a tank containing an established resident of the same species, that there was tumultuous fighting accompanied by increases in the discharge frequency of both individuals. Lissmann (1958) noted that two fish (Gnathonemus senegalensis) separated by a visual but not by electrical barriers in an aquarium, seemed to sense one another's electrical discharges. Mechanical disturbance of one individual caused it to increase its frequency and the fish in the other compartment usually followed suit. Disturbances in the first compartment made while the first fish was not present, did not affect the discharge rate of the other fish.

Szabo (quoted in Lissmann, 1961a) suggested the increases in frequency in one species of mormyrid are effective in eliciting a discharge cessation of another species. Numerous studies have been performed testing the responses of electric fish to artificial stimulation (Lissmann, 1958; Watanabe and Takeda, 1963; see review of work in Bullock, 1969).

Bullock (1969) presents evidence that the discharge of one electric eel (Electrophorus electricus) causes other electric eels to approach the site where one was discharging. In one series of experiments an eel was captured in a net and suspended in a tank containing several electric eels. When the fish in the net maintained a steady high frequency of discharge it caused a significant attraction of other electric eels. In another experiment, one electric eel was isolated from a group of 11 others in separate pools. The isolated eel was connected to the others electrically with the use of dipole electrodes. The isolated fish was disturbed or fed thus causing it to increase its frequency. This caused attraction to the electrodes and elevation of discharge frequency of the 11 eels in the other tank. When the connection between the two tanks was broken, then disturbance to the single fish had no effect on the activity of the other fish.

The most complete study to date of the use of electrical signals in communication, has been a study of the agonistic social behavior of Gymnotus carapo by Black-Cleworth (1970). In her study, Black-Cleworth emphasized the analysis of the contest of electrical displays, and their effects upon the recipients of the displays. She was able to distinguish four types of electrical discharge patterns used in agonistic behavior. The Normal Discharge of Gymnotus, is a steady train of pulses. It serves to identify the species, aid in location, and convey the size of individuals. To other Gymnotus kept in the aquarium, the Normal Discharge acts as a stimulus for attack. SID's or sudden increases in the discharge frequency followed by decreases to the original frequency, were associated with the tendency to attack. SID's served the function of threat displays, causing the recipient to retreat. Discharge Breaks were periods of silence in the discharge lasting less than 1.5 seconds. They were given prior to attacks, and served as a moderate intensity threat display. Discharge Breaks caused the other fish to retreat or do nothing. Discharge Arrests were periods of silence in the electric discharge that lasted for more than 1.5 seconds. They resulted in approach by the other fish without subsequent action. Discharge Arrests function as appeasement displays in Gymnotus. Black-Cleworth's study, although confined to the non-reproductive behavior of Gymnotus is clearly a major advance in the understanding of electrical communication. Other studies have also added to our knowledge of electrical communication such as Valone (1970) and Moller (1970).

The use of electrical communication in the reproductive behavior of electric fish is completely unexplored to date. Lissmann (1958) clearly pointed out that it would be of great interest to look at the electric signals of Gymnarchus niloticus during the breeding season. Gymnarchus is a species that will attack and even attempt to eat a source of electric signals similar to its own.

Aside from the observations of Budgett (1901) who described the nesting behavior of Gymnarchus, very little is known of the breeding habits of electric fish. The modes of reproduction of gymnotid fish

is unknown (Breder and Rosen, 1966).

Electrical communication is confined to certain fishes. Other modalities are available to fishes and certain patterns are beginning to emerge that help to explain the choice of one modality over another. One factor is the function of the signal in the animal's social behavior. Another is the ecological context of the signal. Olfactory signals, for example, seem well adapted for long distance orientation due to the remarkable ease of generating signals many times threshold. The visual modality, being accurately localizable, is useful in conveying complex temporal and spatial signals. The visual modality has limited value at night or where obstructions interfere with straight line transmission in muddy water, for example.

Concurrent with the evolution of the electrical object locating system (Lissmann, 1958), electrical communication has evolved in fishes in response to the biological problems of species and sex recognition, of behavioral orientation and timing. Some of the properties of the electrical modality are as follows: 1) Conduction time of signals is rapid, in fact, instantaneous. 2) There is no persistence to signals; they have rapid fade-out, unlike some chemical signals that linger. 3) Like sound, the signals are nearly omnidirectional. 4) The signal is capable of crooked line transmission, not being limited by objects in the environment. Electrical communication is not affected by vegetation, or by muddy water. 5) The sender directs his own energy into the production of signals rather than depending upon some ambient energy. Most visual signals depend upon ambient light. The intensity of the electrical signals will evolve to a level that is sufficient to overcome background noise. 6) The distance of electrical communication is short, on the order of 1 to 10 meters. Electrical signals are attenuated in the same way as the potential field around a dipole. 7) The electrical system is non-specialized in that it is not used exclusively for communication. It is well known that electric fish are capable of sensing conducting and nonconducting objects in their environment by detecting distortions in their own electric field (Lissmann, 1958; Lissmann and

Machin, 1958). The mechanisms for localizing objects differing in conductivity from water have been the subject of studies on several species (Hagiwara and Morita, 1963; Hagiwara, Kusano and Negishi, 1962; Hagiwara, Szabo, and Enger, 1965a and b; Bullock and Chichibu, 1965; Suga 1967a,b).

In order to fully appreciate the uses of electrical signals in communication, both in the reproductive and non-reproductive social behavior, and to begin to study the influence of the ecology on the forms and modalities of social signals, I felt that it was necessary to do field work. This paper presents some of the results of my studies of gymnotid fishes from the New World tropics. The first part of the paper will be an introduction to the ecology of gymnotids, with an emphasis on the daily cycles of activity, the annual cycle of activity, on the movements, and on the spacing of the fish. There is an emphasis on the ecology of two species of gymnotids: Sternopygus macrurus and Eigenmannia virescens, two species that differ in their ecology and their patterns of electrical communication. The remainder of the paper presents evidence for the use of electrical communication in these two species.

II. METHODS

A. Period of Study

This research represents 12 months of field work in Trinidad, West Indies and in Guyana, South America. I spent two months, July and August of 1969, at the New York Zoological Society's Tropical Research Station, Simla, Arima Valley, Trinidad investigating the behavior of Gymnotus carapo, the only gymnotid species present in Trinidad.

During the month of September, 1969 I worked in Guyana, South America making preliminary observations on the ecology and behavior of several species of gymnotids. I traveled to Bartica, Mahaica and the coastal region surrounding Georgetown, and to the Rupununi District in the interior of Guyana. On March 3, 1970 I returned to the Rupununi District of Guyana to continue my observations on gymnotids. I remained in Guyana through the rainy season until August 15, 1970. During 1971 I returned to the study site in The Rupununi District from April 12, 1971 until June 28, 1971. The observations that I made, thus span a period of three years, encompassing three rainy seasons and part of two dry seasons. They represent a total time in the field of 12 months.

B. Study Sites

All observations were confined to small streams, ponds, and swamps. No attempt was made to study the gymnotids in the main rivers or large ponds, although some fish were collected from the Takutu River (Rupununi, Guyana) during the dry season in 1970 when the water was very low, and from several ponds on the Rupununi Savanna during the dry season. Although the ecology of large rivers in the neotropics is quite different from the ecology of small streams and swamps, my attention was focused on the small bodies of water only. An important feature of the study was the necessity of being able to wade in the water. Many of the observations made in the field depended upon accurate spatial localization of individuals (although it was impossible to individually identify fish). This would have been impossible in a larger body of water where observations would have had to have been conducted from a boat or from the shore. Steinbach (1970) has made general ecological observations on gymnotids in the

Rio Negro, Brazil in a large body of water; however, Lissmann (1961a) and Lissmann and Schwassmann (1965) observed gymnotids in smaller bodies of water.

Trinidad. All of my observations in Trinidad were confined to the northern part ($10^{\circ} 30' \text{ N}$; $61^{\circ} 15' \text{ W}$) in clear streams running off the Northern Range (3000 feet) and in several swamps in the North-east.

I observed Gymnotus carapo in the Arima River, the Mausica River, and the Guanapo River, all of which flow west into the Caroni Swamp in the western part of Trinidad, and in the Barro River, the Aripo Savanna, and the Nariwa Swamp, all of which drain in the eastward direction into the Atlantic Ocean. Although I searched for Gymnotus on the northern side of the Northern Range in the Marianito River, I found no evidence for its presence, as reported by Price (1955).

Guyana. Some preliminary observations were made in Guyana on the coastal area around Georgetown and in the Botanical Gardens in Georgetown. The main research area, however, was in the Rupununi District, 420 km from the coast. Since there were no field stations in Guyana, a primitive camp was constructed to serve as a laboratory. The camp was located 16 km east of the village of Lethem at the base of the Kanuku Mountains on the edge of Moco-moco Creek ($3^{\circ} 19' \text{ N}$, $59^{\circ} 39' \text{ W}$, Fig. 1).

Two sites in Moco-moco Creek were observed extensively during this study. The first site was in the area immediately around the camp. This area lies just at the base of the Kanuku Mountains. Here the shallow creek flows rapidly over rocks and rapids, between banks with steep sides. The second site lies 4 km downstream from the camp, in a flat low-lying area where the deeper creek meanders slowly over sand and mud bottom among the giant Moco-moco plants (Montrichardia sp., Araceae) that give the creek its name. The low-lying area becomes flooded during the wet season, forming a large area called Kumaka Swamp. These two areas are shown on the map in Fig. 1. Both of these study sites were located in forest except for the open swamp savanna in Kumaka Swamp shown on the map. The water in this creek was usually clear.

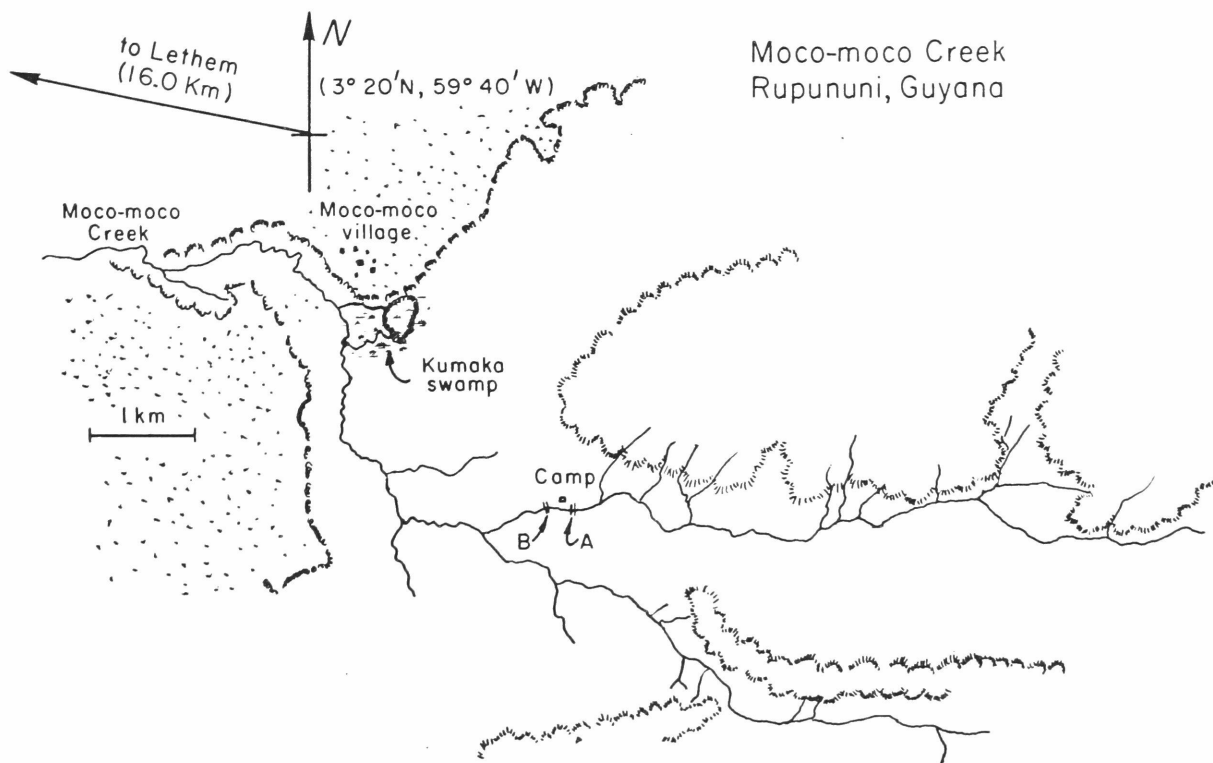


Fig. 1. Map of the main study area in the Rupununi District of Guyana. The locations of study sites A and B, as well as Kumaka Swamp are indicated. Savanna is represented by a dotted pattern, the remainder of the map represents forest. The approximate location of a bluff, forming the base of the Kanuku Mountains that lie to the south of the camp, is shown as a scalloped line. Taken from photograph made by Huntington Aerosurveys, Ltd., October, 1953, film no. 22, frame 084.

Other locations on the Rupununi Savanna were also observed but not systematically. Travel over the savanna was relatively easy by jeep thus permitting visits to various sites to compare the ecology of different regions.

C. Aquarium Studies

Extended visual observations of gymnotids were possible only with the use of aquaria. To minimize the disturbance to the fish caused by transport and by extended periods in captivity under extremely crowded conditions, aquarium studies were conducted while I was in the field. In 1971 I made systematic observations of agonistic and sexual behavior of Eigenmannia virescens in these field aquaria. Freshly caught specimens were observed at night in a 76 liter or a 108 liter aquarium illuminated from behind by the light from a single candle surrounded by red celophane. The tanks were supplied with fresh creek water at least once every three weeks. The water was aerated with battery powered air pumps, and sometimes planted with plants from Kumaka Swamp. Fish being used for aquarium observations were kept individually in 10 to 20 liter tanks made from heavy duty plastic bags or in 15 liter tins used by tropical fish exporters as holding tanks for aquarium fish. A wooden tube was placed in each tank as a hiding place for the fish. The fish were identified individually by taking note of small scars, and naturally occurring deformities, as well as naturally occurring patterns of coloration of the skin. For example, in 1971 one Eigenmannia (#46) had approximately 2 cm of its tail regenerating; another (#16) had a small notch in its anal fin 3 mm from the end. These small differences could be used to confirm the identification of an individual during the aquarium observations. Since the fish were usually kept isolated and were never observed in groups larger than three individuals, the identification of an individual was rarely confused. On three occasions, however, when confusion did occur, the correct identity of the individual was determined by comparing the discharge frequency to previously made tape recordings. The fish were never kept in the holding tanks for more than 12 days (average = 4.8 days), and they were not fed during the period of captivity. After observations

were completed on a group of fish, the individuals were sexed and then preserved in formalin.

D. Detection of the Electric Signals

The electric signals from the fish were detected with two electrodes immersed in the water. The electrodes were made of 2 mm diameter copper wire each with an exposed surface area of 2.8 cm². These copper electrodes were soldered to copper wires that were insulated except at the tip, and shielded. The two electrodes were mounted at the ends of two rectangular plastic rods held in the shape of a "V". The distance between the electrodes could be varied between 0 and 55 cm by altering the angle of the "V". Normally an electrode spacing of 20 cm was used because it provided adequate sensitivity and yet was not cumbersome and could be used as a probe among tangled vegetation along the bank of the creek. The shielded cable leading to the electrodes was rarely more than 3 meters in length.

The potential difference between the two electrodes was amplified with one of two amplifiers or "fish detectors". The first amplifier, made by Round Hill Associates, model AA-100, was a portable, battery powered audio amplifier and pre-amplifier; it was used as a general purpose fish detector. This amplifier was flat to within 3 db from 100 Hz to 12 kHz with a gain of 70 db (3×10^3). The output of the amplifier was connected to an 8 ohm loudspeaker and the entire assembly was mounted in a plexiglass box. Since the electric discharges from gymnotids consist of a series of brief pulses similar to nerve spikes, the discharges were audible once they had been transduced by the loudspeaker. This amplifier was selected for its cheapness and durability under rugged field conditions. Although the entire fish detector was accidentally immersed in water several times, both the amplifier and speaker operated normally after several hours drying in the sun. One disadvantage of the amplifier was that it did not respond to low-frequency electrical signals. One species, Sternopygus macrurus produced an electric discharge with a fundamental frequency in the range from 55 to 140 Hz. The amplifier begins attenuating the signal over this range, thus making this species slightly more difficult to detect than species with higher frequencies.

The amplifier was powered by a 12.6 V mercury battery. It has an advantage over a normal dry cell because it maintains a relatively constant voltage output throughout its life. The battery was changed immediately if the voltage under load fell below 10V. Since the gain of the amplifier was related to the voltage of the power source, the constant voltage source provided by the mercury battery insured an approximately equal gain of the amplifier throughout the study.

The second amplifier, MR1 & MR2, used for measurements of field strength and discharge waveform and for all tape recordings was an amplifier with higher gain and better overall frequency response. This amplifier employed a low noise integrated circuit operational amplifier as its first stage. The response was flat from 3 Hz to 30kHz and the maximum gain was 80 db (10^4). This amplifier proved to be more suitable for detecting the low discharge frequency of Sternopygus macrurus than the general purpose fish detector. The second amplifier was designed by Mr. Mike Rosetto of the Rockefeller University.

The spectrum of noise of thermal origin for the two amplifiers, measured at 25° C (input shorted) is shown in Fig. 2. In this figure I have plotted the RMS noise measured in Volts and divided by the 3 db bandwidth of the measuring system (Federal Scientific Ubiquitous Spectrum Analyzer, UA-7B). The AA-100 amplifier has a peak noise output of $2 \times 10^{-7} \text{ V} / \text{Hz}^{1/2}$ at 500 Hz. Low-frequency noise of this amplifier is attenuated with the low frequency cutoff filter. The MR2 amplifier has better noise characteristics, being nearly uniform across the spectrum from 10 Hz to 10 kHz and having an RMS noise level of only $2 \times 10^{-8} \text{ V} / \text{Hz}^{1/2}$. Therefore, with the amplifier set to its widest bandwidth (30 kHz), the RMS noise level was 3.5×10^{-6} Volts. Since the thermal noise sets the lower limit of sensitivity of the amplifier, this means that the minimum sensitivity of the fish detector to electric fields within the 3 Hz to 30 kHz bandwidth when the electrodes were spaced apart by 20 cm ($S/N = 1$) was $0.17 \text{ } \mu\text{V}$ per cm, a sensitivity that is of the same order of magnitude as that of most fresh water electric fish (Machin and Lissmann, 1960; Bullock et. al., 1972b).

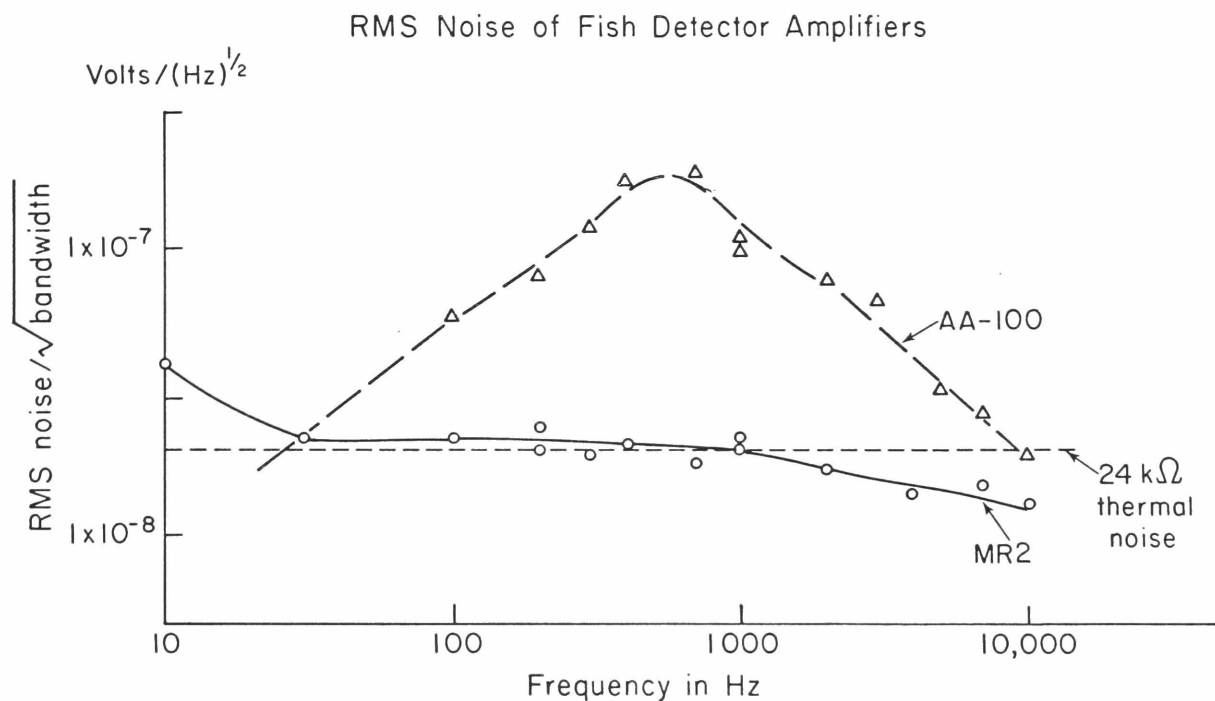


Fig. 2. Spectrum of noise from the two amplifiers used as fish detectors in this study. The noise spectra were measured with the input of the amplifiers shorted, at 25°C. A line representing 24×10^3 ohm thermal noise is indicated.

Signals from the amplifier were tape recorded with a Uher 4200 or 4400 Report Stereo tape recorder. The amplifier output was recorded on channel 1 and a voice commentary was recorded on channel 2. For most recordings, a tape speed of 3 3/4 i.p.s. was used. The 5 db frequency response of this tape recorder at 3 3/4 i.p.s. was 40 Hz to 16 kHz (manufacturer's specifications).

E. Spatial Localization of Individual Fish

The "V" shaped plastic rod supporting the dipole electrodes was mounted on the end of a four-foot stick used for probing the stream in search of a fish. A fish was located by making slow sweeping movements from one side of the stream to the other while slowly progressing up or down stream. Considerable care was taken while probing in the vicinity of rocks, logs or other objects under which a fish could be hiding. While the systematic search with the electrode was going on, I listened at all times to the output of the loudspeaker for the slightest sound resembling an electric fish. Once a sound had been heard it was usually a simple matter to move the electrode in the direction and orientation which gave the largest signal, and eventually to localize the fish to within a few centimeters. One measure of the maximum distance at which I could detect an average sized adult (150-250 mm) Gymnotus carapo in the Mautica River of Trinidad (specific conductivity, L , of water = 1.85×10^{-4} mho/cm) yielded a value of 2.5 meters, however the distance at which the fish could be detected was greater in the direction parallel to the longitudinal axis of the fish, as would be expected if the electric field surrounding the fish were a perfect dipole. The average maximum distance of detection of 11 well isolated Gymnotus in the up and downstream direction in the Mautica River was 2.1 meters.

The range at which a fish could be detected depended upon the size of the individual. The fry of Gymnotus carapo 10-20 mm in length, found in the Aripo Savanna in Trinidad (specific conductivity of water, L , = 6.84×10^{-5} mho/cm) could be detected at a distance of approximately 5 cm from one of the poles of the electrode.

The distance at which a fish could be detected also depended to a certain degree upon the species. The sporadic low frequency discharges of Electrophorus electricus, the electric eel, carried over long distances. One electric eel found in the Ikuwali creek in the Rupununi could be detected at a range of 6 to 10 meters. The relatively high frequency tone discharges produced by Apteronotus albifrons and Eigenmannia virescens were also easy to detect at long distances. These discharges contrasted with the noise produced by the fish detector amplifier and the electrical noise generated by atmospheric disturbances and thus could be detected at lower levels than the discharges from other species which produce pulse-like discharges.

Spatial localization of an individual depended upon the situation. In the simplest case, that for Gymnorhamphichthys hypostomus, in which solitary individuals bury themselves under 1 to 2 cm of sand during the day in the middle of shallow creeks, the exact position of the individual could be determined by moving the electrode close to the fish. In addition, the orientation of the fish could be determined by rotating the dipole electrode around until the null direction was determined. The fish was perpendicular to the null direction of the dipole electrode. Once the location had been established, it could be confirmed by a very gentle touch of the electrode on the sand over the fish. If the fish was buried within a few centimeters of the place where the electrode touched, it would usually give a slight increase in the frequency of its discharge. The frequency elevation is a response to mechanical stimulation and is characteristic of all of the pulse fish (Bullock, 1969).

The position of a solitary individual hiding under an undercut bank, deep inside logs, or among large piles of collected debris in the stream, could be approximated even though it was impossible to probe with the electrodes close to the fish. This was done by slowly scanning past the general location from which the signal was coming and determining the point at which the signal becomes the strongest with the same electrode orientation. The distance under the bank could not be determined by this method.

Spatial localization of an individual which is close to other individuals was more difficult. However, the task was simplified by reducing the separation of the electrodes and thereby the overall gain of the amplifier and very carefully probing the region of interest. Since neighboring fish in a cluster usually differed slightly in the frequency of their discharge, it was possible to orient with respect to one discharge at a time and thereby position the individuals in a cluster. It was impossible, however, to determine the locations of individuals in a cluster if their numbers were more than 4 or 5. If two fish in close proximity were discharging with exactly the same frequency, it is conceivable that they would not have been detected by this method. This situation would not occur in those species that show a Jamming Avoidance Response (Bullock, 1969) such as Eigenmannia and Apteronotus.

It was often difficult to determine how many individuals were present in large clusters of fish. This was particularly true for the pulse fish where the discharge frequency of each individual is approximately the same. Nevertheless, an attempt was made to estimate the number of individuals occurring in clusters by very careful probing with the electrodes with the gain of the fish detector reduced and by probing first one individual and then another while listening for slight increases in the frequency. To provide a check on this method, I caught all of the members of a cluster several times for an accurate count of their number. The result of this check indicated that the fish detector gave moderately accurate results if the numbers of individuals were less than 4 in 0.1 m^2 but that if the numbers were greater than 4, my estimates tended to be too low.

Estimates of the number in a cluster of a species producing a tone discharge, such as Eigenmannia, where individual fish have distinctive discharge frequencies was far more satisfactory. By very careful probing over an area with the electrodes, I was able to count each new frequency as I heard it and in this way estimate the number of individuals. This method however also broke down with very large clusters. Since clusters

of Eigenmannia of 20 to 40 individuals are not uncommon, this became a major problem.

In areas where the density of fish was relatively low, I feel that my estimates are an accurate measure of the population level. Under crowded conditions, however, I did not feel confident that I could estimate the population accurately. Some other method should be used under these conditions.

There was no indication that the process of localizing an individual was in any way disturbing to the fish. If the electrodes were kept from touching the substrate near the fish, the discharge frequency of a pulse fish continued in a regular manner. A fish was never seen to change its location as a result of the localization procedure. Very rarely, an individual seemed to respond to the presence of the metal electrodes by turning its electric discharge off. This occurred with one individual of Gymnotus carapo in the Arima River of Trinidad, and one individual of Gymnorhamphichthys hypostomus from Ikuwali Creek in the Rupununi. On both occasions, the fish stopped discharging as the electrode was moved to within 20 cm of their hiding place. I thought that perhaps the fish had sensed the copper wires of the electrode and had responded to this novel stimulus by turning its discharge off. I therefore tested the response of the fish to the presence of the blade of my cutlass. In both cases the discharge ceased for 20 to 30 seconds when the blade was brought to within 50 cm of the fish. This situation was the exception, however. Most individuals did not respond to the presence of the electrodes.

Similarly there was no evidence that my presence in the water affected the fish. When I carefully approached a pulse fish during the night or the day by wading in the creek I detected no change in the discharge frequency. When making a census of the creek or when following fish in the stream at night, I always wore rubber boots in the water. This minimized the electrical spread potentials from my feet and legs which might have been disturbing to the fish.

F. Identification of the Species

The preserved specimens of gymnotids collected during this study

were identified tentatively by consulting various taxonomic works on the fishes of South America. Ellis's (1913) and Eigenmann and Ward's (1905) reviews of the gymnotids provided an introduction to the group, summarizing the previous work on these fish. Schultz (1949) has described the gymnotids from Venezuela, and Fowler (1951) has described the fish from Brazil. Several works on the ichthyology of Surinam have helped in the identification of some of the species found on the Rupununi (Hoedman, 1962a, 1962b; Nijssen and Isbrücker, 1968; Boeseman, 1952). In Trinidad the taxonomic works of Price (1955) and Boeseman (1960) were helpful in identifying the species present on the island.

There seems to be general agreement among taxonomists that the taxonomy of gymnotid fish is in serious need of revision. There are many difficulties in working with this group. Many characters that have been used to classify the species are unreliable. It is possible that the species which I have tentatively called Gymnorhamphichthys hypostomus is actually Urumarā rondoni (Miranda Ribeiro, 1920) but the descriptions of the two species are not sufficient to make the decision (see Curra and Miranda Ribeiro, 1961). As another example, the species which I have identified as Hypopygus lepturus, seems to bear close resemblance to the genus Steatogenes. Hoedeman (1962) decided to place this species in a separate genus because it did not have sub-mental electric organs, the character that defines this genus (Ellis, 1913). A more recent examination of Hypopygus however, has revealed the presence of accessory electric organs in the pre-opercular region (Nijssen, personal communication).

I have compared my specimens to the collection in the American Museum of Natural History, the Museum of Comparative Zoology at Harvard University, the British Museum (Natural History) and the Zoologisch Museum of the University of Amsterdam. One specimen, tentatively put in the genus, Hypopomus, has not been identified and must await further work.

Table I lists the species of fish from the sub-order Gymnotoidei

TABLE I

Members of the sub-order Gymnotoidei (Greenwood, et. al., 1966) observed during the study.

Location	Family	Species
Trinidad, W. I.	Gymnotidae	<u>Gymnotus carapo</u> (Linnaeus, 1758)
Rupununi District, Guyana	Gymnotidae	<u>Gymnotus carapo</u> (Linnaeus, 1758) * <u>Gymnotus anguillaris</u> (Hoedeman, 1962)
	Electrophoridae	<u>Electrophorus electricus</u> (Linnaeus, 1766)
	**Apteronotidae	** <u>Apteronotus albifrons</u> (Linnaeus, 1766) * <u>Sternarchorhamphus macrostomus</u> (Günther, 1870)
	Rhamphichthyidae	+ <u>Hypopogus lepturus</u> (Hoedeman, 1962) <u>Hypopomus brevirostris</u> (Steindachner, 1868) <u>Hypopomus artedi</u> (Kaup, 1856) * <u>Hypopomus</u> sp. no. 3 <u>Eigenmannia virescens</u> (Valenciennes, 1847) <u>Sternopygus macrurus</u> (Bloch and Schneider, 1801) * <u>Rhamphichthys rostratus</u> (Linnaeus, 1766) # <u>Gymnorhamphichthys hypostomus</u> (Ellis, 1912)

* indicates species not previously reported from the Rupununi District
+ collected in the Rupununi (Lowe-McConnell, 1964) but identified as
Steatogenes elegans.

possibly another species: Urumara rondoni (Miranda Ribeiro, 1920)

** synonyms of Sternarchidae and Sternarchus

(Greenwood et. al., 1966) that I observed during my study. In Trinidad, there was one species of gymnotid, Gymnotus carapo. In the Rupununi District of Guyana, I encountered 13 species, four of which had not been previously reported from that District.

G. Identification of the Species Using Electrical Characteristics

During the early phases of the study, I became familiar with the electric discharge of all of the species in the Rupununi as they sound on my fish detectors. Each novel discharge type was investigated: tape recorded and if possible, caught in a net and saved as a specimen. With some experience, the discharge characteristics of most species was learned. The following key is an approximation of the technique which I used in the field for the identification of the species from their discharge characteristics. One species that Lissmann and Lowe-McConnell (personal communication) found in the region around Karanambo in 1958 which is tentatively identified as Porotergus gymnotus (Ellis) is left out of this key because I did not see this species during my study.

Key to the identification of the species of gymnotid fish from the Rupununi District of Guyana based on the audible characteristics of the electric discharge:

- a. Discharge frequency constant; discharge with tonal quality.
 - b. Discharge frequency low (fundamental frequency 50 to 200 Hz, or fourth below middle C or lower on musical scale)
 -Sternopygus macrurus
 - bb. Discharge frequency in mid range (fundamental frequency 250 to 650 Hz or middle C to E above middle C on musical scale)
 -Eigenmannia virescens
 - bbb. Discharge frequency in high range (fundamental frequency 650 to 1300 Hz or G above high C or higher on musical scale)
 - c. Discharge at higher end of range (800 to 1300 Hz)
 -1) Apteronotus albifrons
 - or2) Sternarchorhamphus macrostomus

cc. Discharge at lower end of range (650 to 900 Hz)

.....1) Sternarchorhamphus
macrostomus

or2) Apteronotus albrifrons

aa. Discharge frequency variable; discharge with pulse-like quality.

d. Discharge frequency very low (1 pulse per second or less to 15 pulses per second).

e. Discharge of undisturbed fish in daytime highly irregular; occasional short bursts of pulses of high intensity when disturbed. Average frequency of undisturbed fish 2 to 3 per second

.....Electrophorus electricus

ee. Discharge of undisturbed fish in daytime, stable; frequency: 3 to 6 per second

.....Hypopomus artedi

eee. Discharge of undisturbed fish in daytime, stable; frequency: 7 to 13 per second

.....Gymnorhamphichthys hypostomus

dd. Frequency in a mid range from 20 pulses per second to 60 pulses per second.

f. Lower part of range (20 to 40 Hz) while at rest during the day; when disturbed by gentle probing with stick fish gives a slight elevation in frequency

.....Gymnotus anguillaris

orHypopomus brevirostris

orHypopygus lepturus

ff. Discharge frequency in higher part of range (40 to 60 Hz); when disturbed by gentle probing, fish gives large increases in frequency

.....Gymnotus carapo

ddd. Frequency of discharge in a high range from 70 to 90 pulses per second.

g. Day time observation, fish at rest

.....Rhamphichthys rostratus

gg. Night time observation, fish active

.....Gymnorhamphichthys hypostomus

orRhamphichthys rostratus

aaa. Discharge frequency variable; discharge with a tone like quality, frequency 80 to 100 Hz. Usually from very small individuals

.....Hypopomus sp. no. 3

This key illustrates several ambiguities in the discharge characteristics of several of the species found in the Rupununi District. The fish with pulse-quality discharges proved the most difficult to distinguish, particularly in the mid range of frequencies between 20 and 60 pulses per second. The problem of ambiguity within one habitat on the Rupununi was lessened, since not all species occur within a single habitat. Sternopygus, Eigenmannia and Electrophorus were easily identified under all circumstances.

H. Water Properties

The conductivity of the water was measured with a 1 kHz wheatstone bridge connected across a platinum-coated electrode conductivity cell. The cell constant, K, was 0.1 cm^{-1} . The potential across the bridge was amplified and the null point was determined by listening to the 1 kHz tone on a small earphone. Conductivity measurements were accurate to within 1% of full scale.

The oxygen content of the water was determined by collecting water in an immersible water collecting bottle and measuring the dissolved oxygen with the Hach Chemical Co. OX-2-P dissolved oxygen test kit. This kit uses the Alsterberg modification of the standard Winkler method for dissolved oxygen determination (Alsterberg, 1925).

Other measures of the chemical properties of the water were made with the Hach Model Al-36-10R Water test kit. These tests included:

free acidity, total acidity, alkalinity, total hardness, carbon dioxide, and pH. However, since this test kit was only available for several days in 1971 only a limited sample have all these properties measured.

I. Analysis of Electric Signals

When observing the behavior of electric fish in groups, one is faced with the problem of identifying the individual that produces the electric signal detected with the amplifier. Black-Cleworth (1970) has solved this problem for Gymnotus carapo for situations involving two fish, by measuring the amplitude of the discharge of both fish. The amplitude of the discharge must be measured regardless of the orientation of the fish and she has done this by summing the squared potential from three perpendicular electrode pairs in a large tank.

This method requires considerable electronic equipment, a serious handicap to field studies. Another drawback to Black-Cleworth's method is that only fish that differ in size may be effectively separated by their amplitudes, and in addition, many errors can result due to overlap of pulses.

Another method, employed by Larimer and MacDonald (1968), uses a sound spectrograph to analyze recorded signals. This method has proved to be far more useful for the analysis of electrical signals from more than one fish. Some species of fish produce tone-like discharges that appear as narrow bands on the sound spectrograph. Individuals may be distinguished by slight differences in the fundamental frequency of their discharge. I relied heavily on sound spectrographic analysis of the discharges of Eigenmannia virescens and Sternopygus macrurus. I also used it for the analysis of other species that produce pulse discharges, although there was occasional difficulty in identifying the individual that was producing the discharge.

Tape recorded electrical signals were analyzed with the Kay Electric Sound Spectrograph model 7029-A or with the Federal Scientific UA-7B Ubiquitous Spectrum Analyzer. Since the Federal Scientific spectrum analyzer has only rarely been used for biological research, and because

it has the advantage over the Kay Electric spectrum analyzer in that it operates in "real time", I will describe its operation in some detail.*

The UA-7B analyzer produces a Fourier analysis in the audio range of frequencies once every 50 msec. This Fourier analysis is made up of 500 synthesized filters or filter points spaced linearly across the spectrum. If the selected frequency range is 10,000 Hz, each of the 500 filter points differ by 20 Hz. The filter points act as narrow band filters causing an attenuation of the signal at frequencies differing from the center frequency of the filter point. The frequency difference between adjacent filter points is called β . In the model UA-7B spectrum analyzer, the signal is attenuated by 20 db at a frequency which is $2.3 \times \beta$ above or below the center frequency of a filter point. Similarly, a 40 db decrement is achieved at $5.2 \times \beta$.

Various settings on the analyzer permit one to change the effective bandwidth of the analysis in order to increase the temporal resolution. Thus, a 250 filter point analysis can be performed every 25 msec or a 125 filter point analysis every 12.5 msec etc. The use of this equipment as a pitch extractor is discussed by Weiss, Vogel, and Harris (1966).

The amplitude of the Fourier coefficient of each component frequency in the spectrum is converted linearly into the length of a horizontal line segment which is displayed on the screen of a Tektronix 502 oscilloscope. The line segments corresponding to all of the filter points are arranged end to end in a row along the horizontal axis of the oscilloscope screen to produce a single line ordered from the low frequency to the high frequency. If the Fourier coefficient of a component frequency is small, the line segment is reduced to a tiny dot on the screen, if it is large the line segment is long and will connect two adjacent filter points. Thus, the resulting intensity of any one point along this line is proportional to the Fourier coefficient at that frequency. The line is then photographed with

*further information can be obtained from Federal Scientific Corporation
615 West 131st Street, New York, New York 10027.

continuously moving 35 mm film with a Grass Kymnograph camera to produce a display of frequency vs. time. The amplitude of each frequency component is represented as the darkness of the film. The display produced by this method does not differ significantly from the display produced by the Kay Electric spectrograph (Fig. 3) and it was therefore used extensively in the analysis of tape recorded signals because of the considerable advantage gained from the "real time" operation.

In certain situations, electric fish produce discharges that show only very slight variations in frequency. One social signal consisted of a frequency change of as little as 2% of the steady state frequency. To measure these small variations, the signal was heterodyned to a lower frequency prior to analysis on the spectrum analyzer. The signal was heterodyned by "multiplying" the signal by a constant frequency with a Philbrick SPMI multiplier-divider.

The wow and flutter of the Uher tape recorder was reported to be less than 0.15%, thus, placing a limit to the accuracy of frequency determinations. However, in some cases a 500 Hz sine wave was recorded on Channel 2 while the fish were recorded on Channel 1. This permitted an accurate time reference that allowed a considerable increase of accuracy in frequency measurement. Normally, when two fish were being recorded on the same channel, wow and flutter of the tape recorder could be eliminated by looking at the beat frequency between the two fish. The beat frequency between two fish often appeared as a discrete frequency on the spectrogram when the signal was overloading the input circuit. Overloading the input caused clipping of the waveform and introduced spurious frequencies corresponding to the sums and the differences between the frequencies of the two fish. Since it was useful in this analysis to consider the beat frequency between two fish, the input to the spectrum analyzer was routinely overloaded.

J. Other electrical properties of the electric discharge

The waveform of the electric discharge was investigated with the Sony-Tektronix 323 battery-operated oscilloscope. The input to the oscilloscope was direct from the electrodes and was A.C. coupled. The

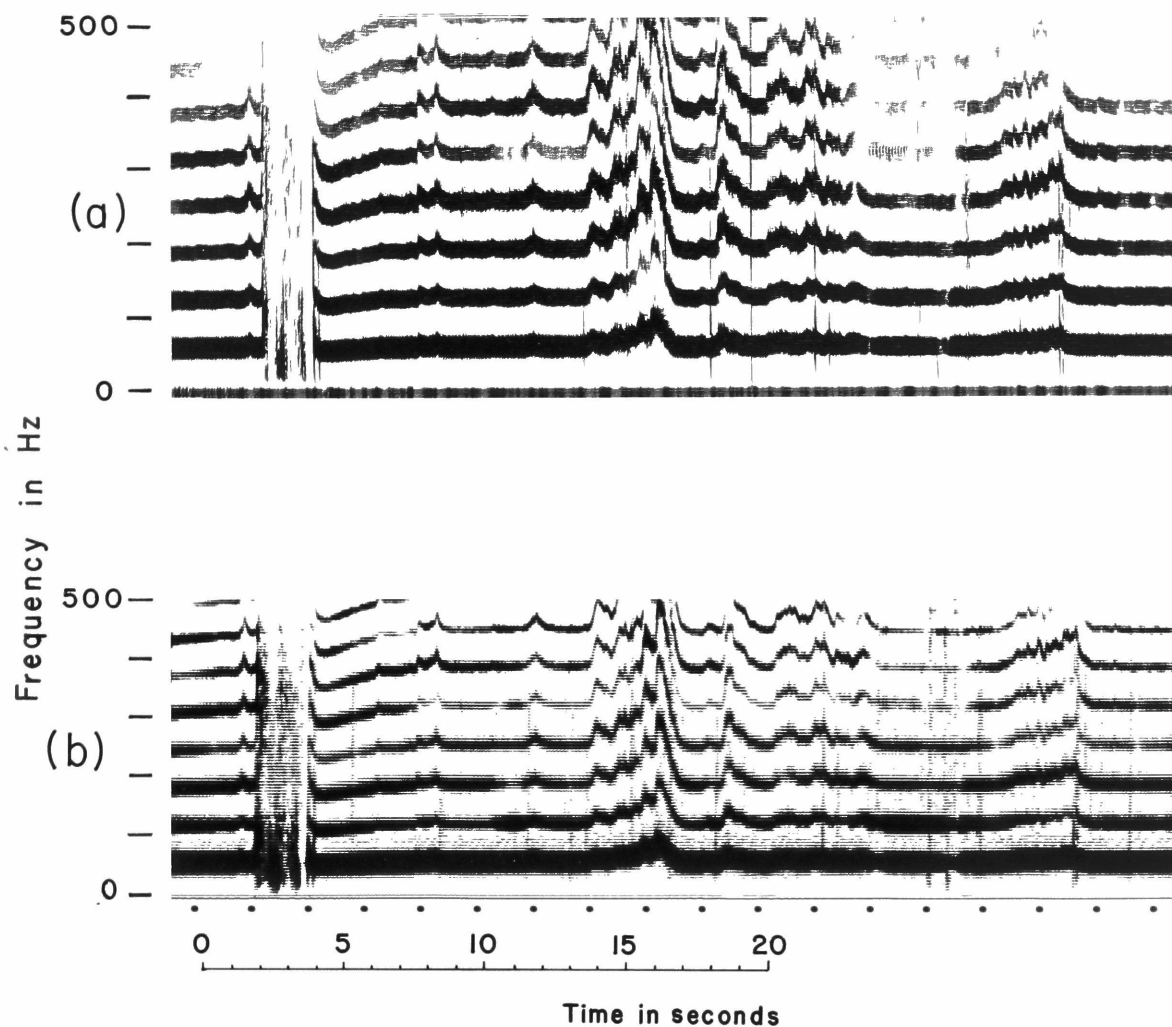


Fig. 3. Sound spectrogram display of the electric discharge of *Sternopygus macrurus* comparing (a) the display produced by the Kay Electric Sound Spectrograph model 7029-A; to (b) the display produced by the Federal Scientific Ubiquitous Spectrum Analyzer model UA-7B.

(a). Frequency range, 5-500 Hz; Bandwidth, 19.0 Hz.

(b). Analysis range, 5 kHz; display width, 1/4; Analysis speed, double recording speed; effective bandwidth (3 db), 7.5 Hz.

discharge waveform displayed on the oscilloscope screen was photographed with a 35 mm camera.

Long term records were occasionally made of the discharge frequency of an individual fish in its hiding place in the stream or of a captive fish in a tank. The discharge of the fish was detected with the fish detector and a standard-sized pulse was made using each fish discharge to trigger a pulse of fixed amplitude and duration. These pulses were then integrated with an R-C circuit of several seconds time constant, and recorded on a portable Rustrak microammeter.

III. ECOLOGY OF GYMNOTIDS FROM THE RUPUNUNI DISTRICT, GUYANA

A. Geography of the Rupununi

The Rio Branco-Rupununi lowlands form a belt of savanna surrounded on all sides by forested uplands. The savanna region, roughly 55,000 square km in area, extends from the Pakaraima Mountains in the north to a gradually rising surface 300 km south of Boa Vista in Brazil. The lowland area has an elevation of 100 to 160 meters above sea level and the peripheral mountain ranges vary in height from 400 to 1000 meters. The savanna extends into the south-western corner of Guyana where it is termed the Rupununi Savanna, or merely the Rupununi.

The Rupununi is divided into two parts, the North Savanna and the South Savanna, by the sharply rising Kanuku Mountains which rise from the lowlands to rounded peaks of over 1000 meters elevation. The northern slopes of the Kanuku Mountains are forested whereas the southern slopes are grassy. It was on the northern side of the Kanuku Mountains, near the border between forest and savanna that most of this work was done.

Water drains from the Rupununi in two main directions. Water from the western part, both north and south of the Kanuku Mountains as far north as the Pakaraima Mountains, flows into the Takutu River and its tributary, the Ireng River. These rivers form the border between Brazil and Guyana. They join the Rio Branco in Brazil which flows south-west until it meets up with the Rio Negro and eventually joins the Amazon River at Manaus. Water from the eastern part of the Rupununi flows toward the Rupununi River which meets the Essequibo River in the north to empty into the Atlantic Ocean on the coast of Guyana. The Rupununi is thus divided into two major drainage systems, the Amazon and the Essequibo.

These two river systems are occasionally connected during very wet years in the vast basin called Lake Amuku which makes contact with the Pirara River, part of the Ireng-Rio Branco drainage, as well as the Bunoni River, part of the Rupununi-Essequibo drainage (Lowe-McConnell, 1964). The Takutu River has not always drained into the Rio Branco.

The Takutu and the Ireng once flowed out of the Rupununi basin to the Proto-Berbice River which emptied into the Atlantic several hundred miles south-east of the present Essequibo River mouth (Eden, 1964; McConnell, 1962). The capture of the Takutu River by the Rio Branco is thought to have occurred since the late Tertiary (McConnell, 1959).

B. Climate of the Rupununi

The seasonal cycle of the Rupununi is dominated by one annual rainy season of four months duration. The single rainy season contrasts with the double rainy season of Georgetown, Guyana, of Manaus, Brazil and of the rest of the forested region surrounding the Rio Branco-Rupununi Basin. Trinidad has an extended rainy season with two peaks of rainfall. A double rainy season is more typical of this latitude according to the scheme of tropical rainfall proposed by Richards (1964). The mean annual rainfall from St. Ignatius, Rupununi is 1,621 mm (Eden, 1964) and 83% of this rain falls between the months of April and August. The microclimate of the Rio Branco-Rupununi Savanna may be a contributing factor to the single rainy season but this phenomenon is not well understood (Eden, 1964).

The weekly rainfall records collected during the study periods of 1970 and 1971 from Moco-moco Settlement are shown in Fig. 4. The total rainfall that I observed in 1970 between March 23 and August 21, was 179.8 cm. In 1971 I recorded a total accumulation of 84.4 cm between April 20 and June 30. Although considerable rain fell during March and early April, 1970, the main rains did not begin until May as they did in 1971. The total accumulation during five and one-half months in 1970 exceeded the average annual figure for St. Ignatius given by Eden (1964). This may be due to the fact that Moco-moco Settlement is at the base of the Kanuku Mountains whereas St. Ignatius is at least 15 km from the mountains. The air in the mountains, being cooler, may cause considerably more condensation than the savanna.

The period between September and March on the Rupununi are a period of virtual drought only interrupted in November or December with a brief period of rainfall, known locally as the "Cashew rains" which

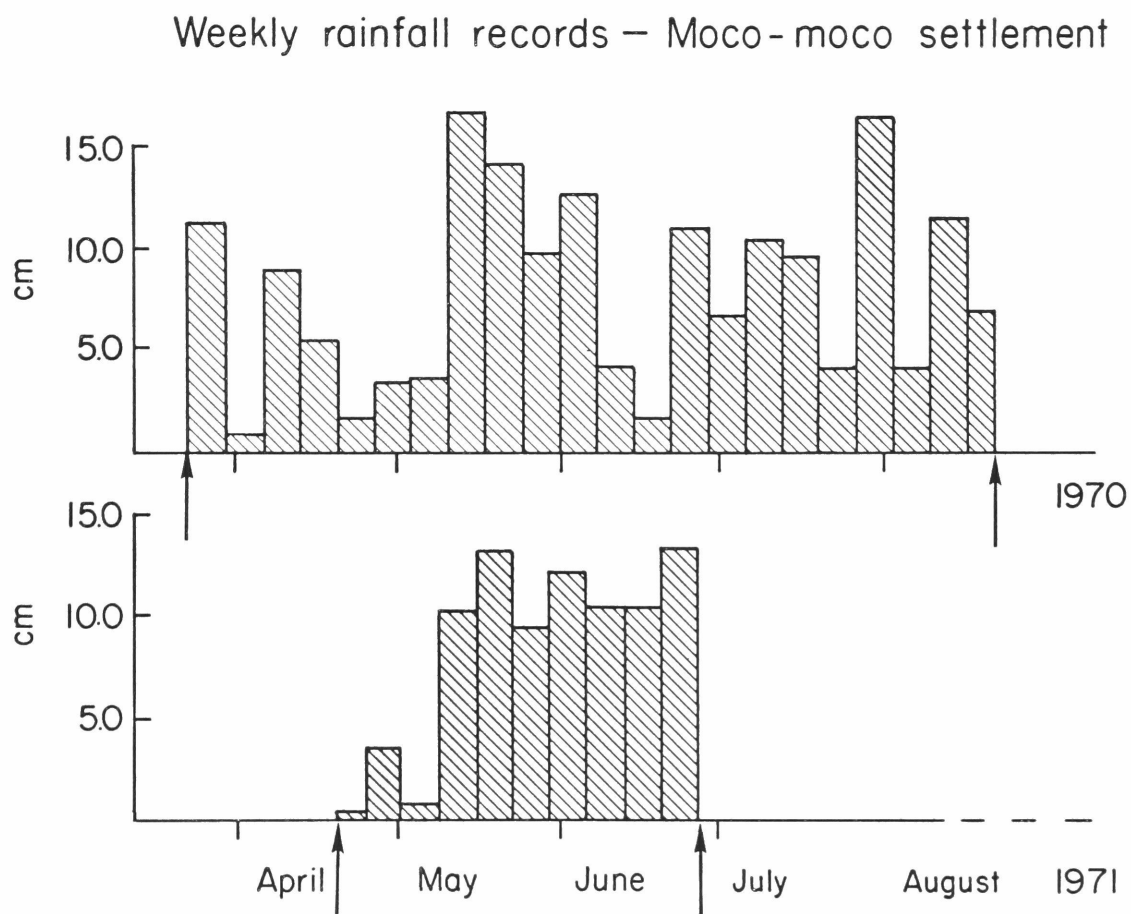


Fig. 4. Weekly rainfall records collected during the study periods in 1970 and 1971. The rain gauge was located near camp in Moco-moco settlement. Arrows indicate the beginning and end dates for which rainfall data were collected.

contribute less than 10 cm to the total annual rainfall. The lack of rainfall during the drought causes the water level in the rivers and their tributaries to fall. The savanna ponds dry up, and many creeks stop flowing, leaving only a series of isolated pools. The savanna turns into a dry, barren desert. In March, 1970 many small creeks originating in the northern part of the Kanuku Mountains between Pirara and Dadanawa were surveyed. All of the small creeks that flow into the Takutu River had nearly completely dried up when checked on March 3 to March 7, 1970 with the exception of Moco-moco Creek and the Saurab Creek. These two creeks continued to flow very slowly. Some of the creeks such as Manari Creek, and Sauariwau Creek were only a series of isolated pools of water about 1 meter deep. The Takutu River was only 10 to 20 cm deep in places on March 17, 1970, and the water was flowing very slowly. The Rupununi River, checked on March 7, 1970 and again on March 29, 1970 consisted of isolated pools, without any above-surface flow.

The main savanna was completely dry in March and early April, 1970 and in April, 1971 except for a few widely separated ponds usually found close to the banks of the main rivers and creeks. Many ponds on the savanna persisted throughout the dry season and the fish that remained in the ponds became more crowded as the dry season progressed.

The rainy season begins with brief, widely-spaced rains in April. Heavy rains follow, occurring regularly throughout May, June, July, and August. My studies began in both years well before the main rains started. In 1970, several heavy rainfalls in April caused the level of Moco-moco Creek to rise and in the lower reaches, to overflow its banks. The flooded areas then dried up later in April when there was less rain. This false start to the rainy season had a significant effect upon the mortality of the fish population (see page 40).

Water levels in the creeks are of major importance to fish ecology. I measured the depth of the creek at a random time during the day for two locations in Moco-moco Creek in 1971. The results are shown in Fig. 5. These data show that water remained at a low level early in April with only minor fluctuations. The response to a heavy rainfall

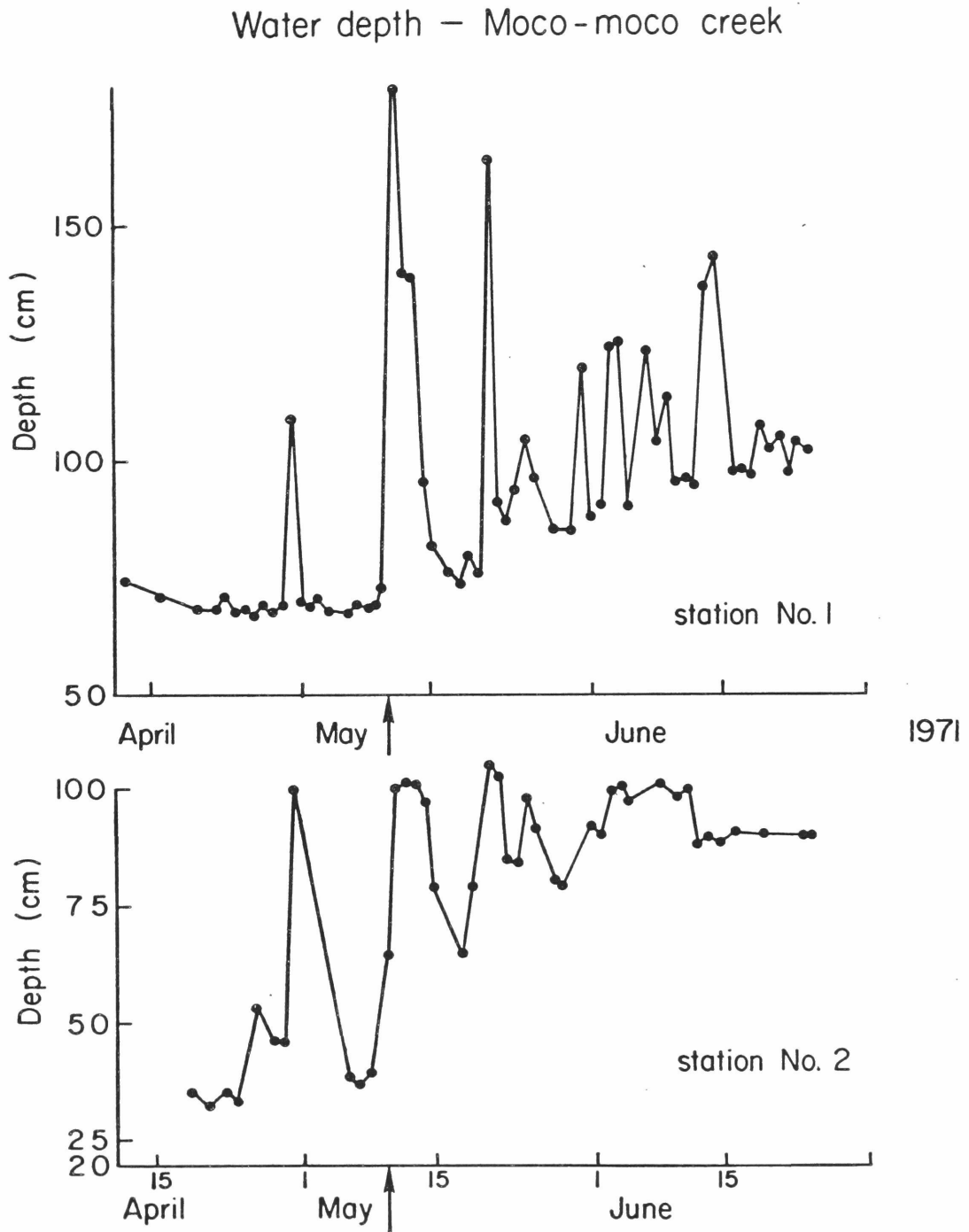


Fig. 5. Water depth measured in two locations in Moco-moco Creek in 1971. Station No. 1 was located near the camp. Station No. 2 was located at the entrance to Kumaka Swamp. An arrow indicates the beginning of the rainy season, defined arbitrarily as the day on which Kumaka Swamp flooded and stayed flooded for the remainder of the rainy season.

during this period was a sudden increase in depth followed by a rapid decrease back to the original level. Later in the rainy season the average level of the creek increased to a higher level and remained there. The depth records were taken at two locations in Moco-moco Creek. Station 1 was near the camp, at the base of the mountains. Here the creek was flowing rapidly over rocks and gravel through relatively steep banks. At station 2, at the entrance of Kumaka Swamp, 4 km from the camp, the creek was flowing slowly over relatively flat terrain with sandy bottom in a meandering pattern. There was extensive flooding of the land near the depth gauge at station 2. There are slight differences in the data recorded from the two stations that can be understood from these differences in position.

During the rainy season which began on May 10, 1971 the variance in water depth at station 2 was much less than the variance in water depth at station 1 ($s^2 = 520.1 \text{ cm}^2$ at station 1, $N = 45$; $s^2 = 115.3$ at station 2, $N = 38$). In 1970, the variance in the depth at station 1 between July 21 and August 22 was 5860 cm^2 , $N = 24$. This effect is due to the fact that the water flowing in the creek at station 1 is confined to a narrow channel with steep sides and there is little flooding, whereas the water at station 2 floods the banks and spreads out over large areas, thus buffering the effect of a large increase in the volume of water. As a result, in the rainy season the low lying regions of the creek provide an environment that fluctuates less than the creek at the base of the mountains.

C. The effect of climate on the ecology of gymnotids

The reproductive activities of the gymnotids and many other fish in the Rupununi are closely regulated by the distinctly seasonal pattern of drought and flood. The annual cycle of activity of the gymnotids can be divided into three phases: the non-reproductive phase that occurs during the dry seasons; the reproductive phase that is triggered by the onset of the rainy season and continues throughout the first half of the rainy season; and the post-reproductive phase, that occupies the latter half of the rainy season. During the non-reproductive season, the fish live in

pools in the creeks and in drying-up ponds on the savanna. As the dry season progresses the fish become more and more concentrated. Food seems relatively limited during this period and there is probably little growth in the fish. Toward the end of the dry season the testes of the males become larger and the eggs of the females turn yellow and begin to enlarge. The reproductive phase is triggered by the onset of the rainy season for most fish. The beginning of the rains, with the resultant flooding increases the food and space available to fish. There is a sudden migration into flooded areas away from the turbulent flows of the main creek for the purpose of breeding. Reproductive behavior continues throughout the beginning of the rainy season, but by the middle of the rainy season most of the fish have already bred. After the fish have bred, the gonads shrink in size again and the fish concentrate their activities on feeding, to put on large stores of fat that will carry them through the dry season. As the rainy season comes to an end, there is another migration back to the main creeks and rivers where the fish remain throughout the succeeding dry season.

D. Gymnotid Ecology in Moco-moco Creek

Study areas: To gather useful information on population levels, species composition and species diversity of gymnotids in Moco-moco Creek, two study areas were set up in the higher reaches of the creek, near the camp, and were observed periodically throughout the study period in 1970. The population levels in these two study areas dramatically reflect the seasonal response of the gymnotids to rainfall.

The two study areas A (35 m long) and B (41 m long), were located near the base of the mountains (Fig. 1). The water flowed swiftly over rocks, coarse gravel, and sand; the banks were high, steep, and in places deeply undercut; trees line the banks, and roots and dead trees extended into the water providing hiding places for the fish. Since the two areas are relatively close to each other and their physical characteristics are similar, the results of censusing one area can be compared to the other. Each study area was censused by systematically scanning the area with the electrodes of the fish detector (AA-100) while listening

for fish. The location of each fish was marked with brightly colored surveyor's tape attached to some object on the bank and note was taken of the nature of the place where the fish was found hiding.

Spatial localization of fish was relatively accurate in these censuses because the fish were well spaced out and the habitat was open. Some error was encountered in the estimation of population levels of certain species. For example, Hypopomus brevirostris, a species that usually is found in small clusters, was sometimes difficult to estimate. It was easy to distinguish between single individuals and groups because one individual produces a series of pulses that are relatively regular in their frequency whereas two fish produce pulses that go in and out of phase with each other, sometimes overlapping completely and sometimes not overlapping at all. The uncertainty came when trying to tell the difference between two and more individuals in a cluster. Since three individuals was the usual upper limit of small groups of Hypopomus caught outside the study area, I recorded a range value of 2 to 3 in these cases of uncertainty. Sternopygus also gave some difficulty when they were found in clusters.

The total population level for each species on each census is shown in Table IIa and Table IIb. Each row of the table lists the total number of individuals of the species, either an exact figure where there was no ambiguity, or else a range value indicating the lowest and the highest possible extremes of the total for that species. At the bottom of the table are shown the number of each species present in each study area averaged for all 18 censuses. The average value was obtained by dividing the totals for the low estimate and the totals for the high estimate by the number of days sampled. If the midpoint of the range of these values is taken as the best estimate, I obtain the percentage composition of the study areas averaged over all days censused. This figure is on the last line of the table.

Hypopomus brevirostris and Sternopygus macrurus were the most abundant species in the study areas; the average numbers of individuals in the two areas were approximately the same. S. macrurus comprised from 30 to 31% of the gymnotid population whereas Eigenmannia virescens was

TABLE IIa

Numbers of gymnotids in study area A determined in 18 censuses in 1970.
 Area: 181 square meters, Length: 35 meters. "H" is the species diversity
 of the study area.

STUDY AREA A

	<u>Hypopomus</u> <u>brevirostris</u>	<u>Gymnotus</u> <u>carapo</u>	<u>Gymnorhamphichthys</u> <u>hypostomus</u>	<u>Sternopygus</u> <u>macrurus</u>	<u>Eigenmannia</u> <u>virescens</u>	<u>Apteronotus</u> <u>albifrons</u>	TOTAL	H
March 16	23-28	1	3	13	5-7	0	45-52	1.555
March 17	29-30	1	3	16	3	0	52-53	1.411
March 19	25-27	1	3	16	2-4	0	47-51	1.444
March 21	27-33	2	2	23-24	2-4	0	55-64	1.424
March 24	29-37	0	1	18-19	2-3	0	50-60	1.211
March 27	28-38	1	3	19-23	1	0	52-66	1.279
March 30	17-20	1	4	12	3-4	0	37-41	1.675
April 1	28-37	0	1	9	1	0	39-48	0.912
April 7	27-35	1	4	6-7	1	0	39-48	1.130
April 10	15-18	0	1	10-11	0	0	26-30	1.139
April 11	19-23	0	1	8-10	0	0	28-34	0.927
April 18	13-18	1	1	5-6	1	0	21-27	1.328
May 20	0	1	0	5	0	1	7	0.770
May 27	0	4	0	4	0	1	9	1.033
June 16	1	0	0	4	0	0	5	0.464
July 9	0	4	0	7	0	0	11	0.761
July 23	6-7	4-5	1	3	0	2	16-18	1.804
August 5	17-20	3-4	2	4-5	2-3	3	31-37	1.868
Average number	16.9-20.6	1.3-1.5	1.7	10.0-10.7	1.2-1.7	0.4	31.6-36.7	1.419
Percent of total	55%	4%	5%	30%	4%	1%	100%	

TABLE IIb

Numbers of gymnotids in study area B determined in 18 censuses in 1970.
Area: 178 square meters, Length: 41 meters. "H" is the species diversity
of the study area.

STUDY AREA B

	<u>Hypopomus</u> <u>brevirostris</u>	<u>Gymnotus</u> <u>carapo</u>	<u>Gymnorhamphichthys</u> <u>hypostomus</u>	<u>Sternopygus</u> <u>macrurus</u>	<u>Eigenmannia</u> <u>virescens</u>	<u>Apteronotus</u> <u>albifrons</u>	TOTAL	H
March 16	17-19	0	6	22-23	1	1	47-50	1.480
March 17	20-25	1	6	16-17	0	4	47-53	1.719
March 19	22-27	0	5	11	9	4	51-56	1.831
March 21	19-24	1	4	25-29	1	4	54-63	1.596
March 24	19-24	0	6	17-19	0	4	46-53	1.561
March 27	24-36	1	5	12-16	3-4	3	48-65	1.652
March 30	12-16	0	5	13	1	2	33-37	1.604
April 1	16-21	0	3	11	1	2	33-38	1.474
April 7	18-25	0	3	13-15	3-4	1	38-48	1.590
April 10	7	0	1	7-8	2-3	1	18-20	1.640
April 11	10-12	1	1	7-8	1-2	1	21-25	1.605
April 18	10-11	1	0	4-5	2-3	1	18-21	1.546
May 20	1	0	0	0	0	3	4	0.500
May 27	0	0	0	4	0	4	8	0.766
June 16	0	0	0	1	0	3	4	0.499
July 9	1	0	0	0	2	3	6	0.985
July 23	4	1	0	0	0	3	8	1.016
August 6	27-28	2	6	0	0	2	39-40	1.236
Average number	12.6-15.6	0.4	3.4	9.2-10.1	1.4-1.7	2.5	29.0-33.3	1.611
Percent of totals	45%	1%	11%	31%	5%	8%	100%	

only 4 to 5%. The species diversity of the two study areas was calculated for each census to indicate the degree of evenness of the species composition of the study areas. I used the formula of Brillouin (1956) as a measure of species diversity. This formula is commonly used when data derive from a sample of the total population. The formula for diversity:

$$H = \frac{1}{N} (\log_2 N! - \sum_{i=1}^s \log_2 n_i!)$$

was calculated using the technique of Lloyd et. al. (1968). N is the total number of individuals, n_i is the number of individuals of each species, s is the number of species in the sample and H is the mean diversity in bits per individual in the sample. In calculating the diversity of the species in the two study areas, I selected the nearest integer to the mid-point of the estimated range of values for each species. The diversity of study area B was slightly higher than study area A, the median value of A was $H = 1.30$ compared to B where $H = 1.56$ (Table IIa,b; Fig. 6).

The most striking feature of the 1970 censuses is the change in the total populations of gymnotids during the wet season. The mean density of gymnotids between March 16 and April 18 (dry season) was 0.25 gymnotids/square meter (s.d. = 0.07, $N = 12$) for study area A and 0.23 gymnotids/square meter (s.d. = 0.08, $N = 12$) for study area B. There was a steady decline in numbers of fish as the wet season began until finally the population reached a low level of 4 to 5 individuals of all species per study area on June 16, 1970. The lowest density recorded was 0.02 to 0.03 gymnotids per square meter, and this occurred during the wet season. The population levels begin to increase again toward the end of the wet season and on the last census the population level had nearly reached the same level as before the rains. The study was discontinued in 1970 before the end of the rainy season.

Fig. 6 shows a plot of the total number of all species present in the two study areas. The decrease in numbers of individuals in the study areas during the wet season was caused by a migration of the fish from

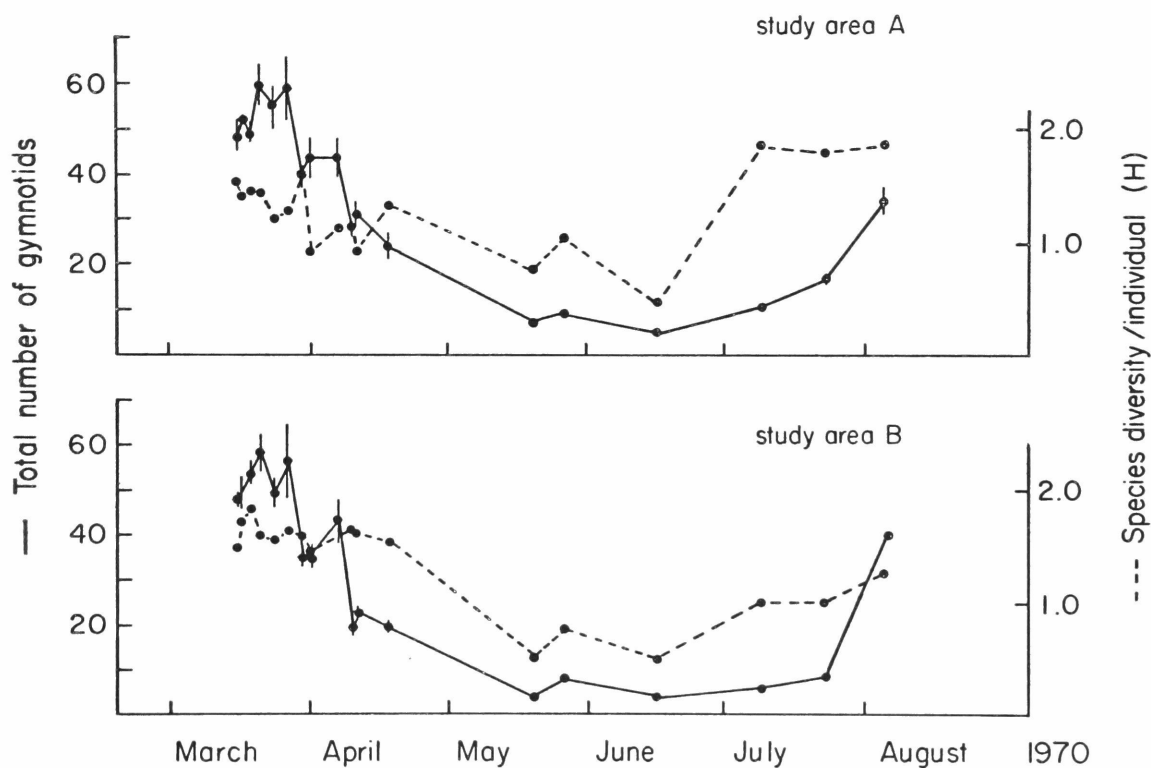


Fig. 6. Population levels and species diversity of two study areas in Moco-moco Creek during the dry season, and wet season in 1970. The total number of gymnotids is plotted as a solid line in each case. The line passes through the mid point of the estimated range of values for each day. The vertical line through each point indicates the range. The species diversity of each study area is calculated for each census and plotted as a dashed line.

these study areas that lie at the base of the mountains, to lower lying areas where the creek floods into Kumaka Swamp. In summary, the gymnotids are found in the higher reaches of Moco-moco Creek during the dry season with an average density of 0.23-0.25 fish per square meter, but once the rainy season has begun and new areas are flooded, the fish migrate to flooded areas.

In 1971 the pattern was repeated: a similar migration down to the lower reaches of the creek took place with the first flood. Evidence for this migration was again seen from the sudden decrease in population levels of gymnotids. In six separate censuses taken prior to May 11, 1971 I obtained an average of 67.5 ($s = 15.3$) individuals of Eigenmannia virescens in a 215 meter stretch of Moco-moco Creek near the camp whereas after the heavy rainfall on May 11 (3.95 cm) on three separate censuses. I obtained an average value of 4.3 ($s = 2.1$). Similarly on May 10, 1971 the positions of 13 Sternopygus macrurus were mapped in a location approximately 30 meters downstream from study area B. When this area was checked on May 14, at the first opportunity following the heavy rainfall and flood, only one of the positions formerly occupied by Sternopygus macrurus was now occupied. Thus in both 1970 and 1971 the majority of individuals of all species left the higher regions of the creek in response to the first sign of flooding and heavy rainfall.

In 1971 I was able to observe the fish as they made their migration into the breeding areas in flooded regions of Kumaka Swamp. The first heavy rain occurred on April 26, 1971. Prior to this date, Kumaka swamp was completely dry. On April 26, however, after a heavy rainfall in the mountains (only 0.4 cm near the camp) the creek rose and the water started to flow into the swamp. Hypopomus brevirostris was very common at the entrance to the swamp immediately after the water began to flow into the swamp. Within 20 minutes, many Hypopomus had penetrated several hundred meters into the swamp. After one hour, many Eigenmannia had also entered the swamp. I did not detect any other species on the first day. On April 27 I found that Hypopomus, Eigenmannia, and Gymnorhamphichthys were common in this area.

After this rain, the water level fell and water stopped flowing into the swamp and the water in the swamp stood in pools, where the fish were trapped. The water rose again on May 11, 1971 and this time it continued to flow into the swamp for the remainder of the rainy season. Five seine hauls across the flow of the water into the swamp on May 11 (6' x 5' x 1.8" mesh), at 1400 hours yielded 2 Sternopygus macrurus, 2 Hypopomus brevirostris, 10 Eigenmannia virescens and 6 Gymnorhamphichthys hypostomus. It was unusual to find any gymnotids moving about during the daytime but the normal activity cycles seem to be upset by the beginning of the rainy season. Possibly the first fish to arrive in the breeding ground have an advantage over others that come later in terms of setting up territories or some other factor, thus making it important to enter the swamp early even at the expense of traveling during the daytime.

The migration into the swamp is triggered by the first rainfall which causes flooding. In some years, early rainfalls that cause flooding are not followed by a continuous rainfall that keeps the level of the swamp up. Thus the initial flooding may dry up. This occurred in 1970 after an early false rainy season in April flooded Kumaka swamp. By April 29, 1970 there were only a few remaining isolated pools of water left in the swamp, and in these pools, I found many individuals of Hypopomus brevirostris and Hypopygus lepturus as well as many other small characins, cichlids and catfishes. The fish trapped in these pools were probably eaten by birds. Bird footprints were especially common around these pools and I observed several herons (Ardeidae) and vultures (Cathartidae) perched in trees around the pools. Thus early migration, although perhaps of advantage to species setting up territories was also hazardous.

Rising water seemed to trigger the migration of gymnotids into newly flooded areas. With each flood during the rainy season, there would be another migration into a new area. I noted that there were many fish concentrated around the entrance to Kumaka Swamp on May 11, 1971 when the water first rose but that the numbers steadily declined as more and more fish entered the swamp. On May 21, 1971 after another heavy rainfall, there was extensive flooding of new areas. During this flooding I observed

an additional migration, in which Eigenmannia virescens and Hypopomus brevirostris were common.

E. The Mode of Reproduction of Gymnotid Fish

There is no information in the literature regarding the modes of reproduction of gymnotid fishes. Breder and Rosen (1966) discuss some anecdotal evidence that suggests that perhaps Gymnotus carapo is a mouth brooder or else brings forth its young alive.

Ellis (1913) mentions a similar common belief among the natives of South America for Electrophorus electricus. Although I was not successful in my attempts to observe the natural sequences of reproductive behavior, I made sufficient observations to conclude that the gymnotids on the Rupununi lay eggs that are fertilized externally. The following evidence is in support of this view:

1) Many gymnotids were dissected, their ovaries and testes were examined, but no embryos were found. Gonadal tissue in all stages of development was examined for nearly all species of gymnotids from the Rupununi. There were cases of ripe gonads for most species, but there was no evidence for internal fertilization or embryonic development in any of the material.

2) The reproductive tract of gymnotids is unsuitable for internal development or fertilization. There are no intromittent organs present on any of the gymnotids although there are small urogenital papillae on many species (Ellis, 1913). With females in ripe condition, gentle pressure caused the eggs to pass easily down the ovarian duct and out the genital pore. Milt passed easily through sperm ducts and out the genital pore to the exterior. Gentle pressure on the abdomen released milt in ripe males.

3) The eggs of gymnotids are well suited for external development. The eggs that are stripped from a ripe female Sternopygus or Apteronotus albifrons are quite sticky. When released under water, they cling to sticks or leaves. The shells of these eggs appear slightly hardened.

In one case, spawning occurred in an aquarium, but it was not witnessed. Eigenmannia males and females were sometimes kept in aquaria for observations of reproductive behavior during the breeding season in 1971. On June 11, 1971, I discovered a total of 72 larvae were hiding between rocks at the bottom. There were two occasions prior to June 11 on which I left a male and a female overnight in the same tank and did not observe them: once on June 3-4 and again on June 8-9. The eggs could have been laid and fertilized on either of these two occasions. June 3-4 is the most likely occasion because the female left overnight at this time had many small eggs and a few large ripe eggs in her ovary when she was examined on June 4.

There were no specialized brood pouches in the mouth or elsewhere in any of the species of gymnotids from the Rupununi. I never saw any cases of larvae in the mouth of adults. This evidence suggests that mouthbrooding does not occur in these species.

F. Nest Structure and Parental Care in Gymnotids

Two nests were seen for Gymnotus carapo, but none were found for any other species. The two nests were discovered in the daytime on July 7, 1969, in a narrow (1 x 400 meter) drainage ditch in the Aripo Savanna in Trinidad. Both nests were depressions or excavated holes 5 to 10 cm deep, 15 cm long, 10 cm wide, in the loose sand at the bottom of the 10 to 20 cm deep ditch. Both were well protected, one by a large log that had fallen across the stream, and the other by a large leaf from the palm, Maurita flexuosa, that had fallen in the water over the nest site. A single adult male was present in each case. In one of the nests the male was lying on its side, its anal fin spread out over the sand at the bottom of the depression. He was covered with a fine layer of sand, and he was not disturbed by the removal of the protective covering. In the depression, and in the surrounding 10 to 20 cm around the depression, there were numerous post-larval Gymnotus all discharging asynchronously. The other nest was less visible, however it was apparent that the male was lying in the depression. Post larval fish were also present at this nest, but they were less concentrated around the depression.

The average length of 4 of the post larval fish from one of these nests was 15 mm. There appeared to be over 100 juvenile fish present in each nest.

G. The Annual Cycle of Reproduction: The Reproductive Phase

The reproductive phase for most gymnotids living in Moco-moco Creek was triggered by the onset of the rains. Sternopygus provides an exception to this general pattern since it is breeding in the creek before the rains. Evidence for seasonal breeding triggered by the beginning of the rains is based on the condition of the gonads of the fish, and on the dates of discoveries of larval and post-larval fish.

In 1971 I captured over 140 Eigenmannia virescens for use in observations in aquaria. Captures made between April 15 and May 10 were in the higher region of Moco-moco Creek, fish captured after May 11 were from Kumaka Swamp. These Eigenmannia were examined after the experiments were completed to determine their sex and gonadal condition. Table III shows the proportion that had large or small gonads. The fish with enlarged gonads included those fish which were either developing IV, gravid, or spawning in the system of classification of maturity stages of Kesteven (1960) as summarized in Bagenal and Braum (1968). Those with small gonads correspond to the virgin, maturing virgin, and developing (III) or spent in the same classification scheme.

It can be seen from Table III that the proportion of the fish with enlarged gonads is small during April in the period before the rains when the fish are still crowded in the stream waiting for the rain to come. In May, the proportion of fish with enlarged gonads has increased markedly. Nearly 75% of the males caught in Kumaka Swamp had enlarged gonads during this period. Then again when the fish were sampled in June, the proportion of fish with enlarged gonads had decreased slightly once more. Many of the fish caught during this month had recently-spent gonads.

Although my observations in 1971 did not continue past June 24, data from 1970 indicated that during the months of July and August there were few fish with enlarged gonads. Nearly all of the specimens examined at

TABLE III

Date (1971)	Sex	Gonads Enlarged	Gonads Small	Total
April 15-28	males	2	4	6
	females	1	5	6
May 3-28	males	25	6	31
	females	20	15	35
June 1-24	males	9	13	22
	females	18	22	40

Reproductive condition of adult Eigenmannia virescens from Moco-moco Creek and surrounding flooded areas (Kumaka Swamp). Entries contain the number in each gonadal condition.

(N = 140).

this time had gonads that were completely spent. Data on gonadal condition before and during the breeding season for other species is less systematic, but isolated observations of gonadal condition indicate a similar pattern in Hypopomus brevirostris, Hypopomus artedi, Hypopygus lepturus and Gymnorhamphichthys hypostomus.

The dates of onset of the breeding seasons can also be estimated from the dates of appearances of larvae and post-larvae of different sizes. Both in 1970 and 1971 I made periodic surveys within Kumaka Swamp to determine the first date for detecting electrical impulses from larval fish. The first larvae were detected on May 29 in 1970 and May 26 in 1971. These larval fish were found in the flooded swamp forest near Moco-moco Creek where many of the adults were breeding. They were buried in leaf litter in the bottom of the stream in very quiet areas near the edge of the flow of water at depths of up to 50 cm. The larvae were so small that they could only be detected at a distance of 2 to 3 cm with the AA-100 fish detector. Possibly these fish were overlooked earlier. Attempts to catch the larvae proved very difficult until a fine-mesh net was used. The first larval fish were caught in 1970 on June 1, several days after they were first detected with the fish detector. One specimen of Hypopomus brevirostris caught on June 1 had a length of 7 mm. Four specimens of Gymnorhamphichthys hypostomus caught on the same day ranged in size from 14 to 22 mm. I also detected but did not catch Eigenmannia virescens larvae on this date. In 1971 I exercised considerable care in probing through the leaf litter in Kumaka Swamp in search of larval fish during the month of May. I wanted to be sure that I did not overlook very small fish. The first larvae were detected on May 26 (Hypopomus brevirostris) and caught on May 28. The median size of these larvae was 7 mm ($N = 7$), and upon investigation I noted that the yolk sacks were near the final stages of absorption.

The larval and post-larval fish were collected at random times throughout the breeding season to determine the approximate rate of growth of the young and to provide an estimate of the time of hatching of the eggs of each species. The sizes of larval and post-larval

gymnotids as well as their date of capture are shown in Fig. 7. A line connects the medians of the samples from the same day. I have included in this figure data from fish collected by two techniques. Using the first technique I systematically searched through the leaf litter on the bottom of the swamp in an effort to localize very small larvae. Once localized I used a very fine-mesh net to capture the fish. With the second technique I made collections of small fish by passing a 75 cm diameter hoop net with 1/8 inch mesh through the water in a thick mat of water plants (Polygonum sp.) in Kumaka Swamp where many of the fish appeared to be breeding. Small fish were brought out into the open water by walking through the plants and deliberately disrupting them so that the fish came out in the open. This method yielded numerous small fish, all of which were collected.

The plot of length vs. date, yields an approximate growth curve for each species. With the exception of Sternopygus macrurus, all of the species appear to have a similar origin (Fig. 7). If growth is assumed to be linear throughout the early phases of development, then the length-date data for each species may be fitted, using the method of least squares, to a straight line. When this is done, data for all of the species shown in the figure with the exception of Sternopygus macrurus in 1971, and Hypopomus brevirostris in 1970 have non-random correlation coefficients ($p < .01$). The regression lines describing growth of all species shown in Fig. 7, with these two exceptions, extrapolate back to zero length at dates between May 18 and May 26. Since Kumaka Swamp was flooded on May 14 and on May 10 in 1970 and 1971 respectively, the zero-length date (hatching) derived for "linear growth" indicate that spawning must have occurred within a few days after flooding. It is unlikely that extremely small fish such as those caught on May 28 - June 2 could have swum the 1/2 km into the swamp, and it is impossible that spawning could have occurred in the swamp before the flood because the swamp was completely dry except in small isolated pools, until May 10. Thus these data indicate that some species spawn in the swamp immediately following the first flood, in May. Although I searched in

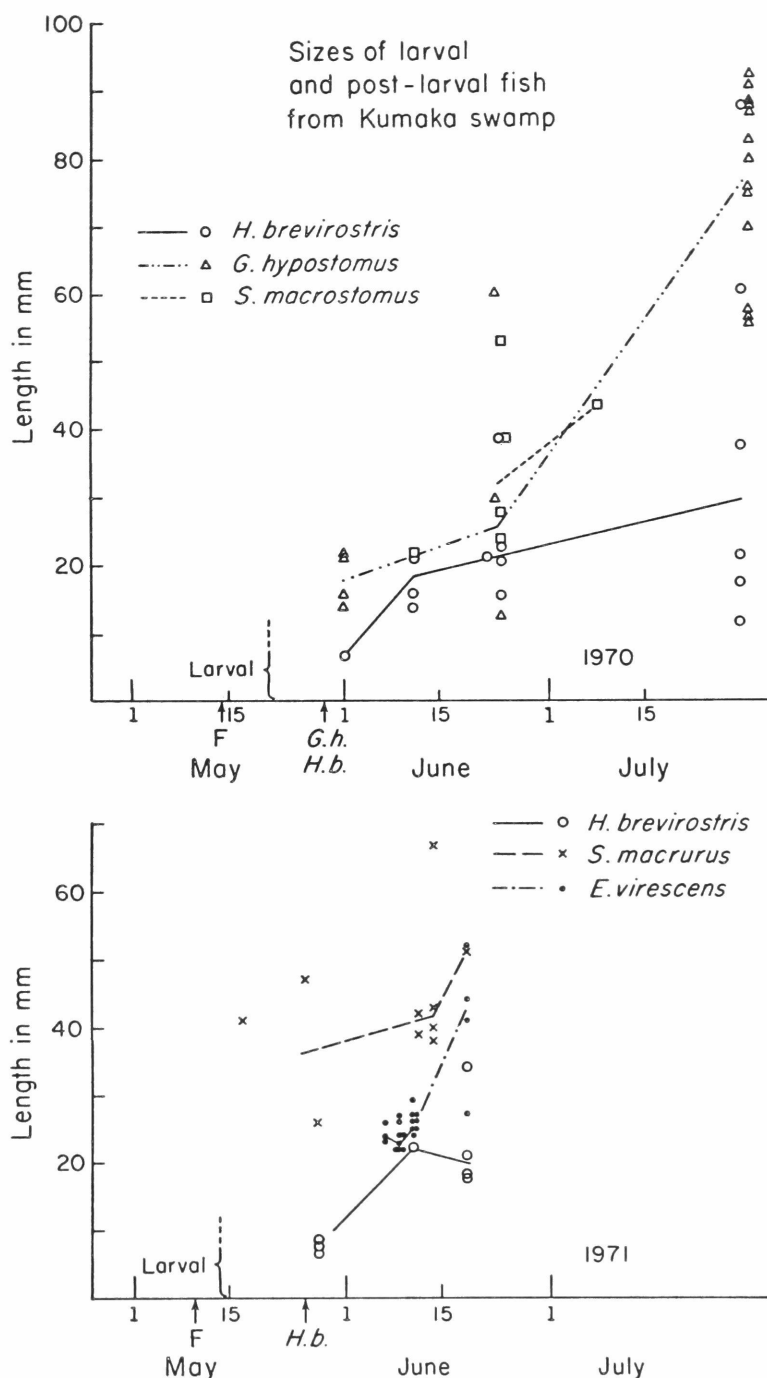


Fig. 7. Sizes of larval and post-larval fish from Kumaka Swamp vs. the date of capture for 1970 and 1971. Each symbol indicates a single fish of the species shown in the keys. A line for each species passes through the median length for any given day. The date at which the swamp flooded for the first time is indicated by an F in the figure. G. h. and H. b. refer to Gymnorhamphichthys hypostomus and Hypopomus brevirostris, and the arrows point to the date at which I detected, but did not capture, the first larval forms of these species. The larvae continue absorbing their yolk sacks until they are approximately 5 to 10 mm long.

Moco-moco Creek for small fish, I never was able to find any prior to the onset of the rainy season.

Clearly, one exception to this general picture of breeding adults spawning immediately as the water rises is indicated for Sternopygus macrurus. Even though the correlation coefficient between length and date of capture is not significant ($r = 0.34$; $v = 9$), the discovery of a small Sternopygus in Kumaka Swamp of 41 mm on May 17, 1971 (7 days after the flood) could have occurred only if the small fish had hatched in the main creek, and had been washed into the swamp with the rising water. Since it was caught within 200 m of the main creek, this is a likely explanation. It thus appears that Sternopygus macrurus begins breeding before the onset of the rainy season, its breeding site being somewhere in the main creek rather than in Kumaka Swamp. This conclusion is supported by examination of the gonadal condition of Sternopygus captured in the creek in early April. One female Sternopygus, length 460 mm, found deep in an undercut bank in Moco-moco Creek on April 20, 1971 was ripe with eggs. She was so close to spawning, the eggs came out into the net as soon as she was caught. A large male, length 546.5 mm with testes that were enlarged to fill the abdominal cavity was present in the same hiding place. Before disturbing this pair, I recorded electrical activity from the male that I interpret to be courtship song for this species (see page 93). Although no other ripe females were caught, a considerable proportion of individuals caught between April 20 and May 10 had enlarged gonads. I captured 39 individuals of Sternopygus macrurus in 1971 and examined their gonads. The gonadal state is indicated in Table IV using the same procedure as I used for sexing Eigenmannia. This Table shows that a large proportion of individuals captured in the three week period before the onset of the rains, had enlarged gonads. This fact, considered along with the early appearance of Sternopygus young, strongly suggests that Sternopygus breeds in the creek before the rains. Length data show that juvenile Sternopygus are consistently longer than any other species found in Kumaka Swamp possibly because Sternopygus has an early start to breeding.

The breeding period for gymnotids continues throughout the rainy

TABLE IV

Reproductive condition of Sternopygus macrurus from Moco-moco Creek and surrounding flooded areas (Kumaka Swamp). Entries contain the number in each gonadal condition.

		Gonads Enlarged	Gonads Small	Total
April 20 - May 10	males	6	4	10
	females	4	6	10
	immatures	0	3	3
May 11 - May 30	males	0	2	2
	females	1	2	3
	immatures	0	3	3
June 1 - June 20	males	2	2	4
	females	0	0	0
	immatures	0	4	4

season. With each sudden rainfall and consequent flood, additional fish perform a lateral migration into unoccupied areas for the purpose of breeding. On June 13, 1971 a particularly heavy rainfall flooded new areas and caused fish to begin their breeding in an area that previously had not been flooded. By July and August, however, most fish caught had spent gonads, and having finished their breeding efforts had begun the post-reproductive phase of the annual cycle.

H. The Annual Cycle of Reproduction: The Post-Reproductive Phase

During the final month of the rainy season, the fish begin to put on stores of fat to be used during the dry season. All of the fish caught in August, 1970 had very small gonads and were instead remarkably full of fat in the abdominal region.

Coinciding with the deposition of fat in these fish is a reverse lateral migration back to the main body of the creek. This can be seen from the populations of gymnotids shown in Fig. 6. By August 6, the population levels of the study areas A and B had nearly reached the population levels typical for the period before the onset of the rains in 1970.

Fish hatched in Kumaka Swamp continued to reside there until the end of the rainy season when they too returned to the main creek. Larger individuals returned to the creek earlier than smaller ones. This is demonstrated for Gymnorhamphichthys hypostomus by showing that post-larvae sampled in the main creek are significantly larger than post-larvae caught at nearly the same time in Kumaka Swamp. In a random sample of Gymnorhamphichthys from Kumaka Swamp taken on July 30, 1970 in which an effort was made to include all fish, even very small ones, by careful scanning over the sand and leaf litter bottom, the mean size of post-larvae was 74.2 mm (s.d. = 21.7, N = 24). On July 31, 1970 however, a collection of Gymnorhamphichthys post-larvae from the main creek had a mean length of 126 mm (s.d. = 19.0, N = 11). These samples differ significantly in their central tendency when tested with the two-tailed Mann-Whitney U test (Siegel, 1956) ($Z = 4.6$, $n_1 = 24$, $n_2 = 11$, $p < .01$). These samples did not include any adult fish that would have biased the

mean toward higher values. Adults were considerably larger than juveniles and could be distinguished easily. Another sample of Gymnorhamphichthys taken on April 2, 1970, that included only fish at least one year old (the fish had not yet bred), had a mean length of 164.6 mm (s.d. = 22.3 mm, N = 45). All of the individuals in an 80 meter stretch of creek were included in this sample. Smaller fish probably remain in the swamp to take advantage of a multitude of habitats not available in the main creek that may be necessary to insure development. Young Gymnorhamphichthys 40 mm or less, preferred hiding under rotten leaves on the bottom of the stream that flowed through the swamp. The adults were found most commonly buried under sand. Although patches of creek with sandy bottom and patches with leaf litter were available both in Kumaka Swamp and in the main creek, leaves were much more common in Kumaka Swamp because the swamp is in a flooded forest. Possibly the Gymnorhamphichthys young are unable to bury themselves in sand until they attain a certain size or state of development. Thus small fish may prefer to remain in the swamp where leaf litter is more abundant until they are able to utilize the sand as a method of hiding. Young fish of other species seem to follow a similar pattern.

The flow rate of the water may be an important factor for the survival of very small fish. Small fish may not be able to swim against a strong current while a larger fish might have a better chance. If so, a small fish should prefer Kumaka Swamp where the flow rate although highly variable from one location to another was much less than that in the main creek.

In summary, the annual reproductive cycle of most fish on the Rupununi is dominated by a single rainy season. The reproductive cycle is divided into a non-reproductive phase during the dry season; a reproductive phase during the beginning of the rainy season and a post-reproductive phase during the final month of the rainy season. Most species of gymnotids in Moco-moco Creek, including Hypopomus brevirostris, Eigenmannia virescens, and Gymnorhamphichthys hypostomus, seem to follow this pattern. They migrate during the first flood, to Kumaka Swamp to breed. Sternopygus, a notable exception, begins its breeding activities before the beginning

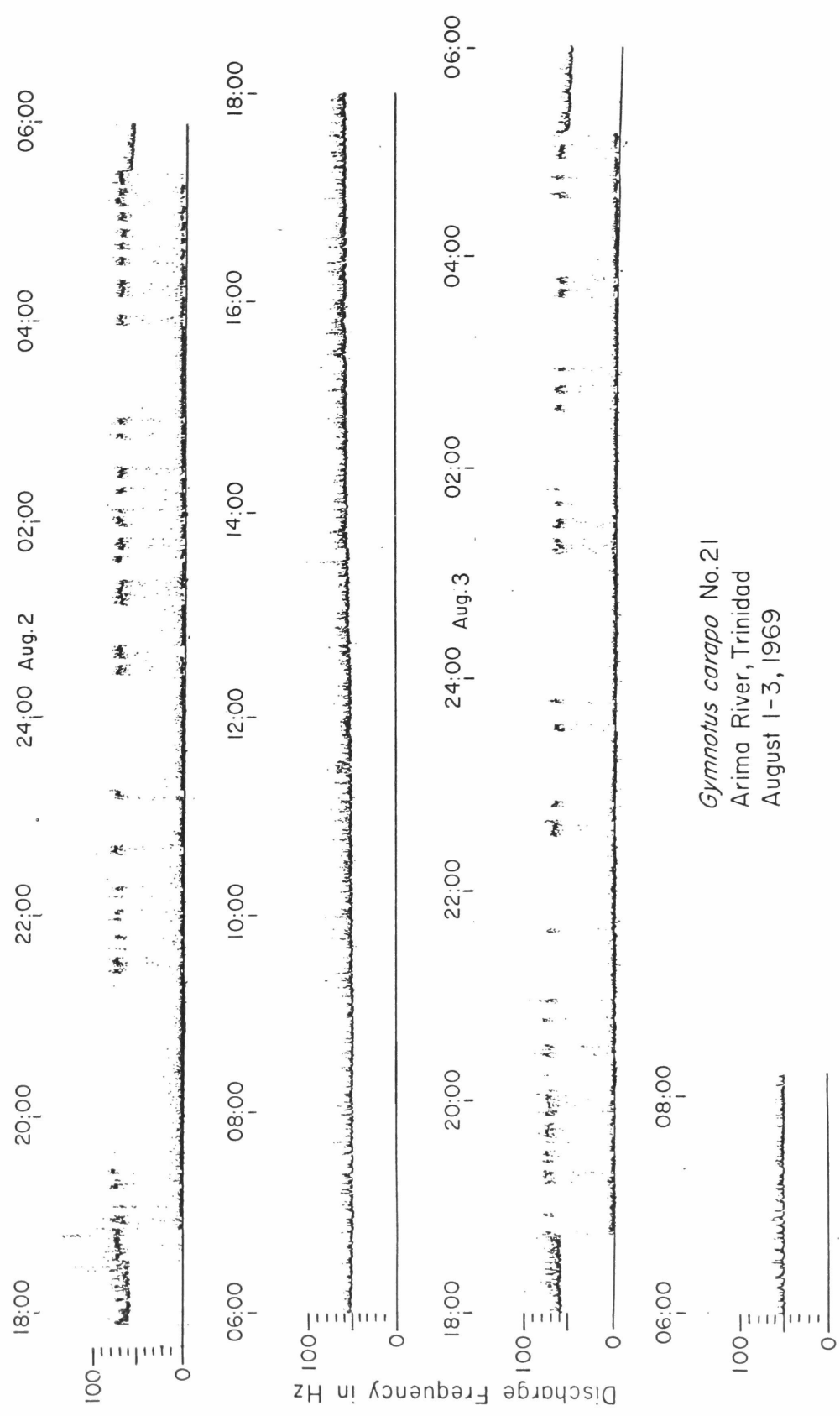
of the rainy season. All species return to the creek during the last part of the rainy season.

I. Diurnal Cycles of Activity

Daily activity cycles of gymnotids are well known from laboratory studies (Lissmann, 1958; Lissmann and Machin, 1958; Lissmann and Schwassmann, 1965; Black-Cleworth, 1970) and from previous field studies (Lissmann and Schwassmann, 1965; Steinbach, 1968; Ellis, 1913; Lowe-McConnell, 1964). Gymnotids are inactive during the daytime and spend their time in well-concealed hiding places. They emerge from their hiding places just at dusk and are active in the main creek or swamp until dawn when they return to their hiding places (Lissmann, 1961a; Lowe-McConnell, 1964). A useful method for following the nocturnal activity rhythm of these fish uses an automatic recording device.

I followed the activities of several Gymnotus carapo in Trinidad in 1969 by monitoring the electric discharge of an individual in its hiding place. Electrodes, secured near the fish in its daytime hiding place, were connected to the fish detector amplifier (MR1). Each pulse from the fish was used to trigger a pulse of constant amplitude and duration. These pulses were then integrated with a several second time constant RC circuit and recorded on a battery operated Rustrak chart recorder. When a fish is present in this hiding place, its discharge frequency is indicated on the recorder. When the fish moves away from the hiding place, the pulse generator no longer is triggered and the chart recorder reads zero. Thus, the chart shows the presence or absence of the fish, and when present roughly indicates its frequency of discharge. The presence of two fish would not be indicated on this chart, nor would differences between the resident and another individual of the same species. The distance from the electrode at which the pulses are no longer triggered is approximately 1.5 meters.

The record shown in Fig. 8 is from a Gymnotus carapo from the Arima River. It starts on August 1, 1969 at 18:00 and continues until August 3 at 08:00. Several features of this chart are immediately evident. First, the frequency of the discharge increases with the onset of darkness



Gymnotus carapo No.21
Arima River, Trinidad
August 1-3, 1969

Fig. 8. Nocturnal activity of *Gymnotus carapo* recorded in the field in the Arima River in Trinidad. The frequency of the discharge of the fish (when present) is recorded as a vertical deflection. See text for explanation of method used to obtain this record.

(18:30 - 18:45), a result consistent with those of previous workers (Lissmann and Schwassmann, 1965; Black-Cleworth, 1970). Second, shortly after darkness, the fish emerged and left the hiding place. This particular individual left its hiding place at 18:50 on August 1, at 18:45 on August 2. Throughout the night, a fish returned for 5 to 10 minute intervals and then left again. It is possible that several individuals, rather than one, are shown in these records. Finally at 05:35 or at 05:10, the fish returned to its hiding place and remained there throughout the day. There was a gradual decrease in frequency once the fish had settled in its hiding place.

Records for other individuals in Trinidad have a similar pattern. These methods have not been used in Guyana because the large numbers of species and the greater overall density of gymnotids would have made interpretation of the results nearly impossible. Observations at night, however, confirm the fact that gymnotids emerge from their hiding places shortly after sunset, enter the main creek, and then return to their hiding places at dawn.

J. Predation and the Diurnal Cycle

Careful hiding during the day is probably important for avoidance of diurnal predators, including predatory birds, mammals, and fish. Once, when I released two adult Eigenmannia virescens into Moco-moco Creek during the daytime, a predatory fish, Crenicichla sp. (Cichlidae) darted out from the bank and devoured both individuals. Another predatory fish in Moco-moco Creek was Hoplias sp. (Characoidei). In the main rivers and savanna ponds on the Rupununi, predatory characins and cichlids such as Serrasalmus sp. and Cichla ocellaris were very common (Lowe-McConnell, 1964). These predators were not seen in the higher reaches of Moco-moco Creek during this study.

Predation is difficult to detect when studying natural populations and it is usually difficult to assign a direct cause for mortality of individuals when there are numerous other factors that could contribute to fluctuations in the population such as disease, food shortage or lack of space. The unusual regenerative ability of gymnotids permits the study

of the intensity of partial predation: predation that does not cause mortality to the prey species. Ellis (1913) showed that gymnotids have a high rate of mutilation and regeneration. Within the subfamily Sternopyginae, which includes many of the species found in Moco-moco Creek, he found that 12% of the specimens (9 species) had injuries. He found injuries in 26% of the specimens from the subfamily Sternarchinae (Aptereronotidae) (11 species). Ellis suggests that the large number of injuries is caused by high levels of predation with a significant number of individuals surviving due to regeneration. The tail and anal fin are the regions most commonly injured.

Eigenmannia virescens collected in Moco-moco Creek and in Kumaka Swamp during the period from April 15 - June 25, 1971 were examined for mutilation and regeneration. In a sample of 126 individuals, 24 or 19% possessed wounds of varying states of regeneration. This is similar to the figure of 15% obtained for Eigenmannia virescens by Ellis (N = 482).

These and the other figures on regeneration presumably reflect partial predation rather than intraspecific aggression because Eigenmannia has a small gape incapable of inflicting this type of wound. In my sample of wounded Eigenmannia, 11 were females and 13 males.

K. Hiding Place Selection

In what is probably an attempt to avoid predators active during the day, gymnotids conceal themselves immobile in hiding places. The following list indicates the different types of hiding places selected by gymnotids in Moco-moco Creek:

1) Under rocks and stones. Rocks and stones lay in the main body of the upper reaches of the creek. Cracks between and under the rocks and stones provided protection for large and small fish.

2) Buried in sand. Fine sand in the bottom of the creek bed was common where the flow of water was not too strong. The sand bottom was more common in the lower reaches of the creek near Kumaka Swamp than near the mountains. Some fish were able to bury themselves in sand.

3) Buried in rotten leaves. Rotten leaves usually collected in

quiet areas, or in areas of backwash from turbulence. In Kumaka Swamp, which was a flooded forest, rotting leaves were present nearly everywhere. Leaf litter sometimes reached a depth of 10-20 cm in quiet areas of the creek.

4) Between small sticks and rootlets. Along the banks of the stream there were often patches of .5 - 1.5 cm diameter sticks or roots forming a loose mesh. Finely subdivided rootlets hung in long tendrils from vines, or from the roots of nearby plants. The cracks between the small stems and roots provided protection for small fish and the mesh of rootlets provided protection for very small fish.

5) Pile of debris. Sticks, leaves, logs and other floating vegetation often build up on a fallen log or a branch, causing a compacted collection of debris, making numerous hiding places in the thick tangle. These piles of debris were usually only temporary, appearing one day and washing away on another.

6) Mat of roots and stems from water plants. Dense growth of grass and water plants were found along the edge of the stream and were frequently found in flooded areas during the wet season. Numerous hiding places were available among these roots and plants for large and small fish.

7) Under or in logs or "tacubas". The local trees, often more dense than water, sink and lie in the stream bottom for many years without rotting. These hard submerged trees are called "tacubas" locally. Hiding places could be found under or inside holes in the submerged logs.

8) Holes in the bank. There were often holes in the clay bank of Moco-moco Creek of unknown origin that provided hiding places for some species. These holes sometimes penetrated 1 to 2 meters under the bank.

9) Undercut banks. In some places the bank of the stream was undercut by currents of water, especially near a bend in the stream. Roots growing into the undercut region provided cover. This was a favorite hiding place for some gymnotids.

10) Hanging from leaves or branches. A small stick from a branch of a tree or a palm leaf hanging in the water was used by some fish as

a substrate on which to position themselves within the flow in the main body of the stream. Hiding was accomplished with the use of protective coloration, and did not depend upon concealment behind a protective barrier.

This list of ten categories of hiding places is an exhaustive catalogue of hiding places for gymnotids in Moco-moco Creek. All gymnotid hiding places could be assigned to one of the ten classes.

To assess such species' preference for the different types of hiding places, I recorded descriptions of the hiding places being used by 531 individual gymnotids of seven species in Moco-moco Creek. Observations were made on July 13 to July 16, 1970 by systematically surveying approximately 1000 meters of Moco-moco Creek in the higher reaches near the camp. Every gymnotid that was detected was recorded and its hiding place was described. When the identification of the species was uncertain due to ambiguity in the electrical discharge, the individual in question was captured for visual identification. The results of this survey are shown in Table V. The ten categories of hiding places are listed against the seven species found in Moco-moco Creek during this survey. The entries in the table are the percentage for each species found in each type of hiding place. For example, 28.4% of the Apteronotus albifrons in the sample were found under rocks (N = 95), while 0% were found buried under sand.

The hiding place preferences for each species can be seen quickly from looking at the table. Apteronotus albifrons usually is found hiding in piles of debris (31.6%) under rocks (28.4%) or in or under logs (26.3%). All of these hiding places, although differing in their structural make-up, provide thick, usually solid cover.

Eigenmannia virescens prefers to hide in similar places, under rocks, in piles of debris and in undercut banks. Eigenmannia was not found hiding in hollow logs in this sample, and was only found in them occasionally during other recorded observations that were not systematic. Another pattern of hiding places similar to Apteronotus albifrons is shown by Sternopygus macrurus, the only difference being that Sternopygus are

TABLE V

Distribution of daytime hiding places of seven species of gymnotids in Moco-moco Creek expressed as the percent of the total for each species July 1970.

	<u>A. albifrons</u>	<u>S. macrostomus</u>	<u>E. virescens</u>	<u>S. macrurus</u>	<u>G. hypostomus</u>	<u>G. carapo</u>	<u>H. brevirostris</u>
	A.	S.	E.	S.	G.	G.	H.
under rocks	28.4	0	37.2	15.6	0	13.7	0
buried in sand	0	0	0	0	100	0	0
buried in rotten leaves	0	0	0	1.6	0	1.1	37.7
among sticks or rootlets	2.1	20.0	0	8.1	0	27.3	52.8
pile of debris	31.6	6.7	32.6	14.0	0	14.8	0
mat of roots or water plants	0	0	9.3	0	0	11.4	0
under or in logs, tacubas	26.3	0	0	29.6	0	21.6	0
holes in bank	0	0	0	7.5	0	1.1	0
undercut banks	11.6	0	20.9	23.7	0	9.1	9.4
hanging from branch or leaf	0	73.3	0	0	0	0	0
TOTALS	100	100	100	100	100	100	100
N=	95	15	43	186	51	88	53
$\frac{H}{H_{max}}$	0.537	0.249	0.502	0.720	0	0.724	0.371

($H_{max} = 3.322$)

sometimes found hiding in holes in the bank whereas Apteronotus is not.

Gymnorhamphichthys hypostomus is a specialist, hiding only by burying itself in sand. This habit, well described by Lissmann and Schwassmann (1965) is accomplished by positioning the snout near the surface of the sand and then giving pronounced longitudinal undulations of the body that propels the fish into the sand. Gymnorhamphichthys was always found buried in sand (100% of 51 recorded in this sample) and no other fish was ever seen to do this. It is clear that Gymnorhamphichthys, then, is a "specialist" in terms of hiding place selection.

It is possible to calculate a "hiding place diversity" index for each species, employing the information theoretical formula of Brillouin (1962) used previously in calculations of species diversity. Gymnorhamphichthys, being an extreme specialist has a "hiding place diversity", H , of 0.0 bits per individual. For purposes of comparison of one habitat to another it is more interesting to calculate the ratio of the hiding place diversity observed for each species, to the maximum possible hiding place diversity, H_{\max} , available to the species in the particular habitat. The ratio of H to H_{\max} is a measure of the "evenness" of the distribution. A species that selects all hiding places available to it with equal probability, has a high degree of "evenness", and the H to H_{\max} ratio will approach 1.0 (Pielou, 1969). I calculated the maximum hiding place diversity for each species in Moco-moco Creek by assuming equal probability of all ten hiding place categories, employing the formula for diversity of Shannon and Weaver (1949). For ten hiding places, the maximum diversity is 3.322 bits per individual. The result of the calculations of H/H_{\max} are shown at the bottom of Table V.

Another specialist is Sternarchorhamphus macrostomus. It hides during the day suspended at midstream with its lower mandible braced against a small branch or a leaf, its tail trailing downstream with the current from the point of support. Concealment from visual predators is obtained from the close specific resemblance to the sticks and leaves from which it normally hangs. Often the fish assumes an upside-down posture as shown in Fig. 9. Sternarchorhamphus macrostomus is the only



Fig. 9. Photograph of a Sternarchorhamphus macrostomus from Moco-moco Creek, hiding by protective coloration and specific resemblance to the plants from which it is suspended. The flow goes from right to left. This fish is suspended upside down.

species that utilizes disruptive coloration for concealment and small sticks and leaves for attachment. The evenness of its hiding place selection is low (0.249).

Hypopomus brevirostris has a low evenness value (0.371) due to the extensive utilization of rotting leaves on the bottom or small sticks or rootlets found along the bank. Several species including Gymnotus carapo and Sternopygus macrurus contrast with the specialist pattern of hiding place selection. These species have a high evenness value because they are choosing many types of hiding places with similar probability. In terms of hiding place selection, these species would be considered generalists.

Hiding places are a resource that must be available to gymnotids to allow them to survive diurnal predation. Individuals that do not conceal themselves in good hiding places are probably more vulnerable to predators such as Crenicichla. Because at least seven species of gymnotids found in Moco-moco Creek require hiding places during the daytime, and because many of the species utilize similar types of hiding places, hiding places may be a limiting resource when gymnotids are crowded.

Species are in competition when they make demands upon the same resource when that resource is limiting or potentially limiting (Clements and Shelford, 1939; Miller, 1967). When two species are in competition for the same resource, natural selection will favor the species most efficiently utilizing the resource, causing one of the two species to become eliminated according to the theory of competitive exclusion (Gause, 1934). Alternatively, those individuals that avoid competition by specialization in utilization of one resource that other species are not using, will be favored.

The following evidence indicates that hiding place competition exists among gymnotids.

- 1) Dry season conditions cause a decrease in available space and consequently number of hiding places compared to the wet season. Although I had the impression, during the dry season, that every site that appeared

suitable was occupied by at least one individual, it was impossible to tell whether all possible sites were occupied.

2) Two species in Moco-moco Creek show specialization in the type of hiding place selected. Gymnorhamphichthys has the specialized ability to bury itself in sand and Sternarchorhamphus macrostomus hangs from a branch in midstream depending upon disruptive coloration for protection. This specialization probably results from natural selection favoring the avoidance of competition with others.

3) There is considerable overlap in hiding place selection when defined by the ten categories of hiding places shown above. Since there are several species utilizing the same type of hiding place resources, we can assume that these species are potential competitors when the resources are limited.

4) Newly formed hiding places are colonized immediately. Whenever a tree fell into the water, debris began to collect on it, forming hiding places suitable for Apteronotus, Gymnotus, Eigenmannia or Sternopygus. Piles of debris also often appeared during the flood after a heavy rainfall. Newly formed piles of debris were usually soon occupied by several gymnotids. A debris pile that formed during the day was usually colonized during the night and fish were present on the following day. The immediate colonization of these new areas suggests that there is considerable pressure being exerted in other hiding places by overcrowding. During the wet season when more space is available to fish because their population levels in the creek are reduced due to the migration, newly formed debris piles remain for many days with no fish present.

The distribution of hiding places in Kumaka Swamp was compared to that in Moco-moco Creek, at the same time of year. On July 18, 1970 I made a sample by following the main flow of water for 600 meters into Kumaka Swamp starting from the inlet from Moco-moco Creek. I also sampled a large open flooded savanna within this swamp where many fish were breeding. Gymnotids of all sizes encountered by systematic sweeping motions of the electrode were included in this analysis. A total of 233 fish are included.

I found that there were fewer types of hiding places available to the fish in Kumaka Swamp. In particular there were no rocks or stones within the swamp, the bottom being rather muddy or sandy, and the terrain flat, without the large boulders found in the higher reaches of the creek. There were no holes in the bank nor undercut banks in the swamp. Piles of debris were found rarely because the flow of water through the swamp is less than in the main creek thus creating less force to carry debris downstream, and because there were many more obstructions in the swamp making movement of debris nearly impossible. There were five categories of hiding places available to fish, thus H_{\max} takes on a value of 2.322.

The results of this sample are shown in Table VI. They show that Gymnorhamphichthys again is specializing by burying itself in sand, as in the creek. The hiding place evenness index of other species shows some differences between the swamp and the main creek however. The differences presumably reflect the differing species responses to the large increase in available space in the swamp. Hypopomus has a comparatively high diversity index in the swamp when compared to other species, whereas in the creek it was relatively specialized in its hiding place selection.

Apteronotus tends to specialize by hiding among sticks and stilt roots of small trees and shrubs in the swamp. Other species also utilize this habitat. There is extensive use made of the mat of Polygonum acuminatum plants found in the open savanna area of the swamp. Many species of gymnotids are found in the mat of plants during the breeding season. Generally the evenness index is lower in the swamp than in the creek. The median value of evenness for 5 species in the swamp is 0.293 compared to the median for the same 5 species in the creek of 0.502.

In addition to the lower diversity in hiding places in the swamp, there is a great deal of overlap between the species. In particular there was a great deal of overlap in the mat of water plants and in the sticks and rootlets. During these studies, I had the impression that there was considerable homogeneity of hiding place selection in Kumaka Swamp when compared to the main creek.

TABLE VI

Distribution of daytime hiding places for five species of gymnotids in Kumaka Swamp expressed as the percent of the total for each species. July, 1970.

	<u>A. albifrons</u>	<u>E. virescens</u>	<u>S. macrurus</u>	<u>G. hypostomus</u>	<u>H. brevirostris</u>
	A.	E.	S.	G.	H.
buried in sand	0	0	0	100	0
buried in rotten leaves	0	15.2	0	0	37.2
among sticks or rootlets	77.9	10.2	21.6	0	12.8
mat of roots or water plants	23.1	74.6	78.4	0	48.9
under or in logs, tacubas	0	0	0	0	1.1
TOTALS	100	100	100	100	100
N =	13	59	37	30	94
$\frac{H}{H_{\max}}$	0.270	0.419	0.293	0	0.603

$$(H_{\max} = 2.322)$$

This is probably because there was less diversity in the available hiding places so that the fish were forced to overlap extensively in their choice between the available sites. Similarly, the large increase in area and therefore hiding places in the swamp reduces competition and allows the species to coexist in the same types of hiding places that are preferred by all species. It would be of considerable interest to measure the hiding place diversity during the dry season for comparison with the wet season data I have obtained. Previous work comparing niche breadth during wet and dry season in Panamanian fishes suggests increased feeding specialization during the dry season with decreased overlap when compared with the wet season (Zaret and Rand, 1971). Comparison between summer and winter feeding diversity and niche overlap among shorebirds yields similar results (Baker, 1970).

L. Physical Characteristics of the Water

Conductivity: The specific conductance, L , of the water of the study sites was measured with a 1 kHz impedance bridge. The impedance bridge was calibrated periodically using 1% precision resistors. Conductance values are presented in Table VII. In cases where several measures were taken in the same body of water at different times, the mean and standard deviation (s_L) are presented. In Trinidad, clear water had a specific conductance of 1 to 3×10^{-4} mho/cm. The "black" water found in the Aripo Savanna, which had the color of weak coffee, had a much lower value (6.8×10^{-5} mho/cm). The black water in Nariva Swamp did not have a low conductivity value, however. This may be due to the mixing of black water with sea water from the ocean which is only a few miles away.

The conductivity values for Guyana were systematically lower. Clear water running off the Kanuku Mountains in Moco-moco Creek had a value similar to that for the black water in Trinidad. Water in a depression in the savanna near Moco-moco Village predominantly of rain water source, had an even lower conductivity. I did not investigate the reason for this systematic difference in the conductivity of water between Trinidad and Guyana.

The lowest values of specific conductivity that I measured are still

TABLE VII

Conductivity of Water in Trinidad and Guyana

Location	Date	Water Color	Number of Measures	Specific Conductance (mho/cm)	s _L *
Trinidad					
Arima River (4 miles north of Arima)	July - Aug. 1969	Clear	9	1.605×10^{-4}	0.156×10^{-4}
Caroni River (Caroni Pumping Station)	July, 1969	Muddy	1	2.101×10^{-4}	-
Aripo Savanna	July, 1969	Black	1	6.849×10^{-5}	-
Nariva Swamp	July, 1969	Black	7	1.771×10^{-4}	0.092×10^{-4}
Mausica River (4.2 miles east of Piarcó)	July, 1969	Turbid	1	2.315×10^{-4}	-
Barro River	August, 1969	Clear	1	2.907×10^{-4}	-
Guyana					
Botanical Gardens (Georgetown)	September, 1969	Black	1	9.174×10^{-5}	-
Moco-moco Creek at camp	April - July, 1970	Clear	4	4.364×10^{-5}	0.960×10^{-5}
Savanna Pond (2 miles north of Moco-moco Village)	May - August, 1970	Clear	10	5.318×10^{-6}	2.867×10^{-6}

* Standard deviation of values of specific conductance.

greater than that for distilled water at equilibrium with carbon dioxide in the air (7×10^{-7} mho/cm) (Moore, 1962). A specific conductance of 1×10^{-4} is equivalent to aqueous solution of potassium chloride of concentration of 0.0007 Molar when the value of 147 mho/equivalent-cm is used for potassium chloride (Handbook of Chemistry and Physics, 1966). I did not measure conductivity systematically enough to detect differences before and after rainfall, or diurnal variation. This would be an interesting problem for future work.

Dissolved Oxygen: The water in rapidly flowing streams is usually saturated with dissolved oxygen. I measured 9 ppm dissolved oxygen in the Arima River in Trinidad and in Moco-moco Creek in Guyana at temperatures between 23.5 and 25.5°C. Thus in rapidly moving streams, oxygen is not a factor that is limiting the distribution of a species. However, in areas where the water is quiet, and movement is not constantly mixing oxygen into the water, then the dissolved oxygen level falls. In one such case, the flooded swamp savanna in Kumaka Swamp, I observed a gradient of dissolved oxygen from saturation to no oxygen detectable. This gradient ran approximately perpendicular to the flow of fresh water through the swamp, and its location was similar to the distribution of fish in the swamp (Fig. 10). I measured the oxygen concentration at 11 stations in Kumaka Swamp on June 9, 1971 using the Hach Chemical dissolved oxygen kit. The depth of the swamp varied between 10 cm and 1 meter. My samples were taken at 5 - 10 cm depths. The observations are focussed on the most interesting part of the swamp in the southwest corner where the gymnotids were breeding. The oxygen levels at points near the transects were estimated using interpolation, and the approximate lines of equal dissolved oxygen are shown on the map in Fig. 10. Superimposed on the map of the oxygen content are the distribution of Eigenmannia virescens in the swamp as determined on the same day. It can be seen from this figure that Eigenmannia is common in the region that is saturated with oxygen but does not extend into areas where the dissolved oxygen levels fall to 3 ppm or less. It was not uncommon to find Hypopomus brevirostris in the region of 1 to 2 ppm oxygen, but all other species seemed confined to the well-oxygenated areas. H. brevirostris

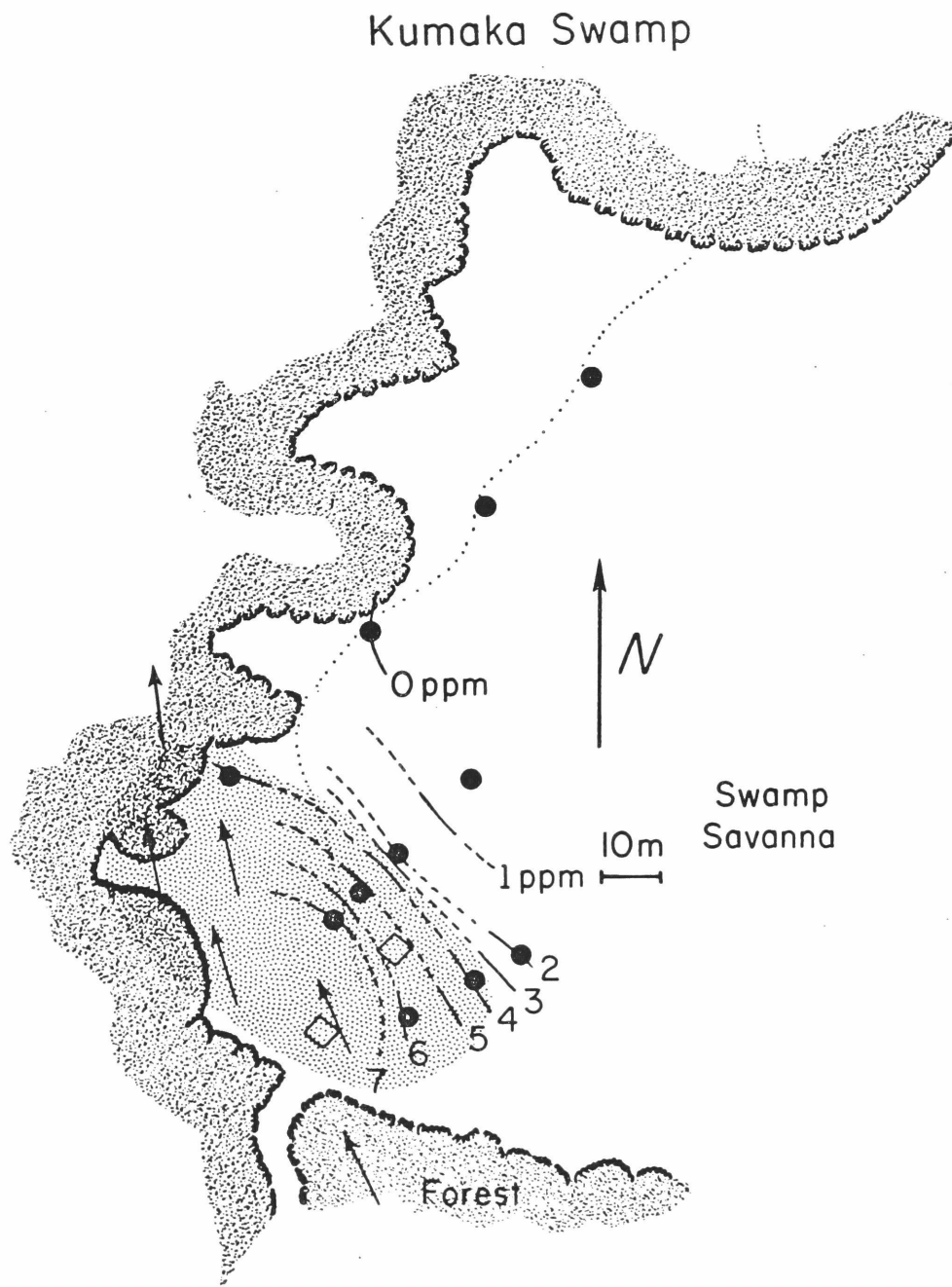


Fig. 10. Concentrations of dissolved oxygen (ppm) measured on June 9, 1971, in the swamp savanna of Kumaka Swamp. Black dots show locations from which samples were taken. Dashed and solid lines indicate approximate lines of equal oxygen concentration. The main flow of water follows the direction of the arrows in the south-west corner of the swamp savanna. The locations of *Eigenmannia virescens* on June 9, 1971 are shown by the stippled area.

is capable of air breathing (Carter and Beadle, 1931) and adults may thus be able to utilize areas of the swamp that are relatively low in oxygen. No gymnotids were found in the deoxygenated area of the swamp.

The dissolved oxygen gradient can be explained by the pattern of water flow in the swamp. The water entered the swamp savanna in the southern corner and flowed in the northwest direction. The flow rate in the estimated center of the flow was 16 cm/sec as measured from surface floating objects. The flow rate decreases perpendicular to the flow and in a large part of the savanna the water is not moving. Since the water is not moving, and since there were no apparent underwater photosynthetic plants in this swamp savanna, the standing water becomes deoxygenated due to the oxidation of vegetable matter in the bottom of the swamp, and due to the action of bacteria. The standing water also becomes warmer than the water in the main flow. The water in the main flow had a temperature of 24.0°C on June 9 whereas the water that was not flowing 30 meters distant from there was 25.5°C. The saturation level of dissolved oxygen in water is inversely related to temperature (Mortimer, 1956). Thus the deoxygenation caused by lack of flow is partly due to use of oxygen by decaying vegetable matter and bacteria, and is partly due to increased temperature.

Gymnotids do not inhabit those areas that are deoxygenated and Eigenmannia is not found in water with dissolved oxygen levels below 3 ppm. Some species of gymnotids, such as Hypopomus may have a greater tolerance than Eigenmannia.

pH: The pH of the water in Guyana was measured using the Hach Chemical pH indicator solution, or using Hydrion Lo Ion pH paper. The pH showed little variation in Kumaka Swamp. Eleven determinations of pH in transects across the swamp savanna all had a pH of 6.0 or 6.5. This is the same value as that measured on two occasions in Moco-moco Creek.

M. Spatial Patterns of Eigenmannia and Sternopygus

When the social organization of an animal is unknown, and when visual observations of individuals are impossible in their natural environment

as is the case with a nocturnal fish, it is necessary to rely on other techniques to describe its social organization. It is possible to learn a great deal from listening to the electric discharges of gymnotids as they interact with each other under natural conditions. Data recorded using this technique will be discussed later. We can also infer something about the social organization and ecology of these fish by an analysis of their utilization of space.

Spatial relationships are important in understanding territorial behavior, individual distance, aggregations of animals, colonial behavior, influence of crowding and other phenomena.

I have analyzed the use of space by Eigenmannia virescens and Sternopygus macrurus, two species that show some striking differences in the spatial patterns, social organization and electrical discharges.

Spatial patterns of organisms are of great theoretical interest to ecologists (see Pielou, 1969). Organisms are usually thought to be either clumped, regularly spaced, or else randomly spaced. If individuals in a population are assigned to the available space without regard for the positions of other individuals, the pattern is random. The number of individuals per unit area will follow the Poisson variate (Pielou, 1969; Clark and Evans, 1954; Hopkins and Skellam, 1954). A clumped pattern is one in which the individuals tend to be closer to one another than expected and a regular or dispersed pattern is one in which the individuals are further apart than expected.

In my analysis of the locations of individuals in their daytime hiding places in Moco-moco Creek during the dry season I found that Sternopygus macrurus is spaced at random whereas Eigenmannia virescens is clumped. To illustrate the contrasting patterns of these two species I have shown in Fig. 11 part A and B and Fig. 12 the locations of all individuals of the respective species in two different study areas. It is clear that Sternopygus is distributed irregularly in suitable locations in the study area whereas Eigenmannia is clumped in large groups. This pattern was seen not only in Moco-moco Creek in all cases during the dry season but also in Ikuwali Creek and Inaja Creek, observed during

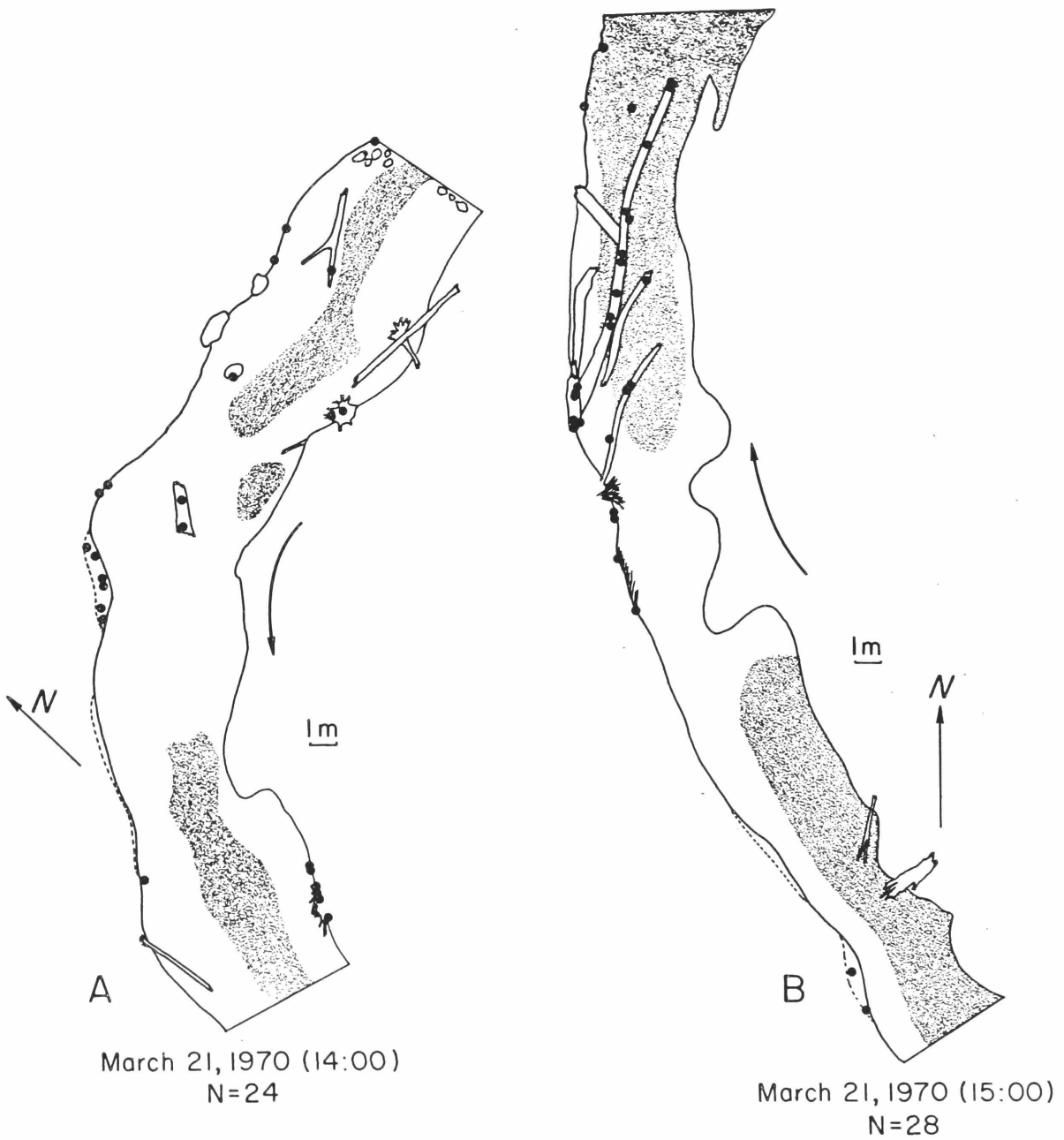


Fig. 11. Spatial pattern of hiding places (daytime only) of Sternopygus macrurus in Moco-moco Creek. The location of each individual on March 21, 1971, is shown as a black dot in the figure. A) Study area A as censused at 14:00. B) Study area B as censused at 15:00.

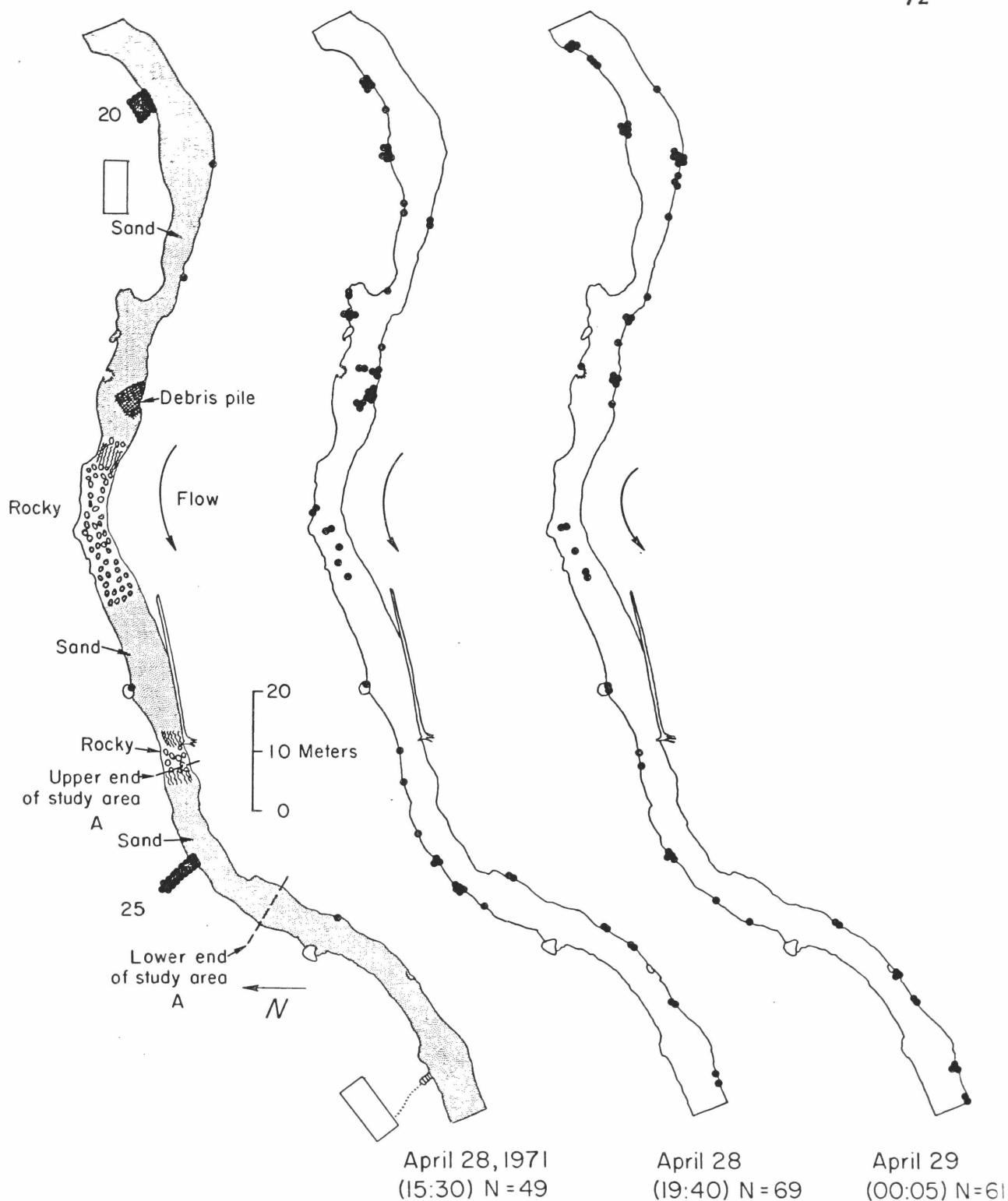


Fig. 12. Spatial patterns of hiding places (daytime on left, night in center and on right) for *Eigenmannia virescens* in Moco-moco Creek. The location of each individual is shown as a black dot. In two cases of large groups, the approximate number of fish in the group is shown to the left of the group.

September 1969. Frequently groups of 15 - 40 individuals of Eigenmannia were found within 1 to 2 square meters in a large pile of debris, or in an undercut bank, protected by tree roots or branches. An occasional solitary individual was not unusual. During the night, the Eigenmannia usually all emerged from the clustered hiding place to enter the creek for the purpose of feeding. A typical pattern for Moco-moco Creek is shown in Fig. 12.

A quantitative analysis of the spatial patterns of organisms relies upon the statistical distribution of the distances between individuals (distribution in statistical sense not spatial sense - see Pielou, 1969). Three methods have been discussed by Pielou (1969); two depend upon the distribution of distances measured from randomly selected points to the nearest individual (Hopkins and Skellam, 1954; Pielou, 1959). The third analyzes the distribution of distances between all individuals and their nearest neighbors (Clark and Evans, 1954).

The Clark and Evans index of dispersion, R , is the ratio of the observed to the expected mean nearest neighbor distance where the expected distance is calculated assuming a Poisson distribution. In two-dimensional space, the Poisson distribution has a nearest neighbor distance of: $1/\sqrt{2\pi\epsilon}$ where ϵ is the density of individuals in the sample area. If the observed nearest neighbor distances are less than expected, then the pattern is said to be clumped and the index, R , will be less than 1. If the pattern is random or the same as a Poisson distribution, the R will be 1, and if the pattern is dispersed, R will be greater than 1. The pattern with maximum dispersion in the two dimensional plane is a regular hexagonal array of points. It has a calculated index of 2.1491. In summary, R varies from zero to 2.1491 as the pattern changes from clumped to dispersed. It is possible to calculate an index, R , for a one-dimensional pattern; however none of the species in Moco-moco Creek followed spatial distributions in one dimension. A single-dimensional analysis would be suitable for species which hide exclusively near a bank, or for individuals living in very narrow streams.

The data collected from several study areas were analyzed using the

two-dimensional procedures outlined above.

The locations of every individual censused in study areas A and B were plotted on a map constructed from measurements made with the aid of a hand held sighting compass and a steel tape. The positions recorded on the map were accurate to within 50 cm. Once the map was constructed, distances between individuals could be estimated by measuring the distances between points.

Data for Eigenmannia and Sternopygus are plotted in Fig. 13 A and B. It can be seen that Sternopygus has an R value that is usually close to 1.0, signifying a pattern that does not differ from random. During April in 1970, five records in study area A indicated a highly dispersed pattern. R attained a value of 2.06 at one time. Fluctuation in the index, R, during the months of May through August may be caused by the low population levels. In contrast, Eigenmannia has a consistently low R value, corresponding to a clumped pattern. The asterisks in the two figures indicate those data points that do not differ significantly from random ($p \geq 0.05$) when tested with the standard variate of the normal curve according to the method of Clark and Evans (1954). There seems to be no consistent pattern relating population density to pattern of dispersion. In study area A, when the population of Sternopygus began to drop, the index of dispersion increased, indicating a widely separated pattern, whereas in study area B, as the population fell, the pattern became clumped. The most reliable records, however, are those with a large value of N. These values indicate consistent differences between the species.

When the Clark and Evans index of dispersion is applied to all gymnotids in the study area, regardless of species, so that nearest neighbor distances are measured from each gymnotid to the nearest gymnotid, R is found to vary between 0.57 and 0.72 for seven censuses of study area A from March 16 to March 30, 1970. This indicates a clumped pattern. The explanation for the overall clumped pattern may be because hiding places in general are not randomly distributed, but rather are patchy. Edges are preferred by several species and there is a clumping along the edge. Logs are scattered in well separated locations, even a sandy bottom occurs

Moco-moco Creek - 1970
Study area A

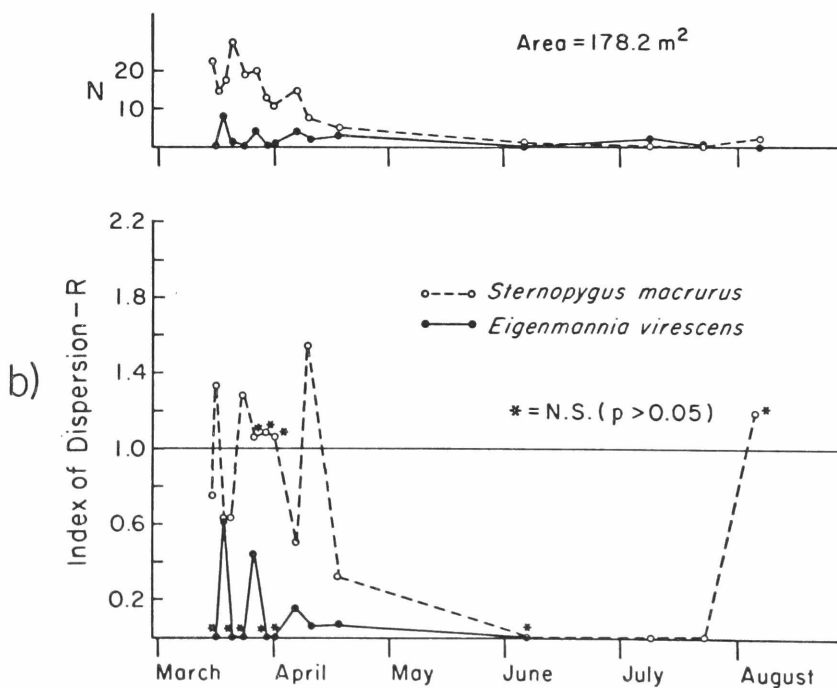
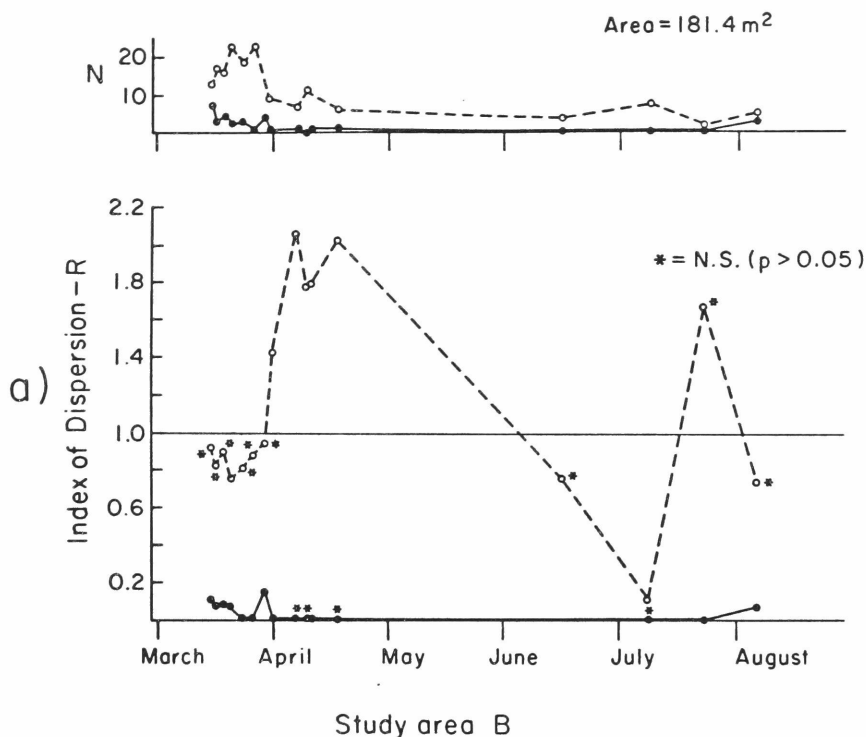


Fig. 13. Population levels (N) and Clark and Evans Index of Dispersion (R) for *Sternopygus macrurus* (dashed line) and *Eigenmannia virescens* (solid lines) in Moco-moco Creek. Measures result from censuses of study areas in creek. a) Study area A. b) Study area B. In the plots of the Clark and Evans Index, the asterisk indicates the points that do not differ from random.

in patches.

To improve the confidence in the measure of dispersion for Eigenmannia virescens, for which there were only a few individuals in study area A or B, a study area of larger size was set up in 1971. This study area, 215 meters long, with a total area of 1246 square meters was large enough to include several clusters of Eigenmannia during any day. When censuses were taken, some difficulty was encountered when estimating the distances between individuals within the cluster. Therefore I arbitrarily used an average separation of 0.3 meters.

The results of nine censuses conducted during April and May 1971 are shown in Table VIII. The data for day and night are presented separately because of the large differences in locations of individuals during the day and night. It can be seen from the table that the value of R is in all cases but one, less than 1.0. The day and night time nearest neighbor index do not differ when the R values are tested using the Mann-Whitney U test. Both patterns show individuals closer together than expected. Eigenmannia, therefore, shows a clustered distribution in the creek.

I had the impression of a more dispersed spatial arrangement for Eigenmannia during the night compared to the day. However, the Clark and Evans index is insensitive to differences in group size. It shows no difference between a single large cluster and dispersed pairs of individuals. This drawback is mentioned in the original paper by Clark and Evans. Therefore, I have devised another measure to illustrate the spatial pattern of Eigenmannia that differentiates between the day time and the night time activity.

Two individuals are said to belong to the same cluster if they are found within a certain minimum distance of each other. A convenient distance is equal to one half the expected nearest neighbor distance calculated for a Poisson distribution. This distance is considerably less than the random distance so it was used to define a cluster. When this criterion is used, I find Eigenmannia confined to a few clusters during the day time: 50% of the individuals can be found in one to two of the largest clusters. The total number of clusters in study area is low. During the night, however, there are a larger number of clusters, and 50% of the individuals are

TABLE VIII

Clark and Evans dispersion index for Eigenmannia virescens in Moco-moco Creek, 1971. Area = 1246 square meters.

	Date	Time	N	$R=r_o/r_e$	P
DAY	April 21	11:20	69	.510	**
	April 28	15:30	49	.850	*
	May 14	15:20	2	.024	**
	May 19	14:00	6	.763	NS
NIGHT	April 21	19:15	56	.771	**
	April 21	23:00	93	.650	**
	April 28	19:40	70	.496	**
	April 29	00:04	69	.476	**
	May 19	19:50	5	1.594	†

* or ** Pattern clumped: departure from random significant at 0.05 or 0.01 level respectively.

† Pattern dispersed: departure from random significant at 0.05 level.

Mann-Whitney U test of differences in R between Night and Day, N.S.
p = 0.548.

found in the 8 or 10 largest clusters.

The data that summarizes the number of clusters and the approximate composition of the clusters are presented in Table IX. It can be seen that there is a consistent difference between night and day. When the day and night values were compared using the Mann-Whitney U test, the two differed with $p < .05$. Daytime clusters tended to be larger and fewer, nighttime clusters tended to be more numerous, containing fewer individuals. This is consistent with the pattern illustrated in Fig. 12.

The spatial pattern for Eigenmannia was different in Kumaka Swamp. The swamp is a less patchy environment, being a uniform spread of Polygonum sp. (Polygonaceae) in a thick mat providing numerous hiding places for adults and small fish under leaves, under the leaf debris and among the stems of the plants. The hiding places are more uniformly distributed than they appear to be in the main creek.

Spatial localization of individuals in Kumaka Swamp was difficult with my detector because of the thick tangle of plants that made it hard to move the electrode. An attempt was made to assess the spatial relationships between individuals in the following way: before the rainy season started, two 5 x 5 meter square plots were cleared by cutting the tops off of the plants and removing the cut stems and leaves. The roots, stems and leaf litter were left to provide hiding places for the fish. These areas could then be censused with the fish detector. The overall density of fish in these specially prepared plots seemed to be normal.

Four daytime censuses were conducted in the 5 x 5 meter plots and each fish was localized and plotted on a map. The four measures were then analyzed with the Clark and Evans index and were found to be a dispersed pattern. The results are shown in Table X. Thus, individuals remained separated by approximately 1 meter.

In summarizing the spatial relationships of Sternopygus and Eigenmannia, Sternopygus is distributed at random or else is somewhat dispersed, whereas, Eigenmannia is clustered into groups. The term, "random," refers to the mean nearest-neighbor distances. It is clear from Fig. 11, that Sternopygus does not select hiding places at random, but rather chooses spots that

TABLE IX

Analysis of clusters of Eigenmannia virescens. Moco-moco Creek, 1971.
Area = 1246 square meters.

	Date	Time	Number of Fish	Number of Clusters*	Number of Clusters Containing 50% of Individuals†
DAY	April 21	11:20	69	10	1
	April 28	15:30	49	6	1
	May 19	15:20	6	3	1
	June 11	14:00	1	1	1
NIGHT	April 21	19:15	56	30	8
	April 21	23:00	93	37	9
	April 28	19:40	70	31	9
	April 29	00:04	69	29	9
	May 19	19:50	5	5	3

* Two individuals are considered to be members of the same cluster if the distance between them is 1 meter or less.

† To determine this value, clusters are ranked from largest to smallest. The number of clusters is thus the minimum figure necessary to include 50% of the total population.

Mann-Whitney U test of differences between day and night values: Number of clusters, $p = .03$. Number of clusters containing 50% of individuals, $p = .008$.

TABLE X

Clark and Evans dispersion index for Eigenmannia virescens in Kumaka Swamp.
Data obtained from two 5 x 5 meter plots.

Date	Number of fish	$R = r_o / r_e$	p
May 17, 1971	8	1.414	.01 < p < .05
May 19, 1971	12	2.124	p < .001
May 24, 1971	11	1.338	.01 < p < .05
May 24, 1971*	18	1.687	p < .001

*refers to plot number 2.

provide suitable protection such as under rocks, under logs, and under the bank as discussed in Chapter III K. Neither Sternopygus nor Eigenmannia select hiding places at random. The two species differ in the use of the suitable space, however. Eigenmannia tends to clump together into large clusters, whereas Sternopygus tends to distribute itself throughout the available space. An individual Eigenmannia will be likely to hide in a place that is close to other individuals rather than separated from other individuals. Sternopygus seems to select its hiding places without regard for the presence of other individuals.

It would be impossible to quantify the total area which is suitable for hiding. A given sunken log may, or may not, have holes which may, or may not, be visible to the observer. Most hiding places are not visible even with underwater inspection, thus it is not possible to determine whether Sternopygus is maximally dispersed within the suitable habitat. It appears from this analysis, that Sternopygus has no tendency to form large groups as has Eigenmannia. In addition, individuals are tolerated at relatively close range. Territoriality, individual distance, and other forms of social spacing which could be operating in Sternopygus are not excluded from this analysis. It is possible that Sternopygus is maximally dispersed within the suitable habitat.

Data on the age and the sex of the individuals in the study areas are not available, thus it is not possible to analyze spacing patterns within these groups. There were several instances where several adult male Sternopygus were found close to each other, however. This is discussed in more detail in Chapter IV D.

During the night, the spatial patterns for Eigenmannia differed from that during the day. The change is from large clusters to smaller clusters that are well dispersed. In the breeding season, in Kumaka Swamp, where hiding places are fine-grained, the pattern for Eigenmannia is dispersed, or spaced apart further than expected based on a Poisson distribution.

IV. THE ELECTRIC DISCHARGE CHARACTERISTICS OF RUPUNUNI GYMNOTIDS

A. Tone and Pulse Fish

The electric discharges of the gymnotids of the Rupununi fall into two natural groupings based on their auditory characteristics as transduced by a fish detector (see Methods). The two types are Tone discharges and Pulse discharges. Tone discharges consist of pulses that have durations long with respect to the period between pulses and in which the frequency is normally constant. Pulse discharges consist of pulses that are brief with respect to the period between pulses, and in which the frequency is variable. The names, Tone, and Pulse, recall the differences in the "sound" produced by the fish detector.

This classification scheme is the same as that proposed by Lissmann (1961a). His "type I" discharge corresponds to "Tone" discharges and his "type II" discharges correspond to "Pulse" discharges. Other authors have used other classification schemes. Steinbach (1970) used the waveform, polarity, and frequency of the discharge to distinguish six arbitrary classes of gymnotids from the region of the confluence of the Rio Branco and the Rio Negro in Brazil. This classification scheme is difficult to use in the field, however, even with the use of a portable oscilloscope. Steinbach's illustrations, moreover, do not include waveforms for many species, G. carapo, for example. Bullock (1969) distinguishes four classes of discharges based on discharge frequency and patterns of frequency variation. This classification scheme is similar to the one I have used with some minor exceptions. Bullock's group "a": low frequency, variable interval, discharge includes the same species that I include in the group of fish with Pulse discharges. Group "b" or high frequency, constant interval discharges corresponds to Tone discharges. Group "c" in Bullock's system is intermediate between Tone and Pulse fish. Only one species, Hypopomus occidentalis is known to belong to this group. The interval between discharges is stable but the fish is capable of producing large, sustained, frequency changes. These characteristics were similar to those I observed for Hypopomus sp. no. 3 from the Rupununi, but further work needs to be done on this species. Group "d" discharges, those for

which there are no known frequency changes, were not encountered among Rupununi gymnotids. Bullock gives examples of two species that belong to group d: Steatogenes sp. and Gymnarchus niloticus. Although I never found Steatogenes among Rupununi fishes, I did have a chance to make recordings from Hypopygus lepturus (Hoedeman), a closely related species.¹ Hypopygus lepturus recorded at 28°C had a steady state discharge of 43 Hz, but produced SID's (a sudden increase in frequency followed by a decrease back to the steady state frequency; Black-Cleworth, 1970) that resulted in frequency changes of 2 to 3 Hz. The SID's were given in response to mechanical stimulation. Bennett (1971) reports a similar finding for Steatogenes sp.

With the exception of Hypopomus sp. no. 3, I have classed the gymnotid fishes of the Rupununi into two groups, Tone and Pulse. Further work is necessary to clarify the classification of Hypopomus sp. no. 3. Tentatively it is classed as a Pulse fish because the pulses are brief with respect to the period between pulses, and the frequency is variable.

B. Waveforms and Frequency Stability of Tone and Pulse Fish

Eigenmannia virescens and Sternopygus macrurus both produce Tone discharges. The waveforms of their discharges recorded from a monopolar electrode near the head of the fish are shown in Fig. 13. As can be seen from these waveforms, the duration of the individual pulses is nearly as long as the interval between pulses. A spectrogram display, shown below the waveform, indicates that the normal discharge of these two species consists of a constant frequency, shown as a straight line on the spectrogram. Gymnotus carapo, a Pulse fish, has a discharge in which the pulses are brief with respect to the period between pulses and in which the

¹ Possibly Hypopygus lepturus should be included in the genus Steatogenes since it has been recently discovered that Hypopygus has supplementary electric organs in the head region (Nijssen, personal communication). Submental filamentous electric organs are the major character used in defining the genus, Steatogenes (Steindachner, 1880). Since Hoedeman (1962) found none, he described it as a new genus.

frequency is variable. The waveform of the discharge (Fig. 13), was recorded from a freely moving fish with a dipole electrode. The spectrogram of the discharge, shows that the frequency is variable.

Note that when the discharge of Sternopygus, Eigenmannia, or Gymnotus is displayed on a sound spectrograph, that there are numerous harmonics above the fundamental. These harmonics are present because the discharge is not sinusoidal, but rather a pulse train. The amplitudes of the harmonics are displayed as section displays in Fig. 13. The even harmonics (2, 4, 6, etc.) have a weaker contribution than the odd harmonics (fundamental, 3, 5, etc.) in Sternopygus and Eigenmannia. Note that the discharge of Gymnotus, made up of pulses, produces many harmonics above the fundamental of approximately equal amplitude. The relative amplitudes of the harmonics depends to a certain extent upon the orientation of the recording electrodes with respect to the fish, but this has not been studied systematically.

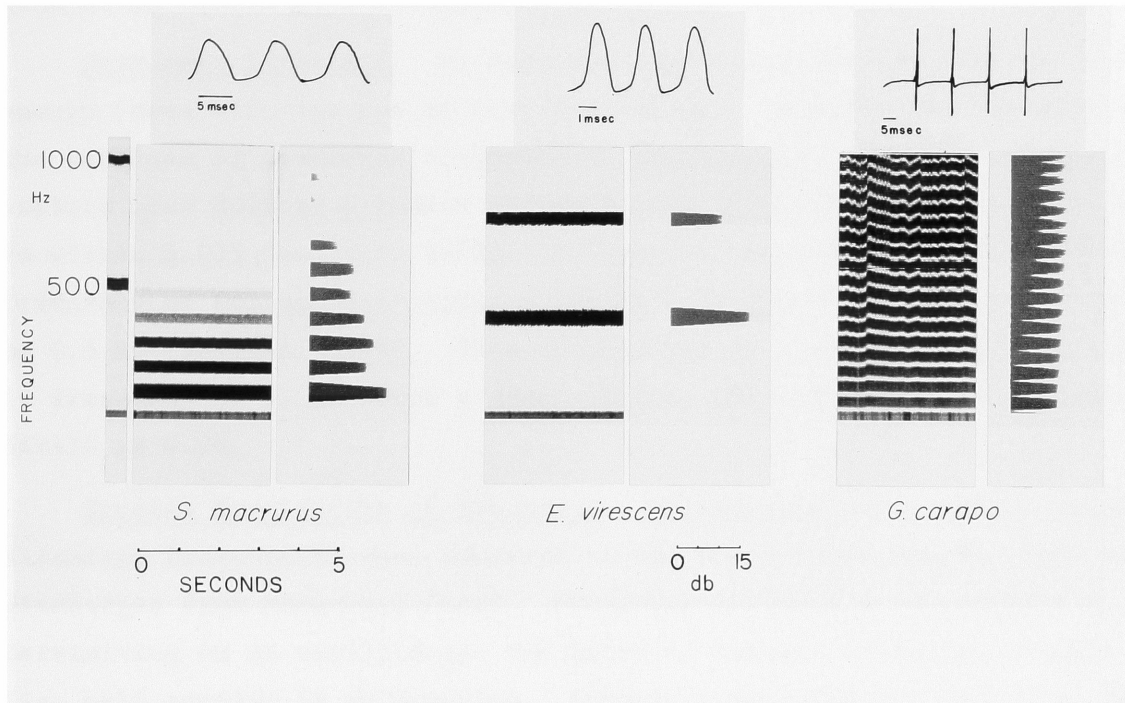


Fig. 14. The electric discharge of three species of gymnotids from Moco-moco Creek: *Sternopygus macrurus*, *Eigenmannia virescens*, and *Gymnotus carapo*. Top: waveform of the discharge traced from a photograph of an oscilloscope screen. The waveforms of *S. macrurus* and *E. virescens* were recorded from a monopolar electrode near the head of the fish. The waveform of *G. carapo* was recorded with dipole electrodes from freely swimming fish. Bottom: spectrogram displays of the discharge of each species. Spectrograms made with Kay Electric 7029-A sound spectrograph; range, 10-1000; bandwidth, 37.5 Hz. The left-hand display is frequency vs. time where the amplitude is the darkness of the trace. The right-hand display is amplitude vs. frequency of a section of the display shown on the left.

V. ELECTRICAL COMMUNICATION IN STERNOPYGUS MACRURUS

Normal Discharge. The electric discharge of Sternopygus macrurus consists of head-positive pulses of 8 to 12 msec duration that are superimposed on a head negative base line (Bennett, 1961; 1971). The net potential integrated over one complete discharge cycle is zero due to the head negative baseline (Bennett, 1971). The pulse repetition rate varies from 50 Hz to 150 Hz when measured at 25°C.

Frequency Stability. My frequency measuring devices were not accurate enough (even with the use of beat frequencies) to permit measurement of the variance of discharge frequency in Sternopygus. Bullock and his co-workers have devised a method for measuring frequency that is accurate to within 0.01% (Bullock, 1969). A "typical" standard deviation of the frequency of Sternopygus macrurus during a 10 minute sample was found to be 0.5 Hz (Bullock, 1969). This corresponds to a coefficient of variation in frequency of 0.5%. Over a short period, the frequency may vary by as little as 0.2%.

Species Specificity of Discharge. Sternopygus has a unique range of discharge frequencies when compared to the three other species with Tone discharges from Moco-moco Creek. Frequency measures were obtained by determining on an oscilloscope the interval between discharges from a fish held captive in an aquarium. Frequency measurements were also made on undisturbed fish in the field, by making a tape recording to be spectrographed later. The measurements made in the field, showed no apparent differences from those made in aquaria. All discharge frequencies were corrected to 25°C using a Q_{10} of 1.5 (Enger and Szabo, 1968). Sternopygus discharges at frequencies between 50 and 150 Hz. (\bar{x} = 91.2, s.d. = 27.9, N = 47). The frequency range of Eigenmannia virescens is higher (250 to 600 Hz) and the combined ranges of Apteronotus albifrons and Sternarchomphus macrostomus is even higher (750 to 1250 Hz). Fig. 15 shows the distribution of normal discharge frequencies, corrected to 25°C, for the four species of Tone fish in Moco-moco Creek. It is clear that Sternopygus has a unique range of discharge frequencies when compared to the 3 other

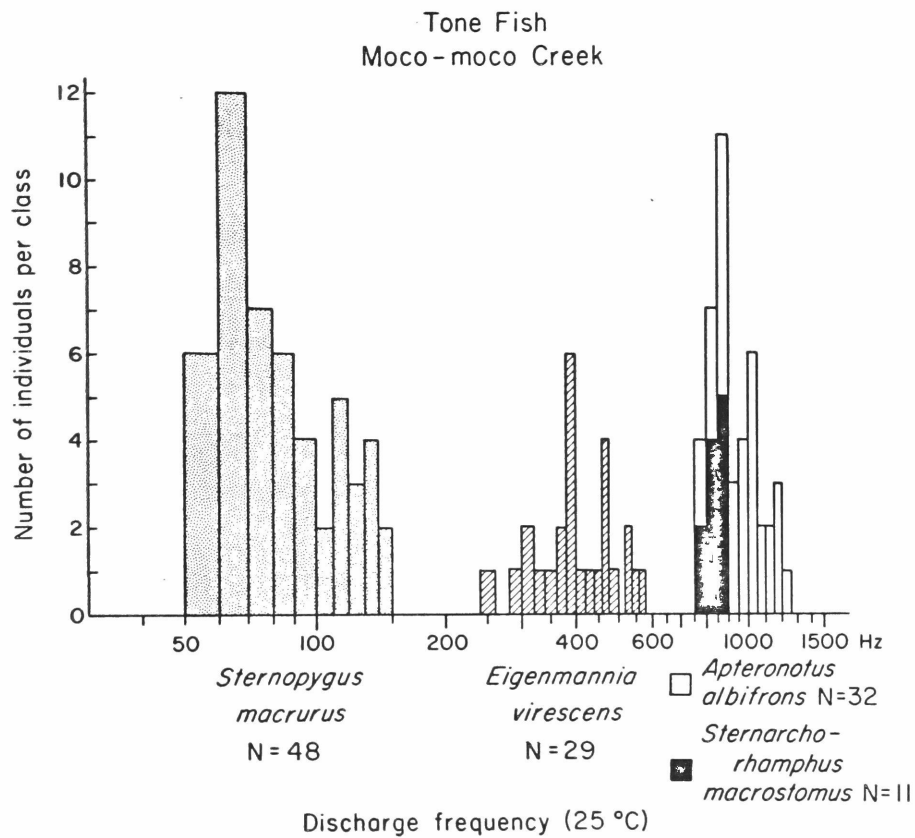


Fig. 15. Distribution of discharge frequencies, corrected to 25°C, of all species of gymnotids with Tone discharges from Moco-moco Creek. *Sternopygus*, has a unique frequency range from 50 to 250 Hz, *Eigenmannia* has a unique range from 240 to 600 Hz.

species with Tone discharges.

Since the range of frequencies of Sternopygus is broad when compared to the standard deviation of frequency of any one individual, it would be especially suitable for the discharge frequency to mediate recognition of intraspecific classes, on the basis of sex, age-class, etc. Since there is no overlap in frequency of Sternopygus and any other species of Tone fish in Moco-moco Creek, it would be especially suitable for the discharge frequency to be the basis of a species recognition signal. Frequency then, may have some important role in signal identification.

A. Sex Differences in the Electric Discharge

The sex of captured fish was determined by dissection since I could find no external morphological cues to aid in identification. Those fish with gonads so small that they could not be sexed in the field were called immature.

Male and female Sternopygus in breeding condition differed in the frequency of their electric discharge (Fig. 16). The average frequency at 25°C of 16 males was 66.8 Hz (s.d. = 13.9 Hz), whereas the average discharge frequency of 12 females was 120.1 Hz (s.d. = 19.7 Hz) and the average of 10 immatures was 92.3 Hz (s.d. = 26.0 Hz). It is possible that the frequency difference between males and females is established early in development and maintained throughout life. Alternatively, the frequency difference may become apparent only with sexual maturity, and possibly, only during the seasonal breeding period. Fig. 17 shows the discharge frequencies of males, females, and immatures, vs. their total length. Length was measured from the tip of the snout to the top of the caudal filament. The reproductive condition of the fish are also shown in this figure. If the gonads are beginning to develop, are developed, or are spent, then the fish is classed as a reproductive, labeled "R" in the figure. If the gonads are small, virgin, and show no signs of developing, then the fish is classed as non-reproductive, "NR" in the figure. Clearly when reproductive males are compared to reproductive females, there is no overlap in the discharge frequency. There does not seem to be any pattern to the frequencies of immature fish; thus the

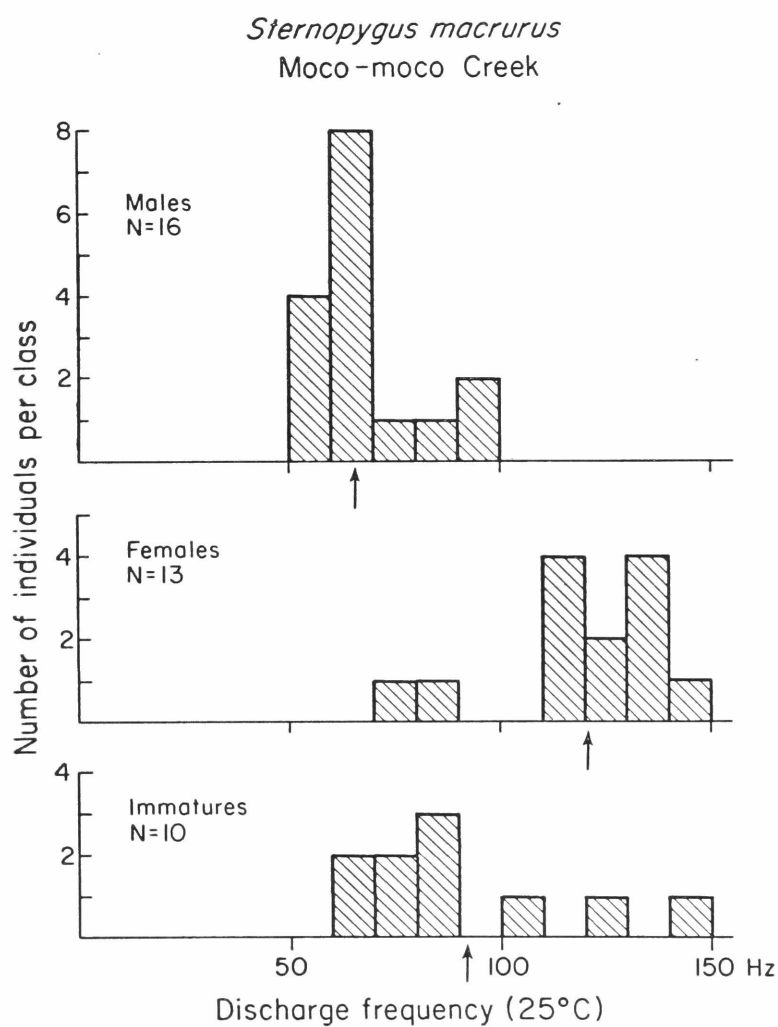


Fig. 16. Distribution of discharge frequencies, corrected to 25°C, of *Sternopygus* males (top), females (center), and immatures (bottom). Means of each distribution are shown by arrows.

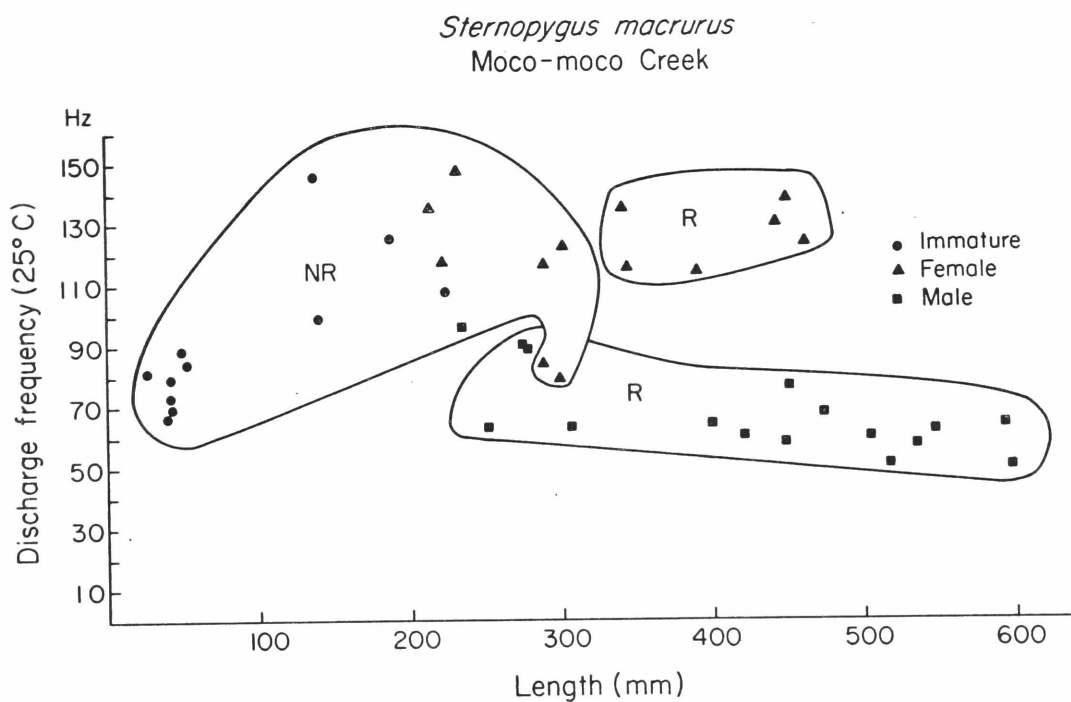


Fig. 17. Discharge frequencies of immature (circles), female (triangles), and male (squares) *Sternopygus macrurus* from Moco-moco Creek plotted against length from tip of snout to end of caudal filament in mm. Fish in reproductive condition are labelled, "R". Fish in non-reproductive condition are labelled, "NR".

frequency difference must largely result from some developmental frequency change. It is not known whether the frequency difference between males and females is seasonal. Other parameters of the discharge, such as waveform and polarity, did not differ between males and females. The amplitude of the discharge was related to the size of the fish.

It is interesting that sexual maturity is delayed in Sternopygus until the fish are quite large (300 mm). All of the fish that I caught that were less than 300 mm had completely undeveloped gonads. Although the ages of the fish are unknown, a fish that is 300 mm is estimated to be at least 2 and possibly 3 years old. This figure is arrived at after consideration of the fact that the smallest Sternopygus captured during April and early May in 1971 were 100 to 200 mm long. These individuals hatched in the previous breeding season, one year earlier. Thus, if a Sternopygus achieves a length of 100 to 200 mm in one year, it may take 2 or 3 years to achieve a length of 300 mm. Delayed maturity in Sternopygus contrasts with Eigenmannia which seem to breed in the first rainy season after they hatch (age: 1 year).

B. Variation in the Discharge

The discharge of Sternopygus varied in several ways that were easily distinguished from the closely regulated frequency described above. These variations are of two types: "Rises" and "Interruptions".

A Rise is any increase in the resting frequency followed eventually by a decrease back to resting (Fig. 18). Some Rises are "simple" since there is only one frequency maximum in the Rise, while others are "complex" because there are several points within the Rise at which the frequency goes through a maximum. One Sternopygus male in Moco-moco Creek, recorded on May 2, 1971, produced simple Rises that lasted from 0.3 to 2.5 seconds (\bar{x} = 0.8 seconds, N = 35) with a maximum increase in frequency of 1 to 43 Hz (\bar{x} = 6.5 Hz, N = 35). Complex Rises given by the same individual had durations between 0.7 and 4.0 seconds (\bar{x} = 1.9 seconds, N = 39), and had maximum frequency changes of 1 to 85 Hz (\bar{x} = 18.9 Hz, N = 39). The number of frequency maxima per complex Rise varies between 2 and 6.

An Interruption is any temporary cessation of the electric discharge

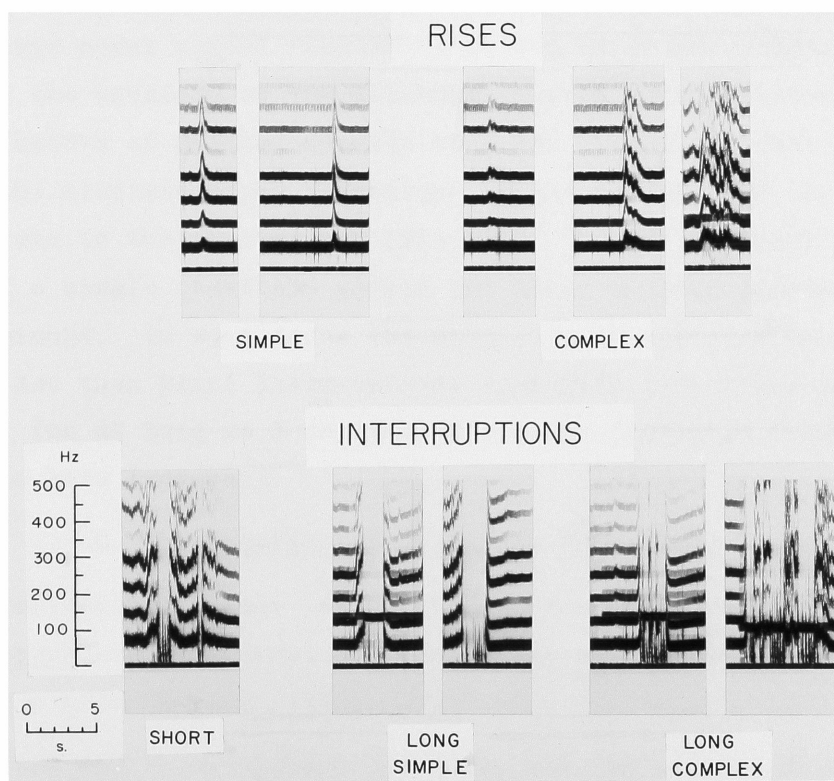


Fig. 18. Examples of discharge variations produced by *Sternopygus*. Each example is a selected spectrogram made with the Kay Electric spectrograph; range, 5-500; bandwidth, 19.0 Hz. The time and frequency scales apply to all examples. The dark bank passing through some of the spectra at about 100 to 150 Hz is the playback tone that elicited the Rises and Interruptions.

(Fig. 18). Interruptions given by the same male as above lasted from 0.3 to 1.7 seconds (\bar{x} = 0.8 seconds, N = 21). Usually Interruptions occur within Rises, following an increase in frequency and preceding a decrease back to the normal frequency. Often the frequency goes below the normal frequency for a second or two following the Interruption, only to return again back to the normal frequency. Short Interruptions had durations of 1 second or less, and long Interruptions lasted for more than 1 second. The discharge never ceases completely during an Interruption. Oscilloscope records of the waveform of the discharge during Interruptions reveal low amplitude bursts of pulses, usually at a low frequency, that do not resemble the electric organ discharge. These pulses make low frequency contributions to the spectrogram (Fig. 13). Simple Interruptions are made up of a single cessation within the Rise, whereas complex Interruptions occur in groups. In some cases the discharge is elevated to a higher frequency and then brief Interruptions alternate with brief periods of discharge, for as long as 5 seconds before the discharge frequency returns back to the base frequency.

C. The Function of Discharge Variations

The following evidence indicates that Rises and Interruptions function in Sternopygus much as normal song functions in unmated Chaffinches in attracting a mate (Marler, 1956).

1) Rises and Interruptions are given only by males. I detected trains of Rises and Interruptions from eight individuals. Of these eight, three were captured and were found to be males in breeding condition, and the other five had frequencies within the male range (55 to 70 Hz).

2) Rises and Interruptions were given only during the breeding season. All Rises and Interruptions that I detected were given during April or May. This was judged to be the breeding season from inspection of the gonads of the fish and from sizes of larval and post-larval fish (Fig. 7).

3) Rises and Interruptions were given only by males who occupied hiding places. They were given when a female swam past the male.

I made extended recordings of the patterns of Rises and Interruptions

from two male Sternopygus at night. One recording was made on May 1, 1970 from a site 600 meters upstream from the camp. Other males were present nearby, and they also gave Rises and Interruptions. A 200 second segment of the electrical activity recorded at 21:19 on that day is shown in Fig. 19A. There are periods of normal discharge, broken occasionally by simple Rises and an occasional complex Rise. Complex Interruptions are common in this sequence. The complex Interruptions show a certain degree of stereotypy for this individual. They begin with an increase in frequency, and end with a decrease back to and even below the base frequency. There are several Interruptions grouped together within the complex, and the duration from the beginning to the first Rise to the return to the base frequency is about 3 to 4 seconds.

The second example was recorded at 21:20 on April 28, 1971 from a male hiding in a hollow log in Moco-moco Creek (Fig. 19B). The activity from this solitary male was normally a constant frequency; however sequences of electrical activity did occur. Interruptions were generally simple, and the duration of Interruptions was usually long. Rises were common but were usually simple rather than complex. Again, no temporal patterning was seen. The male in example (B) showed a definite response to a passing Sternopygus female. The female (frequency = 150 Hz), shown by the arrow in line 3 of the example, came close enough to the electrodes to create a trace on the spectrogram. The male probably detected the presence of the female long before its discharge was apparent on the spectrogram. An Eigenmannia (frequency = 330 Hz) also passed close to the electrodes in this example (arrow in line 2), and it is possible that the Sternopygus is also responding to presence of the Eigenmannia.

D. Site Attachment and Territoriality

During April and May, large, low-frequency male Sternopygus showed persistent attachment to well-protected sites even at night when it is normal for them to leave for feeding. The sites were usually separated from each other by more than 5 meters. In two sites, however, I noted the presence of several males within 2 meters of each other. One site, a deeply undercut bank that was protected by the roots of a nearby Mora

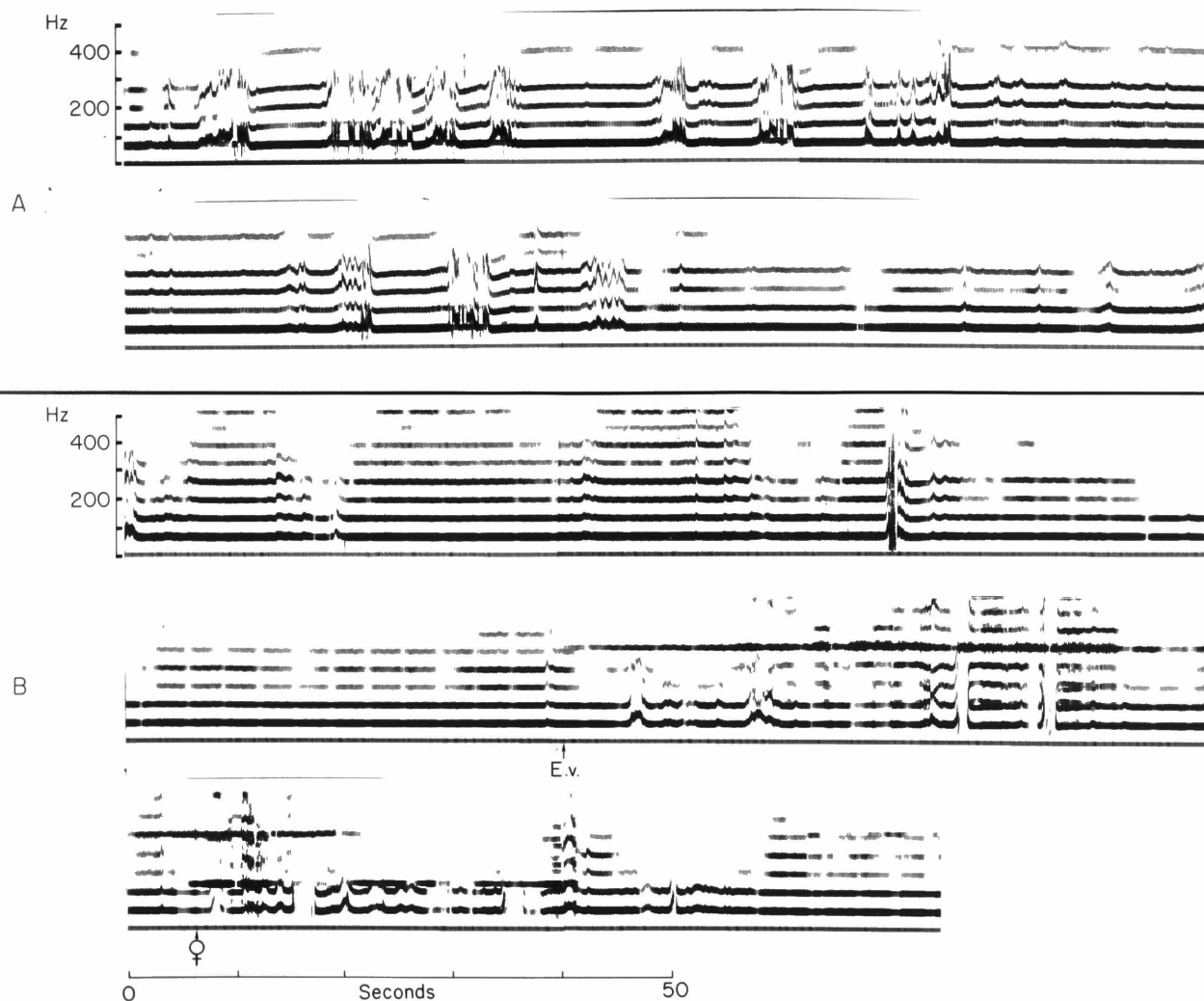


Fig. 19. Examples of naturally occurring sequences of Rises and Interruptions recorded in the field from two different male Sternopygus. A) Recording made on May 1, 1970, 21:19. B) Recording made on April 28, 1971, 21:20. Moco-moco Creek. Kay Electric Spectrograph; Range, 5-500 Hz; Bandwidth, 19.0 Hz. "E.v" shows the discharge from an Eigenmannia; "♀" shows the discharge of a Sternopygus female.

tree (Mora excelsa, Caesalpinieae), was occupied by 4 to 6 large males. Spectrographic analysis of recordings made on May 1, 1970 from this site show that more than one male was giving Rises and Interruptions. Another site, a 5 meter stretch of bank that had numerous holes of unknown origin, provided hiding places for another group of Sternopygus. Again, Rises and Interruptions were given by more than one male present there. An effort was made to catch all of the individuals hiding in this place. A total of 6 Sternopygus were caught. Five were males with lengths between 449 mm and 535 mm, one was an immature fish, 224 mm long. Two large fish were not caught. One was judged to be a female because of the relatively high frequency of the discharge, and the other was judged to be a large male because of the large amplitude, low frequency discharge. As many as five small (less than 150 mm) Sternopygus were detected in this site but not captured.

A territory is any "defended area" (Nobel, 1939; Hinde, 1956). The use of the term "territory" in describing an animal's use of space implies an agonistic defense of a particular area against intrusion by potential competitors. Territoriality in animals usually functions in providing an area for the territory owner to mate, to build a nest, to raise its young, or to feed. Not all functions are necessarily satisfied by each territory. The functions of a territory have been clearly outlined for birds by Howard (1920) and by Hinde (1956). Territorial behavior is well known among fishes, especially among the Perciformes (Baerends and Baerends-Van Roon, 1950; van dem Assem, 1967; Clarke, 1970). Black-Cleworth (1970) has given evidence for territoriality in Gymnotus carapo kept in large aquaria under crowded conditions.

The fact that Sternopygus males occupied specific sites both day and night during the breeding season is highly suggestive of a breeding territory; however, I never witnessed any form of territorial aggression. If this activity occurred at night, it would have been difficult to detect. The fact that several males were often found near each other does not exclude the possibility of territoriality. Many species of birds that nest in colonies have closely spaced territories. The pairing

territories or nesting territories of gulls (Tinbergen, 1956) or the mating territories of many lek species of birds are closely spaced (Wiley, 1970; Snow, 1962). In the case of Sternopygus, a territory could consist of a small hiding place defended against intrusion by conspecifics.

The aggregations of displaying Sternopygus males observed in two locations during this study are reminiscent of the lek mating systems of several species of birds. Although there is very little direct evidence either for or against such a mating system, there are some difficulties, I feel, with a lek system for Sternopygus. In most lek systems, one of the sexes, usually the males, spends most of its time on a display and mating "arena" and does not share in parental care. Care for the young is the exclusive responsibility of the female (Wiley, 1970). With most species of birds which have leks, the female builds a nest and raises the young somewhere distant and distinct from the lek itself. Since Sternopygus probably lays eggs that are externally fertilized, eggs will be deposited where mating takes place. If mating takes place on a display and mating arena, then they will remain there until hatching. This assumes, of course, that Sternopygus do not move their eggs after fertilization as do some cichlids. I observed no special adaptations for carrying or incubating eggs in Sternopygus. If eggs were laid on a communal arena, and if they remain there, this means that (1) the male participates in parental care, a contradiction to a basic feature of most leks, (2) the female remains at the arena to care for the young, or (3) there is no parental care in Sternopygus.

Most likely, there is parental care in Sternopygus. This conclusion is based on: (1) analogy with other species of Rupununi fishes that breed during the dry season and show highly developed parental care (Lowe-McConnell, 1964), (2) analogy with Gymnotus carapo which demonstrated guarding of nests in Trinidad (Chapter III-F), and (3) speculation that eggs left unguarded under crowded dry season conditions during which Sternopygus was found to breed would be subject to intense predation. If there is parental care in Sternopygus, then the female would have to

take over the responsibilities, if the lek mating system is to operate. Because of external fertilization, those responsibilities would have to take place at the site where mating occurs.

Apparently mating does take place between isolated pairs. I observed two instances where one male and one female were found together in the same hiding place isolated from all other Sternopygus, and in which the female was just about ready to spawn. Possibly a female forms a temporary association with a male at a display arena and both of them move to another location for the purpose of spawning. This hypothesis is improbable since the effect of social facilitation of sexual behavior afforded by the lek would then be lost in this case, and because the pair would then be faced with the problem of finding and defending a new hiding place. These arguments do not favor a lek system interpretation, although they are not sufficient to exclude the possibility.

E. Experimental Verification of Species and Sex Recognition

One method that has proved useful in the study of species recognition by song in birds has been the use of playback of recorded vocalizations to territorial males while observing their behavior (Lanyon, 1963; Falls, 1963; Weeden and Falls, 1959; Verner and Milligan, 1971; Emlen, 1972, Bremond, 1967). Attacks, approaches, agonistic postures, and singing rate of a territory owner are usually the quantified responses to playback signals. Playback experiments have been used in studies of auditory communication among fishes, both in cases where sexual differences in acoustic signals were apparent (Tavolga, 1956, 1958a, 1958b; Stout, 1963) and in cases where species differences in auditory signals exist (Delco, 1960).

I used playback experiments to test hypotheses concerning sex and species recognition in Sternopygus. In the experiments, all possible characteristics of the discharge were eliminated except for the fundamental frequency by playing back only pure sine waves of various frequencies. There were no cues in the signal as to polarity, or harmonic structure. No attempt was made to play back pre-recorded electric fish signals.

Sine wave signals were generated with a Hewlett-Packard 204C battery-powered oscillator. They were connected to two copper wires, and fixed in position approximately one meter from the hiding place of the male that was being tested. The amplitude of the signal was adjusted to imitate a large fish. Playback signals were presented to large low-frequency males that showed site attachment. Each experiment consisted of two parts: 60 seconds of control or pre-playback, and 60 seconds of playback. At least two minutes were allowed between experiments, and the order of presentation of signals was randomized. All tests were performed at night. Slight variations were made in the frequencies that I selected within the desired range to prevent habituation to specific frequencies.

In the first series of experiments, I tested the responses of two males to Sternopygus and non-Sternopygus frequencies. The results of 80 different playback experiments to these two males are averaged and plotted as a histogram in Fig. 20. The responses of the two males did not differ appreciably. I have counted the average number of Rises, Frequency Maxima, and Interruptions, subtracted the average number of each response during the control or pre-playback minute, and plotted the results for each of the playback ranges. A Frequency Maximum is defined as a point within a Rise at which the frequency goes through a maximum or a peak value. The mean number of responses for both fish during the pre-playback minute were Rises: 0.36 per minute; Frequency Maxima, 0.50 per minute; and Interruptions, 0.0 per minute. It can be seen that playback of male frequencies (55-72 Hz) tended to reduce the number of Rises and Frequency Maxima, although the responses did not differ from the control period when tested with the Mann-Whitney U Test, two-tailed (Siegel, 1956) ($n_1 = 20$, $n_2 = 20$; Rises: $U = 191$, $p > .05$; Frequency Maxima: $U = 190$, $p > .05$). Playback of frequencies within the female range (130 to 141 Hz) caused a significant increase in all three response categories when compared to the control period (Mann-Whitney U Test, two-tailed, $n_1 = 20$, $n_2 = 20$; Rises: $U = 85$, $p < .001$; Frequency Maxima: $U = 75$, $p < .001$; Interruptions: $U = 112$, $p < .02$). Playback of frequencies corresponding to Eigenmannia's discharge (450-550) caused a slight increase in Rises and

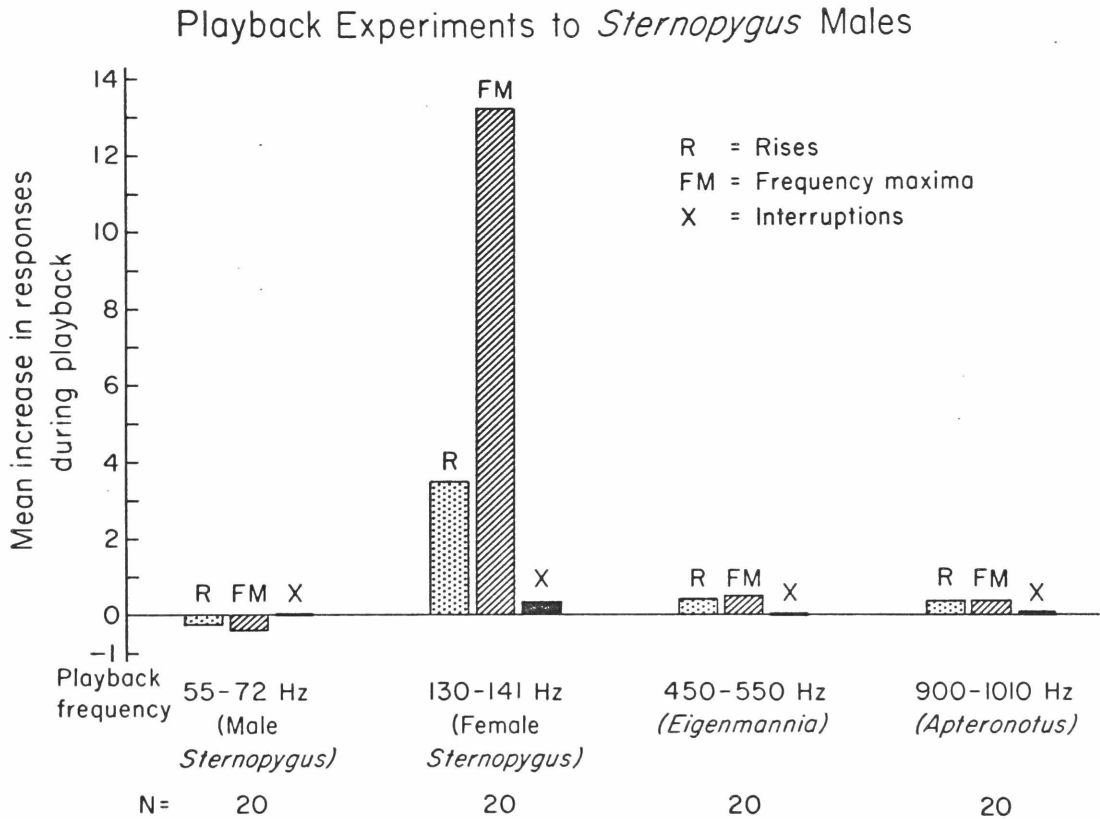


Fig. 20. Mean increases over controls of responses by *Sternopygus* males to playback experiments. The mean number of responses during the control period is subtracted from the mean number of responses during the playback period in each case. Three response measures are shown: (R), number of Rises; (FM), number of times when the discharge frequency reached a maximum; and (X), number of Interruptions. The experiments compare responses to playback of pure sine waves with frequencies corresponding to the electric discharges of male *Sternopygus*, female *Sternopygus*, *Eigenmannia*, and *Apteronotus*.

Frequency Maxima but the increase was not statistically significant ($U > 170$ for all three tests, $p > .05$). Similarly, playback of Apteronotus-like frequencies (900 - 1010 Hz) caused slight increases in frequency but the increase was not statistically significant ($U > 204$ for all three tests, $p > .05$).

In summary, playback of sine waves caused a significant increase in the number of Rises, Frequency Maxima, and Interruptions, when the sine waves had frequencies within the range normally found for Sternopygus females. Playback of male range frequencies tended to inhibit the spontaneous level of rises and frequency maxima (not significant) and playback of frequencies typical of Eigenmannia and Apteronotus discharges tended to increase the number of responses (not significant).

In another series of playback experiments, I tested the responses of males to playback of frequencies within the female range. The purpose of the experiment was to measure the range over which a male will respond. The results of 47 experiments using two different Sternopygus males that showed site attachment are shown in Fig. 21. The results of playback of 12 different frequencies to one male are shown in the top figure (Fig. 21a). The order of presentation of the playback frequencies was randomized as before. The responses of another male are shown on the bottom figure (Fig. 21b). Three trials at each frequency were averaged for each point. In each case the mean number of responses during the control or pre-playback period was subtracted from the playback level, thus in each case the ordinate represents the increase in numbers of responses over control. It can be seen from these two figures that two males respond by giving Rises, Frequency Maxima, and Interruptions during playback of sine waves with frequencies between 80 and 250 Hz. There were no responses to playback of frequencies within the male Sternopygus range (55 - 80 Hz).

There were no responses to frequencies that correspond to exactly twice the male's own discharge. This occurred in both fish tested, even though the two males differed in discharge frequency.

To summarize, two males respond, by giving Rises and Interruptions, to playback of sine waves from 80 to 250 Hz. This range is considerably

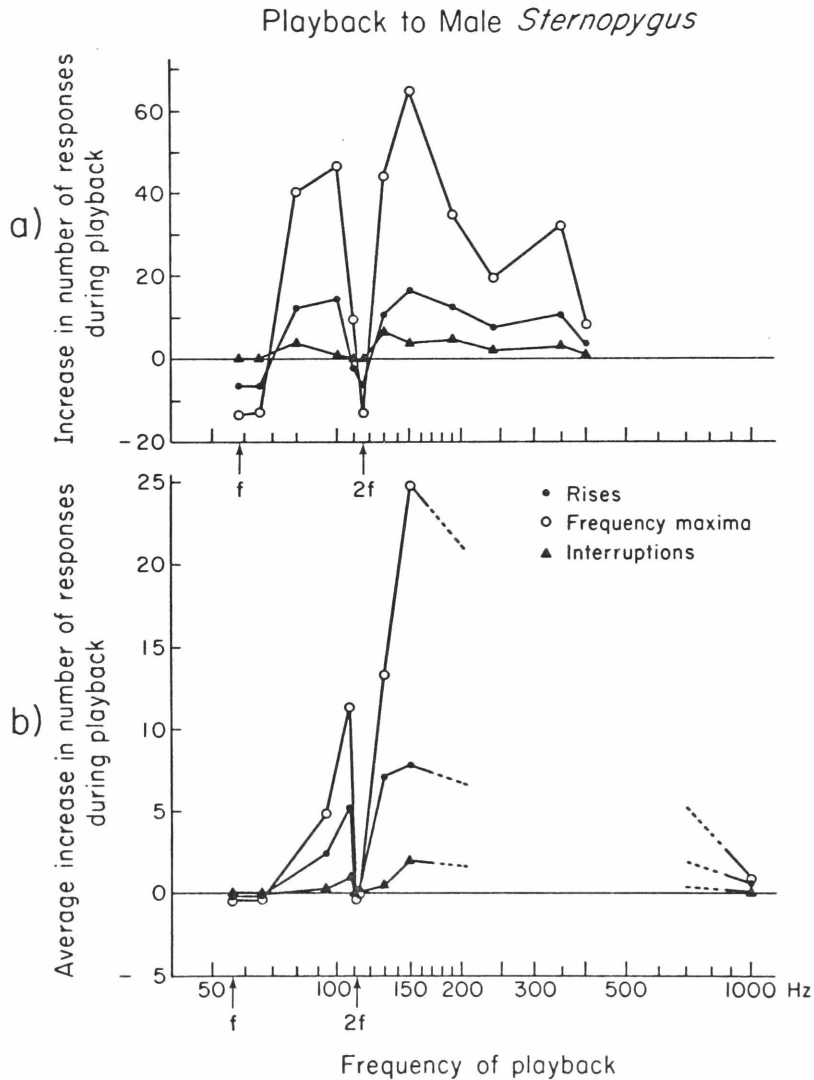


Fig. 21. Increases over controls of responses by *Sternopygus* males to playback of sine waves. The mean number of responses during the control period is subtracted from the mean number of responses per trial during the playback. The frequency of the sine wave is shown on the horizontal axis. (Top) Male 1, one trial at each frequency. (Bottom) Male 2, three trials at each frequency. The discharge frequency of each male is indicated by an "f".

broader than the range of most Sternopygus females. One point within that range that corresponds to twice the male's own frequency was ineffective in eliciting responses.

Although the responsiveness of males is broad compared to the range of females, it is unlikely that a male Sternopygus would ever encounter an individual of another species discharging at frequencies between 150 and 250 Hz. Thus, there may be no particular disadvantage to broad responsiveness. In other localities, where other species of gymnotids occupy this frequency range, it might be expected that the response of males would be more closely related to the range of female frequencies. This situation would be analogous to the calling and song patterns of crickets (Alexander, 1962) and of tree frogs (Littejohn, 1965; Littejohn and Loftus-Hills, 1968) in areas where several species are sympatric and show character displacement, compared to areas where they are allopatric.

The peculiar lack of responsiveness to playback of frequencies exactly one octave above the male's own frequency may be explained by several theories. Possibly the octave contrasts poorly with the male's own discharge, and he, in effect, does not detect it as well as he detects frequencies that are different from the octave. Bullock, Hamstra, and Scheich (1972b) have demonstrated a similar lack of responsiveness in the jamming avoidance response of Eigenmannia and of Sternarchus (Apteronotus) albifrons, when stimuli within 0.05 Hz of the fish's discharge frequency are used. Alternatively, there may be some behavioral inhibition of responsiveness to exactly the octave above the male. A female with a frequency exactly one octave above a male may have special significance to the male, such as his mate. Although isolated pairs of Sternopygus were not common, I found two cases in 1971 of male-female pairs where both fish were in breeding condition and where the male's discharge frequency was exactly one octave below that of the female. In several other instances males were found near females in varying states of reproductive condition and in which there was no simple relationship between their frequencies. It was noteworthy that in the two cases in which an octave relationship existed, both males and females were very close to spawning condition.

It is possible that when a male and a female Sternopygus come together for breeding, that either the male or the female changes its frequency so that an octave relation exists between the pair. Mate recognition by frequency would be facilitated if this relationship occurred regularly. Mate recognition is known among birds, and Munding (1970) has evidence for individual recognition by flight calls among American Goldfinches (Carduelis tristis). He also reports evidence for vocal imitation of flight calls among several species of cardueline finches, and imitation of flight calls between pairs of goldfinches. Until further work can be done on the social organization of Sternopygus, the possibility of mate recognition by frequency in Sternopygus remains a speculation.

VI. ELECTRICAL COMMUNICATION IN EIGENMANNIA VIRESCENS

A. Normal Discharge

Eigenmannia virescens produces a tone discharge. It is made up of head-positive monophasic pulses of approximately 2 msec duration superimposed upon a head-negative baseline (Bennett, 1971). The net potential integrated over one complete cycle is zero due to the head-negative baseline. The frequency of the discharge differs from individual to individual; and the range of frequencies for the species in the Rupununi District is from 250 to 603 Hz (Fig. 15).

Frequency Stability. Bullock and his co-workers have made extensive measurements of the frequency stability of Eigenmannia (Bullock, 1969; 1970; Bullock et. al. 1972a). These measurements are technically very difficult, and the interpretation of the results similarly is far more complicated than originally assumed. Eigenmannia is capable of producing a long series of discharges during which the frequency is remarkably stable. The coefficient of variation of the discharge during these "stable" periods is as low as .05% and the intervals between discharges seem to be normally distributed (Bullock et. al. 1972a). The discharge undergoes many seemingly spontaneous changes in frequency and these variations change the overall estimate of the variance to a higher value. A "typical" standard deviation of frequency of the discharge of Eigenmannia during a 10 minute sample is 1 Hz at a normal discharge frequency of 300 Hz (Bullock, 1969). This corresponds to a coefficient of variation of 0.33%. Most likely the time intervals between discharges in a longer (10 minute) sample are not normally distributed due to the spontaneous changes in frequency.

Discharge Frequencies of Males and Females. Males and females differed only slightly in their discharge frequency and there was extensive overlap (Fig. 22). The mean discharge frequency of males collected in Moco-moco Creek and Kumaka Swamp and measured in aquaria, is 403 Hz (s.d. = 103, N = 22). The mean discharge frequency of females is 452 Hz (s.d. = 56, N = 23). When tested with the Mann-Whitney U test, males and

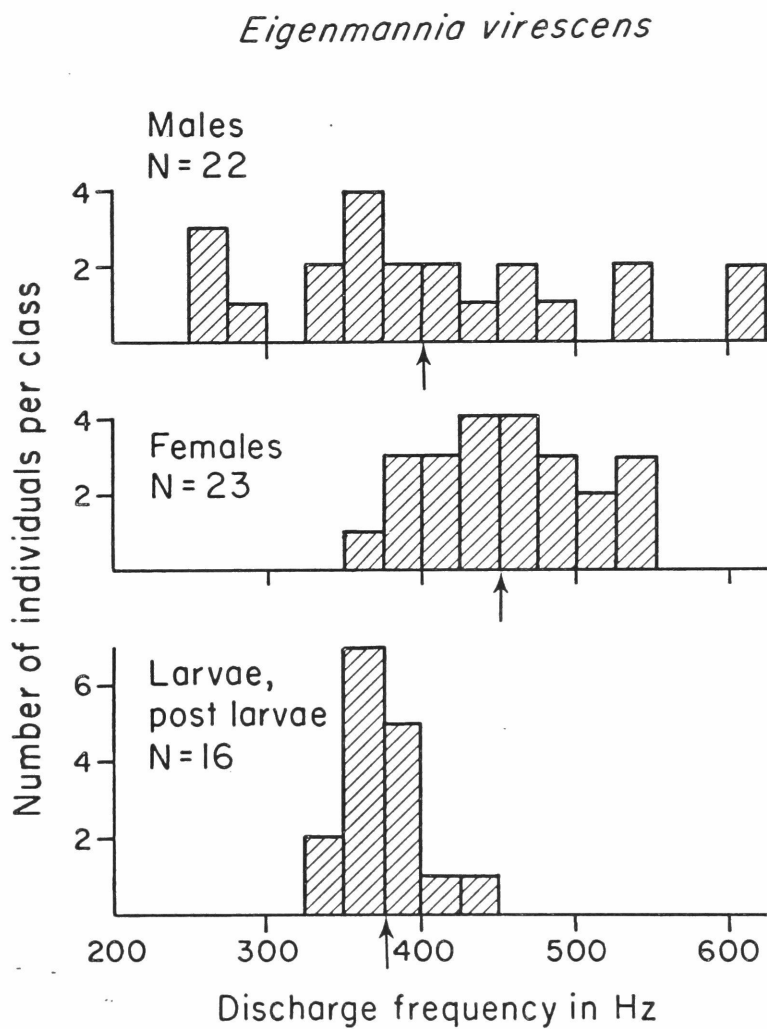


Fig. 22. Distribution of discharge frequencies, corrected to 25°C, of *Eigenmannia* males, females, and immatures. Means of each distribution are shown by arrows.

females were found to differ significantly in the distribution of their discharge frequencies ($z = 2.111$, $n_1 = 22$, $n_2 = 23$, $p = 0.04$, two-tailed test).

The mean discharge frequency of larval and juvenile Eigenmannia virescens is 378 Hz (s.d. = 25 Hz, $N = 16$). There is still extensive overlap between males and females and immatures as shown in Fig. 22. Nearly all of the males and females included in the sample were in reproductive condition. In summary, the discharge frequency of Eigenmannia is unique when compared to all other gymnotids in Moco-moco Creek. Sex differences, although present, are not such that the discharge frequency could be used for unambiguous sex recognition. Unlike Sternopygus in which sex differences were unambiguous, the differences observed in Eigenmannia are only statistical in nature.

B. Discharge Variation in Eigenmannia virescens

Interruptions. An interruption is a temporary cessation of the normal electric discharge. When given by Eigenmannia there is usually a total cessation of the electrical activity during the Interruption. Often, however, some electrical activity occurs during the Interruption, but it differs in amplitude and frequency from the normal discharge. Typically, an Interruption begins with a sudden termination of the electric organ discharge. After a variable length of time, the discharge again resumes; however the pattern followed during the resumption is highly variable. Four Interruptions are illustrated in Fig. 23. This record was obtained from a male Eigenmannia held captive in an aquarium. In the first Interruption that is illustrated, two impulses are nearly suppressed, and a third is partially suppressed. Approximately 33 are suppressed in the second example, 37 in the third and 18 in the fourth. The pattern of discharge resumption in these examples is a gradual increase in amplitude until normal amplitude is achieved. The frequency of the discharge shows a brief recovery from a lower frequency. Other patterns of electrical activity given during the resumption of the normal discharge include patterns such as prolonged discharges at low amplitude and lower or higher than normal frequency. The discharges occurring within the

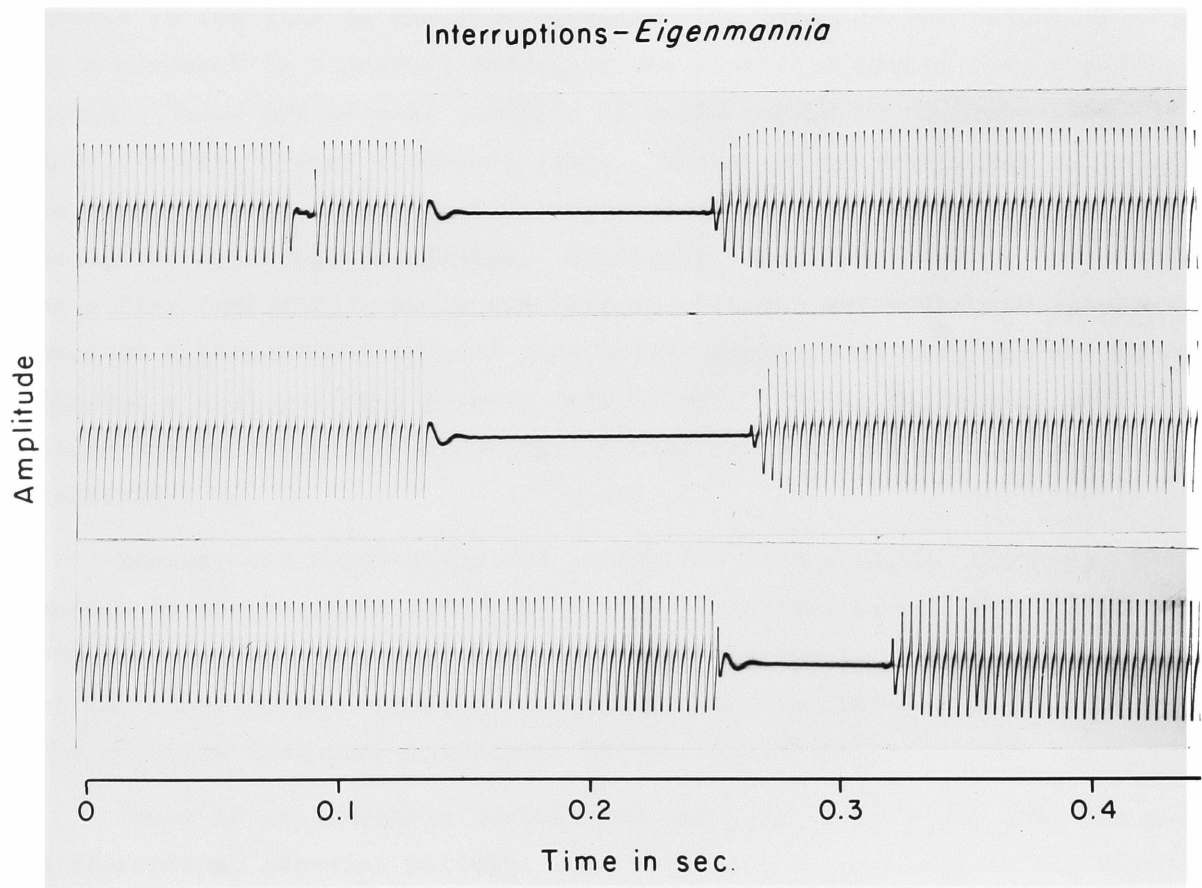


Fig. 23. Oscilloscope tracings of the discharge of *Eigenmannia* during Interruptions.

Interruption quickly subside, however, and the normal discharge resumes.

When an Interruption is displayed on a spectrograph, it appears as a sudden break in the continuous band (Fig. 24). Caution must be exercised when interpreting spectrograph displays, however. Movements of the fish with respect to the electrodes causes frequent "nulls" during the adoption of orientations at which no signal is detected, and these nulls appear as breaks in the line on the spectrograph. The break in the discharge caused by a movement is a gradual fading of the discharge rather than a sudden break. There are several examples of nulls caused by movement (Fig. 24, last example, higher frequency fish). There was no difficulty in learning to differentiate discharge interruptions from nulls due to movement when using the spectrograph display. Similarly, when listening to the discharge on a fish detector, I could discriminate between movements and Interruptions because Interruptions sounded like brief clicks to my ear, whereas movement through a null position gave no such effect. It was difficult, when listening to the fish's discharge to tell which of two fish produced an Interruption.

Because the termination and resumption of the normal discharge is sudden in an Interruption, there are many spectral components to the Fourier analysis at those transition points. The beginning and the end of the Interruption appear as a vertical line on the spectrogram due to the multiple frequency components of the transition.

There is considerable variability among Interruptions; they are not a stereotyped behavior pattern. The variation is greatest in two ways: (1) there are large differences in the duration of the Interruption; and (2) there are many differences in the electrical activity that occurs during the Interruption. Since I have not obtained sufficient data for analysis of variability of electrical activity occurring within Interruptions, I will discuss only variability in the duration of Interruptions.

The duration of Interruptions was measured on spectrograph records. Particularly convenient were spectrograph displays made on the Kay Electric Sonograph at range 10-1000 Hz and bandwidth 37.5 Hz. The measurement of duration was made from the initial transient at the beginning of the

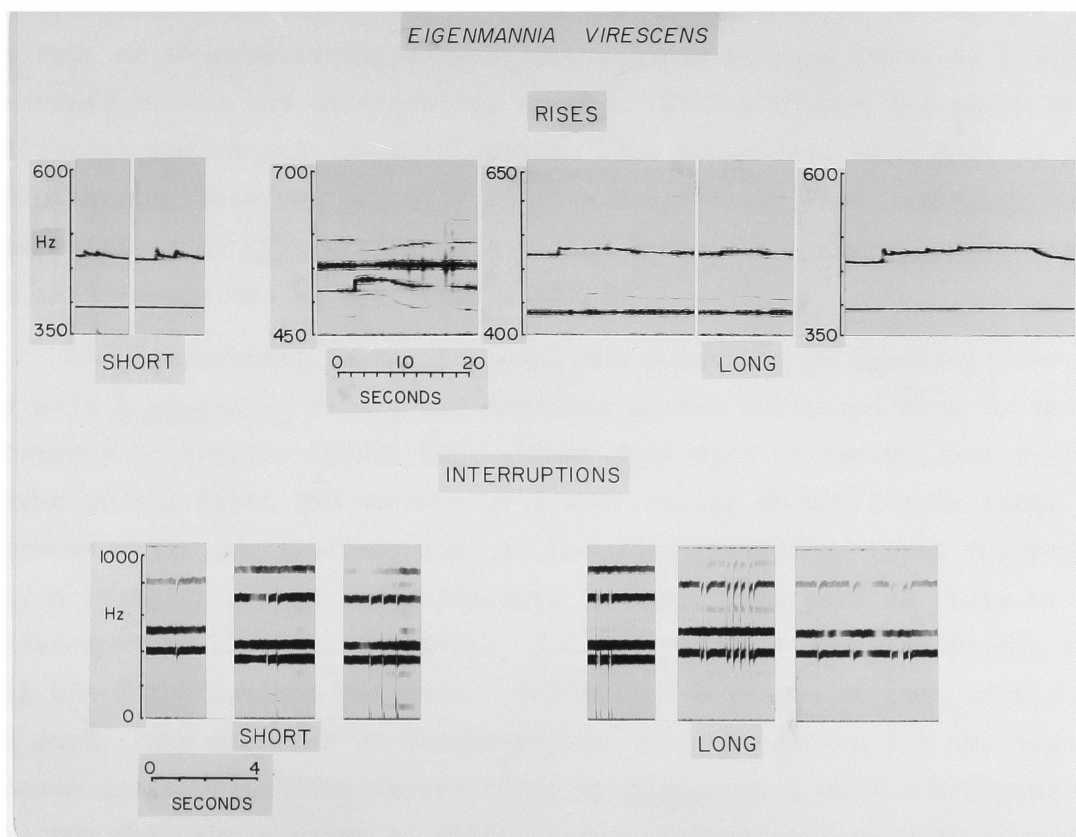


Fig. 24. Variations in the discharge of *Eigenmannia*, displayed spectrographically. Rises: Kay Electric Spectrograph, Range 250 Hz, heterodyned to the base frequency shown on each display; bandwidth, 1.4 Hz. Interruptions: Kay Electric Spectrograph, Range, 10-1000 Hz; bandwidth, 37.5 Hz. Two fish are present in each sample.

Interruption, to the final transient occurring at the resumption of the normal discharge.

I measured the durations of Interruptions given by Eigenmannia males and females during agonistic interactions between pairs of fish in aquaria. The distribution of durations of interruptions is shown in Table XI. This distribution includes all of the Interruptions recorded during the first 100 seconds of 14 arbitrarily chosen interactions between pairs of Eigenmannia recorded during the non-breeding season. Interruptions are given by 7 different individuals in this sample. The recordings were made in August, 1970, during observations made by Jose Torre-Bueno, and during my own observations of Eigenmannia in April of 1971. The median duration recorded in this sample was 40 msec (Table XI).

For comparison, I have measured the durations of Interruptions given by male Eigenmannia during the breeding season delivered when in the presence of females (Table XI). These data were collected from spectrograms of the first 100 seconds of 8 arbitrarily chosen interactions between males and females, both in breeding condition. Only Interruptions given by males are included (in this sample, there were no cases of Interruptions given by females). Four individuals are responsible for all 474 Interruptions measured. The median duration of this sample is 89 msec. The duration of Interruptions observed during the non-breeding season during agonistic interactions of Eigenmannia were considerably shorter than those given by males in sexual interactions with females during the breeding season. This observation suggests that some communicative significance may be attached to the duration of Interruptions in Eigenmannia.

This is similar to a result found for Gymnotus carapo by Black-Cleworth (1970). In Gymnotus, discharge breaks (an Interruption lasting less than 1.5 seconds) were given during aggressive threat, whereas discharge arrests (1.5 seconds and longer) were given during retreat. A critical interval of 70 msec conveniently divides the distributions that I found in these two situations. I call Interruptions with durations less than 70 msec "short", and those with durations 70 msec or longer, "long" (Fig. 24).

TABLE XI

Distribution of the durations of Interruptions given by both male and female Eigenmannia virescens in agonistic interactions compared to those given by males in sexual interactions.

<u>Duration in msec</u>	<u>Agonistic Interactions</u>	<u>Sexual Interactions</u>
up to 20 msec	16.3%	1.9%
20-40	33.7%	7.2%
40-60	28.6%	11.8%
60-80	8.2%	20.2%
80-100	9.1%	18.1%
100-120	3.1%	10.3%
120-140	1.0%	5.9%
140-160	-	7.4%
160-180	-	5.7%
180-200	-	5.5%
200-220	-	2.9%
220-240	-	1.3%
240-260	-	.8%
260-280	-	.4%
280-300	-	.2%
Total number	98	474
Median duration	40 msec	89 msec

Interruptions are often given in bouts of varying lengths. Occasionally only one Interruption is given but usually several Interruptions are given in the bout. To define what is meant by a bout, I have relied upon measurements of time intervals between successive Interruptions. This approach is analogous to that used in the definition of song by Isaac and Marler (1963). They found that the intervals between notes of the vocalizations of the Mistle Thrush showed a bimodal distribution. Short intervals (less than 0.5 seconds) accounted for 99% of the intervals, and the longer intervals (more than 0.5 seconds) accounted for the remaining 1%.

I measured the intervals between all successive Interruptions from real-time spectrograms of 4, ten-minute agonistic interactions between pairs of Eigenmannia made during April, 1971 before the onset of the breeding season. The Interruptions were given by a total of four individuals, two males and two females. The distribution of intervals between interruptions is shown in Fig. 25. There is no evidence for any bimodality in this distribution. Short intervals are the most common and longer intervals decrease in probability in a continuously graded fashion. Although communication signals may show continuous gradations in their physical parameters, it is often useful for the purposes of analysis, to think of signals as belonging to discrete categories, that can be independently tested for their significance. This was done for the intervals between interruptions. I selected the interval length that was greater than 50% of the intervals as a critical interval. Two Interruptions were said to belong to the same bout, if the interval between them was less than 1.5 seconds. It is useful to distinguish five different signals, based on the number of Interruptions in the bout. Single Interruptions are called 1X, two Interruptions are called 2X, and so on up to 4. Five or more are all classed alike and are called 5+X. Examples of 1X, 2X, 3X and 5X are shown in Fig. 24.

Rises. A Rise is an increase in the discharge frequency from the resting frequency that is followed by a decrease back to the resting frequency. I am not including temperature dependent frequency changes in my consideration of Rises. Temperature effects have been considered

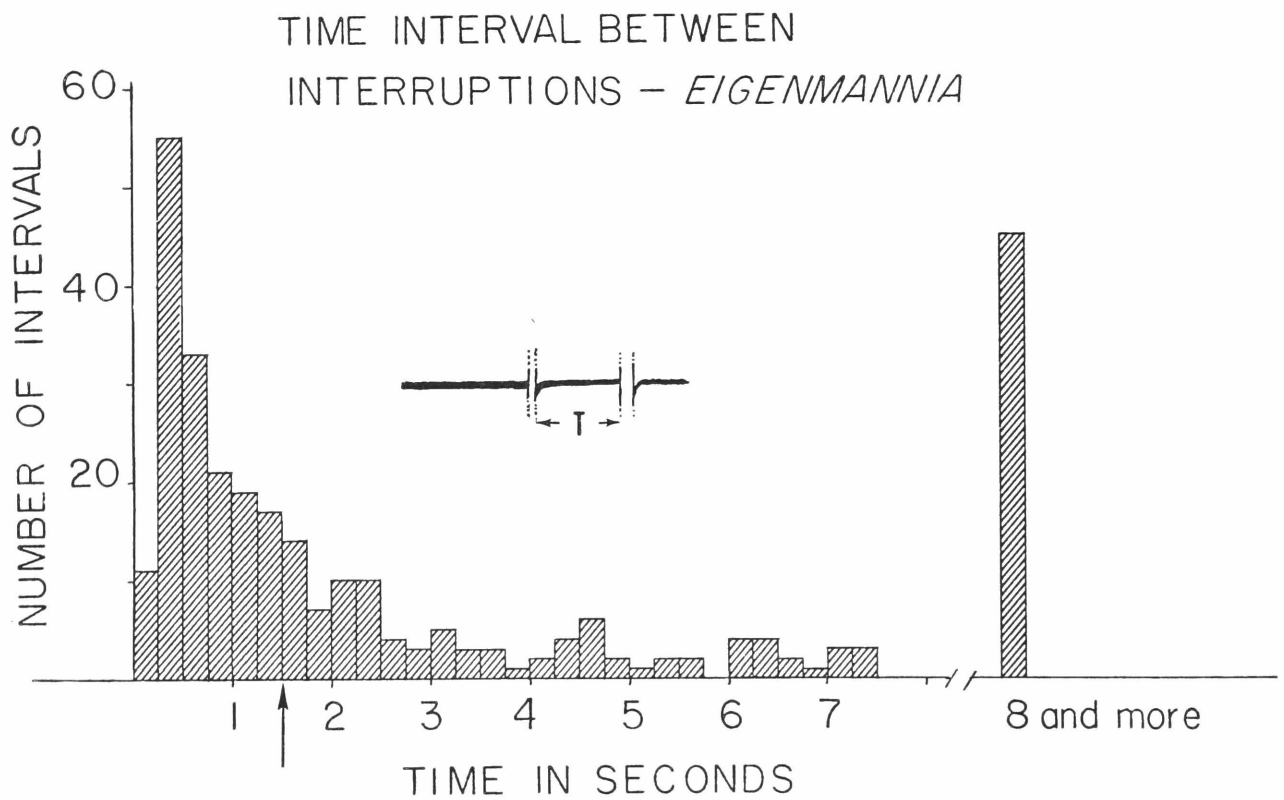


Fig. 25. Distribution of time intervals between successive Interruptions recorded during aggression tests for *Eigenmannia virescens*.

for a variety of species of electric fish by other authors (Coates, Altamirano, and Grundfest, 1954; Lissmann, 1958; Gallon, Mandriota and Thompson, 1967; Enger and Szabo, 1968; Boudinot, 1970). Rises are given during social interactions. I never detected any Rises from isolated fish. Rises can have durations that are as long as 40 seconds, although many are 10-20 seconds and some occur in two seconds or less.

I have distinguished the two classes of Rises: "Long" and "Short". Long Rises are those that last for more than two seconds. They consist of a rapid increase in frequency followed by a prolonged period at the high frequency, followed eventually by a slow decrease back to the resting frequency. The maximum increase in frequency is usually 5 to 20 Hz, and the duration of Long Rises varies between 2.0 seconds and 40 seconds. Short Rises have durations that are less than 2.0 seconds. They consist of a rapid increase in frequency followed immediately by a decrease to the resting frequency. The maximum frequency change is typically 5 to 10 Hz but can be as much as 40 Hz.

Several spectrograms of Long and Short Rises are illustrated in Fig. 24. These spectrograms were made using a narrow bandwidth analysis. When using the Kay Electric Sonograph I played back the tape recorded signal at double speed. This doubles all frequencies and similarly doubles all frequency changes during Rises. The signal was then heterodyned to a lower frequency to bring it within the frequency range of the spectrum analyzer. I used the 5-500 Hz analysis range and narrow bandwidth. The effective bandwidth of this system is 1.4 Hz. In the examples in Fig. 24, two fish are present in each case. Only one fish is giving a Rise however. In the first two examples of Short Rises and in the last example of a Long Rise, the heterodyne signal, a 350 Hz sine wave was recorded on the second channel simultaneously with the fish's discharge. This eliminated slight speed variations in the tape recorder occurring both during the recording and during the playback that smears the trace on the spectrogram. This smearing is shown in the three other examples of Long Rises in Fig. 24.

Bullock et. al. (1972a) describes several types of frequency

variations that occur spontaneously. One, described as a "quasi-periodic, sudden increase in frequency by 0.5 - 1% in less than 0.3 seconds, slowly falling back to the same 'resting' level" is similar to my description of Rises.

C. Descriptions of Movements and Actions During Agonistic Behavior

The movements of Eigenmannia can be broken down into a series of basic units or actions. Although it is difficult to come to any definition of action (Baerends and Baerends Von Roon, 1950; Nelson, 1964), the unit is self-evident after sufficient observations of an animal have been made. Actions are not the movements of individual muscles, but rather, complex, stereotyped sequences of movements of muscles that involve the whole animal. The actions that I will discuss in this section involve only motor actions, the electrical actions have been treated in Chapter VI A. Many actions of Eigenmannia are similar to those of Gymnotus carapo described by Black-Cleworth (1970).

Descriptions of actions are based on observations of 140 individual Eigenmannia in aquaria in Guyana in 1970 and 1971. Additional observations, made in New York on Eigenmannia sp., supplemented the observations made in field aquaria. All observations were made at night.

The locomotion of Eigenmannia, similar to all of the gymnotoid fishes, depends mainly upon longitudinal undulations of the anal fin. The pectoral fins are used for stability and sometimes for slowing the movements in one direction or the other (Ellis, 1913).

Hovering. While hovering, the fish remains in the same position. Normally the body is inclined at a slight angle with the head down near the substrate. The fish is stabilized by sinusoidal undulations originating at both the caudal end and rostral end of the anal fin. Traveling waves move down the fin and meet in the middle. Alternate beating of the pectoral fins helps in stabilization. The skin and musculature of Eigenmannia are nearly translucent in the region around the anal fin. With a light source behind the aquarium, I could clearly see the sinusoidal undulations of the fin as moving bands of light caused by differences in light transmission by the pinnalis analis muscles (Ellis, 1913). During active Hovering,

the bands of light and dark moved both from the tail and from the head meeting in the middle of the anal fin. During inactive Hovering, there was no movement of the anal fin except for very slight fanning motions along the dorsal-ventral axis that seemed to stabilize the fish.

Forward and Backward Swimming. Normal swimming was accomplished by sinusoidal motions of the anal fin. During forward swimming, the undulations progressed from the rostral end of the fin to the caudal, and during backwards swimming, the action was reversed. Lissmann (1961b) has recorded the motions of the dorsal fin of Gymnarchus niloticus using cine film, and has confirmed the direction of movement of the undulations in this species. It was my impression, using the transmitted light as an aid in following the motions of the anal fin, that rapid swimming either forward or backward was accomplished by increasing the speed at which the undulations traveled along the fin. Forward and backward swimming were accomplished with equal facility.

When frightened, Eigenmannia gives a very rapid jerk to the entire body in a serpentine fashion that propels the fish rapidly, for a short distance. Lissmann (1958; 1961b) has suggested that during this type of anguilliform swimming (Gray, 1933) the electrical object location system does not function normally.

Feeding. I was not able to observe normal feeding behavior in the field without disturbing the fish with my light. This description is based on aquarium observations both when artificial food were provided (Tubifex tubifex) or when no food was present, but the fish appeared to be searching for small items of food on the bottom. The fish moves slowly over the bottom with its head near the substrate and its tail held upwards at an angle of 30° to 50° . Slow movements are occasionally interrupted by brief twitches. Several quick beats of the pectoral fins brings the fish's head closer to the substrate, and its orientation closer to the vertical, for a fraction of a second. The fish then relaxes back to the normal attitude. Twitching was associated with prey capture when Tubifex were present. The motion brings the terminal mouth in contact with the substrate. Feeding also takes place from the

surfaces of plants introduced into the aquarium. In this case, the angle of the fish is more nearly horizontal as it moves slowly near the surface of a leaf or a stem, taking very small items off the plants.

Attack. When two fish are introduced into the aquarium they usually display clear agonistic behavior. During the initial interactions between two fish there is fighting, and both fish give attacks. Later on, the fighting is largely one-sided, and one fish gives most of the attacks. Attacks include cases where an actual physical blow is delivered by one fish to the other, or where a vigorous pursuit takes place but a blow is not delivered because the other fish is out of reach. There are three forms of attack.

1) Butt. A Butt is a rapid forward approach to the opponent which ends in physical contact between the tip of the snout of the aggressor and the body surface of the opponent. Most Butts are delivered to the rostral end of the opponent and commonly delivered to the abdomen, to the region around the pectoral fins, and to the side of the head. Butts are the basic form of attack in Eigenmannia. Fig. 26, part 4 illustrates a Butt that is directed at the origin of the anal fin at mid body. A visible recoil in the opponent can be seen from many Butts.

In the photograph the opponent (the lighter fish) recoils slightly by Rolling as if in response to the Butt.

2) Slide Slap. A Side Slap is a blow that is delivered using the side of the head. It is usually given from a Parallel Position or Anti-Parallel Position, by arching the body so that the head is bent toward the opponent. In a single rapid motion, a slap is delivered to the body of the opponent. This is shown in Fig. 26, part 2.

3) Chase. A Chase is a rapid pursuit of one fish by the other, in which the chased fish swims around the tank in attempt to get away from the aggressor. In the confines of an aquarium, a Chase may take the form of a circle.

Threats. Threats are agonistic actions in which there is no contact made with the opponent. The intention to attack is clear, the effect is

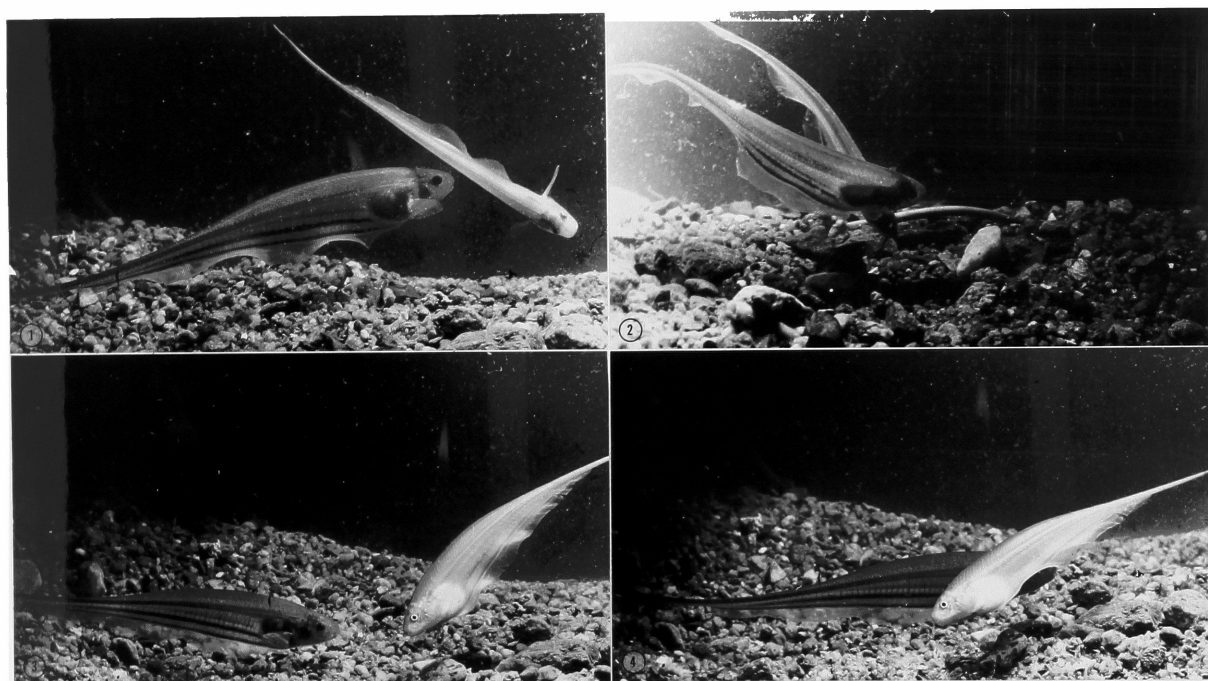


Fig. 26. Photographs of *Eigenmannia virescens* during agonistic encounters. 1) shortly after a Butt by fish in foreground, the fish in background gives a Roll. 2) Serpentineing with Side Slap by fish in foreground. 3) Facing. 4) Butt by darker fish, Roll by lighter fish.

similar to an attack, but no contact is made. There are two types of threats.

1) Dart Toward. A Dart Toward is a rapid motion toward the opponent similar to the motion seen in a Butt. It is discontinued abruptly just short of the opponent however. After the aggressor has come to a stop, it swims back approximately to the starting point. Darts were usually performed by swimming forwards toward the opponent, but were occasionally performed by swimming backwards towards the opponent.

2) Drive. A Drive is an approach to the opponent from underneath or from above that uses a process of translation of the body in the dorsal or ventral direction. When the aggressor gave a Drive towards the opponent the opponent usually swam backwards slowly to retreat.

Orientation and Display. When two fish interact, they often adopt postures or characteristic orientations with respect to each other. Some postures and orientations immediately precede or follow attacks or retreats.

1) Parallel Position. The two fish line up parallel to each other, head to head and tail to tail, separated by distances up to 10 cm. This is equivalent to Baerends *et. al.*'s (1950) lateral display, or Black-Cleworth's (1970) parallel lateral display.

2) Anti-parallel Position. The two fish align themselves parallel to each other but facing in opposite directions. Fish in the Parallel or Anti-parallel Position will show mild agonistic interactions by giving Slaps to the head or to the tail.

3) Facing. The two fish are oriented so that their heads are near each other, and their tails oriented away. The distance between the heads varies up to 15 cm. This is shown in Fig. 26, part 3.

4) Dart Away. This is similar to a Dart Toward but is directed away from the other fish.

5) Serpentining. This is the same as Serpentine defined by Gymnotus (Black-Cleworth, 1970). The two fish are aligned in a Parallel or Anti-Parallel Position. Their bodies touching along the whole length. They produce large longitudinal undulations of their bodies, and the peaks of

the undulations strike the opponent. Serpentineing occurred during the initial stages of fighting before dominance was established. It is shown in Fig. 26, part 2.

6) Approach. Any action or movement that brings two separated fish closer together. Approaches can be Forward or Backward depending upon the direction of swimming.

7) Retreat. A rapid movement of one fish away from the other fish. A Retreat can be accomplished either by forward swimming or by backward swimming.

8) Roll. The fish tilts over slightly on its side and after a short period of time it returns to a vertical orientation. Rolls were given in response to Butts and they usually were given such that the dorsal side was presented to the opponent. The Roll may be a method of cushioning the shock of a Butt in that the fish rotates as if in response to the Butt. Alternatively the fish in the Rolled position, may present less surface area to the opponent, so that Butts are less likely. A fish in the Rolled position is shown in Fig. 26, part 1.

These actions and orientations form the basic motor patterns used in agonistic behavior in Eigenmannia.

D. The Role of Electrical Actions in the Agonistic Behavior

Having described both the electrical actions and the motor actions of agonistic behavior in Eigenmannia I will now proceed with an analysis of the system of electrical communication.

In the case of Sternopygus, electrical signals convey information about the species and about the sex of an individual. The motivation of the signaler also can be conveyed by electrical signals. With Sternopygus, the motivation to attract a female is clearly encoded in the series of Rises and Interruptions that the male gives from his hiding place. We can infer communication of motivation or intention if we can show that there is some behavioral change in the recipient that is appropriate to the particular motivational state of the signaler (Marler, 1961, 1967).

To discern meaning in electrical signals, I have relied upon the

classical approach to the study of motivation of displays, as outlined by Tinbergen (1959), and by Hinde (1970). The motivation of a display can be determined by an analysis of (1) the situation in which it is given, (2) the behavior which accompanies the display, (3) temporal correlations between the display and events of known motivation, and (4) the nature or form of the display itself.

I have attempted to use some of these methods in my approach to the study of electrical communication in Eigenmannia. These techniques were also used by Black-Cleworth (1970) in discerning the meaning of electrical signals used by Gymnotus carapo.

In the first analysis, I have attempted to describe the context or situation in which certain displays are given. This is helpful in understanding the origin and nature of signals. As Hinde (1970) points out, we can infer that there is aggressive motivation behind displays that are directed at intruders at a territorial boundary, and we can infer that there is sexual motivation behind signals given only in the presence of a mate.

Data regarding the context or situation of different electrical actions were collected during aggression tests run between pairs of Eigenmannia. The tests lasted for 10 minutes each. Observations were made in aquaria, electrical activity and voice commentary were recorded on a tape recorder. A total of six fish were tested, and each fish was allowed to interact with every other one. The fish were kept isolated between tests.

In order to evaluate the context of an interaction between two fish, it is essential to know the dominance relationship between individuals. When a fish is in a dominant role, its behavior will differ markedly from situations in which it plays a subordinate role. Dominance relationships have been a subject of intense analysis in studies of primate social organization. Struhsaker (1967) used diadic supplantations to obtain food or space to define dominance in Vervet Monkeys. Kawai (1958) determined dominance between diadic pairs by giving pairs of monkeys that were far enough away from the rest of the troop to avoid interaction, a sweet

potato test. The winner of the test was called the dominant monkey for that particular diadic pair. Sade (1967) used the winner of fights between individuals in diadic situations to define dominance.

Since I have confined by attention to interactions between no more than two individuals at a time, the outcome of some sort of competition experiment for food or space between the two individuals should reliably predict dominance relationships between the individuals. Pairs of fish were allowed to compete for occupancy of a single hiding place during the daytime. Fig. 27 shows two individuals placed together in the aquarium during the daytime. The two fish were isolated prior to the test. In the top photograph (Fig. 27, part 1) the fish in the foreground is giving a Side Slap to the tail of the fish in the background. This is one of many attacks that is delivered to the fish during approximately 10 minutes after the two fish have been introduced. When the hiding place is discovered (a wooden tube lying on the bottom center of the tank) the fish that discovers it enters immediately. Soon, however there is a contest for occupancy of the hiding place, the inside one emerges to try to defend it. Butts are given frequently. Eventually one fish takes possession of the hiding place and the other is left outside (Fig. 27, part 2). Usually a stable occupancy was established within 15 minutes of the beginning of the test. Each test took one hour, and the individual that occupied the hiding place at that time was recorded. The results of these competition experiments are shown in Table XIIa. The identity of the winner of the test is shown on one side, and the identity of the loser is shown along the top. Each X in the table indicates the results of a single trial. Clearly there is a dominance order among these five fish. Fish 1 was subordinate to all fish; it never won in the competition for a hiding place. Similarly, fish 8 never won a competition except when it was placed with fish 1. At the top of the dominance order, there is a triangle. Fish 2 was dominant to all other fish except 10, fish 3 was dominant to all other fish except 2 and fish 10 was dominant to all others except fish 3. Fish 9, an individual that was included in some of the aggression tests to be considered later, died before these tests could be performed.

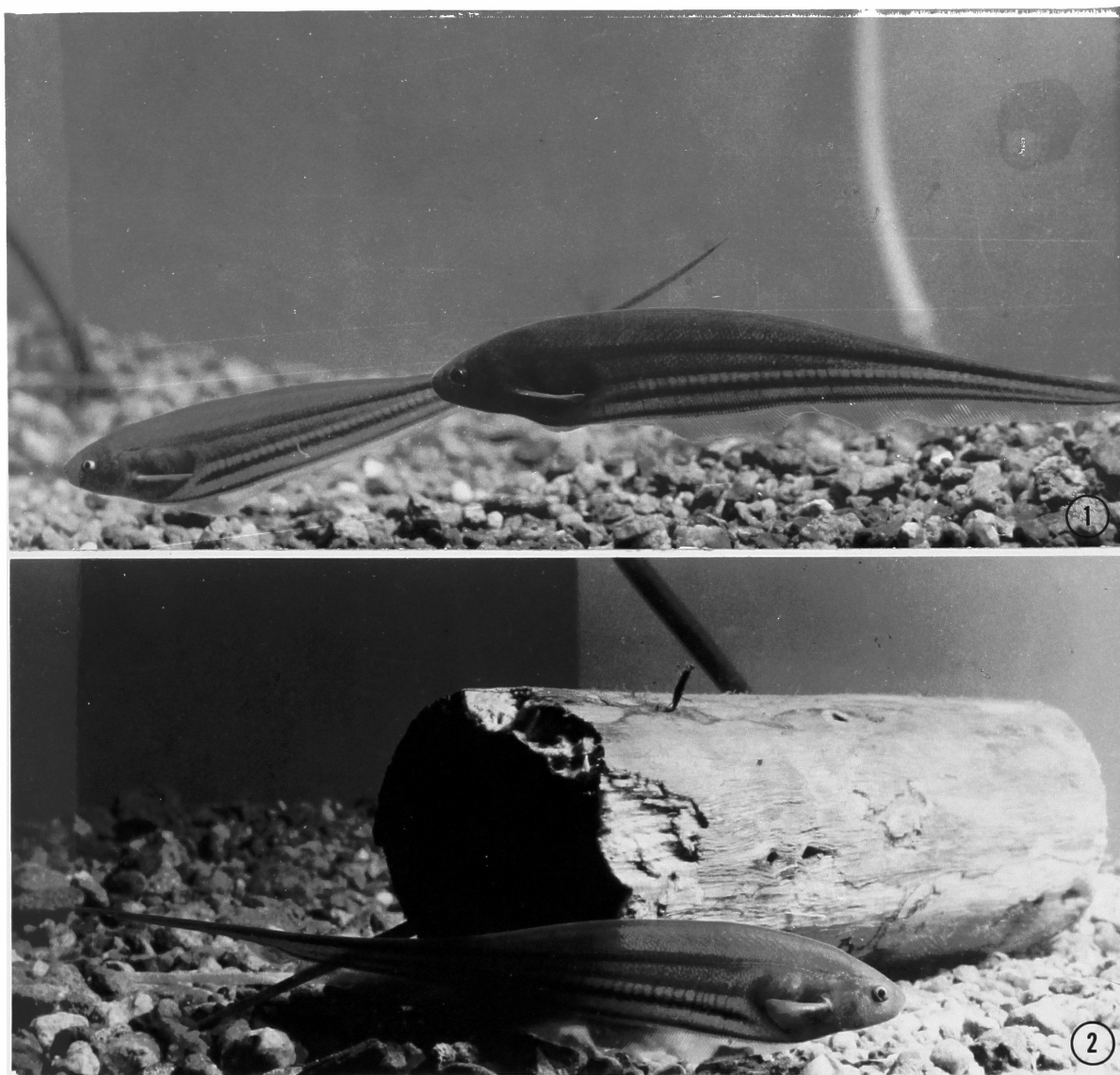


Fig. 27. Competition for a hiding place. 1) Fighting. 2) Final outcome.

TABLE XII

- a) Outcome of competition experiments between pairs of fish for occupancy of a single hiding place during the daytime. Each "x" represents the outcome of a single one-hour experiment.

		Loser of competition. (Outside of hiding place at end of one hour)				
	FISH	2	3	10	8	1
	2		xx		xx	xx
	3			xx	xx	xx
Winner of competition. (Inside hiding place at end of one hour)	10	xx			xx	xx
	8					xx
	1					

- b) Results of aggression experiments between pairs of fish. Each member of the pair is assigned the role of most or least aggressive based on the total number of Attacks given by each fish.

		Least Aggressive					
	FISH	2	3	10	8	1	9
	2		xxx		xx	xxxx	x
	3			xxx	xx	xx	x
Most Aggressive	10	xxx			xxx	x	x
	8					xx	x
	1						xx
	9						

The dominance order determined by this method is approximately predictable from the relative lengths of fish (Table XIII) but does not relate to sex or weight. Thus the shortest fish, fish 1, was lowest on the ranking, and fish 8 was the next shortest. The fish in the triangle of dominance were of approximately equal length. It is not clear why a triangle dominance relation existed between these fish. There are no apparent relationships between these fish regarding length, weight, sex or sexual development that could have predicted the result.

The dominance ordering of fish in the competition experiment paralleled exactly the ordering that I observed for the aggressiveness of individuals that were placed together for night time aggression tests. The most aggressive individual of a pair is defined as the one who, after ten minutes of interaction, has given the greatest number of Attacks. Attacks in this usage include Butts, Chases, Side Slaps, Dart Towards, and Drives. The outcome of 31 aggression tests between the six fish is represented by an "x" in the appropriate square in Table XII, part b. Clearly the ordering of aggressiveness is the same as the ordering of dominance in obtaining a hiding place. Note that fish 9 is the least aggressive fish of all.

The average rate of occurrence of actions, both motor and electrical are listed for fish in the Dominant role, and for fish in the Subordinate role in Table XIV. The rates are expressed as the number of events per ten minute test. In each test, a fish was assigned a role as Dominant or Subordinate based on the outcome of the daytime competition experiment. The average rates of events given by each individual, and by individuals of each sex are also shown in the table so that comparisons can be made of males and females, and of different individuals. The main result of the analysis can be seen from comparing the average number of responses per 10 minute test for fish in the Dominant role (TOTALS: dominant) to those in the Subordinate role (TOTALS: subordinate).

As I have already indicated, Attacks (Butts, Side Slaps, Chases, Drives, Darts) are given by the Dominant fish, and not by the Subordinate fish. Similarly, Approaches (Forward Approaches, Backward Approaches)

TABLE XIII

Descriptions of fish used in Aggression Tests, Eigenmannia virescens

Fish Number	Sex	Length in mm	Weight in grams	Gonadal Condition
2	male	142.6	5.05	testes large developing
3	female	146.5	4.80	ovaries granular developing
10	female	147.2	4.30	virgin not developing
8	female	112.0	4.40	eggs developing not ripe
1	male	103.0	3.40	testes small not developing
9	?	?	?	?

were given more often by Dominant fish than by Subordinate fish. Displays (Parallel Position, Anti-Parallel Position, Serpentine, Dart Away, Facing) were given by Dominants and Subordinates equally frequently, thus implying no particular role to positions and orientations. Retreats (Retreat Forwards, Retreat Backwards, and Roll) were given by the Subordinate fish more often than by Dominant fish. Interruptions of the discharge (both long and short Interruptions) were given almost exclusively by the Dominant fish. Short Rises were given by fish in the dominant role more often than by fish in the subordinate role, but the result was not statistically significant. Short Rises occurred rarely. Long Rises were given largely by fish in the Subordinate role. The mean values of rates of actions for each fish were used to test the significance of the differences between fish in Dominant and Subordinate roles. The results of the two-Tailed Mann-Whitney \underline{U} Tests ($n_1 = 5$, $n_2 = 6$) are shown at the bottom of the table.

When the actions of males are compared to the actions of females, (Sub-totals at bottom of Table XIV) the differences in the rates are minor. Only one difference is suggestive, that Short Rises are given more frequently by females, but this is not statistically significant. Although individuals differ somewhat in their actions, it is clear that the role as dominant or subordinate is the most important factor in determining the number of actions in a given test.

E. Simultaneous Electrical and Motor Actions

The analysis of the context of electrical signals was further refined by considering the motor actions that are given at the same time as electrical actions. For the purpose of this analysis, the criteria for association of two events, electrical and motor, had to be defined precisely.

Data were taken from all 31 of the aggression tests, lasting 10 minutes each. A real-time spectrogram was made of each test and it was aligned with a real-time spectrogram of the voice commentary on motor actions. The voice commentary was transcribed, in code form, onto the spectrogram so that an accurate temporal comparison could be made. A

two second allowance was given for slight delays in the voice commentary. I determined the motor actions that occurred simultaneously with all electrical actions differing from the normal discharge (including Interruptions and Rises). A motor action was considered to be simultaneous with an electrical action, if it occurred within 0 to 2 seconds from the time that the electrical action started. Only one motor action, the first to occur within the 2 second limit, was scored. If there was no motor action recorded during this period or if the two fish were hovering, or were separated, I recorded a "no action" score.

Simultaneous actions were scored for the following electrical events: 1X or a single Interruption (separated from all other by 1.5 seconds or more); 2X, or bouts containing 2 Interruptions; 3X; 4X; and 5+X (5 or more Interruptions); Short Rises, and Long Rises.

Using the above method, I have counted the number of times that motor actions occurred simultaneously with each electrical action and recorded the scores in Table XV. The motor actions are the same as those described in Chapter VI B, except that Side Slaps are included with Butts, and Retreats both Forward and Backward are lumped, and called Swim Away. Below each entry in Table XV are the percentage of the total responses for each electrical action. As an example, the electrical action, "IX", occurred a total of 348 times. It occurred simultaneously with "No Action" 46% of those times; with Butts, 25%; with Chases 7.8%; and with Darts Toward 10%.

Interruptions are given normally simultaneous with Attacks, and with Threats. They are given rarely with Approaches, Mutual Displays and almost never with Retreats. Short Rises are given at the same time as Attacks, as Threats, and as No Action. Long Rises are given simultaneously with Retreats, No Action, and Mutual Displays, but never with Attacks or Threats. These results follow a pattern that is consistent with the result obtained from looking at the electrical displays given by fish in dominant and subordinate roles. Interruptions, clearly, are given by dominant fish, during Attacks, and during Threats. Short Rises are also given during Attack. Long Rises on the other hand, are given largely by

TABLE XV

The observed frequencies if first motor events occurring simultaneously with electrical events. Data from 31 Aggression Tests, Eigenmannia virescens.

		Simultaneously Occurring Motor Event																
		ATTACKS		THREATS		APPROACHES			MUTUAL DISPLAYS					RETREATS		NO ACTION		
		Butt	Chase	Drive	Dart to.	Approach	Back. Appr.	Follow	Parallel	Anti-P.	Serp.	Dart Away	Face	Swim Away	Roll	No Action	TOTALS	
Electrical Event	Interruptions	1X	87 25%	27 7.8%	1 0.3%	35 10%	6 1.7%	2 0.6%	4 1.1%	9 2.6%	6 1.7%	3 0.9%	0 0%	5 1.4%	2 0.6%	1 0.3%	160 46%	348 100%
		2X	60 36.6%	15 9.1%	0 0%	12 7.3%	5 3%	3 1.8%	3 1.8%	5 3%	4 2.4%	2 1.2%	0 0%	1 0.6%	1 0.6%	52 31.7%	164 100%	
		3X	21 29.6%	0 0%	0 0%	6 8.5%	0 0%	2 2.8%	0 0%	6 8.5%	3 4.2%	5 7%	1 1.4%	0 0%	0 0%	27 38%	71 100%	
		4X	45 57%	5 6.3%	0 0%	5 6.3%	1 1.3%	0 0%	0 0%	2 2.5%	3 3.8%	3 3.8%	0 0%	0 0%	0 0%	15 19%	79 100%	
		5+X	55 49.5%	11 9.9%	3 2.7%	12 10.8%	1 0.9%	0 0%	3 2.7%	4 3.6%	5 4.5%	3 2.7%	0 0%	0 0%	0 0%	14 12.6%	111 100%	
Rises	Short	9 30%	4 13.3%	1 3.3%	6 20%	0 0%	0 0%	0 0%	0 0%	1 3.3%	0 0%	0 0%	0 0%	0 0%	0 0%	9 30%	30 100%	
	Long	0 0%	0 0%	0 0%	0 0%	2 1%	0 0%	1 0.5%	9 4.6%	8 4.1%	0 0%	0 0%	2 1%	90 45%	1 0.5%	84 42.6%	197 100%	
Column totals		277	62	5	76	15	7	11	35	30	16	1	8	93	3	361	1000	

subordinate fish, and they are given during Retreat.

One hypothesis regarding the simultaneous occurrence of Electrical and Motor Actions is that they occur independently, and that there is no association between the two. If there is no association, one can predict the frequencies of occurrences of simultaneous actions from the products of the probabilities of occurrences of the motor and electrical actions taken separately. An $R \times C$ test for independence is a statistical test of this hypothesis. I preferred to use the G -test or the log likelihood ratio test described in Sokal and Rohlf (1969). When the G -test of independence is applied to the 7×15 table (Table XV), the result is $G = 310.15$ (d.f. = 84, $p \ll .005$). The significance of the result was tested by consulting a table for the χ^2 distribution. The probability that the electrical and motor actions are independent is thus very small. Electrical and motor actions are therefore not independent, but rather associated with each other. Clearly one type of association is between Interruptions and Attacks, another is between Long Rises and Retreats.

The data for simultaneous actions are sufficiently detailed to permit an analysis of the context of electrical signals that are very similar, such as Interruptions occurring in bouts of differing lengths. "Is 1X given in the same context as 2X?" and so on. To determine whether two signals differ in their context, I have compared the simultaneously occurring motor actions in a test for homogeneity (Simpson, Roe and Lewontin, 1960). Two signals are said to be homogeneous if they do not show a reasonable difference in the distribution of simultaneous motor actions. The test for homogeneity is a $2 \times n$ G -test similar to the test of independence discussed above. Each signal is compared, in turn, with every other one in a 2×15 cell G -test. The degrees of freedom are 14, and the value of G , along with the significance when compared to the critical values of χ^2 , are indicated in Table XVI. The results of these calculations show that 1X and 2X have a homogeneous distribution of simultaneous actions, thus we must assume that the signals are similar if not identical in context. Comparison of 1X and 3X or more than 3X, however, show significant differences. In this particular case, the

TABLE XVI

Result of G -test of hypothesis that any pair of electrical events are homogeneous with respect to simultaneously occurring motor events. Each test is made on a 2×15 matrix, d.f. = 14. Entries in table are the value G , and the probability of H_0 . Data from 31 aggression tests, Eigenmannia virescens.

		1X	2X	3X	4X	5+X	Short	Long
Discharge Interruptions	1X	0 N.S.	17.1 N.S.	38.6 **	30.4 **	62.4 **	13.0 N.S.	410.5 **
	2X	-	0 N.S.	31.0 **	18.7 N.S.	29.6 **	15.1 N.S.	252.5 **
	3X	-	-	0 N.S.	27.1 *	43.6 **	24.6 *	153.6 **
	4X	-	-	-	0 N.S.	10.4 N.S.	15.8 N.S.	219.1 **
	5+X	-	-	-	-	0 N.S.	13.0 N.S.	280.6 **
Rises	Short	-	-	-	-	-	0 N.S.	111.8 **
	Long	-	-	-	-	-	-	0 N.S.

** = p less than 0.01

* = p less than 0.05

N.S. = p greater than 0.05

degree of heterogeneity seems to increase, as indicated by the value of \underline{G} , as the differences between numbers of Interruptions in the bout increase. The largest value of \underline{G} is achieved when comparing 1X to 5+X. Similarly, 3X is only slightly different from 4X, but quite different from 5+X; 4X does not differ from 5X. The reason for the difference between 2X and 3X while there is none between 2X and 4X is not known. In most cases there is no significant difference between Interruptions and Short Rises, but the difference between Interruptions and Long Rises is highly significant.

The results of these tests of homogeneity have indicated that the context of electrical signals differ. There are large differences between Interruptions and Long Rises, and there are significant differences between Interruptions of bout lengths that differ. The larger the difference in the bout length, the larger the difference in the contexts. Returning then to Table XV to discover the source of these differences, we find that the likelihood of Butts being associated with Interruptions, increases with the bout length. There is only a 25% association between Butts and 1X, but a 50% association between Butts and 5+X. Similarly, there is a reduced chance of No Action associated with long bouts of Interruptions, as shown by the 46% figure for 1X and the 13% figure for 5+X. There are no other apparent trends in the associations between motor actions and Interruptions of different bout lengths.

There is a continuous gradation of signals that consist of Interruptions as a basic unit. The rate of delivery, or the number of Interruptions in a bout, codes in a graded fashion the intensity of the underlying motivation. In this case, the number of Interruptions occurring in a bout is related to the tendency to attack in aggressive situations.

F. Responses to Electrical and Motor Actions

Communication is not demonstrated merely by showing that signals are produced that encode information. It is also necessary to show that the signals are received, and that the information somehow changes the behavior of the recipient. This can be done by looking at the responses to signals.

The sequences of behavior observed in the aggression tests were considered to be an endless exchange of actions or stimuli and responses.

An action of one fish is a stimulus to which the second fish responds. The response of the second fish becomes the next stimulus to which the first fish responds and so on. If the first fish performs two different actions in succession, then it is considered as an action by the first eliciting a no response in the second followed by a No Action in the second eliciting a different action in the first and so on. If a response of a fish does not occur within 10 seconds of an action, it is scored as a No Response. This method is similar to that used by Hazlett and Bossert (1965) and by Black-Cleworth (1970).

The actions that I considered in this analysis were either isolated motor actions, isolated electrical actions, or simultaneous motor and electrical actions as defined in the previous analysis of simultaneous events. To consider all the possible motor actions separately would have been prohibitive, thus certain classes were lumped. The action Attack (B), includes Butts, Side Slaps, and Chases; Threat (T) includes Drive and Dart Toward; Approach (A) includes Forward Approach and Backward Approach; Display (D) includes Parallel Position, Anti-Parallel Position, Serpentine, Dart Away and Facing; Retreat (R) includes Forward Retreats, Backward Retreats and Rolls; No Motor Action (NM) was a class signifying no observable motor action, which included Hovering. The electrical actions were similarly lumped. Bouts of Interruptions 1X, 2X, and 3X were lumped as one action, and 4X and 5+X were lumped as another. Short Rises were rare, and they were lumped with Long Rises. This procedure of combining actions resulted in a total of 6 Motor actions (B, T, A, D, R, and NM) and 4 electrical actions (1-3X, 4+X, Long Rises and Normal Discharge). All 24 possible combinations of these actions are listed in Table XVII. The responses to these actions are shown in the columns following each preceding action. To simplify the table response actions are listed without regard for the simultaneously occurring electrical action.

The responses to motor actions are much as one would expect intuitively. For example, the response to an Attack (B) with normal discharge, is usually No Motor Response (NM), or Retreat (R), but it is rarely an Attack (A) or a Threat (T). It is interesting that Threats cause Retreats even through there is no actual physical contact made.

TABLE XVII

Responses of one fish to electrical and motor actions of the other fish. Motor responses that occur simultaneously with electrical responses are lumped without regard to the electrical response. Data from 15 aggression tests.

		- Response Action -						
		NM	B	T	A	D	R	Totals
Normal Discharge	NM	116	300	101	92	47	19	675
	B	191	2	1	2	31	89	316
	T	77	1	3	0	8	40	129
	A	54	5	3	2	21	35	120
	D	39	50	0	5	33	22	149
	R	115	72	23	31	9	3	253
1X to 3X	NM	68	1	0	1	2	10	82
	B	58	1	0	0	9	24	92
	T	10	0	0	0	0	1	11
	A	11	0	0	0	0	6	17
	D	5	1	1	0	4	3	14
	R	1	1	0	0	0	0	2
4X or more	NM	21	0	0	0	0	6	27
	B	37	0	0	0	4	14	55
	T	1	0	0	0	0	4	5
	A	4	0	0	0	2	1	7
	D	9	0	0	0	2	1	12
	R	0	0	0	0	0	0	0
Long rises	NM	22	22	11	9	6	1	71
	B	1	0	0	0	1	0	2
	T	0	0	0	0	0	0	0
	A	1	0	0	0	0	0	1
	D	2	1	1	0	3	0	7
	R	12	8	1	3	0	0	24
Totals		855	465	145	145	182	279	2071

NM = no observable motor action

B = attack

T = threat

A = approach

D = display

R = retreat

Other features of this analysis are of interest, Displays (D) are followed by Attacks (B), Retreats (R) and by other Displays (D). Retreats, are often followed by no motor response (NM), but often they are followed by Attacks (B). Comparisons of the responses to other actions can be seen from inspection of the remainder of the table.

G. Responses to Electrical Displays

The most interesting part of the table, from the point of view of electrical communication signals, are the responses to electrical signals that are given alone - without the simultaneous occurrence of a motor action that could also be causing a response. The response to pure electrical signals are shown in the NM rows of Table XVII, and these rows are extracted, and expressed as a percent of the total response in Table XVIII. It can be seen that Interruptions tend to produce Retreat, and inhibit Attack. Long Rises, on the other hand, are followed by Attack, by Threat, or by Approach, and rarely by Retreat. We see from this analysis that Interruptions serve as aggressive threats, causing the opponent to Retreat once they are given. The number of Interruptions in the bout has communicative significance to the recipient, apparently conveying information to the recipient of the increased underlying motivation to Attack. Bouts of Interruptions that include 1 to 3 Interruptions (1-3X) cause only a few Retreats (12% of the total responses) and an occasional Attack. Bouts that include 4 or more Interruptions (4+X) are followed by 22% Retreats, and no Attacks. The signal that appeared to be graded in intensity in terms of the underlying motivation to attack, also appears to be graded in intensity in terms of the reception of the signal and the immediate response to it. The difference in responses to Interruptions occurring in different bout lengths, is slight, and it is not statistically significant, probably due to the small numbers observed in each category. It is suggestive of a trend in the data, however, one which is consistent with expectation.

It is possible to test whether two electrical signals are homogeneous with respect to the responses that they elicit in the recipient fish much in the same way that signals were tested for homogeneity using the

TABLE XVIII

Responses of one fish to the electrical actions of the other fish during aggression tests. Cells contain the percentage of the total for each display. Data from 15 aggression tests.

	- Response Action -						number of electrical actions
	NM	B	T	A	D	R	
- Preceding action -							
Normal	17.3	44.4	14.9	13.6	6.9	2.8	675
Discharge							
1 - 3X	82.9	1.2	0	1.2	2.4	12.2	82
4+X	77.8	0	0	0	0	22.2	27
Long	31	31	15.5	12.7	8.4	1.4	71
Rises							

NM = no observable motor action

B = Attack

T = Threat

A = Approach

D = Display

R = Retreat

simultaneously occurring actions. The preceding actions were tested in this manner, using the G-test as before. The results are presented in Table XIX. Electrical signals are compared to each other in terms of the responses that they elicit. Table XIX part A shows that Interruptions differ from the Normal Discharge. In addition, Interruptions differ from Long Rises. As indicated earlier, Interruptions occurring in short bouts do not differ from Interruptions occurring in long bouts. When the electrical signals that are given simultaneous with various Motor Patterns are compared (Table XIX part B - F), there are rarely any significant differences between electrical events. This is probably because direct motor actions override the effectiveness of electric signals. For example, the response to an Attack is greater than to an electrical signal that may or may not accompany Attack. Thus there seems to be no difference between Interruptions and Normal Discharge when both are given simultaneous with Attack (Table XIX part B). An alternative explanation for the apparent homogeneity of electrical actions that are given simultaneous with motor actions is that there are so few occurrences of events in these cases, that statistical tests cannot detect fine differences that may exist. One test of homogeneity of electrical actions occurring simultaneous with motor actions is of interest. When simultaneous with Threats, 1-3X elicits different responses than 4+X (Table XIX part C). By consulting the original frequency data (Table XVII) it can be seen that this difference is due to the fact that short bouts of Interruptions given with Threats, cause only an occasional Retreat, and often No Response from the recipient, whereas the long bouts of Interruptions given during Threats, causes only a few No Responses and several Retreats. The 4+X with Threat is more effective in eliciting retreat than the 1-3X with Threat. This result is in accordance with what is expected from the underlying motivation of the two electrical signals.

An electrical action can be a response to an electrical or motor action of the other fish. Long Rises were given in the absence of any Motor Action as a response to actions by the other fish. These responses were lumped into the No Motor Response category in the earlier analysis.

TABLE XIX

Results of G test of hypothesis that two electrical signals are homogeneous with respect to the responses that they elicit. Electrical signals occurring simultaneously with different motor actions are considered separately. Each cell contains the value of G , the degrees of freedom, and the level of significance.

A. Simultaneous with no motor action:

	Normal Discharge	1-3X	4+X	Long Rises
Normal Discharge	0 df=5 N. S.	197.6 df=5 **	83.7 df=5 *	9.2 df=5 N. S.
1 - 3X	- - -	0 df=4 N. S.	3.6 df=4 N. S.	80.8 df=5 **
4+X	- - -	- - -	0 df=1 N. S.	50.0 df=5 **
Long Rises	- - -	- - -	- - -	0 df=5 N. S.

B. Simultaneous with attack:

	Normal Discharge	1-3X	4+X	Long Rises
Normal Discharge	0 df=4 N. S.	1.9 df=5 N. S.	2.5 df=5 N. S.	2.8 df=5 N. S.
1 - 3X	- - -	0 df=3 N. S.	1.3 df=3 N. S.	2.7 df=3 N. S.
4+X	- - -	- - -	0 df=2 N. S.	3.1 df=2 N. S.
Long Rises	- - -	- - -	- - -	0 df=5 N. S.

C. Simultaneous with threat:

	Normal Discharge	1-3X	4+X	Long Rises
Normal	0	5.6	5.2	-
Discharge	df=4	df=4	df=4	-
	N. S.	N. S.	N. S.	-
1 - 3X	-	0	8.2	-
	-	df=1	df=1	-
	-	N. S.	**	-
4+X	-	-	0	-
	-	-	df=1	-
	-	-	N. S.	-
Long Rises	-	-	-	-
	-	-	-	-
	-	-	-	-

D. Simultaneous with approaches:

	Normal Discharge	1-3X	4+X	Long Rises
Normal	0	9.5	2.2	1.6
Discharge	df=5	df=5	df=5	df=5
	N. S.	N. S.	N. S.	N. S.
1 - 3X	-	0	5.8	0.8
	-	df=1	df=2	df=1
	-	N. S.	N. S.	N. S.
4+X	-	-	0	1.0
	-	-	df=2	df=2
	-	-	N. S.	N. S.
Long Rises	-	-	-	-
	-	-	-	-
	-	-	-	-

E. Simultaneous with displays:

	Normal Discharge	1-3X	4+X	Long Rises
Normal Discharge	0 df=4 N. S.	10.7 df=5 N. S.	15.7 df=4 **	10.6 df=5 N. S.
1 - 3X	- - -	0 df=4 N. S.	5.5 df=4 N. S.	3.2 df=4 N. S.
4+X	- - -	- - -	0 df=2 N. S.	6.9 df=4 N. S.
Long Rises	- - -	- - -	- - -	0 df=3 N. S.

F. Simultaneous with retreats:

	Normal Discharge	1-3X	4+X	Long Rises
Normal Discharge	0 df=5 N. S.	1.3 df=5 N. S.	- - -	3.2 df=5 N. S.
1 - 3X	- - -	0 df=4 N. S.	- - -	0.7 df=3 N. S.
4+X	- - -	- - -	- - -	- - -
Long Rises	- - -	- - -	- - -	0 df=3 N. S.

N. S. = p greater than 0.05

* = $0.01 < p < 0.05$ ** = $p < 0.01$

Since it is an interesting response, I present the segregated data on Long Rises as responses in Table XX. This table shows that Long Rises are given as a response to Attacks and Threats. They are also given in response to Interruptions (which act as a threat) and often they are given spontaneously. I often witnessed this in cases where two fish had been fighting but had stopped and were separated from each other. Without any apparent cue, the subordinate fish gave a Long Rise, which was promptly followed by an Approach, with Interruptions, and then Attack. It seemed paradoxical that the subordinate fish would give a signal that would cause the dominant to attack it. Possibly Long Rises are evoked by some subtle cue, given by the dominant fish, that indicates that attack will be soon forthcoming. Under normal circumstances, Long Rises may serve as an aggression-reducing signal much as the hunched posture in a young herring gull, or the head up posture of the ten-spined stickleback (Morris, 1958). In the aquarium situation, it is not unusual that the subordinate fish's signal, which indicates a lack of aggressiveness, will be followed by an attack, much the same as attempts to retreat from the dominant, will be followed by chasing and attack. The available evidence of the context of Long Rises indicate that they are given by the subordinate fish in situations while they are retreating or while they are being attacked by the dominant. The signal seems to convey information to the dominant that indicates the lack of aggressiveness because it causes the dominant to approach and attack it. This evidence suggests that Long Rises are a form of submissive behavior for Eigenmannia. Whether this signal serves any function in the normal situation as an aggression-reducing signal or an appeasement signal, will have to await further work.

In summary, analysis of context, analysis of simultaneous actions, and analysis of response to actions, has revealed that Eigenmannia has a system of electrical communication signals that function in aggressive behavior. One signal, an Interruption, consists of a cessation of the discharge. Interruptions are given in bouts; the number of Interruptions in the bout is directly related to the intensity of the underlying motivation to attack. The number of Interruptions in a bout is apparently communicated to the opponent in aggressive situations. The opponent is

TABLE XX

Preceding actions that elicit Long Rises in aggression tests, Eigenmannia virescens. Entries are the percent of total responses elicited by each preceding action.

	RESPONSE ACTION			
	Electrical	Motor	NM Long Rises	Total no. of Responses
PRECEDING ACTION	Normal Discharge	NM	5.2%	675
		B	3.5%	316
		T	4.6%	129
		A	2.5%	120
		D	0.67%	149
		R	0	253
	1 - 3X	NM	7.3%	82
		B	3.3%	92
	4+X	NM	3.7%	27
		B	9.1%	55

more likely to flee from the fish that gives Interruptions in long bouts than in short ones. Interruptions, then, are a graded system of communication signals. Another signal, a Short Rise, functions as an aggressive threat. It is rare and there are few data available for it. Long Rises, function as a submissive signal; they are given by subordinate fish often during Retreat or in response to Attacks or Threats by the dominant.

H. The Use of Electrical Signals in the Natural Environment

Electrical communication signals are used in communication between Eigenmannia in the natural environment. Since visual observations are impossible under the natural conditions, it is difficult to interpret the context and meanings of these signals. I was able to detect Interruptions regularly, however, and the situations in which I observed them were not inconsistent with the pattern found in the aquarium observations. Interruptions were detected only very rarely during the daytime. During extended periods while I listened to the discharges of Eigenmannia hiding in a large cluster during the day, I detected only the normal discharge of many individuals.

At night, the situation changed, and Interruptions were detected regularly. I observed daytime clusters of Eigenmannia at dusk on several evenings. Just as it became dark I noted brief Interruptions from several within the cluster. Within a few minutes after the first Interruptions were heard, several individuals had emerged from the cluster and were swimming in the main part of the creek. Similarly, at dawn, I detected Interruptions from individuals returning to their hiding places. By 05:00 every morning, the Eigenmannia appeared to begin to travel over long distances in the creek in order to return to their hiding places. As they approached the hiding place, they encountered more and more conspecifics, and usually during encounters, they gave Interruptions. At about 06:00 most of the Eigenmannia had returned to the hiding places and the Interruptions had ceased.

I detected Interruptions from individual Eigenmannia that I attempted to follow on their nightly excursions; the Interruptions were usually given when another Eigenmannia was encountered. Attempts to follow

individuals were difficult because spatial localization of an individual was difficult, and because the identity of an individual was frequently confused after an encounter with another Eigenmannia.

I was able to obtain some information from tracking and it is of interest in interpreting the results obtained in aquaria. I hoped to gain information about the possibility for territoriality from studies of movements of individuals.

I followed the movements of Eigenmannia in Moco-moco Creek by continuously noting the changes of positions of an individual that was localized using an AA-100 fish detector. I paid attention to the presence or absence of other electric fish, that were within the range of detection of my fish detector. An encounter between the fish being tracked and another fish was scored when the second fish could first be detected on the fish detector when the electrode was near the tracked fish. An encounter defined in this way presumably reflects the cases when the tracked individual comes close enough to another individual to detect it. Interruptions are commonly given by Eigenmannia as they encounter other Eigenmannia, but rarely as they encounter other species. Table XXI lists the number of encounters between tracked Eigenmannia and other gymnotids that were accompanied by electrical displays. Nearly half of the encounters with other Eigenmannia are accompanied by an electrical display. Of the 24 encounters with other Eigenmannia in which electrical displays were given, 22 of the electrical displays were Interruptions, one was a Long Rise and one was a Short Rise.

Tracking studies in August, 1970 in Moco-moco Creek also showed that Eigenmannia would give Interruptions upon encountering conspecifics in the creek. There was no evidence that Interruptions given by Eigenmannia in these situations had any role in the defense of a territorial boundary. Some typical tracks of Eigenmannia in Moco-moco Creek are shown in Fig. 28. This figure shows the time and place at which the track was begun and finished. The duration of the track in minutes is shown at the right.

In many cases the movement of individuals was limited as illustrated

TABLE XXI

Electrical actions of *Eigenmannia virescens* given during encounters with other gymnotids in tracking studies in Moco-moco Creek in April 1971.

Species Encountered by <u>Eigenmannia</u>	Number of Encounters		Total
	with electrical signals	without electrical signals	
<u>Eigenmannia</u> <u>virescens</u>	24	23	47
<u>Sternopygus</u> <u>macrurus</u>	2	12	14
<u>Apteronotus</u> <u>albifrons</u>	0	3	3
<u>Hypopomus</u> <u>brevirostris</u>	0	4	4
<u>Gymnorhamphichthys</u> <u>hypostomus</u>	0	7	7
Total	26	49	75

Total number of individuals tracked = 32

Total time spent tracking all individuals = 281 minutes

Total number of encounters = 75

Tracks of *Eigenmannia virescens* August, 1970
Moco-moco creek

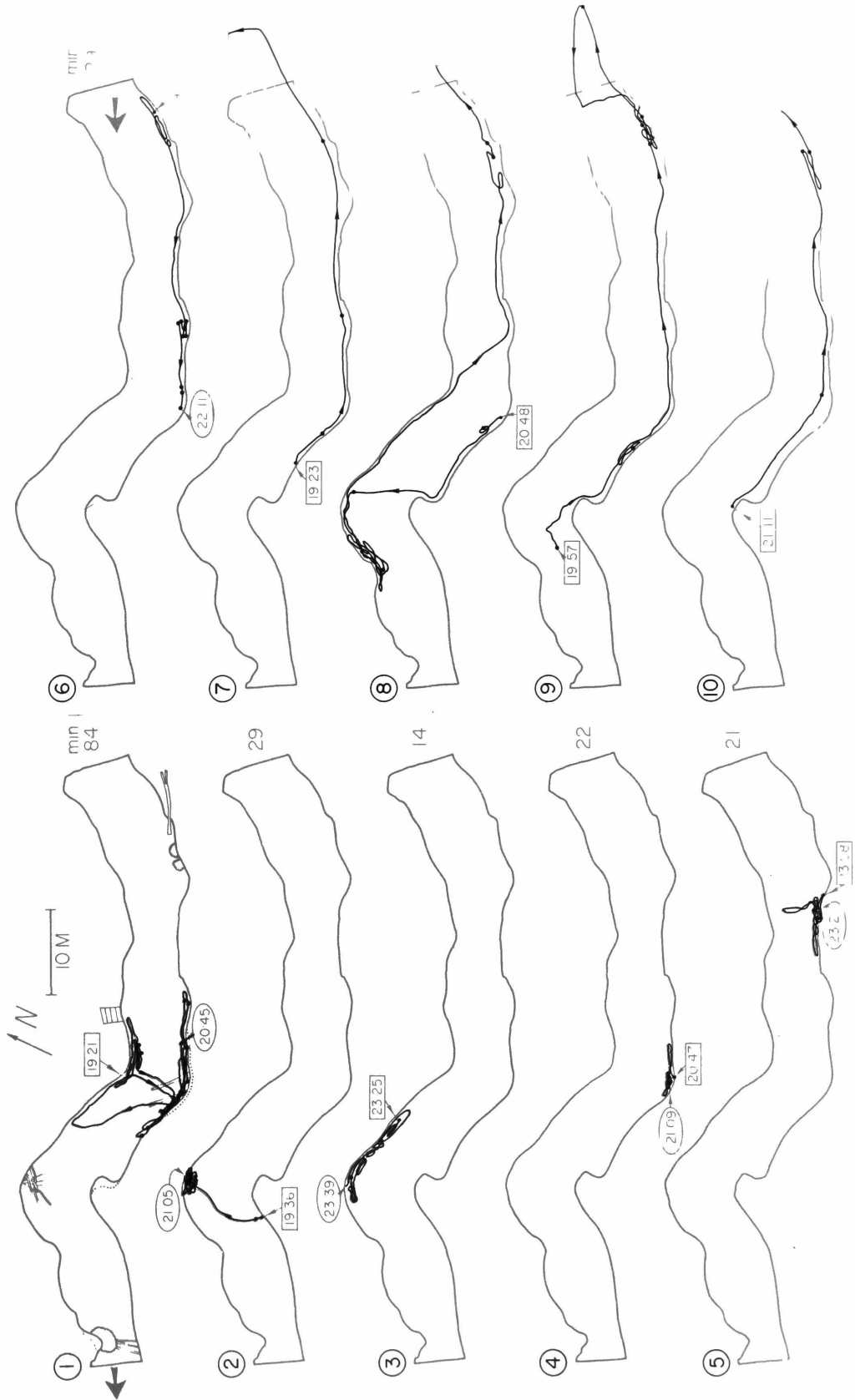


Fig. 28.

by tracks 1 through 6. In other cases, however, the movements were not restricted, and the fish traveled over relatively long distances in straight paths. Positions on the tracks where Interruptions are given are indicated by black dots. In all of these instances another Eigenmannia was present.

Patterns of movements of Eigenmannia at night during August 1970 and during April 1971 are not suggestive of a system of territoriality. The movements of some individuals were confined to a small area, but there was a great deal of variation between individuals. In 33 tracks of Eigenmannia in 1970 for which the average duration was 32 minutes (s.d. = 40.5 minutes), the average distance between the start of the track and the finish was 17 meters (s.d. = 19.0 meters). Longer periods of observation tended to yield longer tracks, thus indicating that movements are not restricted, but rather random.

I. The Role of Electrical Signals in Sexual Behavior of Eigenmannia virescens

During the breeding season in 1971, observations were made in aquaria of Eigenmannia males and females that appeared to be in breeding condition. Female Eigenmannia with enlarged abdomens and 1-2 mm diameter eggs, pale yellow in color, visible through the nearly transparent skin of the abdomen and males with testes that appeared white through the skin, were placed together in aquaria for observations similar to those made during the aggression tests. Attempts to describe sexual behavior of Eigenmannia remain incomplete because I was not able to observe a spawning act. On one occasion, apparently spawning took place in the aquarium in my absence as discussed in Chapter III E.

Spawning did not occur regularly in aquaria because of a multiplicity of possible factors. An attempt was made to imitate the water conditions and the plants (Polygonum sp.) from Kumaka Swamp but this was still unsuccessful. Often a male and female would follow each other around the tank, the male often made gentle Butts to the abdomen, and males and females frequently rested in a Parallel Position. Often the female would swim over surfaces such as the inside of a hollow tube or the undersides of leaves, apparently in search for a place to spawn.

J. Results of Sex Tests

A preliminary survey of the sexual behavior results have indicated that some electrical actions may play an important role in the courtship of Eigenmannia. I conducted 10 minute observations similar to the aggression tests, between pairs of fish during the breeding season. Fish were collected from Kumaka Swamp, and their gonads were well developed. Males and females were easily distinguished externally at this time of year. Tests were conducted in an aquarium with a gravel bottom, but with no plants. On May 24, 25, and 26, 1971, I made ten-minute observations on pairs of Eigenmannia. A total of 20 trials were carried out using 6 females, and 6 males. Seven of these trials were between male-male pairs, seven were between female-female pairs, and six were between male-female pairs. Every trial was tape recorded, with synchronized voice description, and later spectrographed.

The fish interacted aggressively during these trials, and I recorded the total frequencies of actions in the same way that I have done on the aggression trials. The results showing the actions of males compared to the actions of females when in heterosexual paired trials are shown in Table XXIIA. The numbers in this table are the average number of actions per individual per 10 minute trial. The average for males is compared to the average for females. Below each action is the result of the Mann-Whitney U test ($n_1 = 6$, $n_2 = 6$, two-tailed) of differences in the numbers of actions of the males compared to those of the females. The results of the trials indicate that the numbers of actions of the males do not differ significantly from the numbers of actions of the females, except for one action: Short Interruptions. Short Interruptions were given more frequently by males in male-female interactions than by females.

The behavior of females was recorded, both in male-female interactions and in female-female interactions. The average rate of occurrence of events given by females were compared using the Mann-Whitney U test ($n_1 = 14$, $n_2 = 6$), and there were no significant differences in the behavior of the females in these two situations.

The behavior of males was recorded, then, in a similar manner both

TABLE XXII

- A. Comparison between the action of Males to the actions of Females during heterosexual paired encounters. Each entry equals the average frequency of occurrence of events per 10 minute session. Data from tests No. 215-236, Eigenmannia virescens.

	no. of trials	B	T	D	A	R	SH X	L X	SH R	L R
Actions of Males	6	11.7	6.8	33.5	12.0	19.3	31.3	1.5	2.2	4.8
Actions of Females	6	6.1	5.6	32.8	12.1	14.6	12.8	1.1	0.0	3.8
Significance of two-tailed Mann Whitney <u>U</u> test		NS	NS	NS	NS	NS	.05	NS	NS	NS

- B. Comparison of the actions of males when paired with Males to the actions of males when paired with Females. Each entry equals the average frequency of occurrence of events per 10 minute session. Data from tests NO. 215-236. Eigenmannia virescens.

	no. of trials	B	T	D	A	R	SH X	L X	SH R	L R
Actions of males paired with -										
Males	14	4.9	4.1	25.0	9.6	14.3	9.3	0.1	0.3	2.2
Females	6	11.7	6.8	33.5	12.0	19.3	31.3	1.5	2.2	4.8
Significance of two-tailed Mann Whitney <u>U</u> test		NS	NS	NS	NS	NS	0.01	NS	NS	NS

B = Attacks
 T = Threats
 D = Displays
 A = Approaches
 R = Retreats
 SHX = Short Interruptions
 LX = Long Interruptions
 SHR = Short Rises
 LR = Long Rises

in male-female trials and in the male-male trials, and the rates of actions were compared using the Mann-Whitney U test ($n_1 = 14$, $n_2 = 6$). The results of the test, along with the average number of actions per 10 minute session are shown in Table XXIIB. It can be seen that the behavior of males is different in the male-female trials when compared to the male-male trials. The difference lies in the number of Short Interruptions given; it is significantly higher in the male-female interactions.

This result, although preliminary, is suggestive of a possible role of Interruptions in the courtship behavior of Eigenmannia. In these tests, very few Long Interruptions were given (duration more than 70 msec), although during other tests between males and females (see page 111), Long Interruptions were given by males, in the presence of females, and they seemed to have a role in courtship. During these trials Interruptions given by males were given largely in the presence of females, but they were usually Short Interruptions. The complete interpretation of the interactions between males and females during the breeding season will have to await further work.

K. Experimental Verification of Species Recognition

Playback experiments, similar to ones used to test species and sex recognition in Sternopygus, were used to test species recognition in Eigenmannia. There were some major differences in the technique, however. The Eigenmannia were tested in aquaria, the copper playback electrodes were supported on models that were made in the approximate shape of a gymnotid, and response measures included not only electrical responses, but also agonistic motor actions such as Attacks on the model.

The gymnotid-shaped model was constructed from translucent Plexiglass. It was 155 mm long, 22 mm in diameter at the head and 7 mm in diameter at the tail. One of the electrodes was wrapped around the "head" of the model and the other around the "tail." The electrodes were separated by 143 mm. The entire model was supported near the head by a piece of Plexiglass tubing, 7 mm in diameter which carried the wires to the electrodes.

Playback experiments were performed on single Eigenmannia (both

sexes) while they were observed in an aquarium. An experiment began as the Plexiglass model was introduced into the aquarium, 5 cm from the bottom, with the current turned off. The actions of the fish, both motor and electrical, were noted for one minute while the current remained off. Then the current was turned on for two minutes of playback. The motor and electrical actions were again recorded. After the playback, one minute passed with the current off again and the model was removed. At least four minutes were allowed before beginning another experiment with the same fish. The maximum number of experiments on one fish on one day was eight. The fish were held in isolation in holding tanks while they were not being tested.

The fish appeared normal after being introduced into the aquarium. They were generally active, swimming around the entire tank, occasionally showing feeding movements on the bottom, and occasionally swimming back and forth along the glass sides. The fish appeared to react to the introduction of the "silent" model with mild arousal. There were Approaches to the model both backwards and forwards. Occasionally the fish would very gently touch the model with its head, or tail and there were Darts directed at the model. Darts were much more frequent if an aluminum model was used in place of a Plexiglass model, and the fish appeared disturbed. Some fish paid little attention to the Plexiglass model.

When the current was turned on the model, there was nearly always a clear response. The fish approached rapidly giving Darts toward the model. Butts and Side Slaps were directed at the head and tail electrodes, and Serpentineing was common on the head or tail of the model. Fig. 29 part 1 and 2 shows an Eigenmannia responding to the Plexiglass model (the stimulus used to elicit these responses was a 500 Hz sine wave). In the top photograph the fish is Hovering over the tail of the model while making frequent Darts Away from the model. In the lower photograph the fish is Serpentineing on the tail of the model. The responses to playback that I monitored were: Retreats, or Swim Away Forward or Backward; Approaches, both forward and backward; Threats, or Darts Toward and Darts Away; Attacks, including Butts, Side Slaps, Serpentineing. Discharge

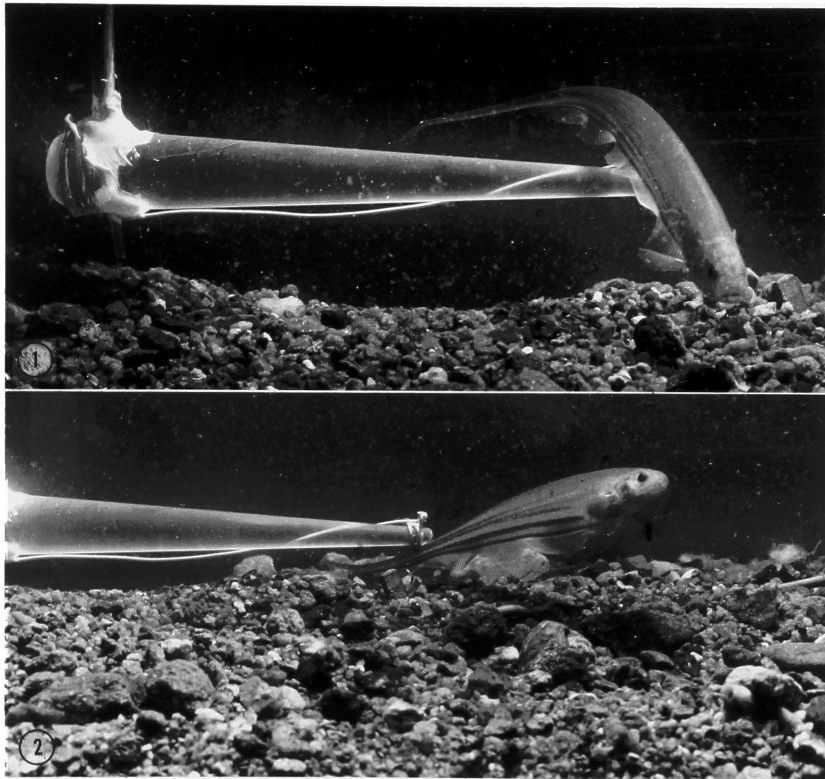


Fig. 29. Eigenmannia attacking the Plexiglass model. 1) Dart Away from "tail". 2) Serpentine on "tail".

Interruptions were given in response to playback, but I did not record any Rises.

Experimental fish general spent slightly more time attacking the tail than the head of the model. In a series of experiments using 13 different fish 60.6% of 656 Butts were delivered to the tail and the remainder to the head. The slight preference for attacking the tail electrode may be due to its smaller size and resulting greater current density. Attacks were only very rarely directed at the side of the model.

In the first series of experiments, I tested the responses of Eigenmannia to sine waves that differed in amplitude. A 500 Hz sine wave, produced by the portable sine wave generator was used as the signal source in the playback experiments. A total of five fish were tested, each was tested once at three different amplitudes of the signal. The greatest amplitude signal measured 1 volt peak to peak between the two electrodes when the electrodes were immersed in the tank. This amplitude is referred to as 0db. Two other signals were reduced in amplitude to -18db and -36db. The fourth playback in which no signal was presented to the model, served as a control. The results are shown in Table XXIII. It can be seen that there are a few Approaches, Retreats, and Darts in response to the silent model. There were both Attacks and Interruptions directed at the model when the sine wave was connected. The number of Attacks was greatest in response to signals at -18db. The number of Darts was greatest in response to -36db. Fewer Attacks and Interruptions were given in response to 0db and to -36db compared to -18db. A 0db signal was considerably greater in amplitude than the amplitude of most Eigenmannia tested, -18db was approximately equal to the amplitude of most fish, and -36db was less than the normal amplitude. It appears therefore, that Approaches, Butts, and Interruptions are given to models which approximately match the amplitude of a normal fish. The amplitude of the playback signal was adjusted to -18db (reference 1 volt peak to peak) in the remainder of the playback experiments.

Sine waves at various frequencies were played back on the Plexiglass

TABLE XXIII

Responses of Eigenmannia to playback of a 500 Hz sine wave of different amplitudes. Playback electrodes are supported on a gymnotid-shaped Plexiglass model. The responses are the totals for all fish tested.

Amplitude of signal	No. of fish	No. trials	R E S P O N S E S				
			RETREATS	APPROACHES	DARTS	ATTACKS	INTER- RUPTIONS
0 db	5	5	10	10	4	18	10
-18 db	5	5	11	15	8	29	55
-36 db	5	5	6	9	30	21	24
no signal	5	5	4	5	7	0	0

model at -18db to Eigenmannia. The results of an experiment that tested the responses to eight different frequencies is shown in Fig. 30. The horizontal axis is the frequency of the sine wave that was used, the vertical axis is the median number of responses per two minute playback period for five fish that were tested. There were two females and three males involved in the test. Each line in the figure represents a different response: Retreats, Approaches, Darts, Attacks, and Interruptions. It can be seen from this graph that the highest median number of Attacks and Interruptions were elicited with playback of frequencies in the range 400 to 600 Hz. Very few responses were given to other frequencies of sine waves. Other responses such as Approaches, Retreats and Darts, do not show any consistent variation with frequency. The range of frequencies that elicit Attacks and Interruptions corresponds well with the range of discharge frequencies recorded for Eigenmannia (Figs. 15, 22). It thus appears that the aggressive actions of Eigenmannia are elicited by electrical stimuli of the appropriate frequency for the species.

In another series of experiments with Eigenmannia I played back pre-recorded electrical signals from five species of gymnotids from Moco-moco Creek. The pre-recorded signals were prepared by recording the signals of captive fish with an Uher Tape recorder at 7 1/2 ips. The playback level was adjusted to 1 volt peak to peak and attenuated to -18db. The five signals used were: Gymnorhamphichthys hypostomus (91 pulses per second), Sternopygus macrurus (71 Hz), Eigenmannia virescens (380 Hz), Apteronotus albifrons (930 Hz), and Sternarchorhamphus macrostomus (930 Hz).

The results of playback of pre-recorded signals to 6 Eigenmannia (2 males and 4 females) are shown in Fig. 31. The median response score (responses per 2 minutes) for the six fish is plotted for each of the responses to each of the stimuli. The median number of responses for all six fish during the control periods were: Retreats, 0.8 per 2 minutes; Approaches, 3.0 per 2 minutes; Darts, 1.0 per 2 minutes; Attacks, 0; Interruptions, 0. Clearly, the aggressive responses (Attacks, Interruptions) are most numerous for playback of the Eigenmannia discharge. Apteronotus albifrons is also quite effective in eliciting aggressive responses.

Responses to Playback *Eigenmannia virescens*

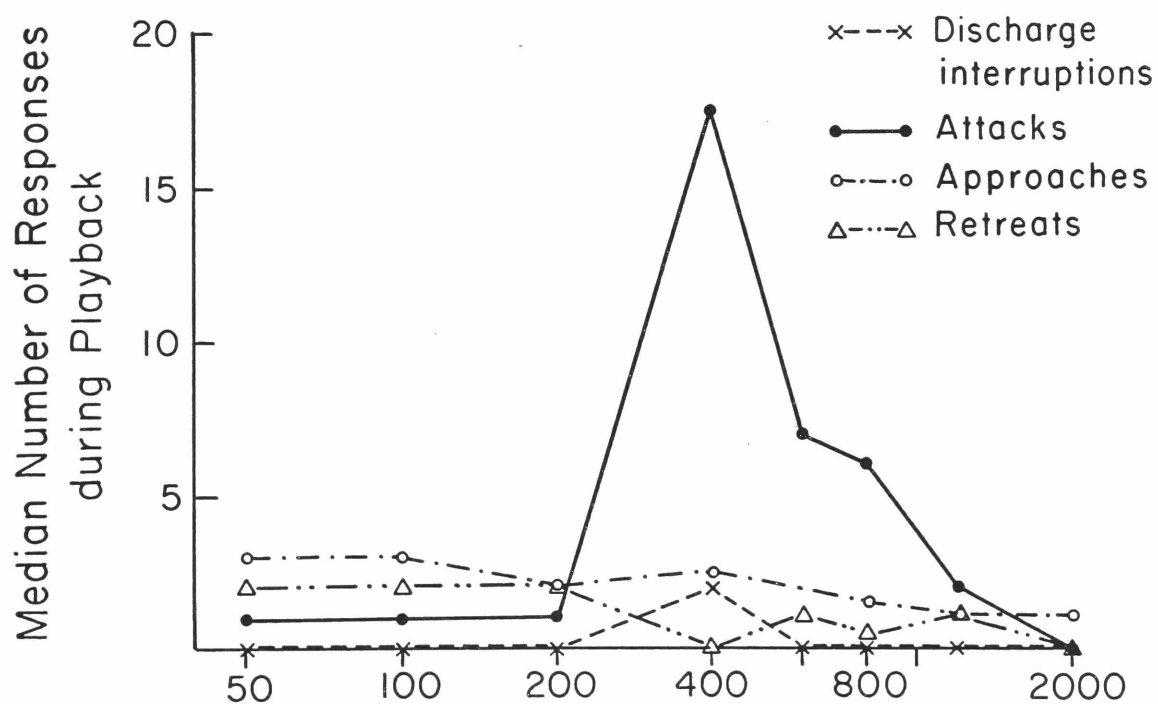


Fig. 30. Responses to playback of sine waves to *Eigenmannia virescens*. Each point is the median value of five trials using five fish.

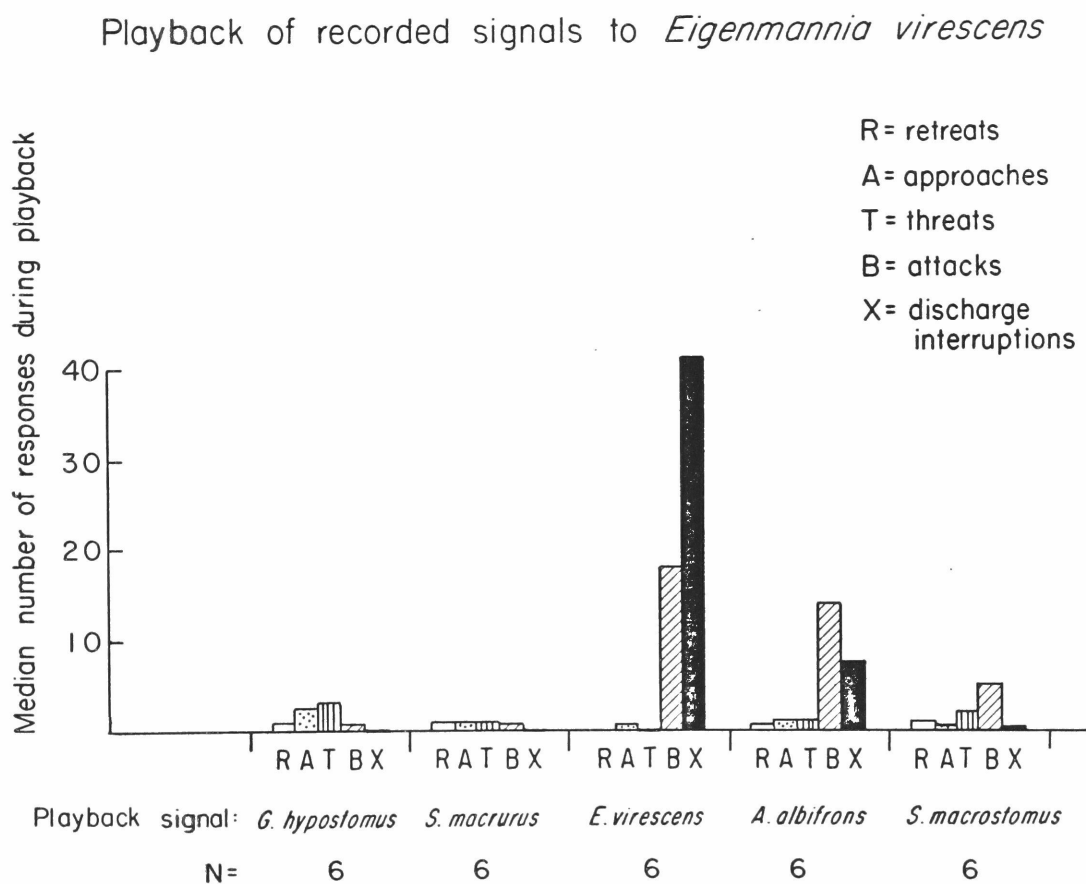


Fig. 31. Playback of tape recorded signals of five species of gymnotids from Moco-moco Creek to *Eigenmannia*. The median number of responses of six fish that were tested is shown on the vertical axis.

Although the median value of Attacks and Interruptions given in response to S. macrostomus were less than in response to A. albifrons the results were not significantly different when tested with the Mann-Whitney U test ($n_1 = 6$, $n_2 = 6$; Attacks, $U = 20$ $p > .02$ two-tailed; Interruptions, $U = 27$, $p = 0.2$, two tailed). There are no differences in the numbers of Approaches, Retreats, or Threats in response to the different playback stimuli. The fact that aggressive responses are elicited from Eigenmannia by playback of its own electrical signals, is consistent with the previous analysis. These experiments support the view that Eigenmannia uses the frequency of the normal discharge for the purpose of species recognition. In this sense the results obtained for Sternopygus are similar to the results found for Eigenmannia.

VII. DISCUSSION

A. Daily Activities of Gymnotids

The gymnotids are inactive during the daylight hours and are active at night. This has been established in previous field studies, in laboratory studies, and confirmed in the present study (Lissmann, 1958; 1961a; Ellis, 1913; Lissmann and Schwassmann, 1965; Lowe-McConnell, 1964; Steinbach, 1970; Black-Cleworth, 1970). On rare occasions, such as on the first day of flooding in 1971, some gymnotids are found swimming into Kumaka Swamp during the daytime. Usually, however, during the day most gymnotids remain concealed under some sort of cover or else protectively camouflaged like Sternarchorhamphus macrostomus. At night, most gymnotids emerge from their hiding places and enter the stream in search of food.

The nocturnal habits of gymnotid fish are most likely the result of selective pressures from two sources: competition and predation. Many species of fish in the Rupununi District show definite circadian activity cycles coincident with daylight. Daylight is important for visual navigation and visual communication. Species that rely upon vision are usually active only during the day. Lowe-McConnell (1964) found that most species of cichlid and characin fish, which depend upon vision, are not active at night. She found Cichlasoma, Geophagus, Acaronia, and Cichla as well as Hoplerethrinus and Hoplias with the aid of a flashlight, hiding at night along the sides of rivers and streams, against rocks or vegetation. Nocturnal fishes in the Rupununi have reversed activity cycles. The gymnotids and many of the nematognaths (catfishes) are nocturnal.

In the clear rivers, streams and ponds of the Rupununi, it is understandable that vision is an important factor which determines activity cycles of fish. It is not obvious that fish that inhabit the large deep muddy rivers of South America will show any daylight induced activity cycles. Steinbach (1970) found large differences in the positions of gymnotids during the night and the day in the Rio Negro, Brazil. More work needs to be done in the large rivers, however to

determine if the activity cycles of fish continue to follow cycles of day-light even in the depths of deep rivers.

Nocturnal behavior may be caused by competition for food or for space with diurnal fishes. If two species that are active during the same time periods compete for the same food, then natural selection will favor those individuals that avoid competition by feeding at different times. Knöppel (1970) has shown that the stomach contents of gymnotids collected in the Igarape Barrow Branco, and in the Igarape Tarumã, from the Brazilian Amazon contain a large percentage of insect larvae, especially Trichoptera, Ephemeroptera and Diptera larvae. In this food habit, they overlap with the food preferences of several of the Cichlidae, notably Aequidens tetramerus, Acaronia nassa, Crenicichla ornata, and C. notophthalmus. The characoid fish Hopterythrinus anilinus also prefers these foods. Thus there is apparent overlap in food preferences between the cichlids, the characins, and the nocturnal gymnotids. Predatory fish that differ in their activity periods may occupy separate ecological niches, thus avoiding competition. There is some evidence that some insect larvae have rhythmic emergence behaviors, and movements that are synchronized with the day-night cycle. MacDonald (1956) studied Chaoborus larvae in Lake Victoria in Africa and found that larvae in the third instar stage inhabit the mud bottom during the day, and migrate upwards into the plankton each night. These larvae escape predation by the nocturnal, bottom feeding mormyrid, Mormyrus kanume. Competition for food for the gymnotids is not completely eliminated by adopting nocturnal habits, of course. Many South American Siluriformes are nocturnal and eat insect larvae, so that they may overlap in food requirements with the gymnotids (Knöppel, 1970).

Nocturnal habits may also be an adaptation to avoid predation. Diurnal fish predators such as the Cichlidae and the characins are particularly common among Rupununi fishes. Hoplias malabaricus (Erythrinidae) and Crenicichla sp. (Cichlidae) were common in Moco-moco Creek, and many other fish predators were common in the main rivers. Lowe-McConnell (1964) suggests that predation is an intense selective pressure among Rupununi fishes that has favored the evolution of spines, bony plates, armour, and

deep bodies. Many predators are diurnal. Lowe-McConnell found that fish caught in gill nets during the daytime were quickly eaten by Serrasalmo species, but that fish caught at night were left unharmed. Lissmann (1961a) suggested that gymnotids avoid predation by being active at night.

An observation of mine on predation of two Eigenmannia released during the day confirms this view (page 54). The high percentage of mutilation observed in gymnotids also suggests intense predatory pressure. Nocturnal predators exist, of course, especially among the nematognaths. Lowe-McConnell (1964) suggests that many species of diurnal fish are inactive and motionless at night in order to avoid detection by nocturnal predators.

If diurnal predation is great, then the soft-bodied, slow swimming, defenseless gymnotids will be unable to survive unless they remain well concealed during the day. Hiding places, then, are of prime importance to gymnotids. Competition for hiding places occurs between gymnotid species during the dry season when the available space is reduced. Many species of fish, other than gymnotids, also compete for some hiding places. Lowe-McConnell (1964) found 15 species of nematognaths hiding inside of dead sticks and logs (hiding place type 7, Chapter III K) from Simoni Creek. Competition for hiding places is reduced for those species which specialize in their methods of hiding. Specialization can occur in two ways. In the first way the fish is morphologically adapted to hide in a particular micro-habitat. Gymnorhamphichthys hypostomus, which buries in the sand, and Sternarchorhamphus macrostomus, which has protective coloration, show this type of adaptation. In the second way, hiding place selection is general, but there is specialized social behavior. Eigenmannia shows specialized social behavior in that it hides in large clusters during the daytime. Clustering in Eigenmannia is a possible mechanism for effective competition for hiding places. Large clusters of Eigenmannia may be more effective in intraspecific competition than isolated individuals. In summary, nocturnal habits in gymnotids may be a response to competition for food, and may be a response to predation. Because they are defenseless, gymnotids must hide during the day. Hiding places are a potential limited resource and this favors the evolution of specialized morphological and behavioral adaptations for hiding.

B. The Seasonal Cycle and Breeding

Tropical freshwater fish face tremendous fluctuations in water levels and in available area during the annual or semi-annual rainy season. A single, rather than double rainy season on the Rupununi makes the contrast with the dry season even more dramatic. Links between the onset of the rainy season and the first spawning of many species of fish are very strong among Rupununi fishes. Lowe-McConnell (1964) summarizes the spawning of most Rupununi fishes by suggesting that those species which are "total-spawners" (all ova ripen and are shed in one batch), including many of the characins, tend to delay their spawning until the rains have started and flooding has occurred. "Partial-spawners," on the other hand are less bound to the beginning of the rainy season; some breed just before the rains, some in the peak of the dry season.

There are many advantages to spawning during the wet season, the most notable being the superabundance of food and space during this short period. There are numerous exceptions of species that spawn the year around, or which spawn slightly before the onset of the rainy season. Lowe-McConnell (1964) carefully discusses six species of fish that seem to spawn during the dry season. Cichla ocellaris, Geophagus jurupari, Cichlasoma festivum, Loricaria sp. and Osteoglossum bicirrhosum, all had spawned either during the middle of the dry season, or else immediately prior to the onset of the rainy season. A stingray, Potamotrygon hystrix, carried nearly ripened embryos during the dry season. Of these six species, four (Geophagus, Loricaria, Osteoglossum, and Potamotrygon) have specialized methods for mouth brooding or incubation that helps to protect the young fish until they attain a certain age. The other two species show well developed nest construction, or defense of young. Numerous other examples are apparent, especially among the Cichlidae, of specialized nest construction, or territorial behavior, and defense of young, that correlate with early spawning behavior. The problem of finding a mate during the wet season flooding may be especially difficult, and the fish that mouth brood or have internal fertilization may be able to reduce this problem by spawning or copulating just before the rains (Nelson, 1964b). The young of early spawners may have competitive advantage

over other species in that the young will be able to obtain more food during the wet season. Similarly the young will not have to remain in the swamps or ponds for as long and suffer the risks of falling water, if they have a head start of several weeks growth.

The habit of early spawning, occurring just before the onset of the rainy season, occurs in Sternopygus macrurus. This is in contrast with other species, notably Eigenmannia virescens, Hypopomus brevirostris and Gymnorhamphichthys hypostomus, which delay breeding until the first flood. The advantages for early spawning are the same as for other species; whether specialized behavior or morphology is responsible for the behavior, is not known, and to make any suggestions would be highly speculative. There are distinct differences in the ecology of Sternopygus and Eigenmannia, however, that are worth reviewing at this point. Sternopygus and Eigenmannia differ in their methods of daytime hiding during the dry season. Eigenmannia forms large clusters of individuals and Sternopygus is spaced seemingly at random in available sites. Sternopygus is a generalist in the selection of sites which it uses for hiding (H/H_{\max} is close to 1.0, Table V). Eigenmannia is similar to Sternopygus both in its selection of hiding places and in the diversity of its hiding place selection. The main difference seems to be in the adaptation for clumping shown by Eigenmannia but not by Sternopygus.

If intraspecific agonistic encounters were to occur between Eigenmannia and Sternopygus over the occupancy of a hiding place, most likely, Sternopygus would win the encounter. The basis for this speculation is that Sternopygus are on the average, larger than Eigenmannia. The largest Eigenmannia that I captured in Moco-moco Creek was 249 mm long and 12.5 g. The largest Sternopygus, on the other hand, was 598 mm long and 302 g. A difference in twice the length and over 20 times the weight, probably makes a large difference in success in defending a hiding place.

Because of its size, Sternopygus may be able to defend a hiding place against intrusion by other species. Taking advantage at its success in defending a hiding place, Sternopygus, may turn the hiding place into a spawning site, and thereby enjoy the same advantages of

early spawning obtained by other species which have specialized morphology for mouth brooding or specialized behavior for guarding young. This argument is highly speculative, of course, but may help to explain some of the differences that I found between Sternopygus and other species of gymnotids in Moco-moco Creek. Further work should be done on the breeding behavior of Sternopygus, including the methods of spawning, care of eggs, and care of young, before some of these questions can be answered. Experiments on intraspecific competition for hiding places could also be performed.

C. Electrical Communication - Properties of the Communication Medium

Any discussion of a communication system must consider the entire process of communication, including the systems for signal emission, signal reception, and signal transmission. A great deal of information has been gathered regarding the mechanisms of production of electricity in fishes, and this has been the subject of a recent comprehensive review by Bennett (1971a). Most of the species of gymnotids and mormyrids have muscle-derived electric organs, that are stimulated at nerve-electric organs synapses (Acetylcholine mediated). The family Aptereronotidae has electric organs that seem to be derived from nerve tissue. Columns of electrocytes fire synchronously and add in series electrically to produce relatively strong electric fields. The linear arrangement of the cells in the body create a field that has properties similar to an electrical dipole. The potential field has been measured for Gymnotus carapo (Lissmann, 1958) and for Gnathonemus petersii (Harder, Schief and Uhlemann, 1964) using monopolar electrodes. The potential field is similar to the field produced by a dipole electrode.

The electric field produced by one fish is sensed by another with specialized electroreceptors embedded in the skin of the fish. Morphologists distinguish two classes of electroreceptors in gymnotids, three classes among the mormyrids. Electroreceptor morphology and physiology has been the subject of another comprehensive review by Bennett (1971b). Those electroreceptors that are ampullary in structure respond to D.C. electrical stimuli with sustained, tonic responses and thus Bennett calls these receptors Tonic Receptors. Other electroreceptors are tuberous in

their structure and they respond to A.C. stimulation with phasic responses; thus Bennett calls these receptors Phasic Receptors. Tonic receptors in Gymnotus carapo normally discharge spontaneously at a steady frequency that varies from one receptor to another (Bennett, 1967; Suga, 1967b). Anodal stimulation with a monopolar electrode causes the Tonic receptor to increase its rate of firing. There is a brief period of accommodation following the initial transient response. Cathodal stimulation causes a brief silent period followed by a recovery to a lower frequency than the spontaneous rate. Tonic receptors are not sensitive to high frequency A.C. stimuli but rather to D.C. stimuli.

Phasic electroreceptors are normally silent, but respond to brief electrical stimuli with a burst of impulses. The response to a sustained electric stimulation is a rapidly accommodating response at the onset of pulses.

Since the electric organ discharge of most species of gymnotids, with the exception of Electrophorus electricus, and a monophasic species of Hypopomus (Hagiwara and Morita, 1963) has no D.C. component it is not sensed by Tonic electroreceptors (Suga, 1967b; Bullock and Chichibu, 1965). The electric discharge of one fish, then, is probably sensed by another fish exclusively by the Phasic electroreceptors. The responses of one fish to the presence of another has not been investigated by electrophysiologists, however, so that this conclusion must remain tentative.

Although Tonic electro-receptors do not respond to the fish's own electric organ discharge they may possibly respond to the summed potentials of its own discharge and that from another fish. Two Eigenmannia placed together produce a summed potential that is amplitude modulated at the beat frequency or difference frequency between the two discharges. Tonic electroreceptors possibly are sensitive to these amplitude modulations, but this has not been investigated.

The distance of communication. One crucial step in communication is the transmission of the signal. The distance over which any communication signal is effectively transmitted depends upon the power of the source, the rate at which the signal is attenuated, the sensitivity of the receptor

and the background noise of the channel. Thus, communication between two animals continues to be effective until the distance between them has increased to the point where the communication signal is indistinguishable from the transmission channel noise. Of course, receptor and integration mechanisms of the central nervous system will evolve to improve the critical ratio of signal to noise for information transfer. Similarly if natural selection operates so as to produce signals that are effective over long distances, then the physical form of signals will evolve to be detectable at a low ratio of signal to noise.

Naturally occurring noise has not been discussed with regard to the electrical communication channel in fish. One source of noise in the electrical communication system could be due to mechanical stimulation of electroreceptors.

Electroreceptors in fish have evolved from ordinary lateral line mechanoreceptors (Lissmann and Mullinger, 1968; Szabo, 1965) and electroreceptors in some elasmobranchs are known to be sensitive to mechanical stimuli (Katsuki *et. al.*, 1951; Lowenstein, 1960; Murray, 1960; Murray, 1967). Gymnotid electroreceptors however, seem to be less sensitive to mechanical stimulation (Hagiwara and Morita, 1963; Hagiwara, Szabo, and Enger, 1965a). Selection should favor a decrease in mechanical sensitivity of electroreceptors while retaining electrical sensitivity because a species could maintain its system of electrical communication and electrical object location while it inhabits fast moving streams where mechanical stimulation is likely to be very great. Thus noise from mechanical sources is probably not a problem for electrical communication.

Other noise sources, particularly noise of electrical origin are likely to be a more severe problem than noise of mechanical origin however. This is especially true in quiet back waters of rivers and in standing swamps where gymnotids breed. The predominant source of electrical noise, aside from electrical signals produced by other species of electric fish, or other individuals of the same species of electric fish, is low frequency electromagnetic noise of terrestrial and atmospheric origin. As Storey (1953) demonstrated in his classic work

on whistling atmospherics, electrical noise in the form of radio waves with frequencies in the audio range (below 20 kHz), can be detected using an audio amplifier connected to a vertical aerial. When the amplified signal is passed directly into a loudspeaker, one can hear atmospheric discharges sounding like "clicks," "swishes," "tweeks," "chinks," and "whistlers" (Storey, 1953).

Storey (1953) triangulated the position of atmospheric "clicks" and found they were localized in storm centers up to 4000 miles from the measuring stations in Cambridge, England. It is generally accepted that the predominant source of natural radio noise of low frequency is produced by lightning discharges (Watt, 1960; Liebermann, 1956a, 1962; Soderberg, 1969). According to Liebermann (1962), there are, on the average, 100 lightning strokes per second somewhere in the world. A brief surge of current such as caused by a stroke of lightning, causes an electromagnetic wave to be generated. These waves are brief, and impulsive and they have many frequency components.

The strength of the electric field produced by the main discharge in a lightning discharge (return stroke) has been measured at various distances from the stroke by various authors (see review in Watt, 1960). The electric field is propagated according to the inverse cube of the distance for distances between 4 and 20 km. Beyond 30 km, the electric field strength is propagated according to the inverse first power of distance (Watt, 1960). Thus radio waves from lightning discharges propagate over long distances with little attenuation. The reason for first-power attenuation is that the electromagnetic waves are reflected from the ionosphere. Liebermann (1956b) detected electromagnetic waves originating from lightning from over 15,000 km from its source. Thunder storms are particularly common over the continents of South America and Africa (Krumm, 1962; World Meteorological Organization, 1956; Crichlow et. al. 1971) and the major component of world wide low frequency electrical noise comes from these regions (Balser and Wagner, 1962). Since lightning is common in South America and Africa and since the propagation suffers little attenuation, it is likely that distant lightning discharges are producing a nearly continuous background of

electrical noise that could affect the detection of communication signals of electric fish. This question was investigated while I was in Guyana.

Electrical noise penetrates water, although there are losses due to reflection. Other authors have detected noise of lightning origin from fresh water and from sea water (Barham *et. al.* 1969; Soderberg, 1969). In Guyana, I detected brief clicks and multiple ringing discharges or "tweeks" with my fish detector when the electrodes were immersed in water. Ringing discharges result from resonant reflections of low frequency electromagnetic waves between the earth and the ionosphere (Liebermann, 1956a, b; Galejs, 1964). When lightning strokes were visible, loud clicks occurred simultaneously. On June 21, 1971 at 23:00, a clear evening during the rainy season, I recorded ten minutes of this low frequency noise for analysis. Copper wire electrodes, oriented horizontally, and separated by 10, 30, or 50 cm were dipped into a quiet region of Moco-moco Creek at a depth of 10 cm. The signal was amplified with the MR2 fish detector amplifier and tape recorded. The frequency response of this system was from 30 Hz to 16 kHz. The noise characteristics of the amplifier were discussed in Chapter II D (Fig. 2). Fig. 32 shows typical clicks and ringing discharges of presumed lightning origin. In the top part of the figure, oscilloscope tracings show typical discharges. The bottom part of the figure is a typical sound spectrograph display of activity during one second. The oscilloscope records are quite similar to those published in Liebermann (1956a). For the purpose of discussion of noise events and their relation to communication, I was interested in the rate at which clicks occur, and their relative amplitudes. From oscilloscope tracings of electrical noise, I determined the frequency of occurrence of events equal to or greater than an arbitrarily chosen series of thresholds or amplitude criteria. The series of amplitudes at which frequency measures were taken were multiples of 15.5, 7.5, 7.5, and 15.0 μ V for electrode spacings of 10, 10, 30 and 50 cm respectively. The noise of the recording system with the electrodes touching was below 5 μ V and thus does not contribute to the result (Fig. 2). Fig. 33 shows data for a total of 6.080 seconds. In this figure each point represents the average number of events per second that have amplitudes that are equal to or greater

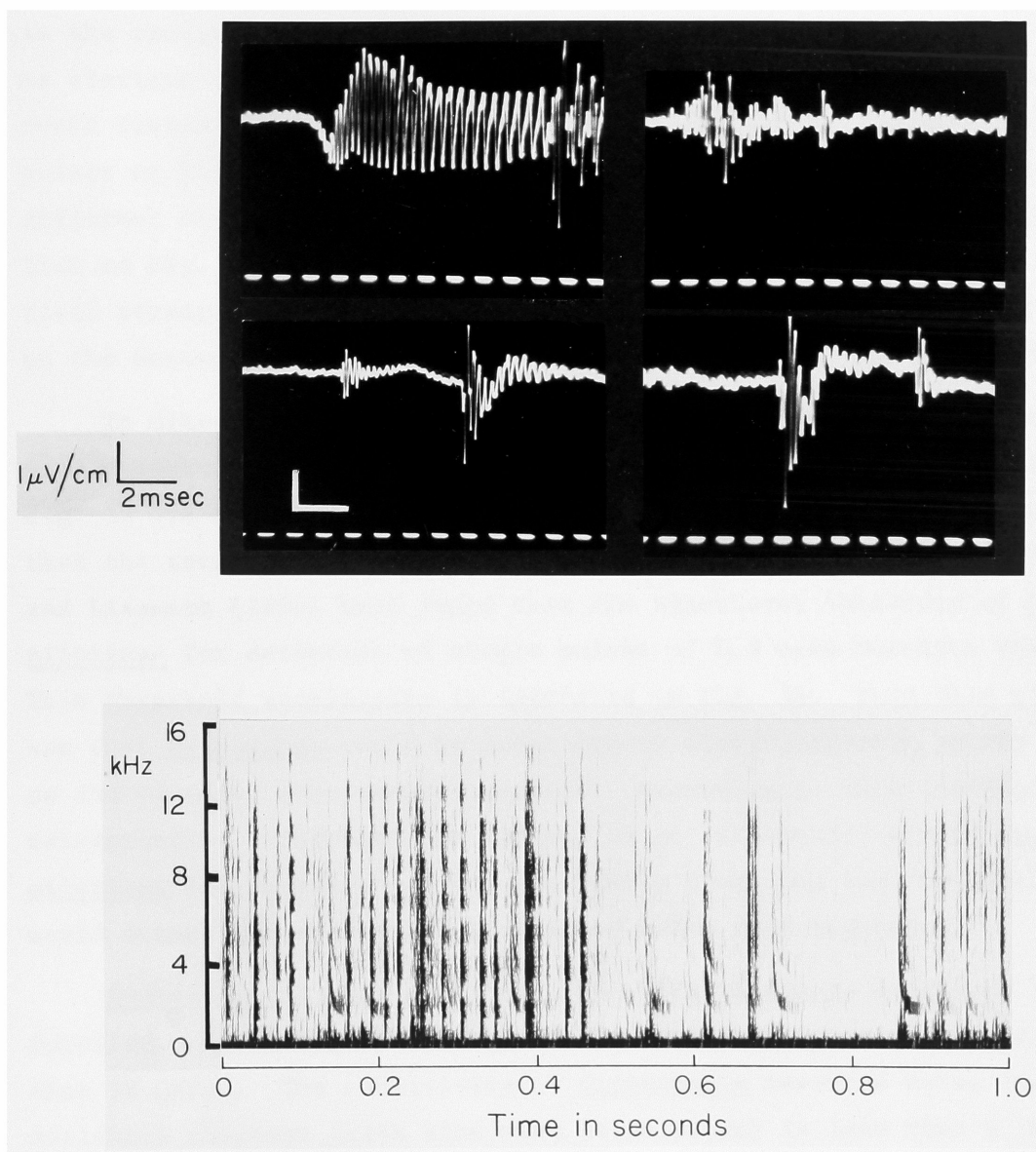


Fig. 32. Examples of naturally occurring electrical noise recorded from Moco-moco Creek, June 21, 1971. Top: Oscilloscope tracings of noise, electrode spacing, 50 cm. Bottom: Sound spectrograph of portion of recording, range 160 to 16,000 Hz; Bandwidth, 600 Hz.

than the value of the abscissa, measured in μV on the top scale. Curves for 10, 30, and 50 cm electrode spacing are shown. Clearly, large amplitude events are more frequent with 50 cm spacing than with 10 cm spacing. This is the result that is expected since the potentials from lightning exist as electric fields. This figure also illustrates that low amplitude events occur frequently and that high amplitude events occur rarely. When the points on Fig. 33 are divided by the electrode spacing, the curves for the different electrode spacings nearly overlap. A single (dashed) straight line on Fig. 33, fitted by eye, shows the frequency of events of various field strengths measured in $\mu\text{V}/\text{cm}$. This curve is referred to the scale on the bottom of the figure. The dashed line has a slope of -2.12.

To determine the effect that lightning noise has on electric fish, some measure of threshold is needed. Most of the impulses shown in Fig. 32 are of approximately 0.2 msec duration. Watt (1960) suggests that the return stroke normally has a duration of 0.2 seconds. Machin and Lissmann (1960) have found that the behavioral threshold of Gymnarchus niloticus for detection of single pulses of 0.2 msec duration was 18 $\mu\text{V}/\text{cm}$. This threshold sensitivity is indicated in Fig. 33. From this plot we see that Gymnarchus would be sensitive to electromagnetic pulses occurring on the average, once every 5 seconds. According to this threshold determination, therefore, it appears as if the sensitivity of Gymnarchus niloticus has evolved to a level slightly less than that at which it would detect the continuous background noise from lightning.

Gymnarchus is more sensitive than this to single pulses of longer duration. Similarly the threshold for sensing pulse trains is far less than 18 $\mu\text{V}/\text{cm}$. The sensitivity of Eigenmannia measured using the jamming avoidance response (with sine wave stimulation) is less than 0.18 $\mu\text{V}/\text{cm}$ (Bullock, et. al., 1972b). Conclusions regarding the probability of detecting electric fields from lightning are tentative and must await accurate behavioral tests using brief pulsed stimuli similar to those recorded for lightning. Tests should be performed under conditions where naturally occurring low frequency noise will not interfere with the results. My speculative conclusion is that electrical noise from lightning is sufficiently great to be detected by electric fish, however,

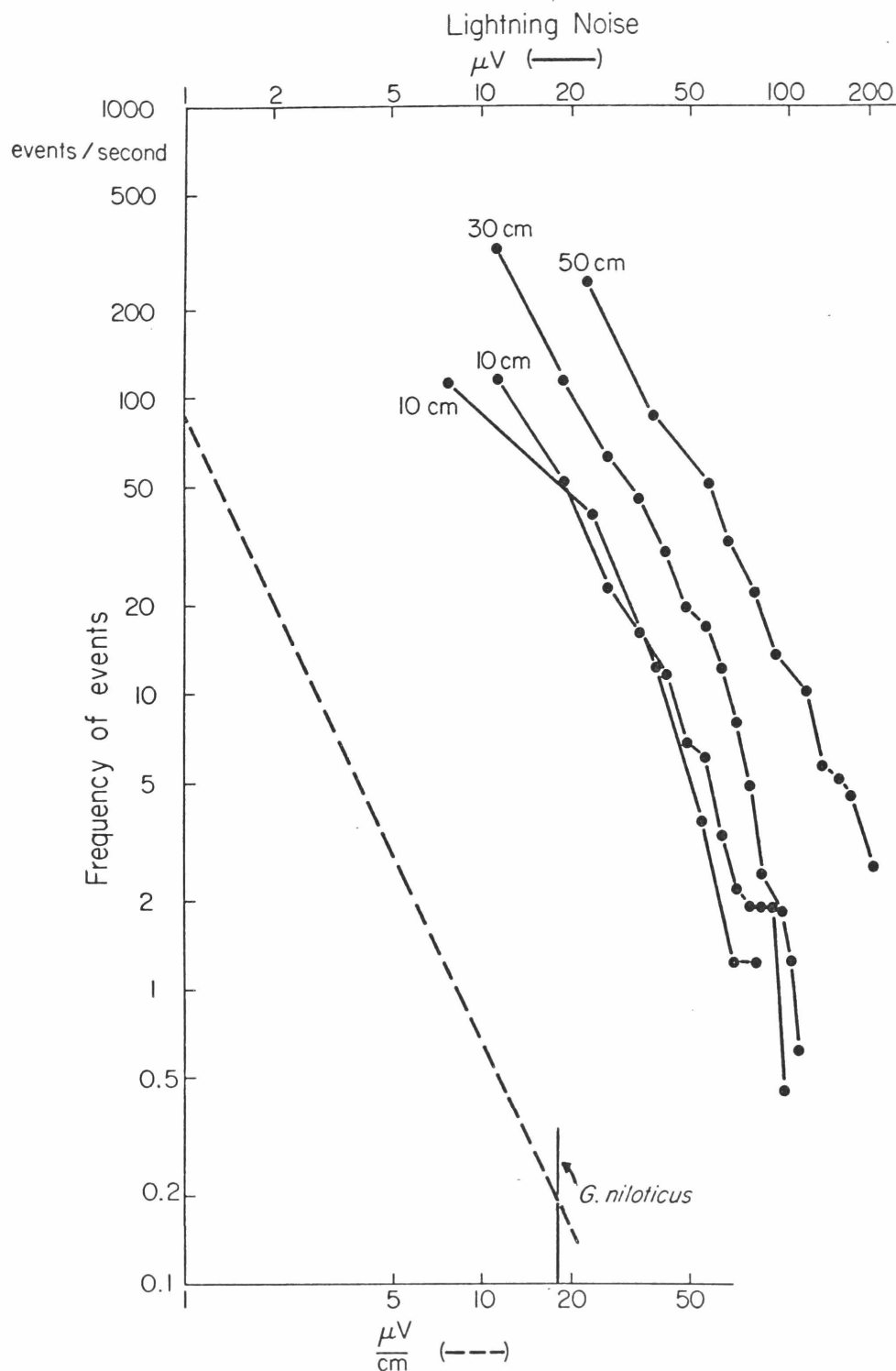


Fig. 33. Plot of the amplitude of electrical noise recorded from Moco-moco Creek, June 21, 1971, vs. the frequency of occurrence of events of that amplitude or greater. Solid lines: the absolute amplitudes of the signals for electrode spacings 10, 30 and 50 cm, referred to scale at top. Broken line: field strength in $\mu V/cm$ determined from the four solid lines fitted by eye, referred to bottom scale. Vertical line at 18 $\mu V/cm$ is the threshold sensitivity of *Gymnarchus niloticus*.

the exact rate of detection of lightning noise is not known.

If the social organization of electric fish is such that long-distance communication with electric signals is advantageous, then natural selection will favor communication signals that contrast well with the background noise. Continuous trains of pulses, both from tone fish and from pulse fish, contrast with the randomly occurring lightning noise. This contrast is achieved because the discharge is stable in frequency. It permits the receiver of the signal to filter out unwanted frequencies and thereby increase the signal to noise ratio.

Certain species of electric fish have discharges that do not contrast with lightning noise. The electric eel is one species. Its discharges occur at random intervals at low frequency. Similarly, many species of mormyrids have randomly occurring discharges. The electric eel, a predator, may gain by being inconspicuous electrically in that it may be able to approach prey without being detected. According to Ellis (1913) who quotes other sources, Electrophorus electricus eats mainly shrimp, and small fishes. Small gymnotids may be part of its diet. Although many mormyrids have randomly occurring discharges, Moller (1970) found that Gnathonemus niger produced a highly regular discharge both when an artificial electrical stimulus was applied, and when natural electric fish pulses were applied. Thus in the presence of a conspecific, the discharge frequency of some mormyrids may be stable, thus permitting long distance communication.

D. The Nature of Electric Signals

The signals used in electric communication serve the function of identification as discussed by Morris (1946) and Marler (1961). In the case of Sternopygus, information regarding the identification of the sex and the species of the signaler are encoded as the frequency of the electric discharge. In Eigenmannia, cues for species identification are also encoded as the frequency of the discharge. The wave form and harmonics of the discharge appear to be unimportant since pure sine waves elicit the species specific responses. Not all species of electric fish can be identified from frequency alone, however. This is particularly true for the fish from the family Apteronotidae from Moco-moco Creek

(A. albifrons, and Sternarchorhamphus macrostomus, Fig. 15). These species overlap in the frequency of their discharge. Moreover, in this case, there are no other apparent electrical cues of the normal discharge that could be used for species recognition. The wave form and polarity of the discharges of both species were investigated and were found to be identical. In fact, the waveform of the discharges of the two species during all stages in development were found to parallel each other, even though there were some developmental changes in waveform within the first month after hatching. It is not known how these two species are able to recognize each other, but it must be by means other than the electrical characteristics of the normal discharge.

Electrical displays serve to communicate the information about the motivation of the signaler. The electrical signals occurring in social situations that I have described in this study are similar to those that others have described for other species. A Rise is an increase in the discharge frequency that is followed, eventually, by a decrease back to the normal frequency. It is given by Sternopygus males that show site-attachment when they are in the presence of electric signals typical of Sternopygus females. Rises are also given by Eigenmannia during agonistic encounters. Rises that are longer than 2.0 seconds are called Long Rises and they are given during Retreat and following attack or threat by the opponent fish. Long Rises in Eigenmannia seem to be a submissive signal. Short Rises have durations less than 2.0 seconds. They are usually given by dominant fish. Rises bear a certain resemblance to Black-Cleworth's (1970) SID for Gymnotus carapo (Sharp increases in frequency followed by decreases to the original level) which were given before, after, and during attacks of conspecifics. SIDs served as an aggressive threat display in Gymnotus, causing the opponent to retreat. The SID pattern recurs in the Pulse gymnotids as a widespread electrical display. Among the Tone fish, the "chirp" display described by Bullock (1969) bears some resemblance to a short rise, and it seems to have an agonistic function.

Electrical displays that consist of increases in frequency also are given by many of the mormyrid species. Bursts of high frequency discharges

in Gnathonemus petersii have some function as an agonistic display (Black-Cleworth, 1970). High frequency discharges of other mormyrids are associated with attacks and with fighting (Möhres, 1957). The major difference between the SID-like displays of the Pulse fish and the Long Rises given by Eigenmannia, is that the Long Rise consists of only a small change in frequency. In many Long Rises, the frequency change amounts to only 2 to 3% of the normal frequency. In addition, Long Rises serve as a display of submissive behavior, rather than aggressive behavior.

The small frequency change is effective as a social signal only because the normal frequency is very stable. If the normal discharge showed a high degree of variability as do the discharges of most of the Pulse fish, then this would not be an effective social signal. It is not known whether other species of tone fish produce long slow frequency changes as social displays. Some apteronotids produce tonic increases in frequency in response to resistance changes (MacDonald, 1970). Eigenmannia and Apteronotus produce changes in their frequency in order to avoid artificial signals of frequencies similar to their own (Watanabe and Takeda, 1963; Bullock, 1969; Bullock *et. al.*, 1972a,b). Eigenmannia produces both increases and decreases in frequency whereas Apteronotus produces largely increases.

Interruptions are a temporary cessation of the normal discharge. In Sternopygus, Interruptions serve as part of the sequences of variations in the normal discharge given by males in the presence of females. Interruptions are given by Eigenmannia both as an aggressive threat, and during sexual encounters. Often Interruptions are given in bouts, and the number of Interruptions in the bout is related to the likelihood of attack. Interruptions are similar to Black-Cleworth's (1970) description of discharge breaks for Gymnotus carapo, which also were given during attacks, and seem to function as a threat display. Long duration discharge cessations, or arrests, function as an appeasement display in G. carapo.

Discharge Interruptions are common to many species of gymnotids and mormyrids. Black-Cleworth (1970) described long duration cessations in

Hypopomus beebei that seemed to serve as an inter-specific appeasement display (during encounters with G. carapo). During this study I detected discharge cessations from Hypopomus artedi, Gymnorhamphichthys hypostomus, and Rhamphichthys rostratus, all given during varying intensities of attack. Bullock (1969) lists several other species that produce discharge cessations. Discharge cessations in Gymnarchus niloticus are similar to those of Eigenmannia. Some discharge cessations are short in duration and are associated with attack on electrodes that carry artificial stimulation (Szabo and Suckling, 1964; Harder and Uhlemann, 1967).

Eigenmannia and Sternopygus from the Rupununi District use their electric discharges for social communication in addition to object location as inferred from other studies (Lissmann, 1958). The normal discharge serves as a communication signal for species recognition. In Sternopygus it also serves for sex recognition. In Eigenmannia, communication of motivation, of the tendency to attack, to retreat, or the motivation for sexual behavior are communicated through modifications of the discharge, both through frequency changes and by discharge cessations.

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