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SOCIAL BEHAVIOR IN THE ELECTRIC CATFISH: THE ROLE OF BEHAVIORAL AND ELECTRIC ORGAN DISCHARGE DISPLAYS IN INTRA- AND INTERSPECIFIC INTERACTIONS

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SOCIAL BEHAVIOR IN THE ELECTRIC CATFISH:
The role of behavioral and electric organ discharge displays in intra- and interspecific interactions.

by

Catharine H. Rankin

A dissertation submitted to the Graduate Faculty in
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ABSTRACT

SOCIAL BEHAVIOR IN THE ELECTRIC CATFISH: The role of behavioral and electric organ discharge displays in intra- and interspecific interactions.

by

Catharine H. Rankin

Adviser: Professor Peter Moller

Using a Resident-intruder Experimental paradigm the African electric catfish, Malapterurus electricus, was observed in inter- and intraspecific interactions. Qualitative and quantitative differences in the catfish's behavior demonstrated that this fish discriminated between conspecifics and members of other species. In interactions with conspecifics, open-mouth and lateral displays were observed. Some of these aggressive interactions escalated to bites with or without electric organ discharges. Discharges were rarely observed during intraspecific interactions. In interactions between conspecifics, residents stayed near their shelter on one side of the tank while intruders stayed on the other side. In contrast, resident and intruder catfish showed few differences in their behavior when their partner was not a conspecific. In interspecific encounters, contacts were limited to brief touches often accompanied by electric organ discharges. The temporal patterning of the electric organ discharges emitted in response to contacts with conspecifics was different from that assosciated with contacts with other species.

An observation of catfish in groups of different sizes, over a period of several days, provided information about territoriality, spacing strategies and the role of electric organ discharges in social behavior. The electric catfish restricted other conspecific's use of shelter sites. Dominance relationships were established following lateral displays with few electric organ discharges observed. Under high population density, electric organ discharges may serve a communication function and "advertize" a territory.

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INTRODUCTION

Current thinking about social spacing no longer rigidly partitions patterns of spatial distribution into tightly defined categories. Animal social spacing is viewed as a continuum of spacing strategies determined by organismic and environmental variables. Territoriality is placed at one end of this continuum and dominance hierarchies at the other (Kaufmann 1983). The position of a group of organisms on this continuum is based on the degree of site attachment and the degree to which an individual has exclusive use of the resources of that site.

In territorial populations, individual members occupy relatively fixed areas from which rival conspecifics are excluded or driven out by the efforts of the resident (Brown 1975). The type of territorial organization that a population establishes, for example mating and feeding territories, and the physical aspects of the territory occupied, such as its shape and size, will depend on a number of organismic and environmental factors such as the age and sex of the animal, its physiological state, population density, the season, habitat characteristics and many others.

In dominance systems the more dominant members have greater access to resources such as food or reproductive partners than do less dominant members. Once a dominance system has been established it is relatively stable. A dominance organization can take on several different forms: 1) a single individual may dominate over all others with no hierarchical relationships within the others in the group, 2) a linear hierarchy and 3) a non-linear hierarchy (Brown, 1975).

Environmental restriction of resources such as food and shelters as well as changing population levels can affect the social organization of a group of animals. Fabricius and Gusstafson (1953) suggested that fish showing dominance hierarchies in aquariums may be organized territorially in the wild. Dominance systems in aquaria may be the result of an inability on the part of the fish to disperse in the limited confines. When a larger tank is provided, territorial organization may replace the dominance hierarchy seen in a smaller tank.

The previous social experience of an individual fish can affect the way it establishes a territory and the way it interacts with others. Differences in familiarity with the encounter site known as "the prior residence effect", refers to the advantage that a resident has over an intruder in its territory. The effects of prior residence on agonistic tendencies can result in territories of different sizes, depending on whether individuals are introduced to an area simultaneously, or are introduced sequentially. Animals already established are able to exclude "latecomers" from much larger areas (Waser and Wiley 1979). Thus, previous social experience may influence spacing behavior by changing an individuals agonistic tendencies.

Patterns of spatial distribution may reflect interspecific interactions as well as intraspecific interactions. In any environment different species coexist, and may compete, although these interspecific interactions have been studied less frequently than interactions between conspecifics (Morse 1980). A proportion of these interspecific interactions may be aggressive encounters. The interactions may be predatory in nature. They may also be between individuals that occupy similar habitats or exploit similar food resources. Several studies have documented defense of territories against non-conspecifics in both birds (Murray 1971; review by Morse 1980) and fish (Low 1971, Myrberg and Thresher 1974, Thresher 1976 and Losey 1982). The best documented cases of interspecific territorial defense in fish are in the reef dwelling herbivorous pomacentrids (damselfishes). Low (1971) found that over 90% of the intruders evicted from Pomacentrus flavicauda's territory were of other species, and that 35 of the 38 species chased off were food competitors while 16 species of intruders who exploited different foods were ignored. Myrberg and Thresher (1974), observing *Eupomacentrus planifrons*, found that the size of the territory defended depended on the species of intruder. The level of aggression displayed by the damselfish was inversely proportional to the taxonomic distance between the resident and the intruder. In a similar study of *Eupomacentrus leucostictus*, Ebersole (1977) was able to relate the degree of aggression displayed toward an intruding species to the degree of overlap in diet between the two. Thus, it appears that damselfish defend territories against food competitors and can make a discrimination among a large number of species of fish, attacking competitors and leaving non-competitors unmolested. This strategy is adaptive in that a resident can protect a food source while not wasting energy attacking non-competitors.

In the studies described above the species of fish that were excluded represented a number of different taxonomic groups and were often highly dissimilar in body form, color and size. Thresher (1976) studied *Eupomacentrus planifrons* to determine the roles played by audition, olfaction and vision in the identification of competitor species. The discrimination was based on visual cues, and most importantly on the body form of the intruder. There were differences in territorial defense when he compared defense against a conspecific with defense against others. Color was important for conspecific territoriality while movement by the intruder was not. In the case of interspecific intruders, color was not important but movement by the other species of fish was a critical factor in releasing territorial aggression against them. Thresher (1976) also noted differences in the posture of the resident damselfish when it directed aggression towards conspecifics when compared to aggression directed towards other species of fish. Based on these differences in intraspecific and interspecific territoriality Thresher argued that interspecific territoriality is not simply a sub-form or "mistaken" expression (as suggested by Murray 1971) of intraspecific territoriality but may be a separate, stable system designed to defend a resource.

For territorial and dominance organizations to function there must be some form of social recognition. In fish this may include recognition processes at interspecies, species, sexual, and individual levels. A variety of sensory channels (e.g., visual, chemoreceptive, mechanoreceptive, tactile and electrical) may be utilized to mediate social recognition (Myrberg 1980). In territorial behavior the territory may be marked or 'advertised' so that it is recognized by intruders. Intruders, in turn, must recognize the signals used to mark a territory. Many fish species use visual (e.g., Thresher 1976), auditory (Myreberg 1980), and chemical signals (Richards 1976) that serve as displays for territorial defense. In addition there is evidence that both visual (Thresher 1981 as cited in Myreberg 1980) and chemical cues (Todd 1971) mediate social recognition in some species of fish that is necessary for stable dominance systems.

Questions of social organization, inter- and intraspecific competition, and the sensory mechanisms that mediate these behaviors, are key issues in behavioral ecology today. The African electric catfish, _Malapterurus electricus_ is a suitable subject to address these questions. Both laboratory and field behavioral studies provide an excellant data basis for the catfish's behavior. Field data suggest a pattern of spatial distribution with which can be compared laboratory findings. The electric catfish emits strong electric organ discharges which have not been studied in a social context and yet may serve as a means of social recognition, as a display to advertise a territory or as a weapon to defend it.

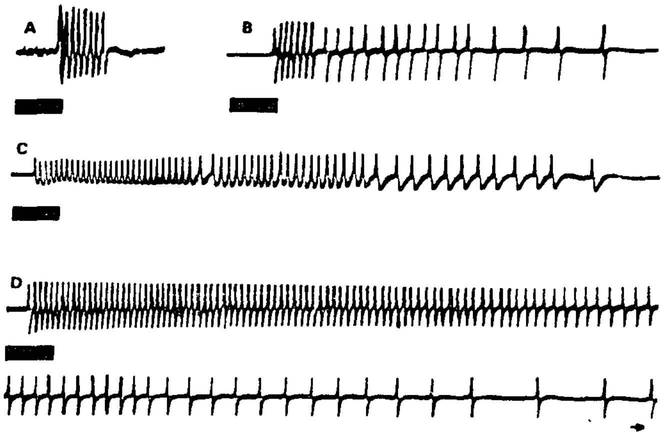
Malapterurus electricus is a slow swimming catfish that lives in the freshwater lakes and rivers throughout Africa. It has been suggested that there are two species of

Malapteruridae: *Malapterurus electricus* and *Malapterurus microstoma*. *M. microstoma* was first described anatomically by Poll and Goss (1969). Like *M. electricus*, *M. microstoma* is compact, torpedo shaped, has barbels about the mouth, no dorsal fin and no protective spines. Poll and Goss noted that both species produce electric organ discharges and no differences were found in either species' electric organs and the electric organ discharges. There are no behavioral or physiological accounts of *M. microstoma*.

Malapterurus electricus is a relatively fast growing, long lived species with an upper age limit of 11 years, an average length of 50.0 cm, and an average standard weight of 2.8kg in the 10th year (Balon and Coche 1974). Specimens up to 137 cm weighing 27 kg have been recorded (Daget 1954). Calculations by Balon and Coche indicated that in Lake Kariba the electric catfish grew 4 to 5 cm a year. They reported that the fish reached sexual maturity in its fifth season when the mean standard length was 23.5 cm and the mean weight was 0.31 kg.

In *M. electricus* the electric organ develops from pectoral muscles and surrounds the body over most of the length of the fish. The EODs are monophasic head negative pulses one to two ms in duration with a repetition rate of 300-500 per second (Bennett 1971). When the animal feeds or is mechanically disturbed a few pulses or long volleys of pulses have been observed (Bauer 1968) (Figure 1).

Figure 1: Examples of Electric Organ Discharges. Volleys range from short bursts (as in A) to long feeding feeding volleys of several hundred pulses (B,C and D). Time marker 20ms.


A
B
C
D

Relatively little is known about the behavior of the electric catfish in its natural habitat. The animals live in turbid and/or black waters where low visibility makes direct behavioral observation almost impossible. Indirect observations, however, have proved useful. For example, Belbenoit, Moller, Serrier and Push (1979) examined catfish EOD behavior in Lake Kainji in Nigeria by "mining" an area with electrodes and monitoring discharge activity. The highest level of EOD activity was observed during the first six hours after sunset. By comparison with laboratory data it was inferred that the catfish were hunting and feeding during the early hours of the night. The same authors reported a previously unknown EOD pattern in which volleys were sometimes preceeded by low frequency trains of 1 to 11 pulses. This pattern was seen in approximately 38% of all volleys recorded during the first four hours after sunset. Belbenoit et al. (1979) suggested that the prevolley could serve : (1) as part of an active electrolocation system or (2) as part of an electromechanical prey locating mechanism to startle prey fish into movement so they could be detected by lateral line receptors (similar to suggestions by Bauer 1968).

Sagua (1980) carried out an analysis of stomach contents of Malapterurus electricus caught in Lake Kainji and the Niger River in Nigeria. The catfish was not a selective feeder but fed on the most readily available prey fish in the habitat. Differences in diet between animals caught in the river and in the lake reflected the relative abundance and availability of the different groups of fish in the two habitats. Over the year the predominant food fish were Clupeidae and Cichlidae. The number of small prey fish found showed that Malapterurus electricus is a voracious piscivore on small schooling fishes. Large size prey fish occurred infrequently and in small numbers. The food items found were representative of both the size distribution and the composition of pelagic schooling preyfish.

Bauer (1968) undertook a detailed laboratory study of the feeding behavior of Malapterurus electricus. He observed that the catfish was a poor swimmer that spent much of the time on the bottom of the tank. Supporting the field data the catfish did show a higher activity level at night. When a prey fish was introduced into the tank (regardless of time of day) the catfish detected the presence of the prey and pursued it. When the catfish approached the prey it thrust forward, opened its mouth creating a suction that pulled the prey into its mouth, and simultaneously began to emit a high frequency electric organ discharge. The discharge would continue, steadily or in shorter bursts until the prey was swallowed. Bauer recorded feeding volleys consisting of 1 to 562 impulses (emitted in from 1ms to 6.8s) with an average of 71 pulses in a volley. The number of pulses emitted correlated with the size of the prey fish. The emission of the feeding EODs depended on the presence of a live prey fish. No discharges were recorded when catfish were fed dead or paralyzed fish or small tubifex worms.

By eliminating senses through surgery Bauer (1968) demonstrated that chemical stimuli that excite taste receptors in the skin, and mechanical stimuli that excite lateral line receptors are the key sensory stimuli in prey detection.

In addition to discharges obtained during feeding, Bauer also recorded discharges in two other situations. The first type was called chase volley because they occurred when large catfish (over 30 cm) were pursuing prey. The chase volley consisted of from 1 to 10 pulses (emitted over 1 to 30ms) with an average of three pulses per volley. Bauer suggested that these volleys may facilitate prey location by startling the prey and forcing it to leave a shelter. The second situation when discharges were observed was when a catfish was mechanically stimulated. The subsequent discharge was called by Bauer a "defensive" volley. It consisted of an average of 16 pulses (range 3 to 67 pulses). Each defensive volley began with a high repetition rate (400-500Hz)which rapidly decreased. Bauer hypothesized that different discharge patterns resulted from different chemical stimuli. By selectively disrupting the taste and lateral olfactory system Bauer demonstrated that predatory behavior was only disrupted by interference with the taste systems.

Little is known about *Malapterurus electricus*' social behavior. Coates and Atz (1954) reported that "In captivity it cannot be kept with other members of its species in a tank; one and only one electric catfish remains." Bauer (1968) reported that catfish housed together fought, often to the death. Balon and Coche (1974) reported that the density of electric catfish in Lake Kariba was high, about 6,994 specimens per hectare. Brichard (1978) found that electric catfish were very common in Lake Tanganyika and that it was not uncommon to observe a number of large catfish (30 to 100 cm) two to three meters apart in shallow rocky areas. Brichard reported that even small fish 3 cm in length were found living separately among the rocks.

These reports suggested that population levels of *M. electricus* are often high and that spacing strategies may be important. The mechanisms that would facilitate intraspecific communication for spacing are as yet unknown.

Malapterurus electricus is a silurid catfish and, like most catfish has 'small pit organs', electroreceptors in the form of ampullary organs. In several species these receptors are sensitive to low frequency weak electric fields (see reviews by Kalmijn 1974 and 1978). Catfish may detect prey fish by fluctuations of weak bioelectric fields around them. Kalmijn demonstrated that *Ictalurus nebulosus* could locate the position of a live goldfish when the only cues available were the bioelectric potentials emanating from the goldfish. Kalmijn suggested that a similar electric sense may be present in *M. electricus* as Bennett (1971) found small pit organs on their skin. Bauer (1968) reported that *M. electricus* could respond to an electrical square wave of 1.5 ms duration and 0.3 mv/cm amplitude. This is within the range of the bioelectrical potentials studied by Kalmijn (1974) in *I. nebulosus*.

As mentioned above, *Malapterurus electricus* generates strong electric fields. Since ampullary receptors in *I. nebulosus* are maximally sensitive to frequencies under 40 Hz (Kalmijn 1974). The question has been raised whether its ampullary receptors can detect some features of the electric catfish's high frequency discharge volley. Some suggestions have been made that single pulses or low frequency pre-volleys (Belbenoit, Moller, Serrier and Push 1979) or even the low frequency tail phase of a feeding volley (1-40 Hz) may be detected. Although there has been little evidence that the electric organ of the catfish is used in an electrosensory system for social communication, data obtained by Kastoun (1971) suggest that the EODs may contain information useful in social interactions. Kastoun connected two tanks containing *Malapterurus electricus* with electric wires and found the fish responded selectively to different types of EOD volleys.

Alexander (1961) suggested that *Malapterurus electricus* may use the discharge in aggressive encounters as either an offensive or defensive weapon and that the electric organ has taken over the defensive function of the spines on the dorsal and pectoral fins in other species of catfish.

In summary, under laboratory conditions, there is a high correlation between EOD patterns and feeding behavior. Therefore EODs recorded in the field were assumed to be part of feeding volleys. There are suggestions that the EODs may be used in social communication among electric catfish if the discharges are detected by the ampullary receptors. There are also suggestions (Alexander 1961; Belbenoit, Moller, Serrier and Push 1979) that the EOD may serve as an offensive weapon against predators.

Malapterurus electricus belongs to one of three groups of so-called strong electric fish. The other two are: the electric eel (*Electrophorus electricus*), and the Torpidinid rays. Strong electric fish generate electric organ discharges of voltage or current high enough to stun or kill other fish. A review of existing data on the electric eel and the Torpedo ray may suggest directions for the studies of the electric catfish, conversely any new findings on the electric catfish may serve to direct future research on the other two groups of strong electric fish.

The electric organs of the strong electric fish are made up of long columns of electrocytes whose embryonic origin has involved the modification of cells in particular muscle groups: the branchial muscles in the torpidinid rays, the pectoral muscles in the catfish and the axial and tail muscles in the electric eel. The electrocytes are innervated by motoneurons and all depolarize simultaneously. This depolarization sums and generates an electric organ discharge. The electric organ discharges are emitted in the form of volleys containing from one to several hundred pulses emitted at high repetition rates (Bennett 1971a). Volleys may consist of several trains of EODs. The strong electric fish emit their discharges intermittently.

While it has been suggested that EODs are used in both predation and defense, and may be used in intraspecific communication (Belbenoit, Moller, Serrier and Push 1979), research to date has concentrated on the role of the strong EOD in predatory behavior (e.g., Bauer 1969, 1979; Belbenoit 1972).

Studies of feeding behavior in the strong electric fish have shown that the strong electric organ discharges are used in prey capture (i.e., Bauer 1968, Bauer 1979, and Belbenoit 1972).

The Behavior of Other Strong Electric Fish

Electrophorus electricus

Electrophorus electricus lives in the freshwater rivers and lakes of South and Central America. It is a member of the suborder Gymnotoidei (Greenwood, Rosen, Weitzman and Myers 1967). It is unique among electric fish in that it has two electric organ systems derived from axial and tail muscle groups. Each produces a different type of EOD; an intermittent low voltage EOD is produced by the Sachs organ and a high voltage EOD is generated by the main organ and Hunter's organ. Like the related weak-electric Gymnotidae, the eel has an electrosensory system in which changes in electric fields produced by the Sachs organ are detected by tuberous organ electroreceptors. This system is used for electrolocation and possibly for intraspecific communication (Bennett 1971).

Although it is not known whether the strong EODs are used in intraspecific communication, discharges are observed during predation. The strong EODs are emitted when the fish is hunting or feeding (Bauer 1979). The frequency of feeding EODs observed by Bauer (1979) was initially high (about 500 Hz), and subsequently decreased to only one or two pulses per second at the end of the volley. Since there was a decrease in amplitude at the end of the feeding response Bauer found it difficult to distinguish between strong and weak EODs. Attacks accompanied by high voltage EODs could be elicited by mechanical stimuli, such as water displacement produced by blowing on the surface of the water near the eel.

Cox (1938) was the first to suggest that the strong EODs might be used for social signalling when he reported that *Electrophorus electricus* could be attracted to an alternating current in the water. Bullock (1973) reported that eels approach other eels while feeding and suggested that this may represent an adaptive response to the presence of food.

Torpedo Rays

The Torpiniform electric rays are found in tropical and temperate ocean waters throughout the world. There are four families of electric rays, Torpedinidae, Hypnidae, Narcinidae and Narkidae (Bond 1980). The bulk of behavioral data has been obtained from the Torpedinidae. The electric organ of Torpedo is composed of large flattened cells, one organ on each side, extending through most of the body.

Unlike the high voltage discharge of Electrophorus electricus the torpidinid rays generate high current EODs of up to 50A (Fessard 1957). Torpedo rays inhabit salt water, which offers low resistance to electrical signals and allows greater current to flow. In fresh water, with higher resistance the voltage produced is not high enough to produce high current. In salt water the strong electric rays produce low-voltage, high-current EODs, while in freshwater the strong electric eels and catfish produce electric signals of high voltage and low amperage.

Like the studies of the electric eel, research on the adaptive significance of the strong EODs in the Torpedo rays has concentrated on predatory usage. Belbenoit (1970, 1981), Belbenoit and Moller (1972) and Belbenoit and Bauer (1972) have examined the relationship between predatory and EOD behaviors in Torpedo marmorata, a North Atlantic species. In this species the capture of prey fish was associated with an initial high frequency EOD volley of 300 to 400 Hz. The EODs immobilized and in some cases killed the prey immediately. When the prey was immobile the ray used its pectoral wings and trunk to surround the prey and manipulate it towards it's mouth. The EOD activity was usually interrupted after the initial volleys of the capture phase, and then reappeared during ingestion. Belbenoit (1981) also recorded electric organ discharges in response to mechanical stimulation. When *Torpedo marmorata* was stimulated with a plastic rod a short volley of electric organ discharges of low repetition rate (less than 170 Hz) was recorded.

Field observations on *Torpedo californicus* Brae and Hixon 1978) indicated that feeding behaviors similar to *T.* marmorata occur in this species. The authors used a flashlight bulb attached to an anesthetized prey fish to demonstrate that the ray was discharging electrically when the prey was captured.

Thus, there is evidence that for two species of torpidinids the electric organ discharge plays a key role in predation. No studies are available on the role of the electric organ discharge in social interactions.

Behavioral Data for Two Silurids

Since little information is available on the social interactions of *Malapterurus electricus*, an examination of the information on social behavior among other types of catfish may suggest behaviors to search for in interactions between electric catfish. Like *M. electricus* the Ictaluridae and the Claridae are both nocturnal piscivores that live in freshwater rivers and lakes.

Todd (1971) and Richards (1976) have studied territorial behavior in the brown bullhead catfish *Ictalurus* *nebulosus*. Todd demonstrated that in laboratory tanks bullhead catfish established territories that were defended against intruders. If the density of fish in a tank was high, Todd observed dominance hierarchies, with aggressive interactions used to establish and maintain rank.

Richards (1976) studied territorial behavior of the bullhead catfish and found that the chemicals for individual recognition were contained in the urine and the mucus of the integument. Both of these substances were used by *Ictalurus nebulosus* to mark territories. Richards found that the bullhead catfish could be trained to discriminate between individual bullheads, between four other species of fish, but could not be trained to discriminate between individuals of another species of fish. Richard's conclusions were that chemoreception was the dominant sensory modality involved in the discrimination of individuals and in establishing and maintaining territories in *I. nebulosus*.

Bruton (1979a, 1979b,1979c) has carried out a series of studies on *Clarias gariepinus* in its natural habitat. He found no evidence for territoriality, but found social facilitation of feeding in two ways. He observed small groups of catfish hunting cooperatively and herding shoals of small schooling fish into shallow water for easy capture. Bruton also observed large numbers of catfish feeding on surface detritus together. Surface feeding was accompanied by loud sucking noises and "smacks" caused by the catfish hitting the ventral side of the head against the water surface. The sounds of feeding attracted other *C. gariepinus* to the area. The catfish stayed tightly grouped during feeding and seemed to be stimulated into more intense activity by the close presence and activity of other catfish. Bruton concluded that social feeding increased the predation efficiency of the individual predator. Bruton observed some aggression between individual *C. gariepinus* prior to courtship and males were observed to engage in fights prior to mating.

A wide range of social behaviors has been observed within the silurid group. In the bullhead catfish territoriality and dominance hierarchies were observed, while in Clarias social hunting was found and dominance struggles were observed in breeding males.

Rationale and Objectives

The objectives of this research are threefold;(1) to develop and test an alternative hypothesis to the current thinking about the role of the EOD as a predatory tool (2) to document the use of EODs in inter- and intraspecific interactions and (3) to contribute to the study of inter- and intraspecific interactions.

Previous research on strong electric fish has focused on the role of the EOD in predation. However, Bauer (1968) and Belbenoit Moller, Serrier and Push (1979) also suggested that the strong EODs may be used in intraspecific communication or as an offensive weapon. Of the three groups of strong electric fish the electric catfish was chosen as subject for the current experiments because as illustrated earlier the largest body of ecological and behavioral data on strong electric fish is available for *Malapterurus electricus*. There is some indication that *M. electricus* may be territorial. In the wild, individuals are captured spaced apart (Balon and Coche 1974, Brichard 1978 and personal observation). *Malapterurus electricus* do exhibit aggression against conspecifics in the laboratory. The strong EODs represent a potential means for intraspecific communication that may be used in territorial advertisement or defence. Field data (Belbenoit et al 1979) on the EODs of *M. electricus* can be compared with laboratory findings. Comparisons of inter- and intraspecific communication have shown that often displays take different forms with conspecifics than with other species (Thresher 1976). The strong EODs may take a different form or be used differently in inter- and intraspecific encounters.

This project will attempt to contribute answers to the behavioral ecological questions of the territoriality-dominance continuum, and the sensory cues that are used in social recognition.

The specific aims of this project were (1) to compile an ethogram of the behavior of Malapterurus electricus in social situations, (2) to correlate EODs and EOD patterns with behaviors observed in inter- and intraspecific interactions, and (3) to determine the preferred patterns of spatial distribution of groups of electric catfish under laboratory conditions.

The study consisted of two experiments. Experiment I was designed to study short-term dyadic interactions of individuals introduced sequentially into a small area using a 'resident-intruder paradigm. Previous work (e.g.,Figler and Einhorn 1983) has shown that the 'prior residence' design maximizes the probability of the expression of territorial or dominance behaviors in pairs of fish.

In Experiment II, a large open field tank was used to observe from one to several fish in a large space, over much longer periods of time. An abundance of shelters allowed the animals to display preferred patterns of spatial distribution.

EXPERIMENT I: DYADIC INTERACTION

In this experiment, observations were made of single electric catfish, pairs of catfish and mixed-species pairs consisting of an electric catfish and a non-conspecific. The motor behaviors and the fish's EOD activity were recorded for comparison in inter- and intraspecific interactions.

Methods

Subjects

The subjects of these studies were 30 Malapterurus electricus, ranging in size from 13-23 cm in total length. It was assumed that these fish were all sub-adults since Balon and Coche (1974) reported that sexual maturity was reached at about 5 years when the length exceeded 23 cm. Each fish was housed individually in a separate 22.4 liter aquarium (41 X 26 X 21 cm) for at least 30 days prior to testing. The water in the home aquaria was maintained at 25±2 C and the water conductivity at about 180±30 uS/cm. The Light:Dark cycle was set at 12:12 with the light phase (fluorescent lights) running from 08:00 to 20:00h. The catfish were fed goldfish (Carassius auratus) and tubifex worms. Records were maintained of length, weight, and EOD amplitude for each animal (Table 1).

To test interspecific interactions, six specimens each of *Carrassius auratus*, *Seratheradon* (*Tilapia*) *melanotheron* (from here on referred to as *Tilapia*) and *Polypterus palmas* were used. The goldfish measured 10-15 cm (too large to be prey) and were chosen to present many of the stimuli associated with the laboratory diet. The *Tilapia* ranged in size from 14 to 18 cm. *Tilapia* constitute a major portion of the catfish's prey in the natural environment (Sagua 1980). *P. palmas* ranged from 25 to 30 cm. This fish is an omnivore, sympatric with the catfish and probably a competitor for food and shelter sites.

M. electricus and *P. palmas* were obtained from a local fish importer. Goldfish and *Tilapia* were obtained from stocks maintained in our laboratory.

To distinguish which of two catfish discharged some animals were rendered electrically 'silent'. This involved a relatively simple procedure. The nerve to the electric organ was bilaterally cut through a midventral incision at the anterior of the fish. Following a 30-day recovery period these silent fish were used as residents or intruders and paired with intact partners.

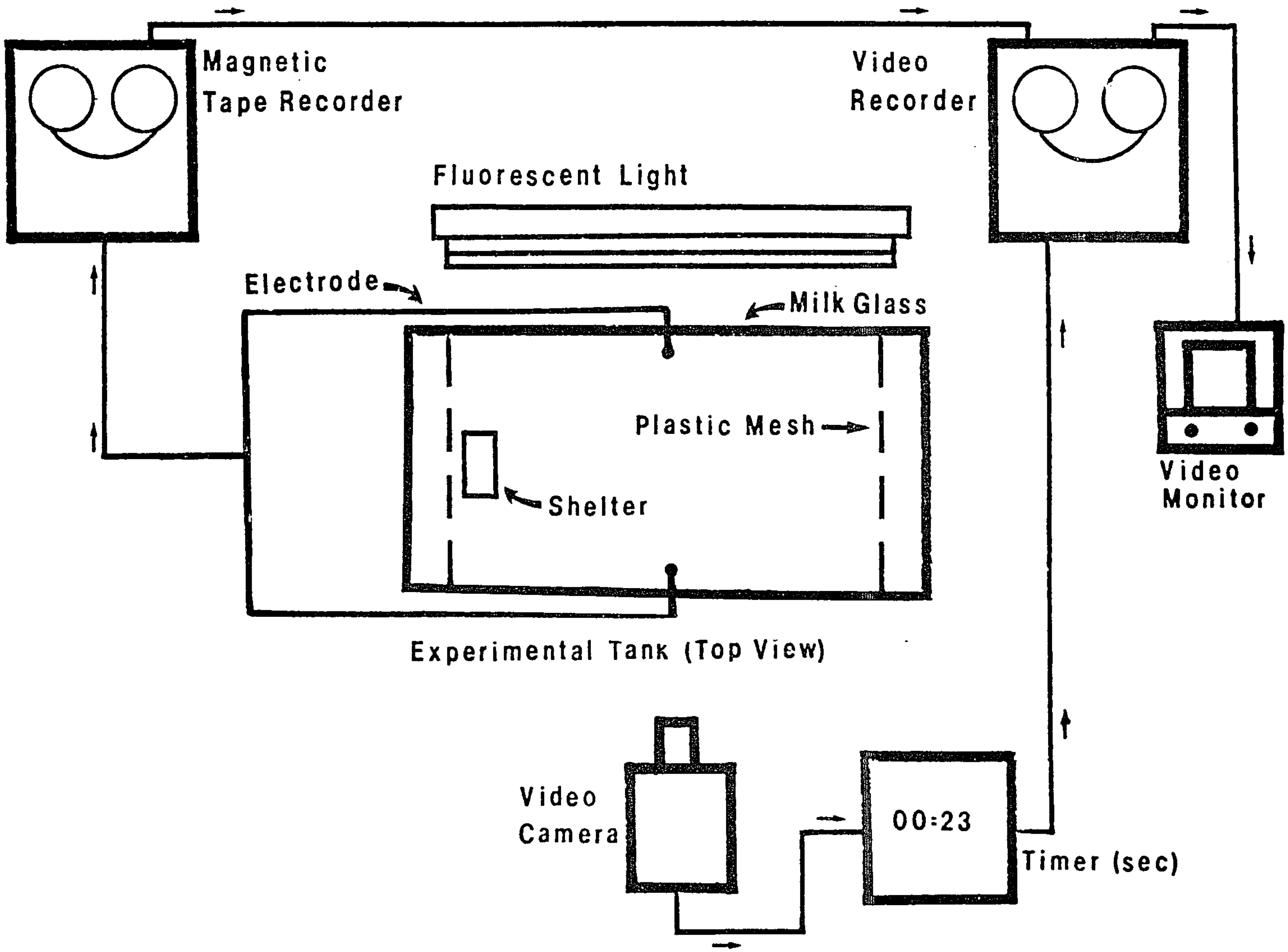
Apparatus

The testing chamber (adapted from Crockett 1983) consisted of an all glass 209 l aquarium measuring W42 x H50 x L91 cm. The water temperature was kept at 25±2 C with the water conductivity maintained at 180±30 uS/cm. The tank was provided with a plastic shelter tube (7.6 cm in diameter and 12.7 cm long) fastened to the floor on one side of the tank (Figure 2).

In order to record the observations on videotape the tank was illuminated from behind and beneath by two fluorescent light fixtures, each fitted with two 40 W cool white bulbs (Norelco, E40CW). The fixtures were mounted 43 cm behind the tank and 43 cm beneath it. These lights provided an evenly diffuse light inside the aquarium when the light was passed through plate milk glass fastened to the back and the bottom of the aquarium. The light was further reduced by covering the lamp with red acetate to produce an illumination of 44 to 88 lux. This illumination was chosed for two reasons. The first was to optimize the shelter attachment of the catfish, being noctural, the light would increase the probability that the catfish would be inactive in the shelter. The second reason was to facilitate filming.

EODs were monitored using a pair of Ag/AgCl electrodes fitted at the center of the front and back walls of the tank

Figure 2: Schematic of the experimental set-up for Experiment I. (Figure is not drawn to scale). Adapted from Crockett 1983.


Magnetic Tape Recorder
Video Recorder
Fluorescent Light
Electrode
Milk Glass
Plastic Mesh
Shelter
Video Monitor
Experimental Tank (Top View)
Video Camera
00:23
Timer (sec)

(50.8 cm apart) and recorded on magnetic tape (Sony TC-270 two channel tape recorder). Behavioral interactions were recorded on videotape (Sony AV 3200 camera, Sony AV 3600 video recorder).

Procedure

All fish were randomly divided into residents and intruders. There were 6 catfish residents, 2 goldfish residents, 2 Tilapia residents and 2 P. palmas residents. Each catfish resident was tested with 6 catfish intruders and 2 goldfish, 2 Tilapia and 2 P. palmas intruders. Each non-catfish resident was tested with 6 catfish intruders.

A resident was placed in the experimental tank three days before a single intruder was introduced. The overt behavior of both animals and EODs were recorded on videotape for a ten minute trial. Following a trial the intruder was returned to its home tank. The same fish was resident for a week during which 12 different intruders were introduced, each only once. Three trials per day were run with a minimum of three hours intertrial time. The order of intruder presentation was randomized for each resident. No attempt was made to study systematic changes in behavior over the period of a trial or a series of trials. To obtain baseline measures observations were made of the 6 residents alone following the 3 day adaptation period, and also of each of 6 catfish immediately following introduction into the empty tank ('intruders alone').

Analysis

The videotapes were analyzed to obtain the following measures: (1)location data for each of the two fish, and (2) behavior data for each fish. A TRS-80 micro-computer was programmed as an event recorder to calculate frequency and duration of the chosen measures. The location of the fish was determined from a grid placed over the video screen. The grid divided the tank into four quadrants of equal size. The two quadrants on the floor of the tank were labelled "A" and "B"; quadrant "A" was on the left of the tank and contained the shelter. Quadrants "C" and "D" were the highwater areas of the tank. As a fish swam about the tank during a trial it was scored in a quadrant when more than 50% of its body crossed into the quadrant. If a fish settled on the dividing line between quadrants it was scored in the quadrant it had previously been in.

From observations of interactions a list of 16 behaviors was generated.

1. 'Inside shelter'; a fish occupied the shelter with more than 25% of the body.
2. 'Outside shelter'; a fish occupied the shelter with less than 25% of of the body inside the shelter, or touching the shelter with some part of the body.

3. 'Resting'; the fish lay motionless on the floor of the tank, and was not in contact with the shelter.
4. 'Swimming'; the fish was actively moving about the tank.
5. 'Hovering' maintained a stabilized position in midwater.
6. 'Pushing'; one fish physically moved the other fish.
7. 'Contact'; any physical interaction between the two fish.
8. 'Chasing'; when one animal swam rapidly after the other following a contact.
9. 'Fleeing'; one fish swam rapidly away from the other fish.
10. 'Lateral display': the fish line up head to tail (see Figure 3b).
11. 'Biting'; one animal placed its mouth over part of the other animal (see Figure 3 C and D).
12. 'Approach'; one fish swam toward the other fish in a straight line.
13. 'Following'; one fish swam along the path taken by the other fish, within a distance of 10 cm.
14. 'Open Mouth'; one fish opened its mouth wide (see Figure 3a).
15. 'EOD': occurrence of electric organ discharges.

For the analysis a number of the above behavior categories were combined or modified. Because an assessment of motivational factors underlying 'Approach', 'Chase', 'Flee' and 'Following' proved to be difficult. Thus these categories were combined with 'Swimmming' to form a new category 'Active'. Further, since there were no significant differences in frequency and duration when the fish was inside or outside the shelter, data for both categories were pooled forming a new category 'Sheltering'. Catfish never hovered in midwater, but goldfish and Tilapia did. The behaviors 'Push', 'Lateral Display', 'Bite' and 'Open Mouth' occurred exclusively in encounters between conspecifics.

Statistical tests were done on the means of the frequency and time measures. Univariate analyses of variance were used to discover differences between resident catfish paired with different species of intruders, and differences in the behavior of intruder catfish when placed with different species residents. A one-tailed t-test was used to test differences between resident and intruder catfish. If not otherwise stated the level of significance was $p< 0.05$.

For the behavior 'EOD' only the frequency measure was used. A software package (Applescope RC Electronics) was used to analyze the recorded EODs. From the screen of the Applescope the number of EOD pulses and the duration of the volley was recorded. A discharge volley consisted of one to several trains of EOD pulses. Univariate analyses of variance were used to test differences in the 'EOD' measures (Figure 1).

Since EOD volleys were observed only during contacts a ratio of mean number of EOD volleys to mean number of contacts was calculated. For the analysis of variance the ratio data were transformed using the arcsine transformation in order to provide normally distributed data.

RESULTS

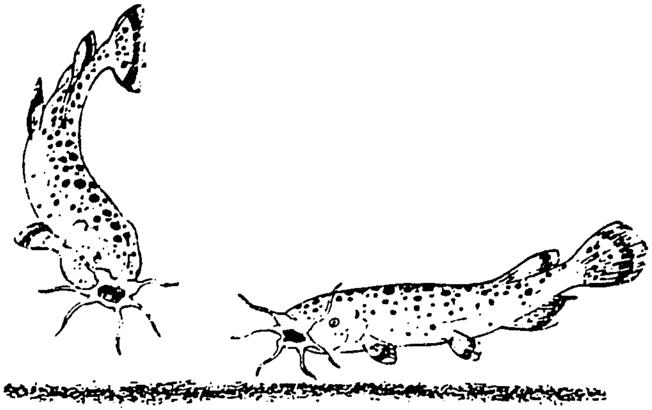
(A) Behavior Description

The first part of the results will provide an ethogram of the behavior of the electric catfish in inter- and intraspecific interactions. This section ('A') provides a descriptive analysis of the behavior of the catfish seperately in inter- and intraspecific encounters. The following section 'B' will provide a statistical analysis of these behaviors.

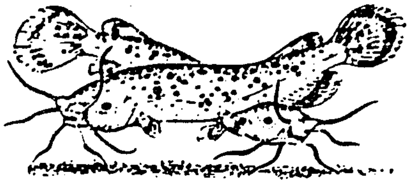
Intraspecific Interaction

In 85% of the trials the resident responded to the presence of the intruder; in the remaining trials no overt response was discernible. Contacts between the two fish lasting several seconds began as touches with the barbels. The first contacts were frequently accompanied by open mouth displays by one or both of the fish (Figure 3a). There was no consistent response to this display by the other fish. Subsequent contacts frequently resulted in lateral displays (Figure 3B). The fish gradually began to 'seesaw' back and forth arching their bodies to push against one another. Lateral displays lasted 5 to 15 seconds. The fish then

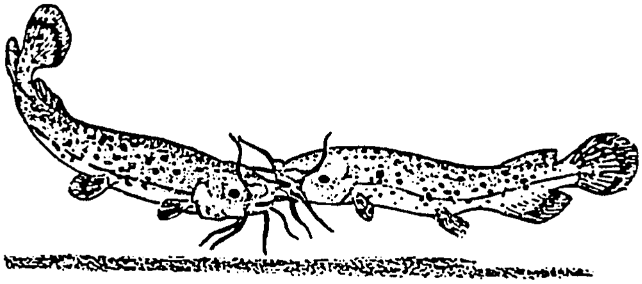
Figure 3: Illustration of four agonistic motor acts. A. Open Mouth Display. B. Lateral Display. C. Barbel Bite. D. Flank Bite. See text for detailed descriptions.



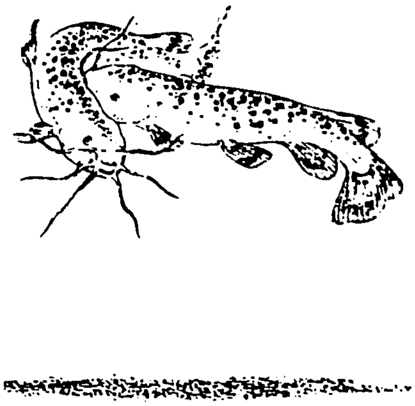
A



B



C



D

broke off and swam away. 'Lateral display' could be resumed on the next contact. 'Lateral displays' were often accompanied by open mouth displays. In approximately 40% of the trials bites occurred. Two different types of bites were observed: a barbel bite and a flank bite. In a barbel bite (Figure 3C) one or both fish gripped the barbels of the other. This grip was maintained for 15 to 20 s while the animals struggled and thrashed about the tank. A flank bite (Figure 3D) occurred when one fish swam rapidly at the side of the other and fastened its mouth to the flank of the victim. This bite was accompanied by much thrashing and twisting as the victim attempted to free itself. The flank bite lasted from a few seconds to several minutes. These bites sometimes left visible bruises. It was only during these forms of bites that EODs were emitted. In the 36 conspecific interaction trials, 234 contacts were observed. Thirty-five bites by residents were observed during 8 of these trials. Few EODs were observed in interactions between conspecifics.

Interspecific Interactions

When a goldfish, a Tilapia or a P. palmas was the partner species, the response of the catfish was different from that when paired with a conspecific. Goldfish and Tilapia are midwater fish and thus spent little time at the bottom of the tank. This made them difficult to be located by the bottom dwelling catfish. Furthermore goldfish and *Tilapia* can see better than the catfish (Ebbesson and O'Donnel 1980) which may have aided in avoiding the catfish. The contacts beween catfish and goldfish or *Tilapia* were of very short duration, usually lasting only 1-2 seconds. More than 50% of these touches were accompnied by EODs. The response of the *Tilapia* and goldfish to a catfish's discharge was to swim rapidly away from the area. On several occasions the shocked fish appeared disoriented and swam into the walls of the tank or the catfish, and on one occasion after a long series of discharge volleys a goldfish appeared to be unconscious for 30 seconds. The catfish sometimes followed the fleeing fish, but more often returned to the area of the shelter.

When the partner species was a *P. palmas* the interactions were more frequent as both *P. palmas* and *M. electricus* are bottom dwellers and so were occupying the same area of the experimental tank. Contacts between catfish and *P. palmas* lasted up to several minutes and were accompanied by EODs more than 50% of the time. *P. palmas* did not always flee in response to the catfish's discharge; when it did not leave the area the catfish ran its barbels the length of *P. palmas* before discharging a second time. Frequently the catfish followed the *P. palmas* contacting it and discharging as they moved about the tank.

Contrasting intra and interspecific interactions the results showed that while locomotor displays were quite frequent in intraspecific interactions such displays were lacking in interspecific encounters where contacts were brief and frequently accompanied by EODs.

(B) Quantitative Analysis

In intraspecific interactions the major differences between residents and intruders were related to the areas of the tank they frequented. In interspecific interactions there were no differences between resident and intruder catfish. Significantly fewer EODs accommpanied contacts in conspecific interactions than in interspecific interactions. The temporal patterning of the EODs emmitted during these interactions was different from that during interactions between a catfish and a member of another species.

Since the focus of this experiment was the social behavior of the catfish, only data on the behavior of resident and intruder catfish (with all species partners) will be presented. A summary of these results is presented in Figure 4. The results of the statistical tests on these data (ANOVAs and T-tests) are presented on Tables 2-5.

Spatial Distribution

Resident catfish spent most of the time in quadrant A, the quadrant with the shelter (Figure 5a). When the

Figure 4: Summary of results of Experiment 1.

R-resident, I-intruder, T-represents T-test I vs R.

↑ indicates significantly higher

↓ indicates significantly lower

* indicates significantly different

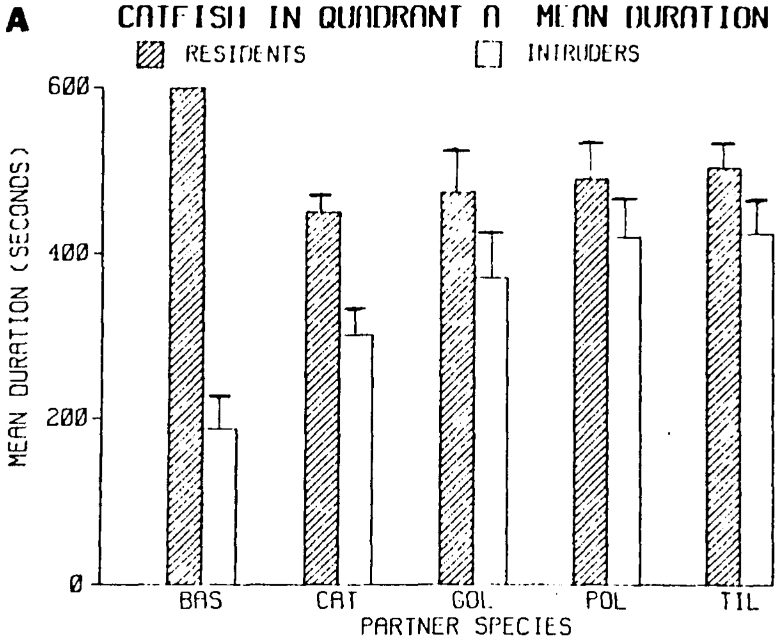
	QUAD A			QUAD B			SHELTER			RESTING			CONTACT			ACTIVITY		
	R	T	I	R	T	I	R	T	I	R	T	I	R	T	I	R	T	I
BAS	↑	*	↓	↓	*	↑	↑	*	↓	↓		↑				↓	*	↑
CAT			↓			↑			↓			↑	↑		↑	↑	*	
GOL																	*	
POL													↑		↑		*	
TIL																	*	

	QUAD A			QUAD B			SHELTER			RESTING			CONTACT			ACTIVITY		
	R	T	I	R	T	I	R	T	I	R	T	I	R	T	I	R	T	I
BAS						↑			↓	↓							*	
CAT	↑								↓	↑	*					↑	*	↑
GOL																	*	
POL																↑	*	
TIL																	*	

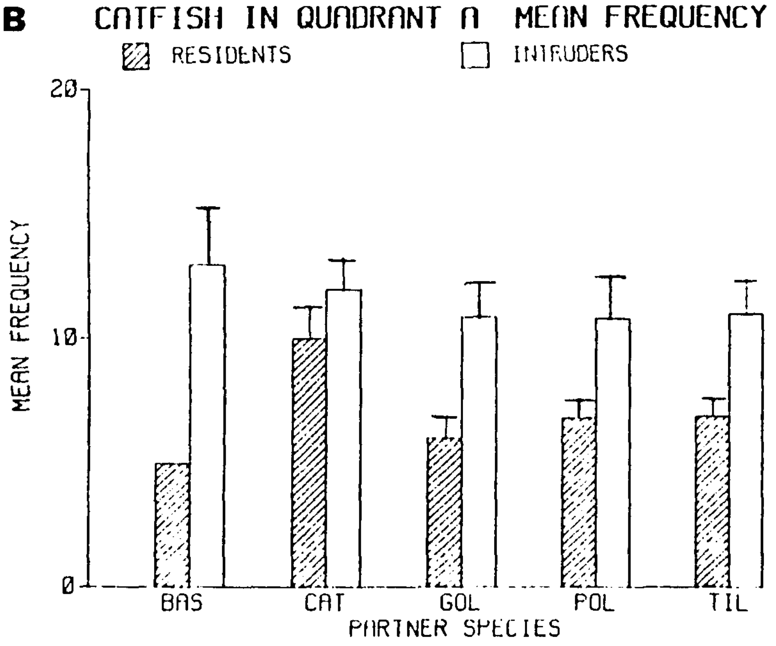
Figure 5: Mean duration of stay (A) and frequency of entry (B) in Quadrant A for 6 resident and 12 intruder catfish. Data is presented for resident and intruder catfish alone (BAS, 6 trials each), when a catfish was paired with a conspecific (CAT, 36 trials), goldfish (GOL, 24 trials), P. palmas (POL, 24 trials), or Tilapia (TIL, 24 trials).

Resident catfish entered Quadrant A significantly more often when paired with a conspecific.

A


CATFISH IN QUADRANT A MEAN DURATION
RESIDENTS
INTRUDERS
600
400
200
0
MEAN DURATION (SECONDS)
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES

B


CATFISH IN QUADRANT A MEAN FREQUENCY
RESIDENTS
INTRUDERS
20
10
0
MEAN FREQUENCY
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES

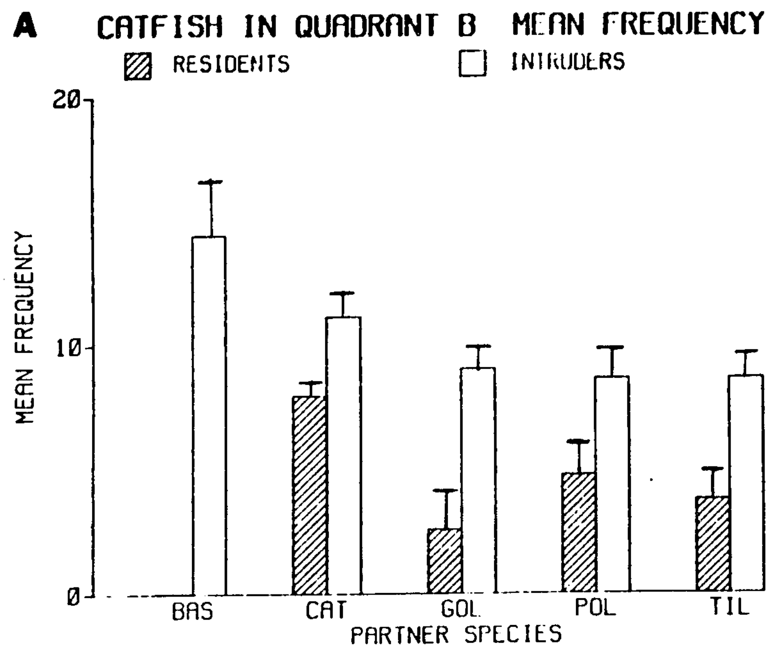
resident was alone, the time spent in this quadrant was significantly larger. On the other hand, an 'intruder alone' spent less time in this quadrant than intruders in the presence of resident fish. In conspecific encounters, residents spent significantly more time in quadrant A than did intruders. When the partner species was a non-conspecific there were no differences in the time measure between resident and intruder catfish.

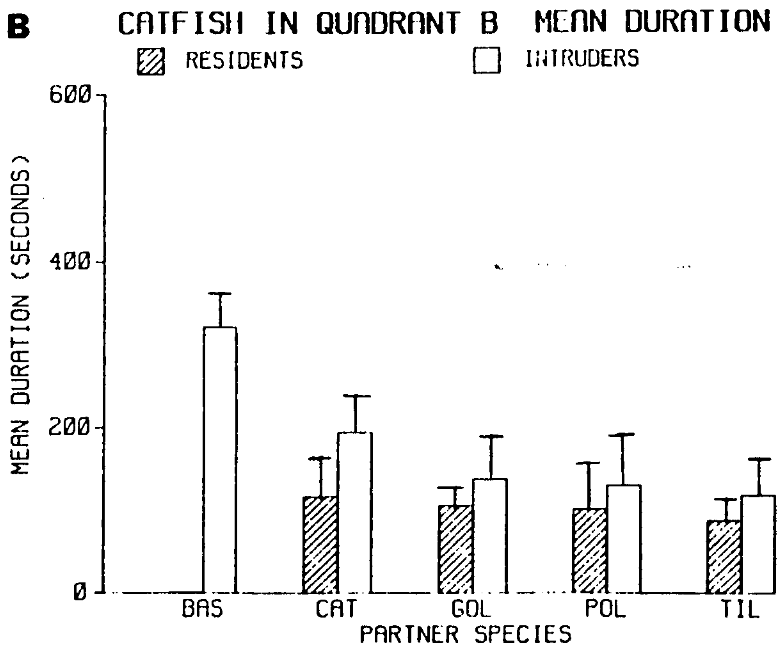
The analysis of the frequency data showed that resident catfish entered quadrant A significantly more often when the intruder was another catfish than when the intruder was another species (Figure 5b). There were no differences in the frequency the catfish intruders entered quadrant A regardless of the resident species.

Resident and intruder catfish spent little time in Quadrant B compared with the time they spent in quadrant A with the shelter (Figure 6a). There were no differences in the amount of time resident catfish spent in quadrant B regardless of the intruder species. Intruder catfish in the absence of a resident spent significantly more time in quadrant B than intruder catfish paired with non-catfish residents. Resident catfish alone did not enter quadrant B (Figure 6b). In conspecific pairings residents spent significantly less time in quadrant B than intruders. Resident catfish rarely entered quadrant B. However, they

Figure 6: Mean duration of stay (A) and frequency of entry (B) in Quadrant B for 6 resident and 12 intruder catfish. Data is presented for resident and intruder catfish alone (BAS, 6 trials each), when a catfish was paired with a conspecific (CAT, 36 trials), goldfish (GOL, 24 trials), P. palmas (POL, 24 trials), or Tilapia (TIL, 24 trials).

Resident catfish paired with a conspecific spent significantly less time in Quadrant B than intruders paired with conspecifics did.


A
CATFISH IN QUADRANT B MEAN FREQUENCY
▨ RESIDENTS
☐ INTRUDERS
MEAN FREQUENCY
20
10
0
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES


B
CATFISH IN QUADRANT B MEAN DURATION
▨ RESIDENTS
☐ INTRUDERS
MEAN DURATION (SECONDS)
600
400
200
0
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES

entered it significantly more often when the intruder was a catfish than when the intruder was a non-conspecific.

Because _M. electricus_ is a bottom dwelling fish the resident and intruder catfish spent little time in the highwater areas of the tank (i.e., quadrants C and D) when compared with the time they spent on the bottom of the tank. Intruder catfish exploring the new environment entered quadrants C and D more often than resident catfish did (Table 6).

There were two important findings in the analysis of the spatial distribution of the fish: (1) resident catfish spent most of their time in quadrant A, i.e. the quadrant with the shelter, they entered it more frequently when the intruder was a conspecific than with any other intruder species. (2) In conspecific pairings, intruder catfish spent significantly less time in quadrant A and significantly more time in quadrant B than resident catfish. There were no differences in the spatial distribution of intruder catfish with non-conspecific residents.

Behavior

Resident catfish alone sheltered significantly longer than resident catfish with any type of intruder. 'Intruder' catfish alone did not shelter at all. Intruder catfish paired with a conspecific resident sheltered for significantly less time than intruder catfish with non-catfish residents. In conspecific pairings resident catfish sheltered significantly longer than intruders (Figure 7a).

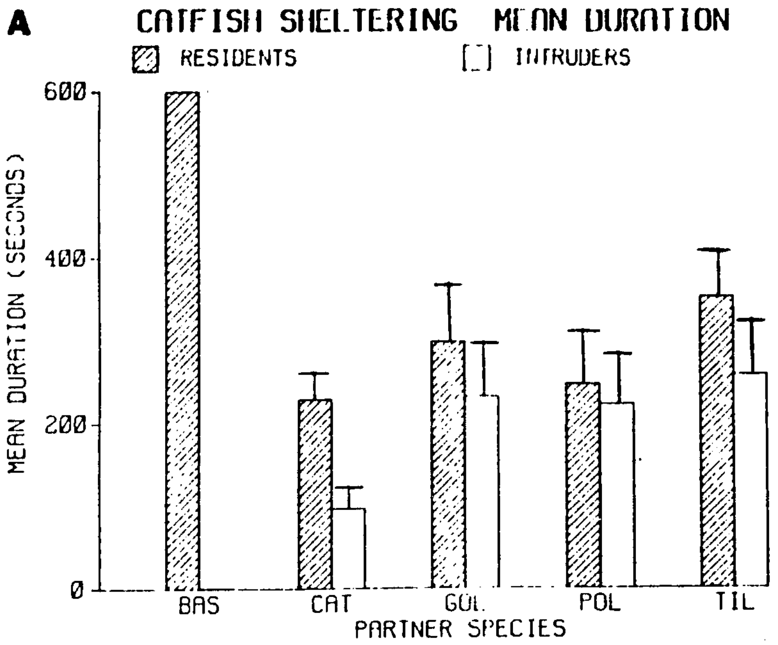
Intruder catfish sheltered significantly less often when paired with a conspecific resident than when paired with residents of another species. When two catfish were paired the resident sheltered significantly more often than did the intruder (Figure 7b).

The spatial distribution and sheltering showed that, regardless of intruder species, resident catfish spent most of the time in quadrant A, and much of that in contact with the shelter. Intruder catfish showed a similar pattern except when the resident was a conspecific. An intruder catfish encountering a resident conspecific spent significantly less time in quadrant A and less time in contact with the shelter. An intruder encountering a resident conspecific spent its time in the adjacent bottom quadrant. It seemed that the resident catfish occupying the shelter restricted the intruding conspecific from spending as much time in this area as it did when paired with 'non-catfish' residents.

Both the duration (Figure 8a) and the frequency (Figure 8b) measures for 'Resting' showed that resident catfish alone did not rest away from the shelter, while residents

Figure 7: Mean duration and frequency of 'Sheltering' for 6 resident and 12 intruder catfish. Data is presented for resident and intruder catfish alone (BAS, 6 trials each), when a catfish was paired with a conspecific (CAT, 36 trials), goldfish (GOL, 24 trials), *P. palmas* (POL, 24 trials), or *Tilapia* (TIL, 24 trials).

A. Mean duration of stay. Intruder catfish paired with a conspecific resident sheltered for significantlty less time than intruder catfish with non-catfish residents.
B. Mean Frequency of 'Sheltering'. Intruder catfish sheltered significantly less frequently when paired with a conspecific than when paired with residents of other species.


A
CATFISH SHELTERING MEAN DURATION
RESIDENTS
INTRUDERS
MEAN DURATION (SECONDS)
600
400
200
0
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES

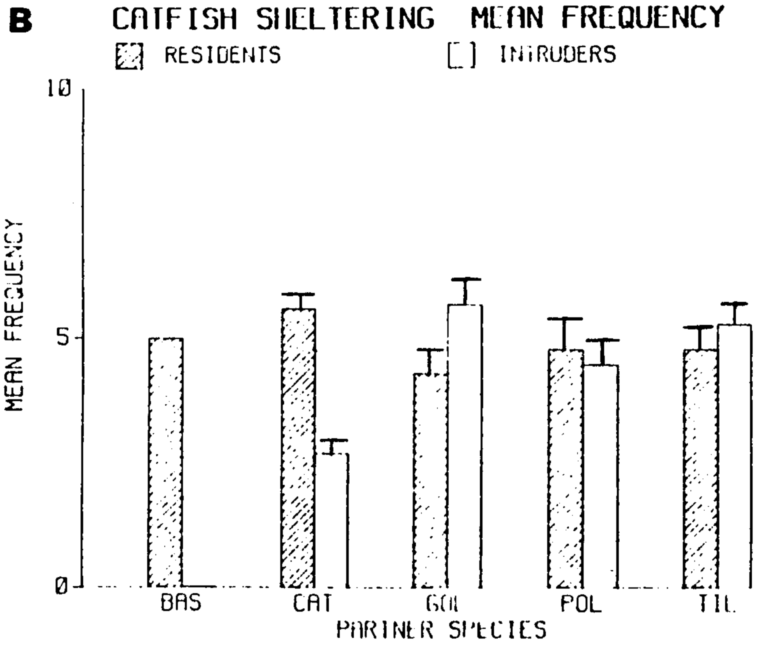
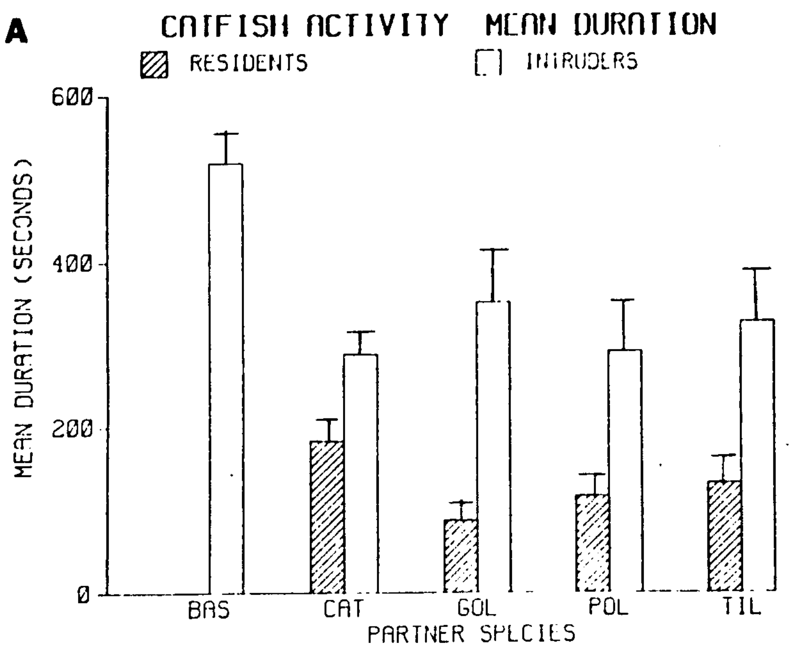
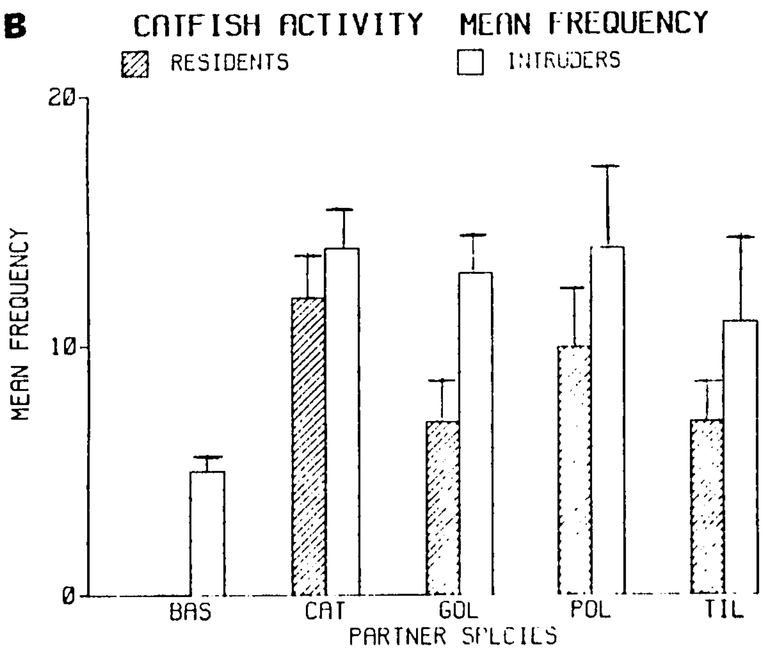

B
CATFISH SHELTERING MEAN FREQUENCY
RESIDENTS
INTRUDERS
MEAN FREQUENCY
10
5
0
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES

Figure 8: Mean duration and frequency of 'Active' for 6 resident and 12 intruder catfish. Data is presented for resident and intruder catfish alone (BAS, 6 trials each), when a catfish was paired with a conspecific (CAT, 36 trials), goldfish (GOL, 24 trials), *P. palmas* (POL, 24 trials), or *Tilapia* (TIL, 24 trials).

A. Mean duration of 'Active'. Intruder catfish were active significantly longer than resident catfish.

B. Mean frequency of 'Active'.


A
CATFISH ACTIVITY MEAN DURATION
RESIDENTS
INTRUDERS
MEAN DURATION (SECONDS)
600
400
200
0
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES


B
CATFISH ACTIVITY MEAN FREQUENCY
RESIDENTS
INTRUDERS
MEAN FREQUENCY
20
10
0
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES

with intruders present did. Intruder catfish rested away from the shelter most when the resident was a conspecific. Thus in conspecific pairings residents stayed in Quadrant A in contact with the shelter, and intruders rested on the floor of the tank in Quadrant B, away from the shelter.

Resident catfish were most active when paired with a conspecific (Figure 9a). 'Intruder' catfish alone were significantly more active than intruder catfish when paired with residents. All intruder catfish were active significantly longer than resident catfish regardless of the partner species present. The frequency data (Figure 9b) showed that resident catfish alone were significantly less active than residents in the presence of intruders.

The activity data suggested that the presence of another fish effected the activity of both resident and intruder catfish. However the effects were opposite; residents became more active in the presence of an intruder while intruders became less active in the presence of an established resident.

Catfish contacted conspecifics and _P_. _palmas_ more often (Figure 10b) and for longer periods of time (Figure 10a) than they did goldfish and _Tilapia_. As pointed out earlier this difference reflects the natural habitats preferred by the various species; catfish and _P_. _palmas_ preferred the bottom of the tank, thus interactions between the two were more frequent than with the midwater goldfish and _Tilapia_.

Figure 9: Mean duration (A) and frequency (B) of 'Resting' for 6 resident and 12 intruder catfish. Data is presented for resident and intruder catfish alone (BAS, 6 trials each), when a catfish was paired with a conspecific (CAT, 36 trials), goldfish (GOL, 24 trials), *P. palmas* (POL, 24 trials), or *Tilapia* (TIL, 24 trials).

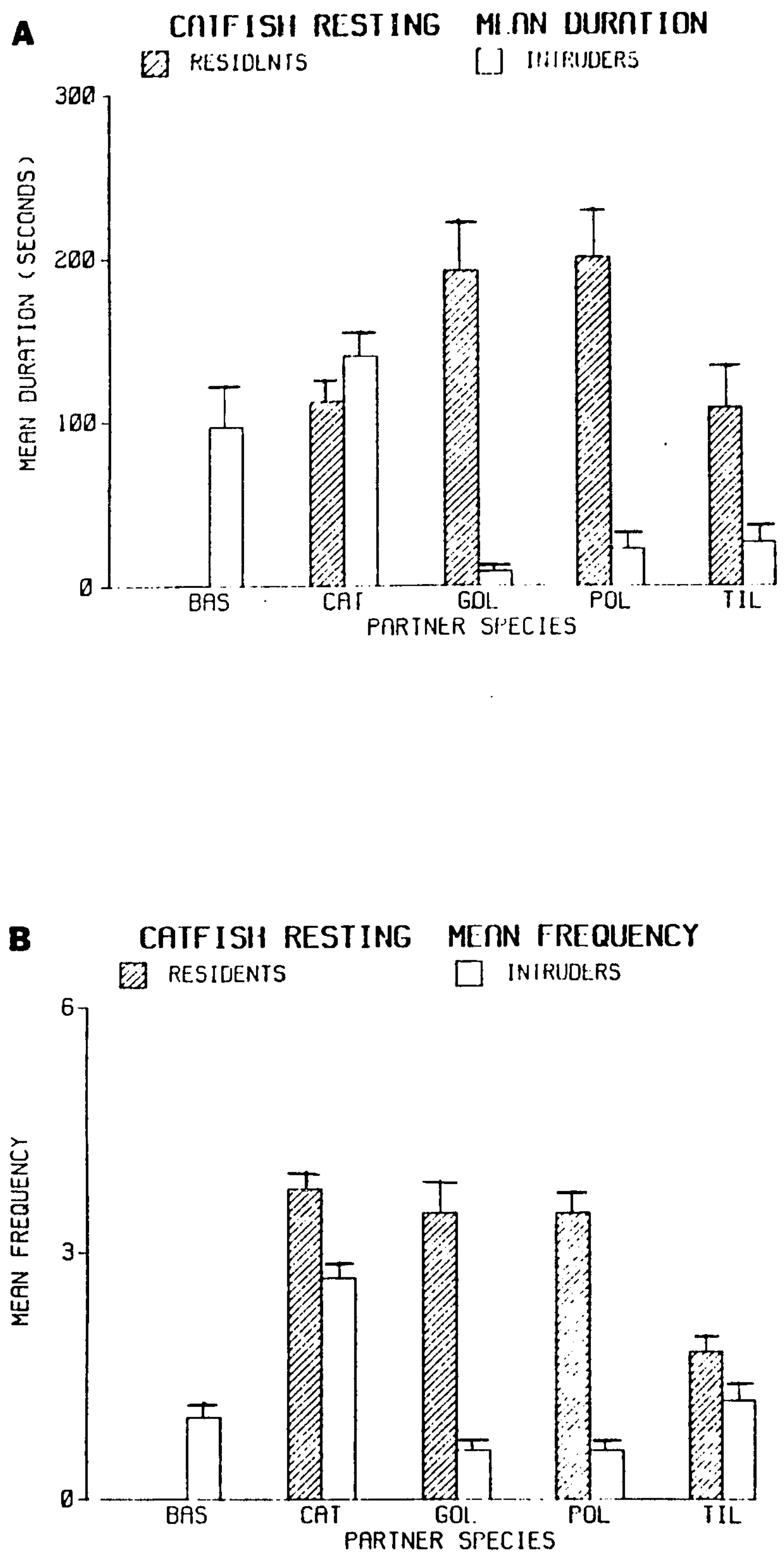
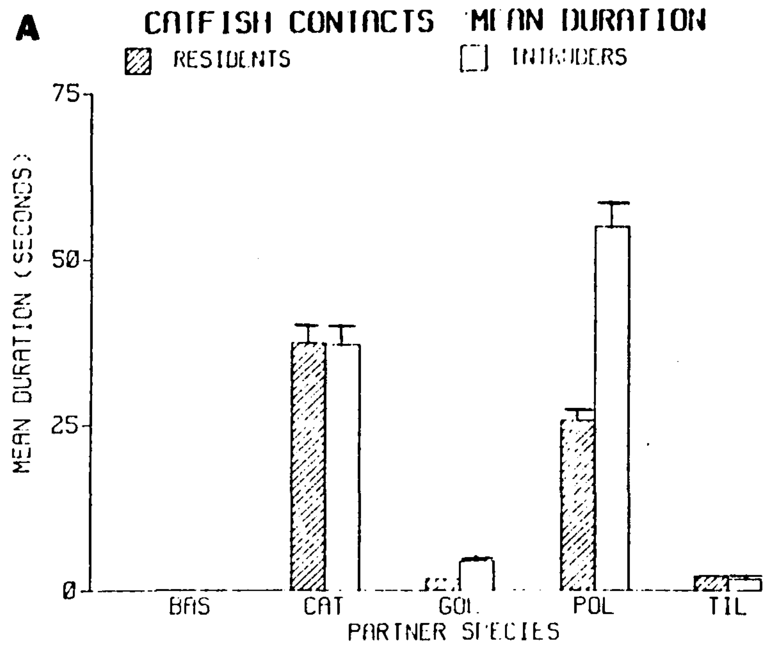

A
CATFISH RESTING MEAN DURATION
RESIDENTS
INTRUDERS
MEAN DURATION (SECONDS)
300
200
100
0
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES
B
CATFISH RESTING MEAN FREQUENCY
RESIDENTS
INTRUDERS
MEAN FREQUENCY
6
3
0
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES

Figure 10: Mean duration and frequency of 'Contact' for 6 resident and 12 intruder catfish. Data is presented for resident and intruder catfish alone (BAS, 6 trials each), when a catfish was paired with a conspecific (CAT, 36 trials), goldfish (GOL, 24 trials), *P. palmas* (POL, 24 trials), or *Tilapia* (TIL, 24 trials).

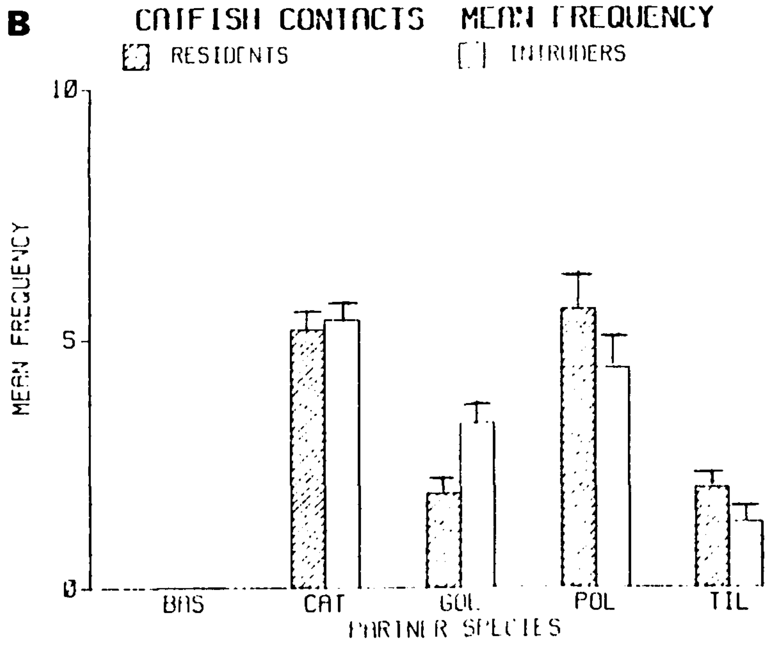
A. Mean duration of 'Contact'. Catfish spent more time in contact with conspecifics and *P. palmas* than with goldfish or *Tilapia*.

B. Mean frequency of 'Contact'.

A


CATFISH CONTACTS MEAN DURATION
▨ RESIDENTS
☐ INTRUDERS
75
50
25
0
MEAN DURATION (SECONDS)
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES

B


CATFISH CONTACTS MEAN FREQUENCY
▨ RESIDENTS
☐ INTRUDERS
10
5
0
MEAN FREQUENCY
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES

Frequency and duration measures for 'Push', 'Lateral Display', 'Bite' and 'Open Mouth' are presented in Table 7. There were no significant differences between residents and intruders on any one of these measures.

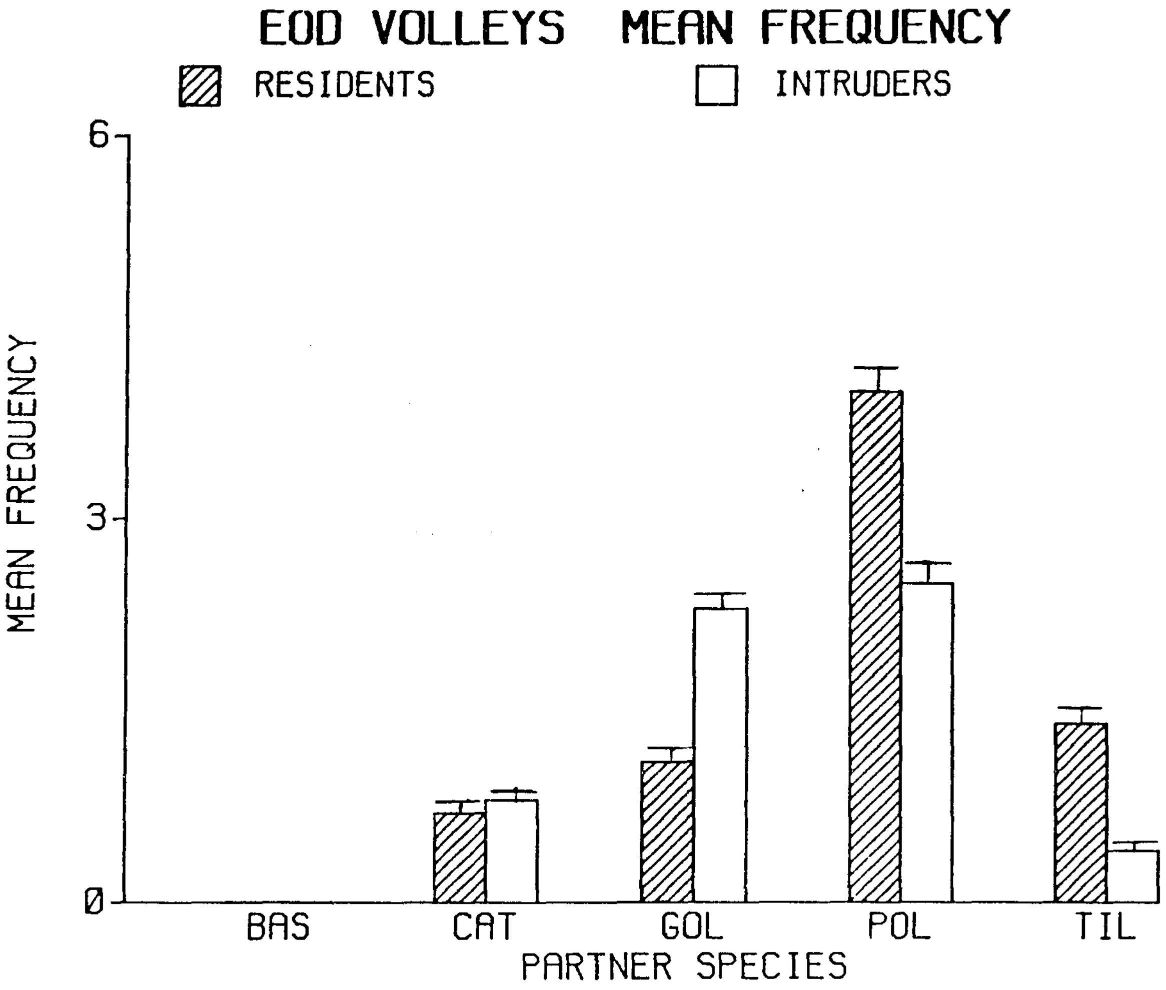
Electric Organ Discharge Activity

Catfish alone did not discharge (Figure 11). Resident catfish discharged significantly more often with *P. palmas* intruders than in the presence of any other intruder species. Intruder catfish discharged significantly more often when the resident was a *P. palmas* or a goldfish than when the resident was a catfish or *Tilapia*.

The observations of the behavior of the electric catfish in inter- and intraspecific interactions indicated that the catfish discriminated between conspecifics and members of other species. This discrimination was manifiested in behavior and EODs. In interactions with conspecifics, the catfish rarely emitted EODs, if it did, then only during bites. This was in contrast to their ready use when other species of fish were contacted (Table 8).

In conspecific interactions sixty-three percent of all bites observed were accompanied by EOD volleys. It was not possible with the present recording system to determine which of the fish was discharging. An attempt was made, however, in a separate series of trials, using one intact

Figure 11: Mean frequency of occurrence of Electric Organ Discharge volleys for 6 resident and 12 intruder catfish. Data is presented for resident and intruder catfish alone (BAS, 6 trials each), when a catfish was paired with a conspecific (CAT, 36 trials), goldfish (GOL, 24 trials), *P. palmas* (POL, 24 trials), or *Tilapia* (TIL, 24 trials).


EOD VOLLEYS MEAN FREQUENCY
▨ RESIDENTS
☐ INTRUDERS
6
3
0
MEAN FREQUENCY
BAS
CAT
GOL
POL
TIL
PARTNER SPECIES

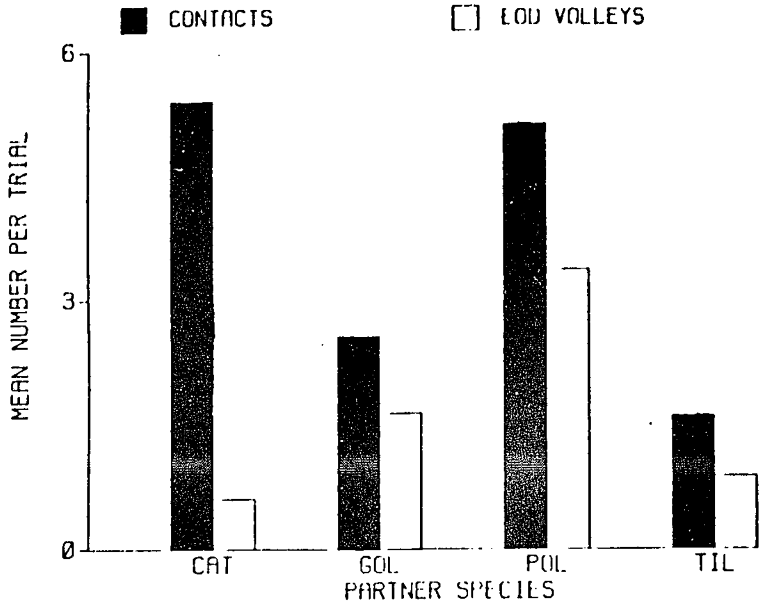
catfish and one surgically 'silenced' catfish. Six trials were run with a 'silent' resident and six with a 'silent' intruder. During these trials, 33 bites were observed, 8 of which were accompanied by EOD volleys. During four of the bites the bite initiator discharged, and in the other four the victim discharged. Thus the use of 'silent' animals could not demonstrate unambiguous assignment of the EODs.

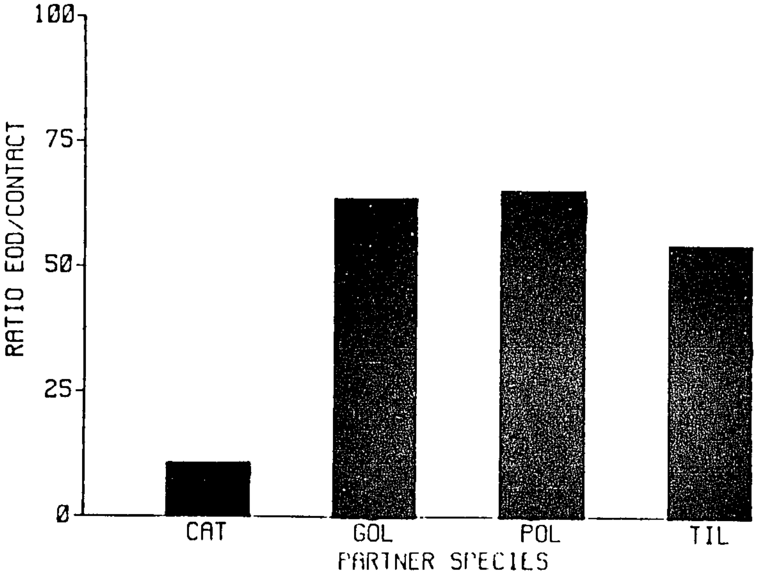
EODs occurred only during bites with conspecifics and brief contacts with other species. To further investigate differences between inter- and intraspecific interactions a ratio of EOD volleys to contacts was introduced (Figure 12a and b). This ratio was significantly lower for catfish/catfish encounters than for encounters between catfish and other species.

A finer analysis of the composition of the discharge volleys indicated significant differences in the temporal patterning of the EODs depending on the species the catfish encountered (Table 9). During conspecific encounters there were significantly fewer trains of EODs per volley than in interactions with the other species. When the four groups were compared there were significantly more EODs in each train emitted during intraspecific interactions. The fewest EODs per train were recorded during interactions with goldfish.

Figure 12: A. Mean frequency of Contacts and Electric Organ Discharge volleys for catfish with conspecific (CAT), goldfish (GOL), *P. palmas* (POL) and *Tilapia* (TIL) partners.

B. Ratio of Electric Organ Discharges/Contacts for conspecific (CAT), goldfish (GOL), *P. palmas* (POL) and *Tilapia* (TIL) pairings. The ratio was significantly lower for conspecific pairings.


■ CONTACTS
□ EOD VOLLEYS
6
3
0
MEAN NUMBER PER TRIAL
CAT
GOL
POL
TIL
PARTNER SPECIES


100
75
50
25
0
RATIO EOD/CONTACT
CAT
GOL
POL
TIL
PARTNER SPECIES

DISCUSSION

Comparing the catfishs' behaviors in inter- and intraspecific encounters there were both qualitative and quantitative differences which showed that the catfish discriminated between conspecifics and members of another species. In interactions with members of its own species open mouth and lateral displays were observed. Some of these aggressive interactions escalated to bites with or without EODs. Electric organ discharges were rarely observed during intraspecific interactions. In interactions with conspecifics residents spent the largest amount of time in contact with the shelter, while intruders spent more time on the opposite side of the tank. In contrast resident and intruder catfish showed few differences in their behavior when the partner was another species. In interspecific interactions the contacts were limited to brief touches often accompanied by EODs. The temporal patterning of EODs emmitted in response to contacts with conspecifics was different from the temporal patterning of the EODs that accompanied contacts with other species.

These results demonstrated that _M_. _electricus_ maintain exclusive use of an area, but that they do so in different ways depending on whether the intruder is a conspecific or not. These differences were apparent in patterns of space utilization, overt behavioral displays, readiness to discharge EOD volleys and the pattern of the emitted EOD volleys. The EODs recorded in the course of this experiment occurred almost exclusively during contacts with other species of fish. Instead of using EODs in encounters with a conspecific, catfish engaged in a series of displays such as lateral and open mouth displays similar to those described by Todd (1972) for *Ictalurus nebulosus* and by Bruton (1979) for *Clarias gariepinus*. The only behavior observed in *M. electricus* which has not been described for other species of catfish was the barbel bite. This bite may have been an attempt by the catfish to disadvantage its opponent by depriving it of sensory input. Both classes of bites, the barbel bite and the flank bite, caused damage in the form of visible bruises to their partners. The EODs that occurred during bites may have been offensive, defensive or simply by-products of physical stimulation due, in the victim to tissue damage or, in the bite initiator, to oral stimulation.

Parker (1974) in his model of assessment strategy states that there is a selective advantage in the ability to compare an opponent's resource holding potential with one's own since an animal could withdraw without damage when the opponent's resource holding potential was assessed to exceed one's own. Furthermore, reliable measures of resource holding potential might be provided by direct trials of strength between combatants. In many cases these tests of strength include pushing and pulling contests, and, in fish, frequently include head and/or tail beating (Parker 1974). Fitting this model, the lateral displays and the pushing that preceeded the escalated fighting and biting in _M. electricus_ could serve in assessing the relative size and strength (resource holding potential) of the opponent. As the model would predict, when the size discrepancy between two fish was large (greater than 5 cm) the smaller fish abandoned the shelter area and fled when the larger fish approached. The most vigorous battles were observed between individuals of the same size.

Like the pomacentrid reef fish observed by Myrberg and Thresher (1974) and Thresher (1976) it appears that _M. electricus_ defends an area of exclusive use from both conspecifics and other species of fish. However, the reef fish discriminate among non-conspecifics, while the electric catfish does not. (In pilot work, an additional three species, _Polypterus ornatopinnus_, _Ictalurus nebulosus_, a Clariad catfish and a crayfish were tested. EOD and contact behaviors similar those described here for interactions with non-conspecifics were observed.) The catfish did not exhibit motor displays, threats or physical attacks to drive away non-conspecifics. The EODs were probably the most efficient weapons to defend the area. Although there were no significant differences in the ratio of EOD to contact for non-conspecifics there were differences in the number of EOD pulses emitted per volley. Weber (1982) found that as catfish were habituated to mechanical stimulation there was a decrease in the mean number of EODs produced per volley. In this experiment the low number of EODs produced in the presence of goldfish could have been due to habituation to the stimulus 'goldfish'. The comparatively 'novel stimuli' _Tilapia_ and _P. palmas_ elicited a greater number of EODs per volley.

Losey (1982) demonstrated that the pomacentrids discriminated among intruder species by observing specific motor patterns during feeding. Fish that did not exhibit these motor patterns were ignored. The discrimination of non-conspecific competitors on the basis of motor patterns would be more difficult for _M. electricus_ than for the reef fish. The visual world of the catfish is restricted by a poorly developed visual system (Ebbesson and O'Donnel 1980) and often turbid aquatic habitats (Belbenoit et al. 1979). Therefore, a parsimonious strategy for the catfish would be to exclude indiscriminately all others from a resource area; and in fact the catfish discharged in response to all other species of fish.

A significant positive correlation between the length of the catfish and the ratio of EOD volleys to contacts characterized encounters with non-conspecifics (Figure 13). The larger a catfish was the more likely it was to discharge when contacting a non-conspecific. The amplitude of the EOD is directly related to the size of the fish, the larger the fish the higher the EOD amplitude. The relationship between the size of the fish and EOD amplitude is shown in Figure 14. The increased probability of larger fish to discharge in response to non-conspecifics, could indicate qualitatively different size-dependent assessment strategies. The discharge amplitude of smaller fish may not be strong enough to discourage intruders, and may even attract electroreceptive predators (such as other piscivorous catfish). Therefore, the adaptive strategy for small electric catfish (this experiment suggested below 15 cm) would be to use their EODs defensively to maintain an area of exclusive use. The four catfish that were under 15 cm in length had a mean ratio of EODs to contacts, during interspecific interactions, of 0.15 compared to a ratio of 0.77 for catfish 15 to 23 cm in length. It is possible that the catfish's strategies change depending on the size of the other fish. This was not tested, in this experiment the size of the non-conspecific was kept constant.

Figure 13: Correlation between length of catfish and the ratio of Electric Organ Discharges/Contact for interspecific interactions. The correlation was significant ($r=+.68$, $P<.05$).

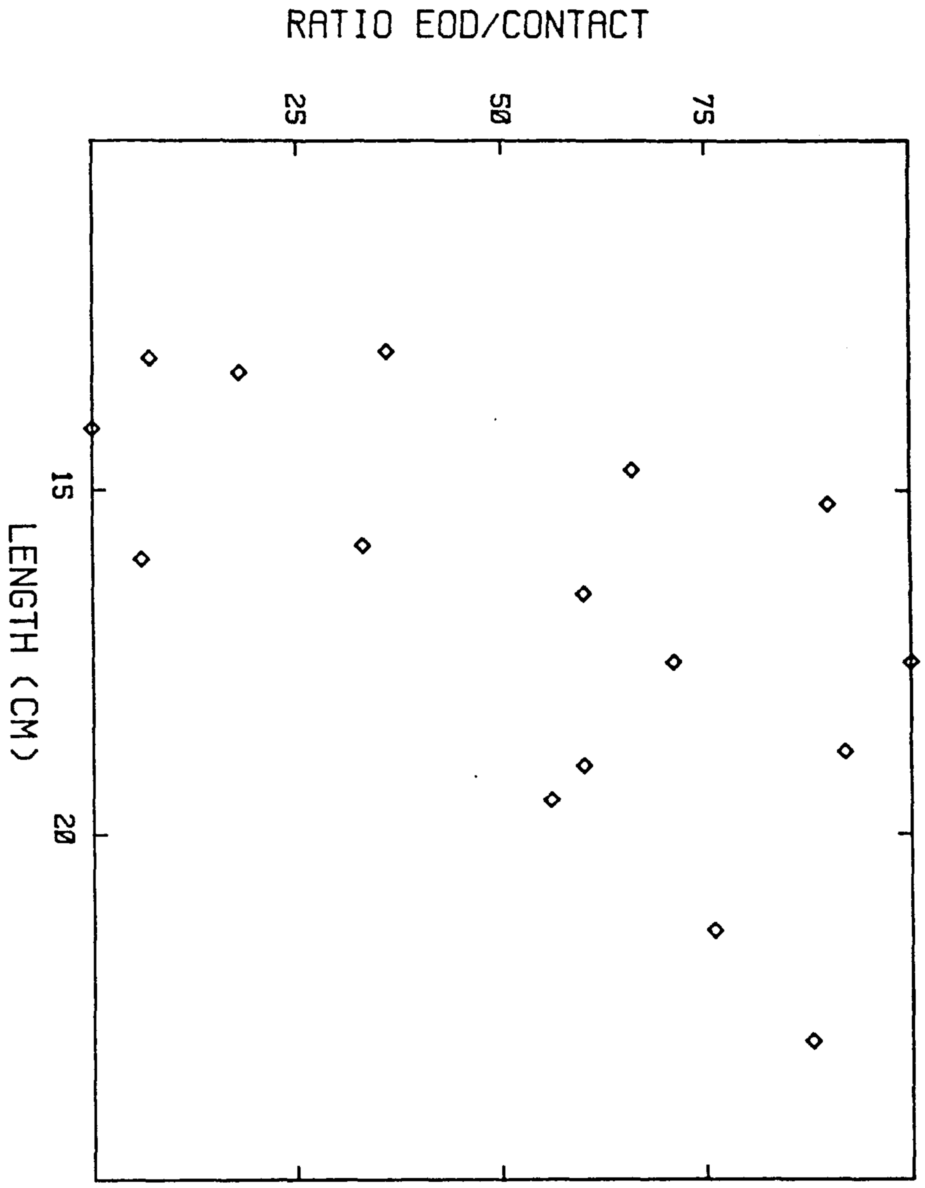
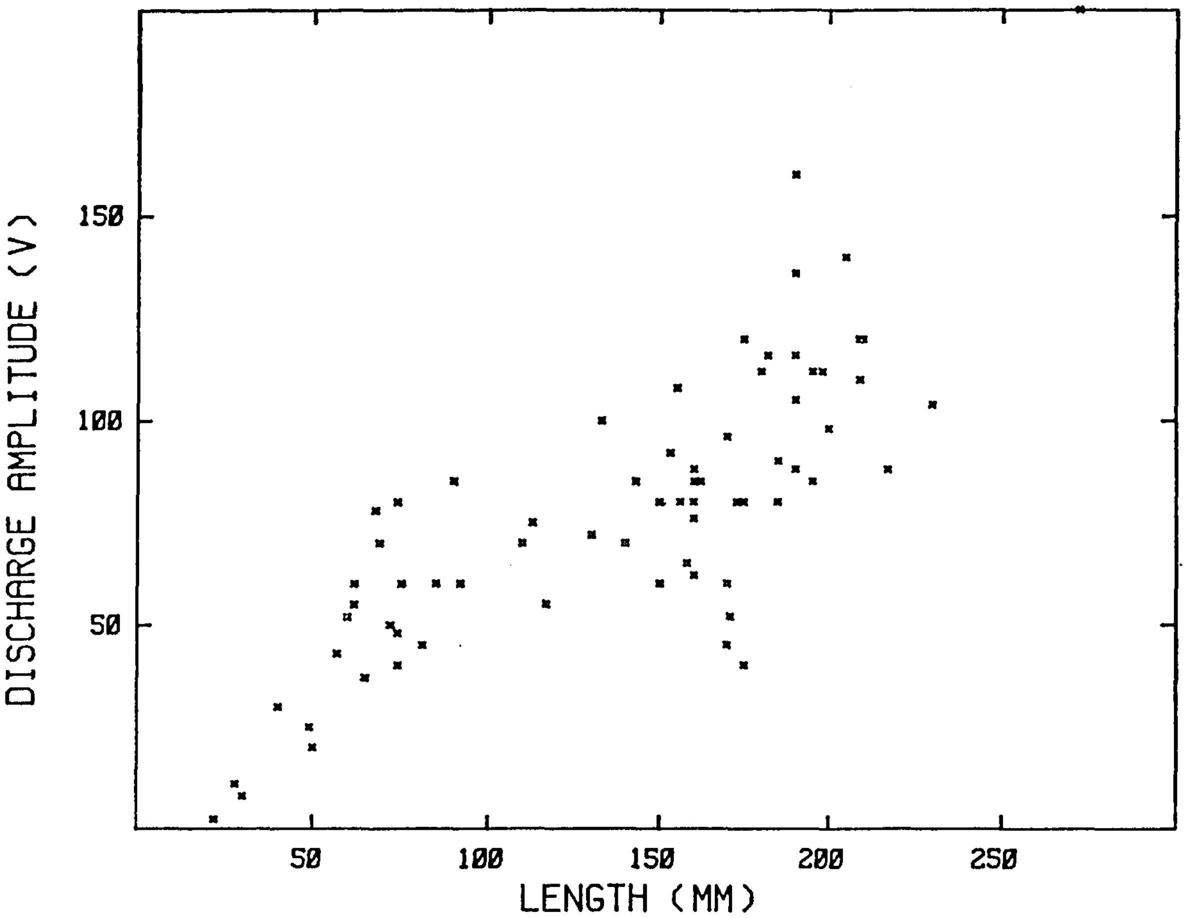

RATIO EOD/CONTACT
25
50
75
15
20
LENGTH (CM)

Figure 14: Relationship between the length of catfish and the Electric Organ Discharge amplitude. As size increases, discharge amplitude increases.



LENGTH-VOLTAGE RELATIONSHIP

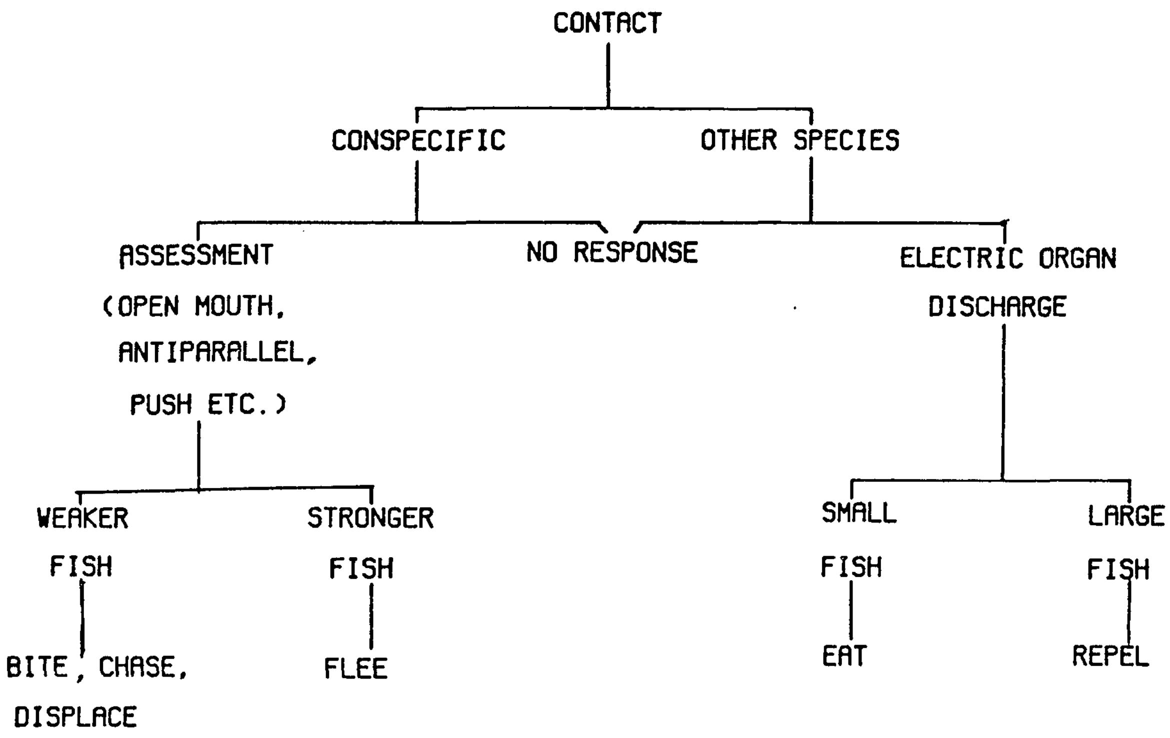
Murray (1971) suggested that interspecific territoriality was a case of 'mistaken identity' in which the opponent was mistaken for a conspecific. In studies of the pomacentrid fish Low (1971) and Myrberg and Thresher (1974) gathered evidence to refute this theory by demonstrating that the territorial fish selectively excluded non-conspecific competitors. The catfish's behavior provides additional evidence against Murray's suggestion.

When _M. electricus_ contacted another fish, a decision was made about the identity of this fish (Figure 15). When the contacted fish was not a conspecific EODs were emitted, causing large fish to flee and small fish to be stunned, resulting in predatory behavior (Bauer 1968). However, when the other fish was a conspecific assessment displays preceeded hostility. Conspecifics exhibited a number of displays that may have served in assessing the opponents relative size and strength. When the conspecific was judged stronger the weaker fish fled. When the fish contacted was judged weaker it was attacked and bitten.

The withholding of EODs during encounters with conspecifics could have several possible explanations. _M. electricus_ may or may not be affected by the EODs of a conspecific. In the first case, the layer of electric organ under the skin of the catfish may act as insulation, or the heavy myelination of the nervous system (Bennett 1971) may

Figure 15: Flow chart suggesting 'Decision processes' in a catfish's encounters with conspecifics and other species.

See text for details.


CONTACT
CONSPECIFIC
OTHER SPECIES
ASSESSMENT (OPEN MOUTH, ANTIPARALLEL, PUSH ETC.)
NO RESPONSE
ELECTRIC ORGAN DISCHARGE
WEAKER FISH
STRONGER FISH
SMALL FISH
LARGE FISH
BITE, CHASE, DISPLACE
FLEE
EAT
REPEL

make it resistant to electric shock. On the other hand, if EODs are effective, their use in conspecific encounters could be viewed as a form of escalation of hostilities. Such an escalation should only follow an assessment of the relative strength of its opponent. In fact during conspecific interactions motor displays were the rule, followed on rare occasions by EODs.

Bauer (1968) classified the fish's electric organ discharge activity according to the number of pulses and the behavioral context. Feeding volleys, defensive volleys and hunting volleys were recorded. In the field, Belbenoit et al. (1979) recorded another discharge pattern, a low frequency pre-volley activity that exclusively preceeded long volleys. No behavior patterns have been identified with this pattern. In the current experiment different temporal patterns of EODs were recorded when the catfish interacted with conspecifics and non-conspecifics. It is possible that the temporal patterning of the EODs into trains of varying length may have contained information that was available to conspecifics. It has become clear that different stimuli do consistently elicit differently patterned EODs. More research into the stimulus control of the pattern of the EODs is necessary before this can be understood.

EXPERIMENT II: OPEN FIELD STUDY

To answer questions on spatial distribution, there were two limitations to the design of Experiment 1. The experimental tank did not provide sufficient space for a fish to flee before fighting escalated to bites and EODs. In addition the presence of a single shelter may have produced artificially high levels of competition. The ten minute trial length may have cut short interactions that may have continued in different forms than those observed. For these reasons Experiment II was designed in a larger area, for a longer period of time and with more shelters available.

Methods

Subjects

The subjects were 15 electric catfish ranging in size from 15-20 cm. Prior to the experiment the subjects were housed and maintained as in Experiment I. Several of the catfish used had been subjects in Experiment I, but had been isolated for 6 months prior to Experiment II. No catfish in this experiment encountered a conspecific it had encountered in Experiment I.

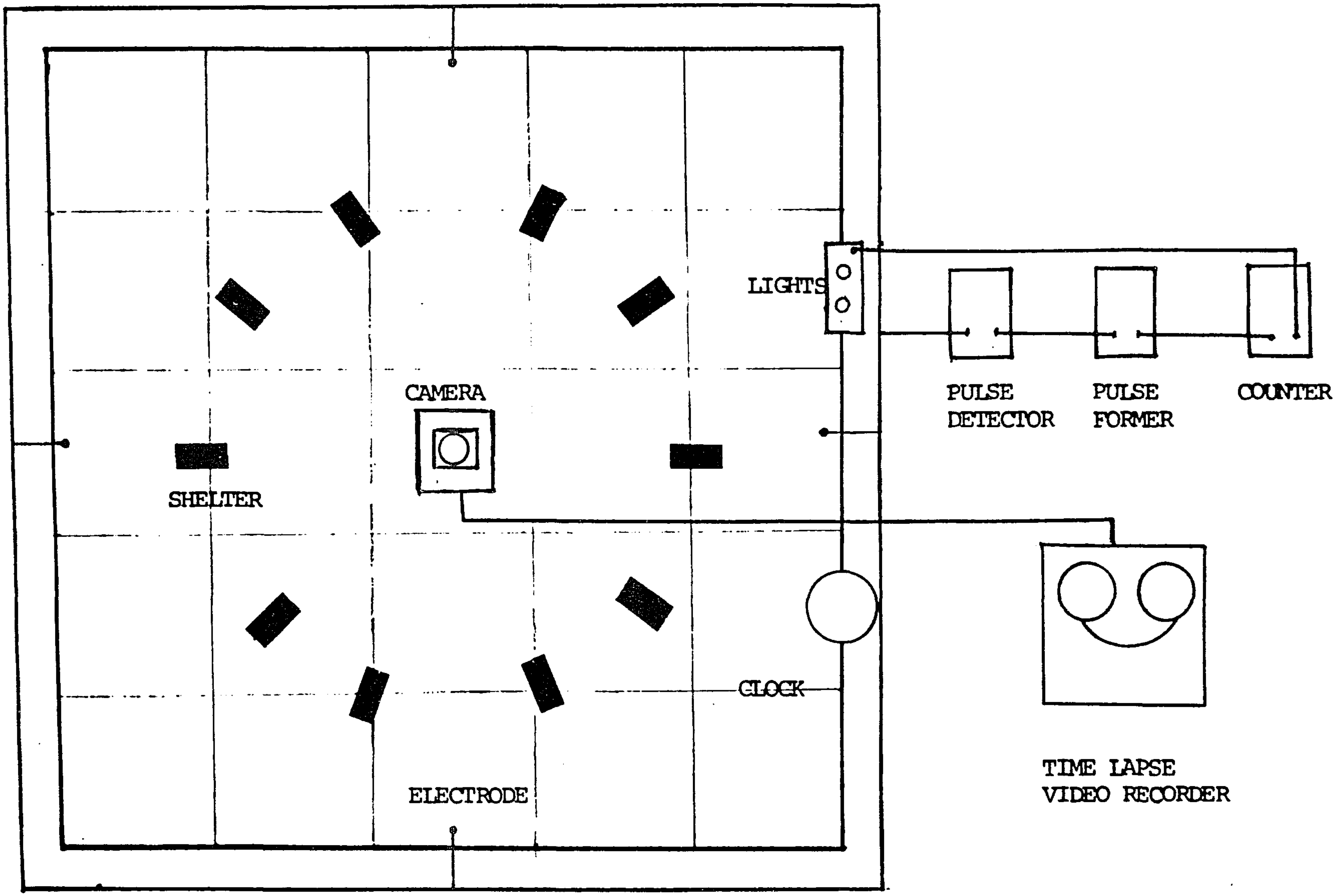
Apparatus

The testing chamber consisted of a large glass tank measuring 150 x 150 x 38 cm. The water was maintained at a depth of 18 cm with a temperature of 25±2 C and a conductivity of 180±30 uS/cm (Figure 16).

To facilitate recording and observations, an orthogonal grid consisting of black lines on white posterboard marked off in 15 cm squares, was positioned under the glass floor of the tank. Ten clay shelters 6 x 6.5 x 15 cm were arranged along the periphery of a circle 1.25 m in diameter The shelters were made of white fired clay and were flat on the bottom and rounded on the top. The distance between neighboring shelters was 29 cm. During the light period of the Light:Dark cycle the tank was lit from above by four 100 watt white light bulbs fixed in 30 cm aluminum reflectors. In addition, four red darkroom bulbs in 21 cm aluminum reflectors were used. These red bulbs alone illuminated the tank during the dark period. (Pilot work had indicated that the animals under the 'light' condition exhibited very little movement. When the white lights were turned off and only the red lights were on, the animals immediately began to swim about the tank.)

A panasonic WV 1040 video camera and a Gyyr Das 300 MK II time lapse video recorder were used to record behavioral data. The camera was suspended from the ceiling 2 m above

Figure 16: Schematic of the experimental set-up for Experiment II. (Figure is not drawn to scale.)


LIGHTS
PULSE DETECTOR
PULSE FORMER
COUNTER
CAMERA
SHELTER
CLOCK
ELECTRODE
TIME LAPSE VIDEO RECORDER

the center of the experimental tank. The video recorder was set to film 2 frames per second. This allowed for eighteen hours of filming on a single one hour 2400m video tape. For data analysis the tape was played back at 60 frames a second. The real time was indicated by a clock (24 cm in diameter) which was positioned beside the tank and was recorded within the field of the camera.

To record the EODs two pairs of Ag/AgCl electrodes were affixed to the midpoint of each side of the tank. The occurrence of EODs activated a pulse detector on a Scientific Prototype 28 V relay rack to produce a brief pulse activating a counter and an array of lights that was mounted on the top of one wall of the experimental tank. In the event of EODs this light would light for 4 seconds and was recorded on videotape (Figure 16).

Procedure

The experimental procedure was an expanded version of the resident-intruder design of the first experiment. In this experiment one, two, three and five fish were observed together. Observations occurred over 15 hours a day for 12 days. The procedure was replicated three times.

In order to identify individual animals on the videotapes, several fish in each replication had a 2 cm round button covered with silver glitter sewn to the skin on the dorsal surface of the head. The surgical procedure required anesthetizing the fish with 20mg per liter water of methane tricaine sulfonate (brand name Finquel). Surgery lasted less than five minutes and involved putting 2 stitches into the button and the skin on the top of the head. Recovery was rapid and the fish was returned to its home tank for 24 hours prior to its introduction into the experimental tank. Pilot observations indicated that the button had no effect on the fish's behavior. Because the button had a tendency to detach in approximately 15 days the surgery to place the buttons on the fish was scheduled one day before the fish was a subject.

In the first replication the first and second intruder had buttons, in the second replication the resident and the first intruder had buttons, and in the third replication the resident and the second intruder had buttons.

The procedure for each replication was as follows. A single fish was released into the center of the tank on day 1 of the experiment at 18:00 h and the recording equipment was activated. The fish was filmed from 18:00 to 9:00 h for three consecutive nights. Filming was restricted to these hours because it was felt that human traffic in and around the experimental area during the day might affect the behavior of the fish. At 18:00 h on day 4 the first intruder was released in the center of the tank. The two fish were then filmed for three nights (18:00 to 9:00 h). On day 7 at 18:00 h the second intruder was released in the center of the tank. The three fish were filmed for the next three nights (same hours). At 18:00 on day 10 two additional intruders were introduced into the center of the tank simultaneously. The five fish were filmed for three consecutive days. On the thirteenth day all fish were returned to their home tanks. After each experiment the tank was drained, cleaned and refilled. It was allowed to stand at least 3 days before the experiment was repeated.

Analysis

Time and/or frequency measures were obtained for the following behaviors.

1. 'Activity': the time any one fish moved about in the tank (determined with the aid of an event recorder).
2. 'Contact': a physical touch between two fish.
3. 'Bite': a flank bite involving two fish as described in Experiment I.
4. An EOD occurrence was scored when the catfish's discharge activated the relay equipment causing the lights to go on. When a contact was observed while the light panel was lit, a 'contact and EOD' was scored. When a flank bite was in progress while the panel lights were on a 'bite and EOD' was scored.

The following were recorded when one or two fish were present.

5. 'Resting': the fish remained motionless in the tank outside of shelters or corners.
6. 'Swimming': the fish actively moved around the tank.
7. 'Hiding': this measure was divided into two subclasses (a) a fish inside a ceramic shelter and (b) a fish in any one corner of the tank.

The following were obtained when two fish were present in the tank:

8. 'Approach': one fish swam toward the other in a straight line.
9. 'Flee': one fish swam rapidly away from the other.
10. 'Displace': one fish swam into an occupied shelter, causing the fish already there to leave.

For all analyses the tapes were viewed at the of 60 frames per second, compressing the 15 hours of real time to one hour viewing time. Time measures obtained in this way were multiplied by 15 to reflect actual time.

Analyses of variance were performed on all data to assess differences among the different population sizes, differences between observation days and across replications.

Spatial Distribution

In order to examine the effects of population size on spatial distribution the positions of two, three and five fish that were hiding was scored every five minutes real time. The choice of five minute samples was a conservative one, as the catfish are sedentary and spent long periods of time inactive. (The time sample in Belbenoit, Moller, Serrier and Push's (1979) was a 50 s recording each hour.) Frequencies were calculated for the number of fish that were in shelters and corners for each five minute sample. Interfish distances were determined from measurements of the distances between occupied shelters and corners (10 minute samples). Univariate analyses were performed on the interfish distance to assess differences among different population sizes and across replications.

RESULTS

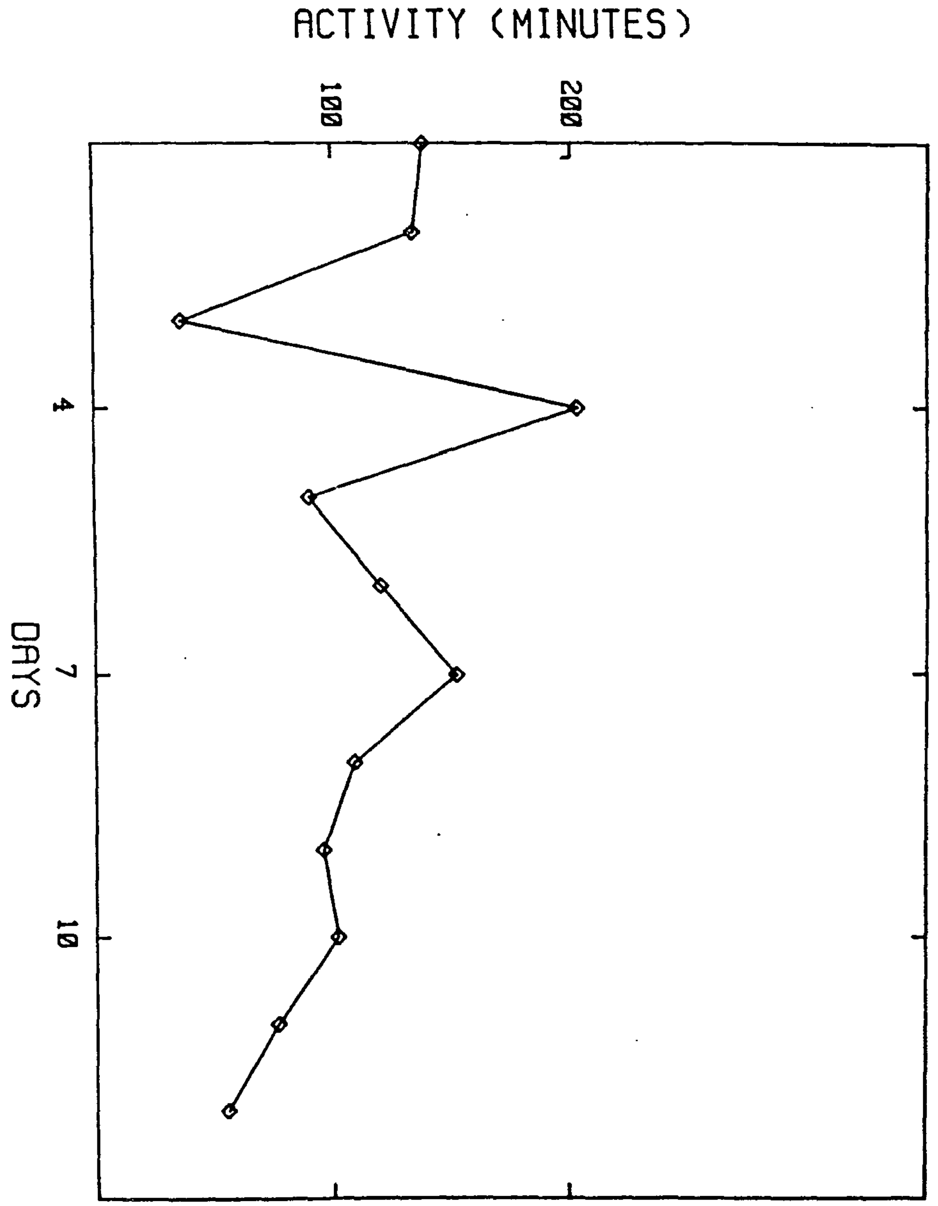
The results of Experiment II support the findings of Experiment I. In each of the three replications catfish restricted a conspecific's use of shelter sites. The dominance relationships were established following lateral displays as observed in Experiment I, however, fewer interactions escalated to bites. At high population density, in one replication, EODs were observed when no contacts were recorded.

Activity

The activity with one fish in the experimental tank was significantly less than when two, three or five fish were together. However, no significant differences in activity were found when two, three or five fish were present. The highest activity was found on the days a new fish was added, F(2,33)=3.62, p=0.05, (Figure 17). The time the fish were active for the 12 day observation period was not different across the three replications.

In order to determine the activity of individual fish within each group, an estimate of the activity level per

Figure 17: Mean activity for replications 1, 2 and 3 on days 1 through 12. Peaks in activity were found on days new fish were added (day 4, 7 and 10).


ACTIVITY (MINUTES)
100
200
DAYS
4
7
10

fish was obtained by dividing the mean activity for each day by the number of fish present (Table 10). The estimate of the activity level for individual fish was the same regardless of the number of fish present and replication.

Contacts and EODs

Contact behavior occurred with greater frequency on those days when new fish were introduced (Table 11). The frequency of contact behavior was the same for the three days when two fish were in the tank. However, with three fish, contacts accompanied by EODS increased from one observation day to the next. These increases were significant, F(2,6)=23.57, p=0.006. When five fish were together significantly more contacts with EODs were observed on the first day than on the subsequent two days, F(2,6)=17.05, p=0.011. In all three replications there were significant differences in contact behavior when 5 fish were together as compared with the contact behavior when 2 and 3 fish were in the tank. With five fish in the tank, more bites, F(2,6)=6.27, p=0.034, more contacts concomitant with EODs, F(2,6)=5.08, p=0.051, and more discharges, F(2,6)=5.20, p=0.048, were counted than when only two or three fish were in the tank.

However, these differences may have been due to the number of fish present, and not due to differences in the behavior of individual fish within a group. To test this, estimates of the frequencies of the contact behaviors for individual fish were calculated. An estimate of the number of contacts an individual fish was involved in, (obtained by multiplying the number of contacts by 2 (since two fish are involved in each contact) and then dividing by the number of fish present) showed no significant differences in the number of contacts per fish regardless of the number of fish present (Table 12). Similar estimates of the number of bites and EODs (obtained by dividing the number of occurances of EODs by the number of fish present) showed no significant differences in the number of bites or EOD occurrences for individuals, regardless of the number of fish present. Thus, differences found among different population sizes were not due to differences in the behavior of individual fish, but were simply a reflection of the increased chance of interaction when more fish were present. There were no significant differences in contact behaviors between the three replications.

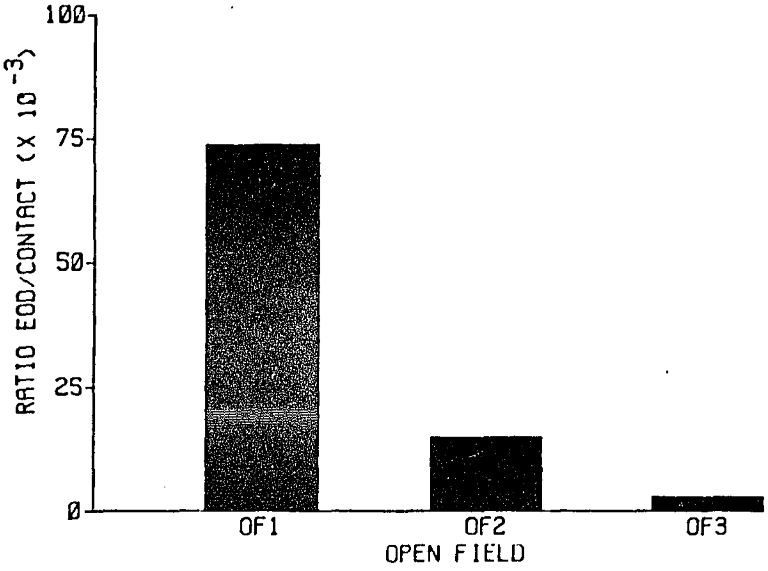
The ratio of EOD occurrences to contacts was significantly higher for the first than for the other two replications, F(2,24)=5.39, p=0.0117 (Figure 18a). The ratio was the same regardless of the number of fish in the tank (Figure 18b). Also, there were no differences comparing these ratios between days.

Figure 18: Ratio of Electric Organ Discharges/Contact in Experiment II.

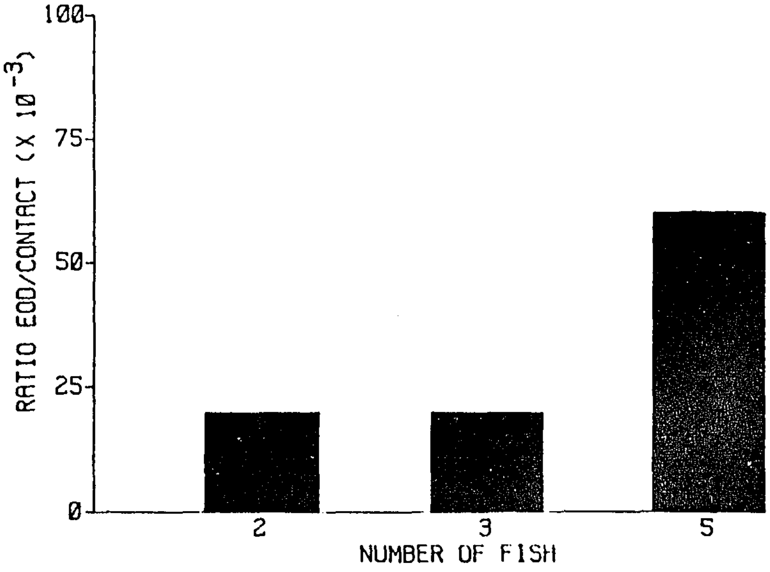
A. Ratio of Electric Organ Discharges/Contact for replications 1, 2 and 3. The ratio was significantly higher for replication 1 than for the other two.

B. Ratio of Electric Organ Discharge/Contact as a function of the number of fish present. There were no significant differences.

A


100
75
50
25
0
RATIO EOD/CONTACT (X 10^{-3})
OF1
OF2
OF3
OPEN FIELD

B


100
75
50
25
0
RATIO EOD/CONTACT (X 10^{-3})
2
3
5
NUMBER OF FISH

In the first replication EODs were observed in the absence of contacts. These EODs were recorded when a fish passed by or contacted the shelter occupied by the dominant catfish.

Behavior of One and Two Fish

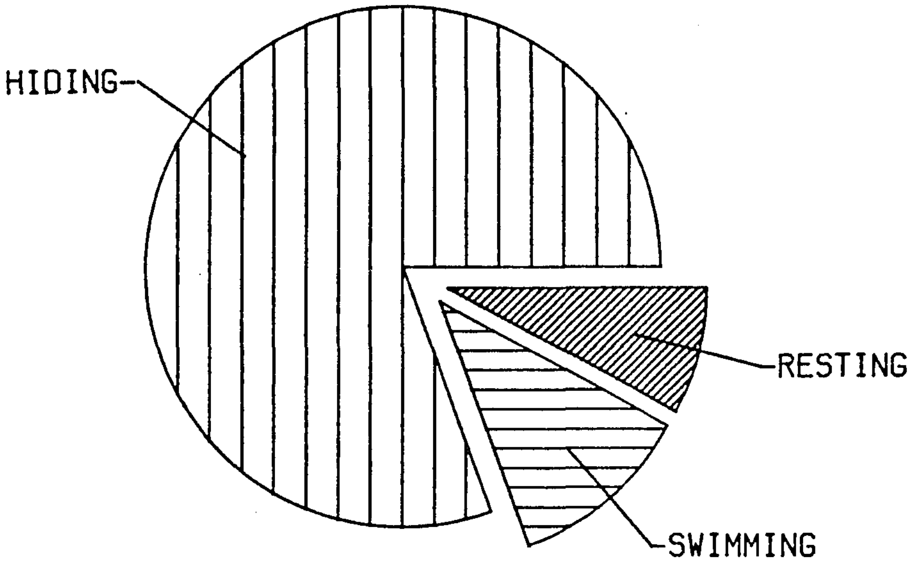
Frequency and duration measures for 'hiding', 'swimming' and 'resting' were obtained for the first three days of each replication with one fish present, and for the second three-day period with two fish present.

The time one fish alone hid (either in shelters or corners), swam or rested remained unchanged regardless of replications or observation days (Figure 19). The fish spent most of the time hiding. Of the three fish observed alone, only one showed a continuing preference over the three days for a single location in the tank. In the first replication, the fish was found in the same corner of the tank 88% of the time. In the other two replications, the fish displayed no preferences and moved about the tank visiting all shelters and corners.

Resident fish alone spent the same time hiding, swimming, or resting as residents in the presence of an intruder (Table 13). There were no significant differences in the frequency or duration of hiding, or in the duration of swimming or resting between a fish introduced into an

Figure 19: Mean duration for one fish alone hiding (in shelters or corners), resting, or swimming.

MEAN DURATION ONE FISH ALONE



empty tank (resident alone) and a fish introduced into a tank already containing an established resident. The frequency and duration of hiding, and the time spent swimming or resting were not significantly different between the resident and the intruder.

When two fish were together, the frequency of the social behaviors 'approach', 'flee', and 'displace' were recorded. The behavior of the resident and that of the intruder were not different. However, an examination of the frequencies of these social behaviors showed two distinct groups of fish. One group showed significantly higher frequencies of displace, T(2)=5.7, p=0.029, and significantly lower frequencies of flee, T(4)=3.08, p=0.037; the other group showed the opposite pattern, low frequency of approach and displace and high frequency of flee. The behavior frequencies for displace and flee differed significantly between the two groups. These differences suggested that the fish in one group were dominant and the fish in the other submissive (Table 14). In replication 1, the resident was dominant while in the second and third replications the intruder was. In each replication, the first interactions were accompanied by lateral displays (as described in Experiment I). Following these interactions (all within the first half hour) no more lateral displays were observed. Furthermore, the fish that broke off the lateral display and fled, remained the submissive fish for the three days that the two fish were together. Dominant fish stayed in the shelters significantly longer than did submissive fish, T(2,6)=7.69, p=0.0068 (Table 15). Submissive fish tended to rest in the center of the tank outside the shelters and corners. In replications two and three, the dominant fish hid in corners and shelters, forcing the submissive fish away from hiding areas. However, in replication one, the dominant fish stayed almost exclusively in the shelters (83.9% of the total time) and spent very little time in the corners (8.5%) leaving them to the submissive fish.

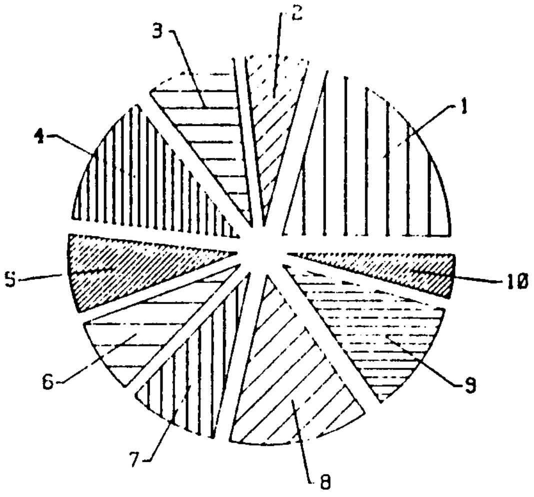
Neither the submissive fish nor the dominant fish selected a particular shelter or corner in which to stay. Instead, the dominant fish frequented all of the shelters, favoring one shelter for several hours, but not exceeding 6 hours (Figure 20, Table 15).

Addition of New Fish

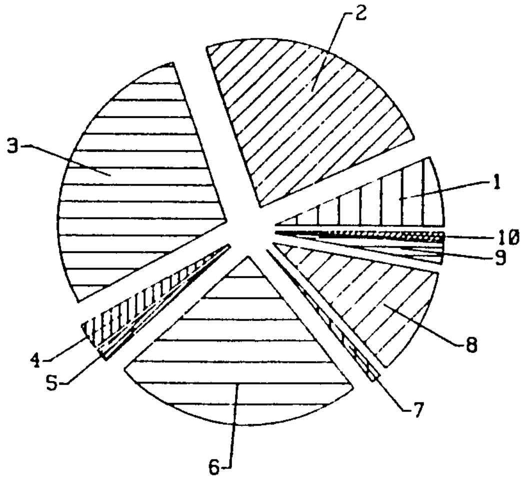
When three or five fish were in the tank the identification of individuals was difficult, especially during the dark hours of the experiment. Therefore the behavior of individuals was not analyzed. However, observations of individuals were made when a new fish was added. In each case the fish that was dominant when two

Figure 20: Time (in percent) the dominant intruder in replication 2 spent in each shelter (Total time in shelter=100%) on days 4, 5, and 6. No single shelter was consistantly preferred.

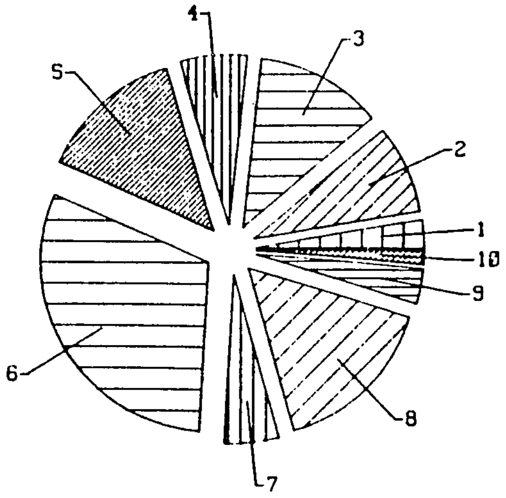
A INTRUDER OPEN FIELD 2 DAY 4 HIDING/SHELTERS



B INTRUDER OPEN FIELD 2 DAY 5 HIDING/SHELTERS



C INTRUDER OPEN FIELD 2 DAY 6 HIDING/SHELTERS



fish were together remained dominant regardless of the number of fish present.

The first contacts between a dominant fish and a newcomer were often accompanied by lateral displays. When the newcomer was smaller than the dominant fish these displays were brief, lasting less than a minute. If the newcomer was equal to or larger than the dominant fish (three cases) the displays lasted several minutes until the dominant fish bit the newcomer. Bites were accompanied by EODs. The interactions ended when the newcomer fled (after 5 to 15 bites). After the initial interactions all of the other fish fled from contact with the dominant fish. No displays were observed between newcomers and non-dominant fish.

Spatial Distribution

The frequency distribution for fish in shelters and corners showed that there were differences in the pattern of distribution for the number of days that the fish were together. The first day a new fish was added patterns of disribution changed. As the time passed the patterns of distribution stabilized (Table 16, 17 and 18). When three fish were together there were very few instances in which all fish were in shelters. When five fish were present they were never all in shelters at the same time. A shelter was never occupied by more than a single fish. The most common pattern of spatial distribution was for the dominant fish and one other fish to be in the shelters, while the other fish were in either the corners or the open areas of the tank. In each of the replications, with five fish together, the fish that was submissive in the 'two-fish' condition occupied the center of the tank, and was never seen in the shelters.

The patterns of spatial distribution were unstable for the first two days the fish were together. Interfish distance measures were analyzed only for the third day of each population size. The mean interfish distance for fish that were 'hiding' was not affected by population size (Table 19).

The data on spatial distribution patterns illustrated that, as population density increased, the number of samples in which all fish were in the preferred hiding areas (as defined by the preference of fish alone)in the tank declined from 53% when two fish were present to 31% with three fish present to a mere 6% with five fish. The instances when no fish was hiding decreased from 12% (two fish present) to 2% with five fish.

DISCUSSION

The observation of electric catfish in groups of different sizes over a period of several days provided information about territoriality, spacing strategies and the role of EODs in social behavior.

Territorial Behavior

In the absence of conspecifics both shelters and corners were the catfish's preferred areas. When a conspecific was present catfish preferred only the shelters.

Laboratory and field studies have demonstrated that familiarity with the environment (prior residence) confers dominance (Waser and Wiley 1979). In Experiment I the resident electric catfish restricted the intruders access to the shelter. In this experiment one might have predicted that the first fish to be introduced into the tank (the resident) should have an advantage over fish introduced later. The results, however, showed that prior residence did not always confer the predicted advantage. In two of the replications the intruder displaced the resident from the hiding areas. Other factors than prior residence must have affected the outcome of encounters between residents and the first intruders.

In a number of species of fish (e.g. Barlow 1976 for Cichlids, Grossman, 1980 for Bay gobies) dominance based on the relative size of individuals has been observed. The size of the catfish may have partly determined the outcome of the encounters. In the first replication, the resident became dominant and was larger (18.5 cm) than the intruder (16 cm), while in the second and third replications the intruders (17.5 cm and 19.0 cm respectively) became dominant and were larger than the residents (16.5 cm and 17.0 cm respectively).

If size were an important factor in determining dominance one would predict that the largest fish will control the preferred areas of the tank as more intruders are added. However, this was not the way the interactions developed. In two of the replications, fish of equal or greater length than that of the dominant fish were introduced into the tank. These fish did not displace the dominant fish from the shelters. Thus neither prior residence nor size accounted for the dominance pattern observed.

Waser and Wiley (1979) discussed the importance of previous social experience in determining the outcome of agonistic encounters. They postulated that a history of wins or losses frequently results in facilitation or repression of aggression towards strangers. A prediction based on such a model is that the dominant fish would remain dominant over later arrivals, and subordinate fish would retain their status. The interactions when the third, fourth and fifth fish were added supported this prediction. The dominant of the two fish retained the use of the shelters and excluded newcomers. In one replication, the subordinate fish as determined in the initial dyadic encounters, continued to be excluded from the shelters and corners for the duration of the experiment, and fled from newcomers. The initial win or loss by an animal had lasting effects on future interactions. In natural populations this effect might be weaker as animals could withdraw from an encounter before serious defeat and, by moving on to new areas, avoid repeated defeats (Waser and Wiley 1979).

To test the factors leading to dominance, prior residence and social experience could be kept constant for all fish by introducing the fish simultaneously into the tank. One would predict that the largest fish would dominate.

The recognition of individuals contributes to the establishment of stable dominance or territorial systems (Morse 1980). Todd (1972) and Richards (1973) demonstrated that recognition of individual conspecifics was based on chemical cues for the catfish _Ictalurus nebulosus_. The results of this experiment indicated that _M.electricus_ was capable of individual recognition. The dominance relationships were established shortly after a fish was introduced to conspecifics. Lateral displays and bites were observed during the first few encounters and rarely seen later in the experiment. Displays apparently were not necessary for recognition, as the submissive fish fled immediately following contact with a dominant fish. The recognition of individuals appeared to require contact or close proximity between two fish, and so may have been mediated by chemical cues.

Chemical cues may also have accounted for the subordinate fish's avoidance of shelters whether or not the dominant fish was currently in residence. Richards (1976) found that Ictalurus nebulosus recognized their own shelters by means of chemical cues provided by urine and mucus from the skin. Bryant and Atema (1982) described the bullhead catfish rubbing on the substrate to mark territories when confronted with the chemical cues of conspecifics. The shelters used in this experiment were porous and presumably absorbed the chemical products (urine, mucus) of individuals that stayed in contact with them. These chemicals may have served as cues to deter subordinates in the same way scent marking in mammals causes conspecifics to avoid another's territory (as reviewed in Morse 1980).

Population Density

The number of individuals within a given area affected the behavior of the individuals as well as the behavior of the group. De Boer (1981) reported that territorial male Chromis cyanea exhibited higher levels of aggression when there was a high population density than when there was a low population density. In this experiment there were no systematic changes in the behavior of individual fish in the three levels of population. However, all of the bites occurred in groups with three and five fish, and no bites were observed when two fish were together. The area provided in this experiment may have been large enough for two fish to avoid escalated encounters while the area in the first experiment was not.

Population density also affects the size and characteristics of territories (Morse 1980). As population size increased from two to five catfish, the tendency for the fish to hide increased. At the same time the higher competition for hiding sites decreased the likelihood that all fish could attain a shelter or corner. In each replication, as population density increased, the size of the territory of the dominant fish shrank. In the first replication this entailed a shift from only the dominant fish in the the shelters, to the dominant fish in a shelter and a conspecific in an unoccupied shelter. In the second replication the dominant fish's territory shrank from corners plus shelters to only the shelters and finally, to tolerating the presence of another fish in one of the unoccupied shelters. In the third replication the dominant fish's territory decreased from shelters and corners to shelters.

Under the conditions of this experiment there was no effect of population size on interfish distance. Interfish distance was measured as interfish hiding distance, and the dominance structure that developed restricted the use of hiding areas. Therefore the measure may not have accurately reflected distances between all individuals. To further test the effect of population density on the size of territories, the simultaneous introduction of different numbers of equal-sized fish into the tank would provide information on the maintenance and establishment of areas of exclusive use ('territories').

Role of EODs

Under the current experimental conditions it was not possible to determine which of the fish discharged when several fish were in the tank together. However, the occurrence of discharges was correlated with certain behaviors so as to make a prediction as to which fish discharged.

In two of the three replications EODs did not appear to play a major role in territorial defense. In Experiment I the few EODs observed occurred most often during or immediately following bites. In these two replications territorial defense appeared to be mediated by physical interactions (bites and lateral displays).

There was some indication in the first replication that as population increased the dominant fish relied more on EODs for territorial defense. With two fish in the tank, the dominant fish physically displaced the subordinate fish and moved in and out of all of the shelters frequently. As population density increased, the dominant fish remained in a single shelter for increasingly longer periods of time. EODs were recorded when other fish passed close by the shelter or contacted the fish. In this case it is assumed that the dominant fish no longer used physical force to repel the other fish, but relied on its EODs to warn away conspecifics.

GENERAL DISCUSSION

Territoriality and Domminance

Social spacing strategies involve a continuum of resource partitioning mechanisms ranging from exclusive use of a resource by a single animal to hierarchical priorities of access, and competition for these resources in dominance systems (Kaufmann 1983). The question has been raised as to how the observed behaviors of *M. electricus* place it onto the continuum. In both experiments, *M. electricus* defended a resource, i.e. the shelters, against conspecifics.

In Experiment II one fish controlled access to all shelters, and repelled others from the area. The fish who were repelled from the shelters (subordinates), did not fight among themselves for position and did not form hierarchies. Thus, in each of the repetitions in Experiment II, there was a single dominant fish controlling the shelters. The tank in Experiment I provided a 38 fold larger water volumn than the tank in Experiment I, but still restricted escape of defeated fish. In the field, when population densities are low, it is unlikely that a defeated fish would remain in that area, but would swim on to an uncontested shelter site. Thus, the population would be organized in territories. However, when the population densities are high, and no shelter sites are left undefended, defeated fish would remain in the area. They would minimize attacks on themselves by avoiding the shelter and the dominant fish, as was observed in Experiment II. Thus, in areas of high population density there might be a number of territories, each one occupied by a dominant individual, with a number of submissive individuals in the area, avoiding the shelter sites.

Kaufmann (1983) suggested that rather than agonizing over whether a species is territorial or maintains dominance systems, more pertinent questions can be asked; for example: "(i) What resources are monopolized by whom, when and under what conditions? and (ii) By what means is monopoly (priority of access) determined and maintained." Based on my results these questions can be answered, at least in part, for *M. electricus*. (i) Shelter sites were defended against both conspecifics and non-conspecifics. Prior residence, size and social expperience all played roles in determining the outcome of agonistic encounters. The shelters were defended both day and night for the duration of the experiment. (ii) Monopoly was determined by interactions beginning as displays and escalating to bites and EODs. In Experiment II the winner of the interaction held the shelters, frequenting them all over each 15-hour observation period. If a subordinate fish was found in a shelter it was chased out. Subordinate fish avoided the shelters most of the time. Chemical cues left in the shelters by the dominant fish could have been responsible for shelter avoidance by the subordinate fish.

Sensory Basis of Social Recognition

Resources are not only defended against conspecific competitors but also against non-conspecifics (e.g. Low 1971, Myrberg and Thresher 1974, and Losey 1982). These interspecific interactions are much less studied than conspecific interactions. In damselfish the topography of the defensive behavior was different when the competitors were conspecifics than when they were members of other species (Thresher 1976). Such a difference in behavioral response indicated that there was a discrimination between conspecific and non-conspecific. In addition, Myrberg and Thresher (1974) and Thresher (1976) demonstrated that damselfish discriminated among a number of non-conspecific species and attacked only food competitors. For the damselfish, visual cues, shape, color, and behavioral patterns were used in species discrimination.

In Experiment I the electric catfish defended the shelter area against conspecific intruders using behavioral displays such as open mouth and lateral displays. On the other hand, the catfish repelled non-conspecifics from the shelter area with electric organ discharges. This defense strategy demonstrated that the catfish were making a discrimination between conspecific and non-conspecific. The catfish did not, however, discriminate among the three non-conspecific species. In Experiment II the social relationships (dominant-subordinate) remained stable after a single encounter, suggesting that individuals may have recognized each other.

The sensory mechanisms underlying species recognition and discrimination as well as individual recognition, were not examined in these experiments. However, the results leave room to speculate about their nature.

The possible means for discrimination are visual, chemical, mechanical, accoustical, and electrical. As pointed out earlier, other species of fish make use of visual information for both individual and species recognition. The electric catfish's visual capabilities are significantly lower than those of most teleost fish (Ebbesson and O'Donnel 1980), and the environment of 'black water' it inhabits restricts the transfer of visual information. Bauer (1968) found that blinding electric catfish did not interfere with their ability to detect and capture prey fish. Thus, it is unlikely that vision plays a large role in social recognition.

Significantly, chemical cues have been implicated in all levels of social recognition in fishes (Myrberg 1980). Other silurids use chemical information to discriminate among a number of other species of fish and to discriminate between conspecifics (Richards 1976). Todd (1971) demonstrated that chemical cues found in the mucus of *Ictalurus natalis* played a key role in the dominance-subordinate relationships between individuals. *M. electricus* has a highly developed chemoreceptive system and uses chemical cues for prey detection and capture (Bauer 1968). In Experiment I the discrimination between conspecifics and other species was made at the moment of contact. I would hypothesize that chemical cues were responsible for the catfish's discrimination between conspecifics and other species of fish in Experiment I, and for the individual recognition that mediated the dominance relationships in Experiment II.

Although most species of fish can use movement-related changes in water pressure through the lateral line receptors to localize other organisms, there is no evidence that any species can discriminate other fish based on these mechanical cues (Myrberg 1980).

Accoustical signals play a role in social recognition in several species of fish, including damselfish (Myrberg 1980, Tavolga 1971). Sounds have been recorded from several species of catfish however, no attempt has been made to record sounds from *M. electricus*. During the experiments reported here I did not observe any behaviors that would suggest sound production (e.g. air gulping, emitting air bubbles). However, auditory cues in social recognition cannot be ruled out.

In weak-electric gymnotid and mormyrid fish electrical signals function for species recognition (Hopkins 1974, Moller 1980), sexual identification (Hopkins and Bass 1981) and possibly individual recognition (Black-Cleworth 1970, Hopkins 1974, Moller 1980). These fish have active electrosensory systems. The use of the EODs in social recognition among strong-electric fish has not previously been investigated. It is possible that the EODs of the electric catfish contain information that might be available to conspecifics. However, the limited use of EODs in conspecific encounters suggests that the discharge may not be a primary means of identification. Electroreception can also act as a 'passive' system when ampullary organs to detect the weak bioelectric fields that surround organisms in the water (Kalmijn 1974). It is unknown whether these bioelectric fields can be used to characterize either species or individuals. It would be interesting to study the catfish's ability to use this information in social recognition.

Electric Organ Discharges

Past research on the use of the strong electric organ discharge have been almost exclusively associated with predatory behavior. The experiments presented here have addressed questions about the role of the strong EODs in both inter- and intraspecific social behavior in the electric catfish, *M. electricus*.

In interspecific interactions the EODs served as an offensive weapon to repel non-conspecifics from a defended area. In intraspecific interactions conspecifics interact through physical touch and displays, and rarely use their EODs. In both experiments the ratio of EODs to contacts was less than 0.10. There were, however, differences in the way the EODs were used. In Experiment I the length of the observation and the space available were limited. The interactions between two fish were brief but intense, and accompanied by many bites. The majority of the EODs recorded occurred during these bites. This was not the case during interactions when two fish were present in Experiment II. There was sufficient space for the subordinate fish to flee, therefore, the interactions did not escalate to fights and bites. The EODs that were observed were concomitant with contacts.

The ratio of EODs to contacts did not change irrespective of the number of fish. However, the behaviors that were associated with the EODs changed. As population density increased to three and five fish the intensity of the interactions increased. When three and five fish were together, EODs were recorded as a fish swam past an occupied shelter without physical contact. As population density increased the EODs became an important signal by which a dominant fish repelled conspecifics.

Brichard (1978) observed large numbers of electric catfish spaced two to three meters apart in shallow rocky areas in Lake Tanganyika. In areas of such high population density the use of EODs to defend territories might decrease physical interactions and thus, lower aggression.

In a field study Belbenoit, Moller, Serrier and Push (1979) reported a daily activity cycle which was correlated with changes in light intensity. There were higher numbers of EODs during the night than during the day. During the first six hours following sunset the volleys consisted of more EODs than daytime volleys. From this Belbenoit et al. (1979) inferred that M. electricus fed most successfully during the early hours of the night.

These long volleys (more than 140 pulses) accounted for approximately 19% of the volleys recorded. If these volleys were, indeed, indicative of feeding, then that left 81% of the volleys without behavioral explanations. The results of these experiments suggest explanations for some of the volleys recorded. There may have been a number of volleys in response to contacts with non-conspecifics. In the turbid water, at night, the catfish may have contacted or been contacted by other species of nocturnal fish that were not prey items and discharged in response to the contact. From Experiment I, one would predict that these EODs would be composed of a series of short trains. Belbenoit et al. did not distinguish trains separately.

The EODs recorded may also have occurred during intraspecific interactions, either violent interactions with bites, or territorial warnings and defense.

Field studies in catfish habitats with good visibility (e.g.,Lake Tanganyika) could test the applicability of this data to natural environments. For continued laboratory investigations of the role of the EODs in social behavior, the results of the second experiment now mandate three changes in the experimental design.

(1) In order to better understand the role of the EODs some method of determining which of the fish discharged must be developed.

(2) In order to better understand the dominance relationships that develop, another method of marking individuals would greatly simplify the task. If buttons were to be used again a more reflective material, or a phosphorescent material would assure the buttons visibility

under low light conditions. Buttons of different shapes and sizes could be used to identify individuals.

(3) In addition, the EOD should be recorded to compare the number of pulses and their temporal patterning with those described in Experiment I and those patterns described by Bauer (1968) and Belbenoit et al. (1979).

The results on the electric catfish's behavior obtained under two different controlled laboratory conditions have elucidated the behavioral displays and environmental parameters that were responsible for the fish's spacing strategies. The particular findings identified the catfish as territorial or dominant depending on the environmental conditions. Thus, the placing of M. electricus and any other group of organisms on the continuum of spacing strategies is not a static, but a dynamic process.

Table 1: Length, Weight and Electric Organ Discharge Amplitude for subjects in Experiment 1

Fish #	Length (cm)	Weight (g)	Amplitude (V)
1	17.5	80	40
2	15.8	60	48
3	19.5	85	64
5	13.3	42	56
6	13.1	40	56
7	19	60	80
9	20.5	108	100
11R	23	185	122
12	18.8	110	104
13R	13.5	35	72
18	17.3	100	80
30R	21.4	105	88
31R	17.5	70	70
33R	14.5	40	64
34	16.5	60	70
35	15.2	55	72
36	16	55	65
37R	20	90	72

R-resident

Table 2: Analysis of Varience for Spatial Distribution Data

Resident Catfish:Duration

	Mean	SE	F	DF	p
Quad A	482.18	15.55	2.19	4,29	0.1068
Quad B	98.67	13.54	1.66	4,29	0.1988
Quad C	6.32	2.43	1.69	4,29	0.1918
Quad D	8.78	2.82	2.01	4,29	0.1321

Resident Catfish:Frequency

	Mean	SE	F	DF	p
Quad A	7.99	.57	7.17	4,29	0.0009
Quad B	5.30	.84	7.94	4,29	0.0005
Quad C	.80	.26	1.74	4,29	0.1813
Quad D	1.27	.41	2.31	4,29	0.0936

Intruder Catfish:Duration

	Mean	SE	F	DF	p
Quad A	343.17	21.81	2.75	4,77	0.0342
Quad B	172.87	18.30	2.30	4,77	0.0668
Quad C	35.68	7.52	.24	4,77	0.9132
Quad D	42.41	7.43	.70	4,77	0.5961

Intruder Catfish:Frequency

	Mean	SE	F	DF	p
Quad A	11.15	.65	.22	4,77	0.9274
Quad B	10.34	.84	.98	4,77	0.4241
Quad C	4.62	.74	.34	4,77	0.8488
Quad D	5.75	.72	.71	4,77	0.5845

This table presents the Analysis of Variance data for the mean duration of stay and mean frequency of entry into Quadrants A, B, C and D for resident and intruder catfish. For resident catfish the ANOVA is based on a repeated measures design. Presented on the table are values for mean, standard error of the mean (SE), the F, the degrees of freedom (DF) and the probability (p).

Table 3: T-Tests for Resident versus Intruder Catfish for Spatial Distribution Data

Duration

	BAS			CAT			GOL			POL			TIL		
	T	DF	p	T	DF	p	T	DF	p	T	DF	p	T	DF	p
Quad A	9.65	5	0.0002	3.53	23	0.0018	1.39	13	0.1850	.945	13	0.3600	1.19	13	0.2530
Quad B	5.03	5	0.0040	2.12	23	0.0457	.52	9	0.6137	.431	12	0.6740	.48	11	0.6450
Quad C	1.37	5	0.2292	1.14	23	0.2679	1.55	14	0.1429	1.64	12	0.1200	1.59	13	0.1340
Quad D	1.61	5	0.1677	1.58	23	0.1282	1.80	13	0.0936	1.81	16	0.0890	1.6	13	0.1160

Frequency

	BAS			CAT			GOL			POL			TIL		
	T	DF	p	T	DF	p	T	DF	p	T	DF	p	T	DF	p
Quad A	3.97	5	0.0160	1.07	22	0.2950	2.66	13	0.190	2.16	13	0.490	3.04	13	0.009
Quad B	11.29	5	0.0001	1.68	18	0.1105	3.34	13	0.0050	1.37	15	0.1910	3.06	14	0.0085
Quad C	1.49	5	0.1949	2.52	23	0.0192	2.19	11	0.052	1.85	12	0.090	1.95	10	0.079
Quad D	2.34	5	0.0668	2.57	20	0.0179	2.78	10	0.0195	1.94	14	0.073	3.15	11	0.0089

Table shows the data for T-Tests for resident and intruder catfish when paired with no partner (BAS), with catfish (CAT), goldfish (GOL), P. palmas (POL) or Tilapia (TIL) partners. Values are for T-test (T), degrees of freedom (DF) and probability (p).

Table 4: Analysis of Variance for Observed Behaviors

	Mean	SE	F	DF	p
Resident Duration					
Shelter	291.8	25.79	5.70	4, 29	0.0031
Active	135.2	15.38	7.22	4, 29	0.0009
Resting	128.8	19.24	2.45	4, 29	0.0285
Contact	22.25	8.63	3.39	4, 29	0.0285
Resident Frequency					
Shelter	5.09	.40	.29	4, 29	0.8790
Active	9.22	1.01	7.34	4, 29	0.0008
Resting	3.14	.4	4.55	4, 29	0.0089
Contact	3.92	.44	10.62	4, 29	0.0001
EOD	1.39	.27	8.77	4, 29	0.0003
Intruder Duration					
Shelter	154.69	22.89	3.63	4, 77	0.0094
Active	320.06	22.93	1.90	4, 77	0.1201
Resting	81.65	16.40	3.64	4, 77	0.0093
Contact	26.62	9.59	1.09	4, 77	0.3664
Intruder Frequency					
Shelter	3.67	.38	5.63	4, 77	0.0005
Active	12.86	1.14	1.4	4, 77	0.2433
Resting	1.69	.31	2.52	4, 77	0.0483
Contact	3.9	.44	5.13	4, 77	0.0011
EOD	1.17	.24	3.31	4, 77	0.0152

This table presents the Analysis of Variance data for the observed behaviors sheltering, active, resting, contact and Electric organ discharges (EOD). Values given are for Mean, standard error (SE), ANOVA (F), degrees of freedom (DF) and probability (p).

Table 5: T-Tests for Resident versus Intruder Catfish for Observed Behaviors

Duration

	BAS			CAT			GOL			POL			TIL		
	T	DF	p	T	DF	p	T	DF	p	T	DF	p	T	DF	p
Resting	2.01	5	0.1002	.60	19	0.5500	1.98	5	0.104	3.02	7	0.021	1.33	6	0.233
Contact				.53	23	0.6000	1.93	13	0.076	.94	14	0.364	.41	14	0.6895
Shelter				3.32	7	0.0100	.54	9	0.60	.26	11	0.799	.95	13	0.3580
Active	12.89	5	0.0001	2.26	21	0.035	3.78	16	0.0017	2.53	16	0.23	2.40	16	0.028

Frequency

	BAS			CAT			GOL			POL			TIL		
	T	DF	p	T	DF	p	T	DF	p	T	DF	p	T	DF	p
Resting	2.24	5	0.075	1.21	13	0.2510	1.93	5	0.1090	2.38	6	0.0560	.63	14	0.540
Contact				.058	15	0.95	1.62	16	0.124	.69	12	0.5000	.76	14	0.461
EOD				.364	20	0.72	1.30	14	0.214	1.00	12	0.335	2.36	6	0.050
Shelter				4.24	15	0.0007	.76	10	0.463	.13	9	0.90	.33	10	0.747
Actlevel	11.07	5	0.0001	.965	19	0.347	1.97	10	0.78	1.06	15	0.3100	1.16	15	0.2630

Table shows T-tests for resident and intruder catfish for duration and frequency of observed behaviors resting, contact, electric organ discharge (EOD), sheltering and active. Values are T-test (T), degrees of freedom (DF) and probability (p) for catfish alone (BAS), and when paired with catfish (CAT), goldfish (GOL), P. palmas (POL) and Tilapia (TIL).

Table 6: Duration and Frequency Data for Spatial Distribution, Experiment I

Duration

	Residents		Intruders	
	PSPECIES=BAS		PSPECIES=BAS	
VARIABLE	MEAN	STANDARD DEVIATION	MEAN	STANDARD DEVIATION
QUADA	600.00	0	188.33	104.46
QUADB	0.00	0	321.67	156.70
QUADC	0.00	0	43.50	77.82
QUADD	0.00	0	43.67	66.33
	PSPECIES=CAT		PSPECIES=CAT	
QUADA	454.14	134.69	302.31	210.38
QUADB	116.56	110.54	194.49	178.29
QUADC	8.58	27.27	41.89	81.19
QUADD	11.19	30.03	49.89	77.53
	PSPECIES=GOL		PSPECIES=GOL	
QUADA	480.92	177.18	371.92	176.50
QUADB	99.38	162.73	137.67	112.53
QUADC	7.00	23.76	35.25	56.75
QUADD	13.00	32.03	56.75	80.18
	PSPECIES=POLY		PSPECIES=POLY	
QUADA	486.17	145.53	421.33	171.74
QUADB	105.42	135.63	130.08	152.42
QUADC	2.83	7.76	23.83	44.06
QUADD	5.92	16.91	22.58	27.86
	PSPECIES=TIL		PSPECIES=TIL	
QUADA	504.75	107.92	425.92	145.82
QUADB	86.83	99.95	118.00	125.33
QUADC	5.42	14.22	26.69	44.39
QUADD	4.25	7.50	26.77	34.12

Frequency

	Residents		Intruders	
	PSPECIES=BAS		PSPECIES=BAS	
VARIABLE	MEAN	STANDARD DEVIATION	MEAN	STANDARD DEVIATION
QUADA	5.00	0	13.17	5.04
QUADB	0.00	0	14.50	3.15
QUADC	0.00	0	5.33	8.73
QUADD	0.00	0	6.83	7.17
	PSPECIES=CAT		PSPECIES=CAT	
QUADA	9.97	6.42	10.94	6.65
QUADB	7.97	9.46	11.22	8.87
QUADC	1.39	3.24	5.33	7.21
QUADD	2.17	4.87	6.67	7.43
	PSPECIES=GOL		PSPECIES=GOL	
QUADA	5.92	3.25	11.50	4.64
QUADB	2.46	1.94	9.08	5.66
QUADC	0.31	0.85	4.75	6.33
QUADD	0.15	0.38	6.17	7.00
	PSPECIES=POLY		PSPECIES=POLY	
QUADA	6.77	2.83	10.83	6.09
QUADB	4.69	6.30	8.67	7.35
QUADC	0.46	1.13	3.42	5.42
QUADD	1.15	3.29	3.92	3.45
	PSPECIES=TIL		PSPECIES=TIL	
QUADA	7.00	2.10	10.77	4.66
QUADB	3.55	2.66	8.69	5.78
QUADC	0.27	0.47	3.31	5.45
QUADD	0.45	0.69	4.00	4.40

Mean duration of stay and frequency of entry for resident and intruder catfish with partners of various species (PSECIES). BAS-no partner, CAT-Catfish partner, GOL-goldfish partner, POLY-P. palmas partner and Til-Tilapia partner.

Table 7: Frequency and Duration of 'Push','Lateral Display', 'Bite' and 'Open Mouth'

	Frequency per trial		Duration (seconds)	
	Mean	SD	Mean	SD
Push	1.4	2.4	3.0	1.6
Lateral Display	2.0	3.4	4.8	5.0
Bite	.4	.9	.9	.5
Open Mouth	.8	1.8	2.2	1.5

The behaviors listed here were observed only during interactions between conspecifics. No differences in the frequency if the duration of these behaviors were found between resident and intruder catfish. Values presented are mean and standard deviations (SD).

Table 8: Contacts, Electric Organ Discharges and Bites

	#	contact	bites	EOD	c+EOD	c+bites
CAT	36	234	35	3	5	22
GOL	24	64	0	0	36	0
POL	24	106	0	0	66	0
TIL	24	35	0	0	20	0

Table shows totals for catfish paired with conspecifics (CAT), with goldfish (GOL), P.palmas (POL) and with Tilapia (TIL). Table shows number of trials (#), total number of contacts, total number of bites, total number of electric organ discharges (EOD), number of contacts accompanied by electric organ discharges (c+EOD) and number of contacts accompanied by bites (c+bites).

Table 9: Analysis of the Electric Organ Discharges

A. Number of Trains within a Volley

	Mean	Standard Deviation
CAT	1.27	.77
GOL	2.41	1.39
POL	2.37	1.70
TIL	2.14	1.35

Scheffe F(3, 123)=2.849,p 0.05

B. Number of Pulses in Each Train

	Mean	Standard Deviation
CAT	15.64	12.59
GOL	5.96	6.03
POL	8.78	6.74
TIL	10.48	7.14

Scheffe F(3, 372)=6.988, p 0.05

The electric organ discharges that were recorded in the presence of catfish (CAT), goldfish (GOL), P. palmas (POL) and Tilapia (TIL).

A. The number of trains of pulses (each train seperated by at least 10 ms) in each electric organ discharge volley.

B. The number of pulses in each train of each electric organ discharge volley.

Table 10: Estimate of Activity per Fish

Day	Rep 1	Rep 2	Rep 3
1	130	213	70
2	17	218	165
3	21	70	16
4	67.7	150.5	67
5	12.5	77.5	43
6	24	65	66.7
7	63	42	50
8	33.9	44	30
9	14.4	57.7	23
10	21.8	12.5	14.2
11	17	12.6	16.4
12	8.9	10	14.4

Table presents an estimate of the number of minutes in each 15 hour observation period that each fish was active in replications 1, 2 and 3. This estimate was obtained by dividing the total activity in each 15 hour observation period by the number of fish present.

Table 11: Contact Behaviors

Rep	Day	#Fish	Contact	Bite	ContEOD	BitEOD	EOD
1	4	2	69	0	9	1	1
1	5	2	1	0	2	0	0
1	6	2	11	0	9	0	1
1	7	3	121	0	16	0	7
1	8	3	82	0	11	0	3
1	9	3	7	0	8	1	0
1	10	5	140	2	31	0	31
1	11	5	132	0	22	0	10
1	12	5	77	8	25	5	30
2	4	2	67	2	2	1	3
2	5	2	70	0	4	0	1
2	6	2	53	0	4	0	0
2	7	3	273	1	14	0	0
2	8	3	185	0	12	0	0
2	9	3	334	10	10	20	30
2	10	5	1103	4	23	3	5
2	11	5	399	2	8	1	1
2	12	5	245	5	12	0	1
3	4	2	85	0	2	0	0
3	5	2	25	0	7	0	1
3	6	2	108	0	17	0	0
3	7	3	489	0	14	1	0
3	8	3	294	0	11	0	0
3	9	3	188	0	7	0	0
3	10	5	561	17	24	80	0
3	11	5	228	0	6	0	0
3	12	5	145	0	10	1	1

Data are reported for replications 1, 2 and 3 for days 4-12 for number of contacts, number of bites, number of contacts accompanied by electric organ discharges (contEOD), number of bites accompanied by electric organ discharges and number of elctric organ discharges alone.

Table 12:Estimate of Contacts, Bites and EODs per fish.

DAY	Contacts Rep. 1	Rep 2	Rep 3	Bites Rep 1	Rep 2	Rep 3
4	69	67	85	0	2	0
5	1	70	25	0	0	0
6	11	53	108	0	0	0
7	14	182	326	0	1	0
8	55	123	196	0	0	0
9	5	222	125	0	10	0
10	56	441	224	2	4	17
11	53	159	91	0	2	0
12	30	98	58	8	5	0

DAY	EODs Rep 1	Rep 2	Rep 3
4	1	3	0
5	0	1	1
6	1	0	0
7	7	0	0
8	3	0	0
9	0	30	0
10	31	5	0
11	10	1	0
12	30	1	1

The estimate of the number of contacts per fish was obtained by multiplying the number of contacts that occurred in a 15 hour obervation period by 2 and dividing by the number of fish present. Estimates of bites and EODs per fish were obtained by dividing the number recorded by the number of fish present.

Table13: Percent of Time Swimming, Resting, in Shelters and Corners

	Rep.	Day	Swimming	Resting	Shelters	Corners
Res	1	1	11	5	5	80
Res	1	2	1.3	.8	1	97
Res	1	3	2.3	0	1	97
Res	1	4	15	1	65	20
Int	1	4	23	11	32	34
Res	1	5	2.6	.1	93	5
Int	1	5	2	.6	.1	98
Res	1	6	4.3	.1	95	1.1
Int	1	6	7.4	.2	11	82
Res	2	1	25	15	11	49
Res	2	2	25	18	23	34
Res	2	3	9	6.8	72	12
Res	2	4	34	46	8	12
Int	2	4	49	5	29	17
Res	2	5	19	48	29	4
Int	2	5	24	2.5	51	23
Res	2	6	20	26	18	36
Int	2	6	20	5	72	4
Res	3	1	8	8	43	40
Res	3	2	21	7	19	53
Res	3	3	2	10	86	2
Res	3	4	23	39	28	10
Int	3	4	31	10	26	34
Res	3	5	11	51	33	5
Int	3	5	11	21	47	21
Res	3	6	22	40	19	18
Int	3	6	23	.1	72.9	4

Table presents the data for the percent of time aone fish alone, and two fish, resident (Res) and intruder (Int), spent swimming, resting, in shelters, and in corners for each 15 hour observation period for each of the three replications.

Table 14: Social Behaviors (Two Fish in Tank)

Replication 1

	Res		Int		Dom		Sub	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Displaced	0.00	0.00	3.00	4.36	0.00	0.00	3.00	4.36
Flee	0.00	0.00	17.33	19.09	0.00	0.00	17.33	19.09
Approach	8.67	11.72	10.33	11.15	8.67	11.72	10.33	11.15

Replication 2

	Res		Int		Dom		Sub	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Displaced	4.67	2.52	0.00	0.00	0.00	0.00	4.67	2.52
Flee	43.67	2.52	0.33	0.58	0.33	0.58	43.67	2.52
Approach	4.33	2.08	44.00	6.08	44.00	6.08	4.33	2.08

Replication 3

	Res		Int		Dom		Sub	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Displaced	5.67	3.06	0.00	0.00	0.00	0.00	5.67	3.06
Flee	64.00	32.45	0.00	0.00	0.00	0.00	64.00	32.45
Approach	5.33	4.62	50.67	29.26	50.67	29.26	5.33	4.62

Table presents the mean and standard deviation (SD), of the frequency of the social behaviors of times displaced from a shelter site, times fled from a partner and times approached partner. The data is presented for residents (Res) and intruders (Int) as well as for Dominant (Dom) and submissive (Sub) fish.

Table 15:Hiding Patterns, Dominant and Submissive Fish

	Rep	Day	Shelters	Corners	Resting
Dominant	1	4	65	20	1
	1	5	93	5	.1
	1	6	95	1.1	.1
	2	4	29	17	5
	2	5	51	23	2.5
	2	6	72	4	.5
	3	4	26	34	10
	3	5	47	21	21
	3	6	72.9	4	.1
Submissive	1	4	32	34	11
	1	5	.1	98	.6
	1	6	11	82	.2
	2	4	8	12	46
	2	5	29	4	48
	2	6	18	36	26
	3	4	28	10	39
	3	5	33	5	51
	3	6	19	18	40

Data from Table & for time in shelters, corners, and resting are reorganized for Dominant and Submissive fish. Note the greater amount of time in shelters for dominant fish and time resting for submissive fish.

Table 16: Spatial Distribution (Two Fish)

Rep	Day	None	1S	2S	1C1S	2C	1C
1	4	2	10	53	71	24	13
1	5	0	2	0	166	9	1
1	6	0	1	25	140	2	0
2	4	52	49	5	20	3	50
2	5	36	55	20	35	2	32
2	6	23	51	22	70	3	11
3	4	40	27	20	38	9	46
3	5	26	88	20	35	0	11
3	6	10	87	32	30	0	21

Observations were made of the location of fish in shelters or corners of the tank every five minutes for each 15 hour obsevation period. Table presents number of observations with no fish in shelters or corners (none) and the number of observations fish were in shelters (S) or corners (C), when there were 2 fish in the tank.

Table 17: Spatial Distribution, Three Fish

Rep	Day	None	1S	2S	3S	1C 2S	2C 1S	1C 1S	3C	2C	1C
1	7	0	43	20	3	3	27	63	0	1	5
1	8	3	18	12	1	96	3	23	0	0	4
1	9	0	1	8	0	167	3	1	0	0	0
2	7	9	42	30	3	22	17	51	0	0	6
2	8	21	26	36	2	8	45	21	0	8	13
2	9	5	58	16	0	0	4	55	0	2	41
3	7	10	41	30	3	22	18	50	0	0	6
3	8	11	39	13	0	7	40	57	0	1	12
3	9	8	64	1	0	0	8	94	0	0	5

Observations were made of the location of fish in shelters and corners every five minutes of each 15 hour observation period. Table presents the number of observations no fish were in shelters or corners (NONE), and the number of observations when fish were observed in shelters (S) and corners (C) when 3 fish were in the tank.

Table 18: Spatial Dstribution, Five Fish

Rep	Day	None	1S	1C	2S	2C	1C 1S	3S	3C	1C 2S	2C 1S	4S	4C	1C 3S	2C 2S	3C 1S	5S	5C	1C 4S	2C 3S	3C 2S	4C 1S
1	10	0	0	0	10	0	0	42	0	13	2	14	0	70	3	1	0	0	0	12	4	0
1	11	0	3	0	33	0	7	6	0	54	0	0	0	12	42	2	0	0	0	16	1	0
1	12	0	1	0	3	0	2	1	0	32	2	3	0	12	76	6	0	0	0	33	9	0
2	10	9	22	34	19	23	21	2	3	8	28	0	0	3	2	4	1	0	0	0	1	0
2	11	6	16	18	19	7	31	4	0	19	35	0	0	0	24	0	0	0	0	0	0	1
2	12	3	13	5	30	7	25	1	0	29	15	0	0	3	22	2	0	0	12	13	0	0
3	10	10	18	12	12	4	35	4	2	29	27	2	2	1	20	2	0	0	0	0	0	0
3	11	1	11	10	4	10	39	3	1	19	57	0	0	3	0	22	0	0	0	0	0	0
3	12	2	3	3	1	1	25	0	0	10	108	0	0	0	11	14	0	0	0	0	1	1

Observations were made of the location of fish in shelters and corners every 5 minutes of each 15 hour observation period. Table presents the number of observations in which no fish were observed in shelters or corners (NONE), and the number of observations when fish were in shelters (S) and corners (C) when 5 fish were in the tank.

Table 19: Interfish Distances

Rep	#fish	Mean IFD	SD
1	2	101	20
1	3	81	30
1	5	89	42
2	2	104	30
2	3	70	32
2	5	87	37
3	2	78	27
3	3	98	36
3	5	101	38

Table shows the mean interfish distance (IFD) in cm for each replication and the standard deviations (SD).

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