THE AGONISTIC BEHAVIOUR OF JUVENILE STICHAEUS PUNCTATUS (STICHAEIDAE)

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THE AGONISTIC BEHAVIOUR OF JUVENILE *STICHAEUS PUNCTATUS* (STICHAEIDAE)

by

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ABSTRACT

Juvenile *Stichaeus punctatus* were obtained while diving at two locations on the Avalon Peninsula. Laboratory observations were undertaken on fish held in aquaria supplied with a continuous flow of seawater and a 12 hr light, 12 hr dark photoperiod.

A qualitative description of the agonistic behaviour was accomplished with seven recognizable actions being observed. These actions are: approach, threat, nip, flee, chase, flatten, and back away. Dominant and subordinate fish showed different frequencies and durations of these actions and also differed in their colouration. The sequence of occurrence of agonistic actions was not random and a sequence diagram was derived. Agonistic behaviour decreased in frequency and bouts involved fewer actions as the length of the encounter increased. Agonistic behaviour and motor activity occur diurnally in the laboratory and in the field. A high level of agonistic and motor activity was observed at dawn.

The sensory modes used by *S. punctatus* during agonistic interaction were investigated using partitioned tanks, models, mirrors, and seawater inhabited by a conspecific. This investigation showed that visual cues must be present in order that agonistic behaviour be observed. Available

space was found to be important in the structuring of agonistic behaviour. A persistent dominance and subordination of individuals was observed in the smaller tank. Territories were established in the larger tank.

The agonistic activity of yearling fish was observed to decrease in the summer and subsequently increase in the fall. It appears that water temperature may be a causal factor in these changes.

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INTRODUCTION

The arctic shanny, *Stichaeus punctatus* (Fabricius), 1780, is a benthic, sublittoral, arctic-boreal blennioid of the family Stichaeidae. Its life history is not well known and there are no published accounts of its behaviour. Leim and Scott (1966) and Andriyashev (1954) give distribution records and morphological descriptions of *S. punctatus*, and present most of the known information on its life history. The report by Collette and MacPhee (1969) on a single juvenile specimen is the most recent published account of the species.

Blennioid fishes have been used extensively in ethological investigations (see review by Gibson 1969) but these studies have dealt mainly with adult fish. Gibson (1968) investigated the behaviour of juvenile *Blennius pholis* and Fishelson (1963) briefly discussed the behaviour of juvenile *Blennius pavo*.

The purpose of the present study was to investigate the agonistic behaviour of juvenile *S. punctatus* both qualitatively and quantitatively, thereby creating a basis for further ethological and ecological investigation. Experiments were done to determine the sensory modes used in agonistic interaction and the relationships of time and space to agonistic behaviour.

METHODS

FIELD STUDY

Juvenile *S. punctatus* were observed and collected while using diving equipment. A slurp gun and fine mesh dipnet were used to collect live specimens. These were transported to the laboratory in a plastic bucket containing approximately 18 l of local seawater. The two field areas were visited at irregular intervals commencing in May, 1969. The dates of the dives at the two areas are presented in Appendix 1.

Field Area Descriptions

The two field areas where *S. punctatus* were observed and collected were in the waters surrounding the Avalon Peninsula of Newfoundland. The major site was in Salmonier Arm with further observation and collecting being done in Logy Bay.

The study site in Salmonier Arm was near the community of Mitchell's Brook. The diving site there is characterised by a rock and pebble beach which continues under the surface to a depth of approximately 7 m. The rocky bottom ends at this depth and adjoins a sand and silt bottom which continues offshore. The fish have been observed inhabiting the rock-sand interface and the rocky area. Juvenile S. punctatus have been observed year around at this location. The greatest numbers were observed during May and June, 1969. No adult specimens have been observed in Salmonier Arm at Mitchell's Brook.

The portion of Logy Bay in which juvenile S. punctatus were observed and collected was Dyer's Gulch, adjacent to the Marine Sciences Research Laboratory. The gulch is characterised by nearly vertical bedrock sides. The bottom is rock and boulder with small areas of gravel. The depth at point of entry is approximately 4 m and the bottom gradually drops seaward to a depth of approximately 19 m. S. punctatus has been observed inhabiting the rocky bottom at depths of 4 to 15 m. Specimens were observed in Dyer's Gulch from August, 1969, until January, 1970. Greatest numbers were observed during August and September, 1969. No S. punctatus were observed during dives before August, 1969 or after January 1970. No adult specimens have been observed in Dyer's Gulch.

LABORATORY STUDY

Fish Holding Conditions

Laboratory observations were initiated in May, 1969, and continued until the spring of 1970. The fish were held at the Marine Sciences Research Laboratory where all laboratory experimentation was conducted. These fish were obtained from Mitchell's Brook and Dyer's Gulch. The main holding tanks were 60 × 29 × 29 cm with a sand and gravel bottom and were supplied with a continuous flow of seawater. Illumination was provided by a 40 watt daylight fluorescent light fixture suspended over the tanks. The photoperiod was controlled and held throughout the study on a 12 hour light - 12 hour dark cycle with lights being turned on at 0700 hours Newfoundland Standard Time. The holding and observation tanks were separated from the rest of the room by a black plastic curtain. Horizontal slits were cut in the curtain to allow observation of the fish without disturbance. Tank temperature was governed by the temperature of the incoming seawater. Daily temperature recordings were kept throughout the study; the data are presented in Appendix 1. Most experimental observations were done in the fish holding room. Similar conditions were provided when observations were done outside the holding room.

The fish fed on foods occurring naturally in the unfiltered seawater supplying the tanks. The food items observed being eaten were amphipods and copepods. This food supply was considered inadequate and supplemental feedings occurred daily. The food was prepared and introduced into the tanks with as little disturbance as possible. Feedings occurred at irregular times to minimise conditioning the fish to a certain time period. The supplemental foods were, in order of frequency of presentation: crushed gonads of *Strongylocentrotus droebachiensis*, live Amphipoda, chopped *Mytilus edulus*, and chopped *Mallotus villosus*.

Few fish died in the laboratory or during transportation to the laboratory. The size, age and sex of these fish are presented in Appendix 2. Aging was done using otoliths and scales. Stomach contents of those fish which died during transportation to the laboratory are also presented (Appendix 2). Live fish were aged by size and specimens used in this study were underyearling unless otherwise stated.

Description of Experimental Tanks

The laboratory observations were done in tanks ranging in size from 24 × 14 × 15 cm to 150 × 51 × 43 cm. Tank bottoms were covered with a layer of sand and gravel.

A continuous flow of seawater was supplied to all tanks unless otherwise stated. Only those tanks which were equipped with special experimental apparatus are described below.

Signals in Agonistic Behaviour

The signal investigation was done in four parts: tank partition, fish model, conspecific water, and mirror tests.

Partitioned Tanks

The first portion of the signal investigation involved the placement of four types of vertical partitions into 24 × 14 × 15 cm tanks. A partition was fixed in position so as to divide the tank into halves with the edges of the partition at mid-front and mid-back of the tank. This allowed simultaneous observation of both halves of the tank. The four partitions were numbered and are described below:

1. Partition no. 1 was a piece of glass, 2.5 mm thick, affixed so that all edges were watertight.

2. Partition no. 2 was a black plexiglass partition, 3 mm thick, with all edges sealed and both surfaces buffed to reduce image reflection.

3. Partition no. 3 was a clear plexiglass partition, 3 mm thick, with numerous 3 mm diameter holes at a distance of from 2 to 4 mm apart. The partition was affixed at the edges but not sealed.

4. Partition no. 4 was a black plexiglass partition, 9 mm thick, with staggered slits. It consisted of a rectangular framework 3 mm thick with two series of black plexiglass strips 6 to 8 mm high affixed on either side. The strips were 3 mm apart, producing horizontal spaces between the strips. The 3 mm spaces on either side of the partition were staggered so that vision through the partition was impossible.

Models

In the second part of the signal investigation tanks of various sizes were used. The three models used were made to resemble juvenile S. punctatus 40 mm long. The models were affixed to a long stiff wire for presentation to the fish. Features of the models, i.e. body outline, fins, eyes, mouth and opercular openings, dorsal fin spots, and chin bars were drawn in India ink on heavy paper. The models were given a thin coat of a brown green watercolour, resembling the body colour of a fish. The features of the three models varied and are numbered and described below:

1. Model no. 1 - posture of body and fins represented a threat posture. The five dorsal fin spots were present and the chin bars absent.

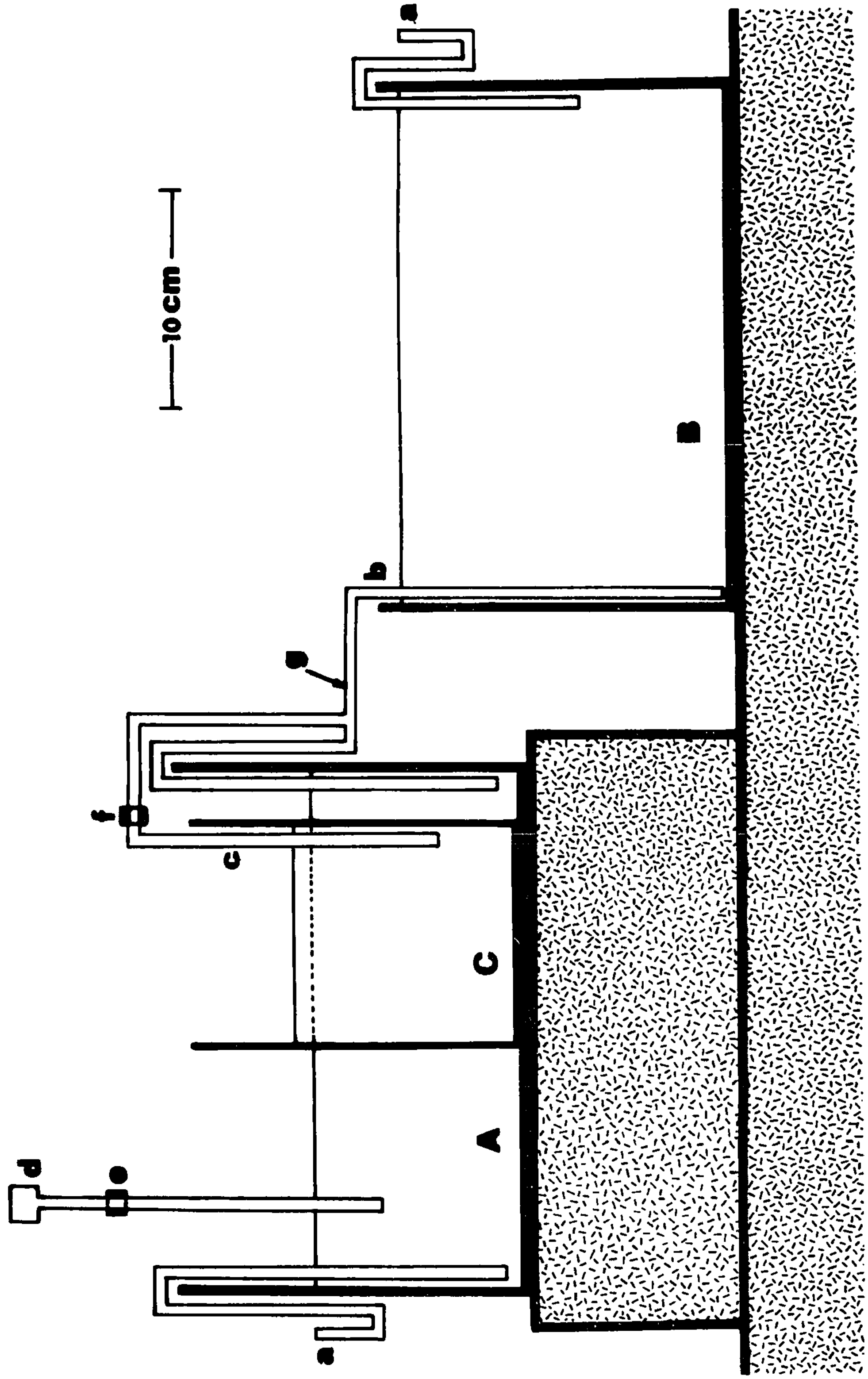
2. Model no. 2 - posture of the body and fins represented a threat posture with dorsal fin spots and chin bars absent.

3. Model no. 3 - posture of body and fins represented a flatten posture. The chin bars were present and the dorsal fin spots were absent.

Conspecific Seawater

In the third portion of the signal study the reactions of fish to conspecific inhabited seawater was investigated. A seawater system as presented in Figure 1 was used. Tanks (A) and (B) were 24 × 14 × 15 cm and had constant level outflow siphons (a). Tank (B) was supplied with an inflow tube (b) which siphoned water from Tank (A). Tank (A) was supplied with seawater taken directly from the seawater outlet in the room. Inflow tube (b) was joined by a stimulus introduction tube (c) by means of a T-connector. Stimulus introduction tube (c) siphoned seawater from a 1000 ml beaker (C) in Tank (A). The flow through the system was regulated by valve (d) on the seawater outlet, clamp (e), and overflow siphon (a) in Tank (A). The flow through Tank (B) was maintained at approximately 200 ml/minute. Clamp (f)

Figure 1. Diagram of the conspecific seawater apparatus. See text for explanation.


10 cm
a
b
g
f
c
C
A
B
d
e
a

on the stimulus introduction tube was closed during non-test situations. Beaker (C) was filled with seawater to a level higher than that of Tank (A) and the difference between the two levels contained 100 ml of seawater. Clamp (f) regulated the flow of the seawater out of the beaker.

In the second part of the conspecific water investigation the same apparatus was used except that a 10 ml syringe was introduced into inflow tube (b) at point (g).

Mirror

In the fourth and final portion of the signal investigation a 24 × 14 × 15 cm tank with a 23 × 15 cm mirror against the rear wall was used.

Changes in Yearling Fish

The tank in which the behaviour of a pair of yearling fish at lowered temperatures was observed had a cooling unit consisting of a system of coiled glass tubing immersed in an ice water bath. The 12 - 13 C water was cooled to 5 - 10 C after flowing through the tubing.

Observation Recording

Recorded observations were made of the particular aspect of the behaviour under investigation at the time. Photographic records were obtained with an Asahi Pentax 35 mm camera. Written records were at times obtained by means of paper and pen but more complete records were obtained with two Ralph Gebrands Co. six pen event recorders. The recorders operated at a chart advance speed of 3 mm per sec and were synchronous to within 1 mm after operating for three hours. During analysis of the records measurements were taken to the nearest whole mm. A keyboard was used to transcribe observations to the event recorders. The keyboard consisted of 11 pushbuttons. One of the buttons operated one pen on both recorders, thus operating as a check on the synchrony of the recorders and as an indicator of the start and end of individual records. The remaining pushbuttons were used to record the observations.

Descriptions of Experimental Procedures

Description of Agonistic Behaviour

The qualitative descriptions of agonistic behaviour were derived from notes taken during observations of the fish and from photographs of the actions. Quantitative data on sequence patterns, action durations, and action frequencies were taken from event records of the motor activity and agonistic behaviour of ten pairs of fish. An encounter occurs when two fish are in the same tank for a period of time. During encounters there are periods when agonistic behaviour is observed. These periods are termed bouts. At the end of a bout or series of bouts one fish was termed dominant and the other subordinate. The criteria for establishing these definitions are as follows:

1. Modal action patterns - the fish which fled or flattened was the subordinate.

2. Colour changes - the darkening of the chin bars and blanching of the dorsal fin spots were characteristic of the subordinate fish. Dominant fish showed a darkening of the dorsal fin spots and a blanching of the chin bars.

Motor Activity Levels in Novel Situation

This series of observations was done using single fish in a 24 × 14 × 15 cm tank. The fish were placed into the tank and left for a period of time before paper and pen recordings of their motor activity, i.e. number of moves, were made. A total of 20 fish were observed and each fish was observed at least twice. Observations were 15 min long and the times of observations were 1, 2, 3, 4, 6, 20, and 24 hr after the fish was placed in the tank.

Agonistic Behaviour and Length of Encounter

The data in this section were obtained by placing two fish from separate holding tanks into a 29 × 20 × 17 cm tank and recording their agonistic behaviour and motor activity during 15 min observation periods 1, 2, and 3 hr after being placed in the tank. Event records were assembled on 5 pairs during 1 and 2 hr observation periods and on 3 pairs during 1, 2, and 3 hr periods.

Diel Activity

The diel occurrence of motor and agonistic activity was investigated in two ways. The first set of observations consisted of direct observation of fish during the 12 hr dark portion of the photoperiod. A short duration flash of light was used during which the position, colour, and posture of 3 or 4 fish were noted. These flashes of approximately 2 sec duration were repeated every 15 to 20 sec for 5 min. Five min observations were done on irregularly spaced days.

In the second part of this investigation 7 fish were held in a 150 × 51 × 43 cm tank supplied with a 12 hr light, 12 hr dark photoperiod with the lights turning on at 1000 hours. The number of moves of all 7 fish and the number of agonistic bouts were recorded for 15 consecutive minutes beginning 5 min before the lights turned on for 7 consecutive days. On two of these days a 5 min observation of agonistic activity was done 40 min after the lights turned on.

Signals in Agonistic Behaviour

Partitioned Tanks

The partition study was done in four parts. All observations were undertaken in the same tank with the partition being changed between observation series. Two fish from separate holding tanks were placed in the partitioned tank, one fish on either side of the partition. At this time inflowing seawater was shut off and the fish left for a period of 2 hr at which time a 15 min event recording of motor activity and agonistic behaviour was made. The fish were then removed and the tank flushed with seawater before replicate testing. In the partitions 1 and 3 series 10 replicates were done, while in partitions 2 and 4 series 5 replicates were done.

Models

The three models described above were presented from outside the tank. They were affixed to a wire and moved slowly toward the fish being tested. Forward movement of the model was stopped either at the tank wall or approximately 5 cm from the fish. The model was held at this point until a response was observed or until 10 sec had elapsed. The model was then withdrawn. Successive presentations to a fish were made with different models separated by an interval of one hour. Each fish received no more than 3 presentations per day. The responses were of four types:

1. Approach - recorded when a fish approached the model without changes in colouration, or agonistic posture.

2. Aggression - recorded when a fish approached the model with agonistic changes in posture, or colouration typical of a dominant fish.

3. Withdrawal - recorded when a fish moved away from the model by backing away or fleeing.

4. No Reaction - recorded when a fish remained stationary, without alteration of its posture or colouration, during the 10 sec presentation of the model.

Conspecific Seawater

The responses of fish to conspecific seawater were observed in two parts utilising the apparatus described above. The first part utilised two fish for each observation. One fish was placed in Tank (B) and the other was placed in beaker (C), as shown in Figure 1. The water flow through the beaker was stopped and the flow through the tank was maintained at approximately 200 ml/min. The fish were left for a period of two hours before recordings were made. Observation began with a 5 min record noting the motor activity and colouration of the fish in Tank (B). Clamp (f) was then opened to allow 100 ml of conspecific inhabited seawater to flow into Tank (B) over a period of approximately 3 min, increasing the flow through Tank (B) to approximately 230 ml/min. Another 5 min recording of the motor activity and colouration of the fish in Tank (B) was made commencing a few seconds after clamp (f) was opened. Both fish were then removed and the water in the system was flushed out and renewed before replicate testing. Ten replicates were done.

In the second part of the conspecific seawater study a fish was placed in Tank (B) and presented with seawater and seawater containing a scraping of conspecific epidermis. During the two hour period after placement of the fish in Tank (B) a small portion of the epidermis was scraped from another juvenile fish and stirred into 25 ml of seawater. Ten ml of seawater containing the scraping and 10 ml of seawater were drawn into two separate syringes shortly before observation began. At the end of the two hour interval a 5 min record noting the motor activity and colouration of the fish in Tank (B) was made. The syringe containing seawater was then emptied into the inflow tube and another 5 min recording was made after which the syringe containing the scraping was emptied into the inflow tube and a third 5 min recording was made. The tank and the syringes were flushed with seawater prior to replicate testing. Ten replicate tests were done.

Mirror

In the fourth and final part of the signal investigation individual fish were placed in a tank and left for a period of one to two hours. The mirror was then placed against the back wall of the tank and left in position until a threat was observed or until 5 min had elapsed. Ten fish were tested.

Agonistic Behaviour and Available Space

This part of the study was done with pairs of fish in two tanks of different sizes, 43 × 25 × 21 cm and 29 × 20 × 17 cm. The bottoms of the tanks had pieces of gravel spread over sand. The positions of the individual pieces of gravel were plotted on outline maps for use as markers. Two fish were placed in each tank and left overnight before observations began. Observations were 15 min long and the position of each fish was marked on an outline map every 15 sec. The positions of the agonistic bouts were noted and the dominant individual in each bout was noted. Observations were made at irregular times of the day for a period of days with one observation per day being made. Following 8 days of observations the fish from the smaller tank were placed in holding tanks. The fish from the larger tank which had been observed for 5 days were transferred to the smaller tank, and observed for 6 days. Two fish from separate holding tanks were observed for 6 days in a second series of observations in the larger tank.

Changes in Agonistic Activity Level in Yearling fish

These observations were undertaken in a number of different situations. The first set of observations used yearling fish from separate holding tanks. Two fish were placed in tanks either 24 × 14 × 15 cm or 29 × 20 × 17 cm in size. The pair was then observed at varying intervals and the number of agonistic bouts was noted. All 15 pairs were observed during their first 15 min in the tank as well as after 1 and 2 hr in the tank. Three pairs were observed after 6 hr and three pairs were observed after 24 hr in the tank.

In the second series of observations a 24 × 14 × 15 cm tank with a central unsealed black partition was used. Two fish were placed in the tank, one on either side of the partition, and left for 2 hr. The partition was then removed and the number of agonistic bouts in the following 15 min was noted. Three replicate tests were done.

In the third set of observations supplemental food was withheld from the fish in two holding tanks for 72 hr. Two fish were placed in a 24 × 14 × 15 cm tank and left for one hour. They were then observed for 15 min and the number of agonistic bouts was noted. Two pairs were observed.

During the fourth set of observations the agonistic activity of two pairs of fish at lower than incoming seawater temperatures was recorded. The first pair was placed in a 29 × 20 × 17 cm tank supplied with cooled seawater. The temperature fluctuated between 5 and 10 C while incoming seawater was 12 to 13 C. Ten minute observations were made at irregular intervals for 4 days during which the number of agonistic bouts was noted.

The second pair was placed in a 29 × 20 × 17 cm tank containing 12 C seawater. The tank was then transferred to a temperature control room held at 1 to 2 C. The tank was aerated and a small quantity of seawater was added every few days. After the initial cooling which took 6 hr tank temperature was maintained at 1 to 2 C. The pair was held at this temperature for 39 days. Observations of 5 min duration were done at irregular intervals for 39 days and the number of agonistic bouts was noted.

The fifth part used the procedure outlined above for investigating motor activity in a novel situation. During 15 min observations the motor activity of the fish which had been in the tank for 2 hr was recorded. Ten fish were observed in this investigation.

In the final series of observations four yearling and three underyearling fish, all collected in September, 1969, were used. They were held in a 150 × 51 × 43 cm tank. The behaviour of these fish was observed for 10 days in October, 1969 and 7 days in November, 1969. The observations were 15 min long and the number of agonistic bouts was recorded.

RESULTS

QUALITATIVE DESCRIPTION OF AGONISTIC BEHAVIOUR

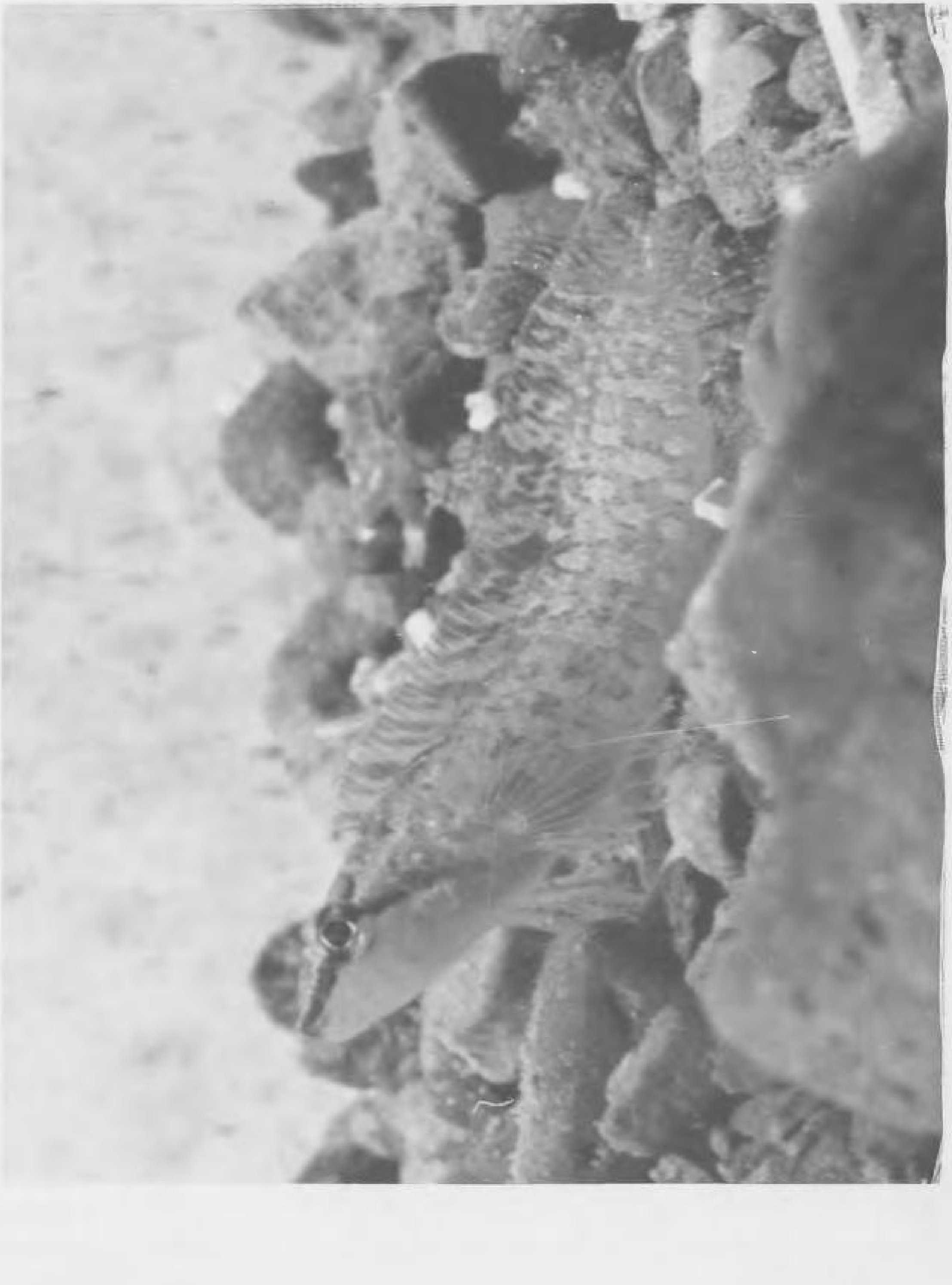
The Modal Action Patterns

The agonistic behaviour of S. punctatus consists of seven recognizable actions, termed "modal action patterns" as suggested by Barlow (1968). Described below are two non-agonistic modal action patterns and the seven agonistic modal action patterns.

Non-Agonistic Modal Action Patterns

Stationary posture - This posture of the fish, shown in Figure 2, is observed when the fish is not moving. The fish is stationary on the substrate with the caudal portion of the body curved so that the tail is at an angle of between 60 and 120 degrees with the longitudinal body axis. The caudal curvature, which starts near the anal region, may be to either side of the body. The pelvic and pectoral fins are in contact with the substrate and support the anterior portion of the body. The pelvics are extended downward forming an angle of between 45 and 90 degrees with the body axis. This angle depends on the contour of the substrate on which the fish is positioned. The pectorals

Figure 2. Stationary posture of a juvenile *S. punctatus*



are extended away from the longitudinal body axis at an angle typically between 60 and 90 degrees, again depending on the contour of the substrate. The dorsal fin is partially erected with the rays typically forming an angle of between 60 and 80 degrees with the body axis. The caudal fin is extended, with the lower rays in contact with the substrate. The anal fin is in contact with the substrate in those places where the bottom topography allows contact. The anal rays are extended between 20 and 60 degrees depending on the contour of the bottom. The head is usually held in line with the body axis but horizontal and vertical movements are common. The body, from the anus forward, is usually not in contact with the substrate with the exception of the tips of the pelvic fins and the lower rays of the pectoral fins.

The description of the stationary posture is presented to allow comparison with the agonistic postures so that easier visualisation of the agonistic actions is possible.

Move - This includes three types of movement by the fish. These are walk, hop, and swim and are described separately below:

1. Walk - This movement is the most common type observed and consists of forward motion derived from resistance of the caudal region of the body, the pectoral

fins, and the anal fin against the substrate. The caudal curvature of the stationary posture is extended and asynchronous adduction of the pectoral fins occurs. The anal rays are adducted in such a way that contact with the substrate is maintained and the rays are erected to between 40 and 60 degrees when contact is lost or when movement ceases. Walking is continued by alternate pectoral adduction and extension with concomitant curvature and extension of the caudal region.

2. Hop - This is a quick forward movement following the stationary posture. The hop is produced by a single synchronous adduction of the pectoral fins with a concomitant single extension of the caudal curvature. The fish is propelled forward and all contact, except for the anal, with the substrate is usually lost. During a hop the dorsal fin is often partially adducted in the anterior region.

3. Swim - This type of movement is accomplished by anguilliform body motions. The head is higher than the tail and the longitudinal axis of the fish forms an angle of approximately 15 degrees with the substrate. The pectoral fins are extended from the body so that the dorsal rays are directed dorso-anterior and the ventral rays are directed ventero-posterior, thereby forming an angle of approximately 20 degrees with the longitudinal body axis. The anterior

portions of the dorsal and anal fins are usually adducted, the degree of adduction becoming less as the fully extended caudal fin is approached. The pelvics are adducted to the ventral body surface. Swimming fish are not in contact with the substrate.

The three types of movement described above are the typical locomotor patterns observed. The term move will include all three types in the remainder of this paper.

Agonistic Modal Action Patterns

Approach - This action consists of the movement of one fish toward another. The approaching fish typically has its head oriented toward the head of the other fish. An approach is produced by one or two types of movement. The more common, walk-approach, is the approach of a fish to another while walking as described above. The other type of approach, hop-approach, is when the fish uses hop movement, described above, to approach the other fish. For recording purposes these two types of approach were not separated and approach in the remainder of this paper includes both types.

Threat - The threat action involves changes in posture and colour which occur while the fish is stationary near or approaching an opponent. Threat consists of various components which vary in their frequency of occurrence. Description of threat will start with the threat posture and proceed to other behavioural elements observed in association with the threat posture.

The threat-posture is shown in Figure 3. The threatening fish is typically positioned at or near the head of the other fish. The dorsal fin spines are erected with the anterior spines erected more than the posterior ones. The first few spines, typically form an angle of 90 degrees with the longitudinal body axis. The head is inclined forming an angle ranging from 10 to 30 degrees with the body axis. As well as inclination of the head there is variable extension of the hyoid and opercular apparatus. Another component of threat posture is the upward arching of the body, as shown in Figure 3B. The amount of arching varies and the anterior portion of the anal fin may lose contact with the substrate during a highly arched threat posture.

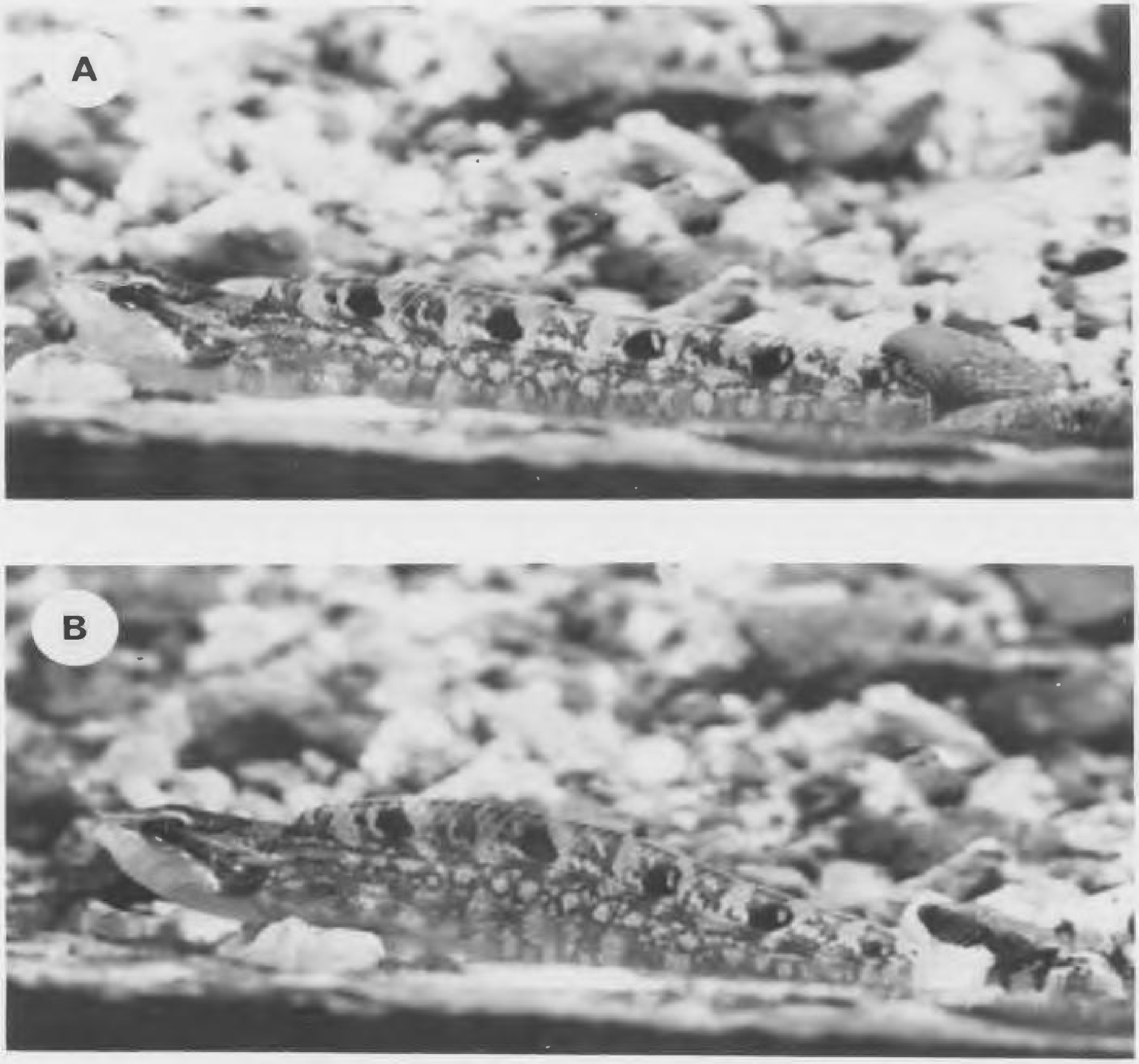
In conjunction with the threat posture described above, four additional components were observed:

1. Threat-approach - The most common of the actions occurring during the threat posture is the movement of the threatening fish toward the other by means of the

Figure 3. Threat posture of juvenile *S. punctatus*.

Photograph A shows dorsal fin erection, opercular extension, and head inclination.

Photograph B shows dorsal fin erection, opercular and hyoid extension, head inclination, and body arching.


A
B

movement walk, described above. This forward motion brings the head of the threatening fish closer to the other fish.

2. Body shake - The second most common action occurring during the threat posture is body shake. This consists of a single lateral shake of the body. The shake is of short duration and usually occurs during a threat posture containing all of the postural components already described. The duration is less than 1/3 sec and the shake is of small amplitude, the body moving laterally 1 to 2 mm.

3. Threat-gape - The third action in combination with the threat posture was observed only twice and on both occasions the fish involved had both assumed the threat posture. A threat-gape is shown in Figure 4. The head is not raised and the opercula are not extended. Instead, the fish opens its mouth, i.e. gapes. The duration of the gape was approximately 3 to 4 seconds in both observations.

4. Threat-wag - The fourth action observed during the threat posture was seen once between two fish but it occurred in several observations of a fish reacting to its mirror image. In the former situation both fish had assumed the threat posture. One fish, during obvious arching of the body, lifted the caudal area from the substrate so that the body was supported by the pelvic and pectoral fins only. The lifted caudal area moved slowly laterally.

Figure 4. Threat gape shown by juvenile *S. punctatus*.

The lateral motions were of small amplitude and there was no forward movement of the body. The fish which performed the threat-wag subsequently nipped the other fish.

Because of limitations of the recording apparatus it was possible to record only threat posture and threat-approach. No recording was made of the variation in the postural components involved in individual threats.

Nip - The action of nipping is of short duration, i.e. less than 1/3 of a second, and observation of the movement is therefore difficult. Nip is a quick forward hop toward the other fish occurring when two fish are less than one body length apart. The short duration and the typical fleeing by the other fish made is impossible to see whether the nipping fish made contact with the other fish. In one observation, however, the nipping fish made contact with the pectoral fin of the other and held the fin in its mouth for approximately one second. The contact was lost when the nipped fish twisted its body and fled. During some of the nips observed in the partitioned tanks it was possible to see the nipping fish with its mouth open and in contact with the tank partition. Typically the initial forward movement of the nip is directed toward the anterior portion of the other fish. The approached fish, however, usually flees and contact, if made, is usually in the middle or posterior portion of the body. During recording, no attempt was made to determine whether or not contact was made.

Flee - This action is a quick forward propulsion of the fish away from the other fish by means of caudal swimming movements. The body is not in contact with the substrate and the pectorals and pelvics are adducted to the body. The caudal swimming motions are of small amplitude and occur in rapid succession, thereby moving the fish through the water quickly.

Chase - This is a swimming action of one fish toward a fleeing fish and involves caudal anguilliform swimming above the substrate. The pectoral and pelvic fins are not always adducted to the body. Swimming speed of the chasing fish is typically slower than that of the fleeing fish. The chasing fish typically settles on the substrate before reaching the other fish.

Flatten - This is a change in the posture of a stationary fish (Figure 5). The components of the act are the depression of the dorsal, anal, pectoral, and pelvic fins. The head is lowered, bringing the chin into contact with the substrate. The anterior spines of the dorsal fin may be lowered more than the posterior spines so that the

Figure 5. Flatten shown by juvenile _S. punctatus_.

height of the dorsal fin may increase gradually toward the posterior end. The pelvic and pectoral fins are typically held close to the body. The caudal fin is not extended fully. Once the fish has attained this posture there is little movement of the body. It was observed, however, that when approached by the other fish there was often a further lowering of the dorsal spines and/or the head if the lowering was incomplete during the initial postural changes.

Recording was made of the presence and absence of the act but quantitative data of the variation in the postural components of the act were not assembled.

Back-away - This act is characterised by a slow lateral or reverse movement of the fish by the use of the pectoral fins and the caudal portion of the body. The pectorals are extended forward while in contact with the substrate and the caudal portion of the body is laterally curved. The fish moves backwards or to one side, depending on the direction of the caudal curvature and on whether one or two pectoral fins are used in the movement. The direction of the movement is away from the other fish involved in the bout.

This act was only rarely observed and was not recorded because of the limitations of the recording apparatus.

The Agonistic Bouts

Agonistic bouts consisted of various numbers and types of agonistic modal action patterns. At the end of a bout a relationship is present in which one fish is dominant and the other subordinate. Dominance is associated with the modal action patterns of nip and chase while subordination is associated with the modal action patterns of flatten, back-away, and flee. Colouration indications of this relationship are also present and are described below. The status of each fish remains the same in successive bouts in an encounter.

Colouration

Colouration of subjects changed in relation to the particular test situation. These changes occur in relation to the agonistic situation as well as to the light intensity of the surroundings. The colouration of fish during the light and dark portions of the photoperiod is described under the section 'Diel Activity'. Agonistic colouration is described below and is related to the agonistic modal action patterns.

The chromatophores of the fish which change during bouts are localised in two areas of the body: the dorsal fin and the chin. The chromatophores in these two areas change rapidly during bouts. Slower changing chromatophores which alter during encounters are on the body of the fish.

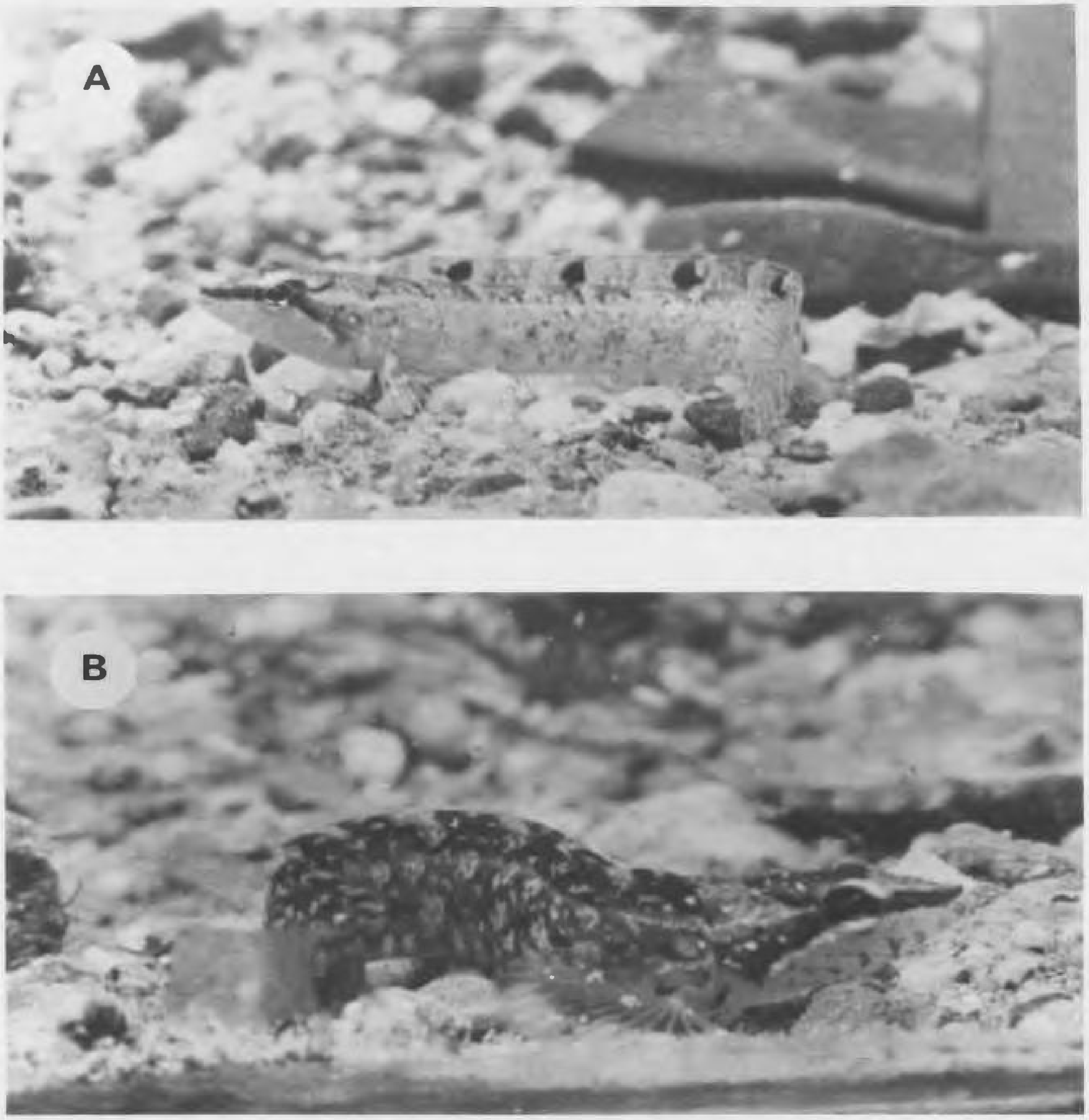
The dorsal fin has five concentrations of chromatophores which blanch or darken depending on the agonistic status of the fish. Dominant fish have darkened dorsal spots (Fig. 6A) whereas subordinate fish have blanched spots (Fig. 6B). Alteration of these spots occurs during bouts with darkening usually occurring during threat and blanching occurring during flatten. The changes in dorsal spot colouration are rapid and the duration of the changes is similar to the mean durations of threat posture and flatten (see Table 1).

The chin also has localised concentrations of chromatophores in the form of six suborbital bars on either side of the head. These vertical bars darken or blanch rapidly and in an opposite way to that described for the dorsal fin spots. Dominant fish have blanched chin bars (Fig. 6A) whereas subordinate fish have dark chin bars (Fig. 6B). Darkening usually occurs during flatten while blanching usually occurs during threat. The duration of the chin bar colouration changes is similar to the mean durations of threat posture and flatten (see Table 1).

Figure 6. Agonistic colouration of juvenile S. punctatus.

A) Dominant fish

B) Subordinate fish


A
B

Body colouration also changes but these alterations usually occur during minutes rather than seconds. The body colouration of a dominant fish is typically paler than that of a subordinate fish (see Fig. 6, A and B).

Colouration of the dorsal fin spots, chin bars, and body were ranked as to their significance in the determination of the dominance or subordination of a fish. Dorsal spots were given first position with three assigned degrees of colour: dark, medium, and pale. In second position were the chin bars with two degrees: present or absent. Third was body colour with three degrees: dark, medium, and pale. Figure 7 shows the data from 10 encounters. This shows that the colouration of dominant and subordinate fish differ as described above with overlap occurring only in the case of body colouration.

QUANTITATIVE DESCRIPTION OF AGONISTIC BEHAVIOUR

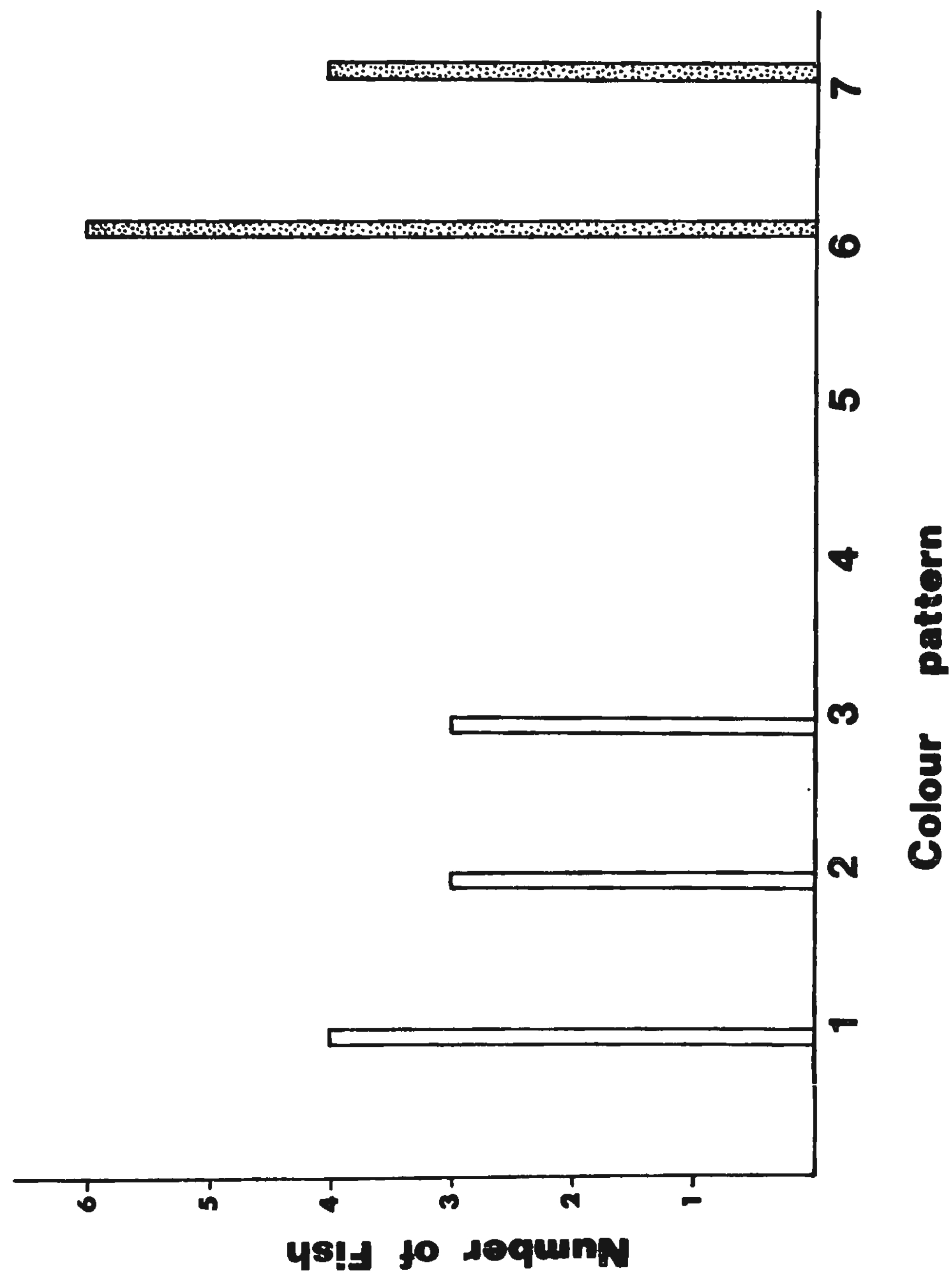
During 10 observations of 15 min duration the modal action patterns were recorded for quantitative analysis of the agonistic behaviour. The actions recorded were move, approach, threat posture, threat-approach, nip, flee, chase, and flatten. Encounter length before observation was 45 to 105 min.

Figure 7. Frequency of agonistic colour patterns of ten pairs of juvenile fish. Clear bars represent dominant fish and stippled bars represent subordinate fish.

Key to colour patterns

Pattern number	Pattern code
1	D A P
2	D A M
3	M A P
4	M A M
5	P A M
6	P B M
7	P B D

The first, second, and third letters in the code represent the dorsal fin spots, the chin bars, and the body respectively. The code letters indicated the degree of pigmentation with D meaning dark, M meaning medium, P meaning pale, A meaning absent, and B meaning present. This system of colour pattern numbers and codes is used in succeeding figures of this type.

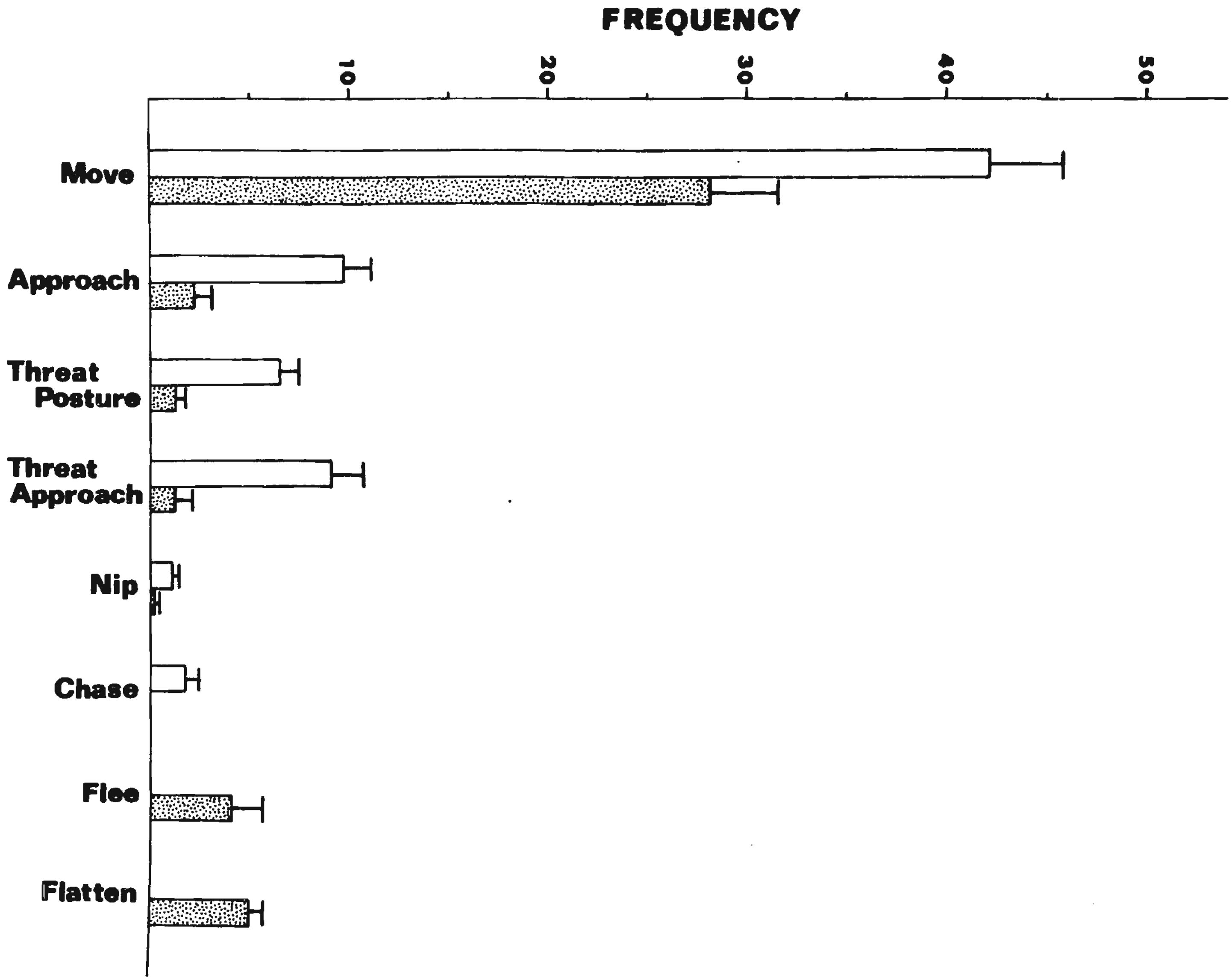

Number of Fish
1
2
3
4
5
6
Colour pattern
1
2
3
4
5
6
7

Frequency and Duration of Bouts and Modal Action Patterns

The mean frequency of occurrence of the actions shown by 10 dominant and 10 subordinate fish per 15 min is shown in Figure 8. Student's t test was used to compare the means for the dominant and subordinate fish and differences were found for each of the modal action patterns. Significant differences ($p < 0.05$) were found for the frequencies of move ($t = 2.74$, 9 d.f.), flee ($t = 2.53$, 9 d.f.), and chase ($t = 2.43$, 9 d.f.) and significant differences ($p < 0.01$) were found for the frequencies of approach ($t = 4.75$, 9d.f.), threat posture ($t = 4.7$, 9 d.f.), threat-approach ($t = 4.5$, 9 d.f.), nip ($t = 4.0$, 9 d.f.), and flatten ($t = 8.1$, 9 d.f.). The typically dominant actions are approach, threat, nip, and chase and the typically subordinate actions are flee and flatten. The mean motor activity level of the dominant fish is higher than that of the subordinate fish.

The mean frequency of bouts per 15 min was 6.2 ± 2 bouts. The mean duration of the bouts was 9.8 ± 1.9 sec. Table 1 indicates that there are differences in the mean durations of the actions of a fish dependant upon the agonistic status of the fish. Significant differences in the mean values of approach ($t' = 9.1$, 18 and 96 d.f., $p < 0.01$), threat posture ($t' = 71.25$, 10 & 65 d.f., $p < 0.01$), threat-approach ($t' = 35$, 10 & 89 d.f., $p < 0.01$), and

Figure 8. Mean and standard error of the mean frequency of occurrence per 15 min of the modal action patterns shown by the dominant fish (clear bars) and the subordinate fish (stippled bars) in 10 observations.


FREQUENCY
10
20
30
40
50
Move
Approach
Threat Posture
Threat Approach
Nip
Chase
Flee
Flatten

Modal action pattern	Duration in seconds Dominant	Subordinate	Probability
Approach	1 ± 0.2	0.9 ± 0.2	$p < 0.01$
Threat posture	7.7 ± 1.6	2 ± 0.8	$p < 0.01$
Threat approach	1.5 ± 0.4	0.8 ± 0.2	$p < 0.01$
Flatten	0	3.3 ± 1.3	$p < 0.01$

Table 1. Mean and standard error of the mean duration in seconds of the modal action patterns shown by the dominant and subordinate fish during ten observations. Significance is based on t test determination of the difference between means.

flatten ($t = 127$, 50 d.f., $p < 0.01$) were found using Student's t test.

Observations involve agonistic bouts and periods of non-agonistic motor activity. Figure 9A shows that there is a significant positive correlation ($p < 0.05$) between agonistic activity and motor activity of the dominant fish whereas the relationship between agonistic activity and motor activity of the subordinate fish is not significant. Figure 9B shows a significant positive correlation ($p < 0.05$) between the motor activity of the dominant and subordinate fish.

Sequence Analysis of Modal Action Patterns in Bouts

The sequence of occurrence of modal action patterns in agonistic bouts was not random. The sequential patterning of the modal action patterns was analysed by assembling a two act sequence table as described by Dingle (1969). The latent period between the action of one fish and the reaction of another fish is a measure of the association between the action and reaction. A latent period of 5 sec was chosen as the maximum latency between two acts in a bout. Periods longer than this were not used in the two act sequence tables. Table 2 shows the observed frequency of the sequences in 62 bouts and the values expected if the

REACTION	ACTION: Approach	Threat Posture	Threat-Approach	Nip	Flee	Chase	Flatten	Totals	Totals as percent of grand total
Move	17 13.8	12 15.4	3 10.8	0 1.8	13 6.4	0 1.4	11 6	56	23
Approach	5 3.7	1 4.2	0 2.9	0 0.5	4 1.7	0 0.4	5 1.6	15	6.
Threat Posture	15 11.3	18 12.7	9 8.9	0 1.5	0 5.3	0 1.1	4 4.9	46	18.
Threat-Approach	0 7.1	10 8	14 5.6	0 0.9	0 3.3	0 0.7	5 3.1	29	11.
Nip	0 1.7	1 1.9	4 1.4	1 0.2	0 0.8	0 0.2	1 0.8	7	2.
Flee	8 13.1	17 14.6	15 10.2	7 1.7	0 6.1	6 1.3	0 5.7	53	21.
Chase	0 2.7	0 3	0 2.1	0 0.4	11 1.3	0 0.3	0 1.2	11	4.
Flatten	15 6.2	8 6.9	2 4.8	0 0.8	0 2.9	0 0.6	0 2.7	25	10.
Totals	60	67	47	8	28	6	26	243	
Chi^2	28.4	9.9	31.9	25.6	100.7	21.7	22.5		
p	<0.01	>0.05	<0.01	<0.01	<0.01	<0.01	<0.01		

Table 2. Frequencies of two act sequences in 62 bouts. Each column corresponds to the initial action and each row to the following reaction. The observed frequencies are the first numbers given in each cell and the expected numbers are given below the observed values.

Figure 9. A. Relationship between motor activity (moves) and agonistic activity (bouts) in ten observations. The data for the dominant fish are represented by dots whereas the data for the subordinate fish are represented by circles.

The regression line for the dominant fish data (line 1) is

$Y = 20.7 + 3.5\,X$; $r = 0.62$; 9 d.f.;

$p < 0.05$.

The regression line for the subordinate fish data (line 2) is

$Y = 13.2 + 2.5\,X$; $r = 0.48$; 9 d.f.;

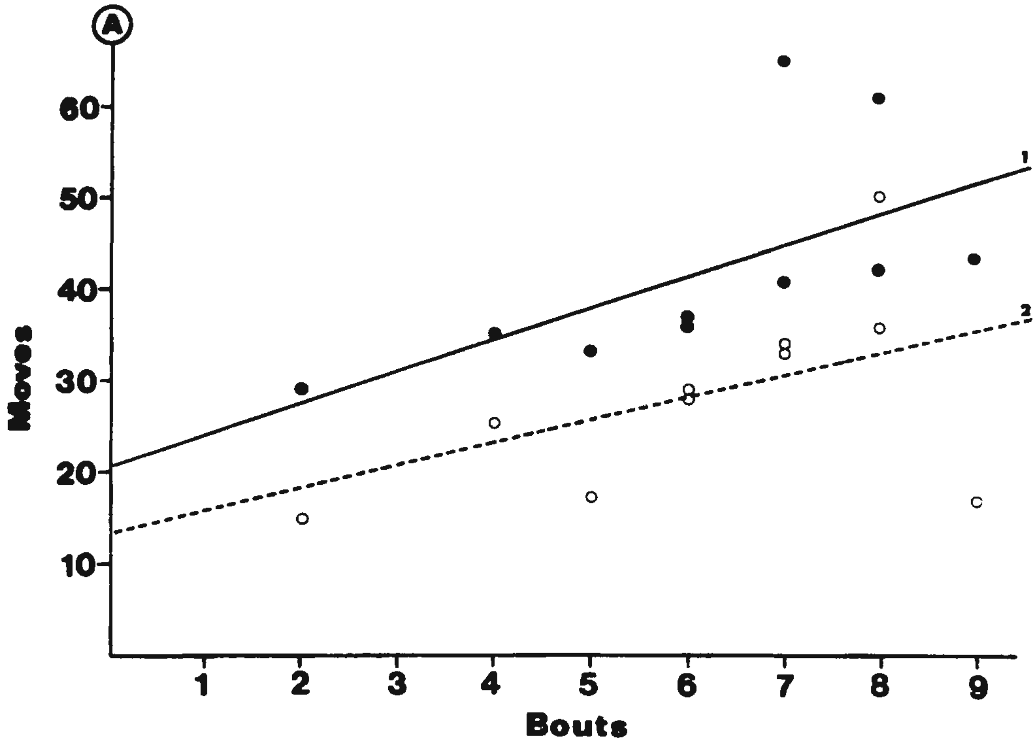
$p > 0.05$.

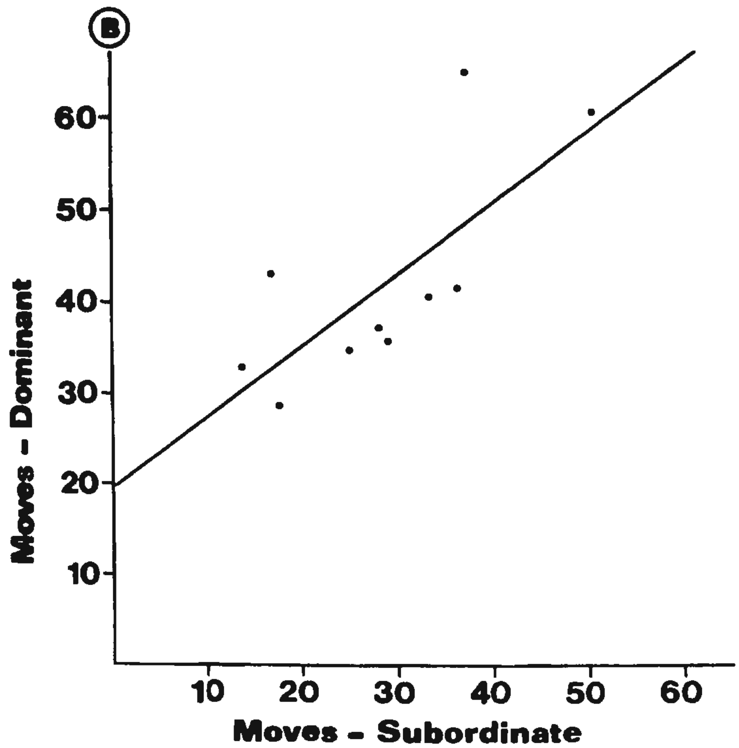
B. Relationship between motor activity (moves) of the dominant and subordinate fish in ten observations.

The regression line for the data is

$Y = 19.5 + 0.8\,X$; $r = 0.71$; 9 d.f.;

$p < 0.05$.


A
60
50
40
30
20
10
Moves
1
2
1
2
3
4
5
6
7
8
9
Bouts

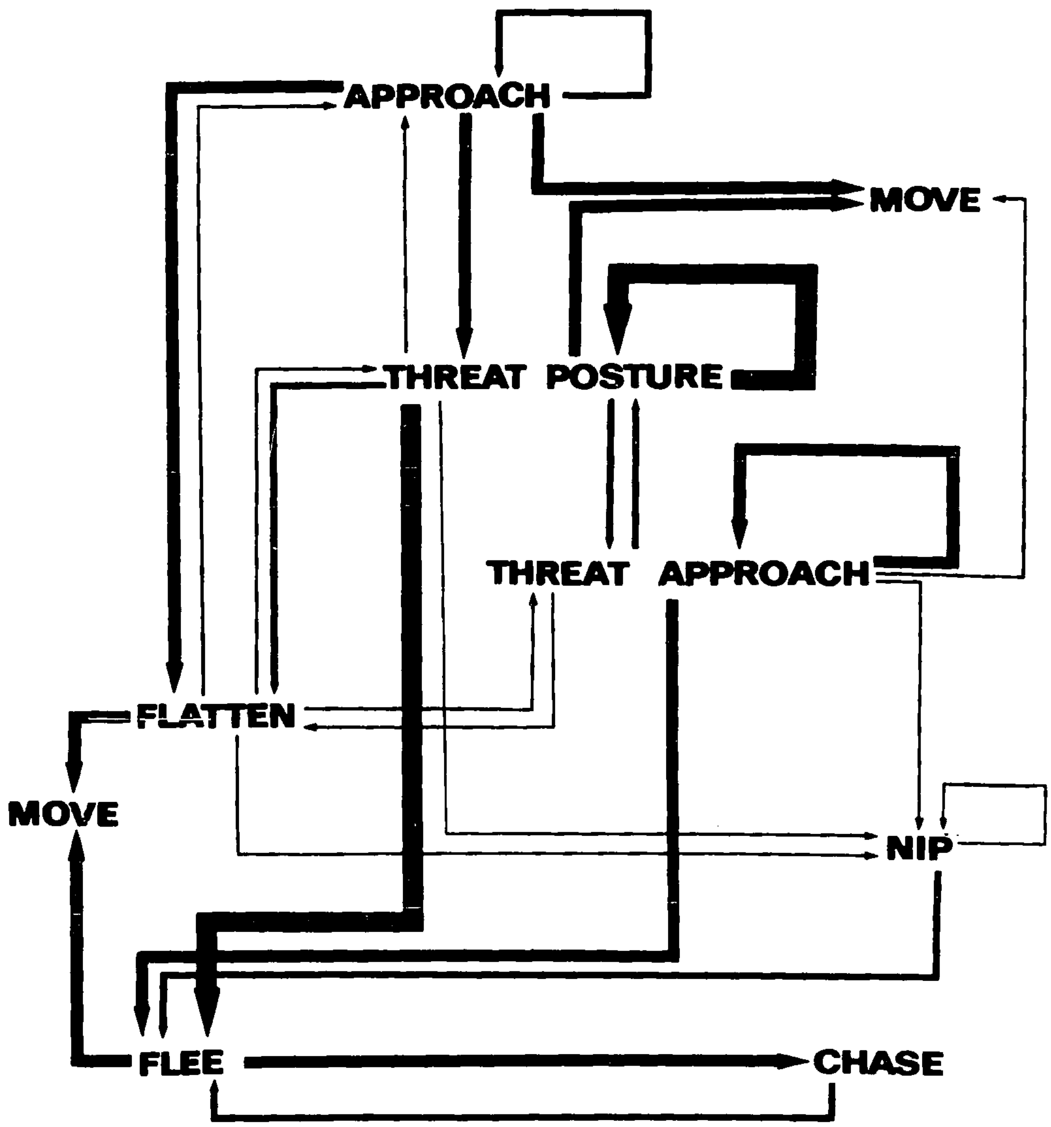

B
60
50
40
30
20
10
Moves - Dominant
10
20
30
40
50
60
Moves - Subordinate

reactions to a specific action were distributed in the same way as the total frequency distribution of the reactions. The observed and expected reaction frequency distributions were compared using Chi-square. The reaction distributions following all actions except the threat posture were significantly different ($p < 0.01$) from the expected distributions. Thus the actions of approach, threat-approach, nip, flee, chase, and flatten were followed by certain reactions. The reactions were different from that expected if the reactions were not influenced by the preceding action. Therefore, all actions, with the exception of threat posture, by one fish had a definite influence on the following reaction of the other fish. The sequence diagram assembled from these bouts is presented in Fig. 10.

MOTOR ACTIVITY LEVEL IN NOVEL SITUATION

When a fish is placed in a different tank it shows quantitative and qualitative changes in its activity as is shown in Figure 11. One hour after a fish was placed in a new tank the mean motor activity was 97.7 moves per 15 min. Subsequent mean motor activity levels were lower than the level observed in the first period. The motor activity observed in the first period consisted of the actions of walk, hop, and swim. In subsequent periods the actions of walk and hop were observed but swim occurred only rarely.

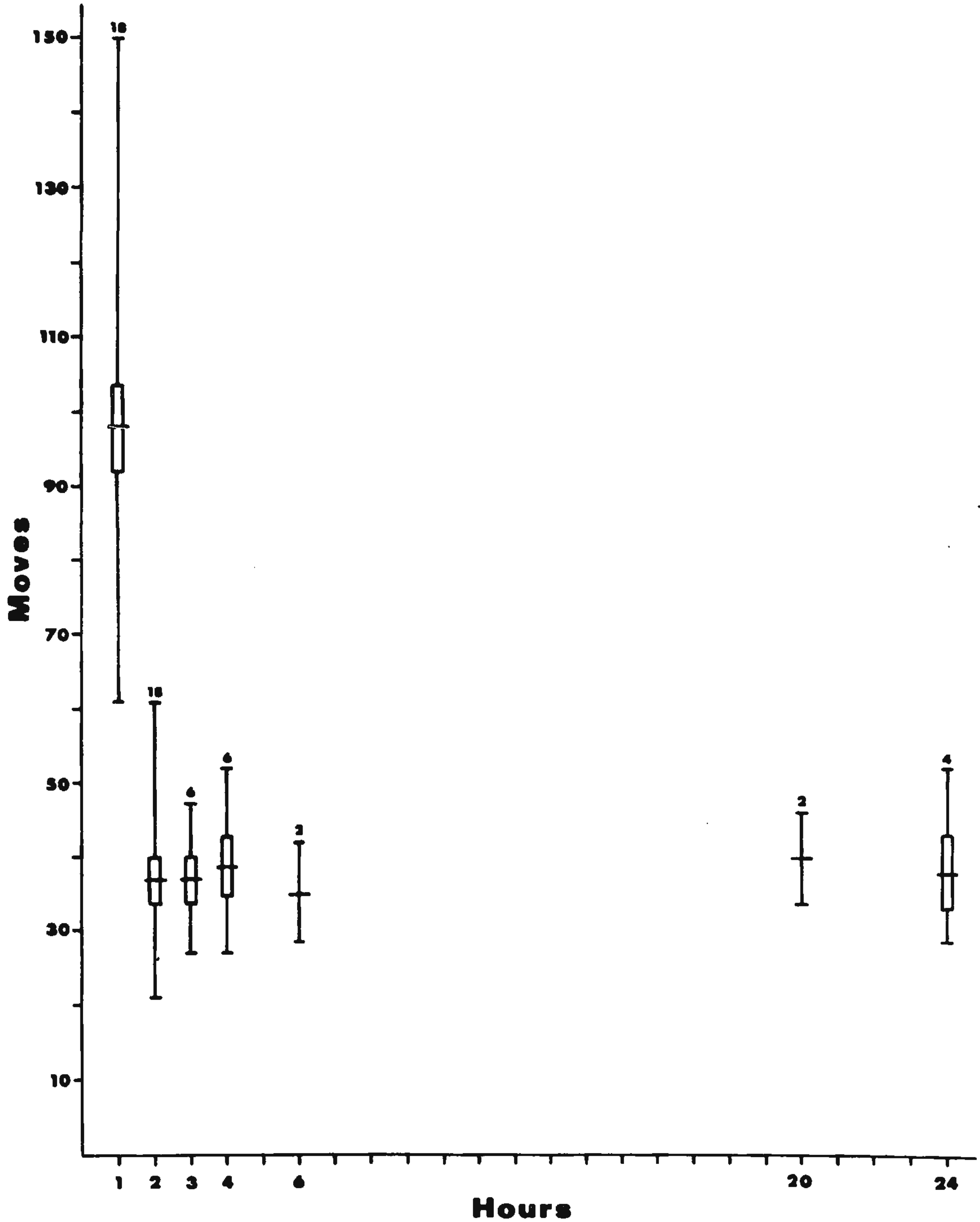
Figure 10. Agonistic sequence diagram derived from the observed values in Table 2. Thickness of the lines indicates frequency of occurrence as shown on the figure and arrowheads indicate the direction of the sequence.



Frequency Key

1-5
6-10
11-15
16-20

Figure 11. Number of moves per 15 min after different lengths of time (hours) in a tank. Mean, standard error of the mean, and range are shown for each time period with the number of fish observed in each time period shown above the upper range value.



18
18
6
6
2
2
4
150
130
110
90
70
50
30
10
Moves
1
2
3
4
6
20
24
Hours

Analysis of variance of the data for the observation periods from 2 to 24 hr indicated that the variation was insignificant ($F = 0.06$; 5&32 d.f.; $p < 0.05$). This indicates that the motor activity level does not change appreciably after the fish has been in a new tank for two hours. These observations were made during the light portion of the photoperiod, between two hours after the lights turned on and two hours before the lights turned off.

AGONISTIC ACTIVITY AND LENGTH OF ENCOUNTER

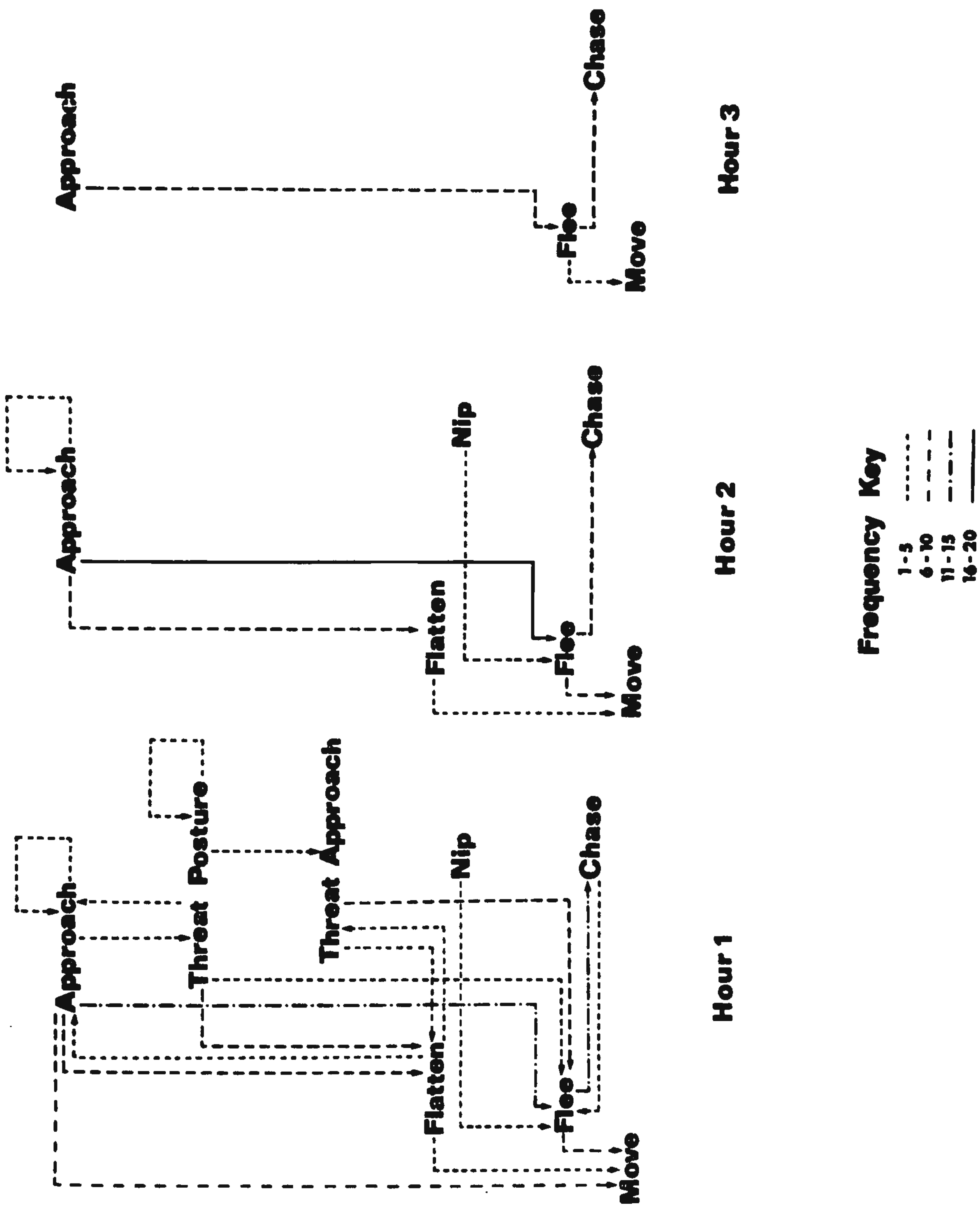
Eight pairs of fish were observed in this series of observations. Three pairs were observed after 1, 2, and 3 hr in the tank and five pairs were observed after 1 and 2 hr in the tank. Frequencies of motor activity, agonistic bouts, and agonistic modal action patterns are shown in Table 3. This shows a decreasing incidence of motor activity in both dominant and subordinate fish and a decrease in the frequency of agonistic bouts. Some of the agonistic modal action patterns also decreased in frequency.

The changes in the structuring of the agonistic bouts are seen more clearly by analysis of the sequences of the modal action patterns in the bouts during the three time periods. The sequence diagrams for hours 1, 2, and 3 are presented in Figure 12. During the bouts occurring after

	Hours after introduction		
	1	2	3
Number of observations	8	8	3
Number of bouts	4 ± 1.2	2.5 ± 0.8	1.3 ± 0.3
Dom. moves	72.8 ± 8.7	49.3 ± 6.8	36.7 ± 7.1
Sub. moves	39.6 ± 14.6	27.5 ± 6.7	20.0 ± 19.0
Dom. approach	8.7 ± 2.6	4.6 ± 1.8	3.0 ± 3.0
Sub. approach	0.5 ± 0.3	0.4 ± 0.2	0
Dom. threat posture	2.3 ± 0.9	0	0
Sub. threat posture	0.5 ± 0.4	0	0
Dom. threat approach	4.4 ± 2.1	0	0
Dom. nip	0.1 ± 0.1	0.3 ± 0.3	0
Dom. chase	1.6 ± 1.0	1.1 ± 1.1	0.9 ± 0.9
Sub. flee	4.9 ± 3.4	2.5 ± 1.4	5.0 ± 5.0
Sub. flatten	1.1 ± 0.6	1.3 ± 0.6	0

Table 3. Mean and standard error of the mean frequency of bouts, motor activity (moves) and agonistic modal action patterns occurring in 15 min observations after encounter lengths of 1, 2, and 3 hours. Dom. means dominant while sub. means subordinate.

Figure 12. Agonistic sequence diagrams for the bouts occurring after encounter lengths of 1, 2, and 3 hr. Line type indicates the frequency of occurrence of the sequences and arrowheads indicate the direction of the sequences.


Approach
Threat Posture
Threat Approach
Flatten
Nip
Flee
Chase
Move
Hour 1
Approach
Flatten
Nip
Flee
Chase
Move
Hour 2
Approach
Flee
Chase
Move
Hour 3
Frequency Key
1-5
6-10
11-15
16-20

one hour the sequences involved all the modal action patterns. In the second hour sequences there were no threat postures or threat-approaches. The third hour sequences are similar to the second hour sequences except that nip, flatten, and mutual approach were not observed.

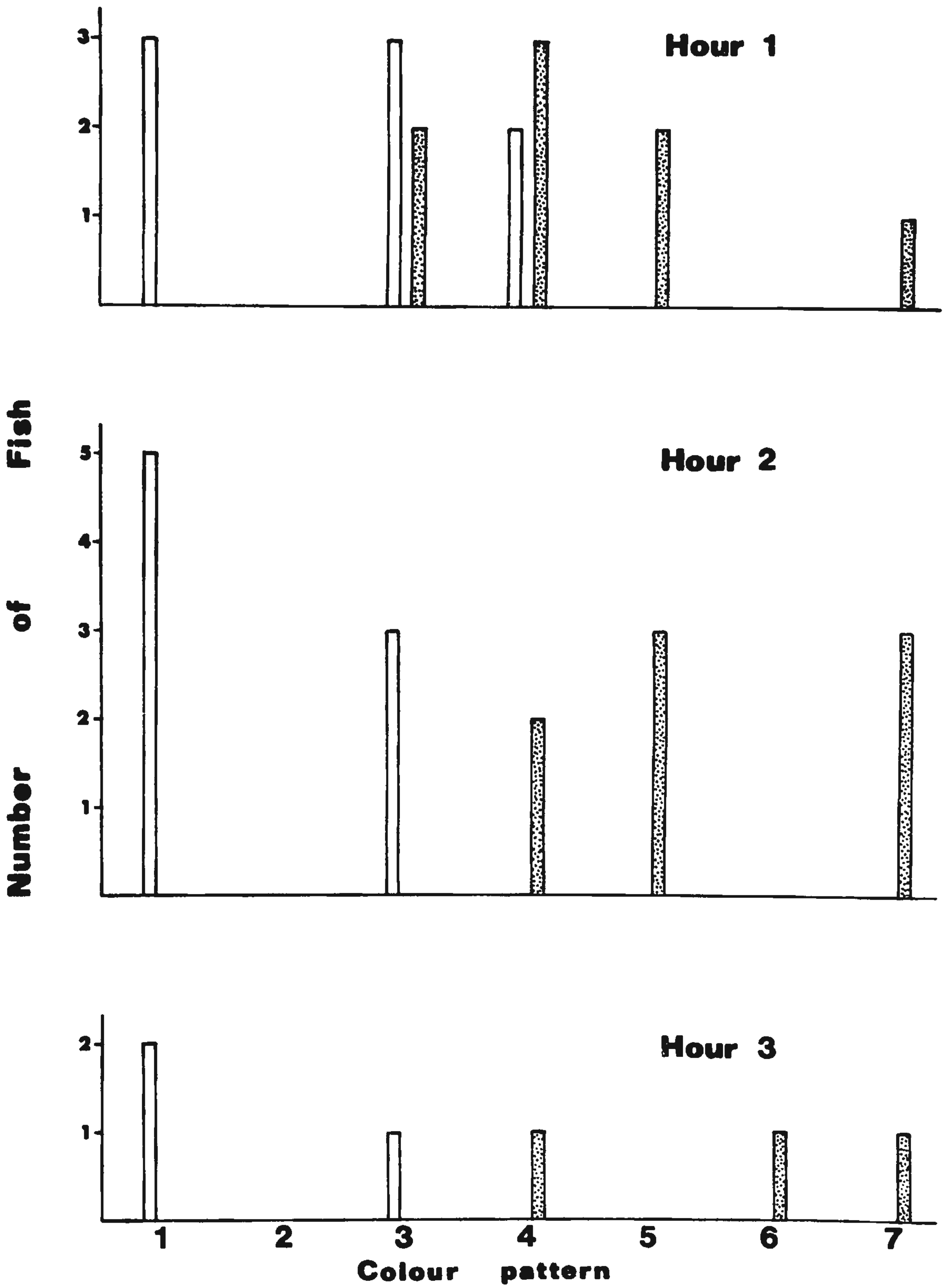
Another indication of the changes in the behaviour during the encounters is seen in the frequencies of colour patterns during the three time periods. Notes on colour were recorded at the end of each observation and the results are summarised in Figure 13. This shows a shift in the colouration of both dominant and subordinate fish away from the typical non-agonistic colour patterns (see 'Diel Activity' for description of non-agonistic colouration).

DIEL ACTIVITY

The diel activity of juvenile S. punctatus was observed in several ways. The motor activity level during the light portion of the photoperiod is indicated by the results of the section 'Motor Activity Level in Novel Situation', where approximately 35 moves per 15 min was the typical motor activity level after a fish was in a tank for two hours or longer.

The typical posture of fish during the light portion of the photoperiod is as described for the modal

Figure 13. Agonistic colour patterns of fish after encounter lengths of 1, 2, and 3 hr. The dominant fish are represented by clear bars and the subordinate fish are represented by stippled bars. Colour pattern numbers are as in Figure 7.


Hour 1
Hour 2
Hour 3
Number of Fish
Colour pattern
1 2 3 4 5 6 7

action pattern of stationary posture. The colouration during non-agonistic periods in the light portion of the photoperiod typically consists of dark or medium dorsal fin spots, absence of chin bars, and pale or medium body colour. Figure 14A is a photograph of a fish taken during a non-agonistic light period.

Night observation of fish held in the laboratory showed definite behavioural differences from the light portion of the photoperiod (Table 4). Of the 19 fish observed, none showed any movement and all assumed a typical posture and colouration. The posture is similar to the modal action pattern of flatten. The colouration consisted of pale dorsal fin spots, presence of chin bars, and medium or dark body colour. Figure 14B is a photograph of a fish taken at night.

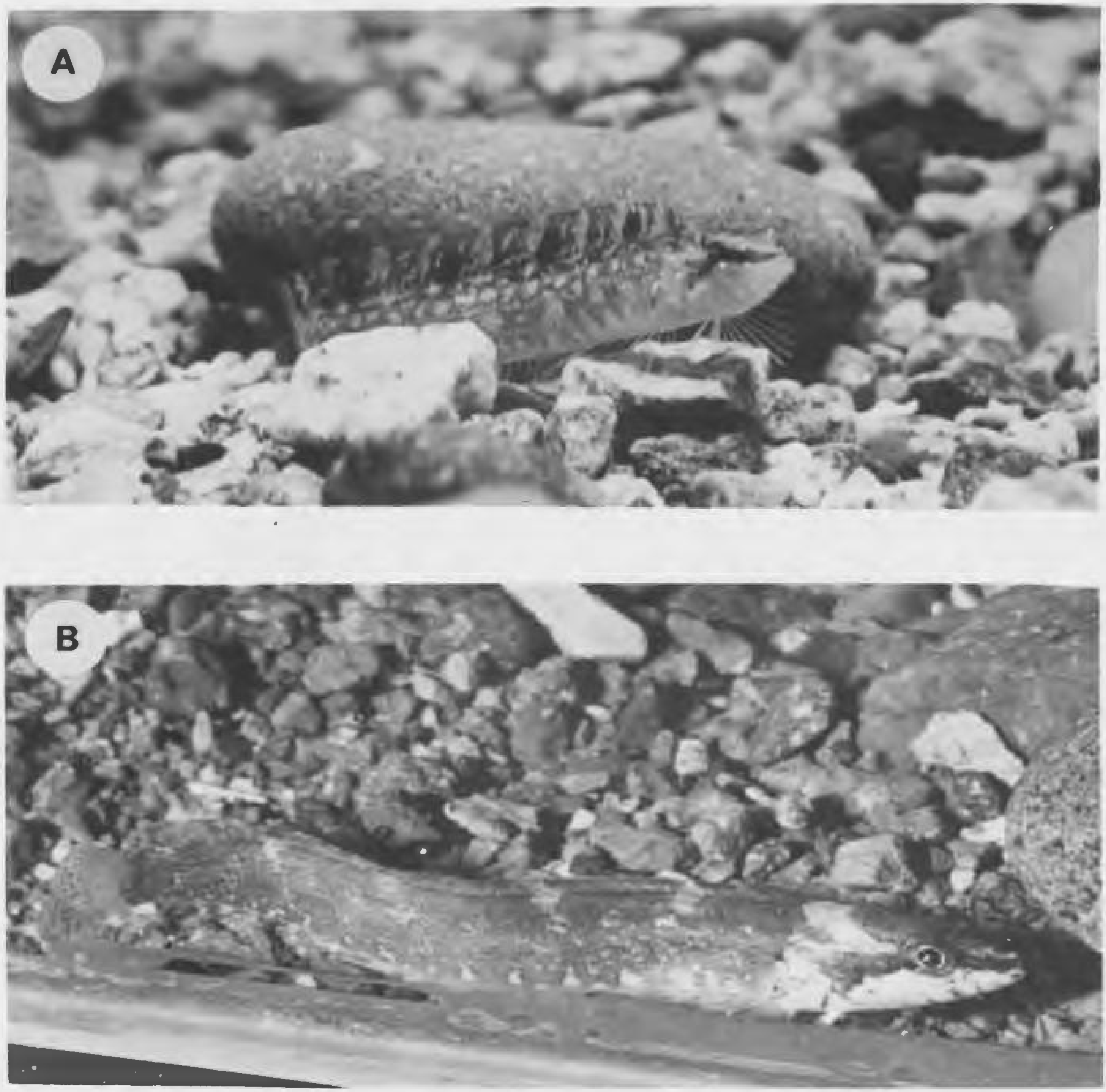
The diel activity of the fish was also observed in the field. Movement, feeding, and agonistic behaviour were observed during day dives. During night dives no fish were seen moving about but fish were observed by turning over rocks.

Further observation were made on seven fish before and after the lights turned on in the laboratory. Figure 15 shows the mean activity per fish during the 5 min before the lights turned on and during the two consecutive 5 min

Figure 14. Diel colouration and postures of juvenile *S. punctatus*.

A. Diurnal

B. Nocturnal



Observation No.	Observation Duration	No. of fish	No. of moves	Dorsal fin spots pale	Chin bars present	Body colour dark	Body colour medium	Head position down	Head position normal
1	5 min	4	0	4	4	4	0	3	1
2	5 min	3	0	3	3	3	0	3	0
3	5 min	4	0	4	4	4	0	4	0
4	5 min	4	0	4	4	3	1	3	1
5	5 min	4	0	4	4	4	0	4	0
Totals	25 min	19	0	19	19	18	1	17	2

Table 4. Nocturnal observations of motor activity (moves), colouration and head position.

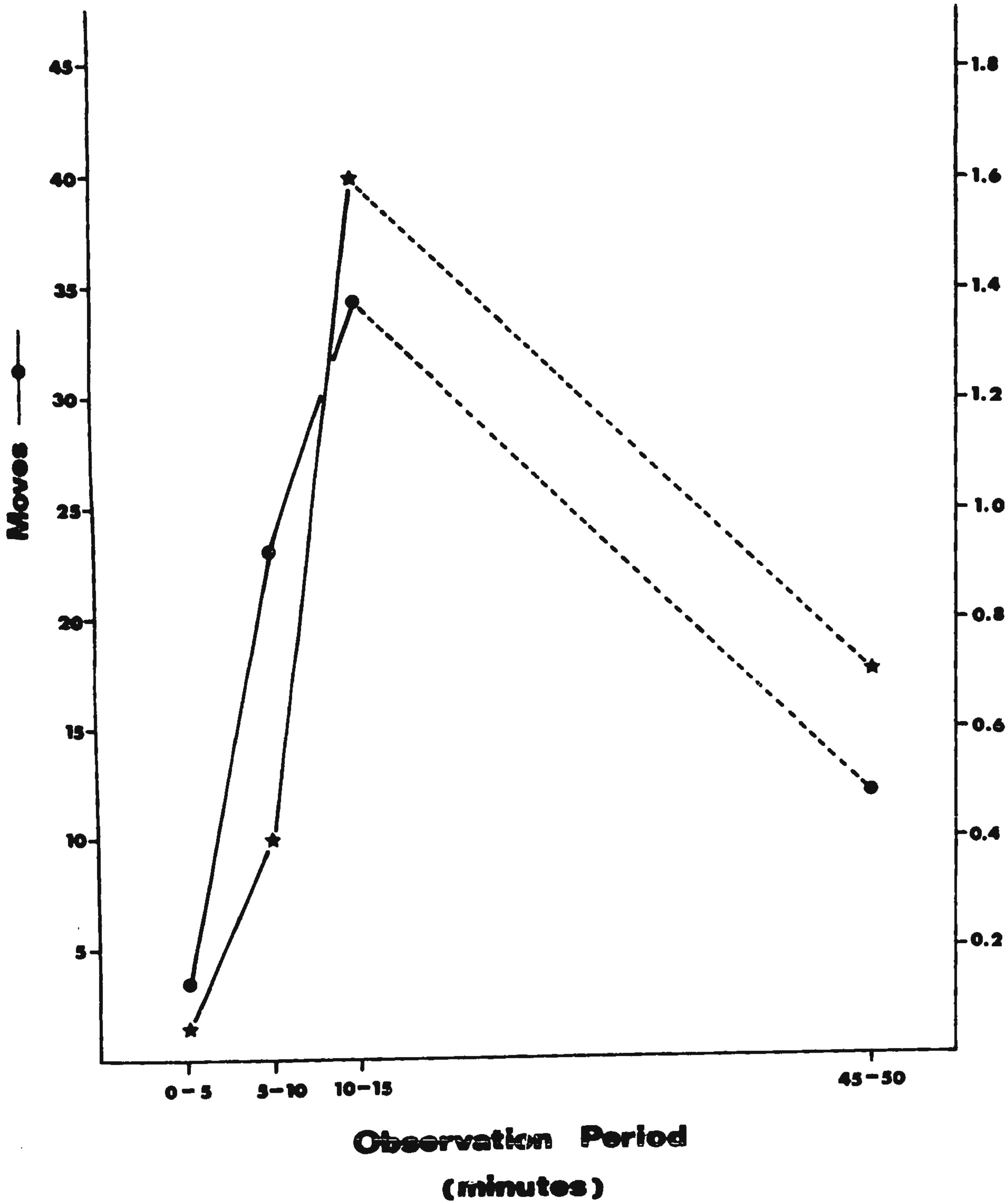
periods after the lights turned on. Both the motor activity level and the agonistic activity level increased after the lights came on. Student's t tests showed differences between adjacent mean values of motor activity and also between adjacent mean values of agonistic activity. The mean motor activity levels in the first two periods were significantly different ($t = 15.97$, 6 d.f., $p < 0.01$) as were the levels in the second and third periods ($t = 5.88$, 6 d.f., $p < 0.01$). The mean agonistic activity levels in the first two periods were significantly different ($t = 3.52$, 6 d.f., $p < 0.05$) as were the levels in the second and third periods ($t = 4.17$, 6 d.f., $p < 0.01$). Two observations of the agonistic activity level of the seven fish were made 40 min after the lights came on. The mean value for this period is shown in Fig. 15. The motor activity mean value for this period was obtained by dividing the typical motor activity level of 35 moves per 15 min by three to give the level in a 5 min period.

SIGNALS IN AGONISTIC BEHAVIOUR

Partitioned Tanks

Records were made of the motor activity and the agonistic modal action patterns observed in the bouts in each partition series. The frequency and duration data are shown in Table 5. Analysis of variance and least significant

Figure 15. Dawn observations of motor activity (moves) and agonistic activity (bouts) per fish per 5 min period. Dotted lines indicate that observations were not done in the 5 min periods between the joined values.


45
40
35
30
25
20
15
10
5
Moves
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
Bouts
0-5
5-10
10-15
45-50
Observation Period
(minutes)

	Partition 1	Partition 2	Partition 3	Partition 4
No. of observations	10	5	10	5
Bout frequency	3.1 ± 0.5*	0**	7.1 ± 1.8***	0**
- agonistic	6.7 ± 1.3*	0**	4.6 ± 1.3*	0**
- non-agonistic				
Move frequency	25.8 ± 3*	33.2 ± 1.8*	46.4 ± 4.5**	33.8 ± 1.8*
Move duration	0.9 ± 0.8*	0.7 ± 0.1*,**	0.6 ± 0.1**	0.6 ± 0.1*,**
Approach frequency	6.5 ± 1.7*	0**	8.4 ± 1*	0**
Approach duration	0.7 ± 0.1*	0**	0.6 ± 0.1*	0**
Threat posture frequency	2.8 ± 0.7*	0*	5.8 ± 1.2**	0*
Threat posture duration	8 ± 1.3*	0**	12.5 ± 2.7*	0**
Threat approach frequency	2.3 ± 0.9*,**	0*	4.7 ± 1.6**	0*
Threat approach duration	1 ± 0.3*	0**	0.5 ± 0.1*,**	0**
Nip frequency	1.1 ± 0.3*,**	0*	3.1 ± 1.1**	0*
Flatten frequency	0.3 ± 0.2*	0*	0.5 ± 0.2*	0*
Flatten duration	1.9 ± 1.7*	0*	5.1 ± 4.4*	0*

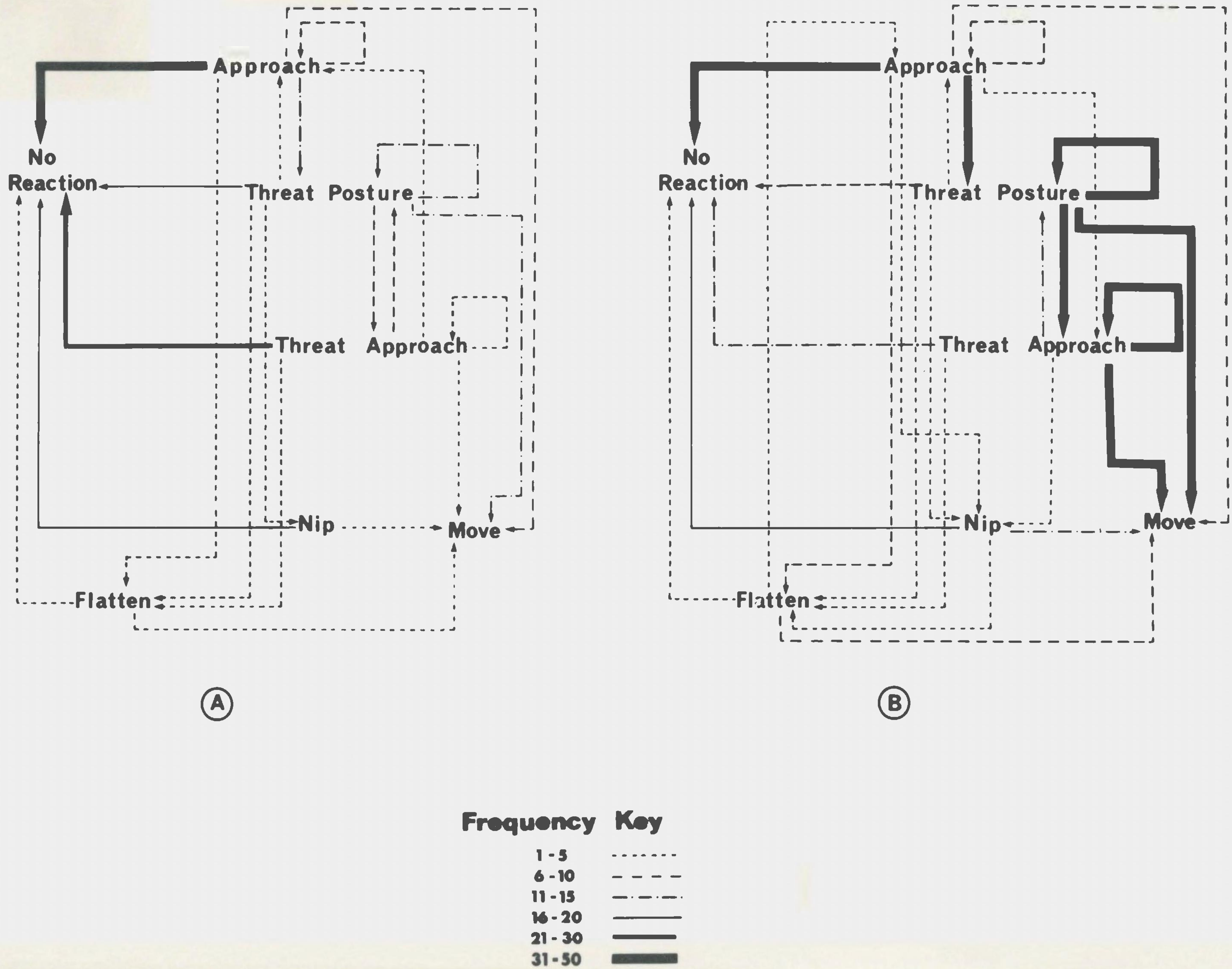
difference (l.s.d.) between means showed that the mean motor activity levels of the fish in series 1, 2, and 4 were not significantly different whereas the mean motor activity level in series 3 was significantly different from those in series 1 (l.s.d. = 12.1, 59 d.f., $p < 0.01$), 2 (l.s.d. = 11.1, 59 d.f., $p < 0.05$), and 4 (l.s.d. = 11.1, 59 d.f., $p < 0.05$). The average duration of move was significantly different between series 1 and 3 (l.s.d. = 0.22, 59 d.f., $p < 0.05$).

In series 2 and 4 no bouts were observed. In series 1 and 3 a significantly different (l.s.d. = 3.1, 29 d.f., $p < 0.01$) mean number of agonistic bouts occurred. The numbers of non-agonistic bouts in series 1 and 3, i.e. bouts in which no reactions were observed, were not different.

The frequency and duration of agonistic modal action patterns in series 1 and 3 were similar. There was, however, a significant difference (l.s.d. = 2.3, 59 d.f., $p < 0.05$) in the mean frequency of threat postures in the two series.

The sequence diagrams assembled from the bouts in series 1 and 3 are shown in Figure 16. Chi-square contingency table analysis of the sequences in the two series showed significant differences. There were insignificant differences in the reactions following the actions of nip ($\chi^2 = 5.57$,

Figure 16. Agonistic sequence diagrams for bouts occurring in tanks containing partitions 1 (A) and 3 (B). Line type indicates frequency of occurrence and arrowheads indicate the direction of the sequence.


Approach
No
Reaction
Threat Posture
Threat Approach
Nip
Move
Flatten
A
Approach
No
Reaction
Threat Posture
Threat Approach
Nip
Move
Flatten
B
Frequency Key
1 - 5
6 - 10
11 - 15
16 - 20
21 - 30
31 - 50

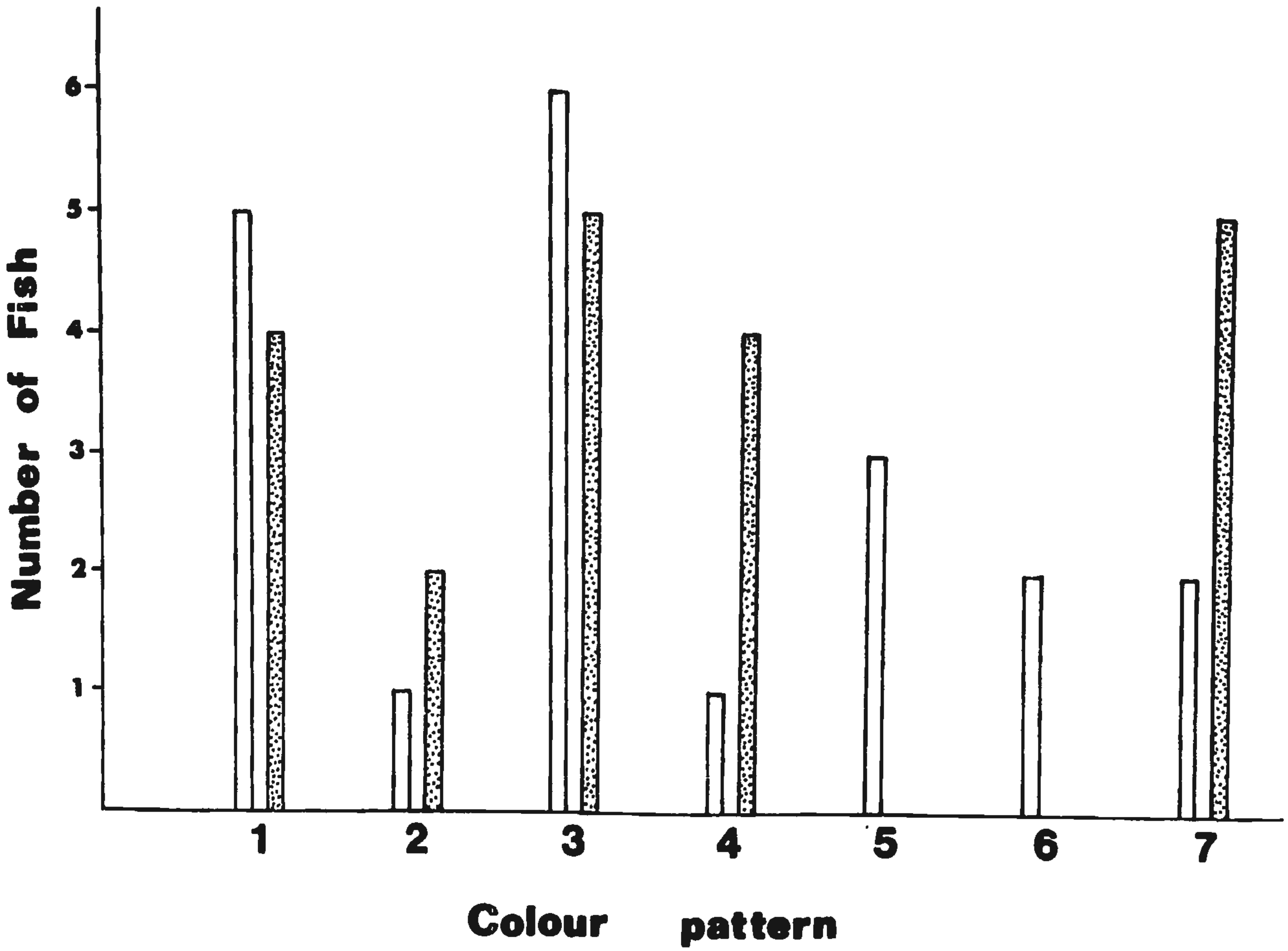
4 d.f., $p > 0.05$) and flatten ($\chi^2 = 0.83$, 2 d.f., $p > 0.05$) whereas significant differences ($p < 0.01$) were found for the reactions following the actions of approach ($\chi^2 = 16.95$, 6 d.f.), threat posture ($\chi^2 = 28.54$, 6 d.f.), and threat-approach ($\chi^2 = 41.95$, 5 d.f.).

The colouration of the fish in series 1 and 3 were recorded at the end of each observation and these results are shown in Figure 17. Chi-square contingency table analysis revealed that the frequency distributions of the colour patterns in the two series were not significantly different ($\chi^2 = 8.8$, 6 d.f., $p > 0.05$).

Models

Table 6 summarises the series of observations involving models. A total of 120 presentations of models were made to 12 fish. The frequencies of the responses to the three models were analysed by a Chi-square contingency table. There is a significant difference ($\chi^2 = 37.45$, 6 d.f., $p < 0.01$) in the ratios of responses shown to the three models. The number of approach responses made to the three models were not different ($\chi^2 = 1.54$, 2 d.f., $p > 0.05$). Model 1 elicited a high number of withdrawal responses and a low number of no reaction responses ($\chi^2 = 14$, 3 d.f., $p < 0.01$). Responses to Model 2 did not differ from the

Figure 17. Agonistic colour pattern frequencies observed in tanks containing partitions 1 (clear bars) and 3 (stippled bars).
Colour pattern numbers are as in Figure 7.


Number of Fish
1
2
3
4
5
6
Colour pattern
1
2
3
4
5
6
7

	Approach	Aggression	Withdrawal	No Reaction	Totals
Model 1	14	9	11	5	40
Model 2	13	12	4	11	40
Model 3	12	2	0	26	40
Totals	39	23	15	42	120

Table 6. Response frequencies to the three models.

overall response distribution (χ^2 = 3.2, 3 d.f., $p > 0.05$). Model 3 elicited a low number of aggression responses, a low number of withdrawal responses, and a high number of no reaction responses (χ^2 = 20.25, 3 d.f., $p < 0.01$).

Conspecific Seawater

In the first part of this investigation observations were made during the 5 min period before and the 5 min period after 100 ml of conspecific inhabited seawater was introduced into the tank. The data are shown in Table 7. The two mean values are similar and no analysis of these results was made. Colouration of the fish did not change greatly and no shift away from the typical non-agonistic colour patterns was evident.

The second part of the investigation involved the introduction of seawater and seawater containing a scraping of epidermis from a conspecific. Motor activity and colouration data are presented in Table 8. The mean number of moves are similar and no analysis was made. The colouration changes were not marked and no shift away from non-agonistic colour patterns was evident.

Fish number	Moves before introduction	Moves after introduction	Colour before introduction	Colour after introduction
1	6	9	5	5
2	10	8	4	4
3	7	11	6	4
4	12	14	5	4
5	9	6	3	3
6	13	11	5	5
7	8	13	6	4
8	11	15	5	4
9	14	10	5	5
10	7	9	4	4
Mean	9.7	10.6		
Standard error	± 0.9	± 0.9		

Table 7. Motor activity (moves) and colour pattern before and after the introduction of conspecific inhabited seawater. Colour pattern numbers as described in Figure 7.

Fish number	Motor activity in periods			Colouration in periods		
	1	2	3	1	2	3
1	10	11	13	5	4	5
2	12	9	7	4	4	4
3	9	8	11	4	5	5
4	13	14	11	6	4	4
5	12	12	14	5	5	4
6	11	9	12	5	5	5
7	10	13	9	5	4	4
8	12	17	11	3	3	3
9	13	11	16	4	5	5
10	14	12	13	5	5	4
Mean	11.5	11.6	11.7			
Standard error	± 0.5	± 0.9	± 0.8			

Table 8. Motor activity (moves) colour patterns before the introduction of 10 ml of seawater (period 1); before the introduction of 10 ml of seawater containing a scraping of conspecific epidermis (period 2); and after the introduction of the seawater containing conspecific epidermis scraping (period 3). Colouration numbers as described in Figure 7.

Mirror

All 10 test fish showed agonistic activity within 3 min after the mirror was placed in the tank. Approach, threat posture, and threat-approach were observed. All fish showed changes in colouration typical of dominant fish, i.e. the dorsal fin spots darkened and the chin bars, if present, blanched. Threat posture followed the first approach to the mirror in all fish.

AGONISTIC BEHAVIOUR AND AVAILABLE SPACE

These observations involved pairs of fish placed in two different tanks. The bottom area of the smaller was 550 cm^2 and that of the larger was 1075 cm^2.

Figure 18 shows a more or less constant level of motor activity during the encounters in the larger tank ($\overline{X}$ = 28.2). Not more than one bout occurred per 15 min (Fig. 19) and, as is shown in Figure 19B, dominance was not restricted to one individual during the encounter. Individuals did, however, achieve dominance in a single bout. In the smaller tank one fish was always dominant and the other fish was subordinate. The level of motor activity of the dominant fish ($\overline{X}$ = 40.4) was always higher than that of the subordinate fish ($\overline{X}$ = 17.6), see Fig. 20, A and B, and the dominant fish did not show the reduction

Figure 18. Motor activity (moves) of the individual fish in the two pairs in the larger tank in daily 15 min periods of observation. The individual fish in pairs 1 (A) and 2 (B) are indicated with fish 1 of each pair represented by the clear bars and fish 2 of each pair represented by the black bars.

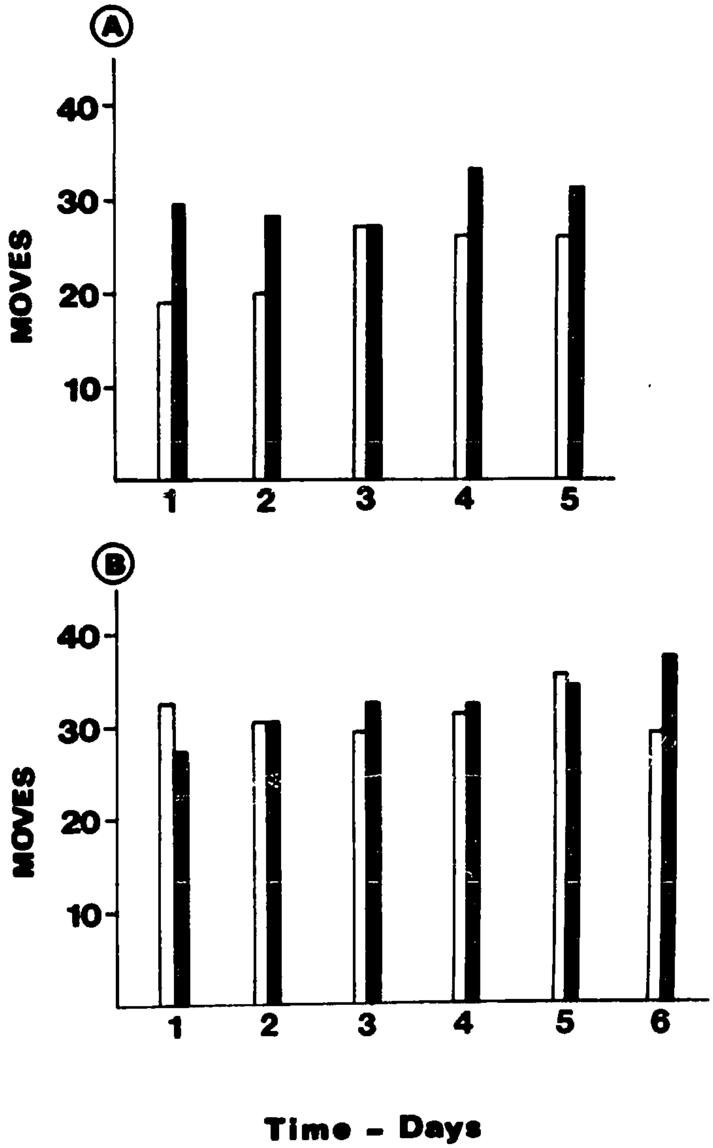
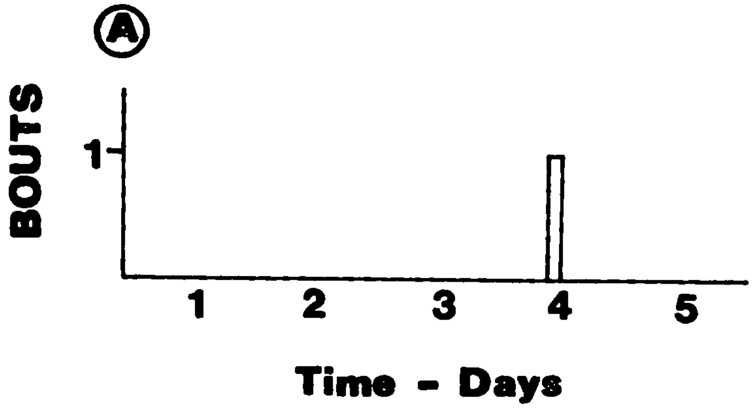
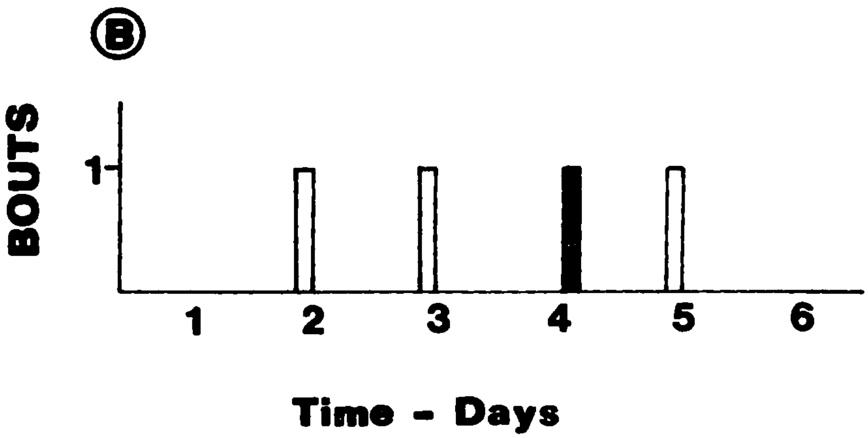

A
MOVES
40
30
20
10
1
2
3
4
5
B
MOVES
40
30
20
10
1
2
3
4
5
6
Time - Days

Figure 19. Agonistic activity (bouts) of the individual fish in the two pairs in the larger tank in daily 15 min periods of observation. The individual fish in pair 1 (A) and pair 2 (B) are represented as in Figure 18. Only the dominant individual in a bout is shown.


A
BOUTS
1
1
2
3
4
5
Time - Days

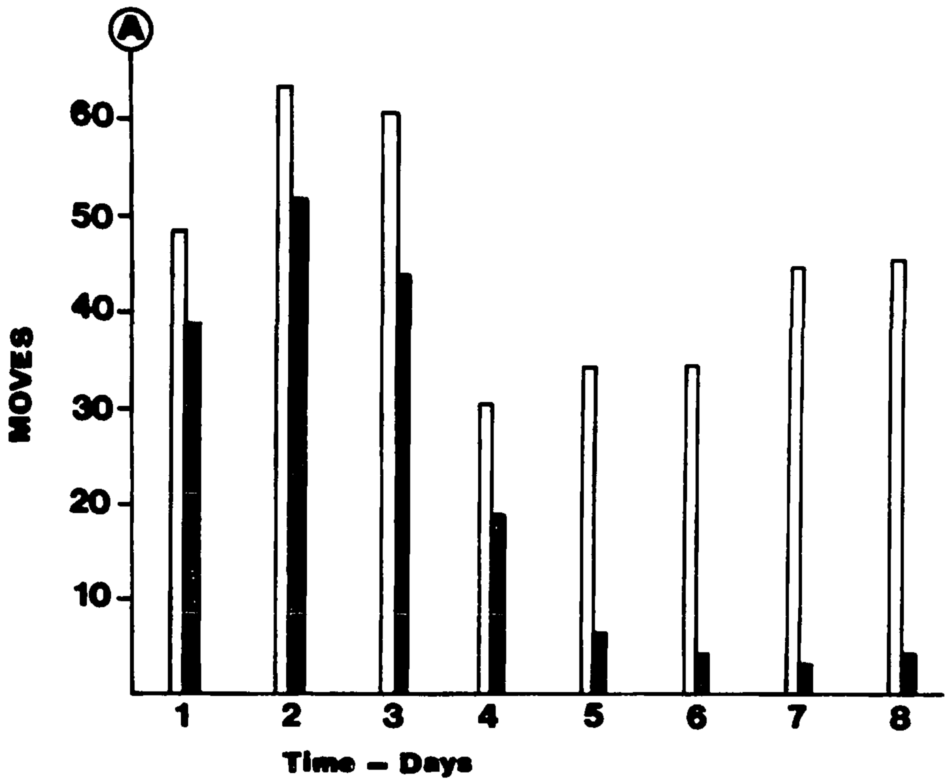

B
BOUTS
1
1
2
3
4
5
6
Time - Days

in motor activity level seen in the subordinate fish. The mean agonistic activity levels of the fish in the smaller tank ($\overline{X}$ = 3.7), see Figures 20 and 21, differed from the levels in the larger tank ($\overline{X}$ = 0.45). The mean levels of agonistic activity in the two tanks were significantly different (t' = 5.7; 10& 13 d.f.; $p < 0.01$). The mean level of motor activity of the dominant fish was significantly different (t' = 3.43; 13 & 21 d.f.; $p < 0.01$) from the mean motor activity level in the larger tank as was the mean level of motor activity of the subordinate fish (t' = 2.44; 13 & 21 d.f.; $p < 0.05$).

Figure 22A shows an insignificant relationship between the motor activity level of the two pairs in the larger tank either singly or combined. A significant positive correlation ($p < 0.01$) was found between the motor activity levels of the dominant and the subordinate fish in the smaller tank (Figure 22B). The data for pair 1 were positively correlated ($p < 0.05$) whereas the data for the second pair were insignificant.

Figure 23, A and B shows an insignificant relationship between agonistic and motor activity levels of the pairs in the larger tank either singly or combined. Figure 24A shows a significant positive correlation ($p < 0.05$) between agonistic and motor activity levels of the dominant fish in the smaller tank. The data for the dominant fish

Figure 20. Motor activity (moves) of the individual fish in the two pairs in the smaller tank in daily 15 min periods of observation. The individual fish in pair 1 (A) and pair 2 (B) are indicated with the dominant fish of each pair being represented by the clear bars and the subordinate fish of each pair represented by the black bars.


A
60
50
40
30
20
10
MOVES
1
2
3
4
5
6
7
8
Time — Days

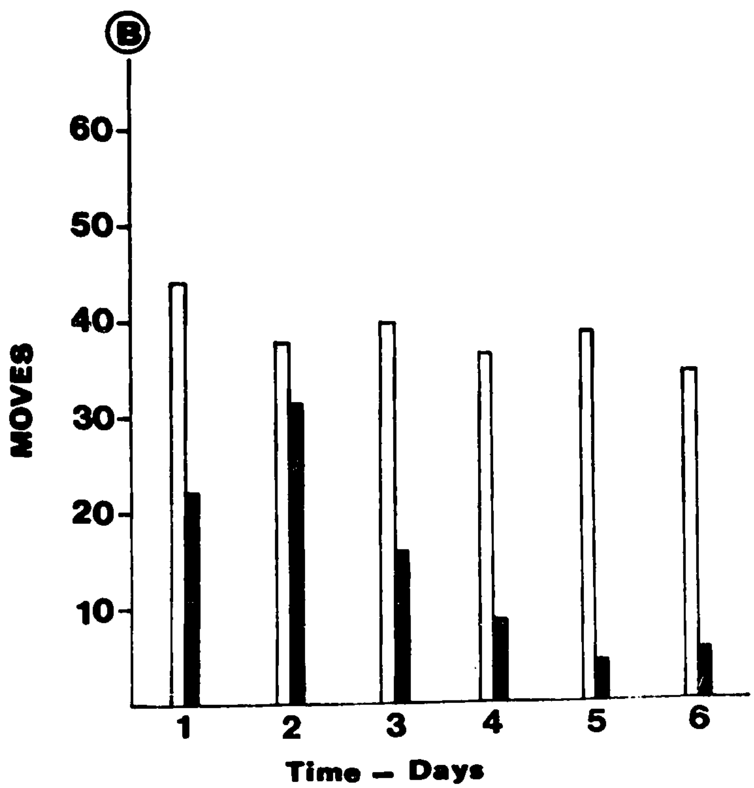

B
60
50
40
30
20
10
MOVES
1
2
3
4
5
6
Time — Days

Figure 21. Agonistic activity (bouts) of the individual fish in the two pairs in the smaller tank in daily 15 min periods of observation. The individual fish in pair 1 (A) and pair 2 (B) are represented as in Figure 20. Only the dominant individual in each bout is shown.

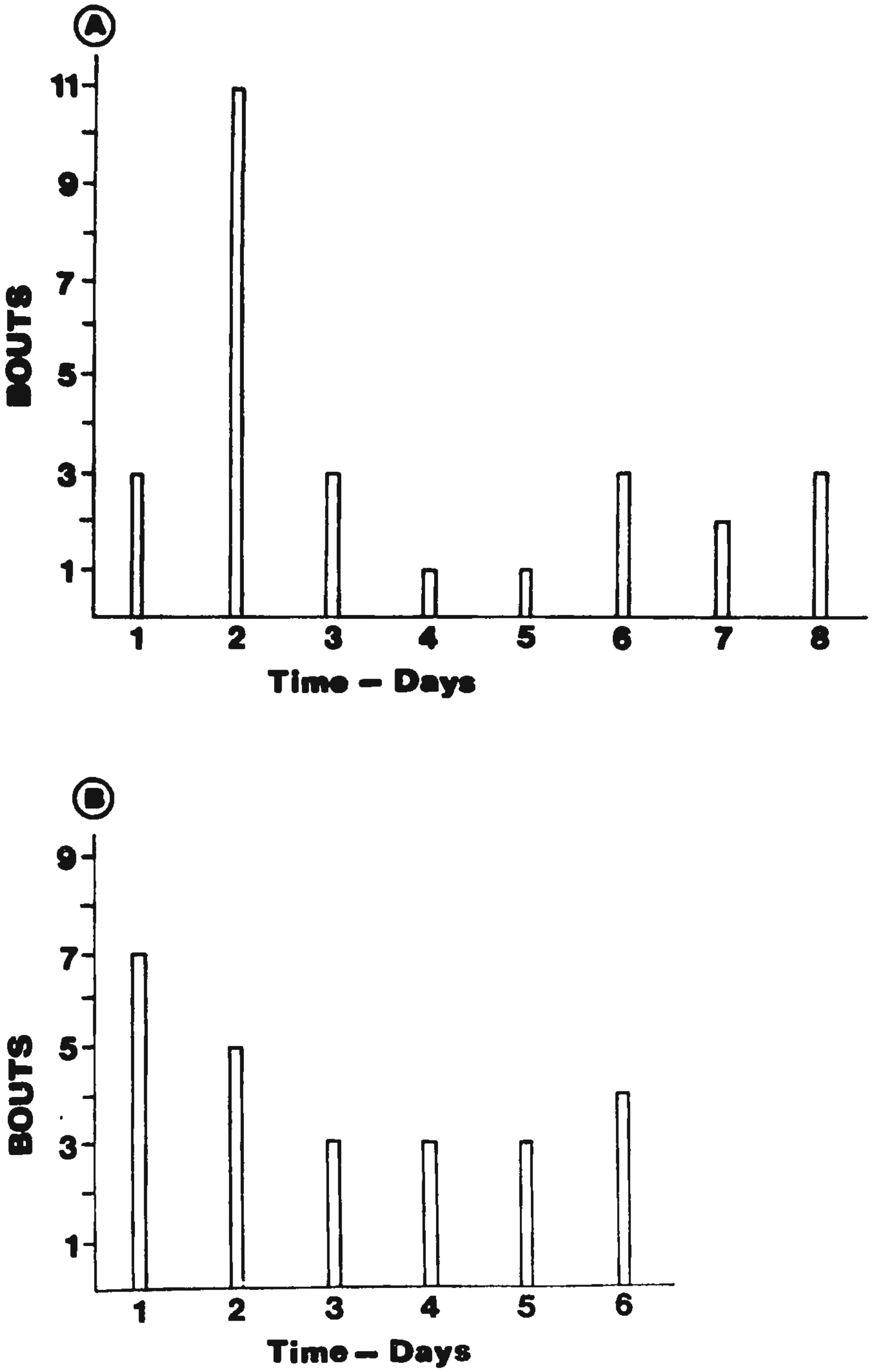

A
BOUTS
11
9
7
5
3
1
1
2
3
4
5
6
7
8
Time — Days
B
BOUTS
9
7
5
3
1
1
2
3
4
5
6
Time — Days

Figure 22. A. Relationship between the motor activity (moves) of fish 1 and fish 2 in the larger tank. Pair 1 fish are represented by the square while pair 2 fish are represented by the dot in this and succeeding figures of this type.

The regression line for the combined data is

$Y = 8.7 + 0.6\ X;\ r = 0.4;\ 10$ d.f.; $p > 0.05$.

B. Relationship between the motor activity (moves) of the dominant and subordinate fish in the smaller tank. Pair 1 and 2 fish are represented as in Fig. 22A.

The regression line for the combined data is

$Y = 33 + 0.4\ X;\ r = 0.73;\ 13$ d.f.; $p < 0.01$.

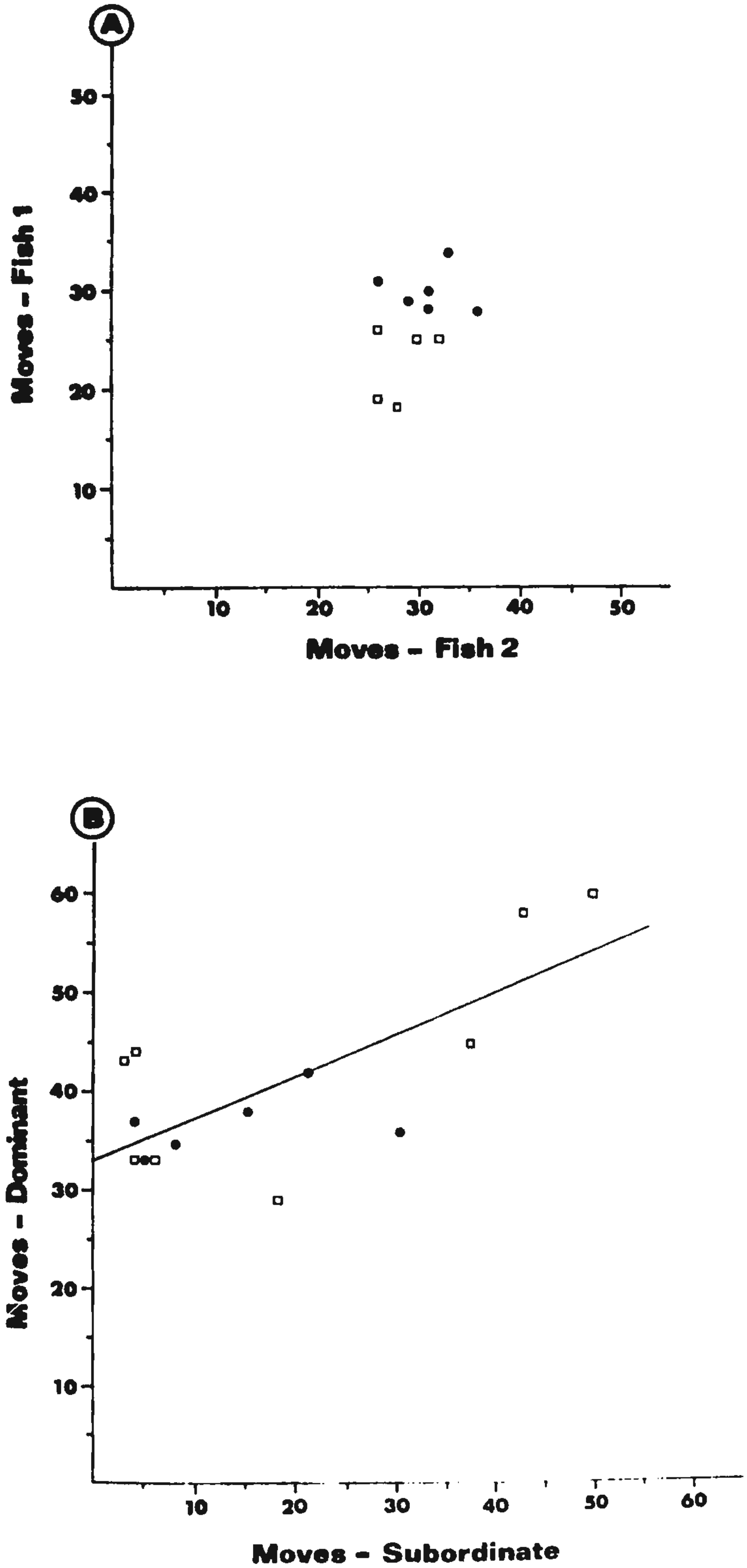

A
Moves - Fish 1
Moves - Fish 2
50
40
30
20
10
10
20
30
40
50
B
Moves - Dominant
Moves - Subordinate
60
50
40
30
20
10
10
20
30
40
50
60

Figure 23. A. Relationship between the motor activity (moves) of fish 1 and the number of agonistic bouts in the larger tank. Pair 1 and 2 fish are represented as in Fig. 22A.

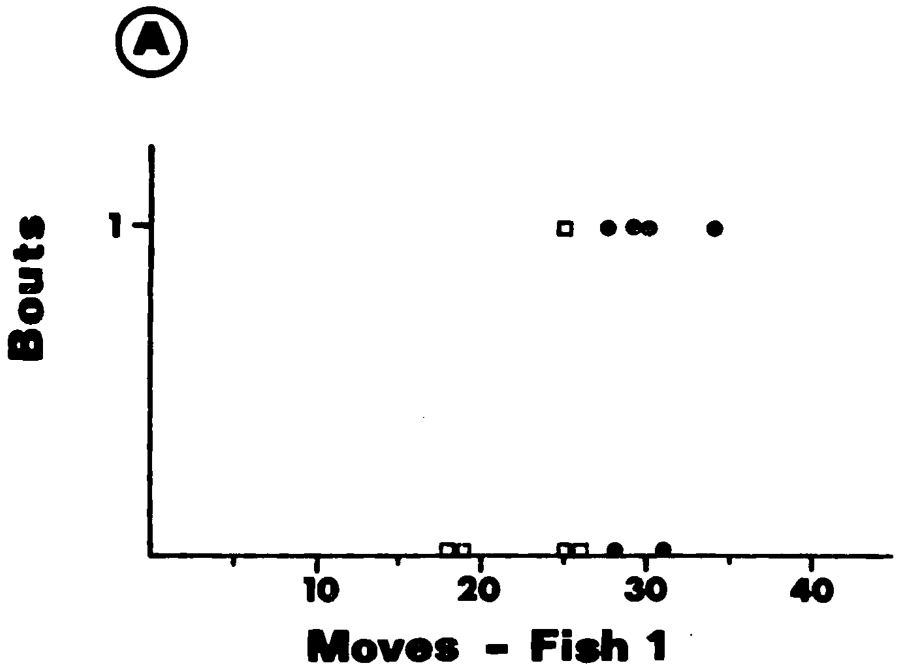
The regression line for the combined data is

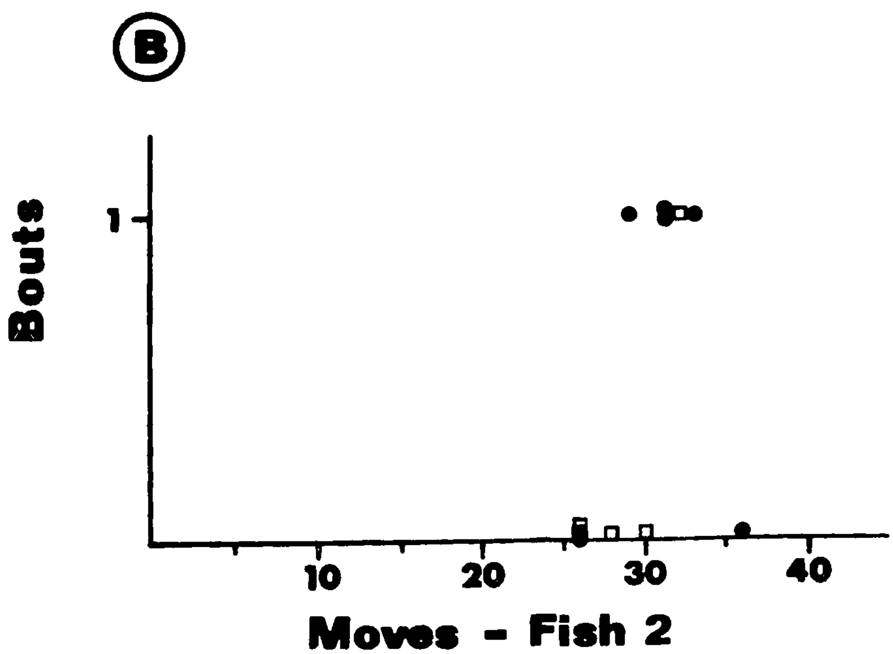
$Y = -1 + 0.06\ X$; $r = 0.51$; 10 d.f.; $p > 0.05$

B. Relationship between the motor activity (moves) of fish 2 and the number of agonistic bouts in the larger tank. Pair 1 and 2 fish are represented as in Fig. 22A.

The regression line for the combined data is

$Y = -24 + 0.9\ X$; $r = 0.46$; 10 d.f.; $p > 0.05$


A
Bouts
1
10
20
30
40
Moves - Fish 1


B
Bouts
1
10
20
30
40
Moves - Fish 2

in pair 1 are correlated ($p < 0.05$) whereas the data for pair 2 are not correlated. A significant positive correlation ($p < 0.05$) was found between the agonistic and motor activity levels of the subordinate fish in the smaller tank (Fig. 24B). The data for the subordinate fish in pairs 1 and 2, taken singly, were insignificant.

Chi-square analysis of the data shown in Figure 25 was made. The expected occupation value was based on the assumption that each quadrate is occupied equally by the paired individuals. The observed occupation of the quadrates by all four fish was significantly different ($\chi^2 > 110$, 13 d.f., $p < 0.01$) from the expected equal occupation values. Chi-square analysis of the occupation of the quadrates which individual fish inhabited was also made. The expected values were based on the assumption that occupaiton of those quadrates which individuals inhabited was equal. The observed occupation by all four fish was significantly different ($\chi^2 > 34$, 5 - 8 d.f., $p < 0.01$) from the expected distribution. Chi-square analysis of the data in Figure 26 was done. Occupation by the dominant fish in pair 1 and by both fish in pair 2 was not different ($\chi^2 < 8.1$, 4 d.f., $p > 0.05$) from that expected if habitation of the quadrates were equal. Occupation of the quadrates by the subordinate fish in pair 1 was significantly different ($\chi^2 = 16.4$, 4 d.f., $p < 0.01$) from the expected equal habitation.

Figure 24. A. Relationship between the motor activity (moves) of the dominant fish and the number of agonistic bouts in the smaller tank. Pairs 1 and 2 are represented as in Fig. 22A.

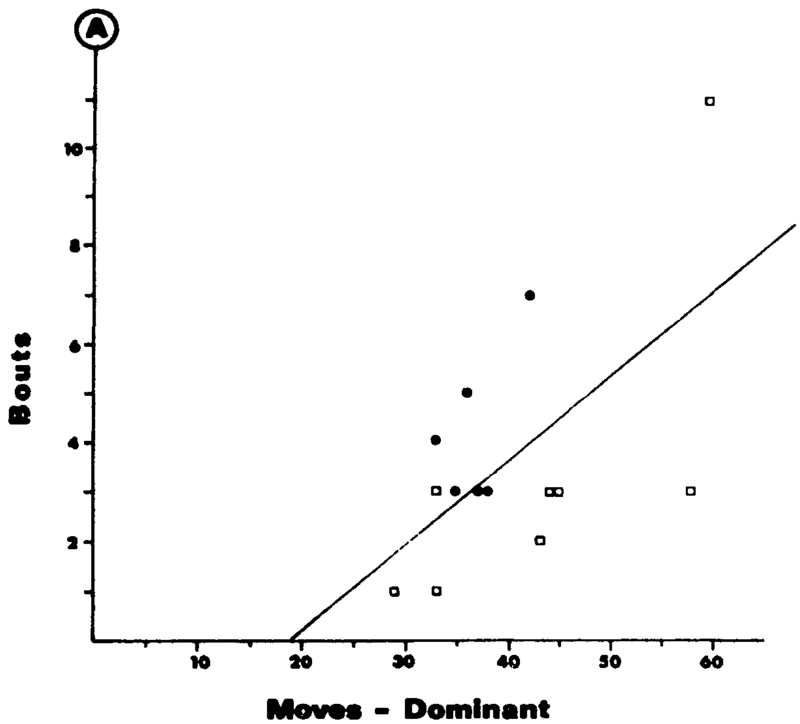
The regression line for the combined data is

$Y = -3.2 + 0.2 X$; $r = 0.59$; 13 d.f.; $p < 0.05$.

B. Relationship between the motor activity (moves) of the subordinate fish and the number of agonistic bouts in the smaller tank. Pairs 1 and 2 are represented as in Fig. 22A.

The regression line for the combined data is

$Y = 1.9 + 0.1 X$; $r = 0.59$; 13 d.f.; $p < 0.05$.


A
Bouts
10
8
6
4
2
10
20
30
40
50
60
Moves - Dominant

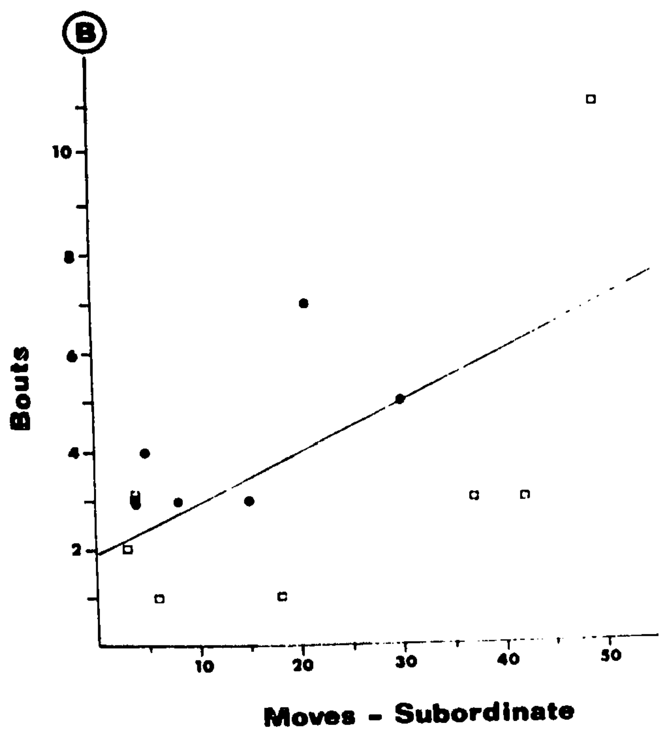
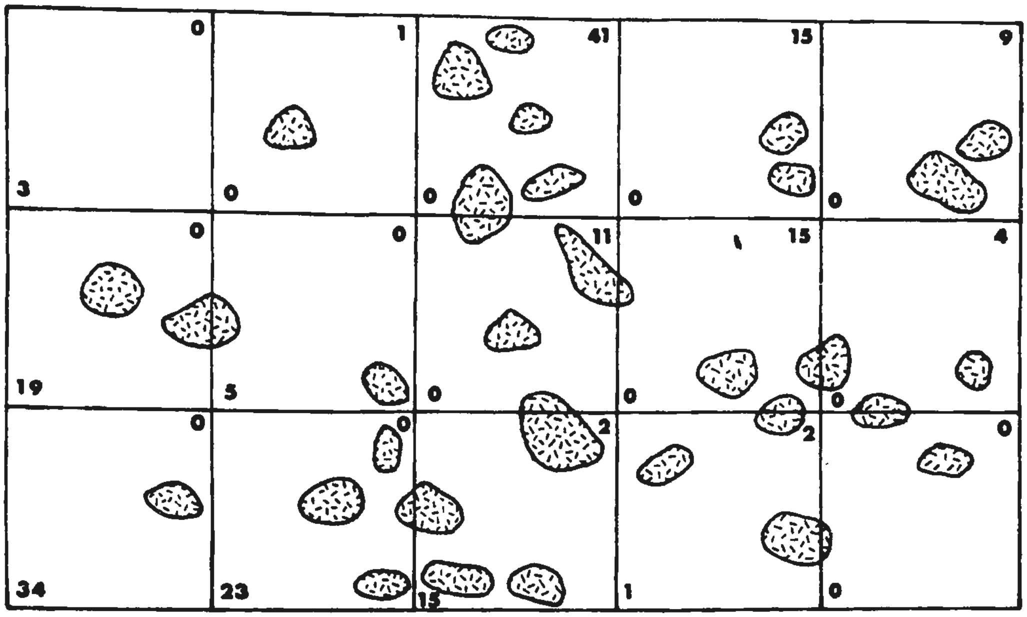

B
Bouts
10
8
6
4
2
10
20
30
40
50
Moves - Subordinate

Figure 25. The percent values of occupation of the quadrates in the larger tank by the individual fish in pair 1 (A) and pair 2 (B). The percent values for fish 1 are given in the lower left corner of the quadrates while the percent values for fish 2 are given in the upper right corner of the quadrates. The hatched areas in the figure represent the major pieces of gravel on the tank bottom.

A


0
3
1
0
41
0
15
0
9
0
0
19
0
5
11
0
15
0
4
0
0
34
0
23
2
15
2
1
0
0

B

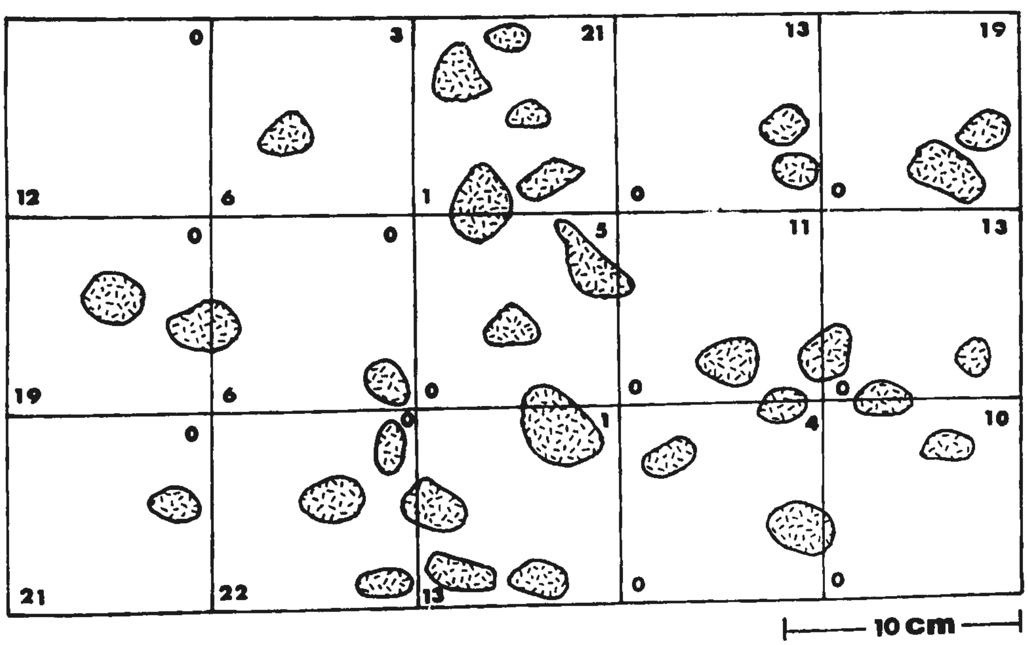
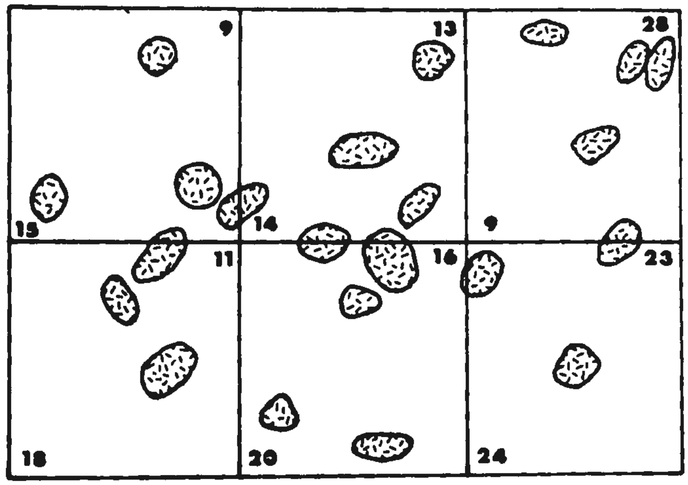
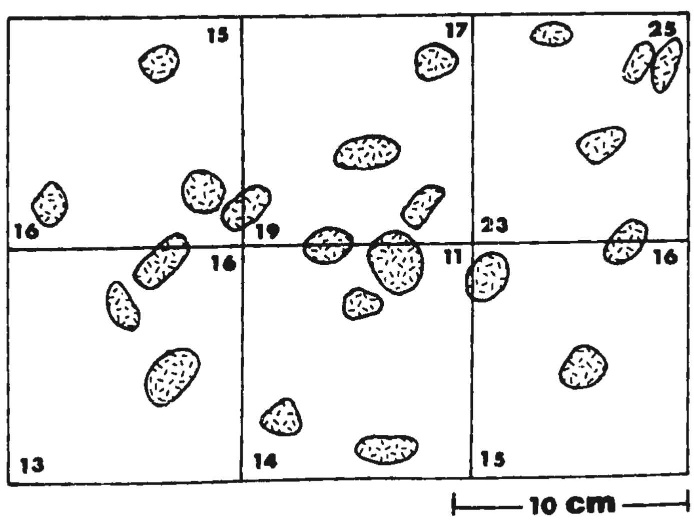

0
12
3
6
21
1
13
0
19
0
0
19
0
6
5
0
11
0
13
0
0
21
0
22
1
13
4
0
10
0
10 cm

Figure 26. The percent values of occupation of the quadrates in the smaller tank by the individual fish in pair 1 (A) and pair 2 (B). The percent values for the dominant fish are given in the lower right corner of the quadrates while the percent values for the subordinate fish are given in the upper right corner of the quadrates. The hatched areas in the figure represent the major pieces of gravel on the tank bottom.

A


9
13
28
15
14
9
11
16
23
18
20
24

B

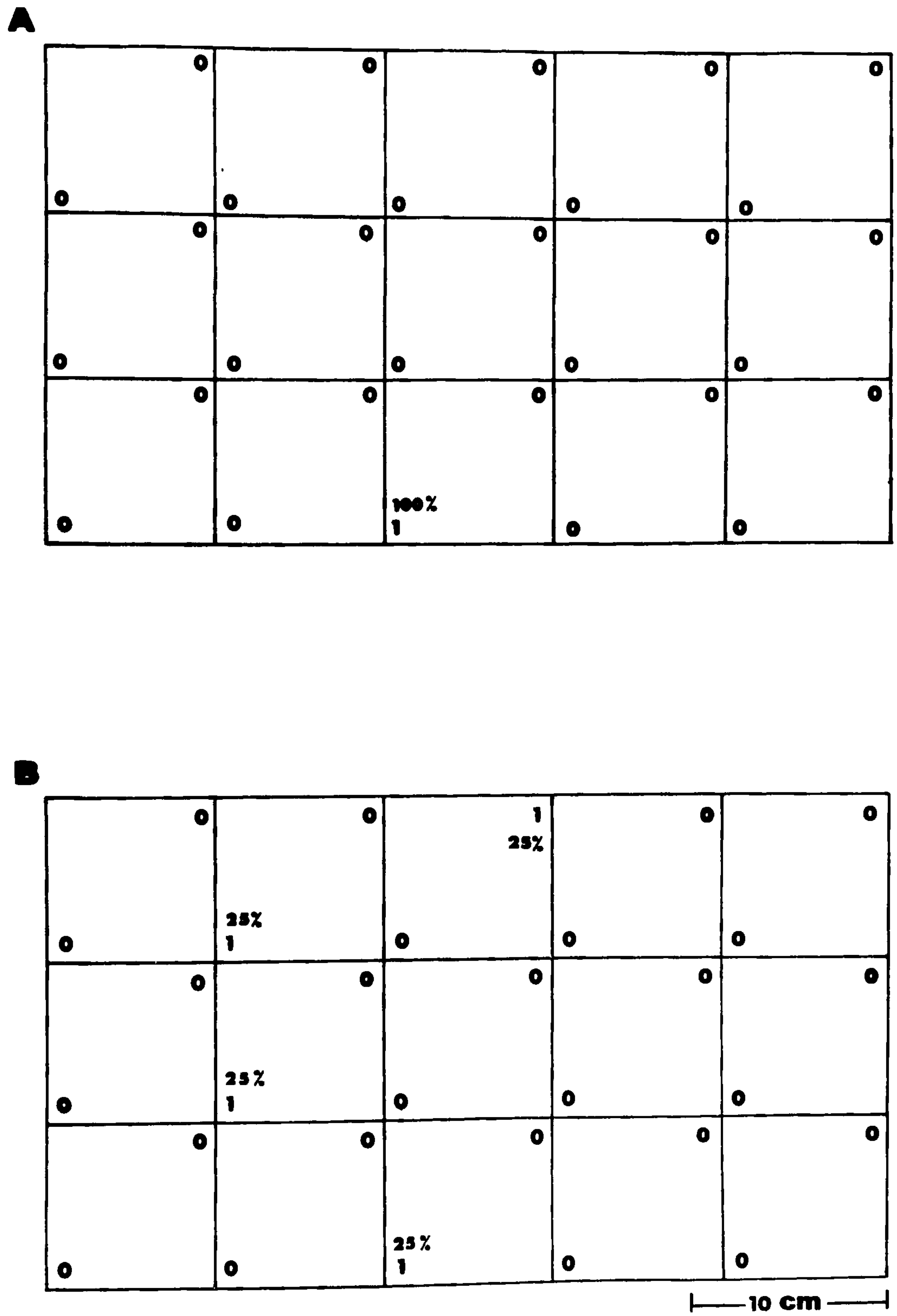

15
17
25
16
19
23
16
11
16
13
14
15
10 cm

Chi-square analysis of the data presented in Figure 27 was not done because of the small number of agonistic bouts observed. Chi-square analysis of the data presented in Figure 28 was done. The observed distribution of the agonistic bouts in both pairs was significantly different ($\chi^2 > 23.8$, 4 d.f., $p < 0.01$) from that expected if the number of bouts in each quadrate were equal.

Figure 29 shows a significant negative correlation ($p < 0.01$) between the occupation of the quadrates by the paired individuals in the larger tank. The data for pair 1 are insignificant whereas the data for pair 2 are negatively correlated ($p < 0.01$). Figure 30 shows an insignificant relationship between the occupation of the smaller tank by the dominant and the subordinate fish. The data for pair 1 are insignificant whereas the data for pair 2 are positively correlated ($p < 0.05$).

Figure 31 shows an insignificant relationship between the occupation of the quadrates by the dominant fish and the agonistic bouts in the quadrates. The data for pair 1 are insignificant whereas the data for pair 2 are significantly correlated ($p < 0.05$). A significant positive correlation ($p < 0.01$) was found between the occupation of the quadrates by the subordinate fish and the agonistic bouts in the quadrates (Figure 32). Individual data for both pairs are correlated ($p < 0.05$). In the relationship between the

Figure 27. The number and percent of the total number of agonistic bouts occurring in the quadrates in the larger tank. The values are presented in the corner of the dominant fish in the bouts. Values for fish 1 and 2 in pair 1 (A) and pair 2 (B) are in the corners described in Figure 25.


A
100%
1
B
1
25%
25%
1
25%
1
25%
1
10 cm

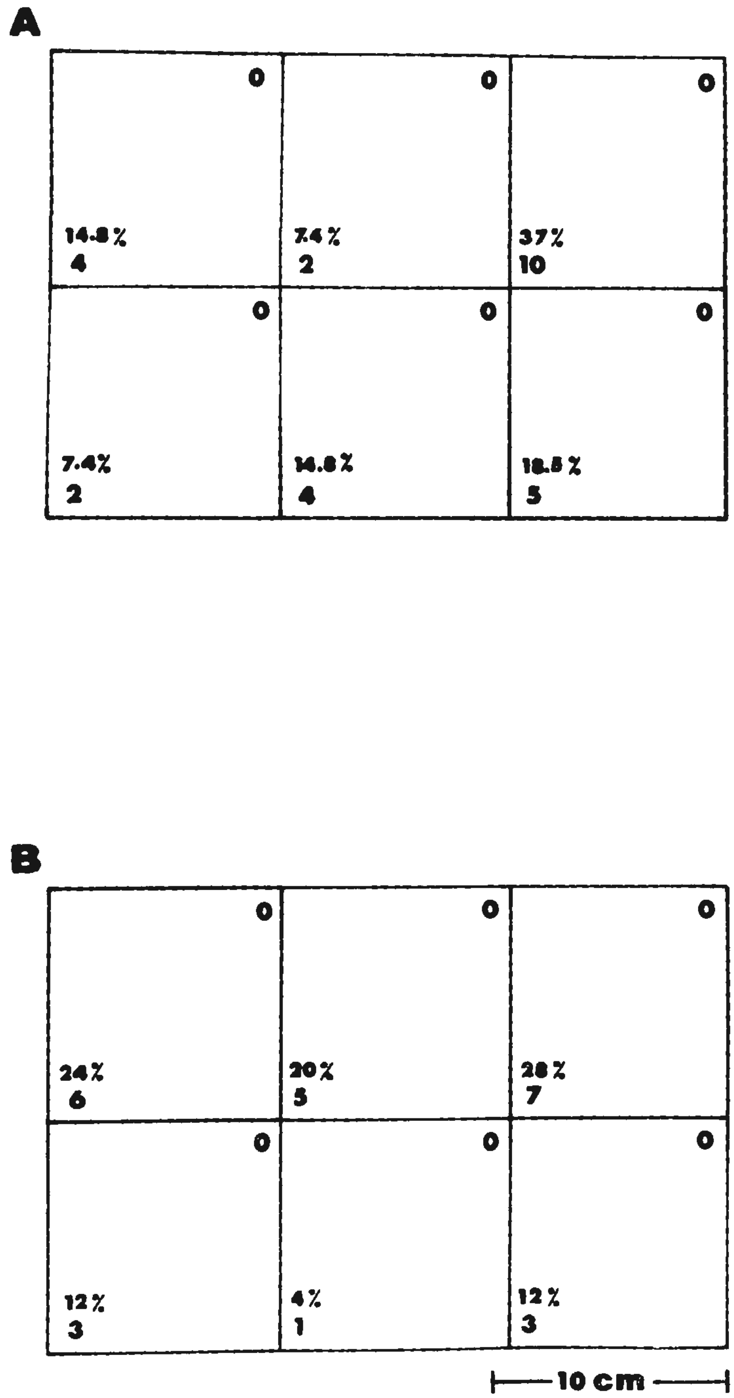

A
0
0
0
14.8% 4
7.4% 2
37% 10
0
0
0
7.4% 2
14.8% 4
18.5% 5
B
0
0
0
24% 6
20% 5
28% 7
0
0
0
12% 3
4% 1
12% 3
10 cm

Figure 29. Relationship between the occupation of the quadrates by fish 1 and 2 in the larger tank. Pair 1 and 2 fish are represented as in Fig. 22A.

The regression line for the combined data is

$Y = 10.1 - 0.5\,X$; $r = -\,0.49$; 29 d.f.; $p < 0.01$.

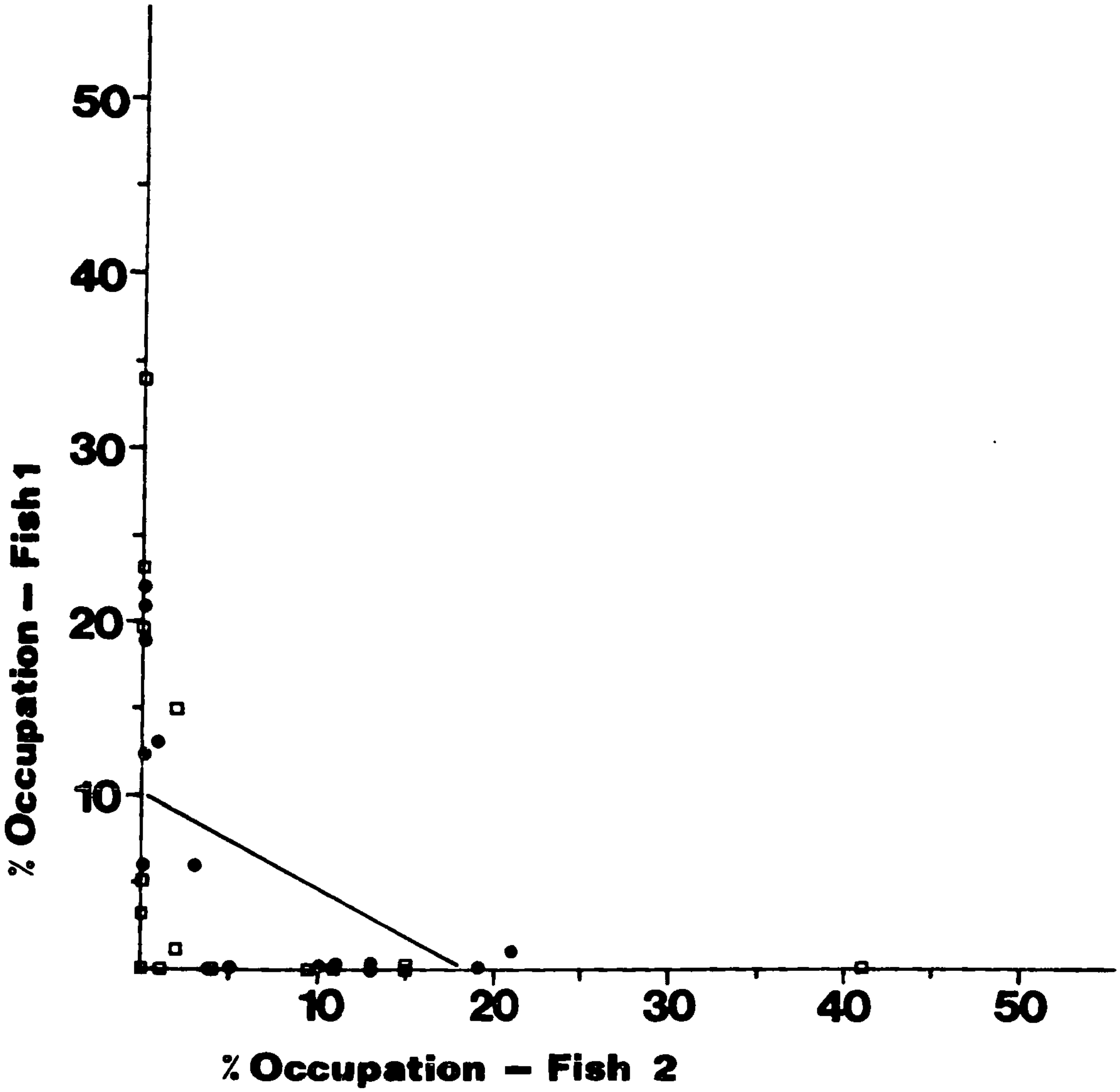

50
40
30
20
10
10
20
30
40
50
% Occupation — Fish 1
% Occupation — Fish 2

Figure 30. Relationship between the occupation of the quadrates by the dominant and subordinate fish in the smaller tank. Pair 1 and 2 fish are represented as in Fig. 22A.

The regression line for the combined data is

$Y = 14.7 + 0.1 X$; $r = 0.16$; 11 d.f.; $p > 0.05$

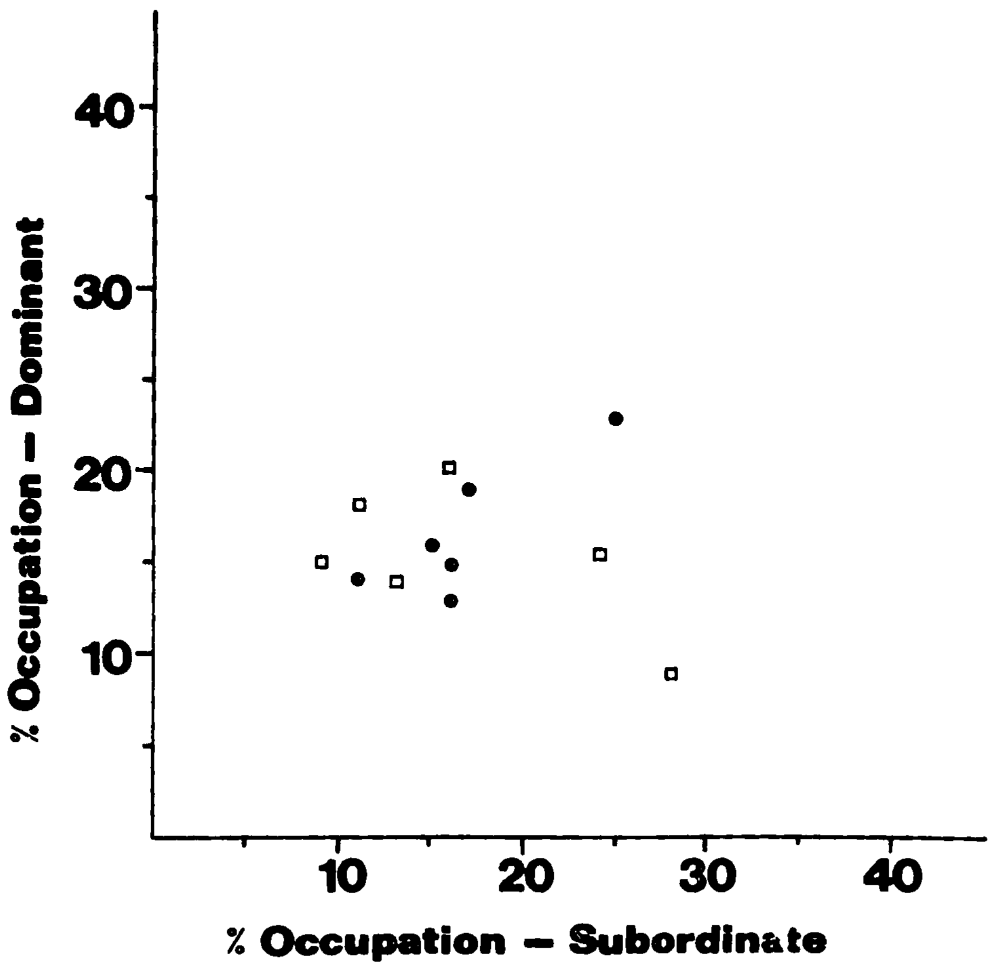

40
30
20
10
% Occupation — Dominant
10
20
30
40
% Occupation — Subordinate

Figure 31. Relationship between the percentage of the bouts occurring in the quadrates and the occupation of the quadrates by the dominant fish in the smaller tank. Pair 1 and 2 fish represented as in Fig. 22A.

The regression line for the combined data is

$Y = 16.8 - 0.01 X$; $r = -0.01$; 11 d.f.; $p > 0.05$

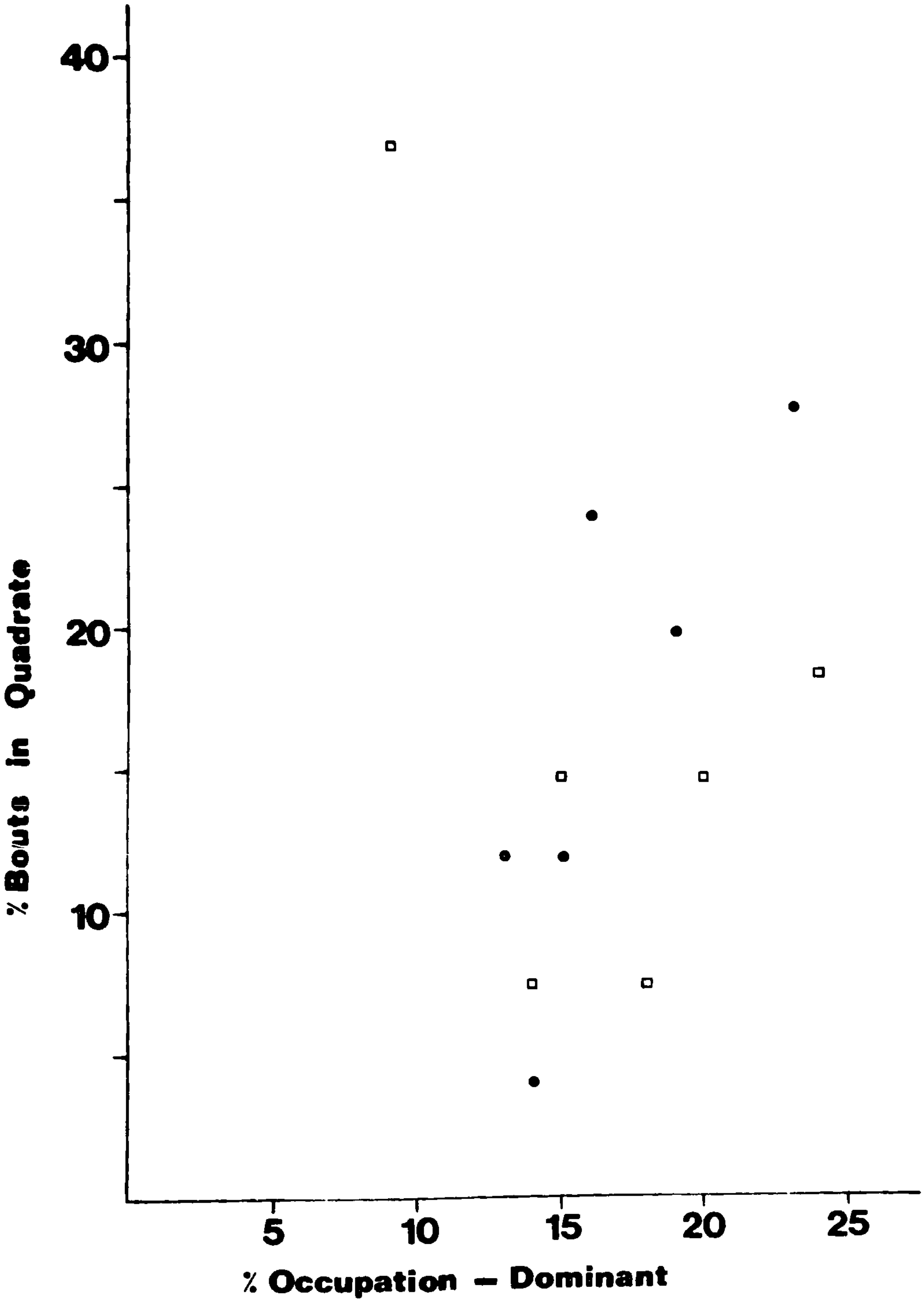
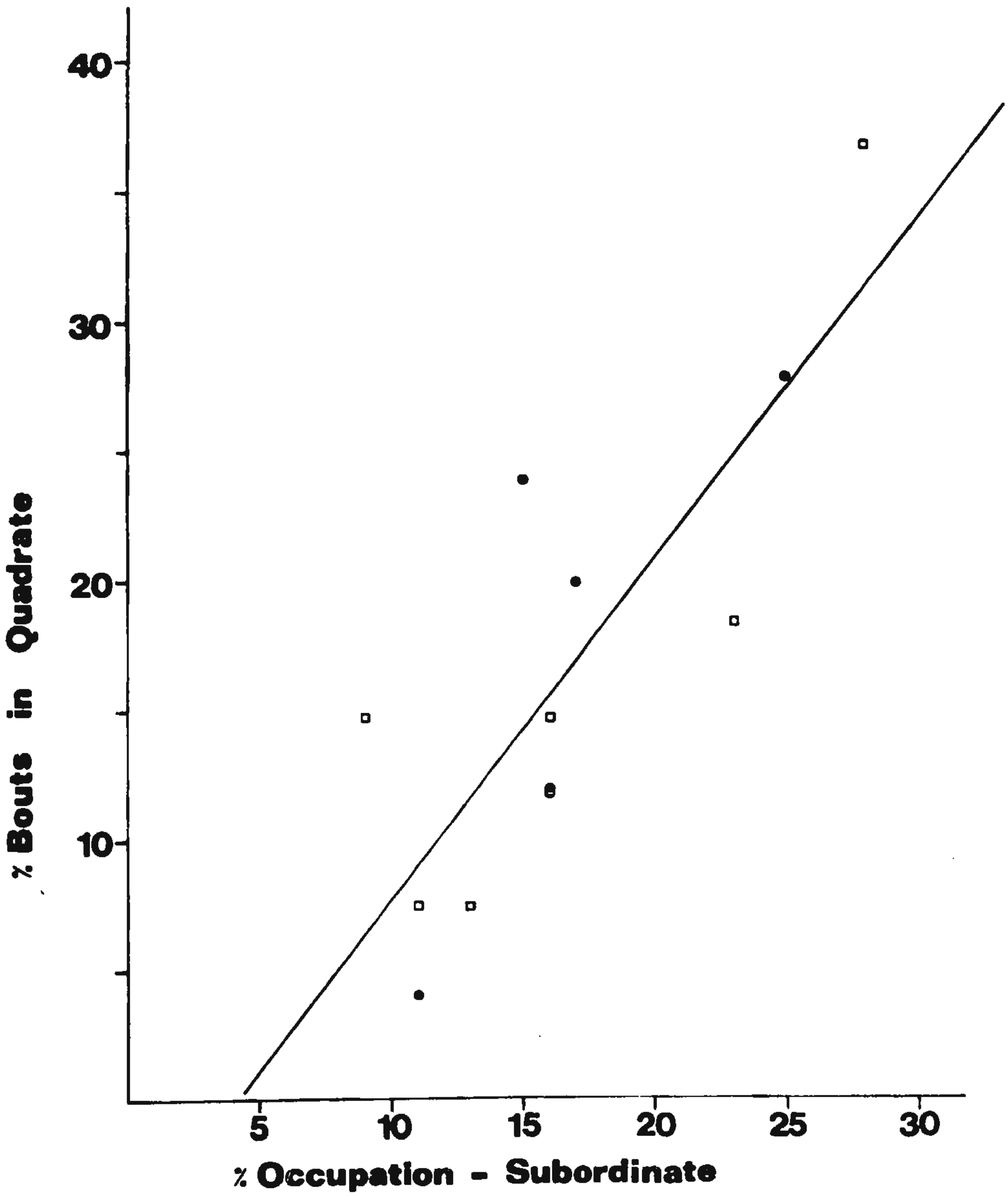

40
30
20
10
% Bouts in Quadrate
5
10
15
20
25
% Occupation — Dominant

Figure 32. Relationship between the percentage of the bouts occurring in the quadrates and the occupation of the quadrates by the subordinate fish in the smaller tank. Pair 1 and 2 fish are represented as in Fig. 22A.

The regression line for the combined data is

$$Y = -5.5 + 1.3X; \ r = 0.82; \ 11 \text{ d.f.}; \ p < 0.01$$


40
30
20
10
% Bouts in Quadrate
5
10
15
20
25
30
% Occupation - Subordinate

occupation of the quadrates and the agonistic bouts in the quadrates in the larger tank, the data for pair 1 (Fig. 33A) are insignificant whereas the data for pair 2 (Fig. 33B) are significantly negatively correlated ($p < 0.01$).

CHANGES IN AGONISTIC ACTIVITY LEVELS IN YEARLING FISH

The level of agonistic activity of fish held in the laboratory decreased during the latter part of July, 1969. The following results were assembled to show the changes in the agonistic activity level.

Observations beginning on 1 August, 1969 are presented in Table 9. As can be seen, only two bouts were observed in a total of 12 hr 15 min of observations. These two bouts were incomplete in that the two threat postures observed were not followed by a reaction by the other fish.

Other observations were made on fish which were separated by a partition prior to observation. The three pairs observed showed no agonistic activity.

Two pairs of yearling fish which had received no supplemental food for 72 hr showed no agonistic activity during 15 min observation period.

Two pairs held at lowered temperatures were observed over a period of days. The pair held at 2 C was observed

Figure 33. A. Relationship between the percentage of the bouts occurring in the quadrates and the occupation of the quadrates by the fish in pair 1 in the larger tank.

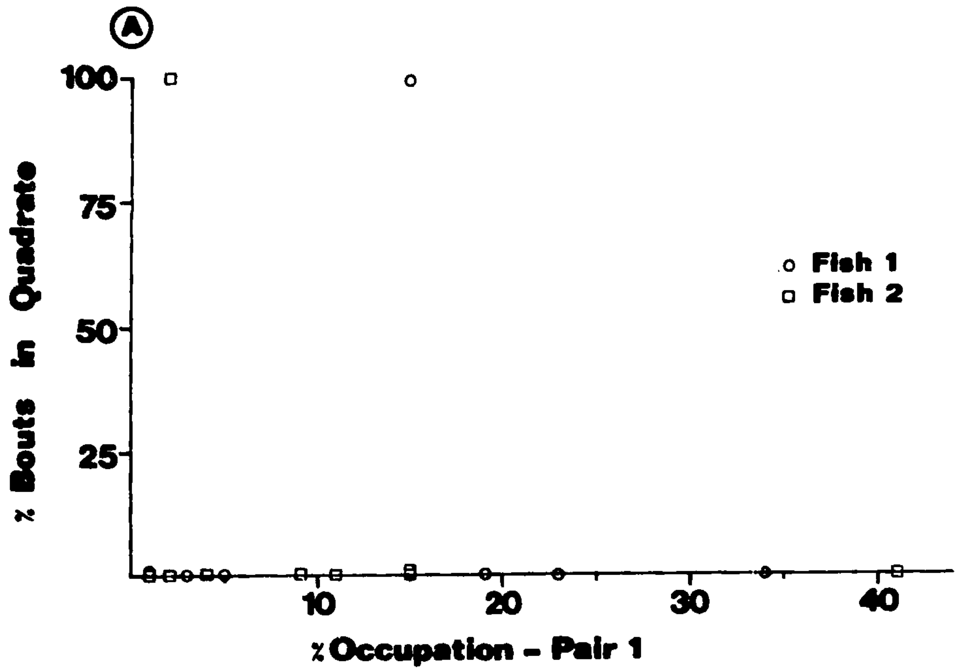
The regression line for the combined data is

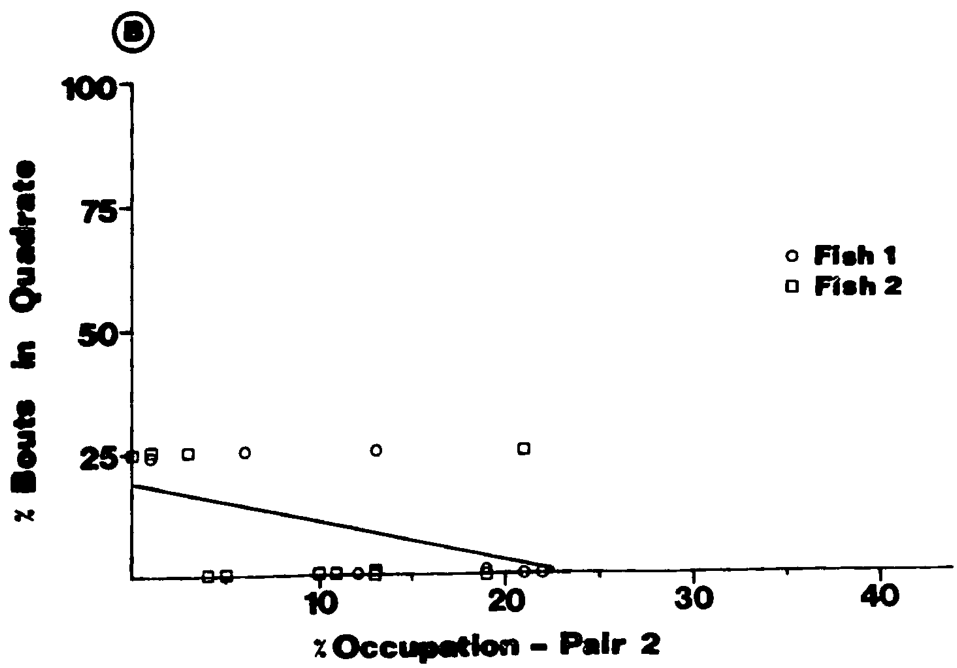
$Y = 17.1 - 0.4 X$; $r = - 0.13$; 15 d.f.; $p > 0.05$

B. Relationship between the percentage of the bouts occurring in the quadrates and the occupation of the quadrates by the fish in pair 2 in the larger tank.

The regression line for the combined data is

$Y = 19.4 - 0.85 X$; $r = - 0.49$; 18 d.f.; $p < 0.05$


A
100
75
50
25
% Bouts in Quadrate
Fish 1
Fish 2
10
20
30
40
% Occupation - Pair 1


B
100
75
50
25
% Bouts in Quadrate
Fish 1
Fish 2
10
20
30
40
% Occupation - Pair 2

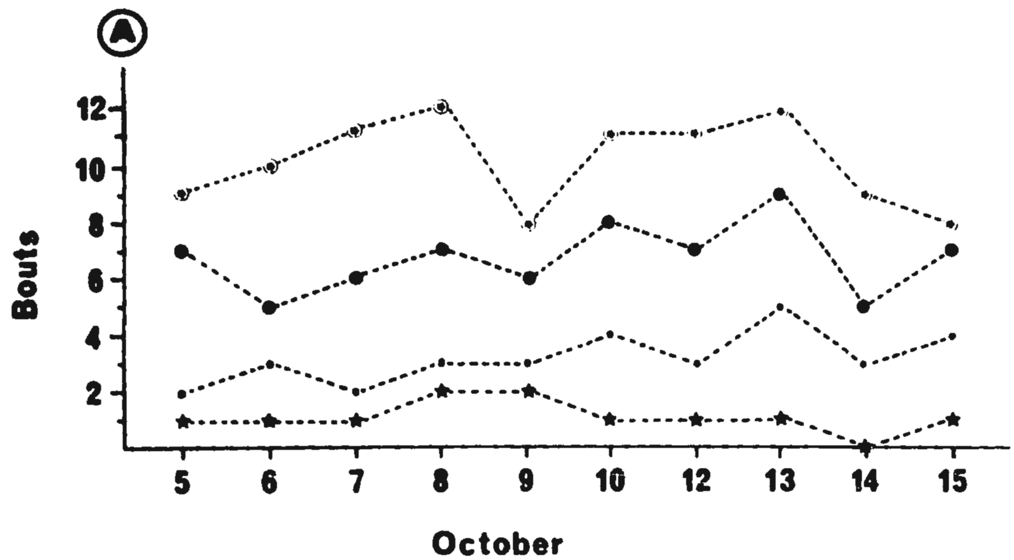
over a period of 39 days. Fifty-one observations, each of 5 min duration, were made. Six observations were made on the first day followed by three observations per day on irregularly spaced days for 39 days. No agonistic bouts were observed. The fish did not feed readily on added food and the level of motor activity appeared to be low. The pair held at 5 to 10 C for four days was observed 16 times, with each observation being of 10 min duration. No agonistic bouts were observed.

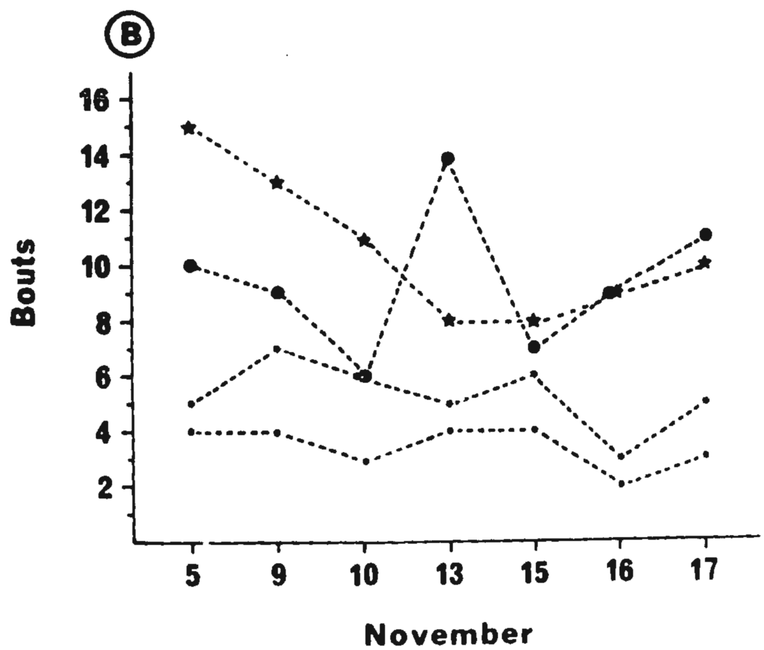
Another series of observations on the yearling fish involved four yearling and three underyearling fish. Notes were made on the ages of the fish involved in the bouts and on whether or not agonistic behaviour was observed in the bouts. Non-agonistic bouts were those in which an approach was not followed by other agonistic actions. Figure 34 shows the number of agonistic and non-agonistic bouts in which fish of the two age groups were involved during the October and November observations. Chi-square contingency table analysis of the data was done. There were significant differences between October and November in the number of agonistic ($\chi^2 = 6.52$, 1 d.f., $p < 0.05$) and non-agonistic ($\chi^2 = 30.9$, 1 d.f., $p < 0.01$) bouts involving yearling fish. The number of agonistic ($\chi^2 = 0.03$, 1 d.f., $p > 0.05$) and non-agonistic ($\chi^2 = 2.15$, 1 d.f., $p > 0.05$) bouts involving underyearling fish were not different

Figure 34. The number of agonistic and non-agonistic bouts in yearling and underyearling fish during the observations in October (A) and November (B), 1969.

The number of agonistic bouts in which underyearlings were involved are represented by dots. The number of non-agonistic bouts in which underyearlings were involved are represented by dots within circles.

The number of agonistic bouts in which yearling were involved are represented by stars. The number of non-agonistic bouts in which yearling fish were involved are represented by stars within circles.


A
Bouts
12
10
8
6
4
2
5
6
7
8
9
10
12
13
14
15
October


B
Bouts
16
14
12
10
8
6
4
2
5
9
10
13
15
16
17
November

between October and November. In October most of the agonistic bouts in which underyearling fish were involved were between two underyearlings ($\chi^2 = 14.5$, 1 d.f., $p < 0.01$). In November a similar difference ($\chi^2 = 4.34$, 1 d.f., $p < 0.05$) was found. In October most of the agonistic bouts in which yearling fish were involved were between yearling and underyearling fish ($\chi^2 = 5.8$, 1 d.f., $p < 0.05$). In November, however, most of the agonistic bouts involving yearling fish were between two yearling fish ($\chi^2 = 8.46$, 1 d.f., $p < 0.01$).

The mean water temperature during the October observations was 9 C while in November it was 6 C.

The mean level of motor activity of 10 yearling fish placed in a new tank was 25.5 ± 2.4 moves per fish per 15 min after two hours in the tank. Student's t test comparison of the mean value for these observations and the typical level obtained in the motor activity level in novel situation study showed a significant difference ($t' = 3.3$; 10 & 18 d.f.; $p < 0.01$). The temperature of the water during the latter study, done in May, 1969, was 4.5 C whereas it averaged 11.5 C during August, 1969, when the above observations were made.

An agonistic bout between underyearling fish was observed in Dyer's Gulch on 13 August, 1969, water temperature 12 C. During the daily dives at Mitchell's Brook from

4 September to 8 September, 1969, there were eight occasions on which yearling fish were in close proximity, about one body length apart, but no agonistic bouts were observed. The water temperature during these observations was 11 to 14 C. Two agonistic bouts have been observed between yearling fish at Mitchell's Brook: one on 16 May, 1970, water temperature 5 C and one on 4 July, 1970, water temperature 7 C.

DISCUSSION

AGONISTIC BEHAVIOUR

Barlow (1968) discussed the concept of behavioural units and suggested the term "modal action pattern" to define the units of behaviour observed in a species. The term embraces the idea that patterns of coordinated movement are clustered in space and time about a mode. The modal nature of the action pattern renders it recognizable. The qualitative and quantitative variations observed in the agonistic behaviour of juvenile *S. punctatus* affirm the use of this term.

Verplanck (1957) defined agonistic behaviour as including attack, threat, appeasement, and flight behaviours. Attack behaviours bring one animal into contact with an opponent in a manner that may cause injury. Threat behaviours elicit further agonistic action, especially flight. In juvenile *S. punctatus* attack and threat behaviours are typically shown by dominant fish. Appeasement behaviours terminate attack or threat while flight behaviour takes the animal away from the opponent. In juvenile *S. punctatus* appeasement and flight behaviours are shown by subordinate fish.

In agonistic behaviour attack, threat, appeasement, and flight behaviours occur in sequences. The presence of common sequence patterns indicates that communication is occurring (Dingle 1969). The agonistic modal action pattern sequences in bouts between juvenile S. punctatus show that communication does occur. Attack is followed mainly by flight responses. Threat is typically followed by threat, flight or appeasement responses. Appeasement and flight are usually followed by no further agonistic action or by threat actions.

Fish may use various sensory modes during communication. Visual signals are often stated to be of prime importance in a species but experimentation to determine the validity of the statement is uncommon. Kleerekoper (1969) states that there is little evidence supporting the use of olfactory signals in agonistic behaviour of fish. Auditory stimuli have been reported to be used during agonistic behaviour in fish (Caldwell and Caldwell, 1967; Brawn, 1961).

Stichaeus punctatus is a diurnally active species which inhabits clear water. Its agonistic behaviour is a complex of posture and colour components. These facts support the hypothesis that visual signals are used during agonistic communication. In the present study the partition experiments were designed to alter the transfer of sensory cues. Visual, olfactory, and auditory modes were selectively altered by the partitions. Agonistic behaviour was observed only when visual stimuli were present. The primary importance of visual cues is supported by the experiments with models and the mirror. The model study indicated that variation in colour and posture are important visual stimuli which are responded to by test fish. Further evidence that olfactory cues, in the absence of visual cues, would not elicit agonistic behaviour was found in the experiments with conspecific seawater. If olfactory signals are present they do not alter the activity or colour patterns of the test fish. The influences of auditory stimuli in the absence of visual stimuli were not investigated but the agonistic behaviour differences observed in the partition experiments may be because of an augmentative influence by auditory cues. Alteration of responses may be caused by auditory signals which could be emitted during certain agonistic actions such as threat posture and body shake.

Assem (1967) reported that male Gasterosteus aculeatus swam continually after being placed in a new tank. After a variable length of time the fish tended to stay in a restricted area and show agonistic behaviour. In the present study the motor activity level of S. punctatus was shown to decrease from an initial high level after placement in a new tank. Thorpe (1963) states that the high level of motor activity following placement in a novel situation is probably indicative of the presence of fright and exploratory behaviour. He suggests that habituation to the novel stimuli reduces the motor activity level. Peeke (1969) states that a major criterion of habituation is temporal persistence. In the present study temporal persistence of decreased motor activity was observed and therefore habituation by S. punctatus to a new tank appears to occur.

The agonistic behaviour of juvenile S. punctatus changes after the dominance and subordination status of the opponents is established. This is interpreted as a learning situation. Dominance and subordination is established during the first few bouts which typically involve most of the agonistic actions of the species in complex sequences. In successive bouts there is a simplifying of the sequences. This phenomenon indicates that there is an ability of the fish to adapt its agonistic responses to the stimulus situation present. This adaptation is assumed to be based on the prior experiences of the opponents in the encounter and the ability of the fish to recognize each other. Further investigation of this assumption is needed.

Space was shown to be one aspect of the environment which influences the agonistic behaviour of S. punctatus. The amount of space available affects both the quality and quantity of agonistic behaviour. If space is limited a constant dominance and subordination of individuals exists in an encounter. If space is not limited dominance and subordination depends on where the bout occurs. Noble (1939) defined territory as "any defended area". In the larger tank both fish occupied territories and the only agonistic behaviour occurred at the border region of the two territories. During the encounters in the larger tank dominance and subordination were transitory and the activity of the two fish was restricted to a certain area which was defended. In the smaller tank the dominant fish established a territory but the space available was inadequate for the establishment of a territory by the subordinate fish. The subordinate fish was always within the territory of the dominant thereby causing the higher level of agonistic bouts.

The decrease and subsequent increase in the agonistic activity level of yearling fish observed in this study indicates the presence of a seasonal factor or factors which affect the level of agonistic activity. Fish held in the laboratory throughout the study, newly caught fish, and fish in the field all showed a low level of agonistic activity during late summer and early autumn. This indicates that the influencing factor(s) exist(s) in the field as well as in the laboratory. Temperature has been reported to affect the agonistic behaviour of fish (Hartman, 1966) and it appears to be correlated with alterations in the agonistic activity of yearling S. punctatus.

AGONISTIC BEHAVIOUR AND ECOLOGY

Stichaeus punctatus fry are pelagic and settlement in the Newfoundland area occurs in July and August (Farwell and Green, unpublished). Field observations indicate that in certain areas newly settled juveniles are very abundant. Yearling fish are relatively uncommon at the two field stations.

One of the functions ascribed to agonistic behaviour is that of population regulation by spacing individuals in the environment. Laboratory observations reveal that this species will establish territories if sufficient space is available. The establishment of territories in the field would serve to space the fish and this may be a factor limiting the number of juveniles in a given area. Further field work is necessary before the natural spatial requirements of *S. punctatus* at different ages can be determined.

Predation and competition may also be factors leading to the reduction in the number of fish in a given area as the age of the fish increases but data supporting this are lacking. Casual observations in the field have revealed that *Tautogolabrus adspersus* and *Myoxocephalus scorpius*, both of which are diurnally active, will attempt to catch the diurnally active juvenile *S. punctatus*.

Intraspecific competition between underyearling and yearling fish may occur in the field during the summer. Laboratory observations show that underyearling fish are dominant during bouts with yearling fish during periods of warm seawater temperature. Occurrence of this situation in the field could be a factor which tends to reduce the yearling population in a given area since yearling fish would be subordinate and move away from dominant underyearling fish. The same situation may be of advantage to the under-yearling fish since a greater number would be able to establish territories in an area.

SUMMARY

1. Agonistic behaviour of juvenile S. punctatus is composed of approach, threat, nip, flee, chase, flatten, and back-away modal action patterns.

2. These modal action patterns occur in a sequential pattern which indicates that the actions are communicative.

3. S. punctatus is a diurnally active species and utilizes visual sensory cues in agonistic behaviour.

4. Solitary fish become habituated to a new tank and maintain a typical level of motor activity.

5. Agonistic responses are altered during encounters.

6. S. punctatus is a territorial species. Persistence of dominance and subordination occurs when space is limited.

7. The agonistic activity of yearling fish appears to be affected by water temperature.

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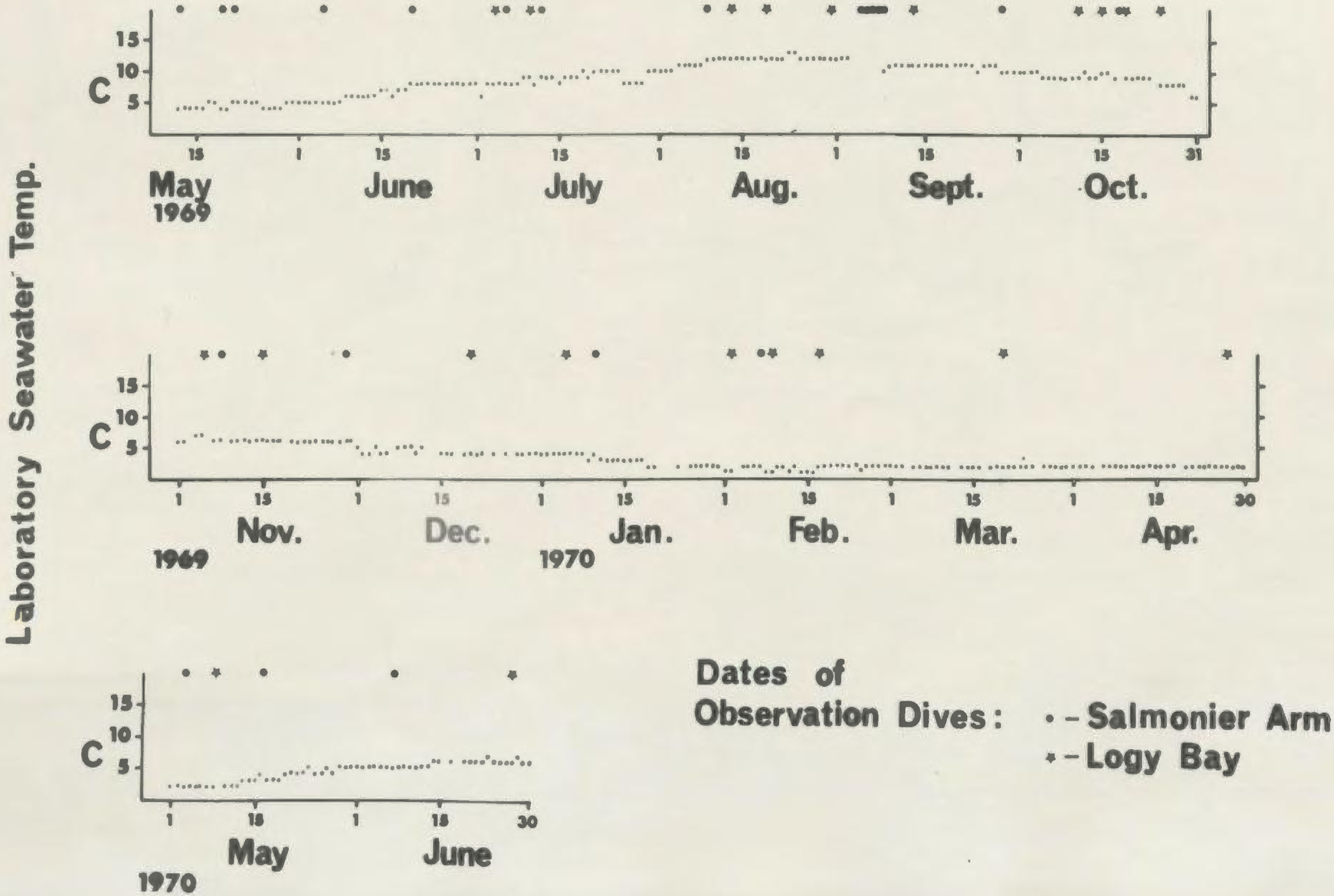
Appendix 1. Daily seawater temperature (degrees C) in laboratory holding tank and the dates of dives at the two field locations.



Laboratory Seawater Temp.
C
15
10
5
15
1
15
1
15
1
15
1
15
1
15
31
May
1969
June
July
Aug.
Sept.
Oct.
C
15
10
5
1
15
1
15
1
15
1
15
1
15
1
15
30
Nov.
Dec.
Jan.
Feb.
Mar.
Apr.
1969
1970
C
15
10
5
1
15
1
15
30
May
June
1970
Dates of
Observation Dives:
• - Salmonier Arm
* - Logy Bay

Appendix 2. Details of fish that died during transport to the laboratory or while held at the laboratory.

Date	Place[1]	Total length (mm)	Age[2]	Sex	Stomach[3] contents
12/5/69	MB	45	<1	Female	A, C, O.
		48	<1	Female	A, C.
		48	<1	Female	A, C.
		51	<1	Male	A, C, O.
19/5/69	MB	59	<1	Female	A, C.
		47	<1	Female	A, C.
		50	<1	Male	A, C.
22/5/69	MSRL	46	<1	Female	-
		44	<1	Female	-
1/8/69	MSRL	51	1^+	Female	-
7/8/69	MSRL	47	1^+	Female	-
9/8/69	MB	55	1^+	Male	A, C, P.
		34	<1	Male	A, C.
13/8/69	DG	36	<1	Male	A, C, Z, P.
30/8/69	DG	39	<1	Female	A, C.
		41	<1	Male	A, C, O.
7/10/69	MSRL	40	<1	Male	-
20/10/69	MSRL	61	1^+	Female	-
26/11/69	MSRL	47	<1	Female	-
10/1/70	MB	69	1^+	Male	A, C.
26/1/70	MSRL	44	<1	Male	-

30/8/69	DG	39	<1	Female	
		41	<1	Male	A, C, O.
7/10/69	MSRL	40	<1	Male	-
20/10/69	MSRL	61	1+	Female	-
26/11/69	MSRL	47	<1	Female	-
10/1/70	MB	69	1+	Male	A, C.
26/1/70	**MSRL**	**44**	**<1**	**Male**	-
		46	**<1**	**Female**	-
1/2/70	MSRL	70	1+	Female	-
		42	<1	Female	-
10/4/70	MSRL	55	<1	Female	-
20/4/70	MSRL	71	1+	Male	-

(1) Place key
MB - Mitchell's Brook
MSRL - Laboratory
DG - Dyer's Gulch

(2) Age key
<1 - underyearling
1+ - yearling

(3) Stomach contents key
A - Amphipoda
C - Copepoda
P - Polychaeta
Z - Zoea larvae
O - Ostracoda

Note: Stomach contents of fish that died in the laboratory were not analysed.