AGONISTIC BEHAVIOUR OF THE AMERICAN LOBSTER

Homarus americanus (Milne-Edwards)

by

JAMES CHARLES EDWARD SCRIVENER

B.Sc., University of British Columbia, 1967

A THESIS SUBMITTED IN PARTIAL FULFILLMENT

OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biology

Accepted for the Faculty of Graduate Studies

[redacted]

Dean pro tem

3 May 1971

We accept this thesis as conforming to the required standard

[redacted] ....

[redacted] ....

[redacted] ....

[redacted] ....

UNIVERSITY OF VICTORIA

November 1970

Supervisor: Dr. D.V. Ellis

ABSTRACT

An investigation was begun in June 1968 to develop an agonistic ethogram for the American lobster, Homarus americanus (Milne-Edwards). Agonistic behaviour consisted of 16 stereotyped behaviour patterns, which were quantitatively recorded during 700 fifteen minute observation periods. Computer analysis of the data indicated that the behaviour patterns were performed as 4 basic chains of activities or sequence pathways, which had side-chains which were often shown more frequently by either males or females. Analysis of responses to displays, demonstrated that one animal performed the aggressive pathway of winners, while its opponent showed one of the two losers pathways. The fourth long complex pathway occurred when both animals showed aggression. There were direct relationships between the difference in body size and chelae size of the combatants and the probability of observing the lobster with the larger win. These influences were complicated by the fact that males were more aggressive than females and that past experience affected aggression. With continued study, the data could be used to develop a model of lobster agonistic behaviour.

[redacted]

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

Figure | Page

Figures | Page

ACKNOWLEDGEMENTS

I am very grateful to Dr. D. V. Ellis, of the University of Victoria, and Dr. R. J. Ghelardi, of the F. R. B. Biological Station Nanaimo for their guidance and encouragement throughout the study.

I am also indebted to Dr. C. Groot, Dr. J. E. McInerney and Dr. C. W. Tolman for offering constructive criticism during the preparation of the manuscript.

Many others generously assisted the author during various stages of the study.

Mr. M. Wilson and assistants built the laboratory in which the work was done.

Dr. D. G. Wilder and his assistants purchased and shipped the lobsters from the East Coast.

Miss T. McMinn assisted during data coding.

The University of Victoria computer centre provided much of the key punch time.

Mr. J. Thompson and his staff, of the Biological Station computer centre provided assistance whenever problems arose during the data processing.

Mr. A. Denbie drew the sketches of the behaviour patterns.

Mrs. G. Glova typed the final draft of the manuscript.

Facilities for the preliminary project were provided by the Vancouver Public Aquarium. The study was financed by the Nanaimo Biological Station of the Fisheries Research Board of Canada and the University of Victoria Biology Department. During this research project the author was supported by an F. R. B. fellowship.

INTRODUCTION

The American lobster, Homarus americanus (Milne-Edwards), is a large and common crustacean occurring from North Carolina to the Strait of Belle Isle (Rutherford, Wilder and Fricker 1967). Despite its availability and commercial importance, only brief notes have been published on its agonistic or other forms of social behaviour. Herrick (1896 and 1911) mentions an "attitude of defence" (standing on the tips of walking legs, chelae raised), swimming behaviour, and resting. Knight (1918) described the resting posture and "fighting posture" (elevated chelae). Other published studies on the ethology of the lobster describe mating, egg-laying and hatching behaviour (Templeman 1934 and 1938).

The purpose of the present study was to develop a quantitative ethogram of lobster agonistic behaviour, to answer some basic questions about it, and to examine lobster agonistic communication. This was accomplished by first describing and naming the stereotyped behaviour patterns and then quantifying these interrelated recordable units. The basic questions asked were: What, if any, are the differences between male and female agonistic behaviour? What characteristics determine which individual will win an agonistic encounter between two lobsters?

The biological information obtained should be of value in managing as valuable a resource as the American lobster fishery. This is, probably, only the second decapod crustacean for which an extensive quantitative ethogram of agonistic behaviour has been developed.

METHODS AND MATERIALS

This study was carried out in two stages. A preliminary investigation was initiated at the Vancouver Public Aquarium, where the basic components of lobster agonistic behaviour were qualitatively determined, and the methods of study and holding were developed. For this work, 16 lobsters were used.

The second phase was carried out at the Pacific Biological Station of the Fisheries Research Board of Canada, Nanaimo, British Columbia. Except for some of the results of the affect of size, all the data presented below were obtained at Nanaimo. Freshly caught lobsters were bought by FRB personnel directly from fishermen on the Canadian east coast and held only briefly before they were shipped west. These animals had not contracted Gaffkemia (a bacterial blood disease) and had no wounds; they had a full complement of walking legs, full-length antennae, and banded claws. A first shipment of 31 lobsters was obtained at St. Andrews, New Brunswick. The lobsters were placed in styrofoam boxes containing dry shavings and freezer packs for shipment by air to Vancouver. They arrived in July 1968 after one day in transit. A second shipment of 35 lobsters was shipped in similar fashion from Prince Edward Island in September 1968.

The experimental animals were kept in 197-ℓ green oval fiberglass holding tanks (Alderdice, et al, 1966). A plywood divider separated the tanks into two compartments each of 2-1/2 square feet. One lobster was kept in each compartment. Animals not in immediate use were kept in an 8-ft (2.5 metres) diameter tank, that had been divided into 21 compartments. All the tanks were supplied with a flow of unfiltered sea water from the Biological Station's non-recycling supply system. Each tank was aerated during most of the study and water temperature monitored by thermograph. During the winter months the temperature generally varied from 8 to 10 C, while during the summer it varied from 10 to 14 C. Fluorescent lights in the study area were controlled by a time switch, which was set each week to the time of sunrise and sunset as reported in local meteorological data. Large windows in the laboratory gave the animals a twilight period before sunrise and after sunset. Surplus lobsters were kept outdoors in the covered 8-ft. tank which was shaded from direct sunlight. All lobsters were fed at least twice weekly on either horse heart, herring, smelts, dogfish, cod, rockfish or molluscs, depending on what was available. Fresh food was used whenever possible. Each lobster was weighed, measured, and marked on the dorsal surface of the carapace with a tattoo machine. Against the red-brown background of the carapace, the white tattoo could be clearly read by an observer 3 metres away. The experimental animals were given at least 30 days to become acclimated to the holding conditions, before they were used in any experiments. This is in accord with the time required for lobsters to acclimate to new temperatures, salinities and oxygen levels (McLeese 1956).

All observations were made in two circular, 6-ft. diameter (1.9 metres), blue fiberglass tanks covered on the bottom with a 10 cm layer of coarse quartz sand. A plywood divider was placed in an observation tank and one lobster was put in each compartment. Handling of the animals appeared to interfere with normal expression of initial agonistic activity. Consequently the lobsters were allowed a rest period of 30 to 40 minutes before observations were begun. To limit handling, a net was used whenever possible, for transferring individuals from one tank to another. After 30 to 40 minutes the divider was removed and agonistic behaviour was observed. The observation-recording period of 15 minutes duration began when the lobsters became aware of each other, as shown by manipulations of their sensory antennae, termed investigative behaviour (see p. 8). The 15 minute period was referred to as an agonistic encounter. The use of two observation tanks permitted the lobsters to recover in one tank, while the observer was recording behaviour and making preparations for the next agonistic encounter in the other tank. With the alternate use of observation tanks a maximum of 15 agonistic encounters could be recorded in one day.

Motion pictures (16 mm) were taken with a zoom lens Bolex H16 camera. These films were analyzed with the aid of a Bell & Howell time motion projector, so that an accurate description could be made of the behaviour patterns. This film was also used to test the consistency of the observer and the recording technique.

The frequency and duration of up to 15 behaviour patterns for each of the two lobsters was recorded during each encounter. For this purpose, a 20 pen Esterline Angus recorder was used, employing either one or two circuits per behaviour pattern per animal. This equipment contains 20 circuits each with a continuously recording ink pen, which marks a chart passing under the pens at a known rate of speed. If a circuit is closed, the pen is deflected by an electro-magnet, until the circuit is opened again. When a behaviour pattern was observed, the appropriate circuit or circuits were closed by pressing a push button key. The circuits were kept closed until the animal stopped showing the behaviour pattern. Seven hundred paired agonistic encounters were recorded with this equipment.

The raw data on recorder chart paper were transferred to coding sheets, for computer processing. The charts were divided off into fifteen 1-minute periods, the first minute beginning with the second which contained the first recorded display. Each second on the chart was examined, to determine if a circuit or combination of circuits was closed during that second. Each column on the coding sheet represented a second in time that a behaviour pattern was exhibited by one of the lobsters. If a particular behaviour occurred, a '1' was placed in the appropriate coding sheet column, otherwise it was left blank. From the coding sheets, the information was punched into computer cards. Programs were written in Fortran IV to determine frequencies, durations and sequences of the behaviour patterns, and to tabulate the responses of one animal to the other during each agonistic encounter (Appendix I). The programs and data were run on an 1130 IBM 16K computer. The output was summarized and graphs drawn for use in the quantitative analysis.

DESCRIPTION OF THE BEHAVIOUR PATTERNS

Sixteen behaviour patterns have been defined and named from the 850 lobster agonistic encounters observed during the last three years. During 700 of these encounters, quantitative data was collected on 15 of the behaviour patterns. Most of the activities were complex motor patterns, involving coordination of many body parts. Applying terms to such patterns was not intended to imply any particular physiological status, but provided simple labels for stereotyped activities which could be recorded quickly and accurately. The behaviour patterns were not all mutually exclusive so that an individual often displayed more than one at a time.

The lobster's normal forward movement and resting posture also need description, to show the difference between agonistic behaviour and general activity. When the lobster is resting, its tail fan, consisting of the uropods and telson, is folded and turned under the abdomen. The cephalothorax usually rests on the bottom. The chelae, bent at the joints with the palms of the claws pointing towards each other, rest on, or are held about 1 cm above the bottom. The antennae point at angles of 45^{o} upwards from the bottom and away from the body axis (Fig. 1).

During normal forward movement, the lobster uses its four pairs of walking legs. The sequence of leg movements appears complex enough to form the basis of a separate study and therefore was not examined in detail. The body is about 3 cm off the bottom, while the chelae and antennae are held as described for resting.

Agonistic behaviour has been defined as "any sort of adaptation which is connected with a contest or conflict between two animals, whether

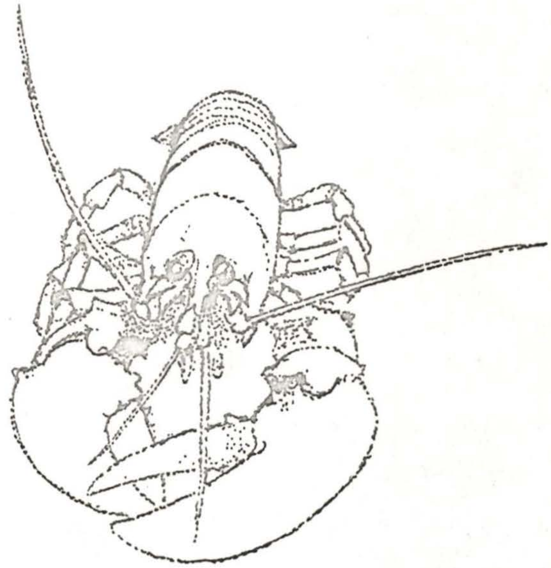


Fig. 1. The resting posture of the American lobster.

fighting, escaping or freezing" (Scott 1958, p. 16). In the present study, the lobster agonistic behaviour patterns were divided into two groups. The first group, called aggressive behaviour, was defined as any agonistic behaviour which directs a lobster towards its adversary. The second group, termed avoidance behaviour, was defined as any agonistic behaviour which directs an animal away from its opponent. During the study, a behaviour pattern was observed which could not be classified as agonistic behaviour, but was associated with it. This activity was classed as investigative behaviour which Scott (1958, p. 19) defined as "any kind of sensory investigation of the environment".

Investigative Behaviour

Antenna pointing

One or both antennae are moved from the normal resting posture (pointing 45^{o} upwards from the tank bottom and away from the body axis), to a position pointing anteriorly, in the direction of the other combatant, and thus parallel to the bottom and the body axis (Fig. 2).

Antenna pointing was a very common behaviour pattern of short duration (1 - 2 seconds). A slight variation sometimes occurred when one lobster was stationary and the other was moving. The stationary lobster demonstrated antenna pointing as described above, but then continued to follow its moving opponent with an antenna. Here the duration was slightly longer (2 - 5 seconds).

Antenna pointing, by one or both lobsters, frequently occurred when they were about 65 - 75 cm apart, either coming closer together or separating. It was deduced that they had just gained or lost sensory contact.

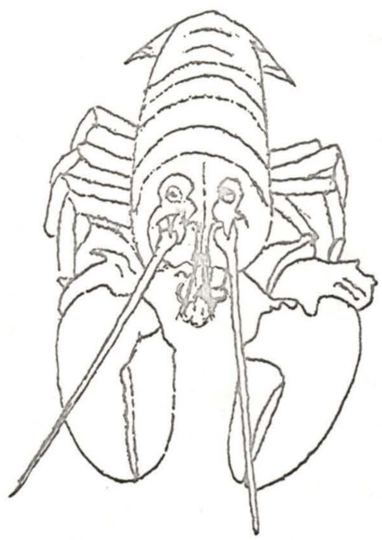


Fig. 2. A frontal view of a lobster antenna pointing.

Aggressive Behaviour

Meral Spread

During meral spread, the lobster stands on its walking legs with its body raised from 4 to 5 cm off the bottom. The abdomen is usually fully extended, with the cephalothorax angled slightly upwards from the horizontal. The chelae are held about 5 cm off the bottom, spread wide apart with their long axes pointing directly at the opponent. Some animals hold the claws fully extended, wide apart and as high off the bottom as possible. Pleopods are held against the abdomen and are not visible from a lateral view. The antennae are pointed at angles of 45^{o} upwards and away from the body axis (Figs. 3 and 4).

Meral spread was observed many times during every agonistic encounter, and showed a maximum duration of approximately 3 minutes.

Following

When one lobster is following another, the abdomen is fully extended, with the tail fan fully opened. The chelipeds are held about 3 cm off the bottom, with the long axes of the palms pointed towards each other distally. The pleopods are stationary as during meral spread, but the antennae are often perpendicular to the body axis (Fig. 3). In this posture the lobster simply follows its opponent. During this behaviour, steps of approximately 7 cm are taken with the second and third pair of walking legs. The first and fourth pair of walking legs appear to be actively moved only half this distance.

Like meral spread, following was observed during every agonistic encounter and had a maximum duration of approximately 3 minutes. A lobster followed at about 0.15 m. per second.

Distinguishing consistently between following, and the lobster's

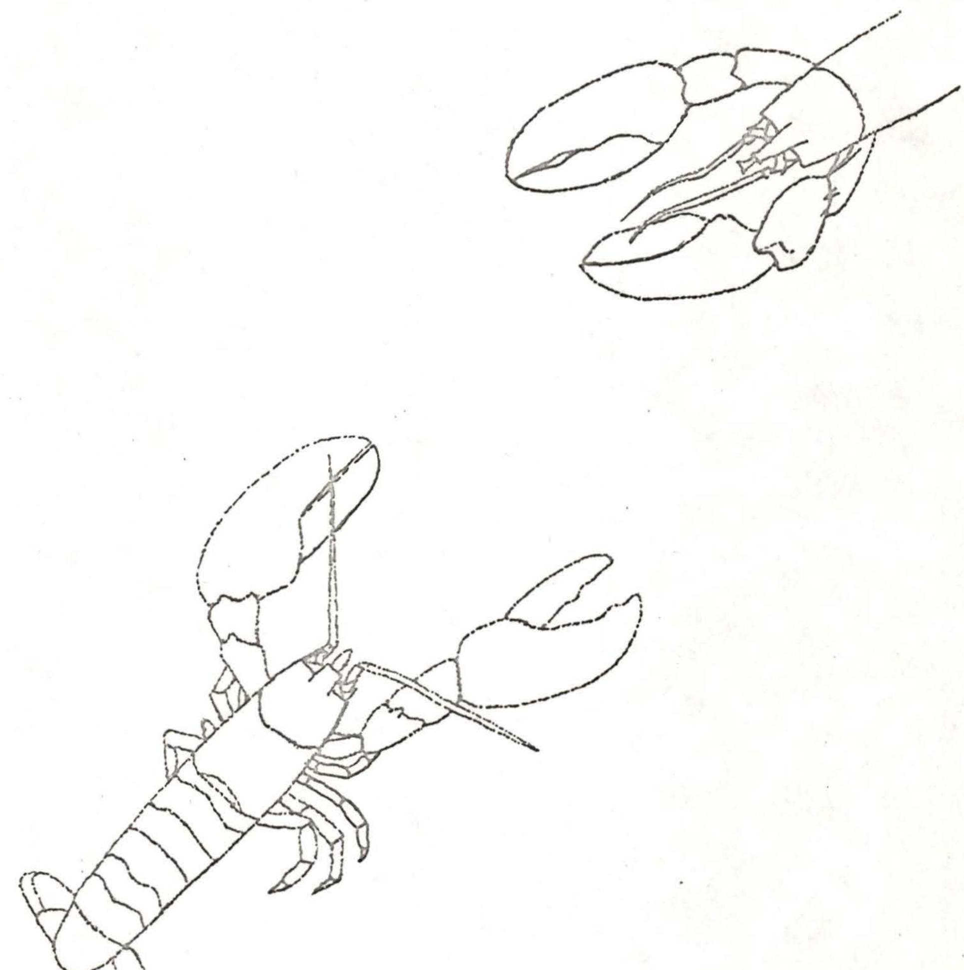


Fig. 3. The lower animal is showing following and meral spread
to its backing opponent.

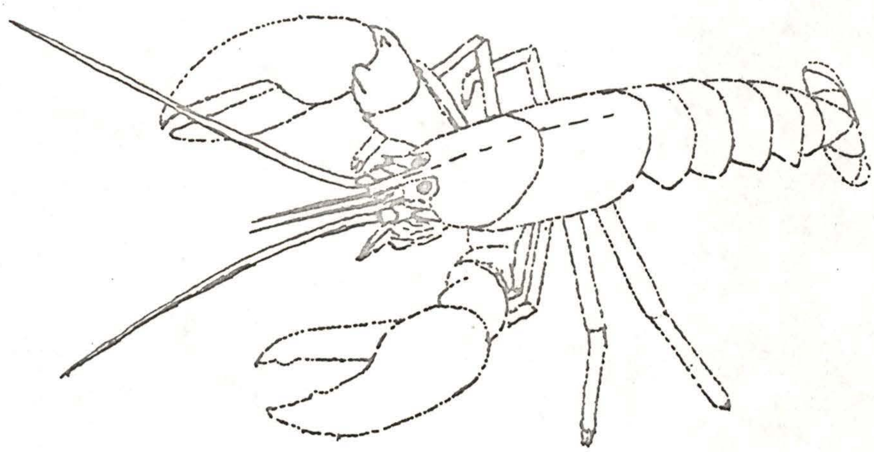


Fig. 4. A lobster demonstrating approaching and meral spread.

normal forward movement, was a problem at first. One useful indication was that the lobster usually responded to its opponent by displaying meral spread as well as following. When an individual demonstrated both simultaneously, the chelae were held in the meral spread posture as described above (Fig. 3). Another distinguishing feature was that the lobster almost always indicated it had detected the opponent by antenna pointing, before it began following.

On rare occasions when there was no obvious indication that sensory contact had been made, the distance at which antenna pointing usually occurred (65 - 75 cm) was considered to be the point at which the lobster detected the presence of its adversary, and changed its normal forward movement to following.

Approaching

Approaching is very similar to following, except that in this case the animal moves towards a stationary opponent that is usually showing neither aggressive nor avoidance behaviour. The abdomen is fully extended, the tail fan expanded and the chelae are held as when following. The pleopods appear to be stationary, but the antennae are often almost parallel to the body axis (Fig. 4). The lobster moves forward towards the other combatant, but at a lower velocity than when following.

Approaching was also a common behaviour pattern, but with a duration of only a few seconds (2-6). It was also commonly shown with meral spread.

Pushing

Pushing occurs when the animals raise their bodies as high as possible on their walking legs and push against each others chelae. The abdomen is extended fully with its tail fan open. The pleopods beat rapidly. Often the cephalothorax and abdomen form an arc, so that the long body axis becomes concave dorsally. The antennae are raised to a vertical position. Walking legs three and four are extended posteriorly, thus producing a greater horizontal force component when the legs are straightened. The chelipeds are spread wide apart with the long axes of their palms pointing directly at, and making contact with, the other lobster.

After prolonged pushing, the long axes of the palms are often turned perpendicularly to the long body axis and now face each other (Fig. 5). The chelae are usually kept closed and only rarely did one animal actually grasp the other.

Long bouts of mutual pushing were common, often lasting 30 seconds. Pushing was observed during three-quarters of the encounters.

Antennae whipping

During this activity, one lobster lashes another by sweeping its antennae back and forth in a horizontal plane. Often when an animal starts antennae whipping, its opponent reciprocates. Usually this activity is combined with pushing or meral spread (Fig. 6).

Antennae whipping was observed in one-third of the agonistic encounters, usually during periods of prolonged pushing. It lasted from 1 to 10 seconds.

Boxing

During a period of continuous pushing one individual occasionally withdrew a chela and then began punching or jabbing its opponent. This activity was called boxing. It had a short duration of 2 to

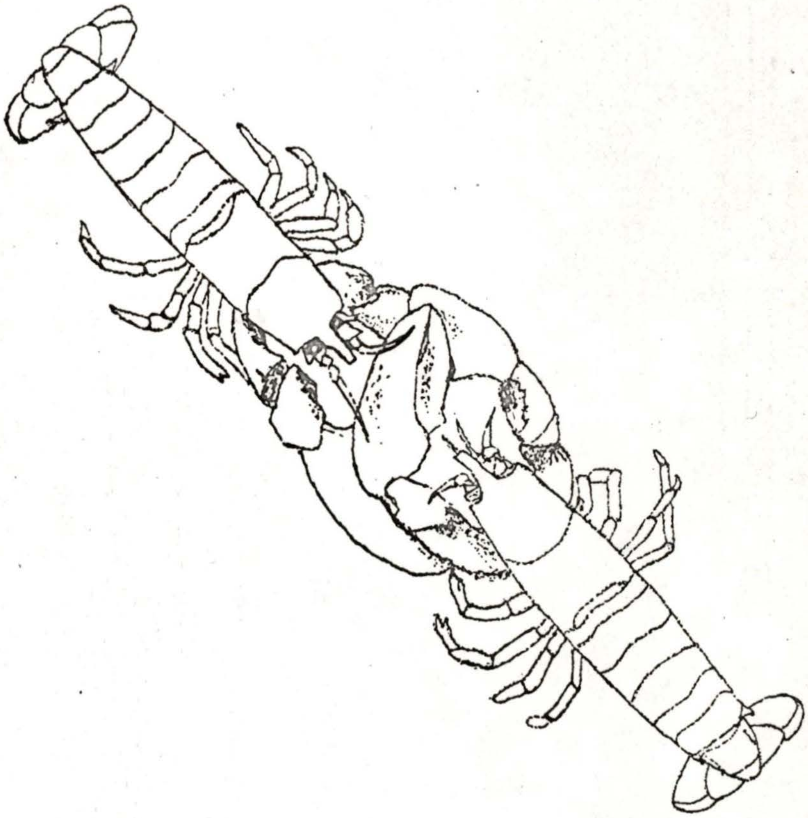


Fig. 5. Both lobsters are demonstrating pushing.

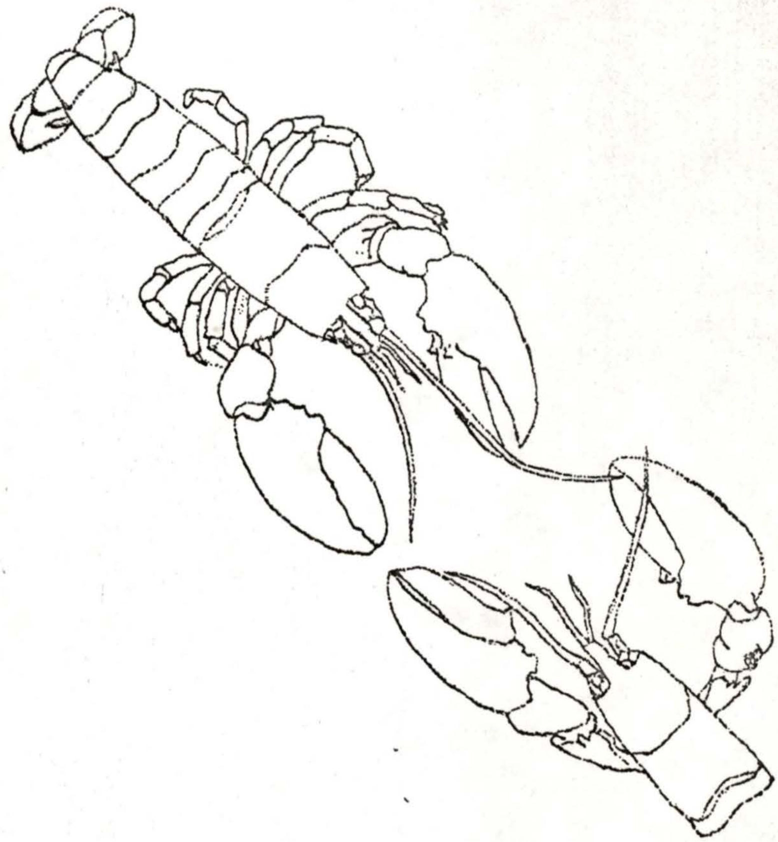


Fig. 6. The upper lobster is antenna whipping.

6 seconds. Boxing was seen in less than one-quarter of the agonistic encounters. It appeared to be a variation of pushing and some lobsters tended to show it more frequently than others.

Rushing

Rushing consists of one lobster with its chelae in the meral spread posture rushing or running toward an opponent. The abdomen is fully extended, with pleopods rapidly beating and tail fan open. During this activity the lobster's body is held about 2 cm off the bottom. At first, the antennae point forward at angles of 45° from the bottom and long body axis, but if rushing continues for more than 2 seconds, they are rapidly turned - as opposed to the usual slow antennae movements - to point backwards at an angle of 20° from the body axis. This movement requires an additional 2 seconds and is often not complete before rushing is terminated (Figs. 7 and 8).

A maximum velocity of 0.7 m. (mean 0.62 m.) per second was recorded during rushing. Steps of approximately 14 cm were taken with the second and third pair of walking legs. This was about twice the distance between footsteps that the lobsters made when they were following. Rushing was observed at least once during each agonistic encounter. Its duration was short (1 - 6 seconds). During long rushes there was a slight variation; the lobster would extend its chelae straight ahead towards the adversary (Fig. 7).

Scissoring

Scissoring occurs when one lobster faces its opponent, with chelae in the meral spread posture (spread wide apart, long axes of the

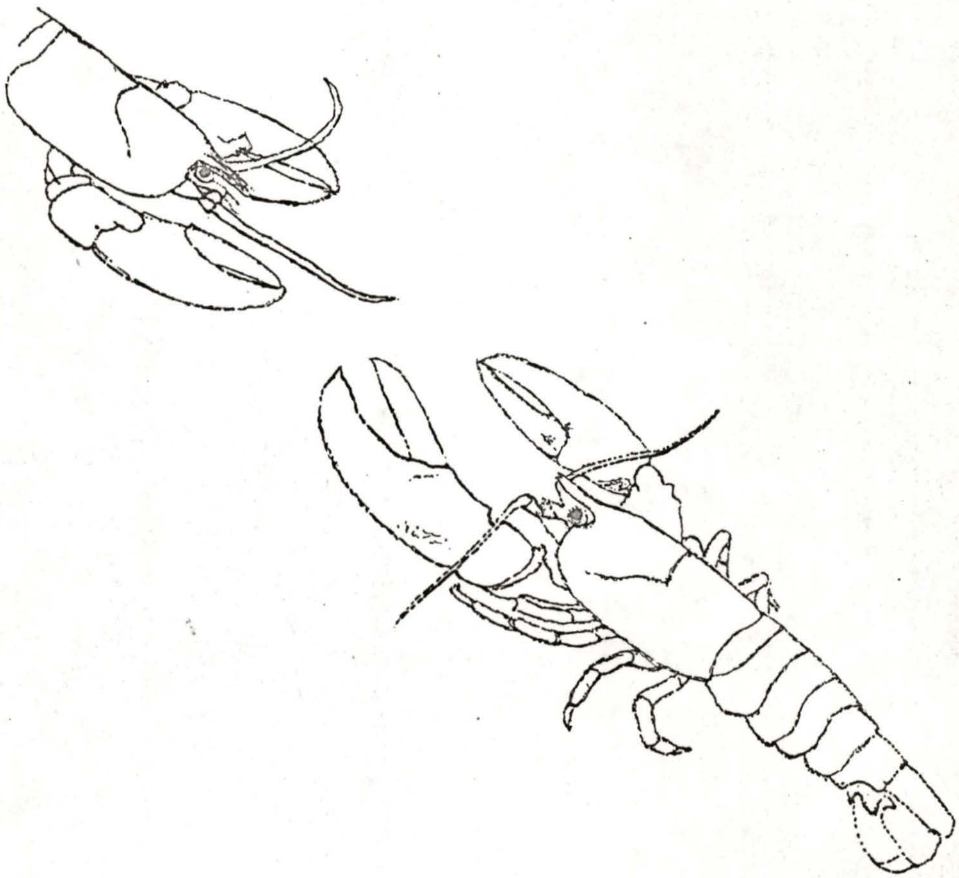


Fig. 7. The lower lobster is rushing, while the upper one is beginning abdomen flexing.

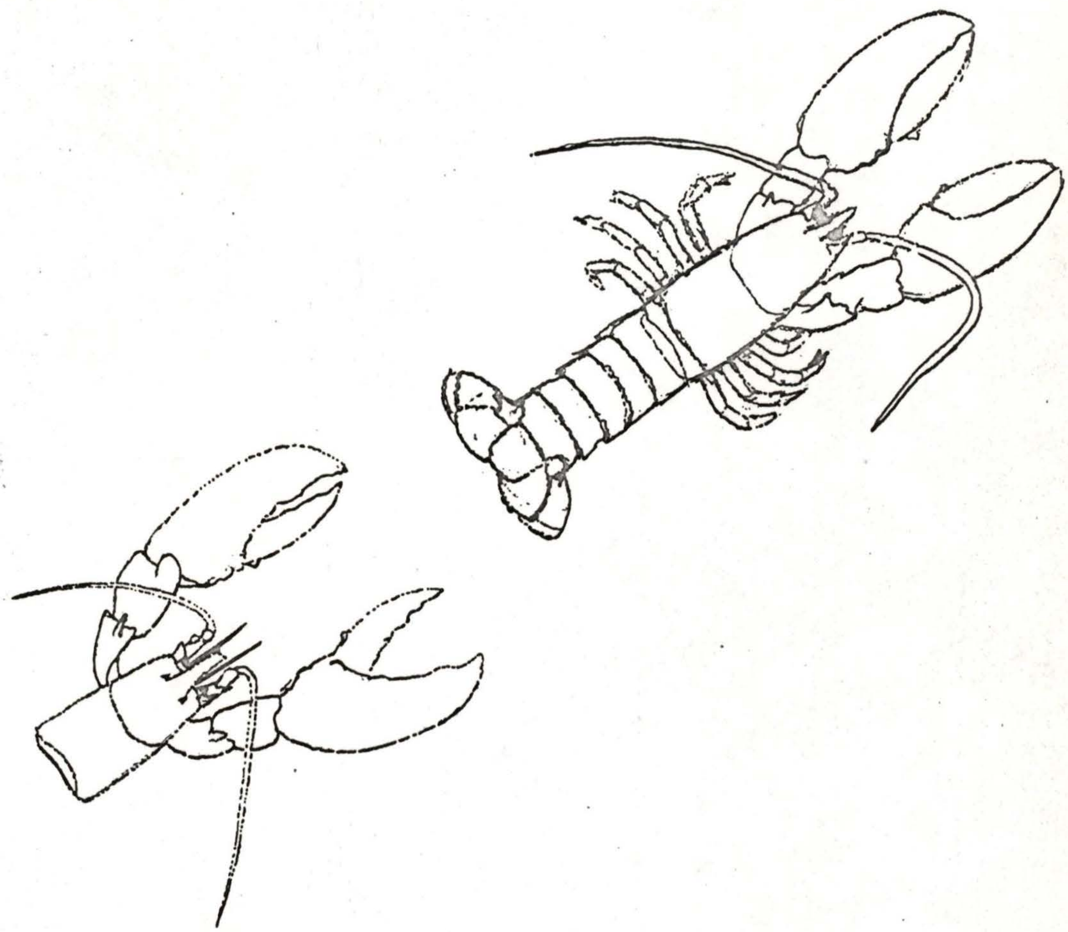


Fig. 8. The lower animal is rushing, while the upper one is running.

palms pointing at the adversary). The chelae are then rapidly brought together in a scissoring motion. As a result, they either strike or pass rapidly in front of the other animal. Simultaneously the lobster raises itself 7 cm off the bottom which is about as far as its walking legs extend (Fig. 9). Sometimes this action is so rapid and vigorous that the lobster leaves the bottom momentarily. Most other body parts remain as they were before scissoring begins.

The duration of scissoring was very short (1 sec.), but it was observed during almost every agonistic encounter.

Rapid turning

This behaviour is shown only by aggressive individuals, when their opponent approaches them from the rear. The abdomen appears to be flexed at an angle and the lobster rotates 180° in less than a second. With its chelipeds in the meral spread posture, it is now facing the antagonist.

A detailed description was not obtained, because rapid turning occurred so quickly and was so rare (observed only 8 times). Frequently a lobster responded to the net, when brought towards it from above, by rapid turning.

Avoidance Behaviour

Backing

When backing, the lobster's tail fan is folded and turned partially under the abdomen, with the stationary pleopods. The antennae are parallel with the bottom, and pointing straight ahead or at an angle of 45° from the long axis of the body. The chelae are pointed in the

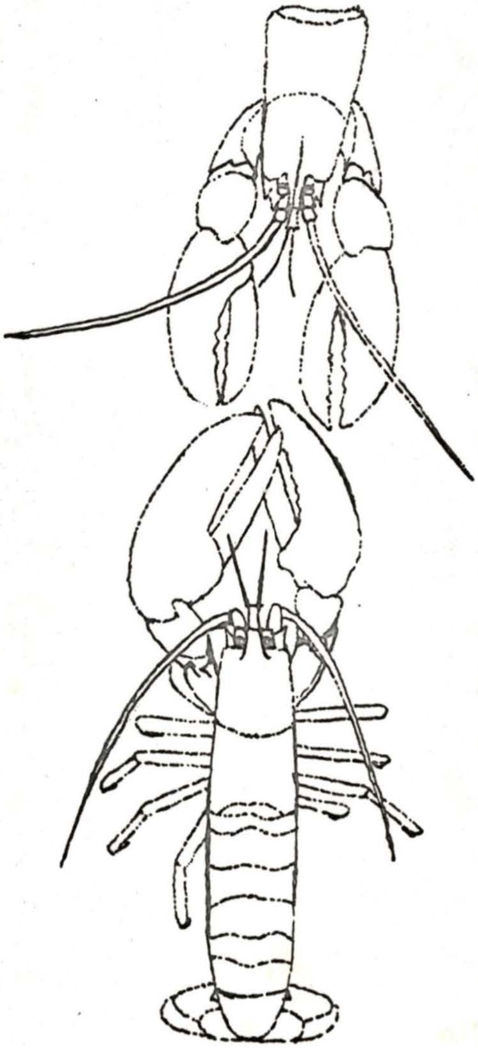


Fig. 9. Scissoring by the lower lobster produces abdomen flexing by the opponent.

direction of the opponent. In this posture the lobster is facing its adversary, while avoiding it by backing away (Figs. 7 and 10).

In a few instances the backing lobster was observed holding its chelae in the meral spread posture. Under these conditions the animal was considered to be backing and displaying meral spread. The movements of the walking legs appeared to be very similar to those shown when following, except that the process was reversed.

Backing was observed during every agonistic encounter, and it was the most common avoidance behaviour pattern. The maximum duration was approximately 3 minutes. A backing lobster moved at a velocity of 0.15 - 0.20 m. per second.

<u>Abdomen flexing</u>

The animal vigorously pushes its body upwards and backwards with the four pairs of walking legs. This raises the individual off the bottom and propels it backwards through the water. As it leaves the bottom, the lobster brings its antennae, chelae and walking legs together anteriorly, to point straight ahead (parallel to the body axis). The legs are now close to the ventral surface of the cephalothorax. This posture produces a streamline body form which is less resistant to backward movement through the water (Fig. 11). The open tail fan is rapidly brought down under the body by contraction of the ventral abdominal muscles (the abdomen is now folded in upon itself). This propels the lobster backwards approximately 1 metre. As it sinks to the bottom, the individual moves the walking legs back to their normal position (perpendicular to the body axis).

The abdomen may be flexed several times, before the animal

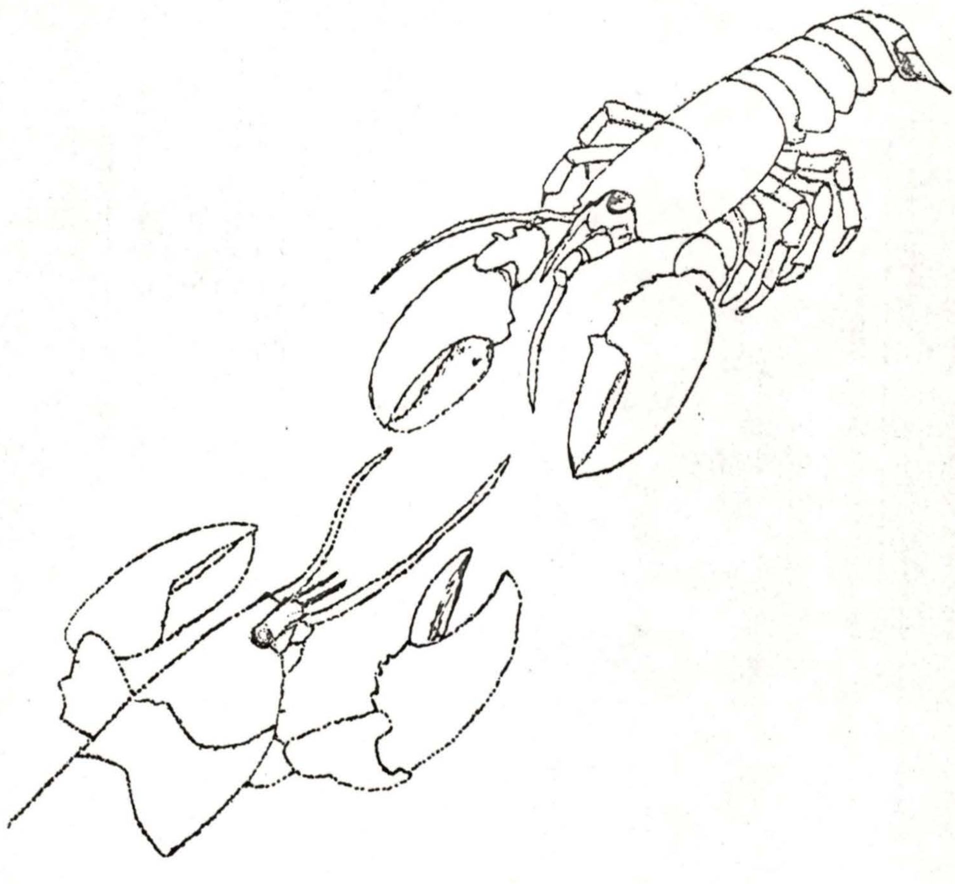


Fig. 10. The upper lobster shows Backing in response to the lower lobsters Meral Spread and Following.

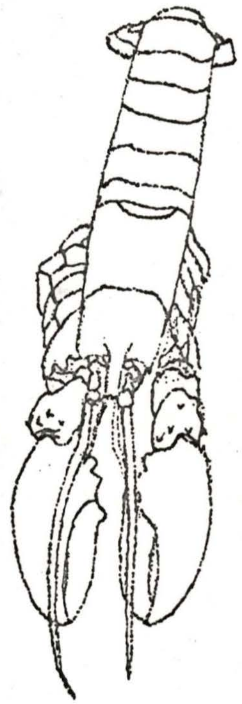


Fig. 11. A lobster abdomen flexing.

returns to the bottom. This is accomplished by folding the tail fan, while the abdomen is being extended; then expanding it, before the abdomen is flexed again. Usually the animal is carried far enough for its advisary to lose sensory contact. When a lobster is approached from the rear it often propels itself completely over top of the opponent.

Abdomen flexing occurred in every agonistic encounter, but its duration was only a few seconds, as the lobster moved up to 3 metres at a velocity of approximately 0.9 m. per second.

Jumping

When a lobster jumps, it flexes the abdomen vigorously in a manner similar to that described for abdomen flexing but the claws are held in the normal meral spread posture and the walking legs remain perpendicular to the body axis. The animal flexes its abdomen only once and is propelled backwards about 60 cm, before returning to the bottom.

Jumping had a maximum duration of only a couple of seconds. Although it occurred in about half of the encounters, it was never recorded on film; therefore a more detailed description could not be made.

Jumping appeared to be a reflex variation of abdomen flexing. The animals did not lose sensory contact when one of them had performed the behaviour pattern, because immediately afterwards they continued their agonistic behaviour.

Walking away

When walking away, the individual moves forward away from its opponent. The abdomen is fully extended with its pleopods stationary and tail fan open.

The chelipeds are held 2 cm off the bottom, with the palms pointing inward about 30° from the longitudinal body axis. The antennae are usually perpendicular to the body axis, but parallel to the substrate. The method and velocity of locomotion is very similar to following (Fig. 12).

The duration of walking away varied from a few seconds to half a minute. It was a common behaviour pattern, but was not demonstrated during every agonistic encounter, because usually a retreating lobster preferred to face its opponent and back away.

Running away

Running away, as the name implies, occurs when a lobster turns away from its adversary and moves away at a rapid velocity. The cephalothorax is held parallel to the bottom, with the abdomen fully extended and its pleopods rapidly beating. The abdomen is often arched upwards with the expanded tail fan about 5 - 7 cm off the substrate. Enough frictional force may be produced, as the water passes up and over it, to keep the lobster firmly on the bottom; thereby providing better traction. The antennae are held parallel to the bottom and perpendicular to the body axis when running begins. If running is continued for 4 seconds or longer, the antennae turn posteriorly so that they become almost parallel to the body axis. The chelipeds are held quite close together with their palms turned outward slightly (Fig. 8). The method of locomotion is similar to that described for rushing.

A mean running away velocity of 0.54 m. per second was recorded. This was slightly slower than that obtained for rushing (0.62 m./sec.). Often running away was observed only a few seconds, before sensory contact

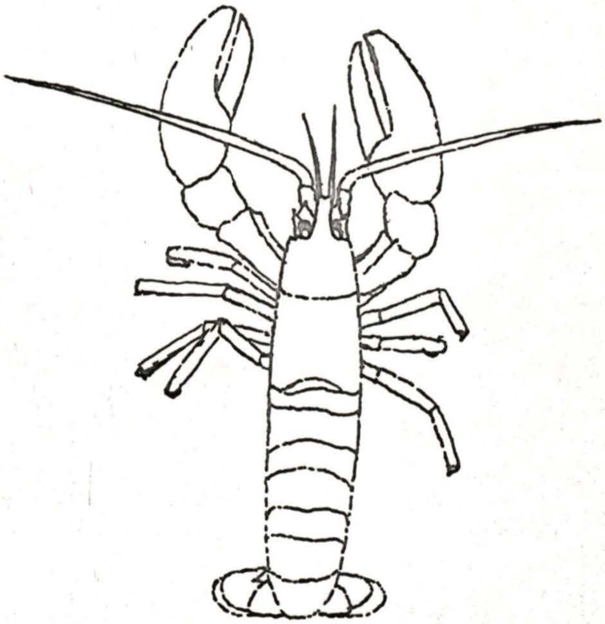


Fig. 12. This animal is Walking Away from an opponent.

between the combatants was lost. It occurred frequently when one animal approached the other from the rear.

Side-ways

During sideways behaviour, the retreating lobster moves sideways away from an opponent, exposing one of its lateral surfaces. The abdomen extends fully, with its pleopods stationary against its ventral surface. The antennae are held in the normal resting posture at angles of 45°, pointing upwards from the tank bottom and away from the body axis. Sideways movement appears similar to normal locomotion among crabs, but is somewhat slower (Fig. 13).

Sideways was observed in about half of the agonistic encounters. Its normal duration was only a few seconds.

To facilitate comparisons, the agonistic behaviour pattern postures are summarized in Table 1.

Discussion of Meral Spread and Antenna Pointing

Meral spread appears to be the threat posture of the American lobster. Manning (1967, p. 92-93) states that "ethologists consider threat to be a direct result of a conflict between attack and escape tendencies, when neither can find separate expression". The supporting evidence is that "threat can sometimes be analyzed into elements belonging both to attack and to escape behaviour". Barnett (1963, p. 87) suggests that among rats threat "has a function like that of many displays, namely, the prevention of injury in a situation which might otherwise result in harmful fighting". Among lobsters meral spread is associated with the aggressive behaviour patterns, approaching and following, and the

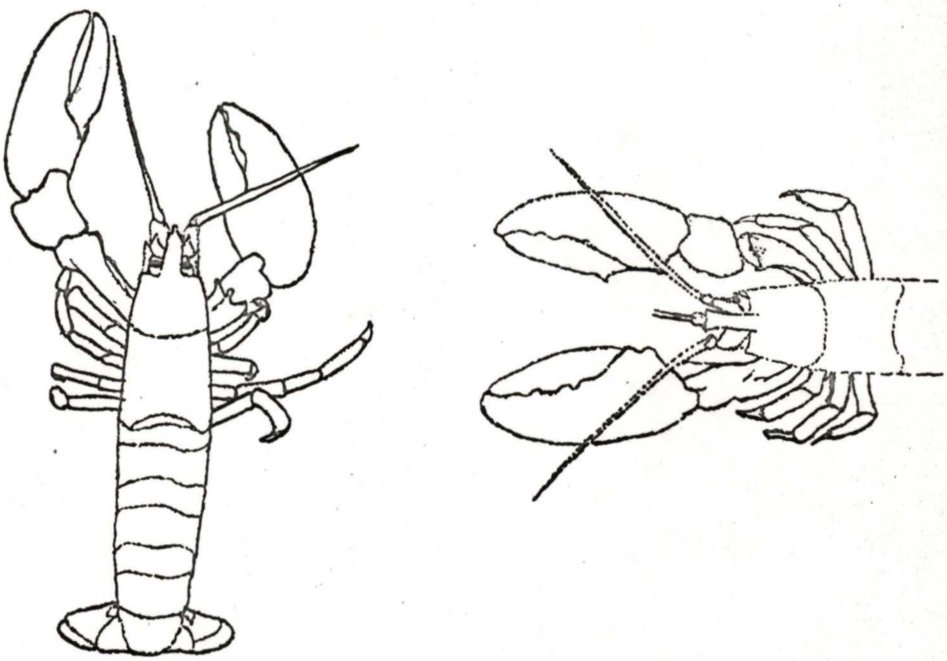


Fig. 13. The lobster on the right is showing Sideways in response to its opponent.

Table 1. A tabular summary of the physical postures and quantitative data on the 15 behaviour patterns.

Behaviour Patterns	Abdomen Position	Tail Fan Position	Position of Pleopods	Cephalothorax Position	Position of Antennae	Position of Chelipeds	Position of Walking legs	Average Duration	Rate of Movement
Antenna pointing	Usually extended	Usually open	-	-	Point anteriorly	-	-	2 sec.	-
Meral spread	Usually extended	-	Stationary	4-5 cm off bottom, anterior higher	45° from body axis and substrate	Held high and wide apart	-	24 sec.	-
Following	Extended	Open	Stationary	3-5 cm off bottom	As Meral spread, or perpendicular to body	-	Moving	21 sec.	0.15 m/sec.
Approaching	Extended	Open	Stationary	3-5 cm off bottom	Usually point forward	-	Moving	3 sec.	-
Pushing	Rigidly extended	Open	Rapidly beating	4-5 cm off bottom anterior higher	Vertical	Touching opponent	Merus 1 & 2 point distally, 3 & 4 point posteriorly	18 sec.	-
Antenna whipping	Extended	Open	-	4-5 cm off bottom anterior higher	Lashing opponent	Meral spread posture	Perpendicular to body	3 sec.	-
Boxing	Extended	Open	-	4-5 cm off bottom anterior higher	Vertical	Jabbing at opponent	Perpendicular to body	2 sec.	-
Rushing	Extended	Open	Rapidly beating	2 cm off bottom	Parallel to substrate, pointing distally or posteriorly	Wide apart or straight ahead	Moving	3 sec.	0.62 m/sec.
Scissoring	Extended	Open	-	Raised to 7 cm above substrate	Usually point posteriorly	Brought rapidly together	May leave the substrate	1 sec.	-
Backing	Partially folded	Folded	Stationary	3-5 cm above substrate	Parallel to substrate and pointing forward or 45° from body axis	Straight in front	Moving	23 sec.	0.16 m/sec.
Abdomen flexing	Vigorously flexed	-	-	Moved off bottom	Point straight ahead	Close together pointed straight ahead	Point straight ahead	3 sec.	0.9 m/sec.
Jumping	Vigorously flexed	Open	-	Moved off bottom	-	Meral spread posture	Perpendicular to body	1 sec.	-
Walking away	Extended	Open	Stationary	2 cm above substrate	Perpendicular to body axis, parallel to substrate	Palms point inwards	Moving	11 sec.	0.15 m/sec.
Running away	Rigidly extended	Open, turned upwards	Rapidly beating	2 cm above substrate	Turn posteriorly	Meral segments close together pointed almost straight ahead	Moving	3 sec.	0.54 m/sec.
Sideways	Extended	Open	Stationary	2 cm above substrate	45° upwards and away from the long body axis	Axis of palms point inwards	Moving	4 sec.	-

avoidance behaviour, backing. By merely demonstrating this posture near the end of an encounter, the winning animal can cause its opponent to withdraw. Meral spread is placed with the aggressive behaviour patterns, because it is shown more often by the aggressive individual (with aggressive behaviour 2961 times, avoidance behaviour 721 times).

This behaviour is called meral spread, instead of chelae spread, for two reasons. First, consistency should be maintained between present and previous names for crustacean threat postures. Wright (1968) discusses "lateral merus" (chelae spread, merus perpendicular to long body axis) and "chelae forward" (merus parallel to long body axis, chelae vertical) displays of many brachyurans. Dingle (1969) names the lateral merus posture of the stomatopod Gonodactylus bredini, "meral spread". Second, the meral segments of the lobster's chelipeds are perpendicular to the long body axis thus spreading the chelae.

Antenna pointing is probably an investigative response to visual stimulation. It can also be a response to a "growl-like" sound that some lobsters are known to produce. When stimulated by handling, highly aggressive lobsters produce a low frequency internal sound (100 - 130 Hz) with maximum sound pressure levels of 16 db above 1 microbar. After being handled several times the sound can also be elicited by visual stimulation (Fish 1966). Visual contact is probably more important here in eliciting antenna pointing, because at least one animal has to detect the presence of its opponent before the sound would be produced. A crude, unsuccessful attempt was made to determine whether the lobsters were making this sound in response to each other, but it could not be identified above the background noise in the observation tanks.

A GENERALIZED DESCRIPTION OF LOBSTER AGONISTIC BEHAVIOUR

A generalized description of an agonistic encounter

The lobsters wandered freely about the observation tank when the divider was removed. Recording of the agonistic encounter began when the lobsters showed antenna pointing, an activity which was interpreted as the first sensory contact. Initially, the animals showed mutual aggression by approaching, showing meral spread, and pushing. When pushing was terminated, one or both individuals withdrew. The lobsters then wandered freely about the tank until they again made sensory contact.

The periods during which aggression or avoidance were shown are referred to as agonistic bouts. There were a number of these bouts during an agonistic encounter. The time between agonistic bouts were termed periods of non-social behaviour.

After a few agonistic bouts with mutual aggression, one individual began to avoid its opponent more frequently than the other. Eventually, if the encounter continued long enough, this lobster consistently avoided its adversary whenever it showed aggressive behaviour. A winner was recognized when the more aggressive animal showed rushing and its opponent responded by abdomen flexing. The time at which the winner became apparent varied greatly from one encounter to the next. After this stage,the defeated lobster avoided the winner whenever it came nearer than half a metre.

Quantitative information about the general description of the agonistic encounters

The initial agonistic bout usually began about a minute after the divider was removed. There were from 2 to more than 14 bouts during an agonistic encounter. The first few agonistic bouts were generally longer than the others (maximum duration 14 minutes), and it was during the last of these, that the outcome of the encounter usually became apparent. Later bouts had a duration between 10 and 60 seconds.

The total time that the lobsters showed agonistic behaviour was termed the total response time (TRT). The TRTs expressed as a per cent of the 15 minute encounter varied between 5% and 96%, with a mean of 38%.

SIMILARITIES IN AGONISTIC BEHAVIOUR BETWEEN THE LOBSTER AND OTHER CRUSTACEANS

Until very recently, little has been written about crustacean agonistic behaviour, other than brief descriptions. Most of the early studies were concerned with dominance hierarchies. Douglis (1946 a and b) and Squires (1965) have observed that confined lobsters form a dominance hierarchy, which was probably governed by size. This has also been found among laboratory populations of many other decapod crustaceans: crayfish, Orconectes virilis (Bovbjerg 1953), Cambarellus shufeldtii (Lowe 1956), and Procambarus alleni (Bovbjerg 1956); hermit crabs, Pagurus longicarpus (Allee and Douglis 1945), Calcinus laevimanus (Reese 1961 and 1962), and Calcinus tibicen (Hazlett 1966 d); spiny lobsters, Jasus lalandei (Fielder 1965); and the shore crab Pachygrapsus crassipes (Bovbjerg 1960). In the two studies by Douglis and Squires, the lobsters were confined at high densities. Unlike Pagurus, Clibanarius (Hazlett and Bossert 1965), Jasus, Panulirus (Lindberg 1955), and Pachygrapsus, the American lobster appears to be solitary, so it probably never reaches densities high enough in nature to form dominance hierarchies.

Bovbjerg (1953 and 1956) and Lowe (1956) named four types of "tension contacts", fight, strike, threat and avoidance, among the crayfish Orconectes virilis, Procambarus alleni and Cambarellus shufeldtii. Their use of the term appeared synonymous with an agonistic bout between two lobsters.

A tension contact involving fighting was similar to a lobster bout of mutual aggression. The duration of fighting was longer than the other types of tension contacts as with mutual aggression bouts among lobsters. The crayfish pushed against each other's chelae using the walking legs for leverage, but unlike normal pushing among lobsters, the chelae were interlocked. If not terminated, one of the animals was eventually forced onto its back. Infrequently one animal physically damaged its opponent (Lowe 1956). Damaging aggression among lobsters never occurred in the observation tank. During fighting, crayfish also performed activities which appeared to be similar to approaching and jumping among lobsters.

The second type of tension contact, "strike", was "a unilateral aggression, in which the aggressor approached with outspread chelae, which were thrust suddenly at another, eliciting a retreat by the latter" (Bovbjerg 1953). Strike activity among crayfish seemed similar to a lobster agonistic bout which contained meral spread, approaching, scissoring, and possibly rushing.

The "threat" tension contact was an approach with outspread chelae as in strike, but this alone was sufficient to cause retreat in the other animal (Lowe 1956). This was probably similar to an agonistic bout containing approaching, meral spread and following seen among lobsters.

The final tension contact involved the elicitation of avoidance in a subordinate crayfish, with no threatening behaviour by the dominant discernible to the observer. This type of agonistic bout was periodically observed among lobsters near the end of an encounter. Bovbjerg and Lowe did not elaborate on the terms "retreat" or "avoidance" so no comparison of lobster and crayfish avoidance behaviour could be made in this regard.

Bovbjerg (1956) also described activities that are similar to antenna pointing and rapid turning, but did not name them.

Fielder (1965) mentioned antennae orientation and the "threat" attitude directed at approaching individuals by the spiny lobster Jasus lalandei. During threat the animal stood high on its legs, waving its first pair of walking legs at the challenger. Among spiny lobsters the first pair of walking legs is not developed into large chelae as in lobsters and crayfish, but have a pointed dactyl at their distal end. The two legs can be brought together as a pair of forceps with barbed ends. Panulirus interruptus assumed a similar aggressive attitude when similarly stimulated. Lindberg (1955) described "swimming" in P. interruptus. The animal flexed the abdomen and expanded the tail fan, pulling itself backwards. The walking legs were brought up close to the body and pointed anteriorly. Swimming appeared identical to abdomen flexing described among lobsters. Similar distances and velocities were attained.

Allee and Douglis (1945) described fighting for shells in the hermit crab Pagurus longicarpus. One animal grasped the chelae and legs of the opponent with its larger chela, and jerked quickly, removing the adversary from its shell. Reese (1962) working with Calcinus laevimanus described threat and a submissive posture. Threat posture consisted of raising the brightly marked larger chela. The submissive posture was observed when a large animal occupied a shell from which it had just removed a smaller hermit crab. The smaller animal would fall over on its side or back making no further effort to defend itself. Under natural conditions one of the crabs often withdrew before it was evicted from its shell. Hazlett (1966 a, 66 b, 66 c, 1967 and Hazlett and Bossert 1965) studied agonistic behaviour among many hermit crabs such as:

Clibanarius cubensis, *C. tricolor*, *Calcinus tribicen*, *Pagarus marshi*, *P. bonairensis* and *Paguristes grayi*. They showed ritualized visual agonistic displays with their ambulatory legs and chelipeds. The legs were raised laterally. The chelae were fully extended anteriorly or 'presented' with the long axis of the palm perpendicular with the bottom. Normally they were held under the body and hidden from view. During an interaction, one individual often moved away before any physical contact was made. Some of the deep water hermit crabs such as *Pagurus politus* lower their bodies close to the substrate, which is believed to have an appeasement function (Hazlett 1966 c).

Dingle and Caldwell (1969) studied the aggressive and territorial behaviour of the stomatopod shrimp *Gonodactylus bredini*. It performed various acts such as: approach, meral spread, lunge-chase, strike, and avoidance, which appeared to be analgous respectively to approaching, meral spread, rushing, scissoring and abdomen flexing described for *Homarus*.

Bovbjerg (1960) briefly described "tension contacts" between crabs of the species *Pachygrapsus crassipes*. These involved threat and pushing behaviour. Crane (1958, 66 and 67) described threat and fighting displays of *Uca maracoani* and *U. rapax*. She has also described aggression in the Australian shore crabs *Heloecius cordiformis* and *Hemiplax latifrons* (Griffin 1968). Shone (1961 and 68) observed the agonistic activities of 34 species of crabs and has described two general types among the brachyurans. The first involved physical interactions, with the exchange of blows and a mutual testing of physical strength. This was found mainly in species of the aquatic brachyuran families. The second involving the semi-terrestrial grapsids and ocypodids was more formalized using optical signals and ritualized displays. Physically damaging fighting was extremely rare. Wright (1968) has classified and discussed the evolutionary history of these displays.

Unlike crayfish and lobsters, crabs do not orientate their antennae towards their adversaries. This may be due to the fact that their main tactile organs are the walking legs; locomotion is lateral with probing movements of the walking legs (Bovbjerg 1960).

Two similarities appear among those decapods for which agonistic behaviour is described. All observers describe a "threat" posture or display, involving the animal raising itself on its walking legs and orienting or displaying its first pair of legs or chelae towards its adversary. All the species studied have some form of pushing display (fighting) during which the chelae are touching or even interlocked. Infrequently fighting leads to physical damage of one individual. This may be rarer under natural conditions for some species, because many of the studies have been done under crowded laboratory conditions. Damaging aggression has occurred among the lobsters in the small holding tanks when the divider has been pushed over, but has never been observed in the 6-foot diameter observation tanks.

BEHAVIOURAL VARIATION DURING THE 15-MINUTE OBSERVATION PERIODS

A 15-minute observation period was chosen as the minimum time in which winning and losing animals of an encounter could always be determined. The object of this section was to determine if agonistic behaviour varied qualitatively or quantitatively during or between encounters. If there were variations, were there any patterns to them or explanations for them.

The frequency histogram of total response times (TRT) expressed as a percent of the 15-minute observation period indicated great variation between encounters (Fig. 14). Differences between various lobster TRT frequency distributions could not be demonstrated by statistical tests which assumed normality, because these distributions were not normal, but skewed towards the higher value ($p < .001$, skewness = 0.9881). Therefore two other indices of behavioural variability were used. Number of seconds per minute during which behaviour was recorded (One-minute Response time or MRT) summarized changes in overall agonistic activity. Frequencies per minute for each behaviour pattern showed changes in the manner in which the overall activity was expressed.

Variation within the encounters

Mean one-minute response times (MRT, Fig. 15) decreased during male/male and male/female encounters from about 32 to 20 seconds. These were significant in a comparison of the first 6 with the last 9 class intervals ($t = 5.27$ $p < .01$, $t = 10.18$ $p < .001$). For female/female and female/male encounters a smaller reduction of 25 - 18 seconds was also

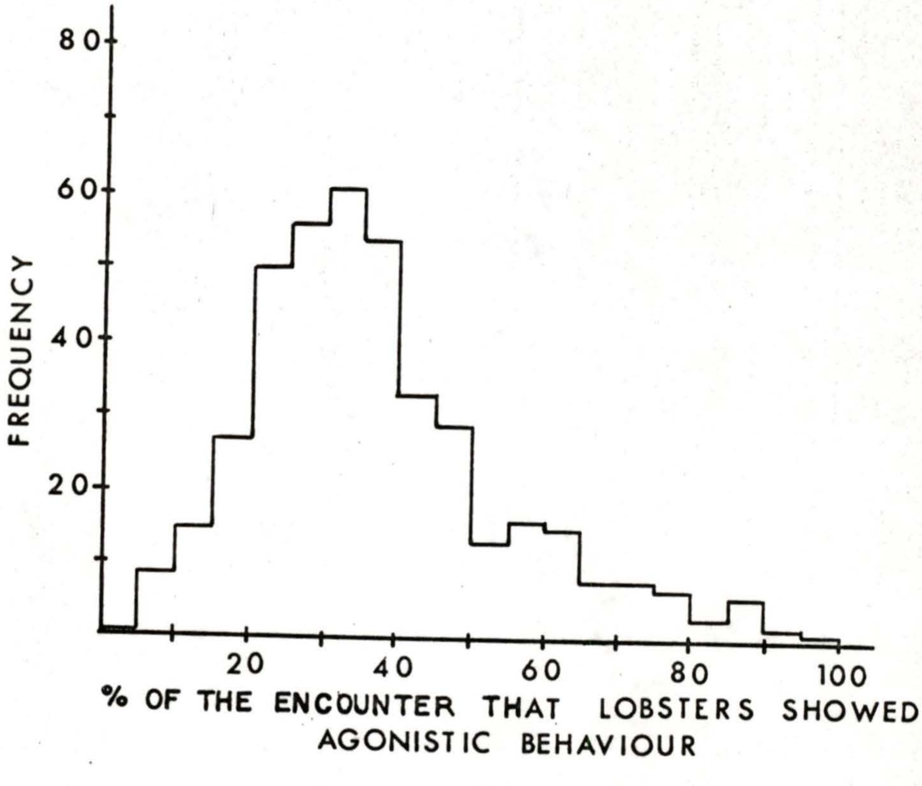


FIG. 14. FREQUENCY HISTOGRAM OF THE PERCENT OF THE ENCOUNTER THAT THE LOBSTERS SHOWED AGONISTIC BEHAVIOUR. NO. ENCOUNTERS = 414

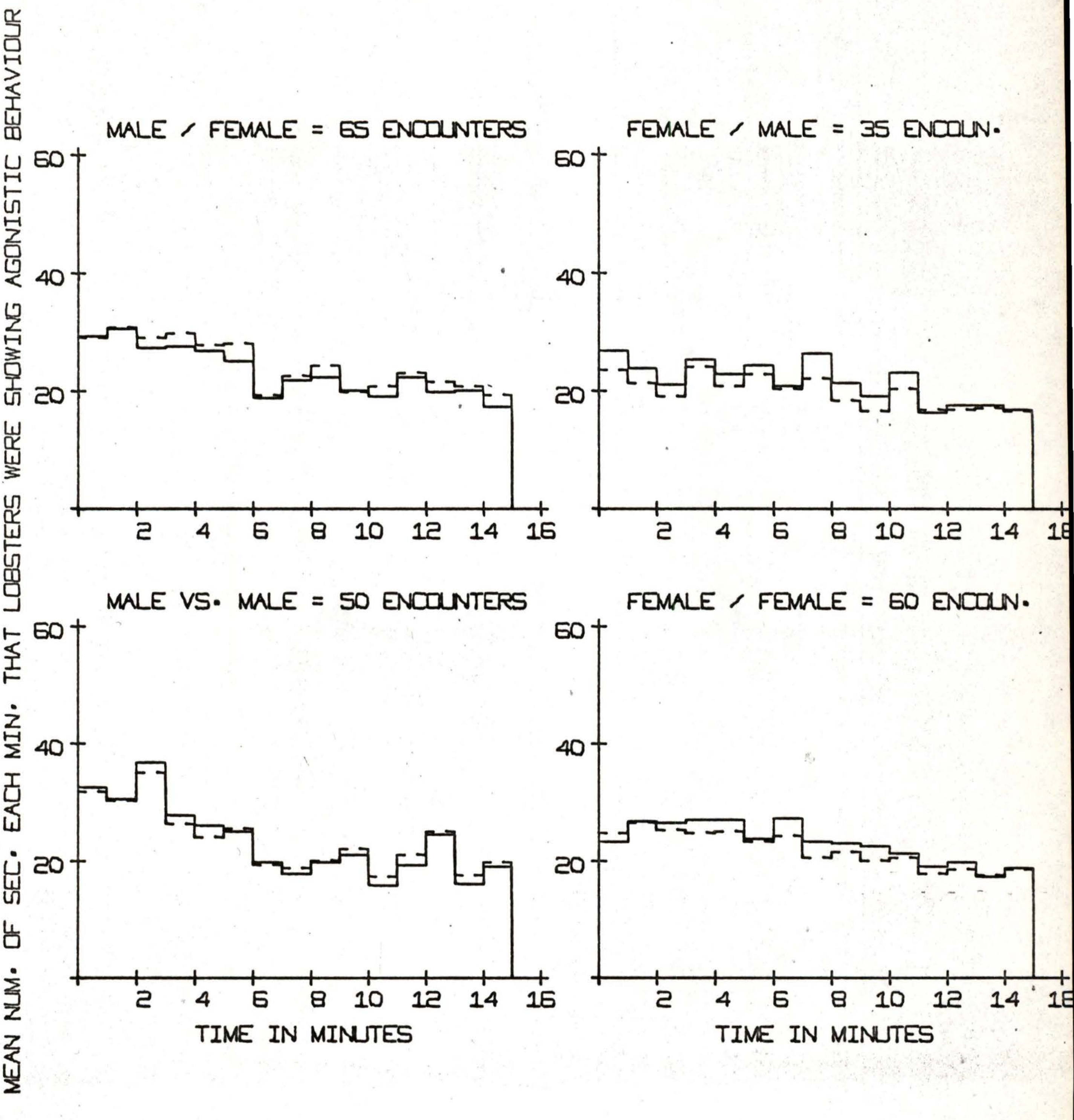


FIG. 15. MEAN ONE MINUTE RESPONSE TIMES FOR EACH MINUTE OF THE 15 MINUTE AGONISTIC ENCOUNTERS (WINNERS - SOLID LINES , LOSERS - STIPPLED LINES).

significant between the first and last half of the encounters ($t = 5.26$ and 4.13, $p < .01$). The amount of agonistic behaviour shown by the lobsters declined throughout the observation periods. Standard deviations of the MRTs for each minute were high (13 - 22) relative to the means, reflecting great variation between encounters or animals or both.

To determine the reason for the high initial mean MRTs, the duration in seconds of each bout - periods of continuous agonistic activity - and their intervening periods of non-social behaviour were tabulated under the minute in which they began (LOBSTER 10, Appendix I). Means were calculated for each of the 15 one-minute intervals and then plotted in a histogram. For example, the mean length of the bouts which began during the first minute of the encounters was 77 seconds. The first few bouts of the encounters were longer than the others, but the mean durations of the periods of non-social behaviour tended to remain fairly stable (Fig. 16). Therefore more agonistic activity took place during the first few minutes of the observation periods, because the first few agonistic bouts tended to be much longer than the others. Low last minute values are to be expected, since recording was stopped abruptly at the end of 15 minutes (Fig. 16).

Mean per minute frequencies for the 15 one-minute intervals of the encounters were calculated, in order to determine which behaviour patterns accounted for the decline in agonistic behaviour. The behaviour patterns were divided into four groups characterized by the rate of decline or the prominence of their frequencies among winners and losers.

Group 1 contains the behaviour patterns pushing, antennae whipping, jumping, boxing and scissoring which among both winners and losers declined in mean frequency (Fig. 17). The commonest activity

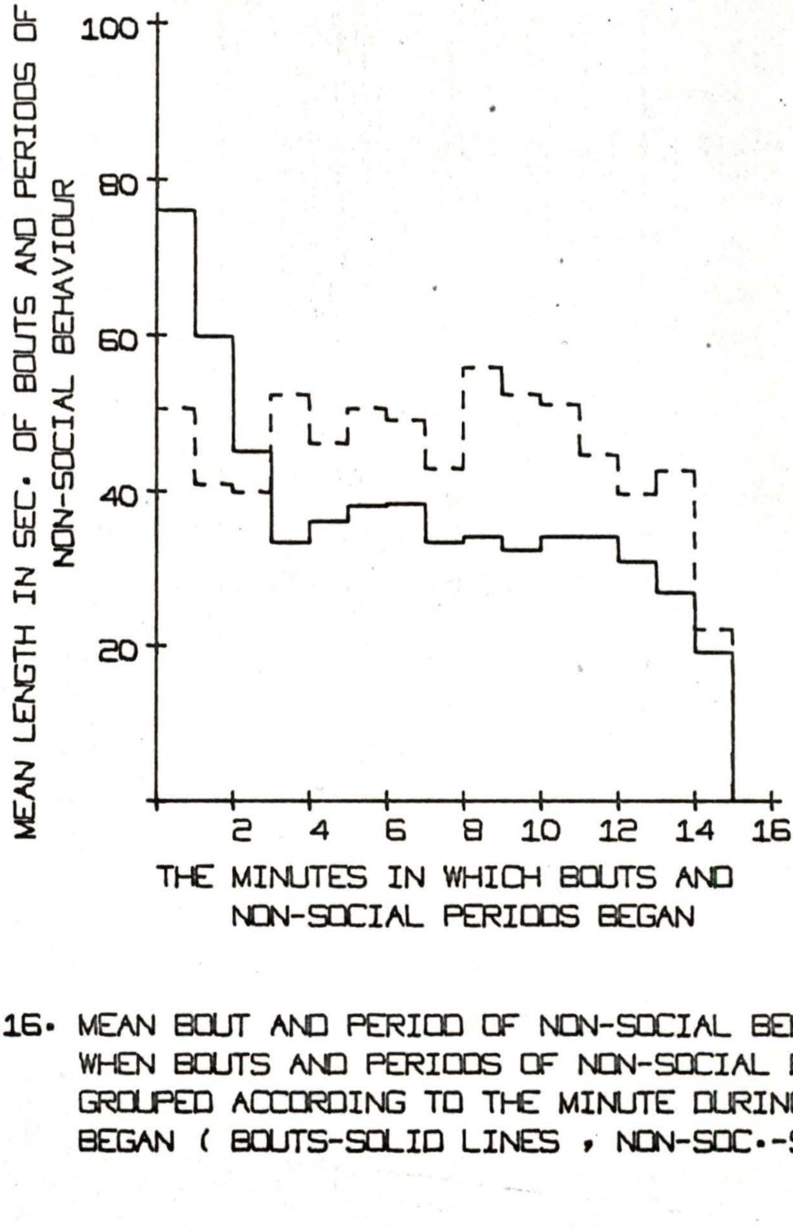


FIG. 16. MEAN BOUT AND PERIOD OF NON-SOCIAL BEHAVIOUR LENGTH WHEN BOUTS AND PERIODS OF NON-SOCIAL BEHAVIOUR WERE GROUPED ACCORDING TO THE MINUTE DURING WHICH THEY BEGAN (BOUTS-SOLID LINES , NON-SOC.-STIPPLED LINES).

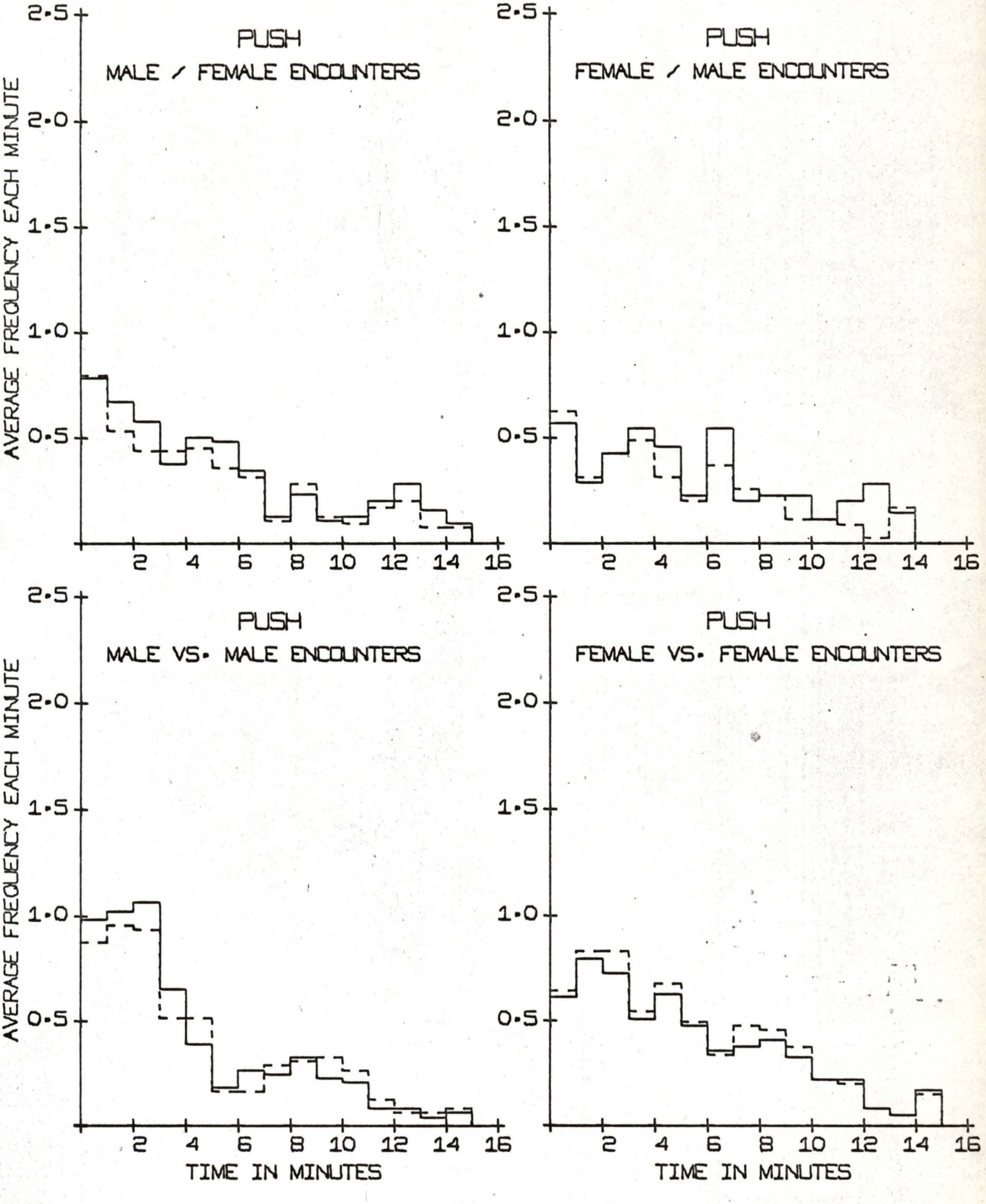


FIG. 17. MEAN FREQUENCIES OF THE GROUP 1 BEHAVIOUR PATTERNS EACH MINUTE OF THE FEMALE VS. FEMALE , MALE VS. MALE , FEMALE / MALE AND MALE / FEMALE ENCOUNTERS (WINNERS-SOLID LINES , LOSERS-STIPPLED LINES)

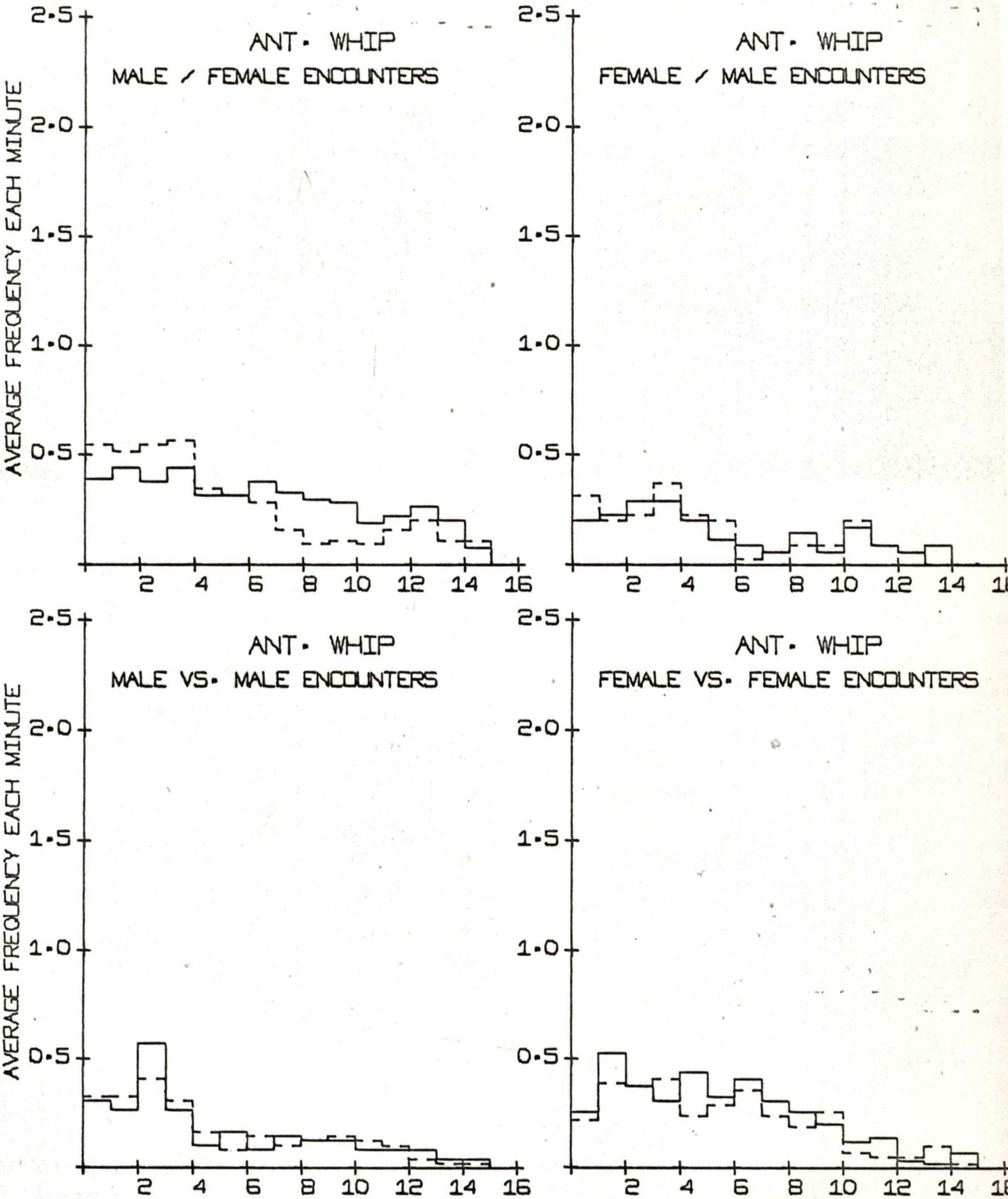


FIG. 17. CONTINUED.

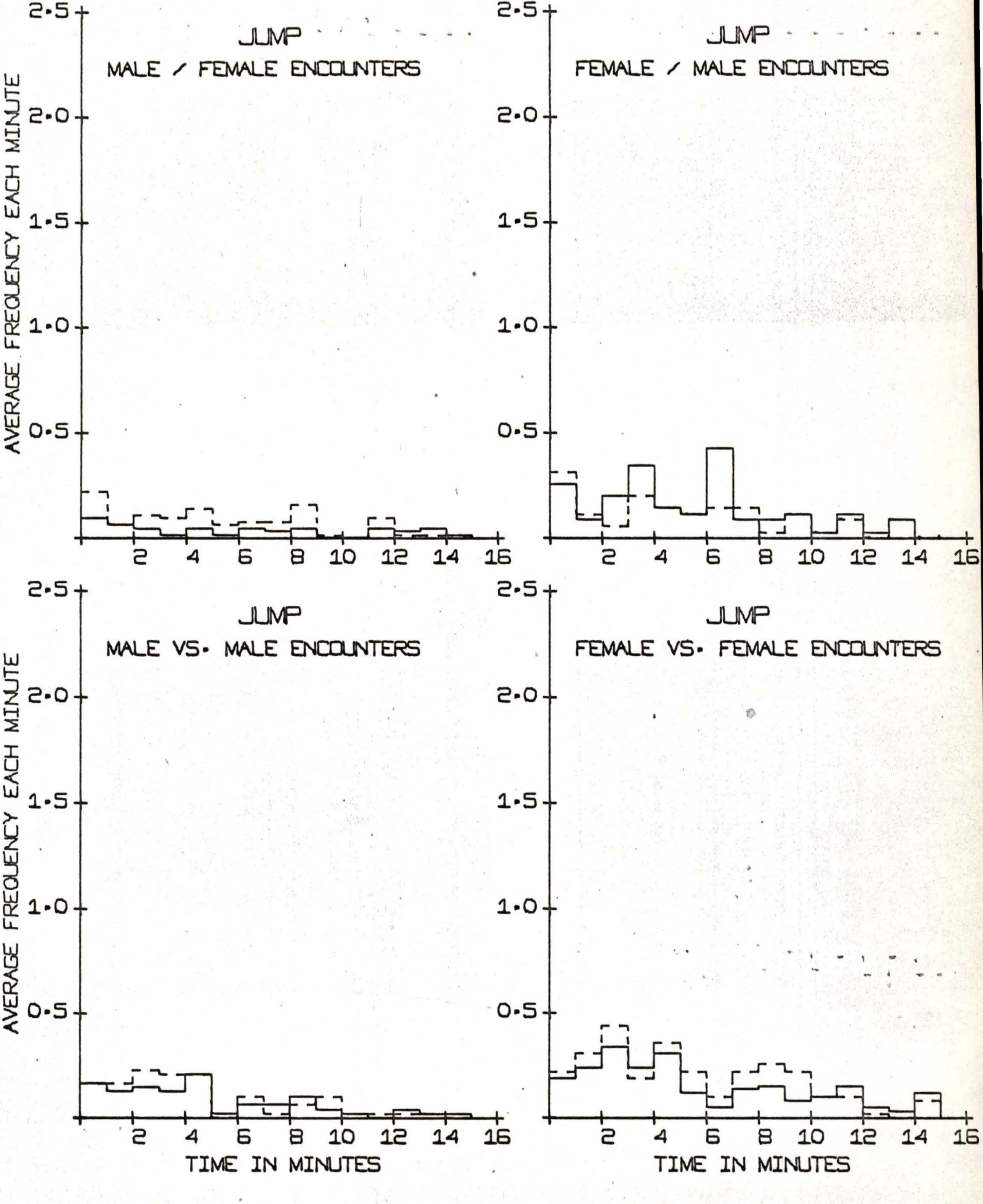


FIG. 17. CONTINUED.

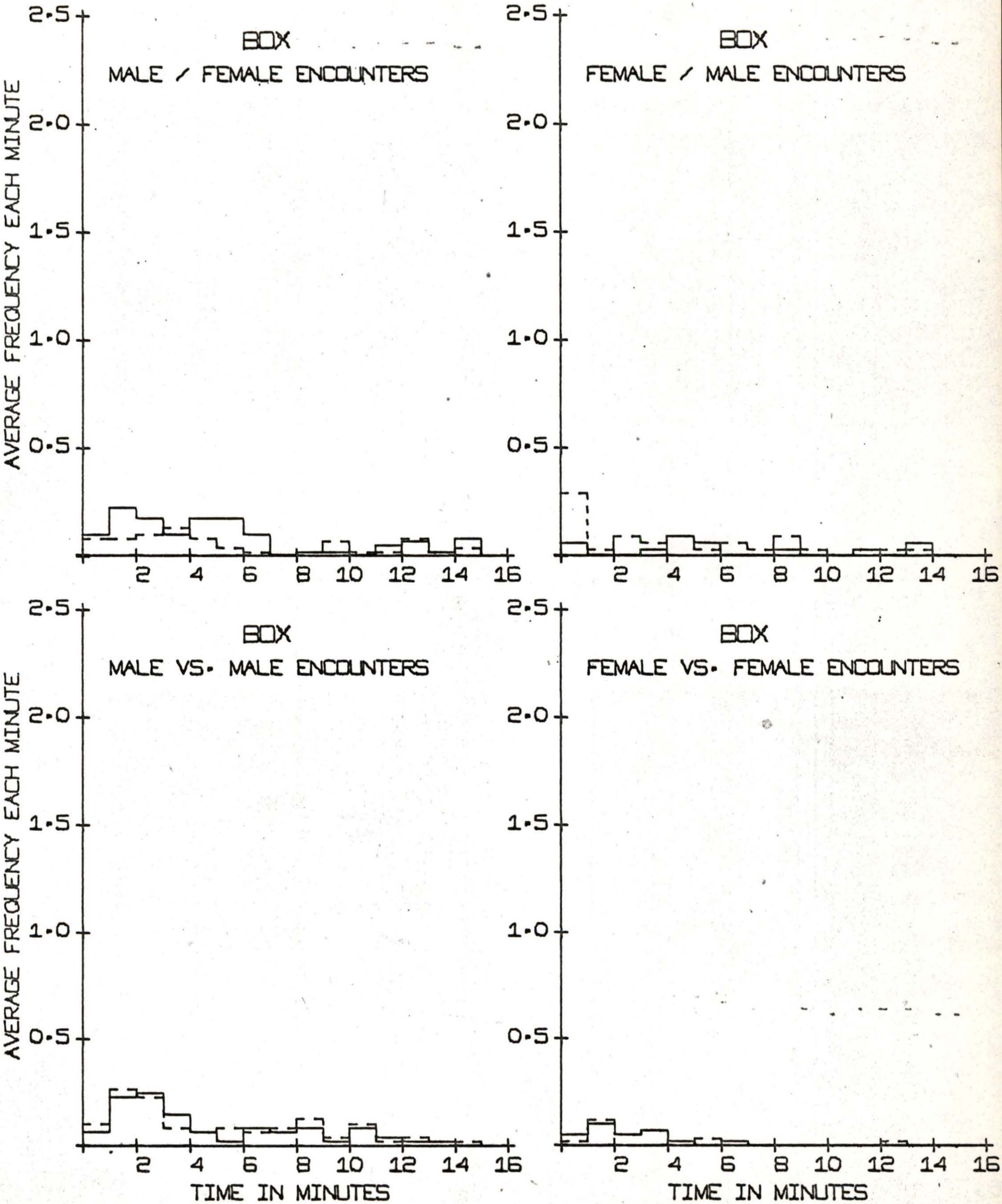


FIG. 17. CONTINUED.

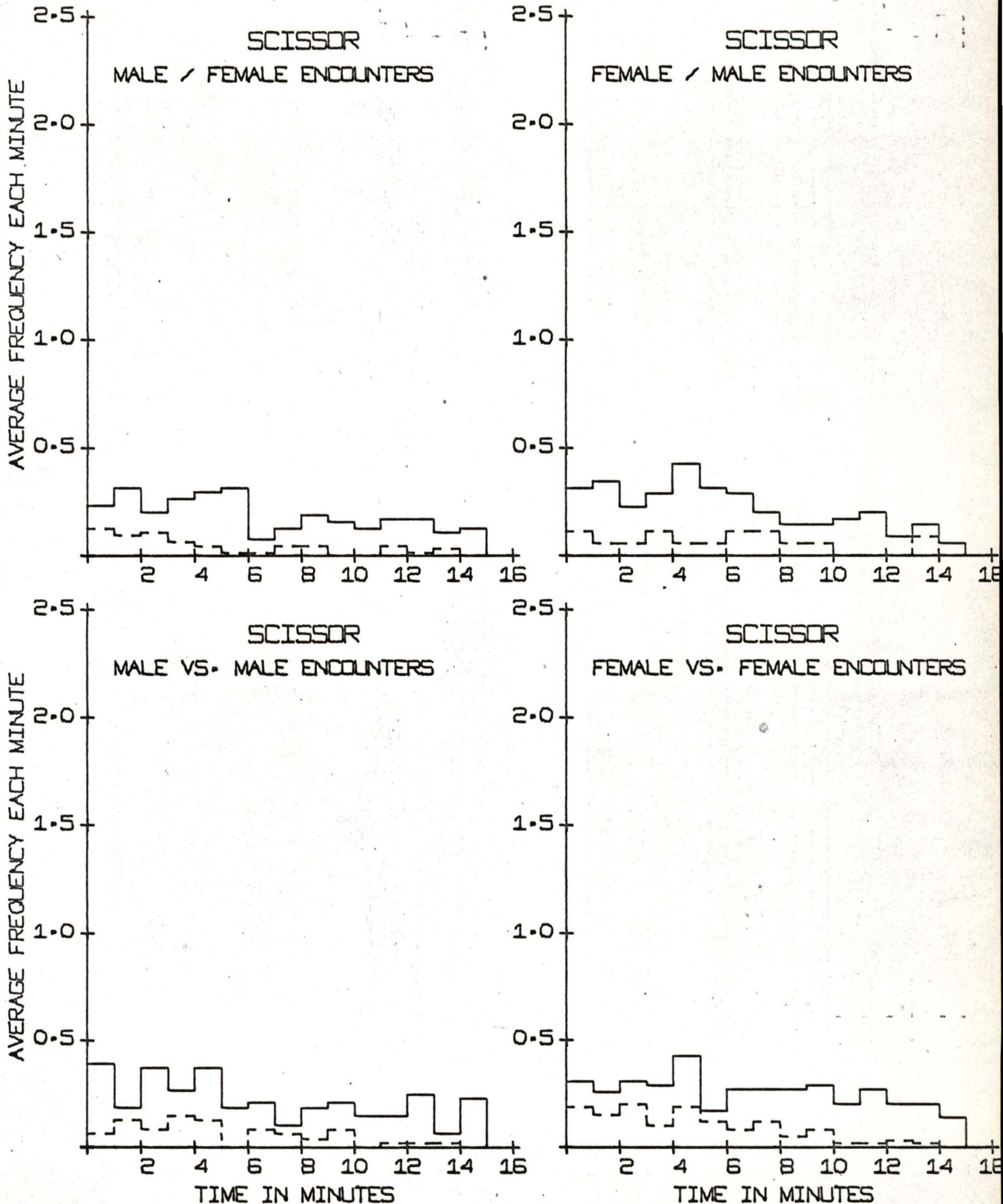


FIG. 17. CONTINUED.

pushing had the highest initial frequency of 0.6 - 1.0 per minute, which dropped almost to extinction by the end of the encounters. Scissoring's average frequency per minute did not always decline as rapidly among winners. The reason will be explained later.

Group 2 patterns, side-ways, abdomen flexing, running away, walking away and backing, were shown mostly or exclusively by losers (Fig. 18). The first three were shown almost exclusively by losers, while the last two were shown by winners, but their mean per minute frequencies usually declined. The mean frequencies of the behaviour patterns in group 2 increased, decreased or simply fluctuated throughout the encounters.

Group 3 patterns were shown mostly or exclusively by winners. Following and rushing were shown almost exclusively by winners, while approaching and meral spread occurred mostly among winners (Fig. 19). When losers showed approaching or meral spread, their mean per minute frequencies declined throughout the encounters.

Group 4 contains the single high frequency behaviour pattern antenna pointing. Its mean per minute frequency was high initially, but after a drop, it often increased (Fig. 20). Antenna pointing was usually the first behaviour recorded during an encounter. This could account for the high mean frequency during the first minute.

The mean frequency data suggests that the group 1 behaviour patterns could account for the drop of the mean MRTs during the 15 minute observation periods. To check this hypothesis, the duration of pushing - the lengthiest group 1 behaviour pattern (p.14) - was removed from the encounter MRTs and mean values were calculated again. The general decline was no longer apparent; mean MRTs simply fluctuated between 16 and 25 seconds

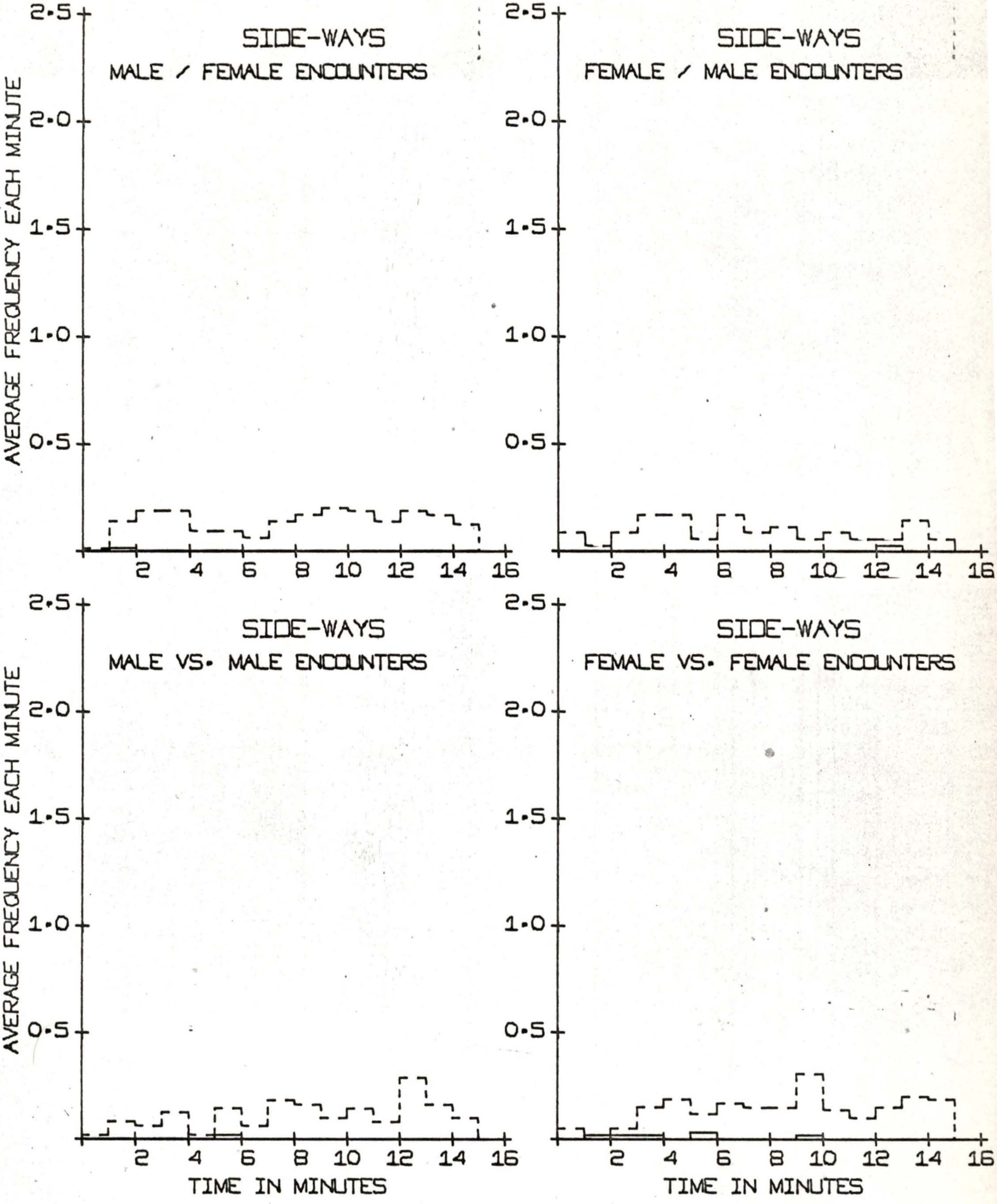


FIG. 18. MEAN FREQUENCIES OF THE GROUP 2 BEHAVIOUR PATTERNS EACH MINUTE OF THE FEMALE VS. FEMALE , MALE VS. MALE , FEMALE / MALE AND MALE / FEMALE ENCOUNTERS (WINNERS-SOLID LINES , LOSERS-STIPPLED LINES)

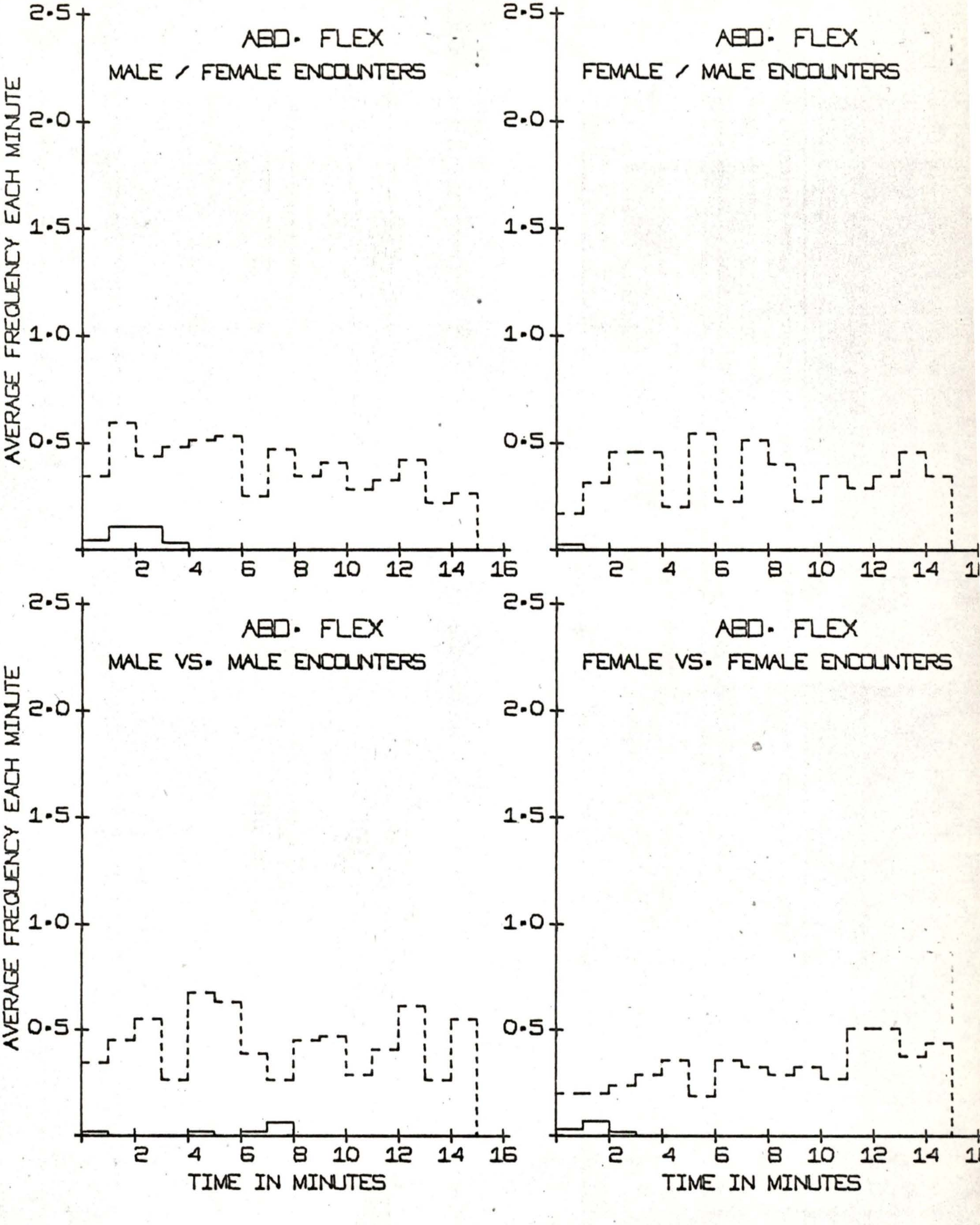


FIG. 18. CONTINUED.

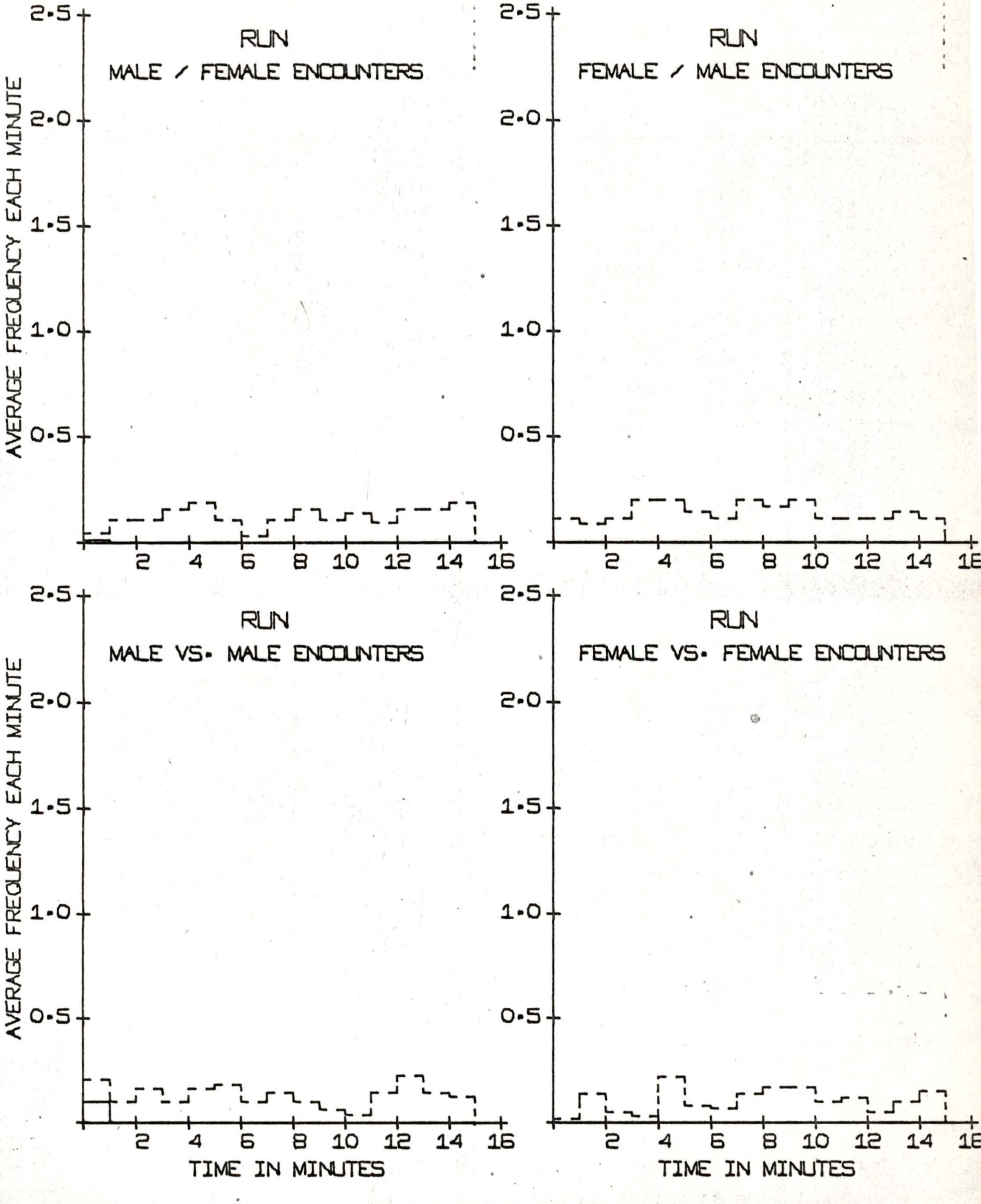


FIG. 18. CONTINUED.

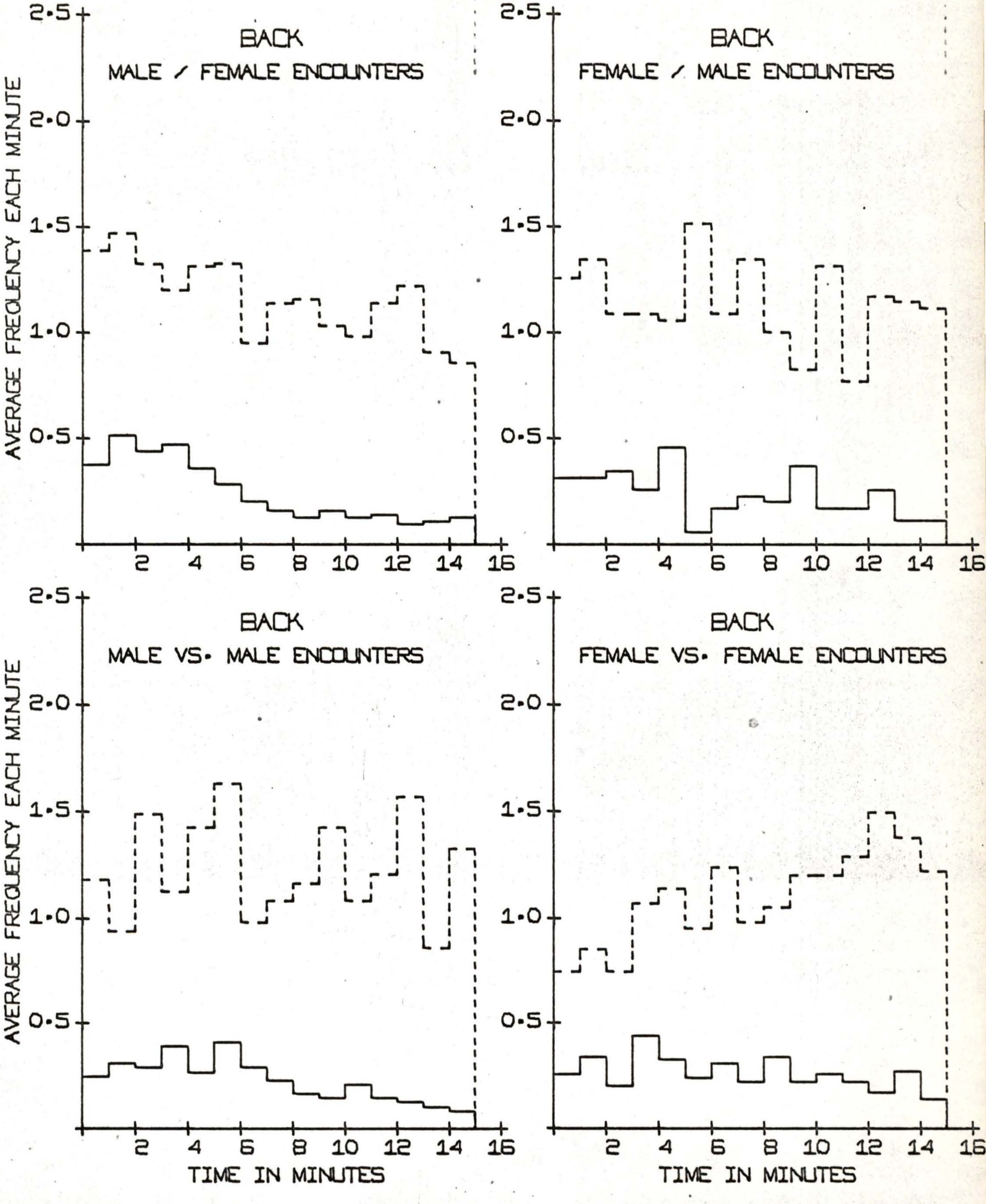


FIG. 18. CONTINUED.

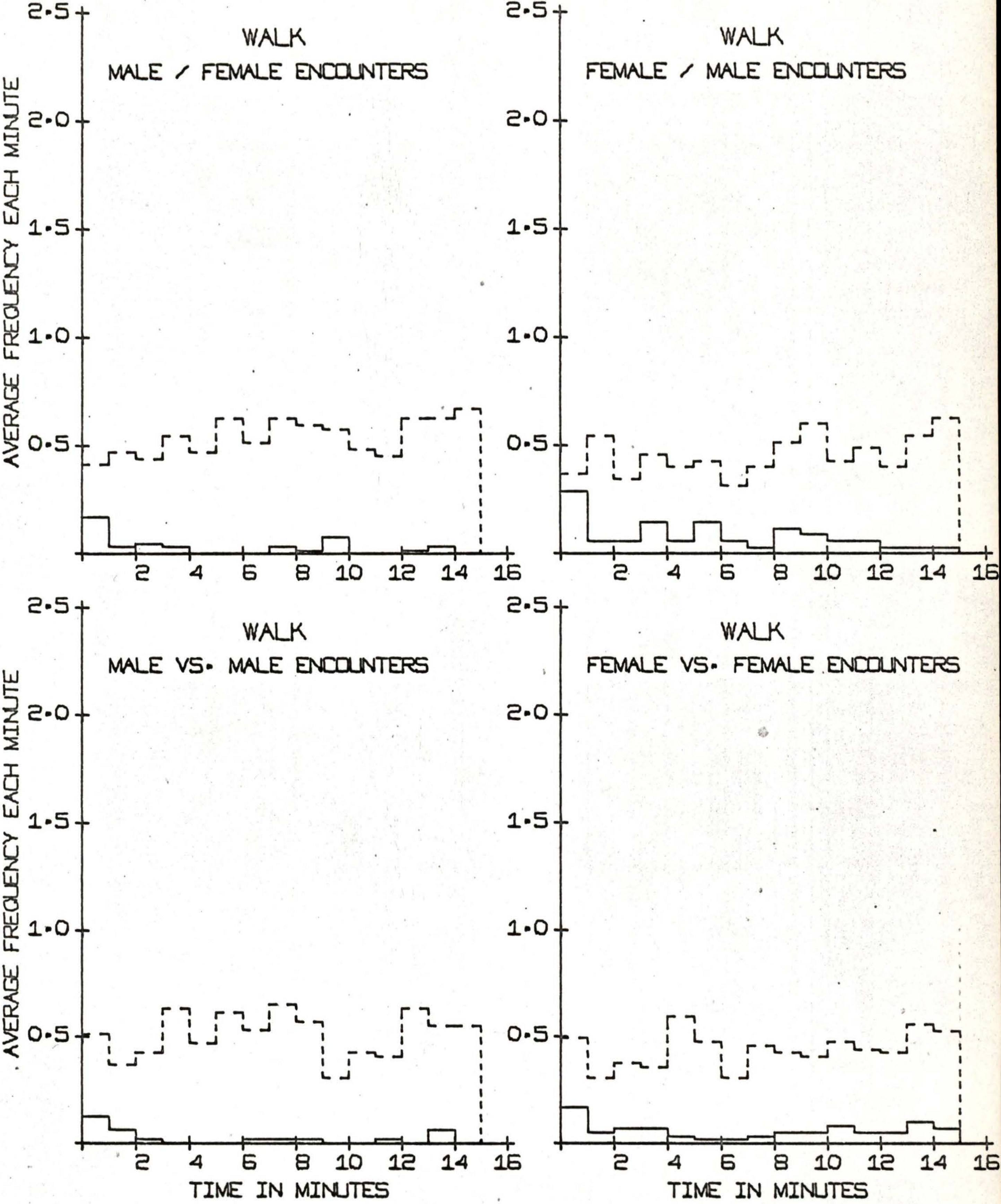


FIG. 18. CONTINUED.

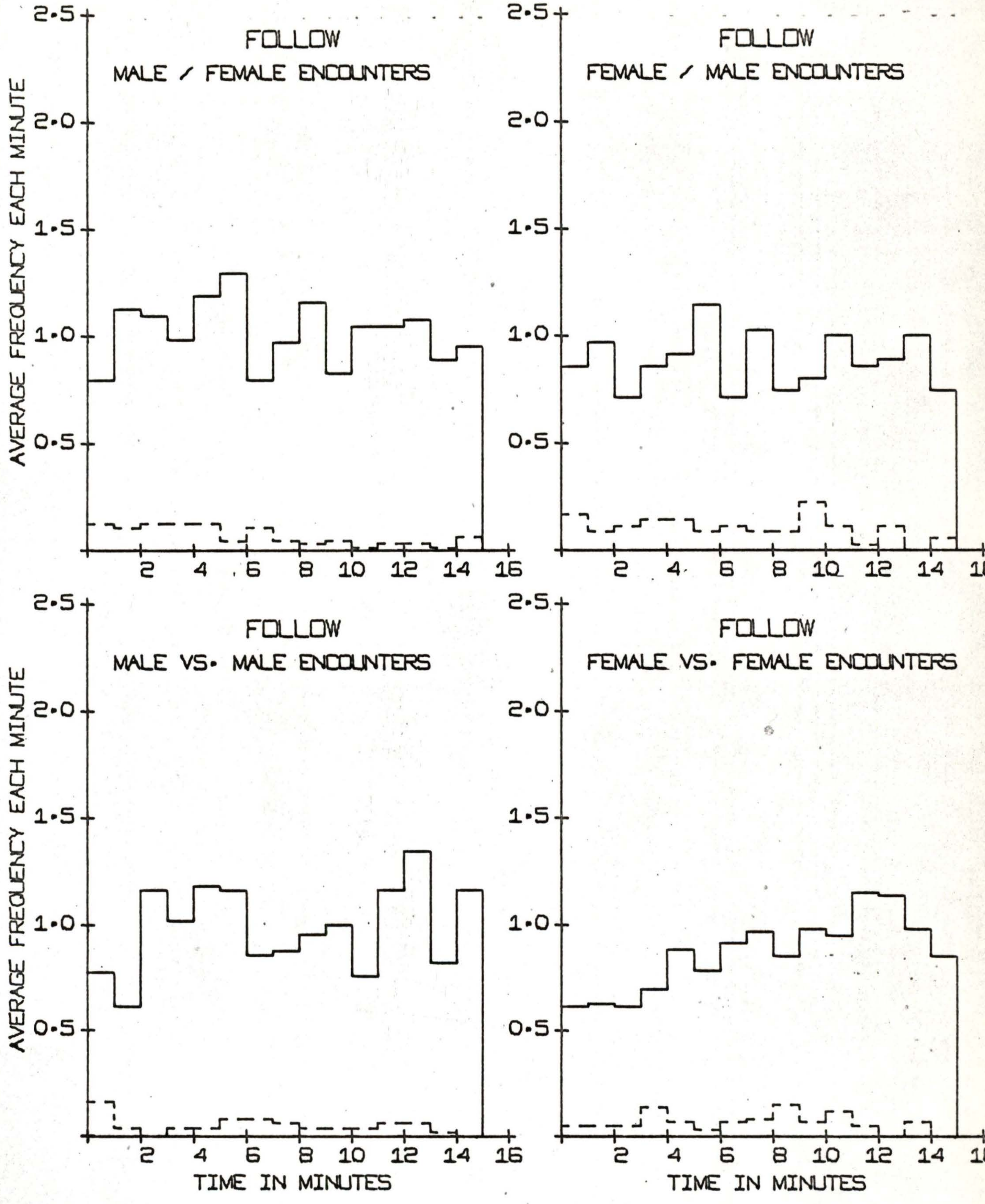


FIG. 19. MEAN FREQUENCIES OF THE GROUP 3 BEHAVIOUR PATTERNS EACH MINUTE OF THE FEMALE VS. FEMALE , MALE VS. MALE , FEMALE / MALE AND MALE / FEMALE ENCOUNTERS (WINNERS-SOLID LINES , LOSERS-STIPPLED LINES)

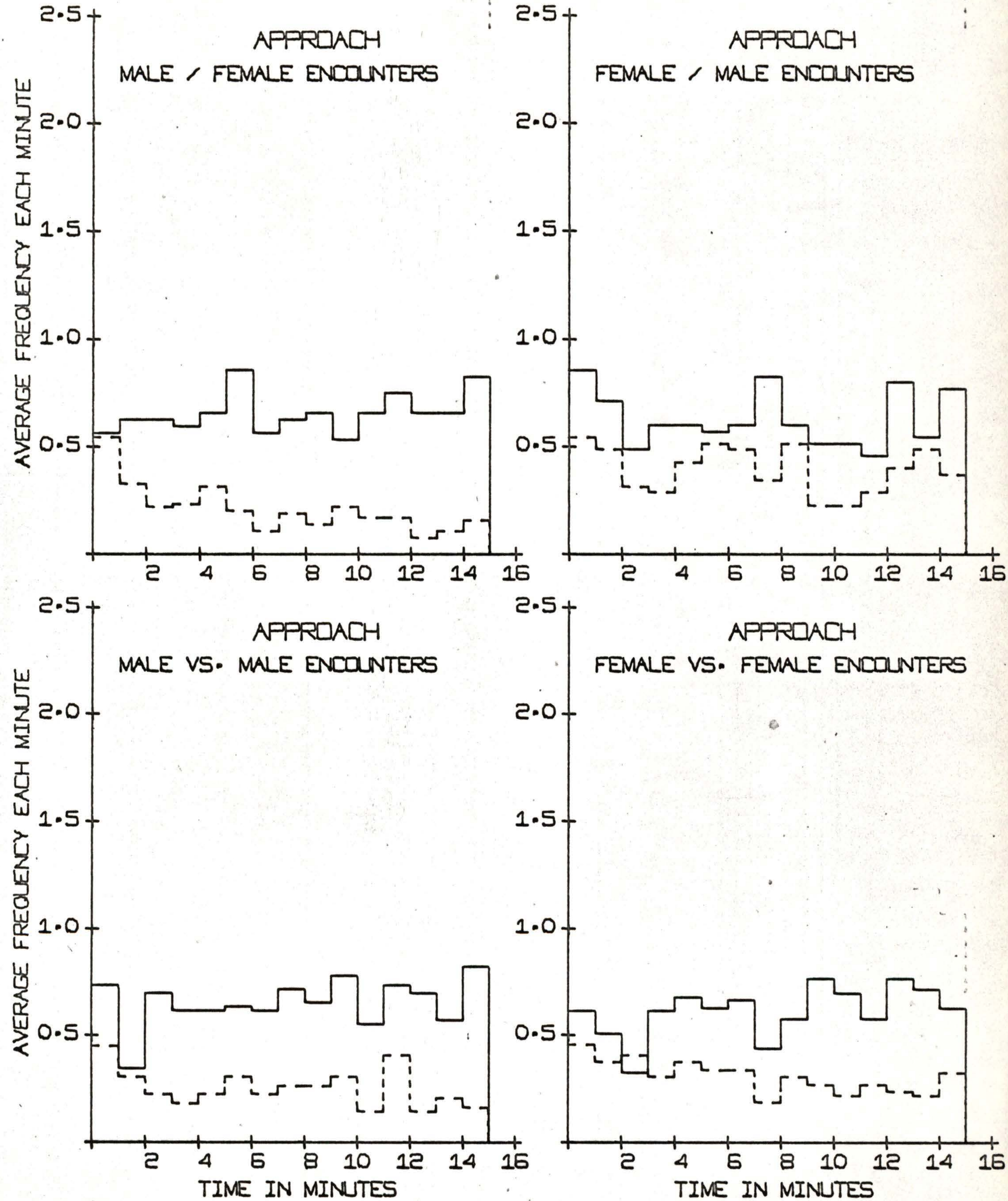


FIG. 19. CONTINUED.

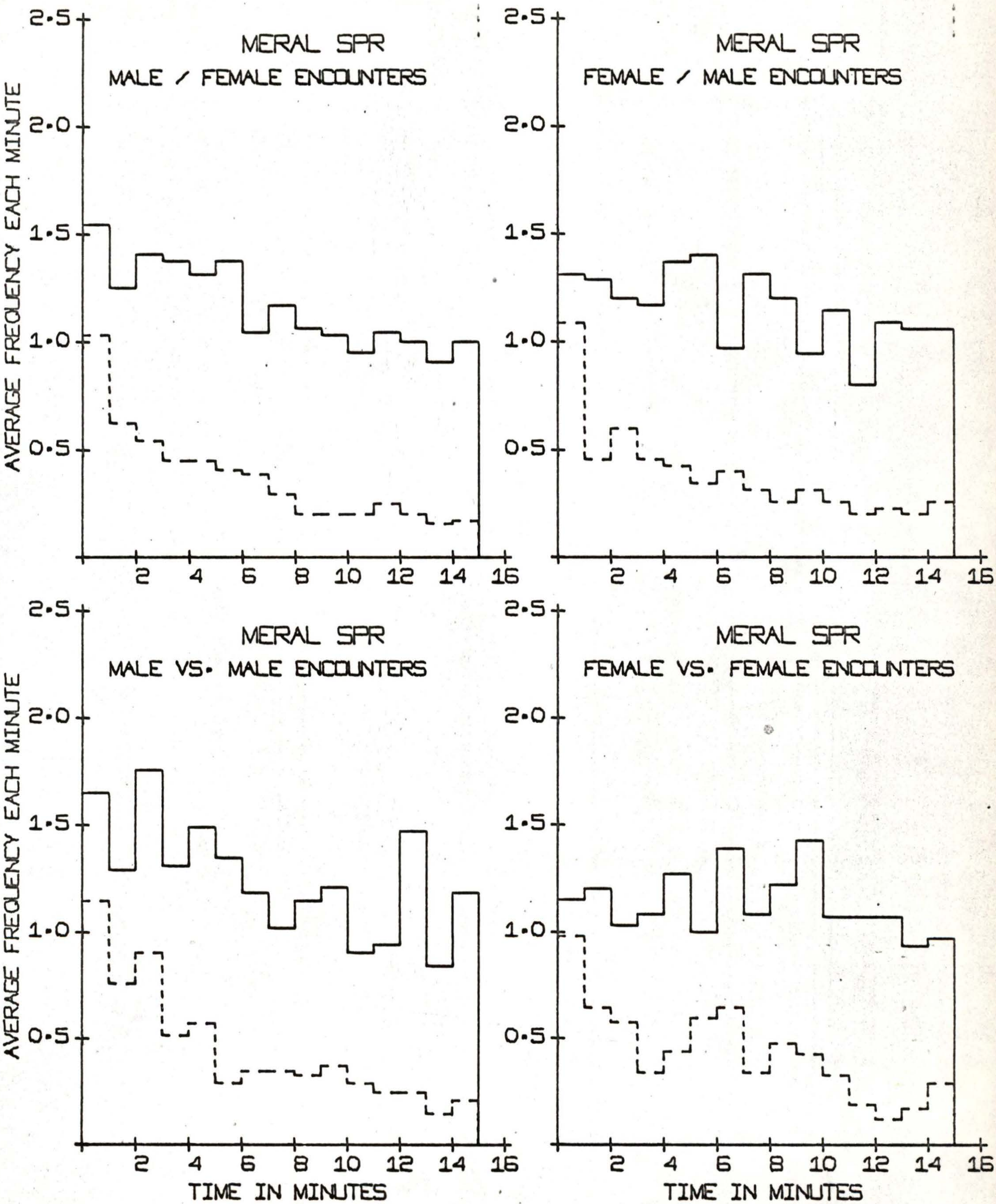


FIG. 19. CONTINUED.

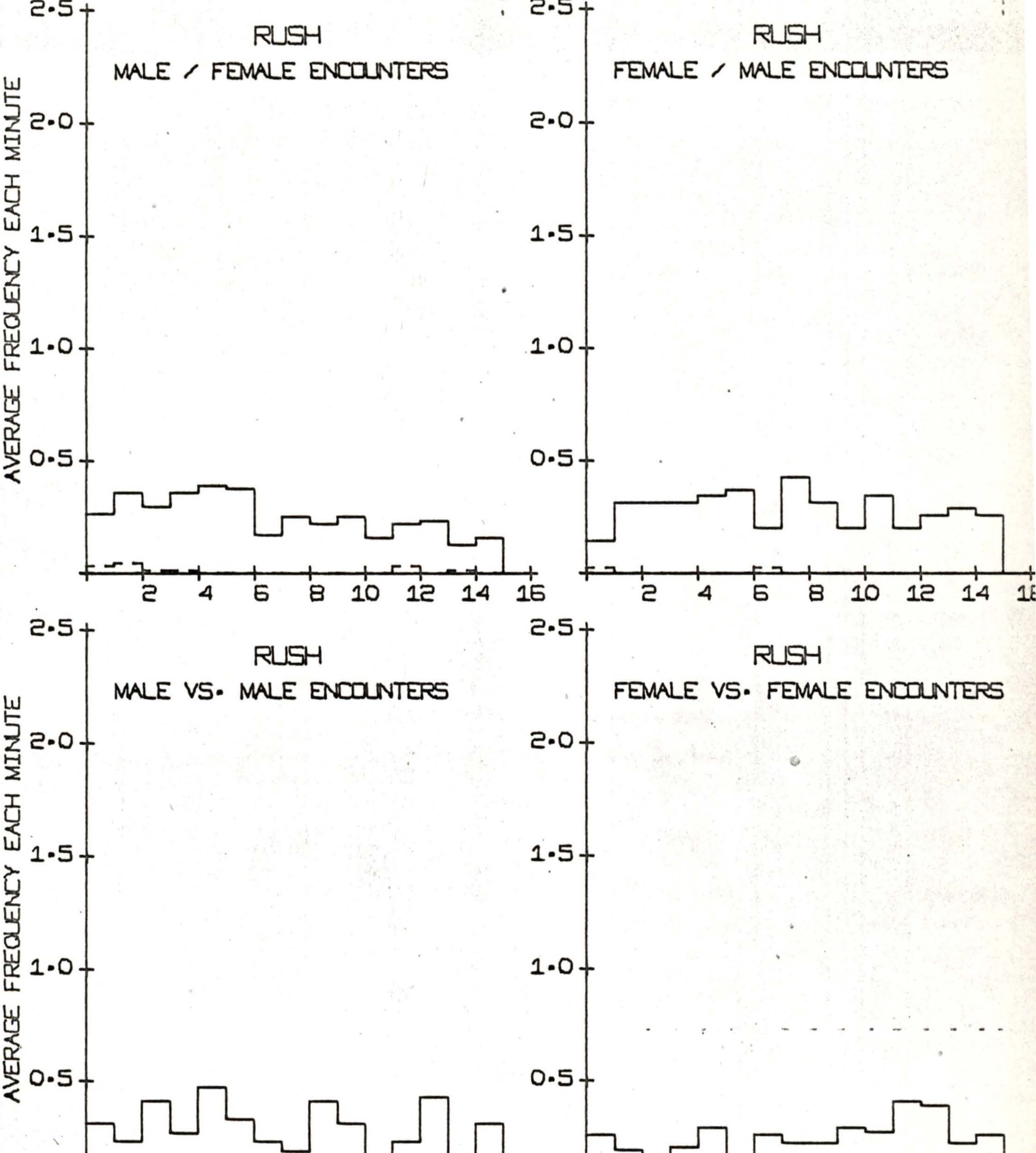
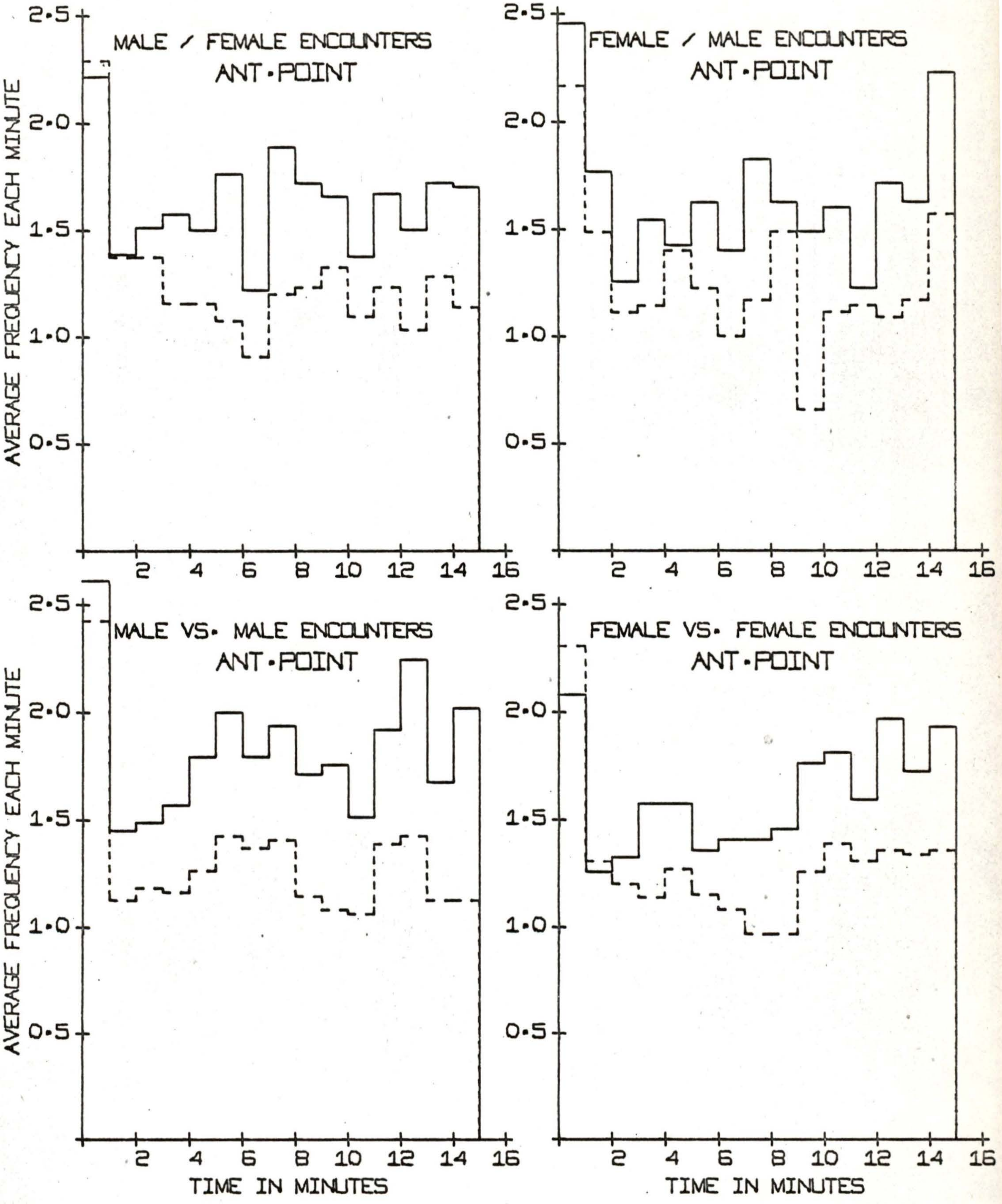


FIG. 19. CONTINUED.



FIG· 20· MEAN FREQUENCIES OF THE GROUP 4 BEHAVIOUR PATTERNS EACH MINUTE OF THE FEMALE VS· FEMALE , MALE VS· MALE , FEMALE / MALE AND MALE / FEMALE ENCOUNTERS (WINNERS-SOLID LINES , LOSERS-STIPPLED LINES)

(Fig. 21). When the group 1 agonistic behaviour patterns were shown during the first few minutes of the observation period, they produced long agonistic bouts which resulted in large initial MRTs.

Variation between encounters

The MRTs of individual encounters ranged from a low (Fig. 22) in which the animals were active for about 20 seconds or less per minute to a high (Fig. 23) in which nearly continuous agonistic activity was observed. In both bases the activity showed no regular temporal patterning during the 15 minute observation period. Typical intermediate encounters produced MRTs which tended to decrease with time (Fig. 24) or oscillated more or less dramatically from one minute to the next (Fig. 25).

To determine whether the agonistic bouts could be used to explain these MRT patterns, the number of bouts in an encounter was plotted against its total response time (TRT). The pattern of points (Fig. 26) fits best around the cubic regression line $\hat{Y} = 3.642 + 0.07140 X + (-1.717 X 10^{-4} X^2) + 1.02 x 10^{-7} X^3$ (Table 2). During the encounters, the number and variation in number of bouts tended to increase until the TRT approached 300 seconds, after which they declined in number and variation. As the TRT approached 900 seconds the number of bouts levelled off at 1 or 2. Therefore the low infrequent MRTs occurred when the lobsters showed only a few short bouts of agonistic behaviour during the observation period. The MRTs from the encounter with the smallest TRT indicate that the shortest lobster agonistic bouts were about 9 seconds (Fig. 22). As the TRT and number of bouts in an encounter

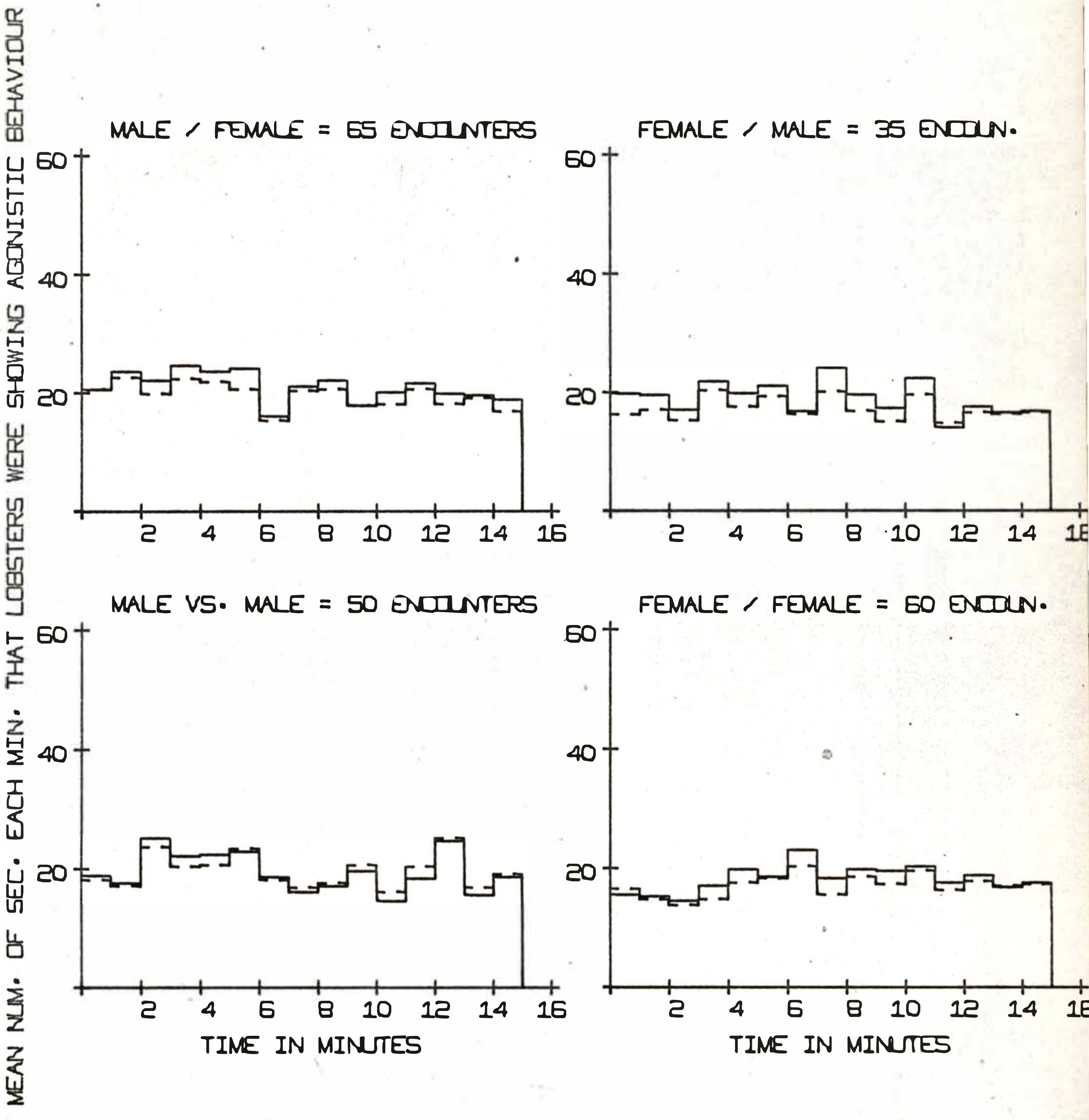


FIG.21. MEAN ONE MINUTE RESPONSE TIMES FOR EACH MINUTE OF THE 15 MINUTE AGONISTIC ENCOUNTERS, WHEN THE DURATION OF PUSHING IS REMOVED (WINNERS - SOLID LINES , LOSERS - STIPPLED LINES).

LOBSTER W WINNER W VS. I MAR.8/69.

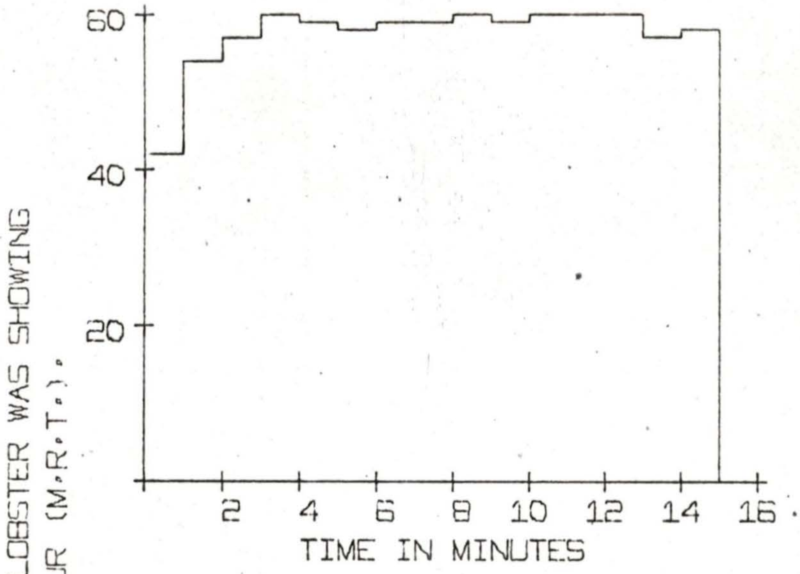


FIG. **23**. THE ENCOUNTER WITH THE LARGEST T.R.T., CONTAINS 2 AGONISTIC BOUTS.

LOBSTER 26 WINNER 26 VS. 4 APR.1/69.

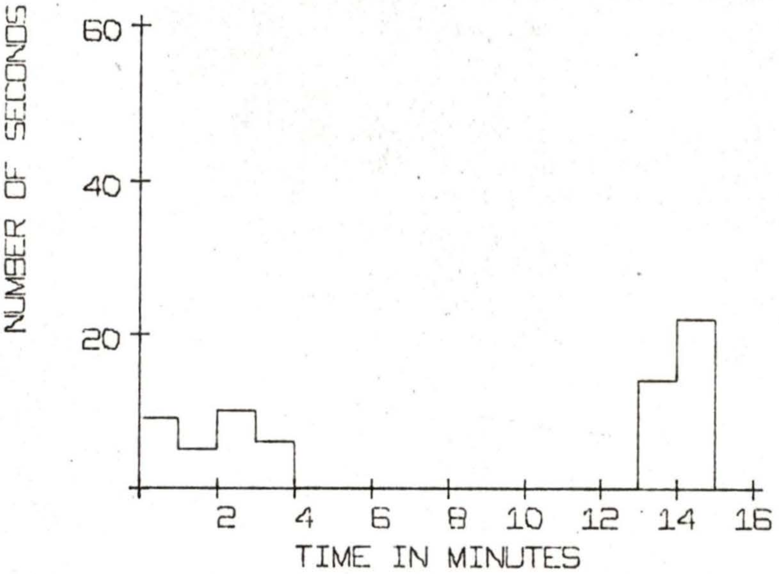


FIG. **22**. THE ENCOUNTER WITH THE SMALLEST T.R.T., CONTAINS 5 AGONISTIC BOUTS.

LOBSTER 19 WINNER V VS. 19 MAR.1/69.

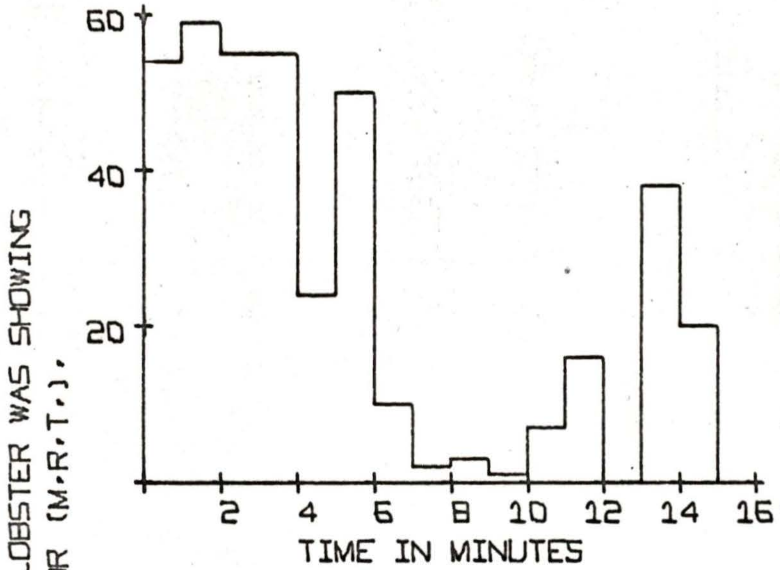


FIG.24. A COMMONLY OBSERVED DISTRIBUTION OF M.R.T.S OBTAINED FROM AN ENCOUNTER CONTAINING 8 AGONISTIC BOUTS.

LOBSTER 20 WINNER 20 VS. X MAR.22/69.

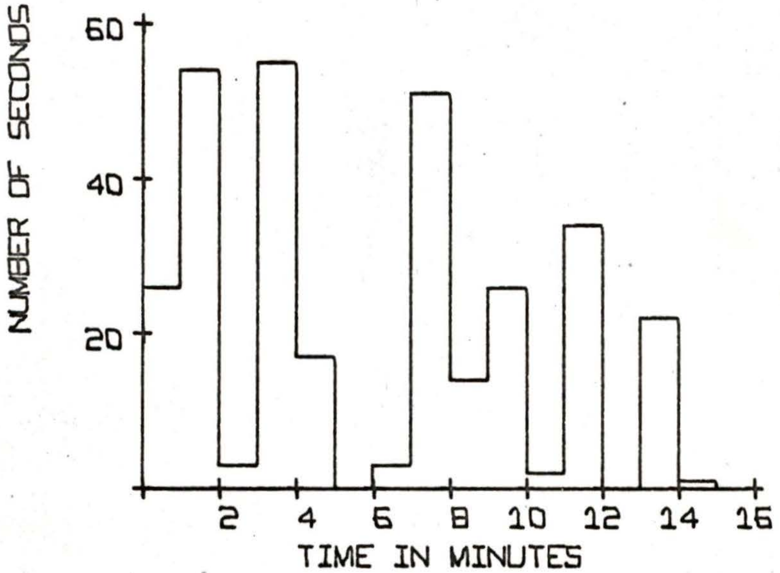


FIG.25. A COMMONLY OBSERVED DISTRIBUTION OF M.R.T.S OBTAINED FROM AN ENCOUNTER CONTAINING 11 AGONISTIC BOUTS.

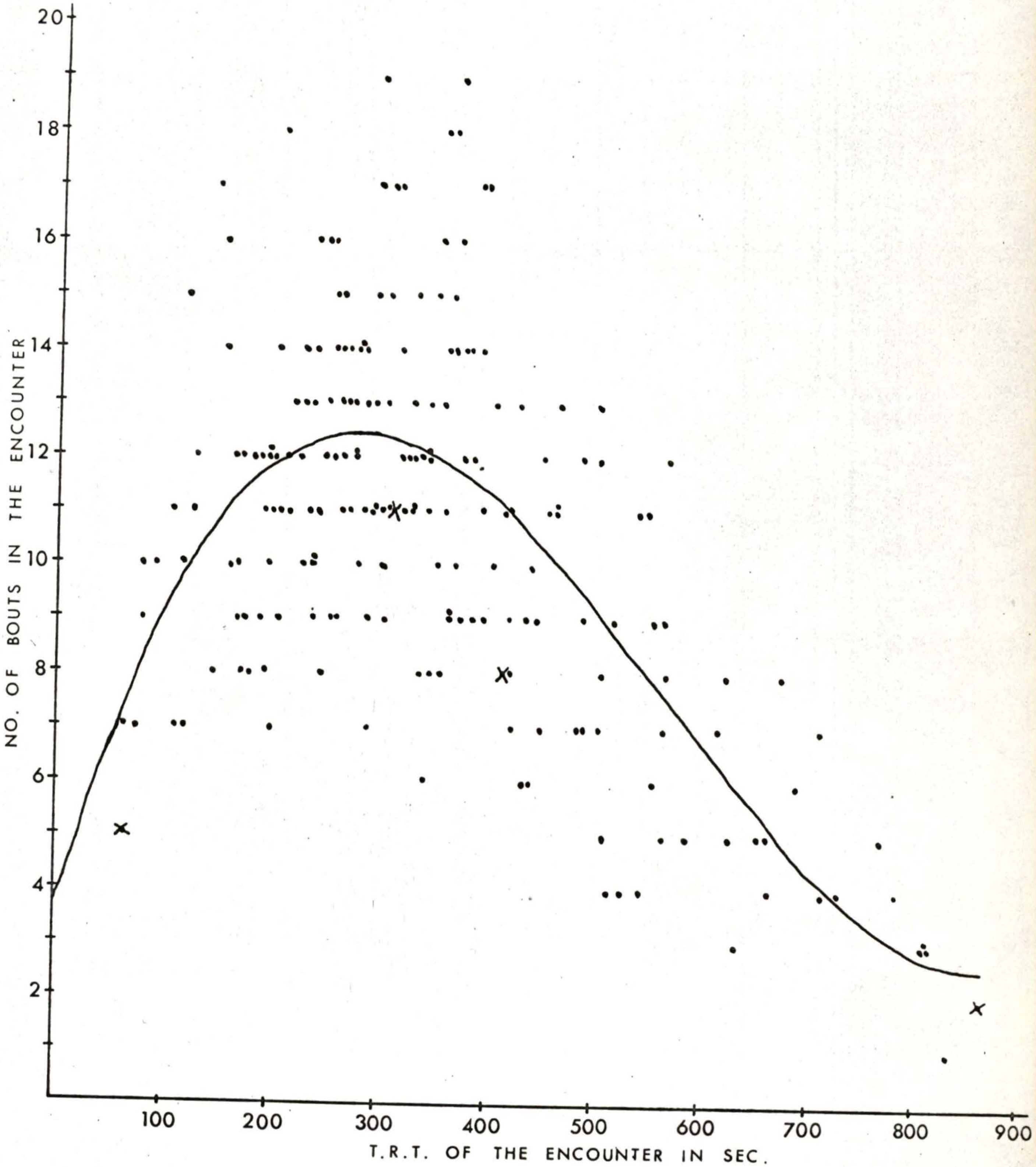


FIG. 26. RELATIONSHIP OF THE NUMBER OF BOUTS AND THE TOTAL RESPONSE TIME FOR 210 AGONISTIC ENCOUNTERS. THE EMPHASIZED POINTS ARE OF THE ENCOUNTERS IN FIGS. 22 - 25.

TABLE 2: Analysis of variance indicating the improvement of fit with each subsequent step in fitting a plynomial to the regression of the number of bouts in an encounter, on the number of seconds spent showing agonistic behaviour in an encounter.

SOURCE OF VARIATION	df	SS	MS	F
Linear regression	1	708.36597	708.36597	101.38***
Quadratic regression	1	392.85522	392.85522	56.23***
Cubic regression	1	124.53564	124.53564	17.82***
About regression	203	1418.31543	6.98678	
TOTAL	206	2644.07227		

Equation for the 3rd degree polynomial

$$\hat{Y} = 3.642 + 0.07140\ X + (-1.717 \times 10^{-4} X^2) + 1.02 \times 10^{-7} X^3$$

increased the MRTs more or less showed an oscillating pattern. This was most pronounced when the bouts were about 60 seconds in duration, but declined during the encounter as the bout length decreased (Figs. 25 and 16). When the TRT was 400 seconds or greater and the number of bouts had decreased, the initial agonistic bouts were long, producing high initial MRTs which decreased as the bout lengths decreased (Fig. 24). As the TRT approaches 900 seconds, the lobsters showed only 1 or 2 very long agonistic bouts which produced the high MRTs (Fig. 23).

Winners in most of the encounters performed antenna pointing, meral spread, approaching and following frequently, but rushed only occasionally (Figs. 27 and 29); while the losers showed antenna pointing, backing and walking away frequently, but performed side-ways, abdomen flexing and running away only occasionally (Figs. 28 and 30). The group 1 behaviour patterns tended to occur only during the first few minutes, whereas the occasionally shown behaviour patterns did not occur until the frequency of the group 1 behaviour patterns had dropped substantially (Figs. 27 - 30).

During encounters with extremely high TRTs, the group 1 patterns were observed throughout most of the 15 minutes, but abdomen flexing, side-ways, running away and rushing did not occur, if at all, until the very end (Figs. 31 and 32).

In encounters with low TRTs, the group 2, 3, and 4 high frequency behaviour patterns, backing, meral spread, approaching and antenna pointing predominated; while following by winners and walking away by losers were shown only occasionally (Figs. 33 and 34).

The evidence suggests that there was great variation between and within lobster agonistic encounters, but the behaviour did follow

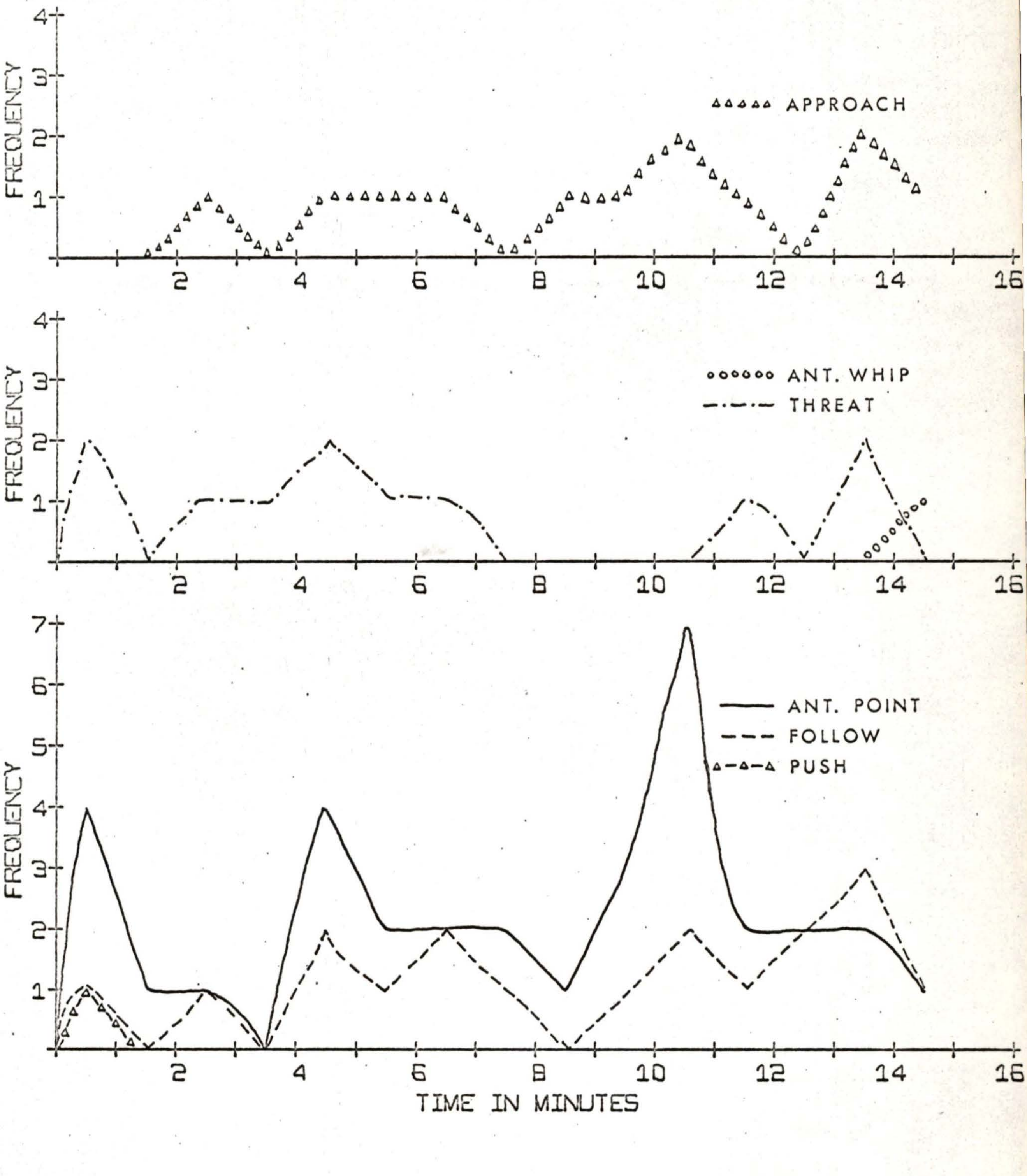


FIG. 27. FREQUENCY OFTHE BEHAVIOUR PATTERNS EACH MINUTE FOR A WINNER FROM A TYPICAL LOBSTER AGONISTIC ENCOUNTER. LOBSTER D WINNER J VS. D MAR.17/69.

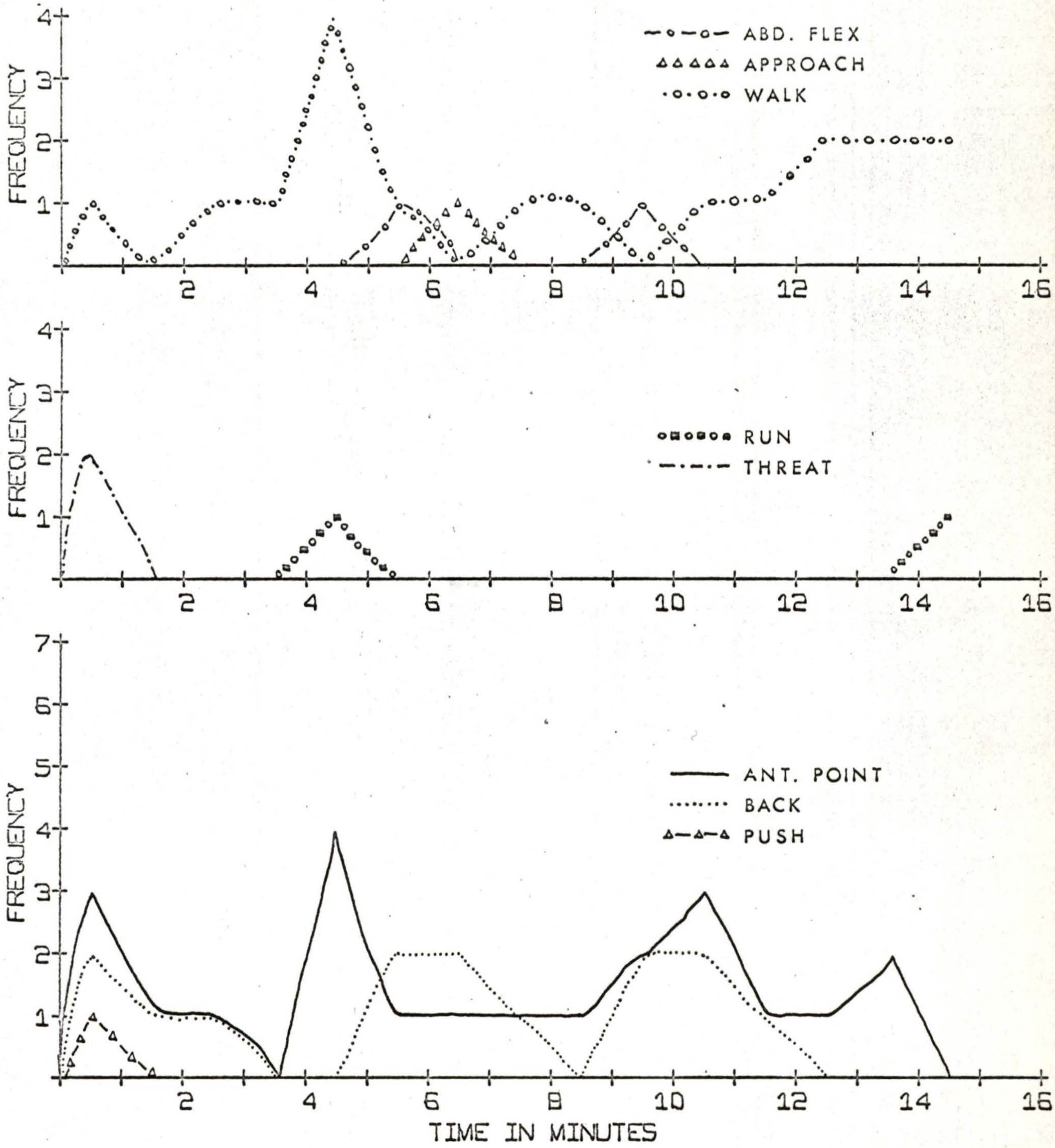


FIG. 28. FREQUENCY OF THE BEHAVIOUR PATTERNS EACH MINUTE FOR A LOSER FROM A TYPICAL LOBSTER AGONISTIC ENCOUNTER. LOBSTER J LOSER J VS. D MAR.17/69.

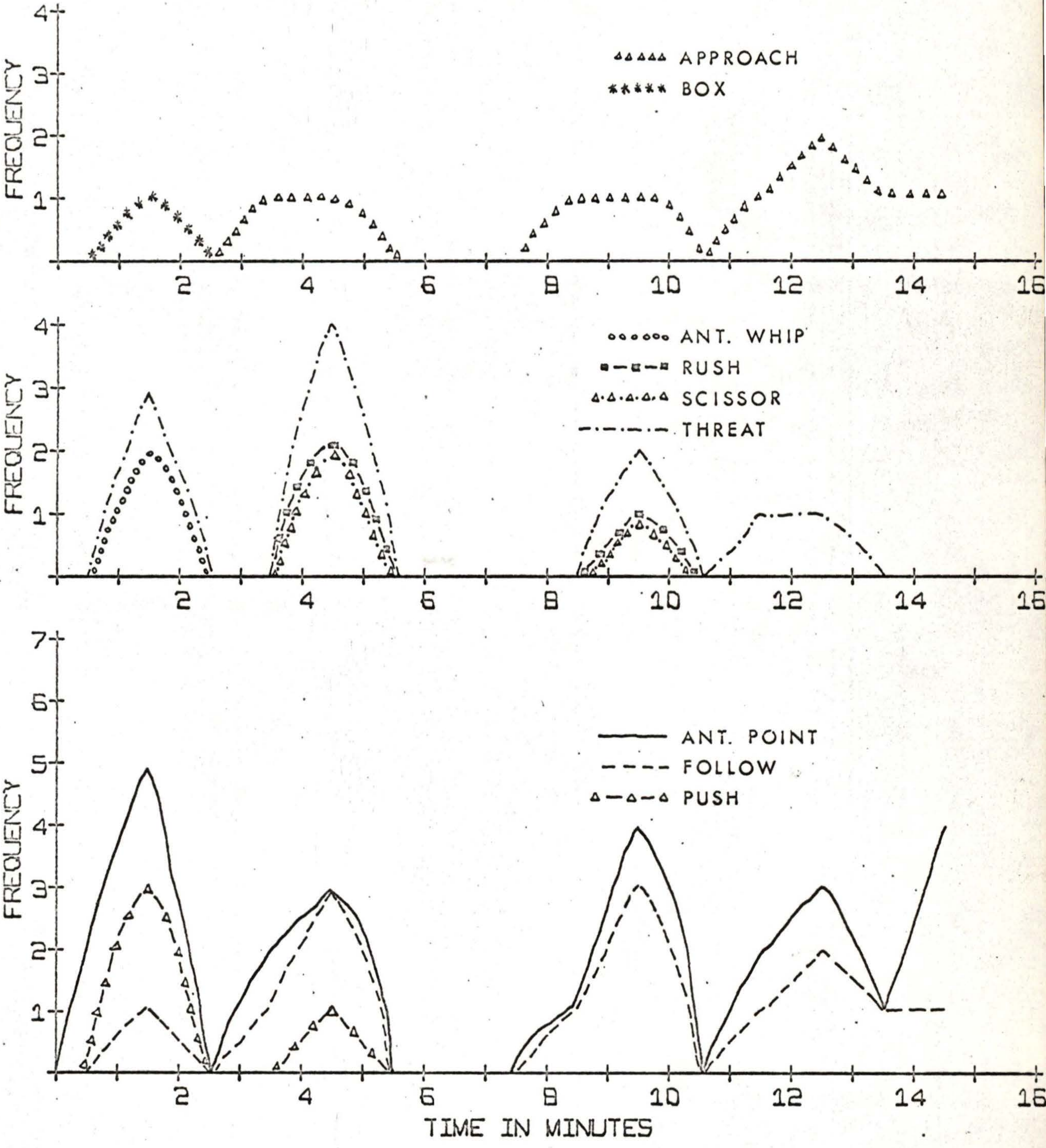


FIG. 29. FREQUENCY OFTHE BEHAVIOUR PATTERNS EACH MINUTE FOR A WINNER FROM A TYPICAL LOBSTER AGONISTIC ENCOUNTER. LOBSTER U WINNER U VS. 23 MAR.15/69.

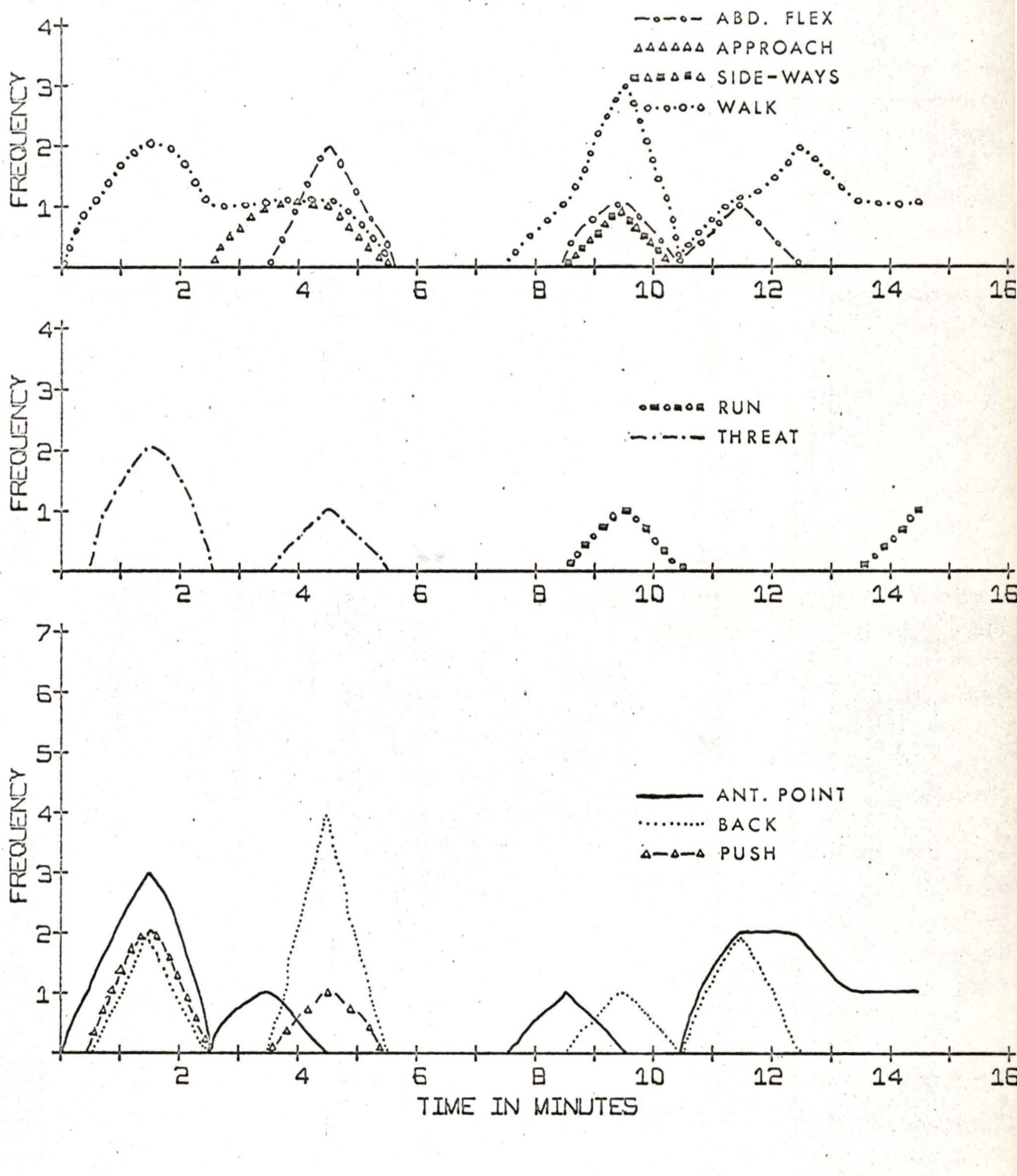


FIG. 30. FREQUENCY OFTHE BEHAVIOUR PATTERNS EACH MINUTE FOR A LOSER FROM A TYPICAL LOBSTER AGONISTIC ENCOUNTER. LOBSTER 23 LOSER U VS. 23 MAR.15/69.

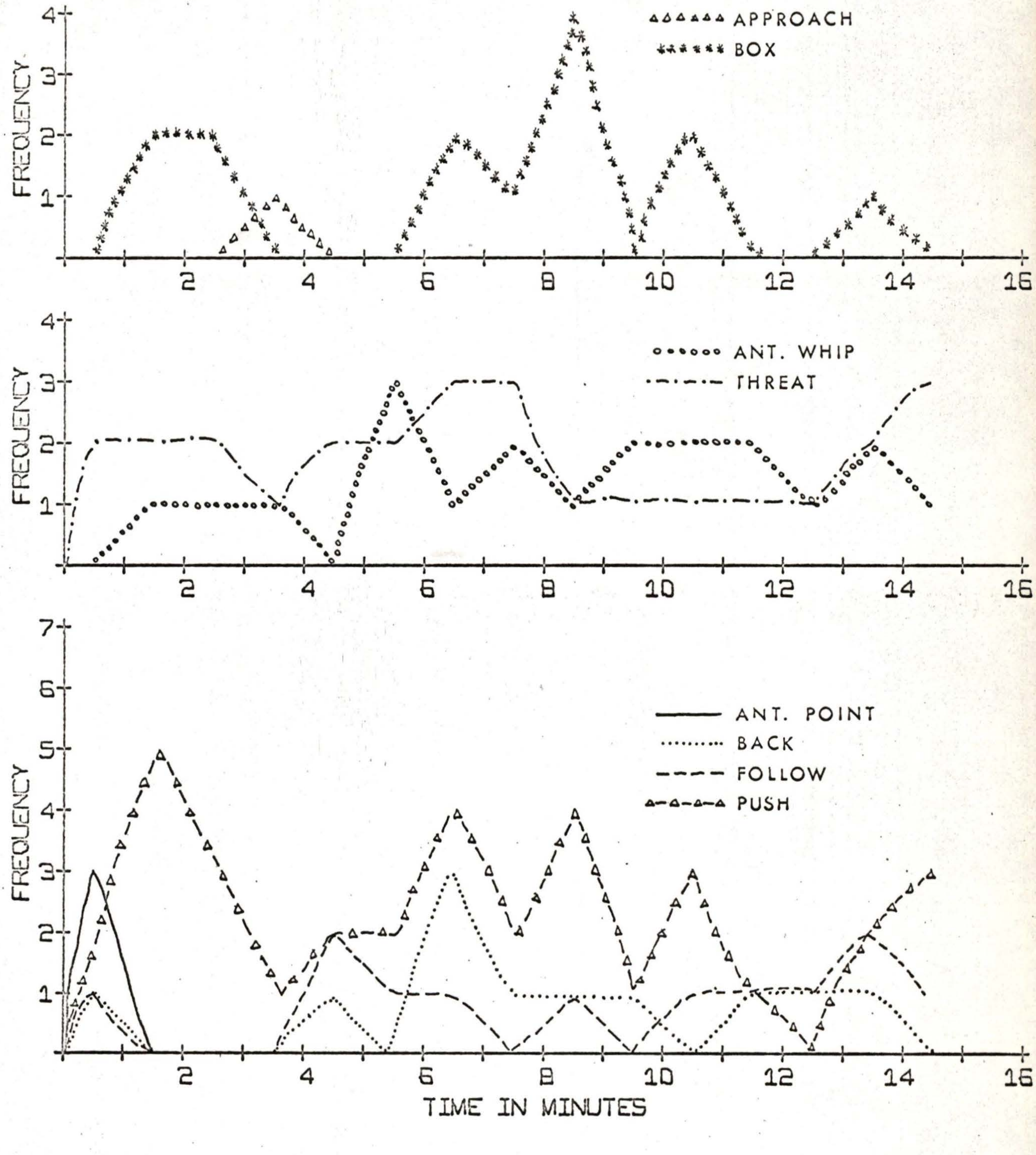


FIG. 31. FREQUENCY OFTHE BEHAVIOUR PATTERNS EACH MINUTE FOR THE WINNER FROM THE ENCOUNTER WITH THE LONGEST T.R.T. LOBSTER W WINNER W VS. I MAR.8/69.

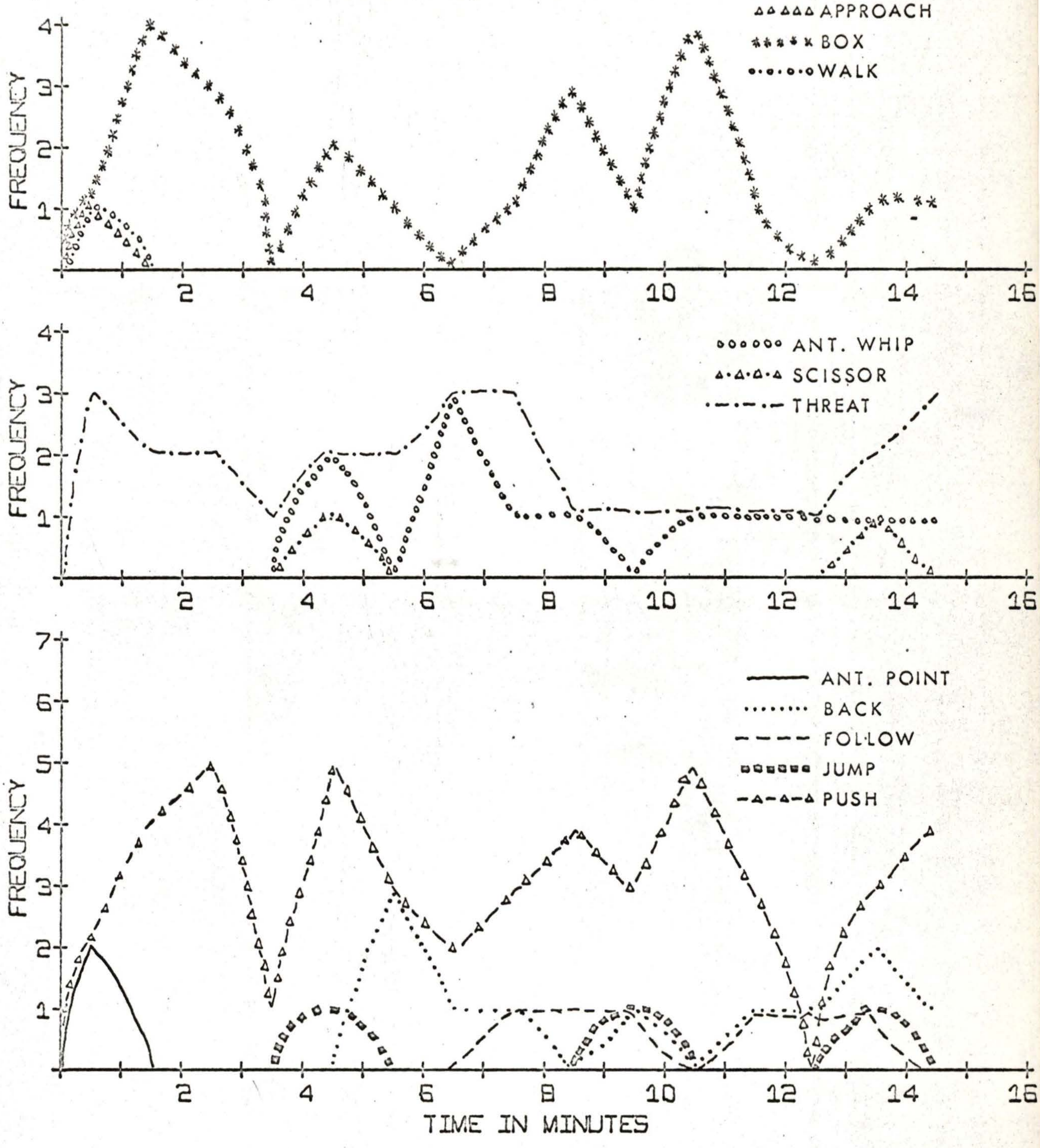


FIG. 32. FREQUENCY OFTHE BEHAVIOUR PATTERNS EACH MINUTE FOR THE LOSER FROM THE ENCOUNTER WITH THE LONGEST T.R.T. LOBSTER I LOSER W VS. I MAR.8/69.

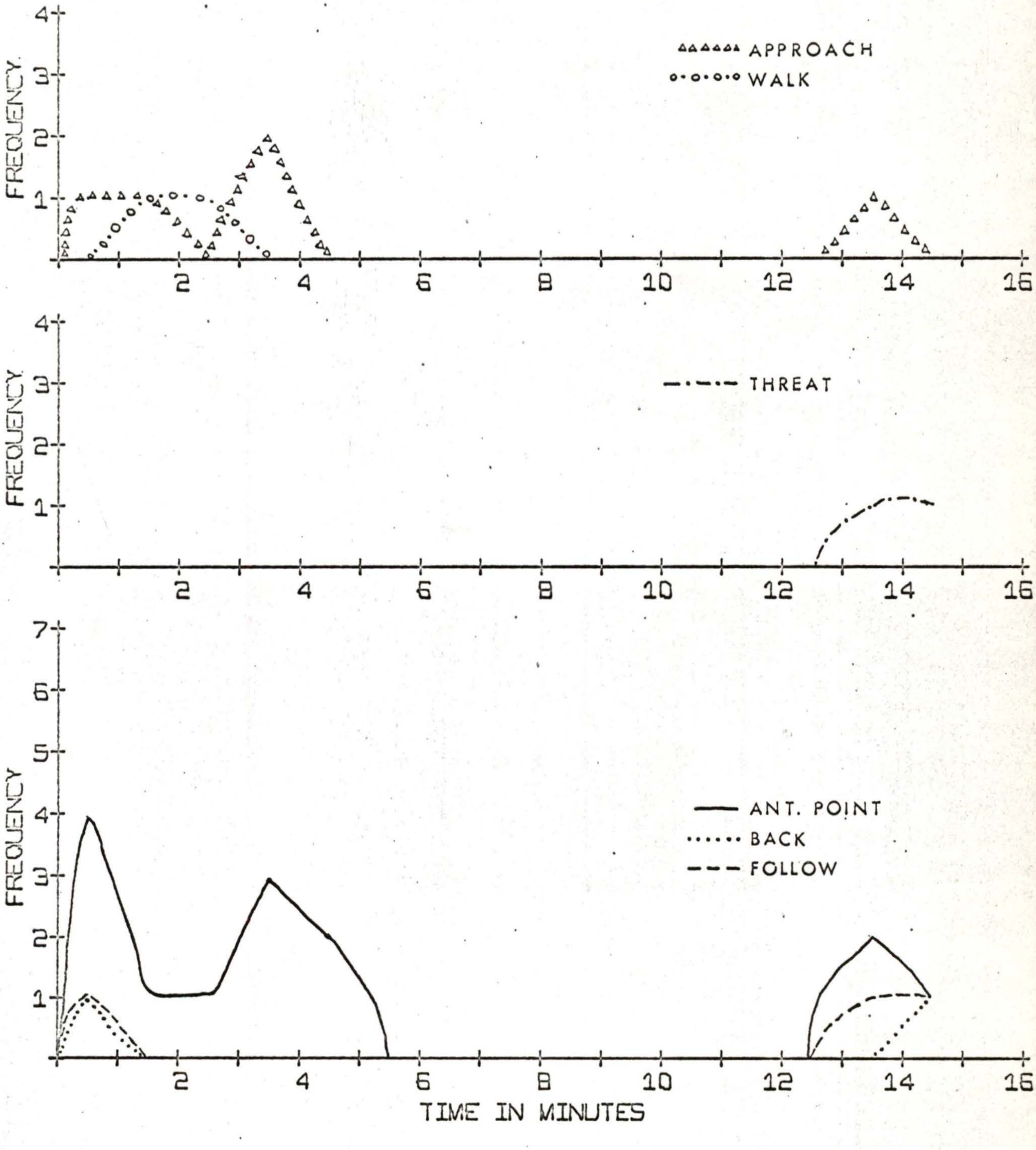


FIG. 33. FREQUENCY OFTHE BEHAVIOUR PATTERNS EACH MINUTE FOR THE WINNER FROM THE ENCOUNTER WITH THE SHORTEST T.R.T. LOBSTER 26 WINNER 26 VS. 4 APR.1/69.

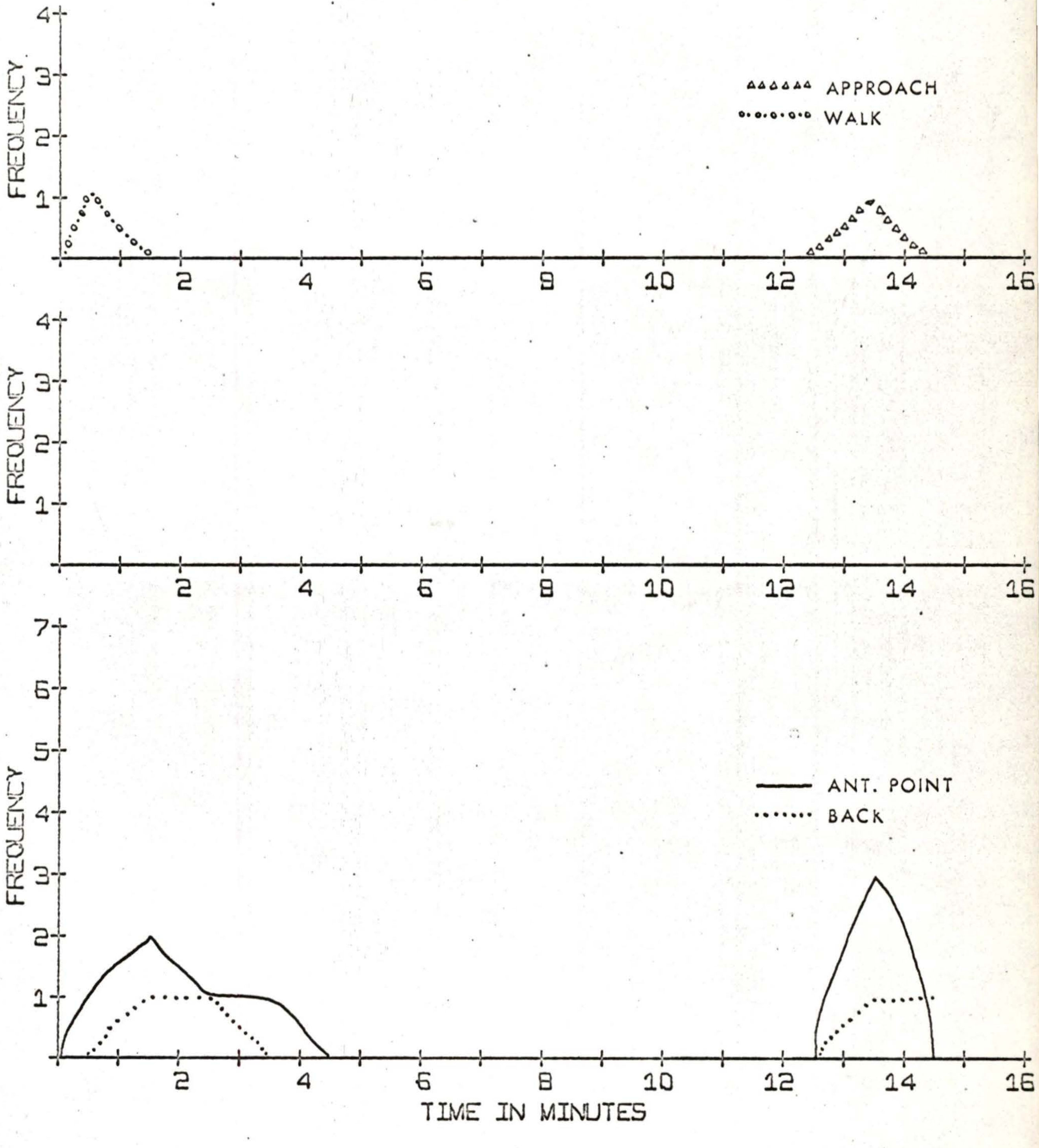


FIG. 34. FREQUENCY OFTHE BEHAVIOUR PATTERNS EACH MINUTE FOR THE LOSER FROM THE ENCOUNTER WITH THE SHORTEST T.R.T. LOBSTER 4 LOSER 26 VS. 4 APR.1/69.

general patterns. Social encounters between two lobsters went through three phases and were of four types. The first phase consisted of long bouts of mutual aggression with frequent occurrence of the group 1 behaviour patterns. This phase could last from 1 (Figs. 27 and 28) to 15 minutes (Figs. 31 and 32), or could be excluded altogether (Figs. 33 and 34). The second phase contained agonistic bouts of less than 1 minute duration, during which group 2, 3, and 4 behaviour patterns were common. This phase could be very long and obvious as in encounter J vs. D and 20 vs. X (Figs. 25, 27, and 28) or very short and obscure as in encounter V vs. 19 (Fig. 24). During phase 3, the agonistic bouts were still shorter and the MRTs no longer fluctuated as extensively as during phase 2. Antenna pointing, following, approaching and meral spread performed by winners and antenna pointing, backing and walking away shown by losers were the principal activities observed during this phase. There were many exceptions to this generalized pattern, but these phases were observed in many encounters. The four types of encounters were those consisting: mainly of phase 1, of all three phases, of phases 2 and 3, and mainly of phase 3.

Male and female differences

Male and female lobsters executed all sixteen behaviour patterns in an identical manner. With two exceptions, they appeared to be shown with similar frequency for similar durations. The exceptions are boxing - shown more often by the males (Fig. 17) - and side-ways - shown more often by the females (Fig. 18).

Boxing had a mean frequency of 1.14 per individual per encounter among the males, while only 0.30 per individual per encounter among the females. Of 100 male vs. male encounters, boxing was shown during 34 (66 boxing not shown). Females showed boxing at least once during 33 encounters and not at all during 112. A 2 x 2 analysis produced a chi-square value of 3.76 ($X_1^2 < .1$). It would appear that males in general showed more boxing than females, but more data is required to demonstrate statistical significance at the .05 level ($X^2 = 3.84$). No difference in duration was observed, because this behaviour pattern is shown for less than 10 seconds.

Side-ways was observed at a mean frequency of 2.12 per encounter among losing females, while only 1.72 per encounter among losing males. It occurred during 63 and did not occur during 37 of the 100 encounters involving males. Females showed side-ways during 107 of their 145 encounters for which data was available. A 2 x 2 analysis produced a chi-square of 2.84 ($X_1^2 < .1$). Female lobsters tend to perform more side-ways behaviour than males, but again statistical significance at the .05 level was not obtained.

Slight variations between male and female pushing were also observed but the main difference was the time at which it was shown. The mean frequency of pushing was the same for both sexes (4.85 and 4.94/individual/encounter in male vs. male and female vs. female encounters respectively), but duration was slightly longer among the females (70.42 sec./encounter for winning females; 61.63 sec./encounter for winning males). The real difference was that females continued to show a substantial amount of pushing at a time during the encounters, when it was rare among males. The mean quantity of pushing declined throughout the encounters for both sexes, but among females the rate was slower (Figs. 17 and 35). Among males it rarely occurred after 5 minutes, but among females it occurred more commonly until 8 to 10 minutes of an encounter had elapsed (Fig. 35).

Lobsters also appeared to show more pushing during unisexual agonistic encounters, than during heterosexual ones (Fig. 17). Means of 66.1 seconds per encounter for the former and 46.2 seconds per encounter for the latter were obtained.

Of the 100 male vs. female encounters, from which the data used in this section was obtained, males won 65 and females 35. A sign test indicates that this was a significant departure from a hypothesis of no difference in the probability of observing a male or female winner (upper .05 confidence limit on 35% = 46%). Males appear to be more aggressive than females.

The consistency of the recording technique

To test the consistency of the recording method, films of lobster agonistic behaviour were projected on a screen and the observed behaviour was recorded, with the same technique used during the encounters (p. 5). The results were analyzed by the computer programs shown in appendix I. This was done during three periods of data collection over a time span of 14 months. The behaviour pattern frequencies from the three recording periods were identical in almost every case, but periodically the durations varied by 1 second and rarely by 2 seconds. Therefore any recording errors obtained during the study are believed to be insignificant and did not affect the general interpretations based on these data.

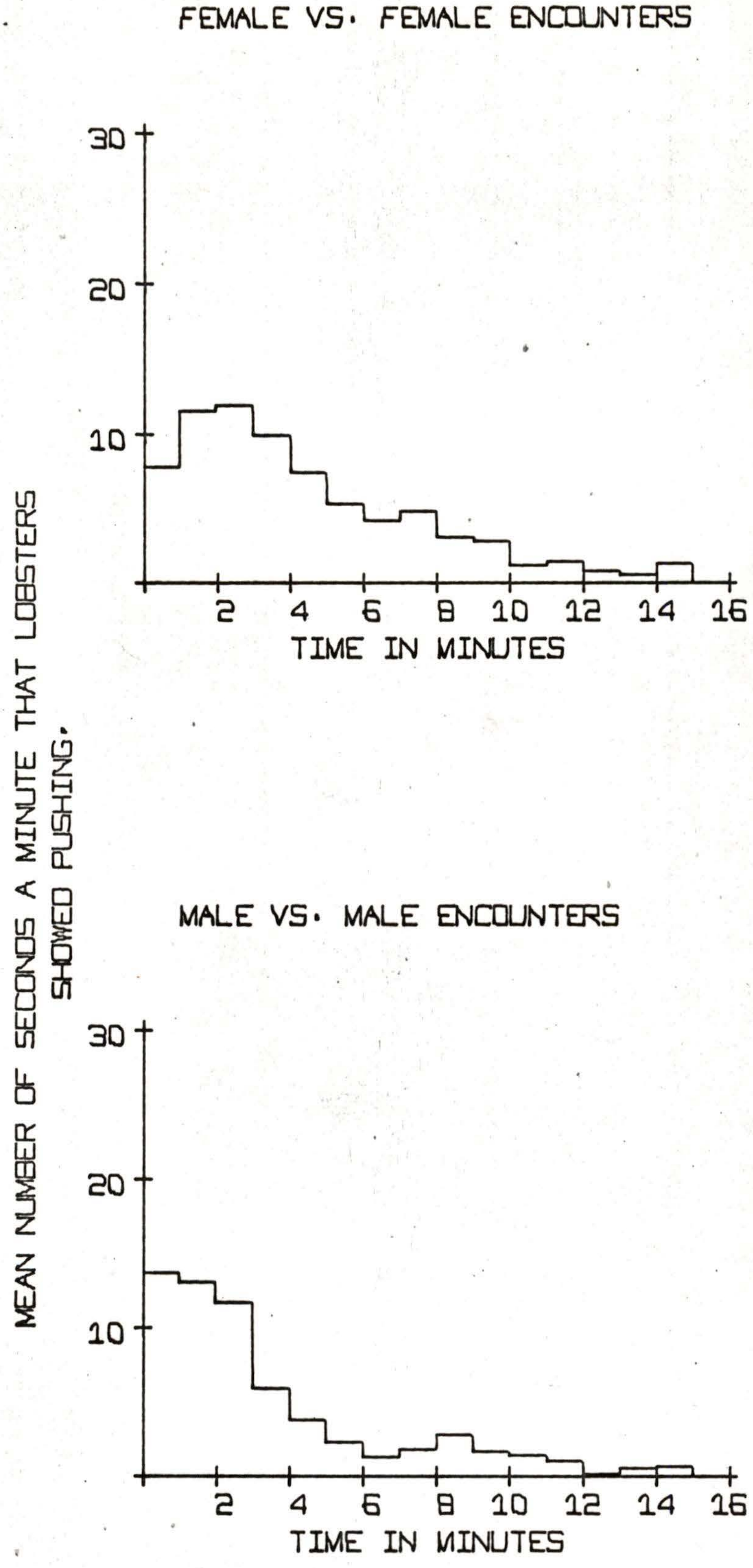


FIG.35. MEAN NUMBER OF SECONDS OF PUSHING EACH MINUTE OF THE ENCOUNTERS.

Discussion

The 15-minute observation period or encounter was an unnatural condition imposed on the study animals. Lobsters would meet, show agonistic behaviour and then separate, but because of the confined conditions, they would inevitably meet again within minutes. The agonistic bouts were more representative of natural lobster interactions, but a fixed observation period was used, first because a definite outcome of winner and loser was desired and second because the collection of single bouts was prohibitively time consuming. This artifact should present no major problem, if the observer was simply searching for generalized patterns and relationships between the behaviour patterns.

A number of generalized conclusions, which should apply to natural lobster agonistic interactions, can be drawn from this examination of the variation within and between encounters. First, the behaviour patterns seem to fit into four basic groups. Second, there appears to be three types of agonistic bout; the very long bouts (1 - 14 minutes) in which the group 1 behaviour patterns occur frequently, the bouts of 20 - 60 seconds duration, in which the group 2, 3, and 4 behaviour patterns are most frequent and the very short bouts (9 - 20 seconds) in which only antenna pointing, meral spread, approaching, following, backing and walking away are shown. Third, males appear more aggressive than females. Fourth, males appear to box more often than females and females show more side-ways than males.

ANALYSIS OF LOBSTER BEHAVIOUR SEQUENCES

One method of analyzing quantified behaviour is to consider the sequences in which animals have performed the behaviour patterns. This can be accomplished by totalling the number of times one activity is followed by another; eg. among winning lobsters meral spread was followed by pushing on 340 occasions and by antenna pointing 1097 times. These frequencies are summarized for easy interpretation in the form of a sequence diagram (Fig. 36) similar to those used by Liley (1966).

The sequence analysis data was obtained from 250 of the 700 quantified agonistic encounters. The remaining 450 encounters were eliminated, because ecdysis, extensive use, exposure to an individual more than once and incomplete data might have affected the results. During 80 female vs. female, 70 male vs. male and 100 female vs. male encounters, 25 male and 27 female lobsters were used 1 - 13 times (average 9.5) over a six month period. Program LOBSTER 8 (Appendix I) tabulated the sequence frequencies from which the winner's and loser's sequence diagrams were drawn.

In these diagrams, the width of each arrow is proportional to the number of times the sequence occurred. To avoid cluttering the diagrams, sequences which occurred less than 30 and 30 - 70 times were omitted and represented by a single line respectively. The more frequent sequence was shaded, while the opposite less frequent one was left white. The frequencies in the boxes indicate the number of times the behaviour pattern was followed by itself. Sequence diagrams are a useful tool for graphically demonstrating both the principal chains of sequences and to some extent the variation within these chains.

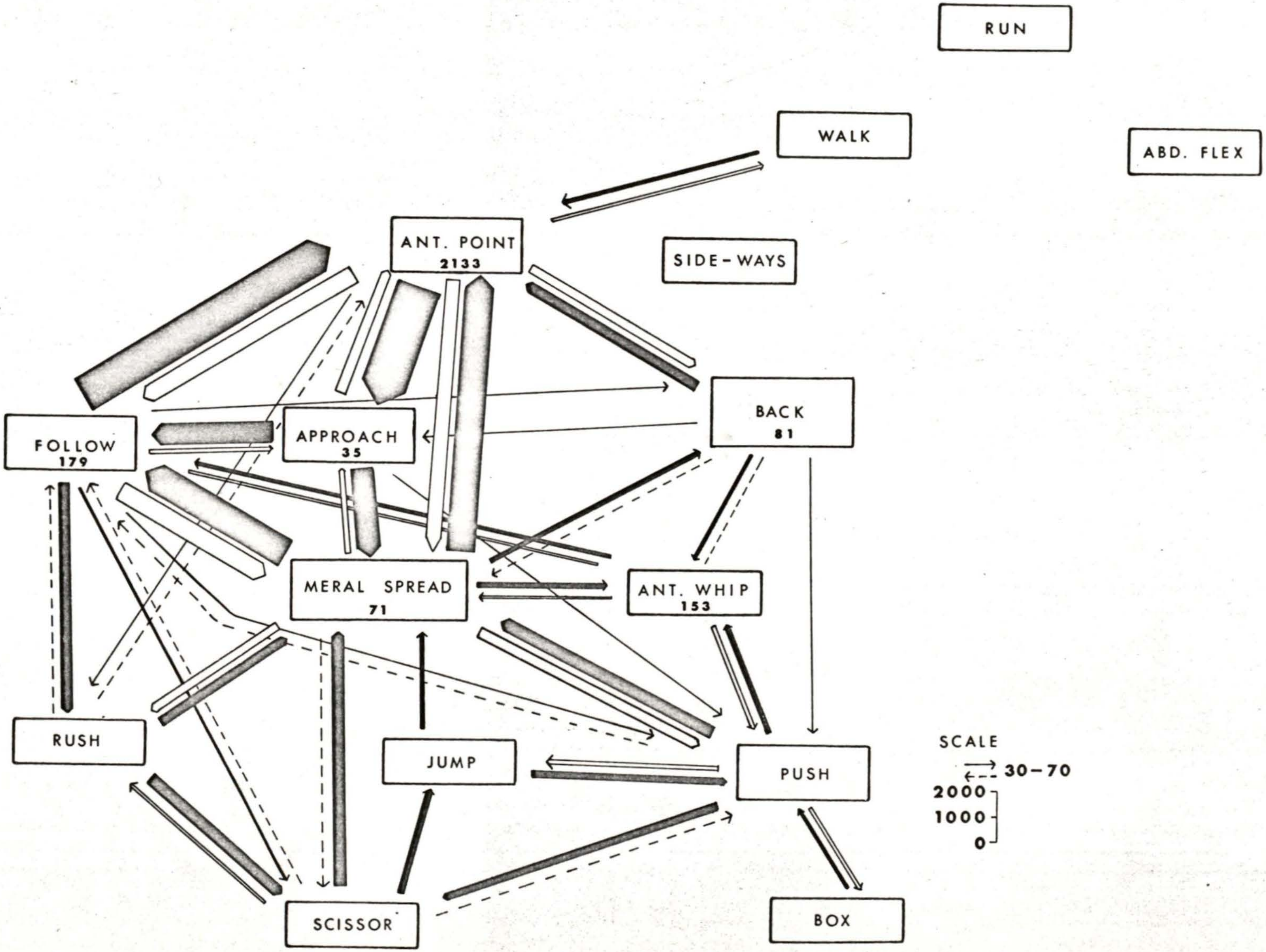


FIG. 36. SEQUENCE DIAGRAM OF WINNING LOBSTER ACTIVITIES FROM 250 ENCOUNTERS. SEQUENCES OCCURRING LESS THAN 30 TIMES ARE OMITTED. FREQUENCIES IN THE BOXES INDICATE THE NUMBER OF TIMES THE BEHAVIOUR FOLLOWED ITSELF.

In each diagram there is a distinct central behaviour pattern around which the other recorded units are assembled. Meral spread among winners and backing among losers have arrows between themselves and almost every other behaviour pattern. This is the arrangement in which the least number of major arrows cross. With the exception of jumping, the behaviour patterns seem to be arranged in a line of increasing aggressive motivation from abdomen flexing and running away in the upper right hand corner, to rushing in the lower left hand corner of the diagram (Figs. 36 and 37). The upper mid-left and the lower mid-right contain the investigative behaviour (antenna pointing) and the behaviour patterns requiring mutual aggression (pushing, antennae whipping, boxing and jumping) respectively.

The most common behaviour pattern among both winning and losing lobsters was antenna pointing. It started and ended almost every chain of agonistic sequences or sequence pathways, as indicated by the large frequency of its repetition (2133, Fig. 36; 1043, Fig. 37).

With antenna pointing as the initial and terminal behaviour pattern, four basic sequence pathways were distinguished from the diagrams. Pathway number 1, the ant. point ⟶ approach ⟶ meral spread ⟶ follow ⟶ rush ⟶ scissor ⟶ meral spread ⟶ ant. point pathway, was seen exclusively among winners (Figs. 36 and 38 a); while number 2, the ant. point ⟶ back ⟶ abdomen flex ⟶ back ⟶ ant. point (Fig. 38 b), and number 3, the ant. point ⟶ walk away ⟶ run away ⟶ walk away ⟶ ant. point pathways (Fig. 38 c), were shown in their entirety only by losers (Fig. 37). Pathway number 4, the ant. point ⟶ approach ⟶ meral spread ⟶ push ⟶ meral spread ⟶

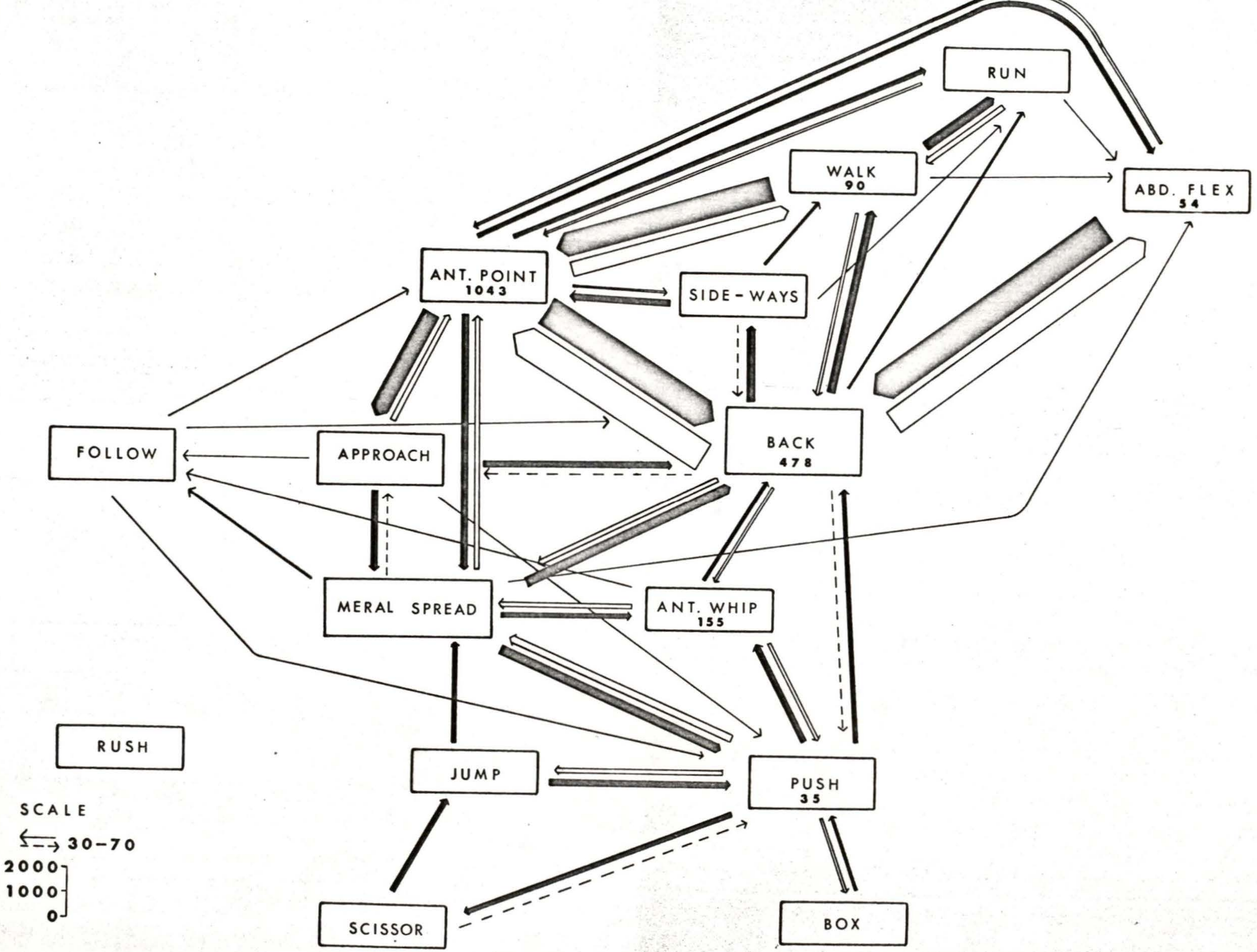


FIG. 37. SEQUENCE DIAGRAM OF LOSING LOBSTER ACTIVITIES FROM **250** ENCOUNTERS. SEQUENCES WHICH OCCURRED LESS THAN **30** TIMES ARE OMITTED. FREQUENCIES IN THE BOXES INDICATE THE NUMBER OF TIMES THE BEHAVIOUR FOLLOWED ITSELF.

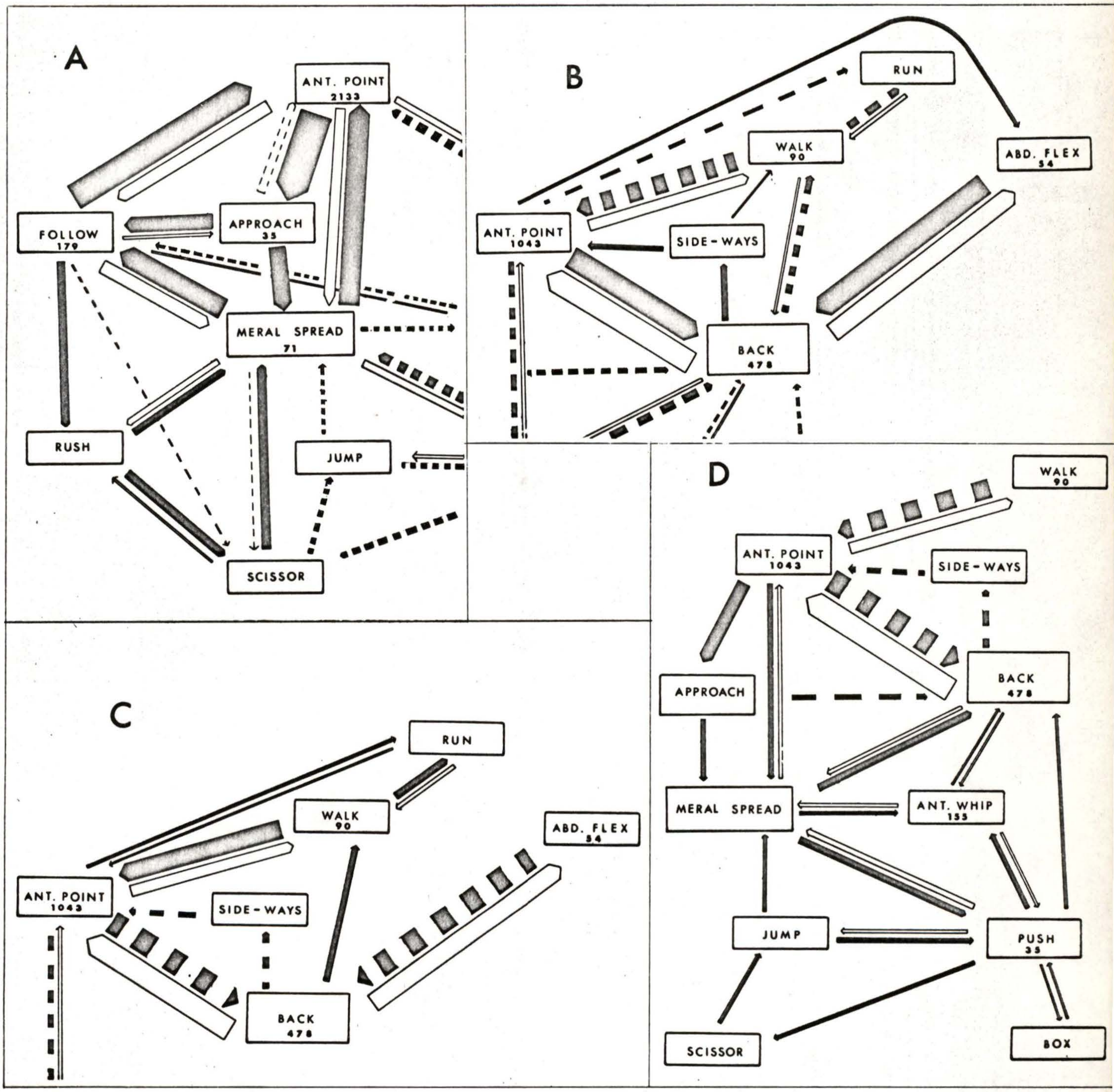


Fig. 38. Sequence diagram extractions which emphasize the 4 basic sequence pathways: A - pathway number 1 from fig. 36, and B-pathway 2, C - pathway 3 and D-pathway 4 from fig. 37.

ant. point pathway, was seen among both winners and losers (Figs. 36, 37, and 38 d). These four basic chains of sequences each had side chain activities, might be partially reversed and might be terminated or entered at various points along the pathways.

Basic sequence pathway number 1 had a number of variations and termination points among its behaviour patterns. Among winners, the most common chains of sequences were either ant. pointing → approaching → meral spread → following → ant. pointing or ant. pointing → approaching → following → meral spread → ant. pointing (Figs. 36 and 38 a). If the lobster was strongly motivated towards aggression, it could proceed from following or meral spread to rushing instead of ending the sequences with ant. pointing. Then the agonistic behaviour ended either meral spread → ant. pointing, or if the animal was close to its opponent scissoring → meral spread → ant. pointing. Periodically, if the opponent did not remove itself from the sensory field of the aggressor, the behaviour proceeded from meral spread to following and through the rushing-scissoring sequences again, before ending with ant. pointing. Often near the end of an encounter, the winner skipped approaching and went directly from ant. pointing to meral spread or following, because the opponent began avoiding the winner immediately after detecting its presence.

Sequence pathway number 2 was the most common one seen among losers (Fig. 37). Rather than turn their back to their opponents, losing lobsters preferred to face them and back away. Often the backing ⇆ abdomen flexing cycle was repeated during a single chain of sequences. If from backing the behaviour proceeded to side-ways, the sequences ended either side-ways → walking away → ant. pointing or more often side-ways ⟶ ant. pointing (Fig. 38 b). When the aggressive opponent was 1 metre or more away, the avoiding individual periodically stopped backing, turned around and began walking away. This chain of sequences ended, when the behaviour continued, walk away ⟶ ant. point.

The third basic pathway (ant. point ⟶ walk ⟶ run ⟶ walk ⟶ ant. point) was not quite as common as the second (Fig. 37). Sometimes the behaviour proceeded directly from ant. pointing to running away and then ended walking away ⟶ ant. pointing. Often the running ⇆ walking away cycle was repeated within a single chain of sequences (Fig. 38 c). This pathway was periodically shown among winners in a reduced form ant. pointing ⟶ walking away ⟶ ant. pointing (Fig. 36).

If both animals in an encounter were aggressively motivated, they showed the fourth basic sequence pathway, which included the group I behaviour patterns pushing, antennae whipping, boxing, scissoring and jumping. The importance of pushing as the central behaviour pattern of this group is clearly demonstrated in the sequence diagrams (Figs. 36 and 37). This sequence pathway was the longest and most complex of the four. When meral spread was followed by pushing, among winners pushing proceeded to meral spread, scissoring, antennae whipping, jumping or boxing (listed in order of decreasing frequency, Fig. 36). If the behaviour returned to meral spread, the lobster reversed the sequence, ended the chain of sequences with ant. pointing or continued into pathway number 1. If the behaviour proceeded to scissoring, the pushing ⟶ scissoring ⟶ jumping ⟶ pushing or meral spread chain of sequences occurred (Figs. 36 and 38 d). When antennae whipping followed pushing: the behaviour returned to pushing; ant. whipping stopped and then started again, while pushing continued; or one of the pathways ant. whipping ⟶

following ⟶ meral spread ⟶ ant. whipping, its reverse (Fig. 36) and ant. whipping ⟶ meral spread ⟶ backing ⟶ ant. whipping (Fig. 37) were observed. When pushing proceeded to jumping the pushing ⟶ jumping ⟶ meral spread ⟶ pushing cycle of sequences was usually observed. Among losers the same chains of activities were observed, but the pushing ⟶ scissoring ⟶ jumping ⟶ pushing cycle was less frequent, and the one involving backing was more frequent than the one involving following (Fig. 37).

Besides being the central behaviour patterns in the sequence diagrams backing and meral spread were also the main interconnecting links between the four basic sequence pathways. Meral spread joined the first and fourth, while backing linked the second, third and fourth. Following and abdomen flexing appeared to be behaviour patterns through which the lobsters could abruptly, though infrequently, change from one basic sequence pathway to another.

Scissoring occurred in basic sequence pathways number 1 and number 4 (involves group I behaviour patterns). The former was shown more often near the end of the encounters, while the latter was observed more often during the first few minutes. Probably, this was the reason why among winners, scissoring's mean frequency per minute did not decline as much near the end of the encounters, as the other group I behaviour patterns (p. 49).

Differences between male and female sequences

There were no qualitative differences between the behavioural pathways used by male and female lobsters. Both sexes showed the four basic sequence chains with their noted variations and side-chains. To determine whether there were quantitative differences significant at the .05 level, the frequency of each sequence, and the totalled frequency of the 14 other possible sequences following a particular behaviour pattern of both sexes were compared in two-way frequency tables. For example, among 135 winning males scissoring was followed on 208 occasions by meral spread and on 206 occasions by one of the other 14 behaviour patterns, and among 115 winning females on 195 occasions by meral spread and on 235 occasions by one of the other 14.

A chi-square value was calculated for each of the 225 (15 x 15) possible single step sequences, where frequencies were 5 or more (appendix II). Tables with frequencies of less than 5 were indicated by 0.00 (Sokal and Rohlf (1969), p. 565, suggest that chi-square tests should not be performed on frequencies of less than 5). Chi-squares were obtained from comparisons between winning males and females and between losing males and females, from all 250 encounters (Tables 3 and 4), from the 70 male and 80 female unisexually paired agonistic encounters (Tables 5 and 6), and from the 100 heterosexually paired encounters (Tables 7 and 8). Chi-squares showing the differences in winner's and loser's behaviour when their opponent was a member of their own and opposite sex were also obtained (males Tables 9 and 10, females Tables 11 and 12).

Females showed a tendency to repeat the agonistic behaviour patterns more often than males. Winning or losing females repeated antennae whipping, approaching and antenna pointing more frequently than males, while winning males repeated only meral spread more frequently than female winners (Table 3 and 4).

There were differences between male and female expression of

TABLE 3 - Chi-square values obtained by comparing the totalled frequencies of 135 male and 115 female winners in two-way tables. * = females significantly greater than males; ! = males significantly greater than females. Chi-squares with lines through them were obtained from frequencies which were too small to appear in the sequence diagram. Boxes emphasize the chi-squares discussed in the text.

INITIAL							SUBSEQUENT BEHAVIOUR								
BEHAVIOUR	SC	PU	BK	SW	RH	AF	JU	AW	FO	AH	MS	BO	WA	AP	RU
Scissor	0.00	2.82	0.00	0.00	1.97	0.00	34.18*	0.00	0.76	0.00	2.02	0.00	0.00	~~10.36~~	0.00
Push	22.81*	~~3.87~~	~~4.23~~	0.00	0.00	0.00	21.44*	0.02	0.66	0.00	4.01!	40.30!	0.00	0.07	0.00
Back	0.00	0.00	3.87*	0.00	0.00	~~8.49~~	0.00	0.11	0.15	0.76	0.02	0.00	0.00	0.18	0.00
Side-ways	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rush	0.88	0.07	0.00	0.00	0.00	0.00	0.00	0.00	9.20!	0.00	2.47	0.00	0.00	4.56!	0.00
Abd.Flex	0.00	0.00	0.94	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Jump	1.05	5.58!	0.00	0.00	0.00	0.00	0.39	0.00	0.00	0.00	9.20*	0.00	0.00	0.00	0.00
Ant.Whip	3.02	0.06	0.00	0.00	0.00	0.00	3.19	9.32*	3.01	0.00	0.14	~~6.73~~	0.00	6.67	0.00
Follow	0.96	0.40	0.80	0.00	11.64*	0.00	0.00	3.00	1.30	1.09	6.40!	0.00	0.00	0.50	0.00
Approach	0.00	3.43	0.01	0.00	0.57	0.00	0.00	0.09	0.89	4.75*	0.39	0.00	0.00	0.08	0.00
Meral Spr.	0.17	1.40	9.88*	0.00	3.75	0.00	0.00	8.16!	0.10	2.61	4.04!	0.00	0.00	0.02	0.00
Box	0.00	0.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00
Walk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.68	0.00
Ant.Point	1.98	4.04	0.42	0.00	1.15	0.00	0.00	0.07	0.77	2.71	1.99	0.00	15.89*	0.07	0.00
Run	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

TABLE 4 - Chi-square values obtained by comparing the totalled frequencies of all losing males and females in 2 x 2 tables. * - females significantly greater than males; ! = males significantly greater than females. Chi-squares with lines through them were obtained from frequencies which were too small to appear in the sequence diagram. Boxes emphasize the chi-squares discussed in the text.

INITIAL						SUBSEQUENT BEHAVIOUR									
BEHAVIOUR	SC	PU	BK	SW	RH	AF	JU	AW	FO	AH	MS	BO	WA	AP	RU
Scissor	0.00	0.01	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Push	0.91	1.26	1.91	0.00	0.00	0.00	*10.86*	*9.60*	0.00	0.00	4.68!	19.42!	0.00	0.00	0.00
Back	0.00	4.18*	0.90	*7.70*	0.00	0.50	0.00	*12.59*	0.00	0.61	0.01	0.00	0.29	1.74	10.97!
Side-ways	0.00	0.00	0.08	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.42	0.30
Rush	0.62	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Abd.Flex	0.00	0.00	0.40	0.00	0.00	0.70	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.24	0.00
Jump	0.00	3.84!	1.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.24	0.00	0.00	0.00	0.00
Ant.Whip	0.00	1.19	2.18	0.00	0.00	0.00	0.00	*5.55*	0.65	0.00	0.20	~~4.11~~	0.00	0.00	0.00
Follow	0.00	0.43	3.89*	0.00	0.00	0.00	0.00	0.20	2.79	0.00	0.26	0.00	0.00	10.46!	0.00
Approach	0.00	1.95	0.01	0.00	0.00	1.22	0.00	0.00	1.62	*4.07*	8.46!	0.00	0.00	1.72	0.00
Meral Spr.	2.87	*4.54*	8.93!	0.01	0.00	2.83	0.00	1.71	0.00	1.98	0.03	0.00	0.35	0.15	0.58
Box	0.00	9.90!	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Walk	0.00	0.00	3.09	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.91	0.00	2.24	0.72	2.84
Ant.Point	0.00	0.82	0.03	*8.39*	0.00	*11.40*	0.00	0.00	~~7.16~~	4.96!	0.04	0.00	3.14	*5.40*	1.65
Run	0.00	0.00	0.00	0.00	0.00	2.31	0.00	0.00	0.00	0.00	0.00	0.00	6.21	*10.02*	0.39

TABLE 5 - Chi-square values obtained by comparing the totalled frequencies of 70 male and 80 female winners in two-way tables. * = females significantly greater than males. ! = males significantly greater than females. Boxes emphasize the chi-squares discussed in the text.

INITIAL BEHAVIOUR	SUBSEQUENT BEHAVIOUR											
	SC	PU	BK	RH	JU	AW	FO	AH	MS	BO	WA	AP
Scissor	0.00	0.39	0.00	2.61	*5.24*	0.00	0.03	0.00	1.72	0.00	0.00	0.00
Push	*4.51*	3.28	0.00	0.00	*9.13*	0.36	0.11	0.00	0.57	24.04!	0.00	0.00
Back	0.00	0.02	3.32	0.00	0.00	0.92	0.00	0.00	1.25	0.00	0.00	1.94
Rush	1.68	0.00	0.00	0.00	0.00	0.00	3.46	0.00	0.75	0.00	0.00	0.00
Jump	0.00	6.35!	0.00	0.00	0.00	0.00	0.00	0.00	*7.40*	0.00	0.00	0.00
Ant.Whip	0.00	3.34	0.49	0.00	0.00	12.89*	0.15	0.00	2.68	0.00	0.00	2.32
Follow	1.58	1.39	1.54	1.78	0.00	5.76*	4.01*	0.00	3.99!	0.00	0.00	0.10
Approach	0.00	4.44*	0.18	0.14	0.00	0.00	0.21	3.58	6.15!	0.00	0.00	0.67
Meral Spr.	2.23	3.60	*17.00*	2.61	0.00	0.94	1.18	2.20	4.39!	0.00	0.00	0.67
Box	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Walk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.02
Ant.Point	1.07	0.00	0.03	6.31!	0.00	0.00	0.20	1.68	0.32	0.00	*12.26*	0.66

TABLE 6 - Chi-square values obtained by comparing the totalled frequencies of 70 male and 80 female losers from encounters in which both animals were the same sex. * = females significantly greater than males. ! = males significantly greater than females. Boxes emphasize the chi-squares discussed in the text.

INITIAL BEHAVIOUR	SUBSEQUENT BEHAVIOUR													
	SC	PU	BK	SW	AF	JU	AW	FO	AH	MS	BO	WA	AP	RU
Scissor	0.00	0.06	0.00	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Push	1.00	1.69	0.02	0.00	0.00	17.70*	4.04*	0.00	0.00	2.84	29.70!	0.00	0.00	0.00
Back	0.00	8.59	0.35	8.47*	0.65	0.00	1.01	0.00	1.32	0.13	0.00	0.28	1.84	7.50!
Side-ways	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.02	0.11
Abd.Flex	0.00	0.00	0.94	0.00	1.03	0.00	0.00	0.00	0.00	0.46	0.00	0.00	0.03	0.00
Jump	0.00	7.57!	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.23*	0.00	0.00	0.00	0.00
Ant.Whip	0.00	2.21	0.67	0.00	0.00	0.00	3.12	1.17	0.00	1.06	1.51	0.00	0.00	0.00
Follow	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.39	0.00
Approach	0.00	0.00	0.97	0.00	0.14	0.00	0.00	0.44	0.00	11.71!	0.00	0.00	0.22	0.00
Meral Spr.	0.00	0.81	6.12!	0.01	1.81	0.04	0.24	2.95	11.77*	0.00	0.00	0.24	0.01	0.60
Box	0.00	0.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Walk	0.00	0.00	0.54	0.00	0.19	0.00	0.00	0.00	0.27	0.05	0.00	0.01	0.00	1.03
Ant.Point	0.00	0.00	2.04	1.52	8.00*	0.00	0.00	1.42	0.54	0.27	0.00	0.33	1.33	0.68
Run	0.00	0.00	0.00	0.00	1.75	0.00	0.00	0.00	0.00	0.00	0.00	12.28!	14.69*	0.09

TABLE 7 - Chi-square values obtained by comparing the totalled frequencies of 65 male and 35 female winners from encounters in which the two animals were of the opposite sex. * = females significantly greater than males. ! = males significantly greater than females. Boxes amphasize the chi-squares discussed in the text.

INITIAL BEHAVIOUR	SC	PU	BK	RH	JU	AW	FO	AH	MS	BO	WA	AP
						SUBSEQUENT BEHAVIOUR						
Scissor	0.00	0.00	0.00	9.79!	* 41.14 *	0.00	1.32	0.00	0.13	0.00	0.00	0.00
Push	* 22.84 *	0.00	0.00	0.00	* 13.51 *	2.86	0.16	0.00	4.32!	11.46!	0.00	0.00
Back	0.00	0.07	1.23	0.00	0.00	0.07	0.00	0.07	1.31	0.00	0.00	0.10
Rush	0.28	0.00	0.00	0.00	0.00	0.00	4.51!	0.00	2.38	0.00	0.00	0.18
Jump	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00	1.89	0.00	0.00	0.00
Ant.Whip	0.00	5.20*	0.35	0.00	0.00	0.38	0.10	0.00	0.28	0.00	0.00	0.00
Follow	0.26	0.06	0.11	* 14.32 *	0.00	0.00	0.12	1.06	3.03	0.00	0.00	1.17
Approach	0.00	0.00	0.00	0.78	0.00	0.00	2.14	1.71	2.44	0.00	0.00	0.61
Meral Spr.	0.27	2.01	0.02	1.81	0.00	6.44!	2.41	0.18	1.00	0.00	0.00	3.53
Box	0.00	1.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Walk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Ant.Point	0.00	0.00	0.49	1.89	0.00	0.20	1.29	0.52	0.78	0.00	* 5.41 *	0.08

TABLE 8 - Chi-square values obtained by comparing the totalled freqiencies of 35 male and 65 female losers from encounters in which the two animals were of the opposite sex. * = females significantly greater than males. ! = males significantly greater than females. Boxes emphasize the chi-squares discussed in the text.

INITIAL BEHAVIOUR	SUBSEQUENT BEHAVIOUR SC	PU	BK	SW	AF	JU	AW	FO	AH	MS	BO	WA	AP	RU
Scissor	0.00	0.00	0.00	0.00	0.00	4.46!	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Push	10.59!	0.00	3.23	0.00	0.00	0.14	*4.69*	0.00	0.00	1.54	0.00	0.00	0.00	0.00
Back	0.00	0.13	2.17	1.15	0.15	0.00	0.00	0.00	7.35!	0.41	0.00	0.42	2.22	1.00
Side-ways	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	2.28	1.92
Abd.Flex	0.00	0.00	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.45	0.00
Jump	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	0.00	0.00	0.00	0.00
Ant.Whip	0.00	0.67	2.87	0.00	0.00	0.00	0.70	0.01	0.00	0.71	0.00	0.00	0.00	0.00
Follow	0.00	1.35	0.39	0.00	0.00	0.00	0.21	0.00	0.00	0.53	0.00	0.00	9.92!	0.00
Approach	0.00	0.00	1.11	0.00	0.00	0.00	0.00	1.46	0.00	0.39	0.00	0.00	2.30	0.00
Meral Spr.	0.00	*7.69*	3.23	0.00	0.57	0.00	1.86	5.16!	7.59!	0.00	0.00	0.00	0.17	0.00
Box	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Walk	0.00	0.00	2.43	0.00	0.10	0.00	0.00	0.00	0.00	1.55	0.00	2.39	2.05	0.32
Ant.Point	0.00	0.00	3.08	*6.78*	3.17	0.00	0.00	0.00	20.88!	1.00	0.00	3.56	4.45*	1.17
Run	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.00	0.00

TABLE 9 - Chi-square values obtained by comparing the totalled frequencies of 70 male winners from male/male encounters and 65 male winners from male/female encounters. * = male/female significantly greater than male/male. ! = male/male significantly greater than male/female. Side-ways, abdomen flexing and running were excluded, because they were rarely shown by winners. Boxes emphasize the chi-squares discussed in the text.

INITIAL						SUBSEQUENT BEHAVIOUR						
BEHAVIOUR	SC	PU	BK	RH	JU	AW	FO	AH	MS	BO	WA	AP
Scissor	0.00	0.21	0.00	16.85	[24.06!]	0.00	2.48	0.00	0.04	0.00	0.00	1.33
Push	[12.64!]	0.05	0.00	0.00	0.62	0.01	1.36	0.00	1.81	2.17	0.00	0.00
Back	0.00	0.41	0.75	0.00	0.00	1.38	0.00	0.00	0.97	0.00	0.00	[4.24!]
Rush	0.32	0.00	0.00	0.00	0.00	0.00	2.07	0.00	0.00	0.00	0.00	0.01
Jump	0.00	1.36	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00
Ant.Whip	0.00	2.30	0.78	0.00	0.00	2.13	*4.18*	0.00	8.74!!	0.00	0.00	0.44
Follow	0.01	1.34	2.06	2.18	0.00	*20.38*	[15.91!]	3.62	0.32	0.00	0.00	0.25
Approach	0.00	0.07	0.31	0.07	0.00	0.00	5.92	0.66	10.53	0.00	0.00	0.02
Meral spr.	5.62*	0.15	5.60*	0.37	0.00	*8.13*	6.18!	0.08	[3.47!]	1.05	0.00	0.20
Box	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	1.59	0.00	0.00	0.00
Walk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.02
Ant.Point	0.23	0.19	0.39	1.21	0.00	0.00	0.19	0.32	4.27!	0.00	2.29	1.84

TABLE 10 - Chi-square values obtained by comparing the totalled frequencies of 70 male losers from male/male encounters and 35 male losers from female/male encounters. * = female/male losers significantly greater than male/male losers; ! = male/male losers significantly greater than female/male losers. Rushing was excluded, because it was rarely shown by losers. Boxes emphasize the chi-squares discussed in the text.

INITIAL BEHAVIOUR	SC	PU	BK	SW	AF	JU	SUBSEQUENT BEHAVIOUR AW	FO	AH	MS	BO	WA	AP	RU
Scissor	0.00	0.00	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Push	3.16	0.00	0.08	0.00	0.00	4.59	0.20	0.00	0.00	0.07	0.00	0.00	0.00	0.00
Back	0.00	0.45	5.18!	0.08	3.19	0.00	0.00	0.00	9.67	1.41	1.65	1.91	9.99*	4.60!
Side-ways	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66	3.47	1.61
Abd.Flex	0.00	0.00	1.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.00
Jump	0.00	3.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.82	0.00	0.00	0.00	0.00
Ant.Whip	0.00	4.18!	1.95	0.00	0.00	0.00	3.20	0.34	0.00	1.87	0.00	0.00	0.00	0.00
Follow	0.00	1.95	0.00	0.00	0.00	0.00	0.93	0.00	0.00	0.06	0.00	0.00	0.31	0.00
Approach	0.00	0.00	3.16	0.00	0.00	0.00	0.00	0.01	0.00	3.83	0.00	0.00	0.02	0.00
Meral Spr.	0.00	5.80!	0.29	0.00	0.74	0.00	0.02	12.68	7.07	0.00	0.00	0.00	0.01	0.00
Box	0.00	9.26!	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Walk	0.00	0.00	0.05	0.00	0.41	0.00	0.00	0.00	0.00	0.44	0.00	0.11	1.27	3.11
Ant.Point	0.00	0.00	7.64!	0.03	1.07	0.00	0.00	1.32	22.24	10.08!	0.00	0.50	0.00	0.40
Run	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	2.34	4.68*	0.00

TABLE 11 - Chi-square values obtained by comparing the totalled frequencies of 80 female winners from female vs. female encounters and 35 female winners from female vs. male encounters. * = female/male winners significantly greater than female/female winners; ! indicates the opposite situation. Side-ways, abdomen flexing and running away were excluded, because they were rarely shown by winners. Boxes emphasize the chi-squares discussed in the text.

INITIAL BEHAVIOUR	SUBSEQUENT BEHAVIOUR											
	SC	PU	BK	RH	JU	AW	FO	AH	MS	BO	WA	AP
Scissor	0.00	0.00	0.00	1.36	0.11	0.00	0.00	0.00	0.74	0.00	0.00	0.00
Push	0.05	0.00	0.00	0.00	0.62	4.32!	0.59	0.00	0.33	0.84	0.00	0.00
Back	0.00	0.51	0.09	0.00	0.00	0.00	0.00	0.07	1.60	0.00	0.00	0.13
Rush	4.53!	0.00	0.00	0.00	0.00	0.00	0.28	0.00	0.83	0.00	0.00	0.00
Jump	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00
Ant.Whip.	0.00	6.43*	0.21	0.00	0.00	4.56!	2.46	0.00	2.95	0.00	0.00	0.00
Follow	2.28	0.06	0.28	2.27	0.00	0.00	3.87!	0.24	0.47	0.00	0.00	1.60
Approach	0.00	0.00	0.00	0.64	0.00	0.00	0.03	0.12	0.80	0.00	0.00	1.76
Meral Spr.	0.07	9.96!	2.11	0.01	0.00	0.15	0.14	0.91	0.96	0.00	0.00	9.06*
Box	0.00	0.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Walk	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Ant.Point	0.00	0.00	0.00	7.23*	0.00	0.22	1.37	0.68	1.75	0.00	0.36	0.04

TABLE 12 - Chi-squares obtained by comparing the totalled frequencies of 80 female losers from female vs. female encounters and 65 female losers from female vs. male encounters. * = male/female losers significantly greater than female/female losers; ! = female/female losers significantly greater than male/female losers. Rushing was excluded, because it was rarely shown by losers. Boxes emphasize the chi-squares discussed in the text.

INITIAL BEHAVIOUR	SC	PU	BK	SW	AF	JU	AW	FO	AH	MS	BO	WA	AP	RU
						SUBSEQUENT BEHAVIOUR								
Scissor	0.00	0.08	0.00	0.00	0.00	9.56!	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Push	7.96!	0.08	4.68	0.00	0.00	2.96	3.37	0.00	0.00	0.25	4.27*	0.00	0.00	0.00
Back	0.00	6.06!	2.44	3.23	0.89	0.00	3.64	0.00	0.63	0.11	0.00	1.86	10.76*	1.82
Side-ways	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.16	0.24	0.18
Abd.Flex	0.00	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.46	0.00	0.00	0.00	0.00
Jump	0.00	0.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.98!	0.00	0.00	0.00	0.00
Ant.Whip	0.00	0.29	0.45	0.00	0.00	0.00	4.00*	0.21	0.00	0.04	0.00	0.00	0.00	0.00
Follow	0.00	0.01	0.16	0.00	0.00	0.00	0.47	0.08	0.00	0.00	0.00	0.00	1.81	0.00
Approach	0.00	0.00	0.04	0.00	0.65	0.00	0.00	0.31	0.00	0.29	0.00	0.00	1.13	0.00
Meral Spr.	0.51	0.03	0.34	0.22	0.68	0.00	1.49	0.17	10.99!	0.10	0.00	0.55	0.30	0.00
Box	0.00	7.23!	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Walk	0.00	0.00	1.02	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.00	5.96*	0.13	3.66
Ant.Point	0.00	0.00	0.03	5.97*	0.38	0.00	0.00	0.00	0.39	5.23!	0.00	6.50!	2.20	0.07
Run	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.04*	1.03	0.00

the winner's basic sequence pathway. Females proceeded from following to rushing, especially when they won over males (Tables 3 and 7); while males showed following ⟶ meral spread ⟶ rushing, especially during male vs. male encounters (Tables 3 and 5). The chi-square obtained for the meral spread ⟶ rushing sequence was not quite significant at the .05 level (Table 3).

Losing males entered the initial stages of the two aggressive pathways (Nos. 1 and 4) more often than females, especially when they lost to females. This involved the ant. point ⟶ approach ⟶ meral spread segment (Tables 4, 6 and 8). From meral spread losing females proceeded to pushing more often than males, especially when they lost to males; while males proceeded more often to backing, when they lost to other males (Tables 4, 6 and 8).

During the second basic sequence pathway females tended to proceed directly from antenna pointing to abdomen flexing more often than males. Also ant. point ⟶ side-ways and back ⟶ side-ways occurred more often among females, indicating their more frequent use of side-ways (Table 4).

During the third basic sequence pathway, ant. point ⟶ walk ⟶ run ⟶ walk ⟶ ant. point, losing females sometimes ended their chain of activities running away ⟶ ant. pointing; while males tended to follow the normal route (Table 4).

The partial display, of this third basic pathway, ant. point ⟶ walk ⟶ ant. point (Fig. 36), seen among winners was much more common among females than males regardless of the sex of their opponent (Tables 3, 5, and 7).

When winning female lobsters showed the fourth basic sequence pathway involving the group I behaviour patterns, pushing proceeded to scissoring and jumping more frequently than among males (Table 3). Scissoring went to jumping before the chain continued jump ⟶ meral spread ⟶ push. When these pathways were shown by males, they tended to return directly from jumping to pushing. This was especially true during male vs. male encounters (Tables 3, 4, 5, and 7). Winning males tended to return from pushing to meral spread or to show the side chain push ⟶ box ⟶ push (Figs. 3, 5, and 7). From meral spread winning females proceeded more often to backing especially during unisexual agonistic encounters (Tables 3 and 5), while winning males proceeded to antenna whipping, especially during male/female encounters (Tables 3 and 7).

Similar male - female differences in the execution of the fourth basic pathway were observed among losers (Table 4). An exception occurred during the push ⟶ scissor ⟶ jump ⟶ push or meral spread sequence, which was possibly due to the fact that it was less common among losers. When males lost to females they tended to show more of the sequence than females that lost to males (Table 8). Losing females also tended to proceed from pushing to the antenna whipping pathways more frequently than males (Tables 4, 6, and 8).

Males and females showed differences in some of the rarer sequences, but more data would be required before these differences should be discussed.

The sequence data from all four types of encounters supports the hypothesis stated earlier, that males are more aggressive than females. Winning males from male/male encounters showed the push ⟶ scissor ⟶ jump sequence and ended their chains of activities back ⟶ ant. point more often than male winners from male/female encounters (Table 9). When males dominated females, they tended to show the ant. whip ⟶ follow ⟶ meral spread ⟶ ant. whip and scissor ⟶ rush sequences, while winning males in unisexual encounters tended to stop following or showing meral spread and then begin them again. Winning females from female/female counters tended to complete the winner's basic pathway more fully (rush ⟶ scissor) and to antennae whip its opponent more often (push ⟶ ant. whip ⟶ meral spread ⟶ push) than winners from female/male encounters (Table 11). Losing males from female/male encounters approached (ant. point ⟶ approach, back ⟶ approach and meral spread ⟶ approach) and followed (meral spread ⟶ follow) much more frequently than losing males from male/male encounters (Table 10). The reverse was true for the ant. point ⟶ back sequence. Males losing to females tended to show the push ⟶ jump sequence more frequently, but this is probably due to the fact that the push ⟶ scissor ⟶ jump ⟶ push sequence was shown more often among winning females. These two sequences were usually seen together after a period of pushing, one animal does one sequence and one animal the other (Table 10). Losing females from female/female encounters showed the push ⟶ scissor ⟶ jump ⟶ meral spread, the ant. point ⟶ meral spread, and the back ⟶ push sequences more frequently than losing females from male/female encounters, while the reverse was observed for the push ⟶ back and the ant. point ⟶ side-ways sequences (Table 12).

The sequence analysis indicates that lobsters showed the agonistic behaviour patterns in the form of four basic sequence pathways. There were quantitative variations in the way males and females performed these basic chains of activities and their side chains, but both sexes used all four pathways. Sequence data also supported the hypothesis, that males are more aggressive than females.

AGONISTIC COMMUNICATION BETWEEN LOBSTERS

Ethologists have often described stereotyped movements or behaviour patterns and ascribed a communicatory function to them, but because of the lack of quantitative data, they have only recently been able to demonstrate the interrelationship of each activity between individuals. Following the development by Shannon of a mathematical theory of communication (Shannon and Weaver 1949), a few ethology studies utilizing his information - quantifying formulae have been made. Haldane and Spurway (1954), and Wilson (1962) analyzed information transfer in the food location systems of the honeybee and the fire ant, while Hazlett and Bossert (1965) and Dingle (1969) studied aggressive communication in hermit crabs and the mantis shrimp *Gonodactylus bredini*.

The data used in the present response analysis was obtained from 23 male and 22 female lobsters during 210 paired agonistic encounters (40 of the usable 250 encounters had been punched inappropriately for this analysis). The recorded behaviour was analyzed by program LOBSTER 9 (Appendix I). This program instructed the computer to search for the start of a behaviour pattern in one animal and then determine the response, if any, of the opponent. The tabulated responses were totalled for the winners, the losers, and both winners and losers of all 210 encounters. When lobsters showed rushing, their opponents responded by abdomen flexing 645 times, backing 589 times, showing no recorded behaviour 31 times, antenna pointing 30 times, showing meral spread and running away 23 times, pushing 15 times, jumping 11 times, walking away 8 times, rushing 4 times, showing side-ways 3 times, and antennae whipping, following and boxing once. A complete matrix of responses to each behaviour pattern is presented in Table 13. The 15 initial acts are listed in the first column and the frequencies of the 16 possible responses are listed in the remaining columns.

The table of responses indicated that lobster agonistic behaviour is a complex behavioural system, even when a simple presentation such as this was used. When one animal showed any of the 15 behaviour patterns its opponent could show almost any of the 16 possible responses. Even though the sequence analysis indicated that rushing was a strong aggressive display, the opponent responded to it by showing almost every one of the possible acts. It is true that abdomen flexing and backing were the most common responses, but no recorded response was observed on 31 occasions.

In order to determine if the behaviour of one animal tended to cause specific responses in the opponent, the following procedure was used. First, the response frequencies were totalled over the initial behaviour patterns (Table 13, column totals). These totals indicated how common each response was. Second, the total number of responses was determined (Table 13, grand total). Third, the frequencies of the responses expected, if the displays of one lobster had no effect upon the response of its opponent, were calculated (Table 14). They were obtained by multiplying the probability of a specific response occurring (column total / grand total, Table 13), by the total number of responses following each initial act (Table 13, row totals). By comparing the expected frequencies with the observed, it was possible to determine whether a behaviour pattern was statistically "directive" or "inhibitive" towards a certain response (Hazlett and Bossert 1965). Scissoring is

TABLE 13 - Frequency distributions of responses observed during 210 encounters. The rows correspond to the initial acts, while columns contain the frequency of the response which heads the column. Row and column totals are also given. Boxes emphasize specific frequencies discussed in the text.

INITIAL BEHAVIOUR	SC	PU	BK	SW	RH	AF	JU	SUBSEQUENT BEHAVIOUR AW	FO	AH	MS	BO	WA	AP	RU	NONE	
Scissor	61	260	420	3	3	354	177	4	1	4	98	1	6	21	10	37	1460
Push	132	1579	52	0	4	22	192	82	15	5	172	57	5	9	1	83	2410
Back	211	45	157	7	384	3	13	350	2001	73	2465	1	38	809	2	499	7058
Side-ways	4	1	6	0	11	0	0	2	84	4	191	0	2	59	0	138	502
Rush	0	15	589	3	4	645	11	1	1	0	23	1	8	30	23	31	1385
Abd.Flex	385	12	8	8	327	0	23	4	371	3	873	0	0	364	0	84	2454
Jump	80	435	32	0	4	13	210	3	13	11	191	1	1	6	1	22	1034
Ant.Whip	10	371	167	4	1	8	8	417	14	5	577	26	20	12	4	80	1724
Follow	0	28	1804	39	0	371	3	51	5	11	365	24	380	149	96	287	3613
Approach	11	51	795	7	11	71	3	15	77	466	414	8	159	719	55	689	3551
Meral Spr.	37	419	1611	27	28	332	47	306	183	137	1544	23	195	424	63	436	5812
Box	3	200	3	0	2	0	3	41	16	1	60	21	1	11	0	32	394
Walk	13	8	26	0	22	0	1	10	480	30	577	0	15	322	0	582	2086
Ant.Point	26	34	1373	80	68	72	4	26	710	1311	1448	28	605	2824	70	2921	11600
Run	12	1	3	0	23	0	4	2	162	2	231	0	1	84	0	61	586
Column Tot.	985	3459	7046	170	892	1891	699	1314	4133	2063	9229	191	1436	5843	325	5993	45669

TABLE 14 - Expected frequencies of responses to the 15 behaviour patterns. Values calculated from Table 13.

INITIAL BEHAVIOUR	SC	PU	BK	SW	RH	AF	JU	AW	FO	AH	MS	BO	WA	AP	RU	NONE
							SUBSEQUENT BEHAVIOUR									
Scissor	31	111	225	5	29	60	22	42	132	66	295	6	46	187	10	192
Push	52	183	372	9	47	100	37	69	218	109	487	10	76	308	17	316
Back	152	535	1089	26	138	292	108	203	639	319	1426	30	222	903	50	926
Side-ways	11	38	77	2	10	21	8	14	45	23	101	2	16	64	4	66
Rush	30	105	214	5	27	57	21	40	125	63	280	6	44	177	10	182
Abd.Flex	53	186	379	9	48	102	38	71	222	111	496	10	77	314	17	322
Jump	22	78	160	4	20	43	16	30	94	47	209	4	33	132	7	136
Ant.Whip	37	131	266	6	34	71	26	50	156	78	348	7	54	221	12	226
Follow	78	274	557	13	71	150	55	104	327	163	730	15	114	462	26	474
Approach	77	269	548	13	69	147	54	102	321	160	718	15	112	454	25	466
Meral Spr.	125	440	897	22	114	241	89	167	526	263	1175	24	183	744	41	763
Box	8	30	61	1	8	16	6	11	36	18	80	2	12	50	3	52
Walk	45	158	322	8	41	86	32	60	189	94	422	9	66	267	15	274
Ant.Point	250	879	1790	43	227	480	178	334	1050	524	2344	49	365	1484	83	1522
Run	13	44	90	2	11	24	9	17	53	26	118	2	18	75	4	77

said to be directive towards abdomen flexing, pushing, jumping and backing, but inhibitive towards following, meral spread, approaching, antenna pointing and no response (Table 15), because the first were shown more frequently than expected, while the second were shown less frequently than expected (Tables 13 and 14). The results indicated that specific behaviour patterns tended to be shown, while others tended not to be shown in response to each initial display (Table 15).

In order to determine if there was any pattern to the responses, a flow diagram was developed. First the most common responses to a specific initial act by the winners were listed; then using these loser responses as initial acts, the commonest responses to them by the winners were listed. The agonistic bouts usually started and ended with antenna pointing, first by the winner, then by the loser. Beginning with a winner's antenna pointing the most common loser response was antenna pointing. The winner responded to this by showing meral spread or approaching. A flow diagram was built up in this manner until the behaviour again reverted back to antenna pointing (Fig. 39 a). The commonest response was indicated by a thick arrow, the second by line arrow and third or fourth by broken arrow. If the commonest response had occurred in the previous step of the flow diagram, the next commonest was represented by the thick arrow. This diagram shows clearly how the basic sequence pathway of winners (ant. point ⟶ approach ⟶ meral spread ⟶ follow ⟶ rush ⟶ scissor ⟶ meral spread ⟶ ant. point) meshed with the common sequence pathway of losers (ant. point ⟶ back ⟶ abdomen flex ⟶ back ⟶ ant. point) during lobster agonistic interactions. The losers showed backing, while the winners

TABLE 15 - The responses to which each display was statistically directive or inhibitive.

	DIRECTIVE	INHIBITIVE
Scissor	Abd. flex, push, jump, back	Follow, meral spr., approach, ant.point, none
Push	Push, jump, scissor, box	Back, follow, meral spr., ant. point
Back	Follow, rush	Push, back, abd.flex, walk, no response
Side-ways	No response	Back, abd. flex
Rush	Back, abd. flex	Most of the others
Abd.flex	Scissor, rush	Back, abd.flex, none
Jump	Push, jump	Back
Ant.whip	Push, ant.whip	Follow, approach, none
Follow	Back, abd.flex, run	Follow, approach, meral spr.
Approach	Approach	
Meral Spr.	Back	Scissor, rush, follow
Box	Push, box, ant.whip	Most others
Walk	Follow, none	Back
Ant.point	None, ant.point, approach	Push
Run	Meral spr., follow	Back, abd.flex

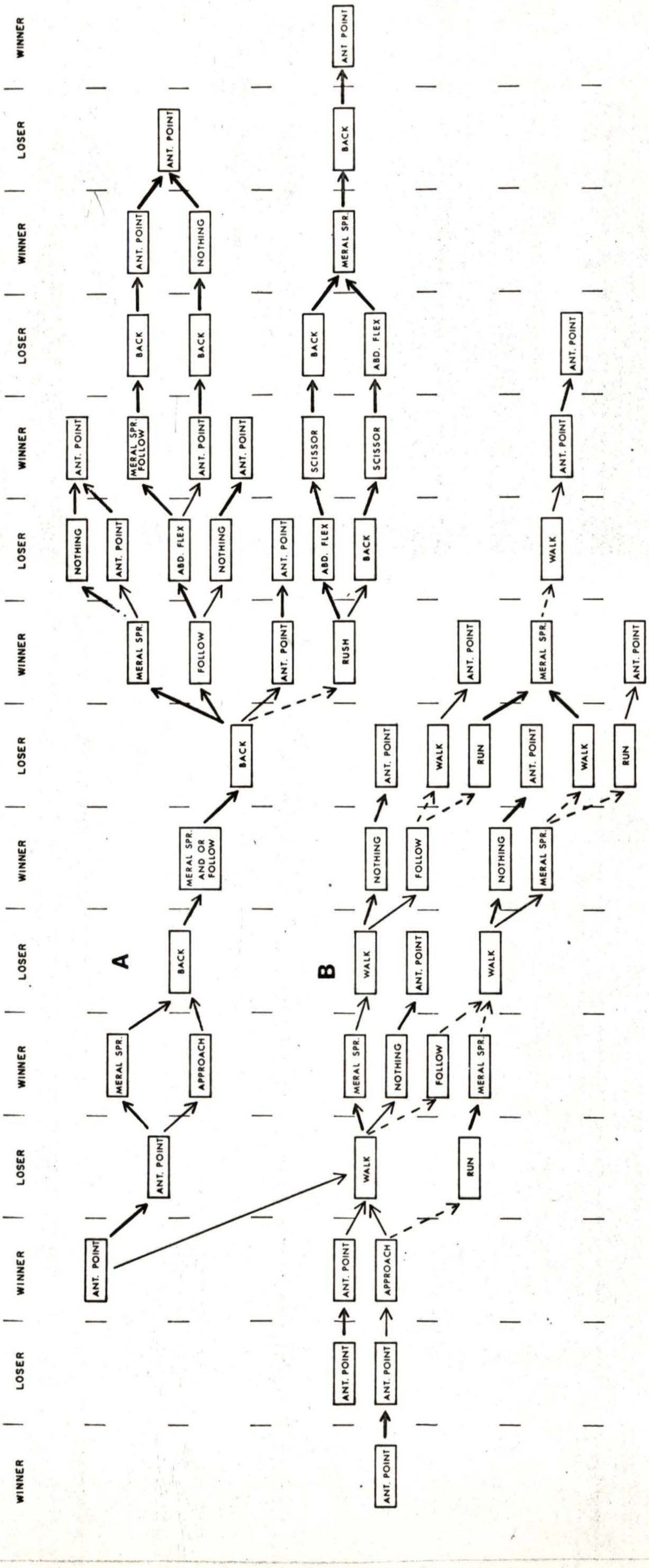


FIG. 39 Flow diagrams of the commonest responses to each display, beginning with antenna pointing which starts each agonistic bout (commonest response - thick arrow, second-line arrow, and third or fourth-broken arrow).

A. The commonest flow of activities; winner performs sequence pathway I, Loser performs sequence pathway II.

B. A common flow of activities; Winner - part of pathway I, Loser - pathway III.

showed following and meral spread. If the winners were very aggressive they demonstrated rushing and scissoring, while the losers abdomen flexed (Fig. 39 a). The less frequent basic sequence pathway of losers (ant. point ⟶ walk away ⟶ run away ⟶ walk away ⟶ ant. point) was often shown in response to the incomplete form of the winner's pathway (ant. point ⟶ approach ⟶ meral spread ⟶ follow ⟶ ant. point, Fig. 39 b). When both lobsters demonstrated the long complex fourth basic sequence pathway, they were required to show mutual aggression (ant. point ⟶ approach ⟶ meral spread ⟶ push ⟶ group 1 behaviour patterns ⟶ meral spread —— ant. point). As the sequence began antenna pointing ⟶ approaching ⟶ meral spread ⟶ pushing the other lobster responded by showing the same behaviour patterns (Table 13, boxes). This is referred to as social facilitation or the mimetic induction effect (Hazlett and Bossert 1965). Social facilitation also commonly occurred later in the pathway, when one of the individuals performed jumping, antennae whipping or scissoring (Table 13, broken boxes). The interrelationship between lobsters showing this pathway could not be demonstrated by flow diagram, because the fourth basic pathway occurred less frequently than the others.

Using the response analysis data, it was possible to estimate the amount of information contained and transmitted by the behaviour patterns. The information present in the average distribution of responses was calculated from

$$H\ (x) = -\sum_{i} p(i)\ \log_2 p(i)$$

where $p(i)$ is the probability of the occurrence of behaviour pattern i (Quastler 1958, p. 14). These were obtained by dividing the grand total of responses into the column totals of Table 13 (appendix II). The logarithm was taken to the base 2 so that the result obtained was in "bits", the basic unit of information theory. A bit has been defined as the amount of information required to make a choice between two equiprobable alternatives (Wilson 1962). The average number of binary symbols (bits) required to store the information of a response (H(x)) equalled 3.375 bits/display (Table 16). This information present in a response was only an estimate of the true value, because the probabilities of responses occurring were only estimates of the true probabilities. The conditional information present in the distribution showing the commonness of the responses could also be calculated, when the initial display of the other member of the agonistic encounter was known. If $p(i,j)$ is the probability that one lobster performed behaviour pattern i, which its opponent responded to by showing j (response frequency/total, Table 13) and $p(j/i)$ is the probability that the opponent responded with display j if the first lobster had performed behaviour pattern i (response frequency/row total, Table 13), then

$$H(x/y) = - \sum_{i,j} p(i,j) \log_2 p(j/i).$$

The difference between these statistics, T(x,y), was a measure of the average restriction on a lobster's display by its opponent, or the amount of information transmitted or communicated per display (Quastler 1958, Hazlett and Bossert 1965). It was the minimum information transmitted, because it was only that which the opponent had confirmed that he had received by his own response. For the lobster it was 0.748 bits/display (Table 16).

The average minimum information transmitted per individual per

TABLE 16 - Average information statistics calculated from the responses recorded during 210 encounters.

TITLES	VALUES
Information present	3.375 bits/display
Conditional information	2.627 bits/display
Information transmitted	0.748 bits/display
Average number of behaviour patterns	76.98 displays/individual/encounter
Average number of bouts during an encounter	10.65 bouts/encounter
Mean bout length	40.07 seconds/bout
Information transmitted during a bout	5.41 bits/individual/bout
Minimum information transmitted per second	.135 bits/individual/second

bout could also be calculated, if the average number of displays per 15 minute encounter per lobster and the average number of bouts per encounter were known. This was found to equal 5.41 bits/lobster/bout (Table 16).

If the average bout length is known, the minimum information transmitted per animal per second can be calculated (Table 16). For lobsters, it was found to be .135 bits/individual/second. This value is very low, because the method ignores the information which was probably transmitted as a function of behaviour pattern duration and possibly intensity, but it was at least a component of the actual average rate of information transfer.

Differences between male and female responses

There were no qualitative differences between male and female responses to their opponent's displays during lobster agonistic behaviour. A display by males or females was statistically directive or inhibitive towards the same responses. The same amount of information was transmitted by the displays; 0.747 bits per display for males and 0.750 bits per display for females.

To determine whether there were quantitative differences in the responses of males and females, the totalled response frequencies of all males and females were compared. Females responded to pushing by scissoring more often than males, even though they both scissored with equal frequency (males = 50 of 491 scissoring, females = 82 of 494 scissoring). This probably reflects the fact that females showed the push ⟶ scissor ⟶ jump ⟶ meral spread side chain of the fourth basic sequence pathway more frequently than males (p.100). Females also showed more scissoring in response to male scissoring (males 26, females 35) and more jumping in response to jumping (males 71, females 139), which indicates that not only did they show this side chain more frequently, but were socially facilitated, when males performed it. The males showed more scissoring in response to abdomen flexing (males 227, females 158). The fact that males showed more boxing in response to pushing (46 to 11) and females showed more side-ways in response to antenna pointing (53 to 27), probably indicates again that male utilized the push ⟶ box ⟶ push and females utilized the back ⟶ side-ways ⟶ ant. point side chains more frequently than their sexual opposites (p.99).

Discussion and Conclusions

The major problem with the analysis of agonistic communication is that it over simplified a complicated system. Five basic assumptions were made.

1. Initial behaviour patterns and responses were independent of previous displays.
2. Almost all information was transmitted visually.
3. Morphological characteristics such as body size and chelae size were not important or had a constant value which was common to all individuals.
4. There was no difference between males and females.
5. The behaviour patterns recorded were constant and there was no variation in intensity.

The first assumption is obviously invalid. Initial activities and their responses were not independent of previous displays. The sequence and response analyses indicated that lobsters followed four basic sequence pathways which meshed together in common patterns (Fig. 39). There were only a few points along these pathways where they periodically switched from one pathway to another. Also, changes in the motivational state of lobsters might not be expressed immediately in the behaviour, but could influence later responses. The information estimates could be too low if the information content of the behaviour patterns varied with the context in which they were shown. In order to determine if the proceeding display of the opponent had any effect on its response to the initial behaviour pattern, the frequencies of the responses following behaviour pattern i could be compared with the frequencies of the responses by the opponent following behaviour pattern i, given that it previously showed behaviour pattern X. This would divide Table 13 into fifteen tables of response frequencies, producing values that are too small for proper comparisons. More data should be obtained before a complete three act response analysis is carried out. While studying aggressive communication systems in hermit crabs, Hazlett and Bossert (1965) obtained a few component "three-act" sequence distributions which could be compared to their "two-act" sequence distributions. They found that the context could affect the distribution of responses at least in a limited way. This was probably also true for responses during lobster agonistic encounters. They had obtained data from 1,000 - 2,000 interactions (bouts), but estimated that the data from about 10,000 interactions (1,000 encounters) would be required before an adequate analysis of three-act sequences could be made.

With the exception of scissoring, pushing, and antennae whipping, which undoubtedly involve the tactile sense, this analysis was based almost solely on one sensory modality, vision. It is possible, that the lobsters were releasing a pheromone or producing sounds during the displays. These factors would increase the information transmitted and could be variations of the visually observed behaviour patterns indicating increased or decreased aggressive motivation and thereby produce a variation in response. Recent evidence suggests that female lobsters produce a sex attractant during molting (McLeese 1970), but it is unlikely that chemical communication is used during agonistic behaviour; first, because the animals moved around quite quickly and second,because the interactions were usually quite short. It is possible though that an interacting pair were producing vibrational messages. When stimulated by handling, lobsters have been known to produce a low frequency internal "growl-like" sound (Fish 1966). This sound was detected when hydrophones were suspended 15 - 25 cm from the animals. During the present study, no sound was detected above the background noise in the observation tanks even with the water turned off.

Another source of variability could be the effect of morphological characteristics such as animal size and claw size. The size of the communicator probably affected the response to his displays. For example, the individual that did nothing in response to rushing might have been much larger than the lobster performing it (Table 13). Size should increase the information content by intensifying or diminishing the displays. Since an increase in the calculated information content depends on an increase in the number of possible responses or a reduced variation in the probabilities of occurrence of each response, this information would be only partially included in the analysis. If size did affect the responses, the information content should increase slightly if there were large size variations between individuals, because the variation in the probabilities of occurrence of each response should be reduced. The displays would also have less restriction on the responses. Therefore, the conditional information (H x/y) would increase, but the information transmitted would decrease. This is exactly what appeared to have happened. During 79 encounters in which the lobsters varied by less than 2 mm. in carapace length, the information content, conditional information and information transmitted were calculated as 3.382 bits/display, 2.629 bits/display, and 0.754 bits/display respectively, while during the remaining 131 encounters they were 3.486 bits/display, 2.739 bits/display and 0.747 bits/display respectively. Hazlett and Bossert (1966) compared the information statistics obtained from size restricted and unrestricted groups of the hermit crab *Clibanarius vittatus*. Their results were similar, but the difference in information transmitted between the two groups was greater than that of the present study (size restricted = 0.34 bits/display, unrestricted = 0.30 bits/display), probably because their test animals were of a greater size range (> 65% variation, present study 26% variation). Even though size differences did affect the information transmitted, the information statistics should represent average values for social interactions between adults in nature, because the size range or size variation of the study animals was similar to those of natural adult lobster populations

(Table 17). It should be made clear though that adults do not represent a very large segment of the southern Nova Scotia lobster population, because an intensive fishery removes much of the stock before maturity (McLeese and Wilder 1964).

The fourth assumption, no difference between males and females, appears to be basically valid. Even though there were quantitative differences between male and female sequences and responses, the average information transmitted per display was very similar (p.113).

There is no way of determining the validity of the fifth assumption without continuing the study. Further ethological research has often indicated that initial descriptions of behaviour patterns were incomplete and that there were subtle variations which were probably indicative of intensity. This would divide the behaviour patterns, producing a greater information content and probably producing a greater restriction on the responses.

Another source of variation could be the effect of facilitation, habituation and conditioning. These three factors have or will be shown to operate during lobster agonistic interactions, but this method of analysis ignored their presence and produced an average overall statistic.

The minimum information transmitted per display, 0.748 bits/display, was similar to those calculated for other invertebrate agonistic communication systems. Hermit crabs transmitted 0.35 - 0.44 bits of information/display (Hazlett and Bossert 1965), while a stomatopod shrimp transmitted 0.78 bits/display (Dingle 1969). These lower values among hermit crabs could be attributed to the fact that they live under more crowded tide-pool conditions. Continual reaction to each other's displays would result in continual turmoil, unless some of the information

TABLE 17 - A comparison of the variation in size of the adult lobster population from five areas along the Atlantic coast of Canada.

ORIGIN OF DATA	CARAPACE LENGTH SIZE RANGES OF AT LEAST 90% OF ADULT POPULATION	% VARIATION IN SIZE	LOCALITY REFERENCE	REFERENCE FOR SIZE OF MATURATION
Miminegash, P.E.I.	64-88 mm.	27	Rutherford, Wilder and Frick (1967)	Templeman (1944)
Isles-de-la-Madeleine, Que.	72-103 mm.	28	Bergeron (1967)	Bergeron (1967)
Gabarus, N.S.	76-107 mm.	29	Rutherford, Wilder and Frick (1967)	Templeman (1944)
Fourchu, N.S.	76-113 mm.	32	Rutherford, Wilder and Frick (1967)	Templeman (1944)
St. Andrews, N.B.	104-145 mm.	28	Rutherford, Wilder and Frick (1967)	Templeman (1944)
Present study	84-114 mm.	26	-	-

transmitted was ignored. The solitary lobster or mantis shrimp (Dingle and Caldwell 1969) which would meet a conspecific less frequently would tend to react more often to the messages transmitted by the communicator.

The rates of transmission are also similar in magnitude. The honneybee and fire ant transmission rates were found to be 0.01 - 2.28 and 0.04 - 1.39 bits/second respectively during food source communication (Wilson 1962). During agonistic communication, it was 0.4 - 4.4 bits/second for hermit crabs (Hazlett and Bossert 1965) and 0.013 - 5.46 bits/second for the stomatopod *Gonodactylus bredini* (Dingle 1969). An average minimum transmission rate of 0.135 bits/individual/second was calculated for the lobster. These are all well below an estimate of 6 - 12 bits/second for the information content of human speech (Quastler 1958). The high estimates of transmission rates obtained for the hermit crabs and stomatopod shrimp are probably misleading. The hermit crab statistics were based upon the length of time it took to attain the postures and not on the number of displays during, or the length of agonistic interactions. The stomatopod transmission rates were based on the average information transmitted per interaction (1.82) which involved an average of 2.4 displays per interaction. The shortest interaction (0.33 seconds) could not have involved 2.4 displays and responses, because invertebrates cannot move around that quickly in an aquatic environment. Both researchers have attempted to calculate extreme rates of transmission from an average statistic.

The information transmission rate calculated for lobsters does include duration, but does not include the amount of information transmitted by the duration. It is only a component of the actual transmission rate. The behaviour patterns and interactions of lobsters appear to have longer durations than those of hermit crabs and stomatopod shrimps. Therefore, the rates of information transmission calculated by this method should generally be higher, for these animals.

The response analysis indicated that the displays are statistically inhibitive and directive toward certain responses. Lobsters respond to an aggressive opponent showing the winner's basic sequence pathway, by performing either loser's pathway. When the fourth basic pathway was observed during an interaction, both individuals were performing it. Despite numerous sources of variability it was possible to measure at least a component of the information communicated by lobsters showing agonistic behaviour. The results indicated that sometimes females responded differently than males, but these differences were not great enough to influence the average information statistics.

FACTORS AFFECTING THE AGONISTIC BEHAVIOUR OF LOBSTERS

When lobster agonistic behaviour had been described and examined, the question - what factors are affecting the outcome of encounters? - was asked. Among marine decapod crustaceans many factors, such as: animal size (Bovbjerg 1956, Fielder 1965, Squire 1965, Hazlett 1968 c), sex (Bovbjerg 1956, Fielder 1965, Hazlett 1966 d), chelae size (Bovbjerg 1956, Lowe 1956), aggressiveness, isolation, starvation (Hazlett 1966b and 66 d), age (Bovbjerg 1956), territoriality (Dingle and Caldwell 1969), the ovigerous condition (Lowe 1956), and ecdysis (Bovbjerg 1953) have been shown to affect agonistic behaviour. The first four of these were examined in this study.

Over a three year period, the outcomes had been recorded for 330 encounters which could be used here. These data were obtained from 40 male and 42 female lobsters which had been used no more than 12 times (mean 8.6). The remaining 520 encounters (observations from 850 encounters in total) were eliminated because extensive use, incomplete data, exposure to another individual more than once and the above factors not studied here might have affected the outcomes.

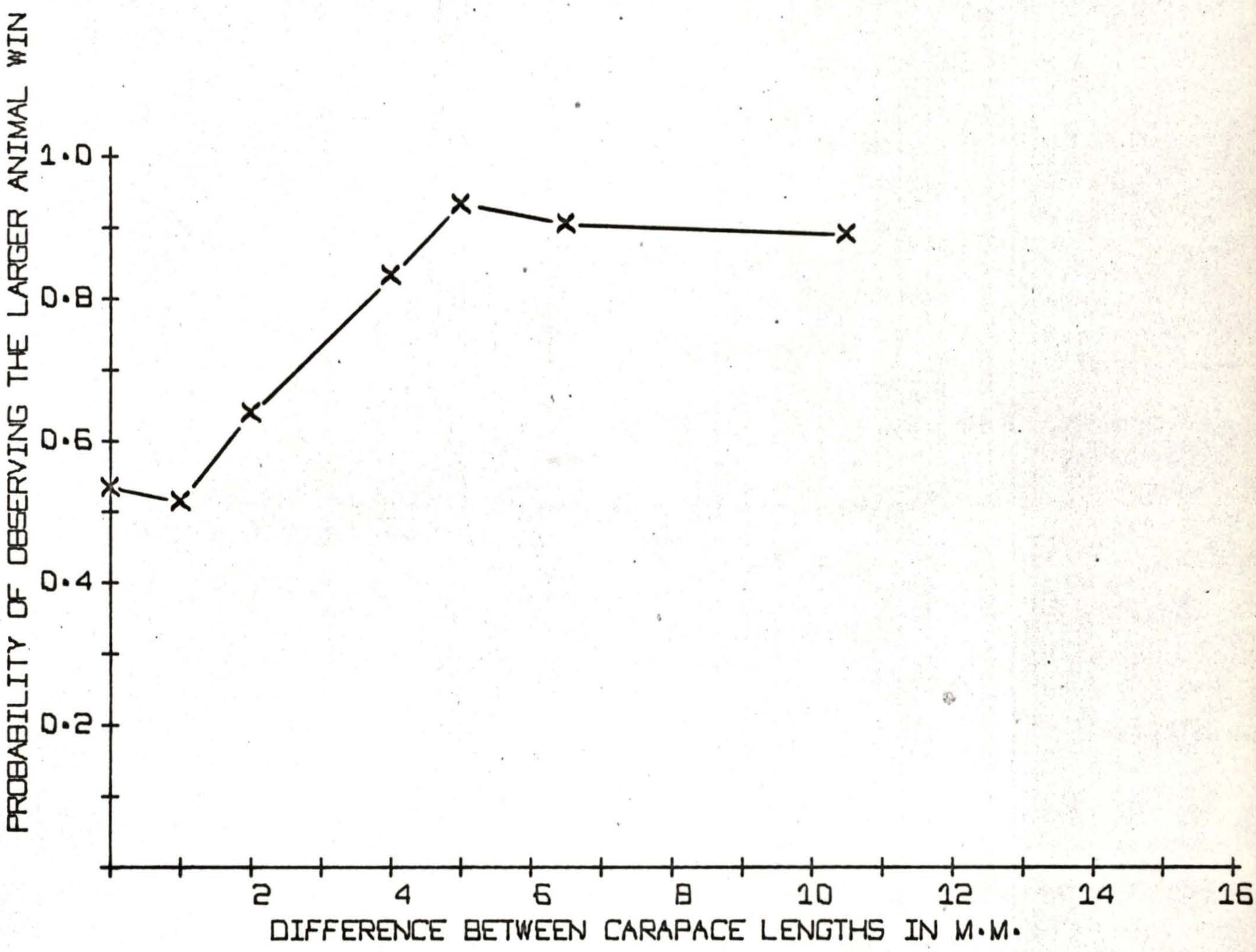
Animal size

There are many documented examples among crustaceans of the size difference between individuals affecting the outcome of agonistic encounters (p.34), but few studies have indicated how much of a size difference is important. Working with the hermit crab *Clibanarius vittatus*, Hazlett (1968 c) found that a 0.8 mm. or greater difference between two individuals' cephalothorax length meant that the larger animal would win at least 90% of the time, and that a 4 mm. difference meant that it would always win. In the present study, carapace length, the distance from the posterior edge of the orbital socket to the dorsal midline of the cardiac region's posterior edge, was used as an indication of overall size.

During 330 lobster agonistic encounters the smaller animal won on 105 occasions or 32% of the time. A sign test showed this to be a significant departure from the null hypothesis (upper .95 confidence limit on 32% was 37.19%). Size therefore did appear to affect the outcome of lobster agonistic encounters, with the larger animals usually winning.

To determine how the size difference between two individuals will affect the probability of the larger animal winning, the difference between the paired animals' carapace lengths, rounded to the nearest mm., were plotted against the percent of the encounters that the larger animal won. This was done for all 330 encounters (Fig. 40), the male vs. male (Fig. 41), and the female vs. female encounters (Fig. 42). Data from the 330 encounters showed that the percent won by the larger animal increased as the difference in size increased, until the percent reached about 90% and levelled off (Fig. 40). Lack of great size variation among the experimental animals prevented extensive data collection among extreme size ranges. The fragmentary data available indicated that the larger animal may always win an encounter if there is a 15 mm. or greater difference in carapace length.

Working with the hermit crab Clibanarius vittatus, Hazlett (1968 c) found that size differences can affect more than just the outcome



FIG·40· RELATIONSHIP OF THE DIFFERENCE IN SIZE AND THE PROBABILITY OF THE LARGER LOBSTER WINNING, BASED ON 330 PAIRED ENCOUNTERS·

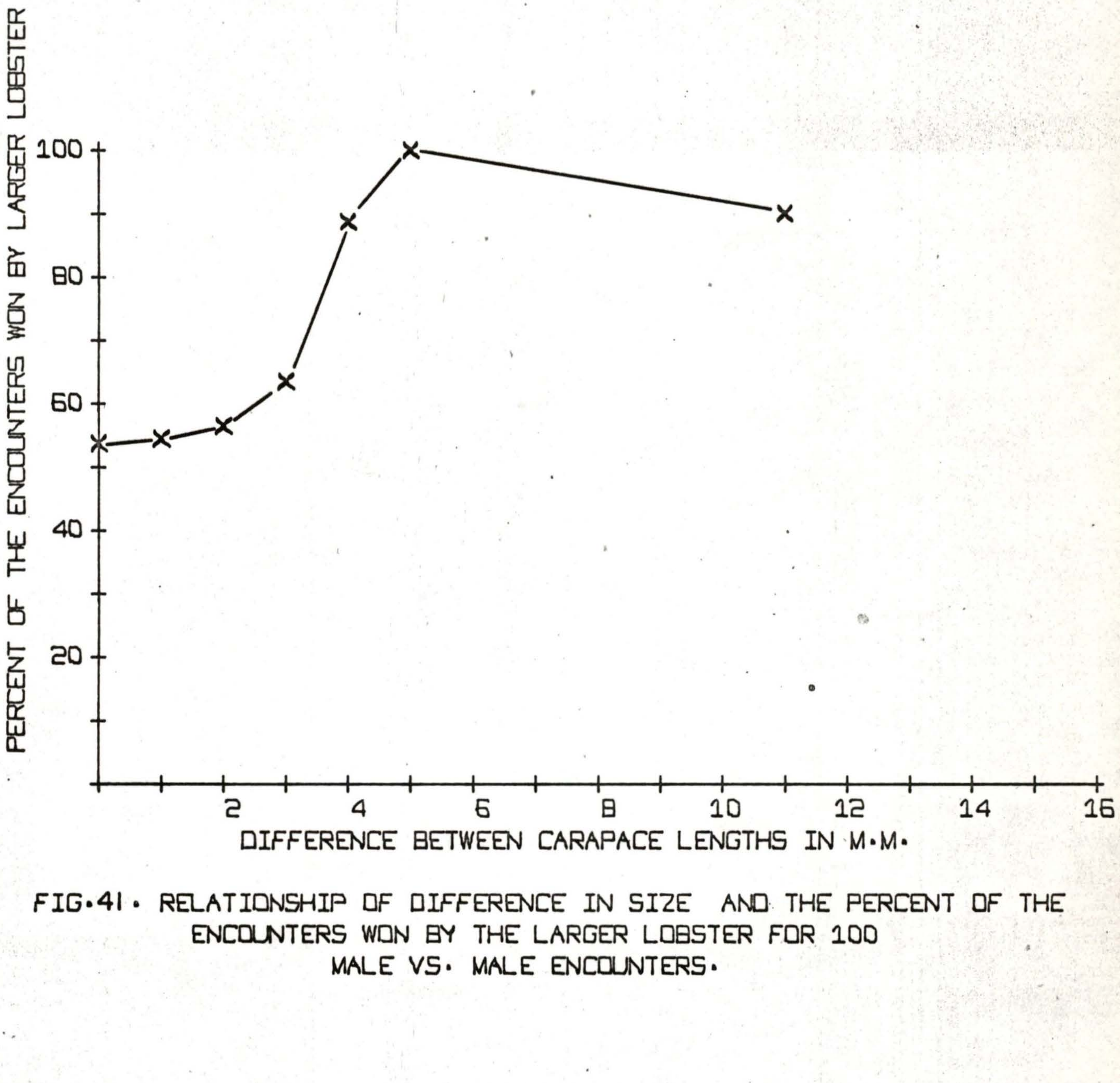


FIG.41. RELATIONSHIP OF DIFFERENCE IN SIZE AND THE PERCENT OF THE ENCOUNTERS WON BY THE LARGER LOBSTER FOR 100 MALE VS. MALE ENCOUNTERS.

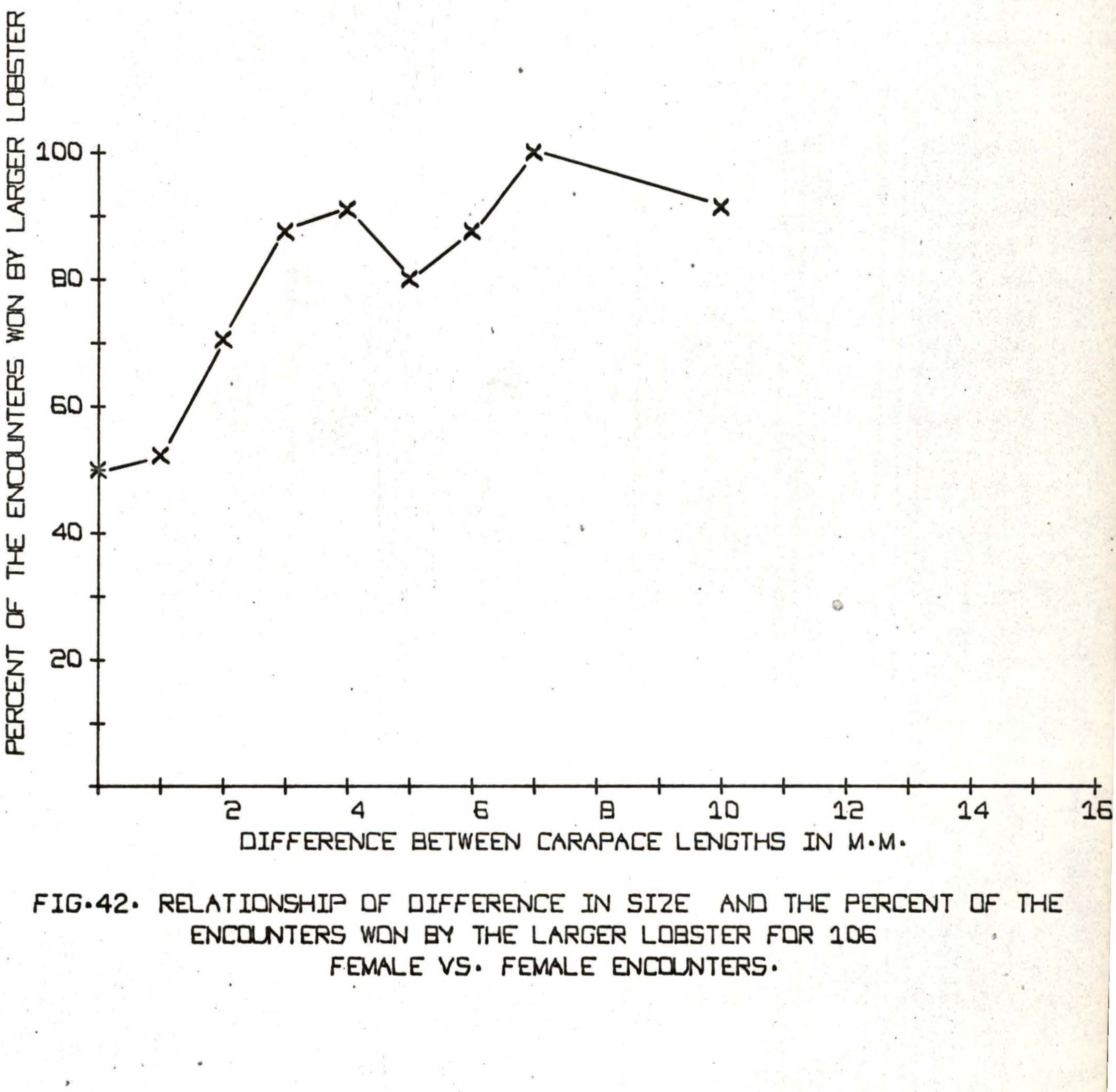


FIG.42. RELATIONSHIP OF DIFFERENCE IN SIZE AND THE PERCENT OF THE ENCOUNTERS WON BY THE LARGER LOBSTER FOR 106 FEMALE VS. FEMALE ENCOUNTERS.

of agonistic encounters. When there was a greater than 15% difference between two individuals' cephalothorax length, the probability of the smaller crab retreating without a display by its larger opponent increased andthe probability of the larger crab executing a display decreased, as the size difference increased. Also the probability of their ignoring each other increased as the size difference increased, until at about a 140% size difference, no aggression took place. Size differences probably affect lobster aggression in a similar manner, but these aspects could not be examined, because the animals used here varied in size by a maximum of only 26% (84 - 114 mm.).

To determine if the sex of the lobster had any effect upon this size factor, the encounters were separated into unisexual (Figs. 41 and 42) and heterosexual agonistic encounters (Fig. 43). When two opposing males had a carapace length difference of 2 mm. or less, the smaller individual appeared to win as often as the larger one, but as the carapace length difference increased from 2 to 4 mm., the percent won by the larger lobster increased to 90% (Fig. 41). During female-female pairings, the larger individual won a majority of the encounters, if there was more than a 1 mm. difference in carapace length (Fig. 42). This may represent a real variation between the sexes, but there were not enough data available to analyze carapace length differences in groups of less than 1 mm. sizes. As with males, the percent of the encounters won by the larger female rose to 90% when there was a 4 mm. carapace length difference between the paired individuals. The low percentages obtained in the 5 and 6 mm. groups were caused by one large female that never won an encounter with another female. When these encounters were removed from the data, the percent won by the larger individuals was

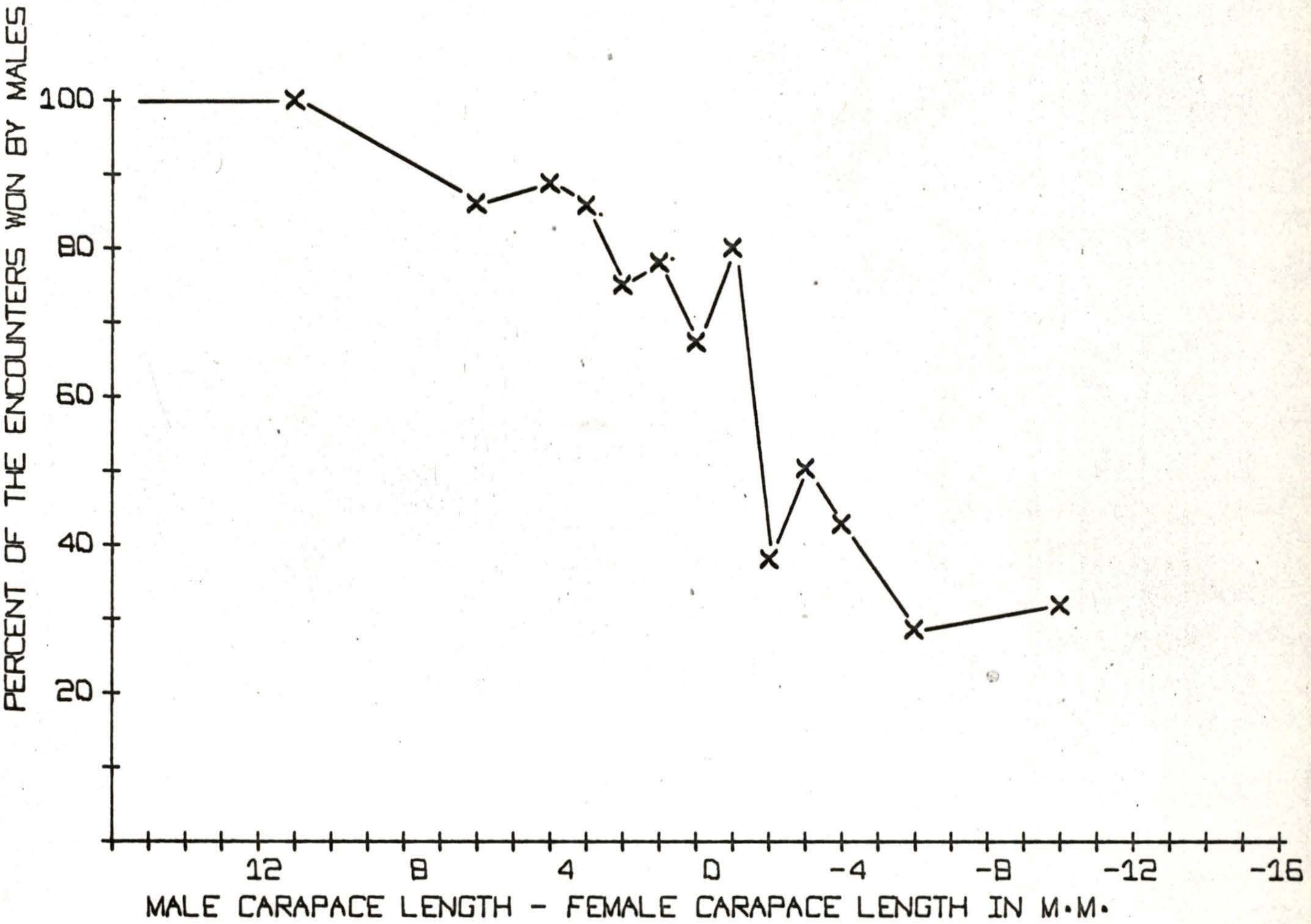


FIG. 43. RELATIONSHIP OF THE DIFFERENCE IN SIZE BETWEEN THE MALE AND FEMALE LOBSTER AND THE PERCENT OF THE ENCOUNTERS WON BY MALES, BASED ON 124 FEMALE VS. MALE ENCOUNTERS.

greater than 90% for all groups with size differences greater than 4 mm. For the heterosexual agonistic encounters, the percentage of encounters won by the males was plotted against the carapace length differences in 1 mm. groups (Fig. 43). The percent won by males was again 90% or greater when his female opponent was 4 or more mm. smaller, but it declined to only 70 - 80% when he was 1 mm. smaller than her. Even when the males were 6 mm. or more smaller, they still won about 30% of the agonistic encounters. If the encounters in which the large losing female took part are excluded, the males still won at least 23.5% of them. This indicates that size and sex were interacting such that maleness enhanced greater size (or possibly vice versa). Females won only 36% of the male-female encounters even though they were larger 53% of the time. Using the sign test, the upper .95 confidence limit on 36% is 45% based on a sample size of 124 (Fig. 43). Therefore the data statistically supports the above conclusion.

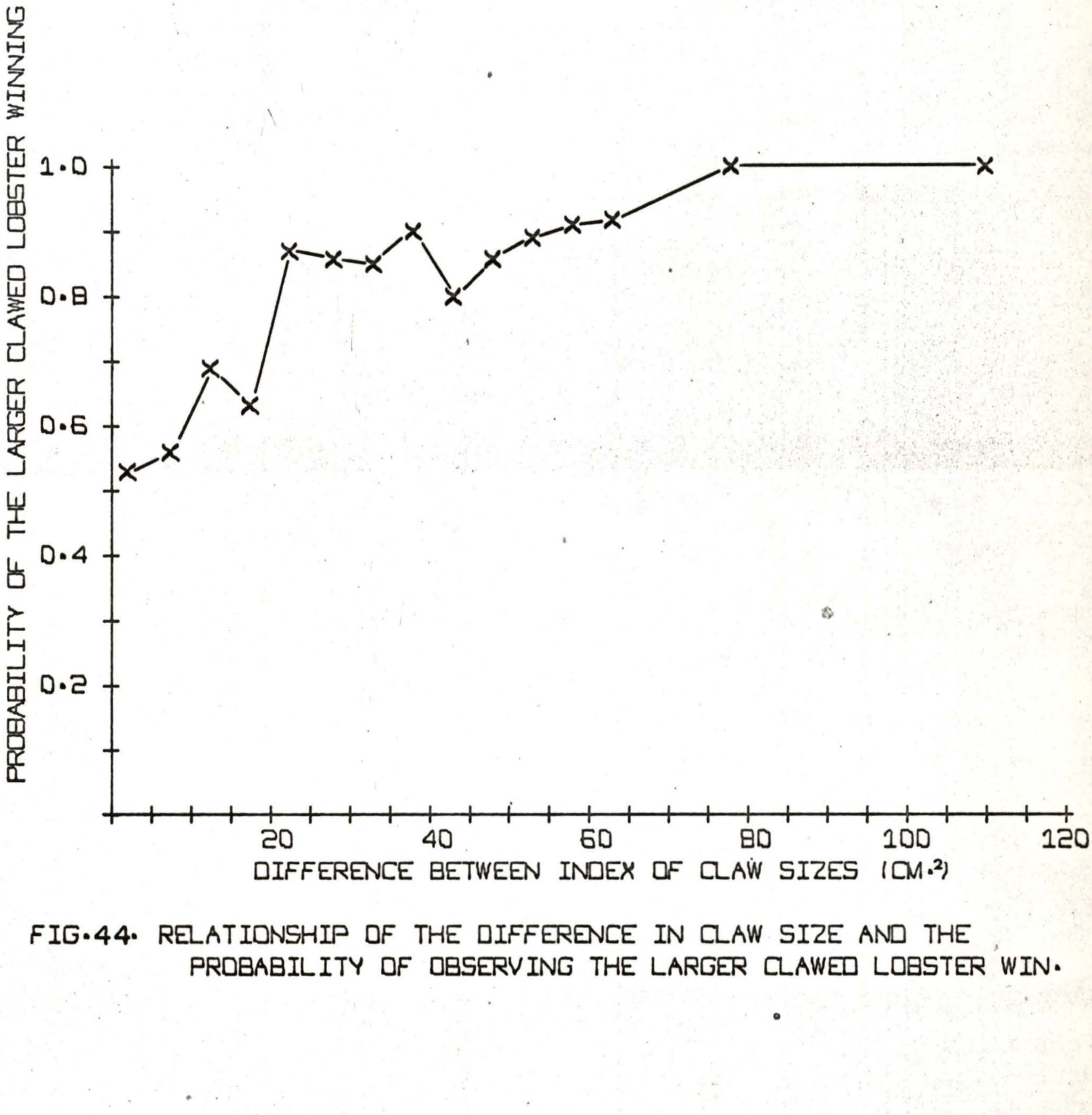
Male dominance was also found among the crayfish Procambarus alleni (Bovbjerg 1956). This appeared to be related to sexual maturity. Working with the crayfish Cambarellus shufeldtii, Lowe (1956) found that size was more important and either males or females could dominate, but in natural populations the females were generally larger and therefore dominated males. This is not the case with lobsters, since males of the same age group are slightly larger and grow faster than females (Wilder 1953, McLeese and Wilder 1964). Therefore under natural conditions both sex and size would favour males in agonistic interactions.

Chelae size

During Bovbjerg's (1956) study of the development of aggressive behaviour in the crayfish *Procambarus alleni*, he found that aggression began as soon as they developed a hard cheliped palm. By the third instar the chelae had formed, but their exoskeletal covering was thin and transparent. Upon molting to the fifth instar, this area of the exoskeleton became hard and opaque and aggressive behaviour began. This association circumstantially suggests that chelae development has some effect on aggression.

To determine whether chelae size could have affected the outcome of the agonistic encounters, a claw size index was developed. The most meaningful measurement is probably volume, but this was difficult to obtain from live lobsters. The index used in the present study was the length of the palm (propodus) in cm. multiplied by its circumference just posterior of the dactyl insertion. The average of pincer and crusher was calculated as a measure of the individual's claw size. Among the test animals, the claw size ranged from 88 to 258 cm^2.

During 261 encounters for which claw sizes were available, the larger clawed animal won 196 or 75% of the time, indicating that claw size could have affected the outcome of the agonistic encounters. The percent of encounters won by larger clawed animals was plotted against the difference in claw size (Fig. 44). A graph similar to the carapace size plot was obtained. The percent won by the larger clawed animal increased as the difference in claw size increased, until it reached 80 - 90% at a claw size difference of 20 - 25 cm^2 (one animal's claws were about 15% larger). Here it levelled off, before increasing again. When one



FIG·44· RELATIONSHIP OF THE DIFFERENCE IN CLAW SIZE AND THE PROBABILITY OF OBSERVING THE LARGER CLAWED LOBSTER WIN·

lobster's claws were 50% larger than its opponent's (greater than 70 cm^2 difference in claw size index), it always won.

Since claw size increases as lobsters grow larger, the test animals might simply be reacting to one, the other or to a mutually related third dimension. To determine whether these factors could be acting independently, first the effect of animal size was removed by using only the 127 encounters in which body size difference was below the limits expected to affect aggression. These were male-male encounters where the size difference was 2 mm. or less (Fig. 41) and female-female encounters (Fig.42), and female-male encounters with a 1 mm. or less size difference. Of the 127 encounters, 63 (50%) were won by the larger animal, 60 (47%) by the smaller and 4 encounters (3%) contained animals of the same carapace length. When claw size was considered, the lobster with the larger claws won 97 (76%) encounters, while the smaller clawed animal won 30 (24%). Using the sign test, the upper .95 confidence limit on 24% is 32.26% for a sample size of 127. Therefore even with the effect of size almost completely removed, the results were still significantly in favour of larger clawed winners. Second, the effect of claw size was removed by using the 73 encounters in which claw size was believed to have little or no effect upon aggression (claw size difference less than 10 cm^2, Fig. 44). Here, 39 and 33 encounters were won by the larger and smaller clawed animals respectively and one encounter contained animals with the same sized claws. When carapace length was considered, the larger lobsters won 50 encounters, while the smaller ones won 23. From the expected 39.5 wins by the larger animals (39 x 73/72) and 33.5 wins by the smaller animals (33 x 73/72), a significant chi-square of 6.08* ($p < .05$) was obtained. This suggests that independent of claw size, that body size was influencing the outcome of lobster agonistic encounters by favouring the larger individual. There appears to be a complex interaction between claw and body size in determining the winner of an encounter.

To determine whether sex had any effect upon the claw size factor, the encounters with animals similar in carapace length were separated into unisexual (Figs. 45 and 46) and heterosexual combinations (Fig. 47). The percent of the encounters won by the larger clawed animal were plotted against the difference in claw size. During male vs. male encounters the outcome of aggression was unaffected by a 10 cm^2 or less difference in the index of claw size, but then as the index difference increased, the percent won by the larger clawed animal increased (Fig. 45). During female-female encounters this increase was much more sudden (Fig. 46). Enough data are not really available here to determine if this difference is significant. During female-male encounters the larger clawed animals won 78% - 100% of the time (Fig. 47). This probably reflects the fact that male lobsters have larger claws than females (McLeese and Wilder 1964) and these larger clawed males were probably winning most of the encounters. The experimental animals had mean claw sizes of 156.5 cm^2 for males and 145.9 cm^2 for females. Of the 99 female-male encounters for which claw size data was available, the males won 65 and the females 34. Males had the larger claws during 53 and the females during 45 encounters. Claw size was equal for one encounter. From the expected 53.5 wins by larger clawed males (53 x 99/98) and 45.5 wins by larger clawed females, a significant chi-square was obtained (5.37*, $p < .05$). Therefore even with the possible effect of

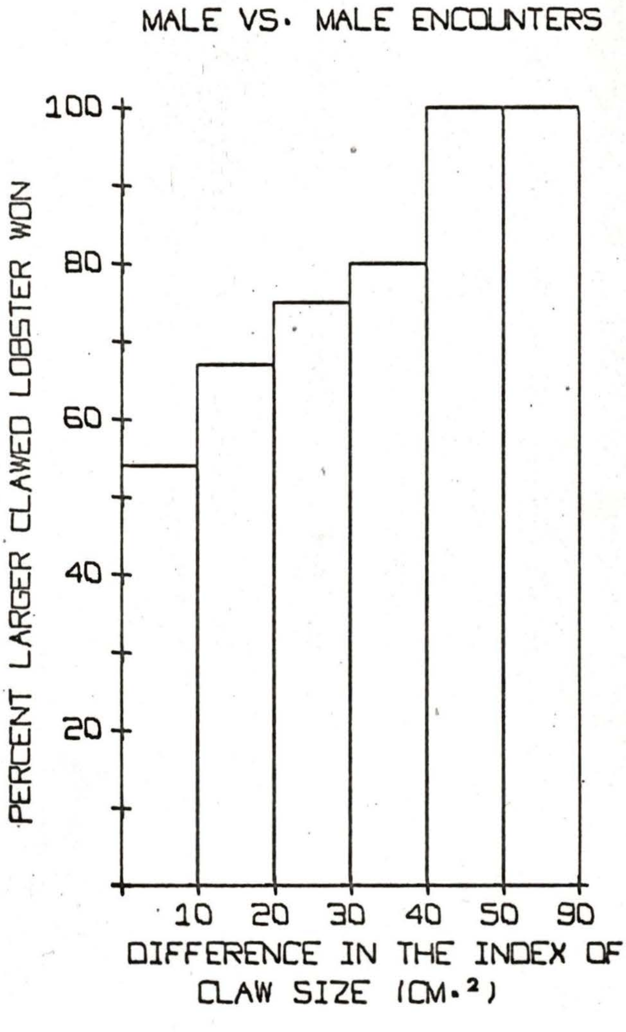


FIG.45. RELATIONSHIP OF THE DIFFERENCE IN CLAW SIZE AND THE PERCENT OF THE ENCOUNTERS WON BY THE LARGER CLAWED LOBSTER, WHEN THE AFFECT OF OVERALL SIZE HAS BEEN REMOVED. BASED ON 43 MALE VS. MALE ENCOUNTERS.

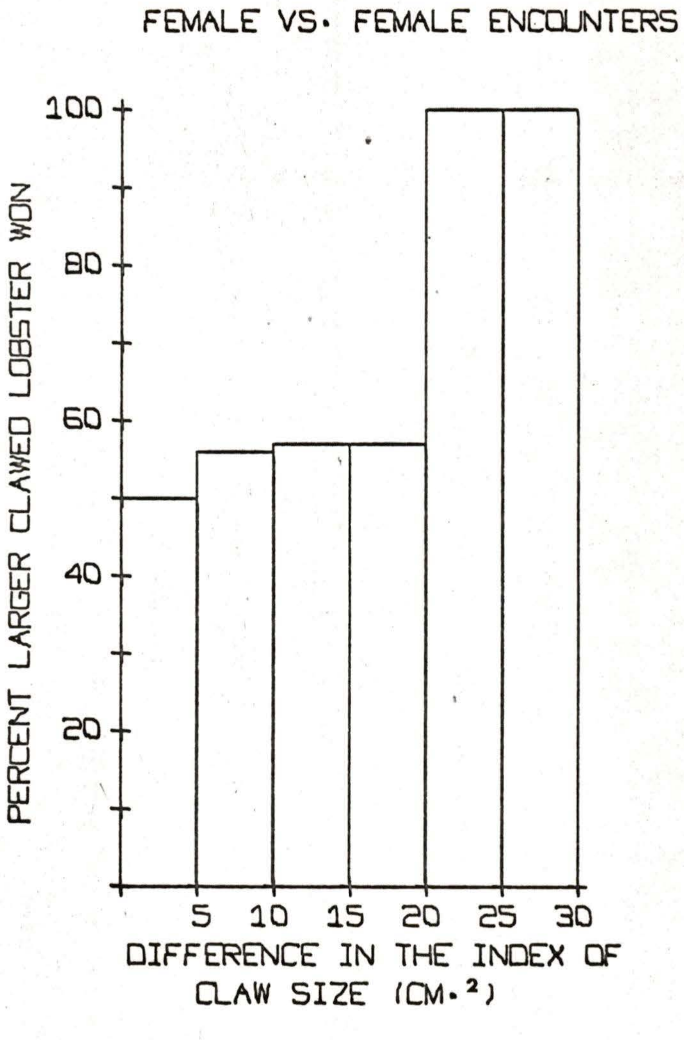


FIG.46. RELATIONSHIP OF THE DIFFERENCE IN CLAW SIZE AND THE PERCENT OF THE ENCOUNTERS WON BY THE LARGER CLAWED LOBSTER, WHEN THE AFFECT OF OVERALL SIZE HAS BEEN REMOVED. BASED ON 44 FEMALE VS. FEMALE ENCOUNTERS.

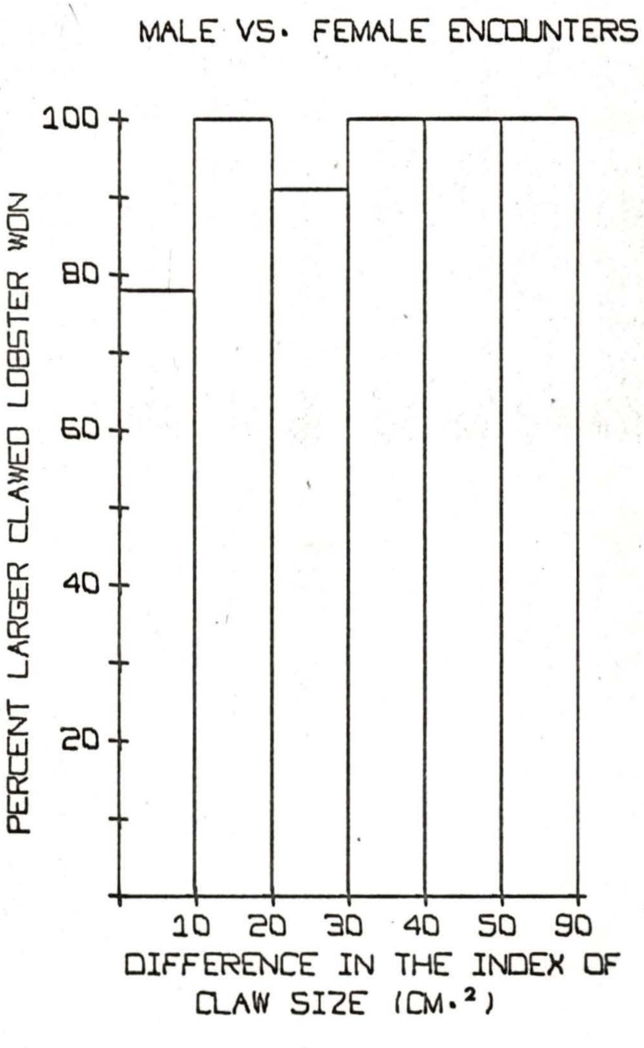


FIG. 47. RELATIONSHIP OF THE DIFFERENCE IN CLAW SIZE AND THE PERCENT OF THE ENCOUNTERS WON BY THE LARGER CLAWED LOBSTER, WHEN THE AFFECT OF OVERALL SIZE HAS BEEN REMOVED. BASEDON 40 FEMALE VS. MALE ENCOUNTERS.

claw size removed, males still won more heterosexual encounters than could be explained by chance. It is possible the larger proportion of male wins were due to a combination of the effects of animal size and claw size. If the nine encounters in which these factors appeared to be unimportant are considered, males won 6 (67%) and females 3 (33%). Assuming 50% male or female wins, the probability of obtaining 3 or fewer female wins during nine encounters is .25. All the data could be retained and much of the effects of these factors could be removed, if the number of encounters in which the factors favoured males or females were known. A conflict between factors in any encounter could be eliminated by determining which one varies more from the known point of no effect. Precisely, which varies most, the difference in claw size from 10 cm^2 or the difference in carapace length from 1 mm. These factors favoured males during 55 and females during 44 of the 99 male-female encounters. Using these values as the expected, a significant chi-square was calculated ($X_1^2 = 4.09$*, $p < .05$).

It appears that males would dominate females in most natural heterosexual interactions, because of a combination of three factors: they are slightly larger, they have bigger claws, and they are inherently more aggressive. Enough data were not available here to demonstrate this third factor statistically when completely independent of the other two, but its affect seems probable.

Aggressiveness

Although animal size and claw size appear to be important factors in determining the outcome of lobster agonistic encounters, small animals with small claws periodically won over larger opponents. Often there was no obvious explanation for this except that the smaller animal appeared to be more aggressive. The factor causing this could be called the animals aggressiveness. It is probably affected by a combination of the animal's genetic make-up, and physiological and psychological state.

The effect of an animal's aggressiveness was particularly apparent during encounters involving lobsters 0 and 9. Lobster 0 was small, but very aggressive, he won ten encounters and lost four. He was the larger individual during one encounter and the smaller during thirteen. He had the bigger claws for six encounters and the smaller ones for eight. The opponents he faced were randomly chosen, so it was unlikely that this data could be the result of his exposure to a proportionally greater number of opponents with low aggressiveness. To test this possibility statistically, the chi-square was calculated using six wins and eight losses as the expected frequency (expected from claw size). A significant value of 4.67* ($p < .05$) was obtained. Lobster 9 was large, but had little aggressive success. She won only one of eleven encounters, even though she was the larger and had the larger claws during seven of these encounters. A significant chi-square of 9.17** ($p < .01$) indicated that exposure to an unusually large number of aggressive opponents should not be used to explain these results.

With the exception of aggressiveness, none of the factors known to affect aggression in crustaceans (p.122) were believed to be influencing one animal more than another. All animals were in the intermolt period during which the least number of physiological changes take place (Passano 1960). No animal was used that had molted less than five months previously nor did any molt less than 2.5 months after being used. All animals were held in isolation, and when data were being collected, most lobsters were used about twice a week. No berried female was used in any encounter, although some females had infertile eggs attached to their pleopods for short periods of time. All animals were fed a varied diet in which food was supplied in excess.

It is possible that an animal's past agonistic experience could be affecting the aggressiveness. To determine whether the past experience could affect the outcome of later encounters, thirteen lobsters were exposed over a three week period to animals they had never seen before. Each of the thirteen lobsters had previously belonged to one of four groups of five that had been exposed to each other eleven times (44 agonistic experiences). The animals in each group varied less than 2 mm. in carapace length and 20 cm^2 in the index of claw size. Eight of these lobsters had experienced more losses than wins and five more wins than losses. The experienced losers won fourteen and lost sixteen of the subsequent encounters, while claw size and animal size data indicated they should have won 21 and lost 9 of them. The significant chi-square of 7.77** indicates that they lost more encounters than could be attributed to chance. The experienced winners won 13 and lost 8, when they could be expected to win 9 and lose 12. The chi-square obtained was not quite significant (3.01, $p < 0.1$). It would appear that there was a change in the outcome of agonistic encounters depending on the past experience of the animals. If this is true, it should be possible to change an experienced winner into a loser.

Lobster J was a very aggressive animal, he had won eight encounters against four other males that were larger by at least 4 mm. in carapace length and 20 cm^2 in index of claw size. He was then exposed to the largest male six times and lost six times. The big male was larger by 14 mm. in carapace length and 80 cm^2 in index of claw size. Afterwards, lobster J was exposed over a three week period to eleven individuals which he had never seen before. He won three of these encounters and lost eight. According to the size and claw size data he should have won at least five of them.

Hypothesis and discussion

Age probably affects lobster aggression through the body size and claw size factors. Unlike many crustaceans lobsters continue to grow throughout their life, even though the molts occur less and less frequently (Passano 1960). Many "giant lobsters" of 20 - 25 pounds have been caught by fishermen. For these reasons older animals would probably dominate their smaller younger opponents during social interactions.

Although the present study has not proven that these four factors are influencing lobster agonistic behaviour, they appear to be excellent predictors of the outcome of agonistic encounters. There seems to be enough evidence to make the following hypothesis.

Animal size, claw size, sex, and aggressiveness, which is influenced by previous experience, form a complex interacting group of factors which influence the outcome of agonistic interactions between lobsters. Animal size and claw size affect aggression by increasing the probability of the larger and larger clawed individual winning.

As the difference in the size of these factors between the combatants increases so does this probability. Adult males tend to win over females, because they are larger, have larger claws and are inherently more aggressive. The past experience of a lobster affects the individual aggressiveness by enhancing its chances of winning, if it is an experienced winner; or by decreasing them, if it is an experienced loser.

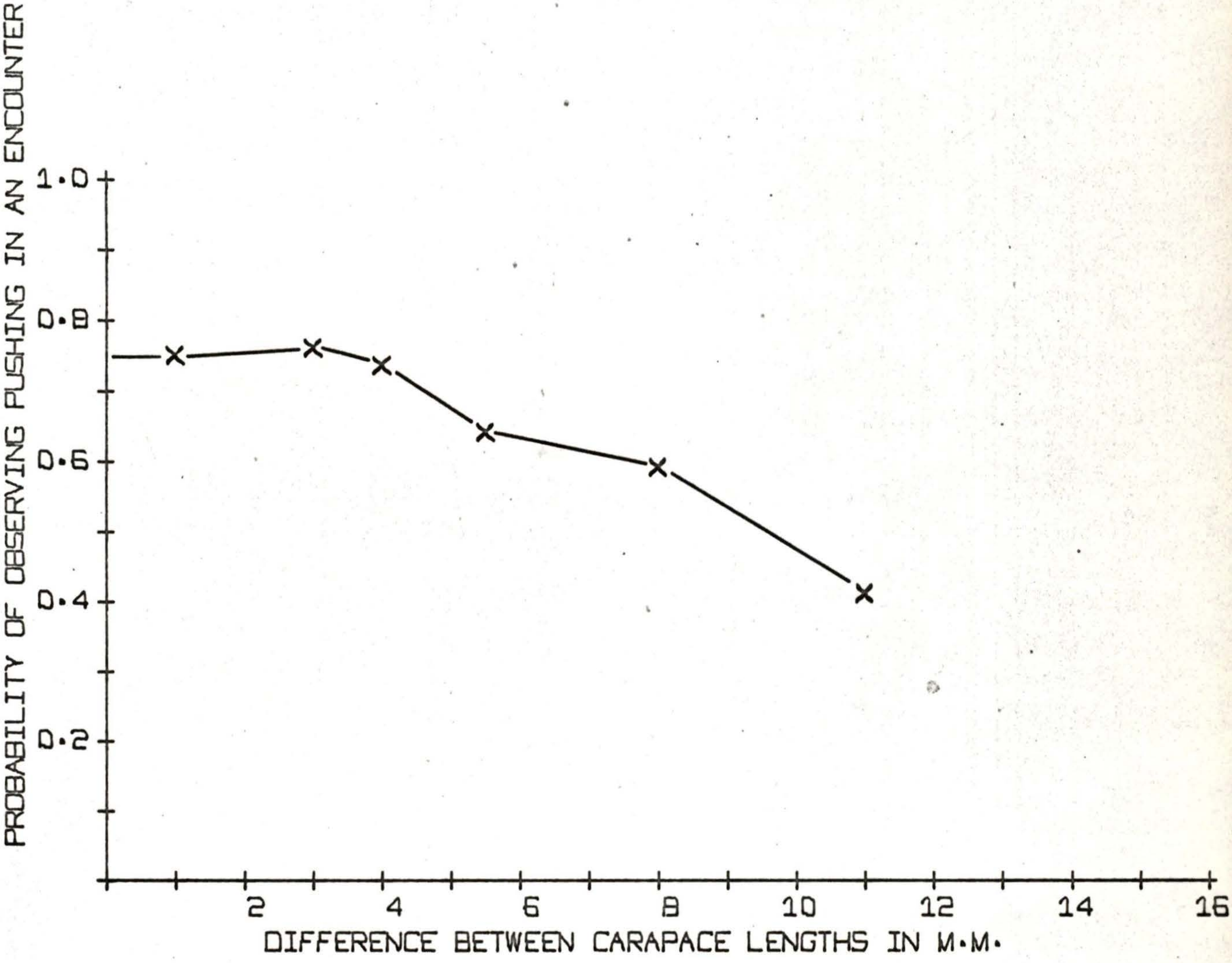
HYPOTHESIS OF LOBSTER BEHAVIOUR DURING AGONISTIC INTERACTIONS IN NATURE

The American lobster is a solitary scavenging decapod which generally occupies a depression in the bottom or a burrow under stones, which it excavates or finds already available (Herrick 1911, Wilder 1959). It avoids high light intensities (McLeese and Wilder 1958) and based on an unpublished study by the author, it appears to be most active during twilight and the early hours of darkness.

The light intensity in the study area was measured at 84.4 foot candles. Summer light intensities just outside the labotatory ranged from 1298 foot candles during heavy rain to 3595 foot candles during bright sunlight. Assuming 5.62% penetration to a depth of 10 metres (based on a typical F.R.B. Pacific Oceanographic Group summer secchi disc reading of 6 metres in Departure Bay, Nanaimo), the laboratory light intensity is similar to the 73.0 - 202.1 foot candles, which would occur at 10 metres (5.62% of 1298 and 3595 foot candles). These 10 metre light intensities would consist mainly of blue-green light (400 - 550 mμ). General Electric fact sheets indicate that 40 watt white fluorescent lamps produce their greatest radiant power between 525 mμ and 650 mμ (peak 580 mμ), but produce little radiant energy between 400 mμ and 525 mμ. Lobster spectral sensitivity ranges from 400 mμ to 600 mμ, with peak sensitivity at 520 - 525 mμ (Kennedy and Bruno 1961). Therefore the lobsters are probably sensitive to a far smaller percentage of the light intensity in the laboratory than in 10 metres of sea water. The light intensity in the study area perceivable by lobsters was far below natural light intensities at 10 metres.

Since lobsters are more active during the late afternoon and evening, it would have been preferable to record agonistic activity at this time. Attempts were made to reverse the activity period by exposing test animals to low light intensities during daylight and higher light intensities at night. The animals became almost inactive except for short periods under the lower light intensity. Lobsters do not appear to have a physiologically controlled diurnal rhythm which is light reinforced, because the activity period can be changed in one day by reversing the photoperiod. Activity appears to be simply a response to a reducing light intensity. Therefore the area in which the animals were held was provided with slightly stronger illumination (they were placed closer to the windows) than the observation tanks. The lobsters were always moved into an area of lower light intensity, when the encounters were recorded.

While foraging, lobsters would probably meet, interact and then separate. These interactions could last from 9 seconds to 14 minutes (Fig. 23). The length of the interaction would depend on the amount of time the lobster spent showing the fourth basic sequence pathway of mutual aggression involving the group I behaviour patterns; pushing, antennae whipping, scissoring, boxing, and jumping. This is the mutual testing of physical strength seen in so many aquatic decapods (p. 37). Pushing is the most important behaviour pattern in this pathway, and its frequency and duration will determine the frequencies and durations of the others (Fig. 38 d). The probability of observing pushing declines as the size difference between the individuals increases (Figs. 48 and 49). Therefore the greater the difference in size or claw size, the shorter the interaction. The encounter would end with one animal retreating by utilizing one of the two avoidance sequence pathways and the other animal pursuing for a short distance by using the winner's pathway. The size and claw size of an opponent are visual signals used



FIG·48· RELATIONSHIP OF THE DIFFERENCE IN SIZE BETWEEN THE PAIRED LOBSTERS AND THE PROBABILITY OF OBSERVING PUSHING DURING THE ENCOUNTER·

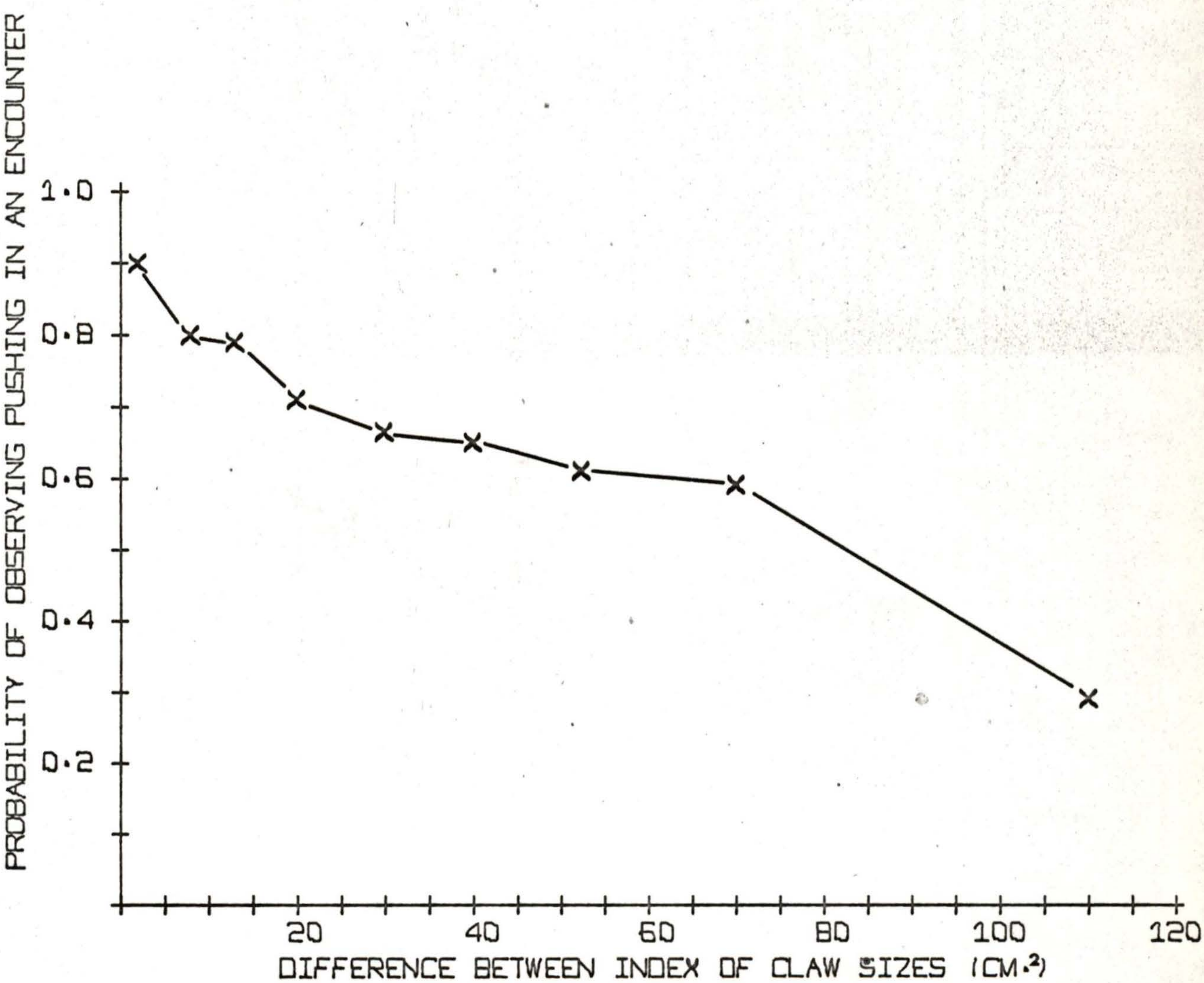


FIG. 49. RELATIONSHIP OF THE DIFFERENCE IN CLAW SIZE OF THE PAIRED LOBSTERS AND THE PROBABILITY OF OBSERVING PUSHING DURING THE ENCOUNTER.

by lobsters to determine whether a mutual testing of strength is required, before one individual decides it should give way. Past experience also influences an individual's decision of whether to show aggression to an aggressor or to retreat. If the opponents are of the same sex pushing will more likely be observed and last longer, than if they are of the opposite sex.

During an interaction the displays will contain approximately 3.375 bits of information per display and at least 0.748 bits per display will be transmitted at an average minimum rate of 0.135 bits per individual per minute. This is a much lower rate of communication than that of human speech, but is similar to other communicating crustaceans.

Among other factors, the size, claw size, sex, and past experience of the lobsters will affect the outcome. The greater the difference in size and claw size, the greater the probability that the smaller or smaller clawed animal will retreat. If one individual is more than 18% larger or has more than 50% bigger claws, it can be predicted to win with complete certainty. If the combatants are of the opposite sex, the female will probably retreat, because males are inherently more aggressive, generally are larger and have larger claws than females. If one of the lobsters has had little success in winning previous agonistic interactions, the probability that it will retreat is greater than if it was an experienced winner.

Lobster agonistic behaviour when compared with other decapods would be classed as primitive aggression (Schöne 1968, Wright 1968). The lobster has not developed elaborate visual displays which have been described among hermit crabs and many shore crabs. This could be due to the fact that they are most active during periods of low light intensity.

The results of this study can provide the preliminary data for developing a model of lobster agonistic interactions, but first detailed quantitative data on the activity, density, size composition, age, territoriality - if any - and spacing in various lobster populations must appear in the literature.

SUMMARY

1. During 1968 and 1969 a study was undertaken, the purpose of which was to develop an agonistic ethogram of the American lobster, Homarus americanus (Milne-Edwards).
2. Lobster agonistic behaviour was divided into 16 stereotyped behaviour patterns.
3. These patterns were placed in four groups: (I) those which declined in frequency among winners and losers during the recording period - pushing, antennae whipping, jumping, scissoring and boxing; (II) those shown by losers - side-ways, abdomen flexing, running away, backing and walking away; (III) those shown by winners - rushing, following, meral spread and approaching; and (IV) an investigative behaviour antenna pointing shown by winners and losers.
4. The length of the periods of continuous agonistic behaviour or bouts depended on whether the group I behaviour patterns were shown. They ranged from 9 seconds to 14 minutes in length.
5. Males showed more boxing, while females showed more side-ways.
6. Lobsters showed the behaviour patterns in the form of four basic sequence pathways: (I) the ant. point → approach → meral spread → follow → rush → scissor → meral spread → ant. point pathway of winners; (II) the ant. point → back → abdomen flex → back → ant. point; and (III) the ant. point → walk → run → walk → ant. point pathways of losers; and (IV) the long complex ant. point → approach → meral spread → push → meral spread → ant. point pathway which required mutual aggression.
7. There were quantitative variations in the way males and females performed the many side chains of the four pathways.

8. An analysis of responses indicated that when one animal performed the winner's pathway I, its opponent usually performed the loser's pathway II or less frequently III.

9. If both animals were aggressive they performed sequence pathway I, which resulted in much social facilitation.

10. Lobster displays contained an average of 3.375 bits of information/display, 0.748 bits of which were transmitted as confirmed by the opponents responses, at a rate of 0.135 bits/individual/second. This is far below estimates for human speech.

11. Body size and chelae size appeared to affect the outcome of lobster agonistic interactions. The probability of observing the larger or bigger clawed animal win, increased as the difference in the sizes increased.

12. Lobsters which were experienced winners tended to win future encounters, while experienced losers tended to lose future encounters.

13. Males tended to dominate females, because they were usually larger, had bigger claws and were inherently more aggressive than females.

14. An hypothesis of lobster agonistic interactions in nature was formed from the results, which with certain additional information could form the basis for a model of lobster agonistic behaviour.

LITERATURE CITED

Alderdice, D. F., J. R. Brett and D. B. Sutherland. 1966. Design of small holding tank for fish. J. Fish. Res. Bd. Canada, 23 (9): 1447-1450.

Allee, W. C. and M. B. Douglis. 1945. A dominance order in the hermit crab, Pagurus longicarpus (Say). Ecology, 26 (4): 411-412.

Barnett, S. A. 1963. A study in behaviour. Principles of ethology and behavioural physiology, displayed mainly in the rat. Methuen & Co. Ltd., London, 288 p.

Bergeron, J. 1967. Contribution à la biologie du homard (Homarus americanus M. Edw.) des Iles-de-la-Madeleine. Naturaliste Can., 94: 169-207 (also in: Travaux sur le Pêcheries du Quebec 14, 1967).

Bovbjerg, R. V. 1953. Dominance order in the crayfish, Orconectes virilis (Hagen). Physiol. Zool., 26: 173-178.

________. 1956. Some factors affecting aggressive behaviour in crayfish. Physiol. Zool., 29: 127-136.

________. 1960. Behavioural ecology of the crab, Pachygrapsus crassipes (Randall). Ecology, 41(4): 668-672.

Crane, J. 1958. Aspects of social behaviour in fiddler crabs with special reference to Uca maracoani (Latreille). Zoologica, 43: 113-130.

________. 1966. Combat, display and ritualization in fiddler crab (Ocypodidae, Genus Uca). In a discussion on ritualization of behaviour in animals and man, organized by Sir Julian Huxley. Phil. Trans. Roy. Soc. Lond. Ser. B No. 772; Vol. 251: 213-226.

________. 1967. Combat and its ritualization in fiddler crabs (Ocypodidae) with special reference to Uca rapax (Smith). Zoologica, 52: 49-77.

Dingle H. 1969. A statistical and information analysis of aggressive communication in the mantis shrimp, Gonodactylus bredini (Manning). Animal Behaviour, 17 (3): 561-575.

Dingle, H. and R. L. Caldwell. 1969. The aggressive and territorial behaviour of the mantis shrimp. Gonodactylus bredini (Manning). Behaviour, 33: 115-136.

Douglis, M. B. 1946 a. Some evidence of the dominance-subordinance relationship among lobsters. Anat. Rec., 96: 553 (abstract).

__________. 1946 b. Interspecies relationships between certain crustaceans. Anat. Rec., 96: 553-554 (abstract).

Fielder, D. R. 1965. A dominance order for shelter in the spiny lobster, Jasus lalandei (H. Milne - Edwards). Behaviour, 24: 236-245.

Fish, J. F. 1966. Sound production in the American lobster, Homarus americanus, H. Milne - Edwards (Decapoda Reptantia). Crustaceana, 11 (1): 105-106.

Griffin, D. J. G. 1968. Social and maintenance behaviour in two Australian ocypodid crabs (Crustacea:Brachyura). J. Zool., 156: 291-305.

Haldane, J. B. S. and H. Spurway. 1954. A statistical analysis of communication in Apis mellifera and a comparison with communication in other animals. Insectes Soc., 1: 247-283.

Hazlett, B. A. 1966 a. Social behaviour of the Paguridae and Diogenidae of Curacao. - Studies of the Fauna of Curacao and other Caribbean Islands. Vol. 23, pp. 1-143.

__________. 1966 b. Temporary alteration of the behavioural repertoire of a hermit crab. Nature, 210: 1169-70.

__________. 1966 c. The behaviour of some deep-water hermit crabs (Decapoda:Paguridea) from the Straits of Florida. Bull. Mar. Science, 16: 76-92.

__________. 1966 d. Factors affecting the aggressive behaviour of the hermit crab, Calcinus tibicen. Z. Tierpsychol., 6: 655-671.

__________. 1967. Interspecific shell fighting between Pagurus cuanensis (Decapoda, paguridea). Sarsia, 29: 215-220.

__________. 1968 a. Effects of crowding on the agonistic behaviour of the hermit crab, Pagurus bernhardus. Ecology, 49 (3): 573-575.

__________. 1968 b. Communicatory effect of body position in Pagurus bernhardus (L) (Decapoda, Anomura). Crustaceana, 14: 210-214.

__________. 1968 c. Size relationships and aggressive behaviour in the hermit crab, Clibanarius vittatus. Z. Tierpsychol., 25: 608-614.

Hazlett, B. and W. H. Bossert. 1965. A statistical analysis of the aggressive communications systems of some hermit crabs. Animal Behaviour, 13 (2-3): 357-373.

Hazlett, B. A. and W. H. Bossert. 1966. Additional observations on the communications systems of hermit crabs. Animal Behaviour, 14 (4): 546-549.

Herrick, F. H. 1896. The American lobster, a study of its habits and development. Bull. U. S. Fish. Comm. 1895, p. 1-252.

__________. 1911. Natural history of the American lobster. Bull. U. S. Bur. Fish. 1909, 29: 149-408.

Kennedy, D. and M. S. Bruno. 1961. The spectral sensitivity of crayfish and lobster vision. J. Gen. Physiol., 44: 1089-1102.

Knight, A. P. 1918. Lobster investigations, Long Beach pond, Nova Scotia 1915. Contributions to Canadian Biology and Fisheries 1917-1918: 51-71.

Liley, N. R. 1966. Ethological isolating mechanisms in four sympatric species on Poeciliid fishes. Behaviour, suppl., 13, 197 p.

Lindberg, R. G. 1955. Growth, population dynamics and field behaviour in the spiny lobster, Panulirus interruptus (Randall). Univ. Cal. Publ. Zool., 59: 157-248.

Lowe, M. E. 1956. Dominance - subordinance relationships in the crayfish, Cambarellus shufeldti. Tulane Studies in Zool., 4: 139-170.

Manning, A. 1967. An introduction to animal behaviour. Edward Arnold (Publishers) Ltd., London, 208 p.

McLeese, D. W. 1956. Effects of temperature, salinity and oxygen on the survival of the American lobster, Homarus americanus (H. Milne-Edwards). J. Fish. Res. Bd. Canada, 13 (2): 247-272.

__________. 1970. Detection of dissolved substances by the American lobster (Homarus americanus) and olfactory attraction between lobsters. J. Fish. Res. Bd. Canada, 27(8): 1371-1378.

McLeese, D. W. and D. G. Wilder. 1958. The activity and catchability of the lobster (Homarus americanus) in relation to temperature. J. Fish. Res. Bd. Canada, 15(6): 1345-1354.

__________. 1964. Lobster storage and shipment. Bull. Fish. Res. Bd. Canada, 147, 69 p.

Passano, L. M. 1960. Molting and its control. In physiology of Crustacea, edit. by T. H. Waterman, Vol. 1 - Metabolism and Growth, Academic Press, New York and London, 670 p.

Quastler, H. 1958. A primer on information theory. In: Symposium on Information Theory in Biology ed. Yockey, H. P., R. L. Platzman and H. Quastler. Pergamon Press 1958, London. 418 p.

Reese, E. S. 1961. Inter and intraspecific dominance relationships of sympatric species of intertidal hermit crabs. American Zoologist, 1: 382 (abstract).

__________. 1962. Submissive posture as an adaptation to aggressive behaviour in hermit crabs. Z. Tierpsychol., 19: 645-651.

Rutherford, J. B., D. G. Wilder and H. C. Frick. 1967. An economic appraisal of the Canadian lobster fishery. Bull. Fish. Res. Bd. Canada, 157, 126 p.

Scott, J. P. 1958. Animal Behaviour. University of Chicago Press, 281 p.

Shannon, C. E. 1949. The mathematical theory of communication. In: The mathematical theory of communication by C. E. Shannon and W. Weaver. University of Illinois Press, Urbana, 117 p.

Schöne, H. 1961. Complex behaviour. In: Physiology of Crustacea, edited by T. H. Waterman, Vol. 2 - Sense Organs, Integration, and Behaviour, Academic Press, New York and London, 681 p.

__________. 1968. Agonistic and sexual display in aquatic and semi-terrestrial brachyuran crabs. Amer. Zoologist, 8: 641-654.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Company, San Francisco, 776 p.

Squires, H. J. 1965. Decapod crustaceans of Newfoundland, Labrador and the Canadian eastern arctic. F. R. B. Manuscript Report Series (Biological) No. 810, 211 p.

Templeman, W. 1934. Mating in the American lobster. Contrib. Can. Biol. Fish. (NS), 8: 423-432.

__________. 1937. Egg-laying and hatching postures and habits of the American lobster (Homarus americanus). J. Biol. Bd. Canada, 3(4): 339-342.

__________. 1944. Abdominal width and sexual maturity of female lobsters on Canadian Atlantic coast. J. Fish. Res. Bd. Canada, 6(3): 281-290.

Wilder, D. G. 1953. The growth rate of the American lobster (Homarus americanus). J. Fish. Res. Bd. Canada, 10(7): 371-412.

__________. 1959. Underwater observations. Ann. Rept. F.R.B.C. Biol. Sta., St. Andrews, N. B. 1959-60 (unpublished) p. 18-20.

Wilson, E. O. 1962. Chemical communication among workers of the fire ant Solenopsis saevissima (Fr. Smith). 2. An information analysis of the odour trail. Animal Behaviour, 10: 148-158.

Wright, H. O. 1968. Visual displays in brachyuran crabs: field and laboratory studies. Amer. Zoologist, 8: 655-665.

APPENDIX I

FISHERIES RESEARCH BOARD OF CANADA

TECHNICAL REPORT NO. 182

COMPUTER PROGRAMS SUMMARIZING ETHOLOGICAL DATA

by

J. C. Scrivener

Department of Biology
University of Victoria

FISHERIES RESEARCH BOARD OF CANADA

Biological Station, Nanaimo, B. C.

April 1970

COMPUTER PROGRAMS FOR SUMMARIZING BEHAVIOURAL DATA FROM SOCIAL ENCOUNTERS BETWEEN PAIRED ANIMALS

Quantitative data on lobster agonistic behaviour were obtained visually from paired animals and recorded on an event recorder, while the encounters were proceeding. Such event recorders permit large amounts of data to be obtained rapidly. Although it is possible to automatically convert such analog data into digital form on tape when it is being recorded, the hardware is expensive, and was not available for this study. However, hand conversion to IBM cards was reasonably quick, and in conjunction with the programs described here, has permitted analysis of a large volume of data.

A series of 10 Fortran IV computer programs were developed for three IBM systems. Programs Lobster 1-3 were run on the University of Victoria's 360 Model 44, 128 K computer. Lobster 4 and 6 will execute under Disc Monitor Version I or II in an 1130. Lobster 7-10 are currently used on the FRB Nanaimo Biological Station's 1130, 16 K computer operating under Version II. The input is read from cards.

For each encounter, data for the two animals are processed separately (Lobster 9 and 10 use the data of both animals). The programs require either twelve (Lobster 1-7) or fifteen behaviour patterns (Lobster 8-10), but dummies can be used to fulfill the requirements. A recorded encounter can last up to 15 minutes. As many encounters as the operator desires can be run in a single job.

The programs are:

Lobster 1. - determines frequencies and durations of 12 behaviour patterns for the first 10 minutes, last 5 minutes and total 15 minutes of a social encounter. Percentages of the totalled durations and the average duration are calculated for each behaviour pattern.

Lobster 2. - runs a sequence analysis, indicating the number of times that each behaviour pattern follows others.

Lobster 3. - combines Lobster 1 and 2 into a single program.

Lobster 4. - determines frequencies and durations of 12 behaviour patterns for each minute of a 15-minute recording period.

Lobster 5. - cancelled.

Lobster 6. - combines Lobster 4 and a variation of Lobster 3 translated for an 1130 Fortran compiler. The program completely fills core and uses overlays in an 8 K machine.

Lobster 7. - is a more efficient form of Lobster 6, developed for a larger core machine. It determines the number of seconds during each minute, the first 10 minutes, last 5 minutes andtotal 15 minutes, that the animal was showing any of the recorded behaviour. The program economizes on printer paper by requiring 69 lines of output per page (8 lines/inch).

Lobster 8. - is an expanded and more efficient form of Lobster 7, which handles 15 behaviour patterns instead of 12. The programs produce the same output, but from different input.

Lobster 9. - runs a response analysis, indicating the frequencies of each possible response of one animal to each behaviour pattern of the other.

Lobster 10. - runs a bout analysis, indicating the lengths of the periods in which the recorded behaviour is being continuously shown and the minute in which each of these bouts start.

Four of the programs (Lobster 7-10) were used extensively during the study and are described and listed below along with examples of input and output.

Program - Lobster 7

(1) Input

The first data card is reserved for a title. Any alpha-numeric characters in columns 1-50 are read and printed at the top of each page of output (TABLE 1 e.g. LOBSTER B WINNER E VS. B AUG. 3/68).

Table 1 is a listing of data cards and shows information on the twelve behaviour patterns recorded during a fifteen minute encounter. Columns 1-9 contain the name of the behaviour pattern. The 10th column is blank, or contains a '5' if this is the last card showing data on the behaviour pattern named in columns 1-9. Columns 11-80 contain data about the behaviour with each column equivalent to one second in time. A total of eleven cards can be used for each pattern. These columns contain a '1' if the behaviour pattern is occurring, and a blank if it is not. The end of a minute is signified by a '3'. If, however, the behaviour continues into the next minute, a '4' instead of a '3' is used. The termination of data is signified by a '6'. Therefore the last card of every behaviour pattern must contain a '5' in column 10 and a '6' anywhere between columns 12-80. Behaviour patterns that were not observed in the encounter were each represented by one card, with their name in columns 1-9, a '5' in column 10 and a '6' in column 12. Time periods during which no behaviour was recorded are excluded in order to fit the data of the 15 minute encounter (900 seconds) onto 11 cards (770 columns). This reduced core, card and keypunch time

TABLE I. listinq of a sample data deck summarized by Lobster 7.

1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	20	1	2	3	4	5	6	7	8	9	30	1	2	3	4	5	6	7	8	9	40	1	2	3	4	5	6	7	8	9	50	1	2	3	4	5	6	7	8	9	60	1	2	3	4	5	6	7	8	9	70	1	2	3	4	5	6	7	8	9	80
L	O	B	S	T	E	R		B					W	I	N	N	E	R				E		V	S	·		B				A	U	G	·	3	/	6	B	·									2	1																														
S	C	I	S	S	O	R											1					1			3	3	3	3																					1									3															3					3							
S	C	I	S	S	O	R									1	3			3															3																																			3	3																3			
S	C	I	S	S	O	R			S																																																								1		6																							
P	U	S	H						S		6																																																																											
B	A	C	K						S		6																																																																											
R	U	S	H											1						1				3	3	3	3										1	1				1	1	1			1									3			1	1		1	1							3				3	1	1	1				
R	U	S	H										1		3			3															3																																			3	3																3			
R	U	S	H						S																																															1		6																									
E	S	C	A	P	E				S		6																																																																											
J	U	M	P						S		6																																																																											
A	N	T	·	W	H	I	P		S		6																																																																											
F	O	L	L	O	W																							3	3	3	3		1	1	1	1	1	1												1									3		1													3								3			1
F	O	L	L	O	W					1	1	1			3			3		1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	3		1		1	1	1	1	1	1	1	1	1	1	1	1	3		1	1
F	O	L	L	O	W				S	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1								1			3			1	1	1		6															
T	H	R	E	A	T								1	1			1		1	1			1	1	3	3	3	3			1	1	1	1	1			1	1	1				1				1	1	1	1	1	1	1	3	1				1			1	1	1	1	1	1	3		1	1	3				1	1		
T	H	R	E	A	T					1	1	1			3	1	1	3															3				1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			3	3																3	1	1	1
T	H	R	E	A	T				S	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1				3	1	1		6																	
B	O	X							S		6																																																																											
A	N	T	·	P	O	I	N	T			1													3	3	3	3	1																												3														3	1		3						1	
A	N	T	·	P	O	I	N	T								3			3	1													3																												3	3	1		1														3			
A	N	T	·	P	O	I	N	T	S																																													1		6																									
R	U	N							S		6																																																																											

requirements. Many decks each containing data of a single animal can be stacked together and run through the card reader as one job. When the operator wishes to terminate the job, a card containing a star in the first column is added to the end of the last deck.

Restrictions

- The 4's and 3's, separating the data into minutes, must all be in the same columns for each behaviour pattern. For example, the 3's on the first data card for each behaviour pattern of lobster B (Table 1) are in columns 5-8, 55, 69 & 73. If the cards are ever in the wrong order, the computer will give an execution error message and stop.
- If 11 cards are required for the data of a behaviour pattern the 80th column on this last card cannot be used.

(2) <u>Output</u>

The output consists of four tables, on two pages, utilizing 69 lines per page (examples Tables 2-5). The title and the name of the observer incorporated in the program is printed at the top of each page.

The first table (Table 2) shows the frequencies of each behaviour pattern for every minute throughout the encounter. Column one in the table names the behaviour patterns. Column two shows the frequency of each behaviour pattern during the first minute of the encounter. The succeeding columns include the frequencies for every subsequent minute. The row under the table shows the totalled frequencies for each column.

The second table (Table 3) presents duration of the behaviour patterns, in seconds, for each minute of an encounter. The first row under the table shows the totalled durations for each column. The next

TABLE 2. FREQUENCIES OF BEHAVIOUR PATTERNS EACH MINUTE OF THE 15 MIN. AGONISTIC ENCOUNTER
AGONISTIC ENCOUNTER

J. CHARLES SCRIVENER

LOBSTER B WINNER E VS. B AUG.3/68. 21

FREQUENCY FOR EACH MINUTE THROUGHOUT AN ENCOUNTER

SCISSOR	2	0	0	0	1	0	0	1	0	0	0	0	0	1	0
PUSH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BACK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RUSH	2	0	0	0	3	2	0	2	0	0	0	0	0	1	0
ESCAPE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
JUMP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.WHIP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FOLLOW	0	0	0	0	2	1	0	1	0	1	1	0	2	2	1
THREAT	4	0	0	0	4	3	1	2	1	0	1	0	0	2	1
BOX	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.POINT	1	0	0	0	1	0	1	1	0	1	0	0	2	1	0
RUN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL FREQ	9	0	0	0	11	6	2	7	1	2	2	0	4	7	2

TABLE 3. DURATIONS IN SECONDS OF BEHAVIOUR PATTERNS EACH MINUTE OF THE 15 MIN. ENCOUNTER.
TRUE TRT IS THE NUMBER OF SECONDS / MIN. IN WHICH BEHAVIOUR WAS RECORDED.

DURATION FOR EACH MINUTE THROUGH AN ENCOUNTER

SCISSOR	2	0	0	0	1	0	0	1	0	0	0	0	0	1	0
PUSH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BACK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RUSH	2	0	0	0	6	4	0	4	0	0	0	0	0	1	0
ESCAPE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
JUMP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.WHIP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FOLLOW	0	0	0	0	7	1	0	4	0	12	26	0	13	40	3
THREAT	7	0	0	0	16	8	2	5	2	0	21	0	0	46	2
BOX	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.POINT	1	0	0	0	1	0	1	1	0	1	0	0	2	1	0
RUN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL DUR.	12	0	0	0	31	13	3	15	2	13	47	0	15	89	5
TRUE TRT	12	0	0	0	26	13	3	12	2	13	26	0	15	50	5
PERC. TRT	20.0	0.0	0.0	0.0	43.3	21.6	5.0	20.0	3.3	21.6	43.3	0.0	25.0	83.3	8.3

TABLE 4. FREQUENCIES, DURATIONS & % OF TOTALLED DURATIONS OF THE BEHAVIOUR PATTERNS DURING THE 1ST 10 MIN., LAST 5 & TOTAL 15 MIN. OF THE ENCOUNTER.
TRT10, TRT5 & TRT ARE THE TOTALLED DURATIONS OF 1ST 10, LAST 5 & TOTAL 15 MIN.
T.R.T.S ARE NUMBER OF SECONDS BEHAVIOUR WAS OBSERVED DURING 15, 1ST 10 & LAST 5 MIN.

J. CHARLES SCRIVENER

LOBSTER B WINNER E VS. B AUG.3/68. 21

TRT10= 89 (TIME10= 14.83 TRT5=156 (TIME5= 52.00 TRT= 245 (TOTAL TIME= 27.22

BEHAVIOUR PATTERNS	FREQUENCIES 10MIN	5 MIN	15MIN	DURATIONS 10MIN	5 MIN	15MIN	(TOTALLED RESPONSE TIMES 10 MIN.	5 MIN.	15 MIN.	AV.DUR.
SCISSOR	4	1	5	4	1	5	4.49	0.64	2.04	1.00
PUSH	0	0	0	0	0	0	0.00	0.00	0.00	0.00
BACK	0	0	0	0	0	0	0.00	0.00	0.00	0.00
RUSH	9	1	10	16	1	17	17.97	0.64	6.93	1.70
ESCAPE	0	0	0	0	0	0	0.00	0.00	0.00	0.00
JUMP	0	0	0	0	0	0	0.00	0.00	0.00	0.00
ANT.WHIP	0	0	0	0	0	0	0.00	0.00	0.00	0.00
FOLLOW	5	6	11	24	82	106	26.96	52.56	43.26	9.63
THREAT	15	4	19	40	69	109	44.94	44.23	44.48	5.73
BOX	0	0	0	0	0	0	0.00	0.00	0.00	0.00
ANT.POINT	5	3	8	5	3	8	5.61	1.92	3.26	1.00
RUN	0	0	0	0	0	0	0.00	0.00	0.00	0.00

TRUE T.R.T.=177.0 19.66 T.R.T.10= 81.0 13.50 T.R.T.5= 96.0 32.00

TABLE 5. MATRIX INDICATING FREQUENCY THAT EACH BEHAVIOUR IN THE ROWS WAS FOLLOWED BY EACH BEHAVIOUR IN THE COLUMNS.

SEQUENCE ANALYSIS

SUBSEQUENT BEHAVIOUR

	SC	PU	BK	RH	ES	JU	AW	FO	TH	BO	AP	RU
SCISSOR	0	0	0	0	0	0	0	0	5	0	0	0
PUSH	0	0	0	0	0	0	0	0	0	0	0	0
BACK	0	0	0	0	0	0	0	0	0	0	0	0
RUSH	5	0	0	0	0	0	0	0	5	0	0	0
ESCAPE	0	0	0	0	0	0	0	0	0	0	0	0
JUMP	0	0	0	0	0	0	0	0	0	0	0	0
ANT.WHIP	0	0	0	0	0	0	0	0	0	0	0	0
FOLLOW	0	0	0	3	0	0	0	1	4	0	2	0
THREAT	0	0	0	7	0	0	0	5	2	0	5	0
BOX	0	0	0	0	0	0	0	0	0	0	0	0
ANT.POINT	0	0	0	0	0	0	0	5	3	0	0	0
RUN	0	0	0	0	0	0	0	0	0	0	0	0

line contains the one minute response times (TRUE T.R.T.). This is the number of seconds during a minute that the animal was showing any of the recorded behaviour. A comparison between the totalled durations and the minute response times could result in a measure of the mutual exclusiveness of the recordable units. The final line expresses the minute response times as a percent of 60 seconds ('****' represents 100%).

The third table (Table 4) is printed at the top of a new page. The first line under the title contains the totalled durations of the twelve behaviour patterns for the first ten minutes (TRT10 = 708), its percent of 600 seconds (10 minutes); the last five minutes (TRT5 = 127), its percent of 300 seconds; and the total fifteen minutes (TRT = 835), and its percent of 900 seconds. Since the lobsters often performed more than one behaviour pattern at a time, it was possible to obtain values greater than 100%. The 1132 printer has no percent character, therefore % is printed as a left parenthesis. The behaviour patterns are named in the first column of the table. Columns two, three and four present the frequencies of each, for the first ten minutes, last five minutes and total fifteen minutes. Columns five through ten show durations and their percent of the totalled durations listed in the line above the table. The final column includes the average durations. Below the table is the total response time (TRUE T.R.T. = 470.0) or the number of seconds during the encounter that the animal was showing any of the recorded behaviour and its percent of 900 seconds. The ten and five minute response times and their percent of 600 and 300 seconds respectively are also printed on the same line.

The final table (Table 5) contains the sequence analysis. It is a 12 by 12 matrix, which lists the number of times the behaviour pattern named in each row is followed by each of the behaviour patterns named in the columns. For example scissor was followed by threat 5 times and not by the others.

(3) Comments

(i) Twelve disc files are allocated for temporary storage of the input.

(ii) The totalled frequencies over fifteen minutes for a behaviour pattern (calculated from Table 2) will not necessarily agree with the total frequency (15 MIN column of Table 4). This occurs because a behaviour pattern sometimes continues into a second minute, so a single occurrence is then recorded twice, once for each minute.

(iii) The sequence analysis only records the start of a behaviour pattern. It does not give special attention to long durations during which other behaviour patterns may stop and start.

(4) PROGRAM LISTING

```
// JOB
// FOR
*ONE WORD INTEGERS
*LIST ALL
*IOCS(2501 READER)
*IOCS(1132 PRINTER)
*IOCS(DISK)
C
C LOBSTER BEHAVIOUR PROGRAM 7, FREQUENCY AND DURATION THROUGH TIME ,(TRT
C      ,FREQUENCY,DURATION,SEQUENCE ANALYSIS
C
      INTEGER A(771),FREQU(12,15),DURAT(12,15),TITLE(50),NAME(12,9)    ,D
     1UR10(12),DUR5(12),FREQ1 (12),FREQ5(12),TDUR(12),DUR,FREQ,TFREQ,TRT
     210,TRT5,TRT,X(12,70),MATRX(12,12),COL,END(12),NDUR(15),NFREQ(15)
      DIMENSION DUR15(15)
      DEFINE FILE 1(770,1,U,NN),2(770,1,U,NN),3(770,1,U,NN),4(770,1,U,NN
     1),5(770,1,U,NN),6(770,1,U,NN),7(770,1,U,NN),8(770,1,U,NN),9(770,1,
     2U,NN),10(770,1,U,NN),11(770,1,U,NN),12(770,1,U,NN)
      A(1)=0
      NN=4
      MM=8
C
C FREQU=MATRIX STORING THE FREQUENCIES OF EACH MINUTE FOR EACH
C          BEHAVIOUR PATTERN.
C DURAT=MATRIX STORING THE DURATIONS OF EACH MINUTE FOR EACH
C                 BEHAVIOUR PATTERN.
C TITLE=STORES TITLE CARD OF DATA DECK.
C NAME=STORES NAMES OF THE BEHAVIOUR PATTERNS.
C DUR10=STORES TOTAL DURATION IN SECONDS OF EACH BEHAVIOUR PATTERN
C           SHOWN DURING THE FIRST 10 MINUTES.
C DUR5=STORES TOTAL DURATION OF EACH BEHAVIOUR PATTERN
C           SHOWN DURING THE LAST 5 MINUTES.
C TDUR=TOTAL DURATION OF EACH BEHAVIOUR PATTERN FOR THE
C               15 MINUTE ENCOUNTER.
C FREQ1,FREQ5,+ TFREQ,STORE FREQUENCIES AS DUR10,DUR5,+ TDUR STORE
C                    DURATIONS.
C DUR=ACCUMULATES DURATIONS.
C FREQ=ACCUMULATES FREQUENCIES.
C END=STORES 6 S INDICATING END OF DATA.
C
C       READ TITLE CARD AND CHECK FOR A STAR
C
   50 READ(MM,1)(TITLE(I),I=1,50)
    1 FORMAT(50A1)
      IF(TITLE(1)-23616)2,60,2
C
C       WRITE OBSERVERS NAME AND TITLE AT TOP OF A NEW PAGE
C
    2 WRITE(3,3)(TITLE(I),I=1,50)
    3 FORMAT('1J. CHARLES SCRIVENER'//11X,50A1)
      DO 41 L=1,12
C
C      READ DATA OF ANIMAL WITH L=BEHAVIOUR PATTERN COUNTER
```

```
C
      J=2
      K=71
    4 READ(MM,5)(NAME(L,I),I=1,9),NUM,(A(I),I=J,K)
    5 FORMAT(9A1,I1,70I1)
      IF(NUM-5)6,7,6
    6 K=K+70
      J=J+70
      GO TO 4
C
C       ZERO STORAGE LOCATIONS
C
    7 DO 8  I=1,15
      DURAT(L,I)=0
    8 FREQU(L,I)=0
      DO 9 M=1,12
    9 MATRX(L,M)=0
      END(L)=0
      N=0
      JJJ=0
      DUR=0
      FREQ=0
      J=1
      K=0
      I=1
C
C       DETERMINE DURATIONS AND FREQUENCIES WITH N=MINUTE COUNTER.
C
   10 J=J+1
      K=K+1
      IF(A(J)-6)100,46,100
  100 IF(A(J)-1)11,14,15
   11 IF(A(J)-A(K))12,10,10
   12 IF(A(K)-3)13,10,10
   13 FREQU(L,I)=FREQU(L,I)+1
      FREQ=FREQ+1
      GO TO 10
   14 DURAT(L,I)=DURAT(L,I)+1
      DUR=DUR+1
      GO TO 10
   15 IF(A(J)-3)10,16,18
   16 IF(A(K)-1)19,17,19
   17 FREQ=FREQ+1
   18 FREQU(L,I)=FREQU(L,I)+1
   19 I=I+1
      N=N+1
      IF(N-10)10,46,10
   46 IF(JJJ-1)47,48,48
   47 DUR10(L)=DUR
      DUR=0
      FREQ1 (L)=FREQ
      JJJ=1
      FREQ=0
      IF(A(J)-6)10,48,10
   48 DUR5(L)=DUR
      FREQ5(L)=FREQ
```

```
C
C     PUT DATA ON DISC FILE
C
      IF(L-4)51,49,55
   49 WRITE(4'1)(A(I),I=1,770)
      GO TO 41
   51 IF(L-2)52,53,54
   52 WRITE(1'1)(A(I),I=1,770)
      GO TO 41
   53 WRITE(2'1)(A(I),I=1,770)
      GO TO 41
   54 WRITE(3'1)(A(I),I=1,770)
      GO TO 41
   55 IF(L-8)57,56,61
   56 WRITE(8'1)(A(I),I=1,770)
      GO TO 41
   57 IF(L-6)58,59,601
   58 WRITE(5'1)(A(I),I=1,770)
      GO TO 41
   59 WRITE(6'1)(A(I),I=1,770)
      GO TO 41
  601 WRITE(7'1)(A(I),I=1,770)
      GO TO 41
   61 IF(L-12)63,62,62
   62 WRITE(12'1)(A(I),I=1,770)
      GO TO 41
   63 IF(L-10)64,65,66
   64 WRITE(9'1)(A(I),I=1,770)
      GO TO 41
   65 WRITE(10'1)(A(I),I=1,770)
      GO TO 41
   66 WRITE(11'1)(A(I),I=1,770)
   41 TDUR(L)=DUR10(L)+DUR5(L)
      DO 200 I=1,15
      NDUR(I)=0
      NFREQ(I)=0
C
C     TOTAL DURATIONS AND FREQUENCIES FOR EACH MINUTE
C
      DO 200 L=1,12
      NFREQ(I)=NFREQ(I)+FREQU(L,I)
  200 NDUR (I)=NDUR (I)+DURAT(L,I)
C
C     PRINT FIRST TWO TABLES OF OUTPUT
C
      WRITE(3,21)
21    FORMAT('0',19X,'FREQUENCY FOR EACH MINUTE THROUGHOUT AN ENCOUNTER'
     1/1X,43('**'))
      DO 22 L=1,12
22    WRITE(3,23)(NAME(L,I),I=1,9),(FREQU(L,I),I=1,15)
23    FORMAT(11X,'*',15(4X,'*')/1X,9A1,1X,'*',15(1X,I2,1X,'*'))
      WRITE(3,24)
24    FORMAT(1X,43('**'))
      WRITE(3,240)(NFREQ(I),I=1,15)
  240 FORMAT(' TOTAL FREQ*',15(1X,I2,1X,'*')////)
      WRITE(3,25)
```

```
25     FORMAT('0',19X,'DURATION FOR EACH MINUTE THROUGH AN ENCOUNTER'/1X,
      143('**'))
       DO 26 L=1,12
26     WRITE(3,23)(NAME(L,I),I=1,9),(DURAT(L,I),I=1,15)
       WRITE(3,24)
       WRITE(3,260)(NDUR(I),I=1,15)
   260 FORMAT(' TOTAL DUR.*',15(I3,1X,'*'))
       DUR=0
       N=1
       M=1
       COL=0
       DO 69 I=1,15
    69 NDUR(I)=0
C
C      PUT DATA FROM ONE CARD OF EACH BEHAVIOUR PATTERN BACK INTO CORE
C
    70 DO 72 L=1,12
       IF(END(L)-6)71,72,71
    71 READ(L'M)(X(L,I),I=1,70)
    72 CONTINUE
C
C         DETERMINE TOTAL RESPONSE TIME EACH MIN. WITH
C                                                N=MINUTE COUNTER.
C                                                L=BEHAVIOUR PATTERN COUNTER.
C                                             NDUR=MINUTE RESPONSE TIME.
C
    94 DO 111 J=2,70
       DO 101 I=1,12
       IF(END(I)-6)102,101,102
   101 CONTINUE
       GO TO 112
   102 L=0
       JJJ=0
       II=0
       K=J-1
   103 L=L+1
       IF(END(L)-6)104,110,104
   104 IF(X(L,J)-6)1050,105,1050
   105 END(L)=6
       GO TO 110
  1050 IF(X(L,J)-1)110,1051,1053
  1051 IF(JJJ-2793)1052,106,1052
  1052 NDUR(N)=NDUR(N)+1
       JJJ=2793
  1053 IF(X(L,J)-3)106,1054,1055
  1054 X(L,J)=0
       GO TO 1056
  1055 X(L,J)=1
  1056 IF(II-3579)1057,106,1057
  1057 N=N+1
       II=3579
C
C         SEQUENCE ANALYSIS       =MATRX
C
   106 IF(X(L,J)-X(L,K))110,110,107
   107 IF(COL-1)109,108,108
```

```
  108 MATRX (COL,L)=MATRX (COL,L)+1
  109 COL=L
  110 IF(L-12)103,111,111
  111 CONTINUE
      M=M+69
      GO TO 70
C
C      CALCULATE M.R.T. AS A PERCENT OF 60 SECONDS AND PRINT THEM
C                                           AT BOTTOM OF PAGE
C
  112 DO 35 I=1,15
      XDUR=NDUR(I)
   35 DUR15(I)=XDUR*100./60.
      WRITE(3,36)(NDUR(I),I=1,15),(DUR15(I),I=1,15)
   36 FORMAT('OTRUE  TRT *',15(I3,1X,'*')/' PERC. TRT *',15(F4.1,'*'))
      TRT10=0
      TRT5=0
      TRT=0
C
C CALCULATE THE TOTALLED DURATIONS FIRST 10 MIN.,LAST 5 MIN.,15 MIN. +
C        THEIR PERCENT OF 600,300,+ 900 SECONDS RESPECTIVELY.
C
      DO 27 I=1,12
      TRT10=TRT10+DUR10(I)
      TRT5=TRT5+DUR5(I)
   27 TRT=TRT+TDUR(I)
      RTRT1 =TRT10
      RTRT5=TRT5
      RTRT=TRT
      PTRT1 =RTRT1 *100./600.
      PTRT5=RTRT5*100./300.
      PTRT=RTRT*100./900.
C
C      PRINT TITLE AND TABLE 3 AT TOP OF NEW PAGE
C
      WRITE(3,3)(TITLE(I),I=1,50)
      WRITE(3,28)TRT10,PTRT1 ,TRT5,PTRT5,TRT,PTRT
   28 FORMAT('OTRT10=',I3,3X ,'(TIME10=',F6.2,5X ,'TRT5=',I3,3X ,'(TIME5
     1=',F6.2,5X ,'TRT=',I4,3X ,'(TOTAL TIME=',F6.2/1X,17('*****')/1X,'*
     2','BEHAVIOUR',3X ,'*',3X ,'FREQUENCIES',3X ,'*',4X ,'DURATIONS',4X
     3 ,'* ( TOTALLED RESPONSE TIMES*'          ,7X ,'*'/1X,'*',4X,'PATTE
     4RNS*',2('10MIN*5 MIN*15MIN*'),' 10 MIN.* 5 MIN. * 15 MIN.*','AV.DU
     5R.*'/1X,17('*****'))
C
C    CALCULATE AND OUTPUT PERCENTAGES OF THE TOTALLED DURATIONS FOR
C              EACH BEHAVIOUR PATTERN.
C
      DO 31 I=1,12
      TFREQ=FREQ1 (I)+FREQ5(I)
      PTRT1 =DUR10(I)*100./RTRT1
      PTRT5=DUR5(I)*100./RTRT5
      PTRT=TDUR(I)*100./RTRT
      RDUR=TDUR(I)
C
C     CALCULATE AVERAGE DURATIONS
C
```

```
      IF(TFREQ-1)29,30,30
   29 AVDUR=0.0
      GO TO 31
   30 AVDUR=RDUR/TFREQ
   31 WRITE(3,32)(NAME(I,J),J=1,9),FREQ1 (I),FREQ5(I),TFREQ,DUR10(I),DUR
     15(I),TDUR(I),PTRT1 ,PTRT5,PTRT,AVDUR
   32 FORMAT(' *',12X,'*',6(5X,'*'),3(8X,'*'),7X,'*'/' *',9A1,3X,'*',3(2
     1X,I2,1X,'*'),3(1X,I3,1X,'*'),3(2X,F5.2,1X,'*'),1X,F5.2,1X,'*')
      WRITE(3,34)
   34 FORMAT(' '17('*****'))
C
C CALCULATE AND OUTPUT THE TOTAL RESPONSE TIME,THE FIRST 10 MINUTES
C          RESPONSE TIME + THE LAST 5 MINUTE RESPONSE TIME.
C
      RTRT1=0.0
      RTRT5=0.0
      DO 37 I=1,10
   37 RTRT1=RTRT1+NDUR(I)
      DO 38 I=11,15
   38 RTRT5=RTRT5+NDUR(I)
      RTRT=RTRT1+RTRT5
      PTRT1=RTRT1*100./600.
      PTRT5=RTRT5*100./300.
      PTRT=RTRT*100./900.
      WRITE(3,1110)RTRT,PTRT,RTRT1,PTRT1,RTRT5,PTRT5
 1110 FORMAT(' TRUE T.R.T.=',F5.1,2X,F6.2,10X,'T.R.T.10=',F5.1,2X,F6.2,1
     10X,'T.R.T.5=',F5.1,2X,F6.2,///)
C
C     OUTPUT SEQUENCE ANALYSIS
C
      WRITE(3,113)
  113 FORMAT('0',30X,'SEQUENCE ANALYSIS')
      WRITE(3,114)
  114 FORMAT('0'33X,'SUBSEQUENT BEHAVIOUR'/14X,'*',1X,'SC',1X,'*',1X,'PU
     1',1X,'*',1X,'BK',1X,'*',1X,'RH',1X,'*',1X,'ES',1X,'*',1X,'JU',1X,'
     2*',1X,'AW',1X,'*',1X,'FO',1X,'*',1X,'TH',1X,'*',1X,'BO',1X,'*',1X,
     3'AP',1X,'*',1X,'RU',1X,'*'/1X,37('**'))
      DO 115 L=1,12
  115 WRITE(3,116)(NAME(L,I),I=1,9),(MATRX (L,I),I=1,12)
  116 FORMAT(14X,'*',12(4X,'*')/1X,9A1,4X,'*',12(1X,I2,1X,'*'))
      WRITE(3,117)
  117 FORMAT(1X,37('**'))
      GO TO 50
60    CALL EXIT
      END
// XEQ
```

Program - Lobster 8

This program was written to perform the same calculations and output the same results as Lobster 7, but handles different input.

(1) Input

The first card is a title card containing any alpha-numeric characters in columns 1-50 as in Lobster 7 (Table 6).

The rest of the data deck contains information on fifteen behaviour patterns. Columns 1-9 contain the name of the behaviour pattern. Column 10 is blank or contains a '5', if this is the last card with information about the behaviour pattern. Columns 11-70 combined, represent one minute of time for the behaviour pattern named in columns 1-9. Each column within this group represents one second in time and contains a '1' if the behaviour is occurring or is blank if it is not occurring. Column 71 has a '4' punched in it, if the behaviour continues over into the next minute, or a '3', if it does not. Columns 72-80 are not read by the computer, but can be used to number the cards (Table 6). This facilitates card sorting if a data deck is dropped. The end of data for each behaviour pattern is signified by a '6', which can be placed anywhere in columns 11-70. A maximum of 16 cards can be used for each behaviour pattern. Behaviour patterns that are not observed during the social encounter are each represented by a single card with their name in columns 1-9, a '5' in column 10, a '6' in column 12, and a '3' in column 71. While this method of data preparation utilizes many more cards than are required for Lobster 7, more information can be obtained.

A job using this program is run in a manner similar to that described for Lobster 7.

TABLE 6. Listing of a sample data deck summarized by Lobster 8.

```
12345678901234567890123456789012345678901234567890123456789012345678901234567890
LOBSTER J   LOSER   23 VS. J   FEB.27/69.        7
SCISSOR  5                1 6                                         3   1
PUSH     5                      1111    1111 6                        3   1
BACK                                         11111            111111114   1
BACK      1111                                                      114   2
BACK      11111111111                                                 3   3
BACK                                              111111111           3   4
BACK            1111111111111                                     11114   5
BACK      111111111     111111                 111111111111111111111113   6
BACK                                                               1114   7
BACK      111111111111111111                                          3   8
BACK     5           1111111111111111111 6                            3   9
SIDE-WAYS                                                             3   1
SIDE-WAYS                                                             3   2
SIDE-WAYS                                                             3   3
SIDE-WAYS5                                                    11 6    3   4
RUSH     5               1 6                                          3   1
ESCAPE                                                                3   1
ESCAPE                                                                3   2
ESCAPE                                                                3   3
ESCAPE                                                                3   4
ESCAPE                                                                3   5
ESCAPE   5           11 6                                             3   6
JUMP     5 6                                                          3   1
ANT.WHIP 5 6                                                          3   1
```

TABLE 6. cont.

1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	20	1	2	3	4	5	6	7	8	9	30	1	2	3	4	5	6	7	8	9	40	1	2	3	4	5	6	7	8	9	50	1	2	3	4	5	6	7	8	9	60	1	2	3	4	5	6	7	8	9	70	1	2	3	4	5	6	7	8	9	80
F	O	L	L	O	W				5																						1		6																																								3				1					
A	P	P	R	O	A	C	H														1	1	1	1																																															3				1					
A	P	P	R	O	A	C	H																																																																				3				2					
A	P	P	R	O	A	C	H																																																																				3				3					
A	P	P	R	O	A	C	H		5																																		1		6																													3				4					
T	H	R	E	A	T				5																				1	1						1	1	1		6																														3				1					
B	O	X							5		6																																																																		3				1					
W	A	L	K						5		6																																																																		3				1					
A	N	T	.	P	O	I	N	T		1				1																																									1																		3				1					
A	N	T	.	P	O	I	N	T																																														1						1										3				2					
A	N	T	.	P	O	I	N	T																																																																		3				3					
A	N	T	.	P	O	I	N	T																																		1													1																		3				4					
A	N	T	.	P	O	I	N	T				1																																															1												3				5					
A	N	T	.	P	O	I	N	T																										1																																							3				6					
A	N	T	.	P	O	I	N	T																																													1									1										3				7					
A	N	T	.	P	O	I	N	T																																																																		3				8					
A	N	T	.	P	O	I	N	T	5								1																				1		6																																		3				9					
R	U	N																																																																												3				1					
R	U	N																																																																												3				2					
R	U	N																																																																												3				3					
R	U	N							5																																																								1	1	1		6	3				4					

(2) Output

The output consists of four tables printed on two pages utilizing 76 lines per page (Tables 7-10). The inclusion of three more behaviour patterns in each table represents the major individual animal output differences between Lobster 7 and 8, but at the end of the job the accumulated sequence analysis for both animals of the social encounters are printed in two tables on different pages. The computer assumes that the first and the other odd decks contain the data of winners, while the second and other even decks contain the data of losers.

(3) Comments

(i) Fifteen disc files are allocated for temporary storage of the input.

(ii) An IBM 1132 printer will not always print more than 76-78 lines per page (8 lines/inch), without skipping the next page of paper. Therefore the observers name and most of the spacing between tables had to be removed from Lobster 8, to make room for the larger tables.

TABLE 7. FREQUENCIES OF BEHAVIOUR PATTERNS EACH MINUTE OF THE 15 MIN. AGONISTIC ENCOUNTER.

LOBSTER 23 WINNER 23 VS. J FEB.27/69. 7

FREQUENCY FOR EACH MINUTE THROUGHOUT AN ENCOUNTER

SCISSOR	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0
PUSH	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BACK	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SIDE-WAYS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RUSH	0	0	0	1	2	1	0	0	1	0	0	0	0	0	0
ESCAPE	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
JUMP	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.WHIP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FOLLOW	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
APPROACH	1	1	0	1	0	1	1	0	1	0	0	0	0	0	0
THREAT	2	2	1	2	4	4	1	1	1	0	0	0	0	0	0
BOX	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WALK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.POINT	2	1	0	2	4	5	2	0	2	0	0	0	0	0	0
RUN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL FREQ	10	5	2	7	12	14	5	2	6	0	0	0	0	0	0

TABLE 8. DURATIONS IN SECONDS. TRUE TRT = NO. OF SEC. / MIN. IN WHICH BEHAVIOUR WAS RECORDED.

DURATION FOR EACH MINUTE THROUGH AN ENCOUNTER

SCISSOR	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0
PUSH	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BACK	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SIDE-WAYS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RUSH	0	0	0	2	2	1	0	0	2	0	0	0	0	0	0
ESCAPE	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
JUMP	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.WHIP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FOLLOW	1	1	2	2	1	7	3	5	8	0	0	0	0	0	0
APPROACH	1	9	0	6	0	2	7	0	3	0	0	0	0	0	0
THREAT	27	18	9	9	18	23	3	8	10	0	0	0	0	0	0
BOX	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WALK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.POINT	2	2	0	2	4	6	2	0	2	0	0	0	0	0	0
RUN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL DUR.	45	30	11	21	26	41	15	13	25	0	0	0	0	0	0
TRUE TRT	44	29	9	18	23	31	11	8	24	0	0	0	0	0	0
PERC. TRT	73.3	48.3	15.0	30.0	38.3	51.6	18.3	13.3	40.0	0.0	0.0	0.0	0.0	0.0	0.0

TABLE 9. Frequencies, durations & % of totalled durations of the behaviour patterns during the 1st 10, last 5 & total 15 min. of the encounter.
TRT10, TRT5 & TRT = the totalled durations of the 1st 10, last 5 & total 15 min.
T.R.T.s = no. of sec. behaviour was observed during 15, 1st 10 & last 5 min.

LOBSTER 23 WINNER 23 VS. J FEB.27/69. 7

TRT10=227 (TIME10= 37.83 TRT5= 0 (TIME5= 0.00 TRT= 227 (TOTAL TIME= 25.22

BEHAVIOUR PATTERNS	FREQUENCIES 10MIN	5 MIN	15MIN	DURATIONS 10MIN	5 MIN	15MIN	(TOTALLED RESPONSE TIMES 10 MIN.	5 MIN.	15 MIN.	AV.DUR.
SCISSOR	3	0	3	3	0	3	1.32	0.00	1.32	1.00
PUSH	1	0	1	6	0	6	2.64	0.00	2.64	6.00
BACK	1	0	1	6	0	6	2.64	0.00	2.64	6.00
SIDE-WAYS	0	0	0	0	0	0	0.00	0.00	0.00	0.00
RUSH	5	0	5	7	0	7	3.08	0.00	3.08	1.40
ESCAPE	1	0	1	1	0	1	0.44	0.00	0.44	1.00
JUMP	1	0	1	1	0	1	0.44	0.00	0.44	1.00
ANT.WHIP	0	0	0	0	0	0	0.00	0.00	0.00	0.00
FOLLOW	7	0	7	30	0	30	13.21	0.00	13.21	4.28
APPROACH	6	0	6	28	0	28	12.33	0.00	12.33	4.66
THREAT	14	0	14	125	0	125	55.06	0.00	55.06	8.92
BOX	0	0	0	0	0	0	0.00	0.00	0.00	0.00
WALK	0	0	0	0	0	0	0.00	0.00	0.00	0.00
ANT.POINT	18	0	18	20	0	20	8.81	0.00	8.81	1.11
RUN	0	0	0	0	0	0	0.00	0.00	0.00	0.00

TRUE T.R.T.=197.0 21.88 T.R.T.10=197.0 32.83 T.R.T.5= 0.0 0.00

TABLE 10. Matrix indicating frequency that each behaviour in the rows was followed by each behaviour in the columns.

SEQUENCE ANALYSIS

SUBSEQUENT BEHAVIOUR

	SC	PU	BK	SW	RH	ES	JU	AW	FO	AH	TH	BO	WA	AP	RU
SCISSOR	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
PUSH	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
BACK	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
SIDE-WAYS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RUSH	2	0	0	0	0	0	0	0	0	0	3	0	0	0	0
ESCAPE	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
JUMP	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
ANT.WHIP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FOLLOW	0	0	0	0	3	0	0	0	0	0	1	0	0	3	0
APPROACH	0	0	0	0	0	0	0	0	2	0	2	0	0	2	0
THREAT	0	1	0	0	1	0	0	0	4	0	1	0	0	7	0
BOX	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WALK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.POINT	1	0	0	0	1	1	0	0	1	6	2	0	0	5	0
RUN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(4) PROGRAM LISTING

```
// JOB
// FOR
*ONE WORD INTEGERS
*LIST ALL
*IOCS(2501 READER)
*IOCS(1132 PRINTER)
*IOCS(DISK)
C
C LOBSTER BEHAVIOUR PROGRAM 8, FREQUENCY AND DURATION THROUGH TIME ,(TRT
C       ,FREQUENCY,DURATION,SEQUENCE ANALYSIS
C    THIS PROGRAM ACCUMULATES SEQUENCE ANALYSIS     UNTIL A * (CALL EXIT)
C         IS REACHED THE ACCUMULATED TOTALS ARE THEN PRINTED.
C
      INTEGER A(961),FREQU(15,15),DURAT(15,15),TITLE(50),NAME(15,9),DUR1
     10(15),DUR5(15),FREQ1(15),FREQ5(15),TDUR(15),DUR,FREQ,TFREQ,TRT10,
     2TRT5,TRT,X(15,61),COL,END(15),NFREQ(15),NDUR(15),MATRX(15,15)
      DIMENSION DUR15(15),MMM(16),IWIN(15,15),ILOSE(15,15)
      DEFINE FILE 1(970,1,U,NN),2(970,1,U,NN),3(970,1,U,NN),4(970,1,U,NN
     1),5(970,1,U,NN),6(970,1,U,NN),7(970,1,U,NN),8(970,1,U,NN),9(970,1,
     2U,NN),10(970,1,U,NN),11(970,1,U,NN),12(970,1,U,NN),13(970,1,U,NN),
     314(970,1,U,NN),15(970,1,U,NN)
      NN=1
      MM=8
      JLOSE=0
C
C FREQU=MATRIX STORING THE FREQUENCIES OF EACH MINUTE FOR EACH
C          BEHAVIOUR PATTERN.
C DURAT=MATRIX STORING THE DURATIONS OF EACH MINUTE FOR EACH
C                BEHAVIOUR PATTERN.
C TITLE=STORES TITLE CARD OF DATA DECK.
C NAME=STORES NAMES OF THE BEHAVIOUR PATTERNS.
C DUR10=STORES TOTAL DURATION IN SECONDS OF EACH BEHAVIOUR PATTERN
C           SHOWN DURING THE FIRST 10 MINUTES.
C DUR5=STORES TOTAL DURATION OF EACH BEHAVIOUR PATTERN
C           SHOWN DURING THE LAST 5 MINUTES.
C TDUR=TOTAL DURATION OF EACH BEHAVIOUR PATTERN FOR THE
C               15 MINUTE ENCOUNTER.
C FREQ1,FREQ5,+ TFREQ,STORE FREQUENCIES AS DUR10,DUR5,+ TDUR STORE
C                   DURATIONS.
C DUR=ACCUMULATES DURATIONS.
C FREQ=ACCUMULATES FREQUENCIES.
C END=STORES 6 S INDICATING END OF DATA.
C
C        READ TITLE CARD AND CHECK FOR A STAR
C
      DO 800 I=1,15
      DO 800 J=1,15
      IWIN(I,J)=0
  800 ILOSE(I,J)=0
      A(1)=0
   50 READ(MM,1)(TITLE(I),I=1,50)
    1 FORMAT(50A1)
      IF(TITLE(1)-23616)2,60,2
```

```
C
C        WRITE OBSERVERS NAME AND TITLE AT TOP OF A NEW PAGE
C
    2 WRITE(3,3)(TITLE(I),I=1,50)
    3 FORMAT('1',11X,50A1)
      DO 41 L=1,15
C
C     READ DATA OF ANIMAL WITH L=BEHAVIOUR PATTERN COUNTER
C
      JJ=2
      KK=61
      N=1
    4 READ(MM,5)(NAME(L,I),I=1,9),NUM,(A(I),I=JJ,KK),MMM(N)
    5 FORMAT(9A1,I1,60I1,I1)
      IF(NUM-5)6,7,6
    6 KK=KK+60
      JJ=JJ+60
      N=N+1
      GO TO 4
C
C      ZERO STORAGE LOCATIONS
C
    7 DO 8 I=1,15
      DURAT(L,I)=0
      FREQU(L,I)=0
    8 MATRX(L,I)=0
      END(L)=0
      JJJ=0
      DUR=0
      FREQ=0
      J=1
      K=0
      I=1
      N1=0
    9 IF(N1-60)10,16,16
C
C      DETERMINE DURATIONS AND FREQUENCIES WITH N=MINUTE COUNTER.
C
   10 J=J+1
      K=K+1
      N1=N1+1
   11 IF(A(J)-6)12,46,41
   12 IF(A(J)-1)9,13,41
   13 DURAT(L,I)=DURAT(L,I)+1
      DUR=DUR+1
      IF(A(J)-A(K))9,14,15
   14 IF(N1-1)9,15,9
   15 FREQU(L,I)=FREQU(L,I)+1
      FREQ=FREQ+1
      GO TO 9
   16 IF(MMM(I)-4)18,17,18
   17 FREQ=FREQ-1
   18 I=I+1
      N1=0
   19 IF(I-11)9,46,9
   46 IF(JJJ-1)47,48,48
```

```
   47 DUR10(L)=DUR
      DUR=0
      FREQ1 (L)=FREQ
      JJJ=1
      FREQ=0
      IF(A(J)-6)9,48,9
   48 DUR5(L)=DUR
      FREQ5(L)=FREQ
C
C     PUT DATA ON DISC FILE
C
      WRITE(L'1)(A(I),I=1,961)
   41 TDUR(L)=DUR10(L)+DUR5(L)
      DO 20 I=1,15
      NDUR(I)=0
      NFREQ(I)=0
C
C     TOTAL DURATIONS AND FREQUENCIES FOR EACH MINUTE
C
      DO 20 L=1,15
      NFREQ(I)=NFREQ(I)+FREQU(L,I)
   20 NDUR(I)=NDUR(I)+DURAT(L,I)
C
C     PRINT FIRST TWO TABLES OF OUTPUT
C
      WRITE(3,21)
21    FORMAT('0',19X,'FREQUENCY FOR EACH MINUTE THROUGHOUT AN ENCOUNTER'
     1/1X,43('**'))
      DO 22 L=1,15
22    WRITE(3,23)(NAME(L,I),I=1,9),(FREQU(L,I),I=1,15)
23    FORMAT(11X,'*',15(4X,'*')/1X,9A1,1X,'*',15(1X,I2,1X,'*'))
      WRITE(3,24)
24    FORMAT(1X,43('**'))
      WRITE(3,240)(NFREQ(I),I=1,15)
  240 FORMAT(' TOTAL FREQ*',15(1X,I2,1X,'*')//)
      WRITE(3,25)
25    FORMAT('0',19X,'DURATION FOR EACH MINUTE THROUGH AN ENCOUNTER'/1X,
     143('**'))
      DO 26 L=1,15
26    WRITE(3,23)(NAME(L,I),I=1,9),(DURAT(L,I),I=1,15)
      WRITE(3,24)
      WRITE(3,260)(NDUR(I),I=1,15)
  260 FORMAT(' TOTAL DUR.*',15(I3,1X,'*'))
      DUR=0
      N=1
      M=1
      COL=0
      DO 69 I=1,15
   69 NDUR(I)=0
C
C     PUT DATA FROM ONE CARD OF EACH BEHAVIOUR PATTERN BACK INTO CORE
C
   70 DO 72 L=1,15
      IF(END(L)-6)71,72,71
   71 READ(L'M)(X(L,I),I=1,61)
   72 CONTINUE
```

```
C
C       DETERMINE TOTAL RESPONSE TIME EACH MIN. WITH
C                                         N=MINUTE COUNTER.
C                                         L=BEHAVIOUR PATTERN COUNTER.
C                                      NDUR=MINUTE RESPONSE TIME.
C
  100 DO 111 J=2,61
      DO 101 I=1,15
      IF(END(I)-6)102,101,102
  101 CONTINUE
      GO TO 112
  102 L=0
      JJJ=0
      K=J-1
  103 L=L+1
      IF(END(L)-6)104,110,104
  104 IF(X(L,J)-6)1050,105,1050
  105 END(L)=6
      GO TO 110
 1050 IF(X(L,J)-1)110,1051,112
 1051 IF(JJJ-2793)1052,106,1052
 1052 NDUR(N)=NDUR(N)+1
      JJJ=2793
C
C         SEQUENCE ANALYSIS       =MATRX
C
  106 IF(X(L,J)-X(L,K))110,110,107
  107 IF(COL-1)109,108,108
  108 MATRX (COL,L)=MATRX (COL,L)+1
  109 COL=L
  110 IF(L-15)103,111,111
  111 CONTINUE
      M=M+60
      N=N+1
      GO TO 70
C
C       CALCULATE M.R.T. AS A PERCENT OF 60 SECONDS AND PRINT THEM
C                                     AT BOTTOM OF PAGE
C
  112 DO 113 I=1,15
      XDUR=NDUR(I)
  113 DUR15(I)=XDUR*100./60.
      WRITE(3,114)(NDUR(I),I=1,15),(DUR15(I),I=1,15)
  114 FORMAT('OTRUE  TRT *',15(I3,1X,'*')/' PERC. TRT *',15(F4.1,'*'))
      TRT10=0
      TRT5=0
      TRT=0
C
C CALCULATE THE TOTALLED DURATIONS FIRST 10 MIN.,LAST 5 MIN.,15 MIN. +
C       THEIR PERCENT OF 600,300,+ 900 SECONDS RESPECTIVELY.
C
      DO 27 I=1,15
      TRT10=TRT10+DUR10(I)
      TRT5=TRT5+DUR5(I)
   27 TRT=TRT+TDUR(I)
      RTRT1 =TRT10
```

```
      RTRT5=TRT5
      RTRT=TRT
      PTRT1 =RTRT1 *100./600.
      PTRT5=RTRT5*100./300.
      PTRT=RTRT*100./900.
C
C      PRINT TITLE AND TABLE 3 AT TOP OF NEW PAGE
C
      WRITE(3,3)(TITLE(I),I=1,50)
      WRITE(3,28)TRT10,PTRT1 ,TRT5,PTRT5,TRT,PTRT
   28 FORMAT('0TRT10=',I3,3X ,'(TIME10=',F6.2,5X ,'TRT5=',I3,3X ,'(TIME5
     1=',F6.2,5X ,'TRT=',I4,3X ,'(TOTAL TIME=',F6.2/1X,17('*****')/1X,'*
     2','BEHAVIOUR',3X ,'*',3X ,'FREQUENCIES',3X ,'*',4X ,'DURATIONS',4X
     3,'* ( TOTALLED RESPONSE TIMES*',7X,'*'/1X,'*',4X,'PATTERNS*',2('10
     4MIN*5 MIN*15MIN*'),' 10 MIN.* 5 MIN. * 15 MIN.*AV.DUR.*'/1X,17('**
     5***'))
C
C   CALCULATE AND OUTPUT PERCENTAGES OF THE TOTALLED DURATIONS FOR
C              EACH BEHAVIOUR PATTERN.
      DO 31 I=1,15
      TFREQ=FREQ1 (I)+FREQ5(I)
      PTRT1 =DUR10(I)*100./RTRT1
      PTRT5=DUR5(I)*100./RTRT5
      PTRT=TDUR(I)*100./RTRT
      RDUR=TDUR(I)
C
C     CALCULATE AVERAGE DURATIONS
C
      IF(TFREQ-1)29,30,30
   29 AVDUR=0.0
      GO TO 31
   30 AVDUR=RDUR/TFREQ
   31 WRITE(3,32)(NAME(I,J),J=1,9),FREQ1 (I),FREQ5(I),TFREQ,DUR10(I),DUR
     15(I),TDUR(I),PTRT1 ,PTRT5,PTRT,AVDUR
   32 FORMAT(' *',12X,'*',6(5X,'*'),3(8X,'*'),7X,'*'/' *',9A1,3X,'*',3(2
     1X,I2,1X,'*'),3(1X,I3,1X,'*'),3(2X,F5.2,1X,'*'),1X,F5.2,1X,'*')
      WRITE(3,34)
   34 FORMAT(' '17('*****'))
C
C
C CALCULATE AND OUTPUT THE TOTAL RESPONSE TIME,THE FIRST 10 MINUTES
C         RESPONSE TIME + THE LAST 5 MINUTE RESPONSE TIME.
C
      RTRT1=0.0
      RTRT5=0.0
      DO 35 I=1,10
   35 RTRT1=RTRT1+NDUR(I)
      DO 36 I=11,15
   36 RTRT5=RTRT5+NDUR(I)
      RTRT=RTRT1+RTRT5
      PTRT1=RTRT1*100./600.
      PTRT5=RTRT5*100./300.
      PTRT=RTRT*100./900.
      WRITE(3,115)RTRT,PTRT,RTRT1,PTRT1,RTRT5,PTRT5
  115 FORMAT(' TRUE T.R.T.=',F5.1,2X,F6.2,10X,'T.R.T.10=',F5.1,2X,F6.2,1
     10X,'T.R.T.5=',F5.1,2X,F6.2)
```

```
C
C     OUTPUT SEQUENCE ANALYSIS
C
      WRITE(3,116)
  116 FORMAT('0',30X,'SEQUENCE ANALYSIS')
      WRITE(3,117)
  117 FORMAT('0'33X,'SUBSEQUENT BEHAVIOUR'/14X,'*',1X,'SC',1X,'*',1X,'PU
     1',1X,'*',1X,'BK',1X,'*',1X,'SW',1X,'*',1X,'RH',1X,'*',1X,'ES',1X,'
     2*',1X,'JU',1X,'*',1X,'AW',1X,'*',1X,'FO',1X,'*',1X,'AH',1X,'*',1X,
     3'TH',1X,'*',1X,'BO',1X,'*',1X,'WA',1X,'*',1X,'AP',1X,'*',1X,'RU',1
     4X,'*'/1X,89('*'))
      DO 118 L=1,15
  118 WRITE(3,119)(NAME(L,I),I=1,9),(MATRX (L,I),I=1,15)
  119 FORMAT(14X,'*',15(4X,'*')/1X,9A1,4X,'*',15(I3,1X,'*'))
      WRITE(3,120)
  120 FORMAT(1X,89('*'))
      IF(JLOSE-1)121,123,123
  121 DO 122 I=1,15
      DO 122 J=1,15
  122 IWIN(I,J)=IWIN(I,J)+MATRX(I,J)
      JLOSE=1
      GO TO 50
  123 DO 124 I=1,15
      DO 124 J=1,15
  124 ILOSE(I,J)=ILOSE(I,J)+MATRX(I,J)
      JLOSE=0
      GO TO 50
C
C     ACCUMULATION IS PRINTED
C
   60 WRITE(3,61)
   61 FORMAT('1J.CHARLES SCRIVENER'//25X,'SEQUENCE ANALYSIS OF WINNERS')
      WRITE(3,117)
      DO 126 L=1,15
  126 WRITE(3,119)(NAME(L,I),I=1,9),(IWIN(L,I),I=1,15)
      WRITE(3,120)
      WRITE(3,129)
  129 FORMAT('1J.CHARLES SCRIVENER'//25X,'SEQUENCE ANALYSIS OF LOSERS')
      WRITE(3,117)
      DO 130 L=1,15
  130 WRITE(3,119)(NAME(L,I),I=1,9),(ILOSE(L,I),I=1,15)
      WRITE(3,120)
      CALL EXIT
      END
// XEQ
```

Program - Lobster 9

This program runs a response analysis, to determine the response of one animal to every behaviour shown by the other, throughout a social encounter.

(1) Input

The same data cards are used for Lobster 8 and 9 (Table 6). During this program the input of both animals are processed together, so the data of the two animals must be treated as a single data deck.

(2) Output

The output consists of two tables which utilize 76 lines on a single page (Table 11 and 12). The titles of both animals are printed in the order in which they were read into the computer. This is followed by a table showing the number of times, if any, that each of the second animal's behaviour patterns were shown in response to each behaviour pattern of the first animal (Table 11). For example, the loser responded to the winner's scissoring by showing backing 3 times and escape once. Column 17 indicates the number of times that the loser showed no recorded response. The second table contains the responses of the first animal to the behaviour of the second animal (Table 12). When the job ends, the computer prints the accumulated frequency totals of the response of the second animal to the first and the first animal to the second.

(3) Comments

(i) Thirty disc files are allocated for temporary storage of the input data.

(ii) One animal responds to the other by:

TABLES 11 & 12. Matrix indicating number of times, if any, each behaviour heading the columns was shown in response to behaviour patterns heading the rows.

TABLE 11.

LOBSTER 23 WINNER 23 VS. J FEB.27/69. 7
LOBSTER J LOSER 23 VS. J FEB.27/69. 7

RESPONSE OF THE LOSER TO THE BEHAVIOUR OF THE WINNER

WINNERS BEHAVIOUR	SC	PU	BK	SW	RH	ES	JU	AW	FO	AH	TH	BO	WA	AP	RU	NONE
	RESPONSE OF THE LOSER															
SCISSOR	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0
PUSH	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BACK	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
SIDE-WAYS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RUSH	0	0	4	0	0	1	0	0	0	0	0	0	0	1	0	0
ESCAPE	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
JUMP	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
ANT.WHIP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FOLLOW	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	1
APPROACH	0	0	2	0	0	0	0	0	0	2	0	0	0	3	0	0
THREAT	0	0	9	0	0	0	0	0	0	0	1	0	0	1	0	4
BOX	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WALK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.POINT	1	0	5	0	1	0	0	0	0	1	0	0	0	4	0	8
RUN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 12.

RESPONSE OF WINNER TO THE BEHAVIOUR OF THE LOSER

LOSERS BEHAVIOUR	SC	PU	BK	SW	RH	ES	JU	AW	FO	AH	TH	BO	WA	AP	RU	NONE
	RESPONSE OF THE WINNER															
SCISSOR	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
PUSH	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
BACK	1	0	0	0	3	0	0	0	7	0	8	0	0	2	0	0
SIDE-WAYS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
RUSH	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
ESCAPE	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
JUMP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.WHIP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FOLLOW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
APPROACH	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
THREAT	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0
BOX	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WALK	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANT.POINT	0	0	0	0	0	0	0	0	0	4	5	0	0	7	0	2
RUN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

(a) Beginning a behaviour pattern during the same second.

(b) continuing a behaviour pattern started earlier, for the next four seconds.

(c) beginning a behaviour pattern within the next three seconds.

These values were used, because periodically the observer detected a two second delay between the time one animal began showing agonistic behaviour and the time the other started. This occurred after they had demonstrated awareness of each other's position.

(iii) The computer assumes that the data of the first animal is that of the winner of the two animal agonistic encounter.

(4) PROGRAM LISTING

```
// JOB
// FOR
*ONE WORD INTEGERS
*LIST ALL
*IOCS(2501 READER)
*IOCS(1132 PRINTER)
*IOCS(DISK)
C
C LOBSTER BEHAVIOUR PROGRAM 9 - A COMPARISON OF BOTH COMBATANTS TO
C   DETERMINE THE RESPONSE OF THE LOSER TO THE BEHAVIOUR OF THE WINNER
C      + THE RESPONSE OF THE WINNER TO THE BEHAVIOUR OF THE LOSER.
C   THIS PROGRAM ACCUMULATES FOR WINNERS + LOSERS UNTIL A * (CALL EXIT)
C         IS REACHED THE ACCUMULATED TOTALS ARE THEN PRINTED
C
      INTEGER X(30,245),NAME(15,9),NUM,A(965),TITLE(2,50),MATRX(15,16),E
     1ND(30),COL,M1(30),WIN(15,16),LOSE(15,16)
      DEFINE FILE 1(970,1,U,NN),2(970,1,U,NN),3(970,1,U,NN),4(970,1,U,NN
     1),5(970,1,U,NN),6(970,1,U,NN),7(970,1,U,NN),8(970,1,U,NN),9(970,1,
     2U,NN),10(970,1,U,NN),11(970,1,U,NN),12(970,1,U,NN),13(970,1,U,NN),
     314(970,1,U,NN),15(970,1,U,NN),16(970,1,U,NN),17(970,1,U,NN),18(970
     4,1,U,NN),19(970,1,U,NN),20(970,1,U,NN),21(970,1,U,NN),22(970,1,U,N
     5N),23(970,1,U,NN),24(970,1,U,NN),25(970,1,U,NN),26(970,1,U,NN)
      DEFINE FILE 27(970,1,U,NN),28(970,1,U,NN),29(970,1,U,NN),30(970,1,
     1U,NN)
      NN=1
      MM=8
C
C X=MATRIX CONTAINING BEHAVIOUR DATA OF BOTH ANIMALS FOR 1 MIN.
C NAME=NAMES OF THE BEHAVIOUR PATTERNS
C A=DATA FOR 1 BEHAVIOUR PATTERN THROUGHOUT THE WHOLE RECORDING PERIOD
C MATRX=ANALYSIS MATRIX CONTAINING RESPONSE OF ONE ANIMAL TO THE OTHER
C END=STOREAGE FOR 6'S INDICATING END OF DATA
C WIN=ACCUMULATOR FOR THE RESPONSES OF THE SECOND ANIMAL TO THE FIRST.
C LOSE=ACCUMULATES OR THE RESPONSES OF THE FIRST ANIMAL TO THE SECOND.
C
C        READ FIRST TITLE CARD AND CHECK FOR A STAR
C
      DO 101 I=1,15
      DO 101 L=1,16
      WIN(I,L)=0
  101 LOSE(I,L)=0
   50 READ(MM,1)(TITLE(1,I),I=1,50)
    1 FORMAT(50A1)
      IF(TITLE(1,1)-23616)2,60,2
C
C READ DATA OF FIRST ANIMAL AND RECORD IT ON THE DISC FILES
C
    2 DO 5 JJ=1,15
      DO 200 I=1,965
  200 A(I)=0
      J=2
      K=61
    3 READ(MM,4)(NAME(JJ,I),I=1,9),NUM,(A(I),I=J,K)
```

```
    4 FORMAT(9A1,I1,60I1)
      J=J+60
      K=K+60
      IF(NUM-5)3,5,3
    5 WRITE(JJ'1)(A(I),I=1,965)
C
C        READ SECOND TITLE CARD
C
      READ(MM,6)(TITLE(2,I),I=1,50)
    6 FORMAT(50A1)
C
C READ DATA OF SECOND ANIMAL AND RECORD IT ON THE DISC FILES
C
      DO 9 JJ=16,30
      DO 600 I=1,965
  600 A(I)=0
      J=2
      K=61
    7 READ(MM,8)NUM,(A(I),I=J,K)
    8 FORMAT(9X,I1,60I1)
      J=J+60
      K=K+60
      IF(NUM-5)7,9,7
    9 WRITE(JJ'1)(A(I),I=1,965)
C
C       ZERO STORAGE LOCATIONS
C
      LOSER=0
 9000 M=1
      DO 10 L=1,15
      DO 10 I=1,16
   10 MATRX(L,I)=0
      COL=0
      DO 100 JJ=1,30
  100 END(JJ)=0
   11 IF(LOSER-1)111,121,50
C
C PUT 1 MIN. OF DATA FOR BOTH ANIMALS BACK INTO CORE
C
  111 DO 12 JJ=1,30
      IF(END(JJ)-6)110,12,110
  110 READ(JJ'M)(X(JJ,I),I=1,245)
   12 CONTINUE
      GO TO 126
  121 M10=0
      DO 123 JJ=16,30
      M10=M10+1
      IF(END(M10)-6)122,123,122
  122 READ(JJ'M)(X(M10,I),I=1,245)
  123 CONTINUE
      DO 125 JJ=1,15
      M10=M10+1
      IF(END(M10)-6)124,125,124
  124 READ(JJ'M)(X(M10,I),I=1,245)
  125 CONTINUE
C
```

```
C RESPONSE ANALYSIS
C   COL=INDICATES THE BEHAVIOUR PATTERN TO WHICH THERE MAYBE A RESPONSE
C   NONE=INDICATES IF THERE IS ANY RESPONSE.
C   M1=398,INDICATES THAT THE PARTICULAR BEHAVIOUR PATTERN HAS ALREADY
C        BEEN RECORDED AS A RESPONSE.
C
  126 DO 33 J=2,241
C
C SEARCH FOR START OF A BEHAVIOUR PATTERN IN FIRST ANIMAL
C
      DO 13 I=1,15
      IF(END(I)-6)14,13,14
   13 CONTINUE
      GO TO 34
   14 JJ=0
      K=J-1
   15 JJ=JJ+1
      IF(END(JJ)-6)16,21,16
   16 IF(X(JJ,J)-6)18,17,18
   17 END(JJ)=6
      GO TO 21
   18 IF(X(JJ,J)-1)21,19,21
   19 IF(X(JJ,J)-X(JJ,K))21,21,20
   20 COL=JJ
      GO TO 22
   21 IF(JJ-15)15,33,33
C
C SEARCH FOR RESPONSE BY THE SECOND ANIMAL
C
   22 L=J-1
      DO 23 I=16,30
   23 M1(I)=0
      LLL=J+3
      NONE=0
   24 L=L+1
      N=L-1
      K1=0
      DO 32 KK=16,30
      K1=K1+1
      IF(M1(KK)-398)25,32,25
   25 IF(X(KK,L)-1)32,26,32
   26 IF(X(KK,L)-X(KK,N))32,28,27
   27 MATRX(COL,K1)=MATRX(COL,K1)+1
      M1(KK)=398
      NONE=1
      GO TO 32
   28 IF(L-J)32,29,32
   29 LL=J
      DO 30 I=1,4
      LL=LL+1
      IF(X(KK,LL)-1)32,30,32
   30 CONTINUE
      MATRX(COL,K1)=MATRX(COL,K1)+1
   31 M1(KK)=398
      NONE=1
   32 CONTINUE
```

```
      IF(L-LLL)24,320,320
  320 IF(NONE-1)321,21,21
  321 MATRX(COL,16)=MATRX(COL,16)+1
      GO TO 21
   33 CONTINUE
      M=M+240
      GO TO 11
C
C WHEN LOSER=0,THE DATA OF A NEW SOCIAL ENCOUNTER HAS BEEN READ AND
C            THIS IS THE RESPONSE ANALYSIS OF THE 2ND ANIMAL TO THE 1ST.
C WHEN LOSER=1,THIS IS THE RESPONSE ANALYSIS OF THE 1ST ANIMAL
C                TO THE 2ND.
C WHEN LOSER=2,BOTH RESPONSE ANALYSES HAVE BEEN COMPLETED.
C
   34 IF(LOSER-1)340,360,50
  340 WRITE(3,35)(TITLE(1,I),I=1,50)
   35 FORMAT('1',10X,50A1)
      WRITE(3,36)(TITLE(2,I),I=1,50)
   36 FORMAT(' ',10X,50A1 //20X,'RESPONSE OF THE LOSER TO THE BEHAVIOUR
     1OF THE WINNER' /1X,94('*')/' WINNERS        *',29X,'RESPONSE OF THE
     2LOSER',29X,'*')
      LOSER=1
C
C     THE RESPONSES OF THE 2ND ANIMALS ARE ACCUMULATED
C
      DO 53 L=1,15
      DO 53 I=1,16
   53 WIN(L,I)=WIN(L,I)+MATRX(L,I)
      GO TO 362
  360 WRITE(3,361)
  361 FORMAT('0',19X,'RESPONSE OF WINNER TO THE BEHAVIOUR OF THE LOSER'/
     11X,94('*')/' LOSERS        *',28X,'RESPONSE OF THE WINNER',29X,'*')
      LOSER=2
C
C     THE RESPONSES OF THE 1ST ANIMALS ARE ACCUMULATED.
C
      DO 55 L=1,15
      DO 55 I=1,16
   55 LOSE(L,I)=LOSE(L,I)+MATRX(L,I)
C
C PRINT OUT OF TABLES
C
  362 WRITE(3,37)
   37 FORMAT(5X,'BEHAVIOUR*',1X,'SC',1X,'*',1X,'PU',1X,'*',1X,'BK',1X,'*
     1',1X,'SW',1X,'*',1X,'RH',1X,'*',1X,'ES',1X,'*',1X,'JU',1X,'*',1X,'
     2AW',1X,'*',1X,'FO',1X,'*',1X,'AH',1X,'*',1X,'TH',1X,'*',1X,'BO',1X
     3,'*',1X,'WA',1X,'*',1X,'AP',1X,'*',1X,'RU',1X,'*NONE*'/1X,94('*'))
      DO 38 COL=1,15
   38 WRITE(3,39)(NAME(COL,I),I=1,9),(MATRX(COL,I),I=1,16)
   39 FORMAT(14X,'*',16(4X,'*')/1X,9A1,4X,'*',16(1X,I2,1X,'*'))
      WRITE(3,40)
   40 FORMAT(1X,94('*'))
      IF(LOSER-1)50,9000,50
C
C     ACCUMULATION IS PRINTED
C
```

```
   60 WRITE(3,61)
   61 FORMAT('1J.CHARLES SCRIVENER')
      WRITE(3,117)
  117 FORMAT('0',15X,'TOTALED RESPONSES OF THE LOSER TO THE BEHAVIOUR OF
     1 THE WINNER'/1X,94('*')/' WINNERS        *',29X,'RESPONSE OF THE LOS
     2ER',29X,'*')
      WRITE(3,37)
      DO 118 L=1,15
  118 WRITE(3,119)(NAME(L,I),I=1,9),(WIN(L,I),I=1,16)
  119 FORMAT(14X,'*',16(4X,'*')/1X,9A1,4X,'*',16(I4,'*'))
      WRITE(3,40)
      WRITE(3,61)
      WRITE(3,130)
  130 FORMAT('0',15X,'TOTALED RESPONSES OF THE WINNER TO THE BEHAVIOUR O
     1F THE LOSER'/1X,94('*')/'  LOSERS        *',29X,'RESPONSE OF THE WIN
     2NER',28X,'*')
      WRITE(3,37)
      DO 131 L=1,15
  131 WRITE(3,119)(NAME(L,I),I=1,9),(LOSE(L,I),I=1,16)
      WRITE(3,40)
      CALL EXIT
      END
// XEQ
```

Program - Lobster 10

This program determines the length in seconds of each period of continuously recorded behaviour and each period of non-social behaviour, for as many social encounters as the operator wishes to run or until the available storage becomes exhausted.

(1) Input

The same input data as for Lobster 8 and 9 can be used (Table 6). The data for both animals are processed together, so the data of a social encounter must be treated as a single data deck.

(2) Output

As the computer reads the data for a single encounter, it prints out the titles of both animals. Below, it prints the lengths in seconds of first the periods of social and second the periods of non-social behaviour in 15 column tables. The column in which they are printed corresponds to the minute in which they started. Finally the total of all periods is printed as an operational check. It should equal 900 seconds (15 minutes).

When the computer reads a card with a star in the first column instead of a new title, the program ends by printing out 3 tables consisting of 15 columns with each representing a minute in the encounters. Each position in a column of the first table contains the length in seconds of a period of continuously recorded behaviour, which started during the minute. The 15 total numbers of seconds of the periods, mean period lengths, sums of the squares of the periods, squares of the totals, and standard deviations of first the social and then non-social behaviour are printed in the second and third table.

Periods of recorded behaviour less than 2 seconds long were counted, but were considered part of a period of non-social behaviour. The total number for each minute was printed under the second table.

(3) Comments

(i) Thirty disc files are allocated for temporary storage of the input data.

(ii) A period of continuously recorded behaviour (a bout) ends, whenever more than 5 consecutive seconds elapse without any of the recorded activity having occurred.

(iii) Bouts of less than 3 seconds duration were excluded, because they were not considered agonistic bouts. The animals indicated that they had detected each others presence by showing an investigative behaviour pattern of 1 or 2 seconds duration, but no agonistic behaviour occurred.

(iv) A carriage control tape specifying 54 lines/page (6 lines/ inch) would be adequate for this program.

(v) Lobster 10's core requirements approach the maximum capacity of a 16 K machine.

(4) PROGRAM LISTING

```
// JOB
// FOR
*ONE WORD INTEGERS
*LIST ALL
*IOCS(2501 READER)
*IOCS(1132 PRINTER)
*IOCS(DISK)
C
C LOBSTER BEHAVIOUR PROGRAM 10 - DETERMINES LENGTHS OF THE AGONISTIC
C          BOUTS AND PERIODS OF NON-SOCIAL BEHAVIOUR + THE MINUTES
C          IN WHICH BOTH START.
C
C    X=STORAGE FOR INPUT DATA WHEN READ FROM DISC
C    A=STORAGE FOR DATA OF 1 BEHAVIOUR PATTERN BEFORE IT IS PLACED ON DISC
C    TITLE=TITLE OF THE ANIMAL + THE ENCOUNTER FROM WHICH THE DATA
C                   WAS OBTAINED
C    END=STORAGE FOR 6S,INDICATING THE END OF DATA FOR A PARTICULAR
C              BEHAVIOUR PATTERN.
C    COUNT=COUNTS THE NO. OF SECONDS EXAMINED BY THE COMPUTER.
C    DETEC=COUNTS THE NO. OF BOUTS OF 2 SECONDS OR LESS OCCURRING
C                    IN EACH MINUTE
C    STOR=MATRIX CONTAINING BOUT LENGTHS + THE MINUTE IN WHICH EACH STARTS
C    LINE=COUNTS THE NO. OF LINES BEING USED ON A PRINTED PAGE.
C    COL=TOTAL NO. OF BOUTS STARTING IN A MINUTE.
C    TOTAL=ACCUMULATES TOTAL BOUT LENGTHS FOR EACH MINUTE.
C    SSQ=SUMS OF SQUARES.
C    ABOUT=STORES BOUT LENGTHS + THE MINUTE IN WHICH EACH STARTS FOR
C           A SINGLE ENCOUNTER.
C    ROW=NO. OF BOUTS STARTING IN EACH MINUTE OF A SINGLE ENCOUNTER.
C    NUM2,TOT2,SSQ2,NONSO + ROW2 ARE USED FOR THE SAME PURPOSES AS COL,
C       TOTAL,SSQ,ABOUT + ROW IN DETERMINING THE LENGTHS OF PERIODS
C       OF NON-SOCIAL BEHAVIOUR.
C
      INTEGER X(30,120),A(960),TITLE(2,50),END(30),COUNT,DETEC(15),
     1STOR(15,200),BOUT,LINE,COL(15),TOTAL(15),ABOUT(15,5),ROW(15),
     2TOT2(16),NONSO(16,5),ROW2(16),NUM2(16),SECON
      REAL MEAN(15),SSQ(15),SSQ2(16)
      DEFINE FILE 1(970,1,U,NN),2(970,1,U,NN),3(970,1,U,NN),4(970,1,U,NN
     1),5(970,1,U,NN),6(970,1,U,NN),7(970,1,U,NN),8(970,1,U,NN),9(970,1,
     2U,NN),10(970,1,U,NN),11(970,1,U,NN),12(970,1,U,NN),13(970,1,U,NN),
     314(970,1,U,NN),15(970,1,U,NN),16(970,1,U,NN),17(970,1,U,NN),18(970
     4,1,U,NN),19(970,1,U,NN),20(970,1,U,NN),21(970,1,U,NN),22(970,1,U,N
     5N),23(970,1,U,NN),24(970,1,U,NN),25(970,1,U,NN),26(970,1,U,NN)
      DEFINE FILE 27(970,1,U,NN),28(970,1,U,NN),29(970,1,U,NN),30(970,1,
     1U,NN)
      NN=1
      II=8
      WRITE(3,43)
   43 FORMAT('1')
      DO 44 L=1,15
      COL(L)=0
      NUM2(L)=0
      TOTAL(L)=0
```

```
      TOT2(L)=0
      SSQ(L)=0.0
      SSQ2(L)=0.0
      DETEC(L)=0
      DO 44 I=1,200
   44 STOR(L,I)=0
      LINE=0
C
C  READ DATA OF FIRST ANIMAL + STORE IT ON DISC.
C
   50 READ(II,1)(TITLE(1,I),I=1,50)
    1 FORMAT(50A1)
      IF(TITLE(1,1)-23616)2,60,2
    2 DO 5 JJ=1,15
      J=1
      K=60
    3 READ(II,4)NUM,(A(I),I=J,K)
    4 FORMAT(9X,I1,60I1)
      J=J+60
      K=K+60
      IF(NUM-5)3,5,3
    5 WRITE(JJ'1)(A(I),I=1,960)
C
C  READ DATA OF SECOND ANIMAL + STORE IT ON DISC.
C
      READ(II,6)(TITLE(2,I),I=1,50)
    6 FORMAT(50A1)
      DO 9 JJ=16,30
      J=1
      K=60
    7 READ(II,8)NUM,(A(I),I=J,K)
    8 FORMAT(9X,I1,60I1)
      J=J+60
      K=K+60
      IF(NUM-5)7,9,7
    9 WRITE(JJ'1)(A(I),I=1,960)
      M=1
C
C  PRINT OUT TITLES.
C
      IF(LINE-46)92,92,90
   90 WRITE(3,91)
   91 FORMAT('1')
      LINE=0
   92 WRITE(3,10)(TITLE(1,I),I=1,50),(TITLE(2,I),I=1,50)
   10 FORMAT('0',10X,50A1/11X,50A1)
      LINE=LINE+3
      DO 11 L=1,30
   11 END(L)=0
      DO 110 L=1,15
      ROW(L)=0
      ROW2(L)=0
      DO 110 I=1,5
      ABOUT(L,I)=0
  110 NONSO(L,I)=0
      MINUT=0
```

```
      JJJ=0
      IB=0
      BOUT=0
      NO=0
      MB2=16
      SECON=0
C
C  BOUT LENGTH ANALYSIS.
C     IB=INDICATES WHETHER A BOUT IS IN PROGRESS.
C     JJJ=INDICATES WHETHER EITHER ANIMAL IS SHOWING ANY RECORDED
C       BEHAVIOUR DURING THE SECOND BEING EXAMINED.
C     NO=COUNTS SECONDS IN WHICH NO BEHAVIOUR WAS RECORDED.
C    BOUT=ACCUMULATES A BOUT LENGTH.
C    SECON=COUNTS SECONDS EXAMINED.
C
 6000 DO 13 L=1,30
      IF(END(L)-6)12,13,12
   12 READ(L'M)(X(L,I),I=1,120)
   13 CONTINUE
      COUNT=0
      MINUT=MINUT+1
      DO 33 I=1,120
      DO 14 J=1,30
      IF(END(J)-6)15,14,15
   14 CONTINUE
      GO TO 34
   15 L=0
   16 L=L+1
      IF(END(L)-6)17,23,17
   17 IF(X(L,I)-6)19,18,19
   18 END(L)=6
      GO TO 23
   19 IF(JJJ-26389)190,23,190
  190 IF(X(L,I)-1)23,20,23
   20 IF(IB-999)21,22,21
   21 IB=999
      ROW2(MB2)=ROW2(MB2)+1
      KK=ROW2(MB2)
      NONSO(MB2,KK)=NO
      TOT2(MB2)=TOT2(MB2)+NO
      SSQ2(MB2)=SSQ2(MB2)+FLOAT(NO)**2
      NUM2(MB2)=NUM2(MB2)+1
      MB=MINUT
      NO=0
      BOUT=0
   22 JJJ=26389
      IF(NO-5)220,221,221
  220 BOUT=BOUT+NO
  221 BOUT=BOUT+1
      NO=0
   23 IF(L-30)16,24,24
   24 COUNT=COUNT+1
      SECON=SECON+1
      IF(COUNT-60)241,240,241
  240 MINUT=MINUT+1
  241 IF(JJJ-26389)25,33,25
```

```
   25 NO=NO+1
      IF(NO-5)33,26,33
   26 IF(IB-999)33,260,33
  260 IF(BOUT-2)261,261,262
C
C  IGNORING BOUTS OF UNDER 3 SECONDS DURATION.
C
  261 DETEC(MB)=DETEC(MB)+1
      IF(MB2-16)2611,2610,2611
 2610 MB2=1
      GO TO 2612
 2611 NUM2(MB2)=NUM2(MB2)-1
      ROW2(MB2)=ROW2(MB2)-1
 2612 NO=NO+NONSO(MB2,KK)+BOUT
      TOT2(MB2)=TOT2(MB2)-NONSO(MB2,KK)
      SSQ2(MB2)=SSQ2(MB2)-FLOAT(NONSO(MB2,KK))**2
      NONSO(MB2,KK)=0
      GO TO 27
  262 COL(MB)=COL(MB)+1
      NUM=COL(MB)
      STOR(MB,NUM)=BOUT
      ROW(MB)=ROW(MB)+1
      K=ROW(MB)
      ABOUT(MB,K)=BOUT
      TOTAL(MB)=TOTAL(MB)+BOUT
      SSQ(MB)=SSQ(MB)+FLOAT(BOUT)**2
      IF(COUNT-5)263,266,264
  263 MB2=MINUT-1
      GO TO 267
  264 IF(COUNT-60)266,263,265
  265 IF(COUNT-65)263,266,266
  266 MB2=MINUT
  267 IF(COL(MB)-200)27,60,60
   27 IB=0
   33 JJJ=0
      M=M+120
      GO TO 6000
C
C  PLACE FINAL BOUT LENGTH OF THE SOCIAL ENCOUNTER IN STOR + ABOUT OR
C        FINAL PERIOD OF NON-SOCIAL BEHAVIOUR IN NONSO.
C
   34 IF(IB-999)36,35,36
   35 IF(BOUT-2)350,350,351
  350 DETEC(MB)=DETEC(MB)+1
      NO=NO+NONSO(MB2,KK)+BOUT
      TOT2(MB2)=TOT2(MB2)-NONSO(MB2,KK)
      SSQ2(MB2)=SSQ2(MB2)-FLOAT(NONSO(MB2,KK))**2
      NUM2(MB2)=NUM2(MB2)-1
      NONSO(MB2,KK)=0
      ROW2(MB2)=ROW2(MB2)-1
      GO TO 36
  351 COL(MB)=COL(MB)+1
      NUM=COL(MB)
      STOR(MB,NUM)=BOUT
      ROW(MB)=ROW(MB)+1
      K=ROW(MB)
```

```
      ABOUT(MB,K)=BOUT
      TOTAL(MB)=TOTAL(MB)+BOUT
      SSQ(MB)=SSQ(MB)+FLOAT(BOUT)**2
      MB2=MINUT
   36 NO=NO+(900-SECON)
      IF(NO-1)361,360,360
  360 ROW2(MB2)=ROW2(MB2)+1
      KK=ROW2(MB2)
      NONSO(MB2,KK)=NO
      TOT2(MB2)=TOT2(MB2)+NO
      SSQ2(MB2)=SSQ2(MB2)+FLOAT(NO)**2
      NUM2(MB2)=NUM2(MB2)+1
C
C  PRINT BOUT LENGTHS + NON-SOCIAL BEHAVIOUR PERIOD LENGTHS OF ENCOUNTER
C
  361 MAX=0
      MAX2=0
      DO 365 L=1,15
      IF(ROW(L)-MAX)363,363,362
  362 MAX=ROW(L)
  363 IF(ROW2(L)-MAX2)365,365,364
  364 MAX2=ROW2(L)
  365 CONTINUE
      DO 366 I=1,MAX
      WRITE(3,45)(ABOUT(L,I),L=1,15)
  366 LINE=LINE+1
      WRITE(3,3650)
 3650 FORMAT(' ')
      DO 368 I=1,MAX2
      WRITE(3,367)(NONSO(L,I),L=1,15)
  367 FORMAT(' ',15('+ ',I3,2X),'+')
  368 LINE=LINE+1
      K=0
      DO 369 L=1,15
      DO 369 I=1,5
  369 K=K+ABOUT(L,I)+NONSO(L,I)
      WRITE(3,370)K
  370 FORMAT(20X,I4)
      LINE=LINE+2
      GO TO 50
C
C  PRINT BOUT LENGTHS,+ CALCULATE SUMS OF SQUARES,SQUARES OF SUMS,
C        MEANS,+ STANDARD DEVIATIONS FOR AGONISTIC BOUTS + PERIODS
C        OF NON-SOCIAL BEHAVIOUR.
C
   60 WRITE(3,37)(L,L=1,15)
   37 FORMAT('1',20X,'LENGTH OF EACH AGONISTIC BOUT AND THE MINUTE IN WH
     1ICH IT STARTED'//1X,15('*MIN.',I2),'*'/1X,53('**'))
      MAX=0
      LINE=0
      DO 39 L=1,15
      IF(COL(L)-MAX)39,39,38
   38 MAX=COL(L)
   39 CONTINUE
      DO 46 I=1,MAX
      IF(LINE-50)41,40,40
```

```
   40 WRITE(3,37)(L,L=1,15)
      LINE=0
   41 WRITE(3,45)(STOR(L,I),L=1,15)
   45 FORMAT(1X,15('* ',I3,2X),'*')
   46 LINE=LINE+1
      IF(LINE-26)461,460,460
  460 WRITE(3,37)(L,L=1,15)
  461 WRITE(3,47)(TOTAL(L),L=1,15)
   47 FORMAT(//40X,'TOTALED VALUES'/1X,15('*',I6),'*')
      WRITE(3,470)(COL(L),L=1,15)
  470 FORMAT(/40X,'NUMBER OF VALUES'/1X,15('* ',I3,2X),'*')
      DO 48 L=1,15
   48 MEAN(L)=FLOAT(TOTAL(L))/FLOAT(COL(L))
      WRITE(3,49)(MEAN(L),L=1,15)
   49 FORMAT(/40X,'MEAN VALUES'/1X,15('*',F6.2),'*')
      WRITE(3,51)(SSQ(L),L=1,15,2),(SSQ(L),L=2,15,2)
   51 FORMAT(/40X,'SUMS OF THE SQUARES'/1X,'*',8(F10.0,4X)/1X,'*',7X,7(F
     110.0,4X))
      DO 52 L=1,15
   52 MEAN(L)=FLOAT(TOTAL(L))**2
      WRITE(3,53)(MEAN(L),L=1,15,2),(MEAN(L),L=2,15,2)
   53 FORMAT(/40X,'SQUARES OF THE SUMS'/1X,'*',8(F10.0,4X)/1X,'*',7X,7(F
     1 10.0,4X))
      DO 54 L=1,15
   54 MEAN(L)=SQRT((SSQ(L)-MEAN(L)/FLOAT(COL(L)))/(FLOAT(COL(L))-1.0))
      WRITE(3,55)(MEAN(L),L=1,15)
   55 FORMAT(/40X,'STANDARD DEVIATION'/1X,'*',15F7.2)
      WRITE(3,56)(DETEC(L),L=1,15)
   56 FORMAT(/30X,'NUMBER OF BOUTS OF LESS THAN 3 SECONDS'/1X,'*',
     115(I4,'  *'))
      WRITE(3,57)(L,L=1,15)
   57 FORMAT('1',20X,'SUMMARIZING STATISTICS OF THE PERIODS OF NON-SOCIA
     1L BEHAVIOUR'//1X,15('*MIN.',I2),'*'/1X,53('**'))
      WRITE(3,47)(TOT2(L),L=1,15)
      WRITE(3,470)(NUM2(L),L=1,15)
      DO 58 L=1,15
   58 MEAN(L)=FLOAT(TOT2(L))/FLOAT(NUM2(L))
      WRITE(3,49)(MEAN(L),L=1,15)
      WRITE(3,51)(SSQ2(L),L=1,15,2),(SSQ2(L),L=2,15,2)
      DO 59 L=1,15
   59 MEAN(L)=FLOAT(TOT2(L))**2
      WRITE(3,53)(MEAN(L),L=1,15,2),(MEAN(L),L=2,15,2)
      DO 61 L=1,15
   61 MEAN(L)=SQRT((SSQ2(L)-MEAN(L)/FLOAT(NUM2(L)))/(FLOAT(NUM2(L))-1.0)
     1)
      WRITE(3,55)(MEAN(L),L=1,15)
      CALL EXIT
      END
// XEQ
```

APPENDIX II

Three programs or variations of them were used for plotting graphs, the chi-square analysis of male and female sequences, and the analysis of response frequencies. They were written in 1130 FORTRAN IV and were developed for use on I.B.M. 1130 or 360 systems. The input was read from cards.

LOBSTER 15

This is the plotting program used for drawing the mean frequency histograms. It was designed for a system using a I.B.M. 1627 plotter, but it could be adapted with few alterations to any plotting system with the basic 1130 routines SCALF, FGRID, FPLOT, and FCHAR.

First the computer reads in the names of 15 behaviour patterns. These are punched in the first 9 columns of 15 cards (1 behaviour pattern/card). The 16th data card contains the title of the 15 graphs. This is punched in columns 1-40. The following 30 cards contain the mean frequency data for the 15 behaviour patterns. The first and other odd cards contain the data of winners, while the second and other even cards contain the data of losers. The first 5 columns are not read, but columns 6-80 contain 15 numbers with a 5 column field per number. These are real numbers with 3 decimal places (e.g. 2.136 or 1.500). Example input is shown in table A2.1. The computer plots 30 histograms, 2 histograms to a graph, and 4 graphs to a page. The histograms of winners are drawn with solid lines, while those of losers are composed of broken lines (examples fig. 17-20).

TABLE A2.1. A LISTING OF INPUT DATA FOR LOBSTER 15.

```
12345678910123456789201234567892012345678940123456789501234567896012345678970123456789 80
PUSH
ANT. WHIP
JUMP
BOX
SCISSOR
SIDE-WAYS
ABD. FLEX
RUN
BACK
WALK
FOLLOW
RUSH
APPROACH
THREAT
ANT.POINT
FEMALE VS.  FEMALE ENCOUNTER TOTAL=60
PUSH 0.6100.7960.7280.5080.6270.4740.3550.3720.4060.3220.2200.2200.0840.0500.169
PUSH  .644 .830 .830 .542 .677 .491 .338 .474 .457 .372 .220 .203 .084 .050 .152
ANT.W .254 .525 .372 .305 .440 .322 .406 .305 .254 .203 .118 .135 .033 .016 .067
ANT.W .220 .389 .372 .406 .237 .288 .355 .237 .186 .254 .067 .050 .050 .101 .016
JUMP 0.1860.237 .338 .237 .305 .118 .050 .135 .152 .084 .101 .152 .050 .033 .118
JUMP  .220 .305 .440 .186 .355 .220 .101 .220 .254 .220 .101 .101 .016 .    .084
BOX   .050 .101 .050 .067 .016 .    .016 .    .    .    .    .    .    .    .
BOX   .016 .118 .050 .067 .    .033 .    .    .    .    .    .    .016 .    .
SCISS0.3050.2540.3050.2880.4230.1690.2710.2710.2710.2880.2030.2710.2030.2030.135
```

TABLE A2.1. CONTINUED.

SCISS		.186	.152	.203	.101	.186	.118	.084	.118	.050	.084	.016	.016	.033	.016	.
SIDE-	0	.0000	.0160	.0160	.0160	.0000	.0330	.0000	.0000	.0000	.0160	.0000	.0000	.0000	.0000	.000
SIDE-		.050	.	.050	.152	.186	.118	.169	.152	.152	.305	.135	.101	.152	.203	.186
ESCAP	0	.0330	.0670	.0160	.0000	.0000	.0000	.0000	.0000	.	.	.	.	.	.	.
ESCAP		.203	.203	.237	.288	.355	.186	.355	.322	.288	.322	.271	.508	.508	.372	.440
RUN		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
RUN		.016	.135	.050	.033	.220	.084	.067	.135	.169	.169	.101	.118	.050	.101	.152
BACK	0	.2540	.3380	.2030	.4400	.3220	.2370	.3050	.2200	.3380	.2200	.2540	.2200	.1690	.2710	.135
BACK		.745	.847	.7451	.0671	.135	.9491	.237	.9831	.0501	.2031	.2031	.2881	.4911	.3721	.220
WALK		.169	.050	.067	.067	.033	.016	.016	.033	.050	.050	.084	.050	.050	.101	.067
WALK		.491	.305	.372	.355	.593	.474	.305	.457	.423	.406	.474	.440	.423	.559	.525
FOLLO		.610	.627	.610	.694	.881	.779	.915	.966	.847	.983	.9491	.1521	.135	.983	.847
FOLLO		.050	.050	.050	.135	.067	.033	.067	.084	.152	.067	.118	.050	.	.067	.
RUSH	0	.2540	.1860	.1520	.2030	.2880	.1180	.2540	.2200	.2200	.2880	.2710	.4060	.3890	.2200	.254
RUSH		.033	.033	.016	.	.	.016	.	.016	.	.	.	.	.	.016	.
APPRO		.610	.508	.322	.610	.677	.627	.661	.440	.576	.762	.694	.576	.762	.711	.627
APPRO		.457	.372	.406	.305	.372	.338	.338	.186	.305	.271	.220	.271	.237	.220	.322
THREA	1	.1521	.2031	.0331	.0841	.2711	. 1	.3891	.0841	.2201	.4231	.0671	.0671	.069	.932	.966
THREA		.983	.644	.576	.338	.440	.593	.644	.338	.474	.423	.322	.186	.118	.169	.288
ANT.P	2	.0841	.2541	.3221	.5761	.5761	.3551	.4061	.4061	.4571	.7621	.8131	.5931	.9661	.7281	.932
ANT.P	2	.3051	.3051	.2031	.1351	.2711	.1521	.084	.966	.9661	.2541	.3891	.3051	.3551	.3381	.355

Variations of this program were used to plot the one minute response times and the mean one minute response times.

PROGRAM LISTING

```
// JOB
// FOR
*ONE WORD INTEGERS
*LIST ALL
*IOCS(2501 READER)
*IOCS(1132 PRINTER)
*IOCS(PLOTTER)
C
C    LOBSTER BEHAVIOUR PROGRAM 15   , PLOTTING AVERAGE FREQUENCIES
C
      INTEGER GRAPH,TITLE(40),NAME(15,9)
      DIMENSION X(15,16),XI(15,16)
      II=8
      DO 1 I=1,15
      XI(I,16)=0.0
    1 X(I,16)=0.0
      DO 42 L=1,15
   42 READ(II,43)(NAME(L,I),I=1,9)
   43 FORMAT(9A1)
      READ(II,2)(TITLE(I),I=1,40)
    2 FORMAT(40A1)
      DO 3 L=1,15
      READ(II,4)(X(L,I),I=1,15)
    3 READ(II,4)(XI(L,I),I=1,15)
    4 FORMAT(5X,15F5.3)
C
C  PLOT AVERAGE 1 MINUTE FREQUENCIES FOR THE BEHAVIOUR PATTERNS
C      DRAWING AND LABELLING GRIDS
C
      PI=3.14159
      T=3.*PI/2.
      GRAPH=0
      ICOUT=0
    7 GRAPH=GRAPH+1
      ICOUT=ICOUT+1
      CALL SCALF(1.6,0.2,0.0,0.0)
      CALL FGRID(0,0.0,0.0,0.5,5)
      CALL FGRID(3,0.0,0.0,2.0,8)
    8 X1=-0.12
      Y=-1.5
      DO 10 I=2,16,2
      CALL FCHAR(X1,Y,0.1,0.1,T)
      WRITE(7,9)I
    9 FORMAT(I2)
   10 Y=Y-2.0
      IF(ICOUT-2)101,12,100
  100 IF(ICOUT-4)101,12,12
```

```
101 CALL FCHAR(-0.25,-4.,0.1,0.1,T)
    WRITE(7,11)
 11 FORMAT('TIME IN MINUTES')
 12 X1=0.48
    Y=2.0
    CO=0.5
    DO 14 I=1,5
    CALL FCHAR(X1,Y,0.1,0.1,T)
    WRITE(7,13)CO
 13 FORMAT(F3.1)
    CO=CO+0.5
 14 X1=X1+0.5
    IF(ICOUT-2)140,140,16
140 CALL FCHAR(0.4,2.4,0.1,0.1,0.0)
    WRITE(7,15)
 15 FORMAT('AVERAGE FREQUENCY EACH MINUTE')
 16 CALL FCHAR(2.25,-7.,0.12,0.12,T)
    WRITE(7,17)(NAME(GRAPH,I),I=1,9)
 17 FORMAT(9A1)
    IF(ICOUT-2)19,18,19
 18 CALL FCHAR(2.75,-4.,0.12,0.12,T)
    WRITE(7,180)(TITLE(I),I=1,40)
180 FORMAT(40A1)
C
C   DRAWING THE HISTOGRAM OF THE WINNER
C
 19 RX=X(GRAPH,1)
    Y=0.0
    CALL FPLOT(+5,RX,0.0)
    DO 20 L=1,15
    Y=Y-1.0
    JJ=L+1
    CALL FPLOT(+2,RX,Y)
    RX=X(GRAPH,JJ)
    CALL FPLOT(0,RX,Y)
 20 CONTINUE
C
C   DRAWING THE HISTOGRAM OF THE LOSER
C
    RX=XI(GRAPH,1)
    Y=0.0
    CALL FPLOT(+5,RX,Y)
    DO 207 L=1,15
    Y=Y-0.3
    CALL FPLOT(+2,RX,Y)
    Y=Y-0.4
    CALL FPLOT(+5,RX,Y)
    Y=Y-0.3
    CALL FPLOT(2,RX,Y)
    JJ=L+1
    X6=XI(GRAPH,JJ)
```

```
      IF(RX-X6)203,207,200
  200 DO 202 I=1,30
      IF (X6-RX-0.1)206,201,201
  201 RX=RX-0.05
      CALL FPLOT(+2,RX,Y)
      RX=RX-0.05
  202 CALL FPLOT(+5,RX,Y)
  203 DO 205 I=1,30
      IF(RX-X6-0.1)206,204,204
  204 RX=RX+0.05
      CALL FPLOT(+2,RX,Y)
      RX=RX+0.05
  205 CALL FPLOT(+5,RX,Y)
  206 RX=X6
  207 CALL FPLOT(+2,RX,Y)
      IF(ICOUT-2)21,22,23
   21 CALL FPLOT(+5,2.75,0.0)
      GO TO 25
   22 CALL FPLOT(+5,-2.75,-18.0)
      GO TO 25
   23 IF(ICOUT-4)21,24,24
   24 CALL FPLOT(+5,4.5,18.0)
      ICOUT=0
   25 IF(GRAPH-15)7,26,26
   26 CALL EXIT
      END
// XEQ
```

LOBSTER 17

This program was used to calculate chi-square values from 2 x 2 tables comparing male and female sequence frequencies. As listed, the program runs on a 360 Watfiv terminal, but it should run on any 1130 or 360 system with only minor changes. Variables are used for the logical unit numbers indicating input-output devices, so that only 2 statements have to be changed to alter the constants. All calculations are done in double precision.

The computer accumulates 4 sets of 15 by 15 frequency matrices. The 1st, 2nd, 3rd and 4th matrix contains the sequence frequencies of male winners and losers and female winners and losers respectively. Each sequence frequency and the total of the other 14 frequencies in the matrix row, of male and female winners are compared in a 2 x 2 contingency table.

	sequence frequency	total of other frequencies
male winner	a	b
female winner	c	d

The chi-square is calculated from the short cut formula

$$X^2 = \frac{(ad - bc)^2 n}{(a+b)(c+d)(a+c)(b+d)}$$

where n is the table total (Sokal and Rohlf 1969 p. 589). This is repeated for all 225 positions in the matrices of losing males and females.

Columns 1-9 of the first 15 data cards contain the names of the 15 behaviour patterns (one behaviour pattern/card). The 80 columns of the next 4 cards contain the titles of matrices 1-4. The remaining cards are sets of array data. Each set is composed of 16 cards. The first card has title information punched in columns 1-50. Characters in columns 51 and 52 indicate whether the following data is from males or females and winners or losers respectively ("M" if male, "F" if female, "L" if loser, "W" if winner). Each of the remaining cards in the set contains a row of a 15 by 15 array. Columns 1-5 are used for labelling and columns 6-80 contain the frequencies with a 5 column field per frequency. Example input of the first 19 cards and one data set of 16 cards are shown in table A2.2. The computer then adds this array to the appropriate matrix. When a star is read instead of a new data set title, the computer stops reading.

Tables 3 and 4 are examples of the chi-square tables that were printed by the program.

TABLE A2.2. A LISTING OF INPUT DATA FOR LOBSTER 17.

SCISSOR
PUSH
BACK
SIDE-WAYS
RUSH
ABD. FLEX
JUMP
ANT.WHIP
FOLLOW
APPROACH
THREAT
BOX
WALK
ANT.PIONT
RUN
TOTALLED SEQUENCE FRQUENCIES OF MALE WINNERS
TOTALLED SEQUENCE FREQUENCIES OF MALE LOSERS
TOTALLED SEQUENCE FREQUENCIES OF FEMALE WINNERS
TOTALLED SEQUENCE FREQUENCIES OF FEMALE LOSERS
MALE LOSERS FEMALE / MALE ENCOUNTERS TOTAL = 35ML

ML4SC	0	4	0	0	0	0	25	0	1	0	1	0	0	0	0
ML4PU	25	3	8	0	0	1	21	18	0	0	38	4	0	1	0
ML4BK	0	8	49	35	0	134	1	1	4	15	20	7	41	201	9
ML4SW	0	0	4	0	0	4	0	0	0	2	0	0	12	16	9
ML4RH	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ML4AB	0	0	161	0	0	4	1	0	0	1	1	0	1	14	0
ML4JU	0	33	5	0	0	1	0	0	0	0	15	0	0	1	0
ML4WP	0	7	15	0	0	0	2	16	7	3	11	1	0	2	0
ML4FO	1	7	6	0	1	1	1	8	2	2	5	0	0	17	0
ML4PP	0	8	57	0	1	1	0	1	11	4	50	3	7	55	0
ML4TH	2	27	60	3	0	6	0	17	18	11	3	2	4	14	0
ML4BO	1	7	1	0	0	0	1	0	0	1	0	2	0	2	0
ML4WK	0	0	8	1	0	10	1	0	0	2	5	0	11	148	26
ML4PT	0	2	165	8	0	16	2	3	8	154	22	1	97	148	29
ML4RU	0	0	0	0	0	5	0	0	0	2	0	1	51	14	2

PROGRAM LISTING

```
$JOB (SCRIVENER,J.C./U0148/050),PAGES=9,TIME=120
C
C   CHI-SQUARE ANALYSIS OF MALE + FEMALE SEQUENCE FREQUENCIES.
C
      DATA LOSER,MULT,MALE/'L','*','M'/
      INTEGER TITLE(16,50),SEX,STAND,X(15,15),ARRAY(4,15,15),
     1SAVE(4,15),LLL(4),NAME(4,80),BEH(15,9)
      DOUBLE PRECISION A,B,C,D,T,X2(15,15)
      II=5
      JJ=6
      DO 2 I=1,4
      LLL(I)=0
      DO 2 L=1,15
    2 SAVE(I,L)=0
      DO 201 L=1,15
      DO 200 J=1,15
      DO 200 I=1,4
  200 ARRAY(I,L,J)=0
  201 READ(II,3)(BEH(L,I),I=1,9)
    3 FORMAT(9A1)
      DO 4 I=1,4
    4 READ(II,5)(NAME(I,J),J=1,80)
      DO 20 I=1,16
      READ(II,5)(TITLE(I,J),J=1,50),SEX,STAND
    5 FORMAT(80A1)
      IF(MULT-TITLE(I,1))6,21,6
    6 DO 7 L=1,15
    7 READ(II,8)(X(L,J),J=1,15)
    8 FORMAT(5X,15(2X,I3))
      IF(SEX-MALE)9,12,9
    9 IF(LOSER-STAND)10,11,10
   10 NUM=3
      GO TO 15
   11 NUM=4
      GO TO 15
   12 IF(LOSER-STAND)13,14,13
   13 NUM=1
      GO TO 15
   14 NUM=2
   15 DO 16 L=1,15
      DO 16 J=1,15
   16 ARRAY(NUM,L,J)=ARRAY(NUM,L,J)+X(L,J)
      LLL(NUM)=LLL(NUM)+1
      K=LLL(NUM)
   20 SAVE(NUM,K)=I
   21 DO 30 I=1,4
      WRITE(JJ,22)
```

```
   22 FORMAT('1')
      DO 24 L=1,15
      IF(SAVE(I,L)-1)26,23,23
   23 K=SAVE(I,L)
   24 WRITE(JJ,25)(TITLE(K,J),J=1,50)
   25 FORMAT(11X,50A1)
   26 WRITE(JJ,27)(NAME(I,J),J=1,80)
   27 FORMAT('0',17X,80A1/1X,87('*')/1X,'*INITIAL    *',27X,'SUBSEQUENT B
     1EHAVIOUR',T88,'*'/1X,'* BEHAVIOUR* SC * PU * BK * SW * RH * AF * J
     2U * AW * FO * AH * TH * BO * WA * AP * RU *'/1X,87('*'))
      DO 28 L=1,15
   28 WRITE(JJ,29)(BEH(L,J),J=1,9),(ARRAY(I,L,J),J=1,15)
   29 FORMAT(1X,'*',10X,'*',15(4X,'*')/1X,'*',1X,9A1,'*',15(I4,'*'))
   30 WRITE(JJ,31)
   31 FORMAT(1X,87('*'))
      DO 40 I=1,2
      M2=I+2
      DO 36 L=1,15
      TOT1=0.0
      TOT2=0.0
      DO 35 J=1,15
      TOT1=TOT1+FLOAT(ARRAY(I,L,J))
   35 TOT2=TOT2+FLOAT(ARRAY(M2,L,J))
      T=TOT1+TOT2
      DO 36 J=1,15
      IF(ARRAY(I,L,J)-5)351,350,350
  350 IF(ARRAY(M2,L,J)-5)351,360,360
  351 X2(L,J)=0.00
      GO TO 36
  360 A=FLOAT(ARRAY(I,L,J))
      C=FLOAT(ARRAY(M2,L,J))
      B=TOT1-FLOAT(ARRAY(I,L,J))
      D=TOT2-FLOAT(ARRAY(M2,L,J))
      X2(L,J)=(((A*D)-(B*C))**2)*T/((A+B)*(C+D)*(A+C)*(B+D))
   36 CONTINUE
      WRITE(JJ,37)(NAME(I,J),J=1,80),(NAME(M2,J),J=1,80)
   37 FORMAT('1',17X,80A1/18X,80A1//10X,'CHI-SQUARE VALUES OBTAINED BY C
     1OMPARING MALE + FEMALE SEQUENCE FREQUENCIES'/1X,117('$')/1X,'$INIT
     2IAL    $',34X,'SUBSEQUENT BEHAVIOUR',T118,'$'/1X,'$ BEHAVIOURS  SC
     3 $  PU  $  BK  $  SW  $  RH  $  AF  $  JU  $  AW  $  FO  $  AH  $
     4 TH  $  BO  $  WA  $  AP  $  RU  $'/1X,117('$'))
      DO 38 L=1,15
   38 WRITE(JJ,39)(BEH(L,J),J=1,9),(X2(L,J),J=1,15)
   39 FORMAT(1X,'$',10X,'$',15(6X,'$')/1X,'$',1X,9A1,'$',15(F5.2,' $'))
   40 WRITE(JJ,41)
   41 FORMAT(1X,117('$'))
      CALL EXIT
      END
$DATA
```

LOBSTER 18

This program was used to tabulate the response frequencies, to calculate chi-square values from 2 x 16 tables comparing the distribution of response frequencies following each display with the distribution of commonness of the responses, and to calculate expected frequencies and information theory statistics. As listed, the program runs on a 360 Watfiv terminal; uses variable locations for the logical unit number constants; and does all complex calculations in double precision.

First the computer accumulates a 15 by 16 array of response frequencies. Then it calculates the frequencies that would be expected to occur if the initial display has no effect on the response, by multiplying the total number of responses to the display (row total) by the total number of times the response was observed (column total) divided by total number of responses observed (array total). The calculations are done in floating point arithmetic and then rounded to the nearest integer. Next it calculates the chi-squares measuring the degree to which the distribution of responses following each initial display is independent of that initial display. This is accomplished by comparing the distribution of column totals (distribution of the commonness of responses) with each distribution following an initial act, using the formula

$$X^2 = \frac{\sum_i (nkj^2/ni.) - n.j^2/n..}{n.1n.2/n..^2}$$

where $\sum_i (nij^2/ni.)$ = the sum of each response frequency in a row squared, divided by itself plus its column total, n.j and n.1 = the row total, n.2 = the array total and n.. = the array total + the row total (Steele and Torrie 1960 p. 371). Finally the computer calculates the information theory statistics using the formulas shown in the text of the thesis (p.110 and 111).

Columns 1-9 of the first 15 data cards contain the names of the behaviour patterns (1 behaviour pattern/card). The 80 columns of the 16th card contain the title of the array. The remaining cards are sets of 15 by 16 matrix data which the array accumulates. Each set consists of 16 data cards. Columns 1-80 of the first card in each set describes origin of the matrix data. Each of the remaining 15 cards contains a row of the matrix. Columns 1 and 2 are used to label the card, while columns 3-80 contain 16 frequencies in 16 fields of 3 columns each (example input table A2.3). A star in the first column of a data set title card indicates that the last data set has been read and accumulated in the array.

Tables 13 and 14 are examples of the output.

References

Sokal R. R. and Rohlf F. J. - Biometry: The principles and practice of statistics in biological research. W. H. Freeman and Company 1969, p. 776.

Steel R. G. D. and Torrie J. H. - Principles and Procedures of Statistics. McGraw-Hill Book Co. 1960, p. 481.

TABLE A2.3. LISTING OF SAMPLE INPUT DATA REQUIRED FOR LOBSTER 18.

SCISSOR
PUSH
BACK
SIDE-WAYS
RUSH
ABD. FLEX
JUMP
ANT. WHIP
FOLLOW
APPROACH
THREAT
BOX
WALK
ANT.POINT
RUN
TOTALLED RESPONSES OF ALL ENCOUNTERS INCLUDING BOTH WINNERS LOSERS
RESPONSE OF MALE WINNERS FROM MALE / FEMALE ENCOUNTERS NO. 2 TOTAL = 65

SC	0	5	1	0	0	1	2	0	0	0	0	0	0	0	0	1
PU	3	46	0	0	0	0	4	4	0	0	5	2	0	0	0	0
BA	39	2	12	0	59	0	1	27	308	11	349	0	0	127	0	42
SI	1	0	0	0	1	0	0	1	12	1	33	0	0	10	0	27
RU	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
AB	68	1	0	0	61	0	2	0	71	1	161	0	0	70	0	12
JU	0	5	0	0	0	0	2	0	0	1	5	0	0	0	0	1
AN	0	20	4	0	0	0	0	35	1	0	32	1	0	0	0	2
FO	0	2	8	0	0	1	0	6	0	0	6	1	2	0	0	2
AP	0	3	2	0	0	0	0	0	7	26	23	0	0	18	0	23
TH	0	17	4	0	1	0	1	14	13	6	56	1	1	11	0	10
BO	0	2	0	0	0	0	0	1	9	1	13	0	0	5	0	3
WA	1	2	4	0	2	0	0	6	107	8	106	0	1	56	0	102
AN	4	2	18	0	9	0	0	6	172	152	257	2	8	183	0	230
RU	2	0	1	0	4	0	0	0	33	0	37	0	0	12	0	9
*																

PROGRAM LISTING

```
$JOB (SCRIVENER,J.C./U0148/050),PAGES=9,TIME=120
C
C   LOBSTER PROGRAM 18    THE RESPONSE ANALYSIS
C
      INTEGER TITLE(16,80),X(15,16),ARRAY(15,16),NAME(4,80),BEH(15,9),
     1  TROW(15),TCOL(16),TOT
      DOUBLE PRECISION  CHISQ(15),STORE,HB,HBA
      REAL PROB(16)
      DATA MULT/'*'/
      II=5
      JJ=6
      TOT=0
      NUM=0
      DO 2 L=1,15
      DO 1 J=1,16
    1 ARRAY(L,J)=0
      TROW(L)=0
      CHISQ(L)=0.0
    2 READ(II,3)(BEH(L,I),I=1,9)
    3 FORMAT(9A1)
      DO 4 J=1,16
    4 TCOL(J)=0
      READ(II,5)(NAME(1,I),I=1,80)
    5 FORMAT(80A1)
      DO 20 I=1,16
      READ(II,5)(TITLE(I,J),J=1,80)
      IF(TITLE(I,1)-MULT)6,60,6
    6 DO 7 L=1,15
    7 READ(II,8)(X(L,J),J=1,16)
    8 FORMAT(16(2X,I3))
      DO 9 L=1,15
      DO 9 J=1,16
    9 ARRAY(L,J)=ARRAY(L,J)+X(L,J)
   20 NUM=NUM+1
   60 DO 21 L=1,15
      DO 21 J=1,16
   21 TROW(L)=TROW(L)+ARRAY(L,J)
      DO 23 J=1,16
      DO 22 L=1,15
   22 TCOL(J)=TCOL(J)+ARRAY(L,J)
   23 TOT=TOT+TCOL(J)
      WRITE(JJ,24)
   24 FORMAT('1')
      DO 25 I=1,NUM
   25 WRITE(JJ,26)(TITLE(I,J),J=1,80)
   26 FORMAT(5X,80A1)
```

```
      WRITE(JJ,27)(NAME(1,J),J=1,80)
   27 FORMAT('0',17X,80A1/1X,92('*')/1X,'*INITIAL    *',29X,'SUBSEQUENT B
     1EHAVIOUR',T93,'*'/1X,'* BEHAVIOUR* SC * PU * BK * SW * RH * AF * J
     2U * AW * FO * AH * TH * BO * WA * AP * RU *NONE*'/1X,92('*'))
      DO 28 L=1,15
   28 WRITE(JJ,29)(BEH(L,J),J=1,9),(ARRAY(L,J),J=1,16),TROW(L)
   29 FORMAT(1X,'*',10X,'*',16(4X,'*'),5('*')/1X,'*',1X,9A1,'*',
     116(I4,'*'),I5)
      WRITE(JJ,30)(TCOL(J),J=1,16),TOT
   30 FORMAT(1X,98('*')/12X,16('*',I4),'*',I5)
      T=TOT
      DO 31 J=1,16
   31 PROB(J)=FLOAT(TCOL(J))/T
      DO 32 L=1,15
      ROW=TROW(L)
      DO 32 J=1,16
   32 X(L,J)=PROB(J)*ROW + 0.5
      WRITE(JJ,33)
   33 FORMAT('1',25X,'EXPECTED FREQUENCIES')
      WRITE(JJ,27)(NAME(1,J),J=1,80)
      DO 34 L=1,15
   34 WRITE(JJ,35)(BEH(L,J),J=1,9),(X(L,J),J=1,16)
   35 FORMAT(1X,'*',10X,'*',16(4X,'*')/1X,'*',1X,9A1,'*',16(I4,'*'))
      WRITE(JJ,36)
   36 FORMAT(1X,92('*'))
      DO 37 L=1,15
      STORE=0.0
      DO 362 J=1,16
      A=ARRAY(L,J)
      B=TCOL(J)
      IF(TCOL(J)-0)360,360,361
  360 B=.001
  361 C=A+B
  362 STORE=STORE+((A**2)/C)
      ROW=TROW(L)
      SUM=T+ROW
   37 CHISQ(L)=(STORE-(ROW**2/SUM))/((T*ROW)/SUM**2)
      WRITE(JJ,38)
   38 FORMAT('1',20X,'ANALYSIS OF RESPONSES'/38X,'CHI-SQUARE',5X,'DF')
      DO 39 L=1,15
   39 WRITE(JJ,40)(BEH(L,I),I=1,9),CHISQ(L)
   40 FORMAT('0',25X,9A1,5X,F7.2,6X,'15')
      HBA=0.0
      HB=0.0
      DO 41 J=1,16
      IF(PROB(J))400,400,401
  400 B=0.0
      GO TO 41
  401 B=ALOG(PROB(J))/ALOG(2.0)
   41 HB=HB+(PROB(J)*B)
      HB=HB*(-1.0)
```

```
      DO 42 L=1,15
      ROW=TROW(L)
      DO 42 J=1,16
      A=FLOAT(ARRAY(L,J))/T
      IF(ARRAY(L,J)-1)410,411,411
  410 C=0.0
      GO TO 42
  411 B=FLOAT(ARRAY(L,J))/ROW
      C=ALOG(B)/ALOG(2.0)
   42 HBA=HBA+(A*C)
      HBA=HBA*(-1.0)
      HBM=HB-HBA
      WRITE(JJ,43)HB,HBA,HBM
   43 FORMAT(30X,'INFORMATION PRESENT =',F6.3,' BITS / DISPLAY'/30X,
     1'CONDITIONAL INFORMATION =',F6.3,' BITS / DISPLAY'/30X,
     2'INFORMATION TRANSMITTED =',F6.3,' BITS / DISPLAY')
      CALL EXIT
      END
$DATA
```

VITA

Surname: SCRIVENER Given Names: James Charles Edward

Place of Birth: Vancouver, B. C. Date of Birth: November 6, 1944.

Educational Institutions Attended, with Dates of Entering and Leaving:

Vancouver City College 1961 to 1962

University of British Columbia, Vancouver 1962 to 1967

to

to

Degrees, Diplomas, etc., Awarded, with Dates and Names of Institutions:

B. Sc. 1967 University of British Columbia, Vancouver

Honors and Awards:

F.R.B. Scholarship, 1968/69 and 1969/70

Publications:

Computer Programs Summarizing Ethological Data J. C. Scrivener (1970)

THE UNIVERSITY OF VICTORIA LIBRARY
MANUSCRIPT THESIS
AUTHORITY TO DISTRIBUTE

AUTHOR: This thesis may be lent or microfilm copies made available:

(a) Without restriction [redacted]

(b) With the restriction that, for a period of five years

(until ------------------) the
DATE

written approval of the following is required:

(1) The Chairman, School of Graduate Studies ------------------------

(2) The Author ------------------------

(3) both the Chairman, School of Graduate Studies, and the Author ------------------------

BORROWERS: The borrower undertakes, by signing below, to give proper credit for any use made of the thesis, and to obtain the consent of the author if it is proposed to make extensive quotations, or to reproduce the thesis in whole or in part.

Signature of Borrower	Address	Date