AGGRESSIVE BEHAVIOUR IN THE DAMSELFISH

STEGASTES PARTITUS

Mission 80.10.B

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ABSTRACT

The aim of the present study was to determine whether within social groups of the damselfish Stegastes partitus, certain individuals elicited significantly more aggression than other individuals in their group.

If such target individuals were found they were removed, sacrificed and histologically examined in an attempt to determine why they elicited marked aggressive behaviour from other group members. The phenomenon of a target individual has been reported in many species including the species under study but rarely has a satisfactory reason been forwarded to explain it.

A detailed study was made of aggressive behaviour by recording interactions between all individuals in any one group. It was found that there were no target individuals. Within each social group there is a strict size dependent hierarchy with an inverse relationship between aggression received and rank among the maturing and mature individuals. Small sexually undifferentiated fish within each group are not incorporated into the social hierarchy with mature individuals until they are close to the stage of sexual differentiation. At this stage they probably start to compete with the more mature individuals of the group for one or more resources. Three hypotheses are put forward in an attempt to determine which resource/s these might be.

INTRODUCTION

It has been observed in studies on the social behaviour of various animal species that within social groupings intragroup aggression may be specifically directed towards certain individuals by one or more group members (Greenberg 1947, James 1949, Myrberg 1972a).

In species that maintain a social hierarchy the aggression is often directed towards the smallest, lowest ranking (omega) or perhaps weakest individual.

Three explanations can be put forward for such behaviour. Lorenz (1963) was inspired to write his book 'On Aggression' because of his observations on aggressive behaviour in fish in which certain fish when attacked by larger or similarly sized fish would direct retaliatory aggression towards smaller individuals which were less likely to be of any danger to them. Aggression was thus redirected towards 'scapegoats' which were smaller or weaker individuals than the aggressor.

Greenberg (1947) wrote of his experiments on sunfish *Lepomis cyanellus* ' the omega seems to be a sort of buffer releasing tension between high-ranking individuals'.

A second possibility which can be forwarded results from a natural tendency or internal motivation for aggression within an individual and if this cannot for some reason be released naturally, it may be released on any available objects animate or inanimate. Rasa (1971) apparently demonstrated the releaser role of small individuals introduced to test fish that had been deprived of a natural release of aggression. She worked on the damselfish *Microspathodon chrysurus* and termed the aggressive motivation 'appetence for aggression'.

A third explanation is that instead of acting as a scapegoat, buffer or as a releaser of aggression, the individual which draws upon itself significantly more aggression than any other group member does so for a reason specific to itself i.e. size, rank, it's own behaviour, stage of maturation or sex.

Myrberg (1972a) working on the bicolor damselfish *Stegastes partitus* (previously known as *Eupomacentrus partitus* - see Emery and Allen 1980) found that within stable groups during the reproductive phase, much aggression was directed at the omega individual. He believed that Greenberg's interpretation that the omega individual was functioning as a buffer applied to the social groups he was working on.

While making field observations on the aggressive behaviour of S. partitus during 1979 and 1980, I noticed that it was not the omega individual in each social group that was the individual receiving more aggression than any other group member but that higher ranking individuals appeared to be the target for intragroup aggression. This finding conflicted with that of Myrberg (loc. cit.).

The aims in carrying out this particular study are: a) to determine whether particular individuals of the bicolor damselfish under natural conditions are the targets of intragroup aggression eliciting more aggression than any other group member; b) to determine if such target individuals are found, why these fish are targets for aggression with respect to the three possible alternative explanations above. In addition to the collection of behavioural data on all aggressive interactions between all fish studied, targets of aggressio where found, will also be examined with respect to size, sex, stage of maturation and rank.

In a study on intragroup aggression, account must be taken of factors that have be shown to affect levels of aggression in social groups of a number of animal specie

Both internal and external factors have been shown to modify social behaviour. There are many factors external to the animal which are important: a) light intensity and water visibility (Stevenson 1967); b) temperature (Schmale 1979); c) lunar cycle (Lobel 1978, Schmale 1979); d) diurnal cycle (Rasa 1971, Myrberg 1972a); e) food supply (Jenkins 1969, Coates 1980); f) density - which affects space and shelter availability (Thompson 1960, Hixon 1946, Shoemaker 1939, Erikson 1967, Frost and Kipling 1967, Boice and Witter 1969, Sale 1972).

In this study every attempt was made to reduce to a minimum external factors while it is hoped to be able to examine something of the internal ones.
The internal factors which are important are: a) age (Schein and Fohrman 1955, Johnsgard 1967, Mckay 1971); b) size (Greenberg 1947, Bovbjerg 1953, Schaller 196 Grant 1970, Myrberg 1972a); c) sex (Schjelderup-Ebbe 1935, Greenberg 1947, Hinde 1956, Thompson 1960, Schmale 1979); d) stage of maturation (Schjelderup-Ebbe 1935, Allee, Collias, Lutherman 1939, Thompson 1960, Chalmers and Rowell 1971); e) individual differences in aggressiveness (Allee 1942, Thompson 1960, Rasa 1971 Ficken et al 1978); f) previous experience (Schjelderup-Ebbe 1935, Braddock 1945, Greenberg 1947).

In order to control for the various temporal factors which can affect levels of aggression, the study had to be over as short a time span as possible. Since

I have only ever found the small discrete social groups required for this study at depths of about 20 m or more the use of a habitat with extended times at the appropriate depths is essential for a study of this sort.

The presence of divers is not believed to affect adversely the behaviour of the fish. Observations made by myself on the social structure of this species using conventional SCUBA compared favourably with similar data taken on this species by Myrberg (1972a)using an underwater TV system. Thresner (1978) was satisfied that diver manipulation in the vicinity of the damselfish Stegastes (Eupomacentrus planifrons did not affect its level of aggression.

SITE

The study took place between the 9th and 16th October 1980. Mission No. 80.10. B The study site was a large very gently sloping sandy area just north of the spar at the end of line E furthest from the Hydrolab. The bubble and spar at this point were visible throughout the study. The depth varied from 18 - 20 m. All collections were taken from this area and at the time of collection sent up to the surface with a support diver. The area was selected during a pre-saturation orientation dive and proved to be very suitable for the present study.

TECHNIQUES

Ten social groups of fish were chosen for the study, eight experimental and two control. Each group was a discrete unit the members of which did not interact with members of other groups, but all individuals were close enough to interact with all others of their group. Each unit was isolated on a patch of rocks and coral rubble by shelter-free areas of sand and consisted of 4-6 individuals which could all be recognised and from 1 - 6 very small fish (juveniles) which had to be lumped together as a unit as they could not be distinguished. For analysis, however, the rate of chases per individual juvenile was sometimes required. To achieve the correct measure, the total chases received by all the juveniles in any one group was divided by the number of juveniles (i.e. in group G rank 5 consisted of two juveniles between them receiving 14 chases. For analysis, the rank of 5 was taken to receive 7 chases per individual). This was considered a valid procedure since there is no correlation between the number of juveniles lumped together and the number of chases given per juvenile in each group (Spearman $Rs = 0.2892$, $N = 12$).

The larger individuals were numbered 1 - 6 in size order (1 = largest). Levels of aggression will, in this study, be determined by the number of times one fish chases another which in its turn is seen to be attempting to avoid the chases. In S. partitus, chasing is the most common act of aggression in the field (Myrberg 1972a,b, pers. obs.). Since all the larger fish are recognisable by size, distinctive marks and location, a picture of the actor and recipient of all aggressive acts can be constructed.

The first Null hypothesis to be tested is that no fish in any one group is chased significantly more than any other in the same group. In order to assess this all the groups were watched and all aggressive interactions between fish recorded. Data were taken on underwater paper resting on formica clipboards by two divers moving between the groups in no pre-determined order. Readings were taken at different times of the day to compensate for any temporal variation there may be in general levels of aggression. All periods of monitoring were timed to the nearest minute so that the time could be standardised for analysis. All groups were not monitor ed for the same length of time. The maximum time spent with any one group before changing to another group was about 20 minutes. Each group was monitored once each morning and each afternoon of the study.

After recording a minimum of 60 interactions in any one group and when it became clear which, if any, individuals were being chased the most, this 'target' individual was removed using the fish anaesthetic Quinaldine (Muench 1958) and each group again monitored in the same way to see if the trend repeated itself and another fish became a target for aggression. Readings were restarted between 45 and 80 minutes after fish removal in all the experimental groups. Experimental group D proved a problem. Up until the last minute fish rank 4 appeared to be chased the most. Just before removals rank 2 was suddenly very active and chased rank 6 for an intense short period. It was decided to remove rank 4 which in the final addition was chased marginally less than rank 6 because the former fish had consistently been chased in previous recording periods whereas most of the aggression received by rank 6 was from this above mentioned single bout with rank 2. This result suggests that the observation period should have been longer on this group but there was no more time to continue.

If certain fish within each group were found to be apparent targets of group aggression the second hypothesis is a Null hypothesis which states that the target fish do not differ in any way with respect to size, sex and stage of maturation consistently from other members of their groups. The target individuals would be removed and sacrificed, the standard length measured to the nearest mm, and the gonads treated histologically for sexing and determining stage of maturation. These removed individuals were to be the only ones sacrificed since large scale collections were not permitted around the Hydrolab facility.

The two control groups were used to test two further Null hypotheses. The first in which an individual was removed in the same way as in the experimental groups and replaced after a few minutes was used to test the Null hypothesis that the removal itself did not affect aggressive behaviour.

The second control group in which no manupulations were carried out was used to test the Null hypothesis that the time lapse between the pre- and post-removal periods did not affect aggressive behaviour within a social group.

There are many factors which affect aggression (see Introduction) and it is not known how important these factors may be in the present study. The study is designed to take account of such factors by the choice of a very short time span to reduce temporal effects, by the methods of data collection and by the choice of statistics. Since even between individual social groups the levels of aggression may be very different the statistics used for the comparison of data across groups will be the Wilcoxon Matched Pairs (Siegel 1956). Such intragroup differences in levels of aggression could result from differences in space available, the group composition and the characteristics of individual fish. Since any deviation

from the Null hypothesis will be unidirectional, one-tailed tests will be used for a priori analysis unless otherwise stated.

Before calculation, all figures were converted to the number of chases per a standard unit of time - 100 minutes - since not all groups were watched for the same length of time. This was an average of all times used and did not necessitate excessive extension of shorter periods of time. Two groups were eliminated because it was subsequently found that they formed part of a much larger group. This left 6 experimental and 2 control groups.

RESULTS

The data collected for each group are shown in their raw form in Appendix B. Individuals in each group were ranked according to which individuals they were chased by and which they chased such that a rank of 1 was assigned to an individual that chased all others and was rarely chased itself. Similarly, rank 2 was chased by rank 1 and chased all others. The tables of results in the appendix are already ranked in the above way.

It may be seen that the ranking order thus formed shows strong linearity with few reversals and is very closely correlated with size (Spearman Rs = 0.9870, N = 30, p 0.01). Only in group E was this not seen to hold where size order is 1, 2, 3, and rank order 1, 3, and 2. All ranking was determined using pre-removal data.

The controls tested for two things. First, group E tested whether the manipulatior itself affected the distribution of aggression within a group. To test for this the pre-removal data were compared with the post-removal data using the Wilcoxon matched pairs. The difference is significant (N = 13, T = 15, p 0.05 - two-tailec Therefore the removal itself could affect the distribution of aggressive behavioui and the pre- and post-removal data cannot be combined to increase sample size.

The second control group tested to see whether the time between the collection of data before removal and after removal had a significant effect on the distributioi of aggressive behaviour within the same group. Group H was used. The time factor does not have a significant effect (N = 15, T = 33) so that the significant effect of removal found above is due to the removal itself and not to the fact that there is a difference of several days between the collection of pre- and

FIGURE 1

Aggressive activity (in the form of chases) received by the individuals experimentally removed and those individuals one and two ranks either side of it.

(The data are summed for all six experimental groups and plotted as median and interquartile range).

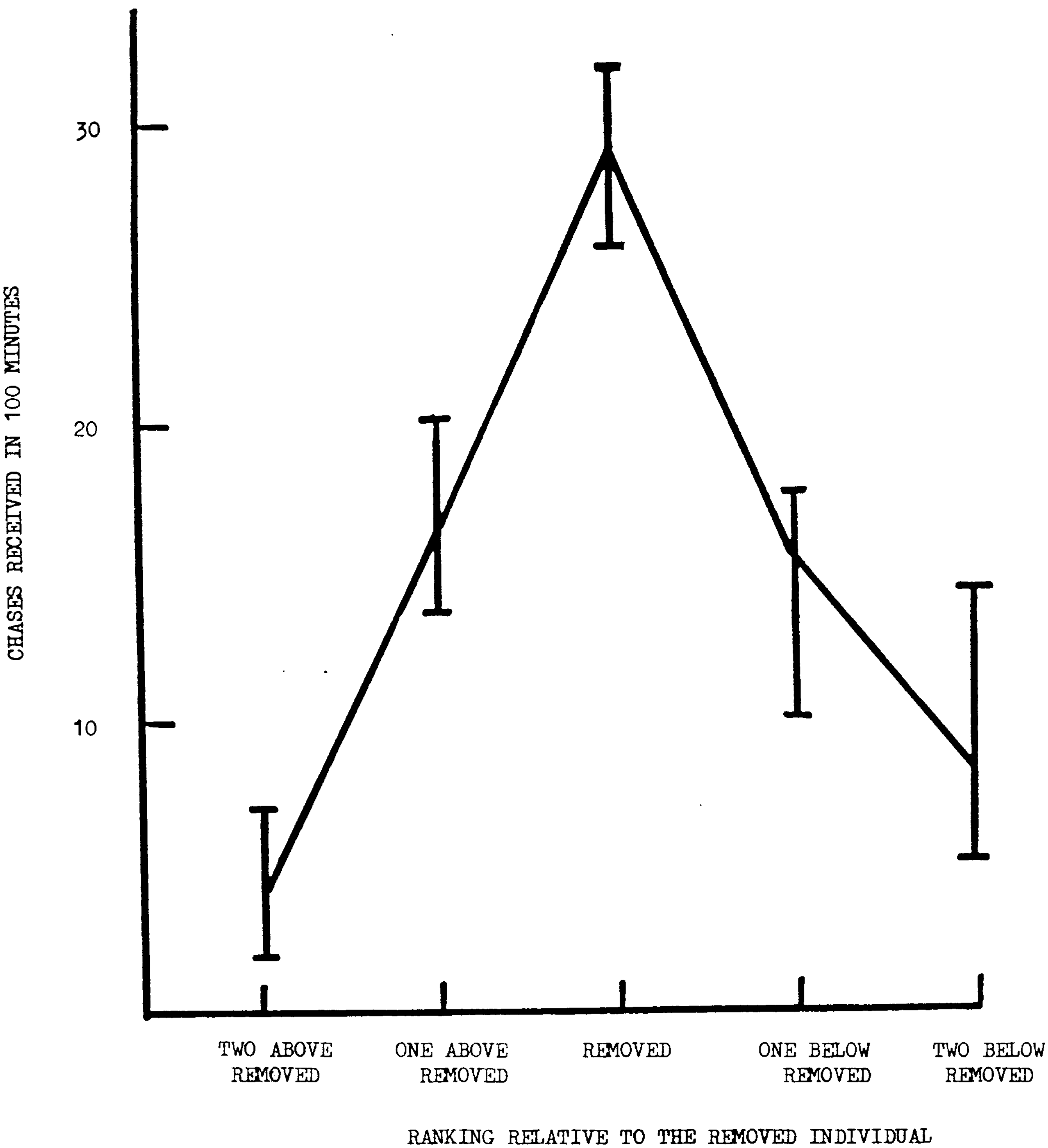


FIGURE 2

Chases received by each rank in each experimental group before removals.

(Group code indicated separately on each plot)

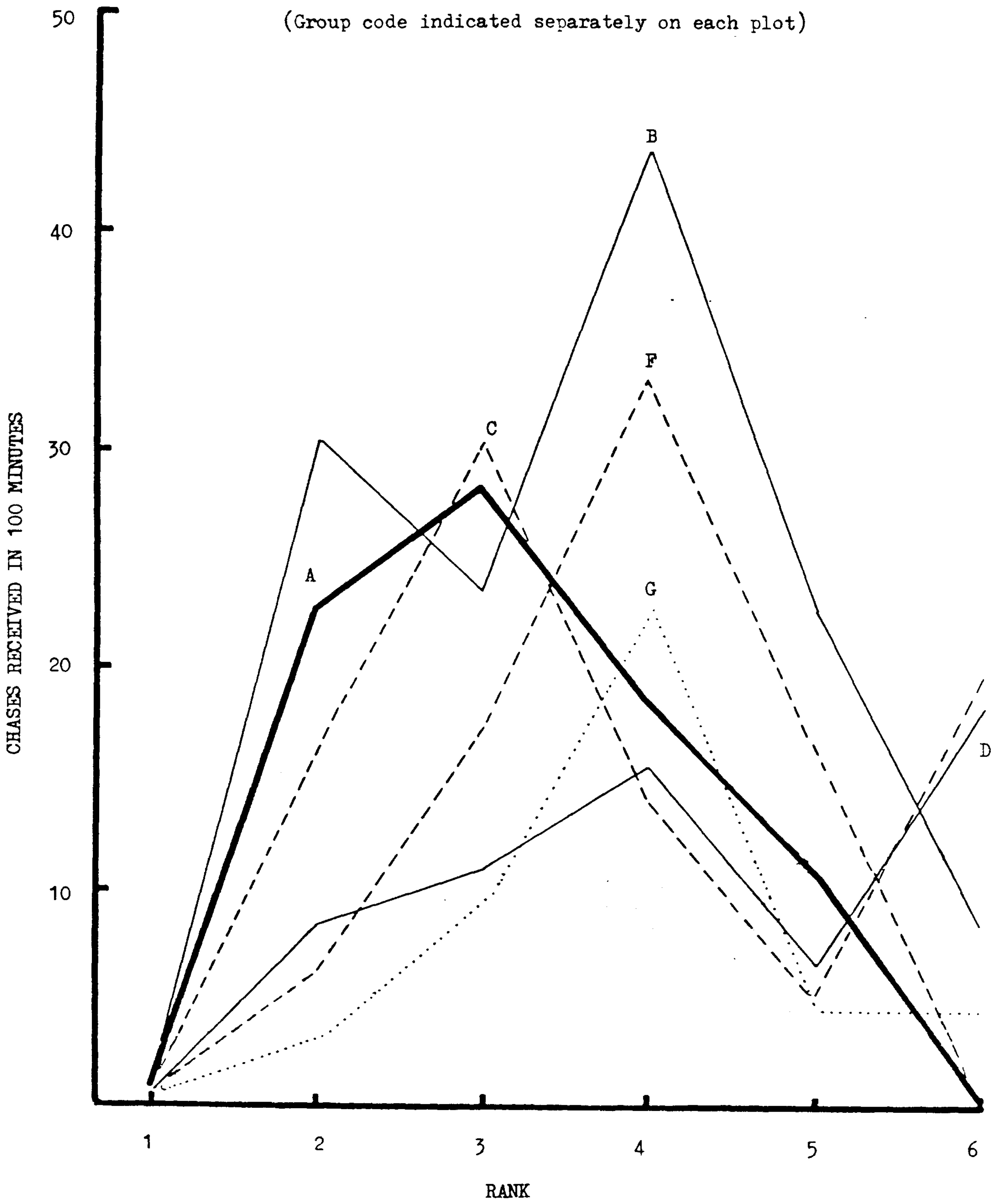


FIGURE 3

Chases received by each rank in each experimental group after removals.

(Group code separately on each plot)

(Two groups were elimated from the post-removal period due to group instability).

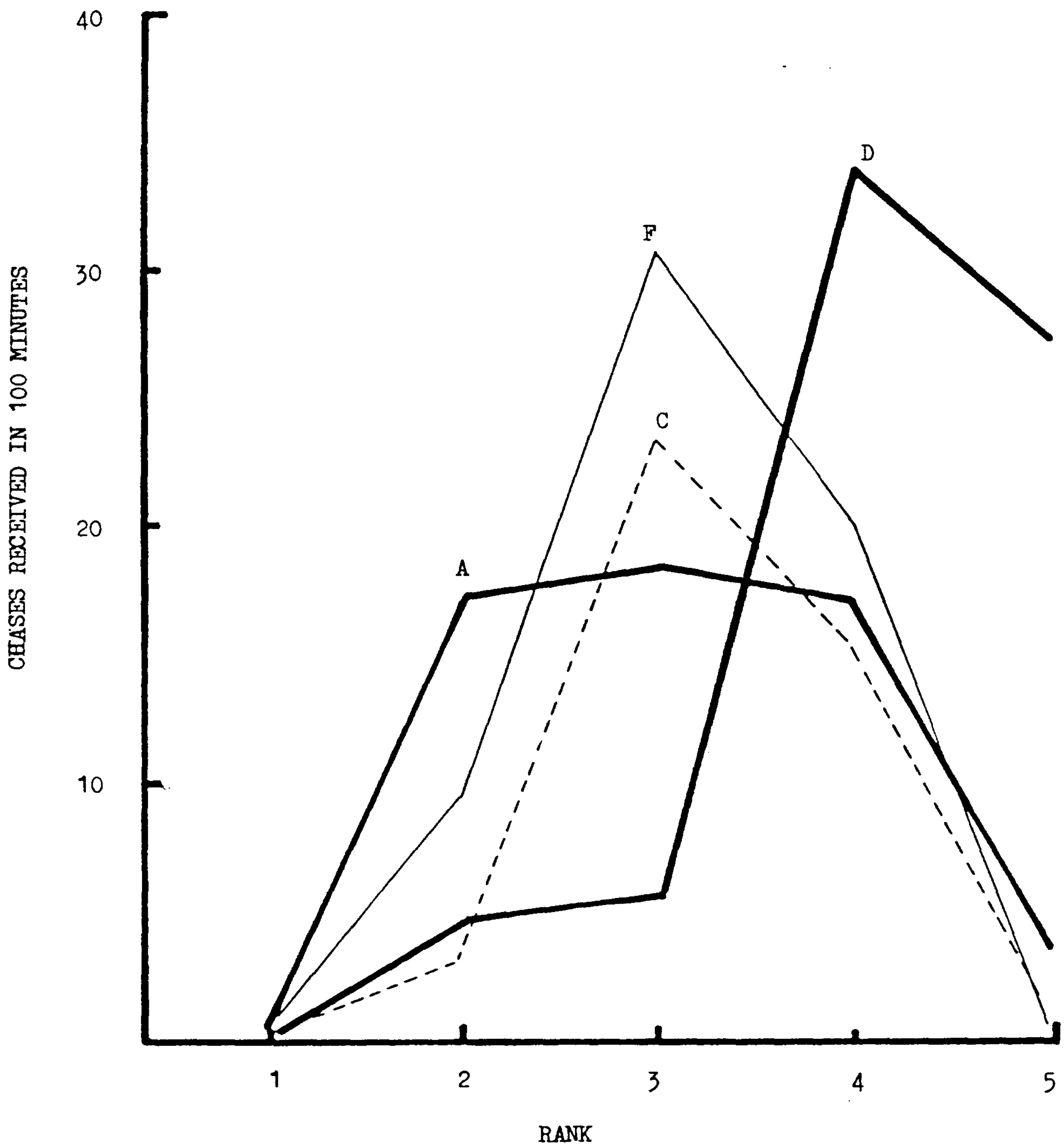


TABLE 1.

Results of the histological examination of six removed individuals from experimental groups.

Fish No.	Group No.	Sex	SL (cm)	Rank
208	F	U	2.6	4
209	B	U	2.7	4
210	C	F/M	3.2	3
211	G	U	3.0	4
212	A	U	2.8	3
213	D	U	2.2	4

M = Mature
F = Female
U = Undifferentiated
SL = Standard Length

DISCUSSION

The data demonstrate a strong relationship between size and rank in social hierarchies of small groups of the damselfish S. partitus. A similarly strong correlation was found by Myrberg (1972a) linking these two factors (Rs = 1, N = 7). This justifies the use of size as an indicator of rank. The hierarchy is linear with very few reversals and between ranks 1 and 4 in some groups and 1 and 3 in others, there is a straight line inverse relationship between chases received and rank.

The results can probably be explained in one of two ways. Either the target individual is being selectively chased by the other members of its group or low ranking individuals are eliciting significantly less aggression than higher ranking ones. If the distribution of chases given to each rank is examined Fig. 4, by plotting chases received by each rank from each rank above it, it may be seen that there is no indication that rank 3 or 4 (removed individual) is selectively chased by the individuals above it in rank. Such a trend would be evidenced by peaks in chases given by each rank to ranks 3 or 4. This Fig. also shows that eac rank chases that individual ranked one below it much more than any other in its group - this is often seen in social groups (Collias 1944, Baerends and Baerends van Roon 1950, Erikson 1967, Eberhard 1969, Borowsky 1973).

The initial hypothesis that there are particular fish within social groups of S partitus which are the targets of intragroup aggression is unfounded. Certain fish appear to be targets of aggression for two reasons: a) there appears to be among higher ranking fish within each group an inverse relationship between rank and chases received and b) the lowest ranking fish for some reason illicit very little aggression from the other group members. Such lower ranking fish are those below rank 3 or 4. This is clearly seen in both pre- and postremoval data (Figs 2

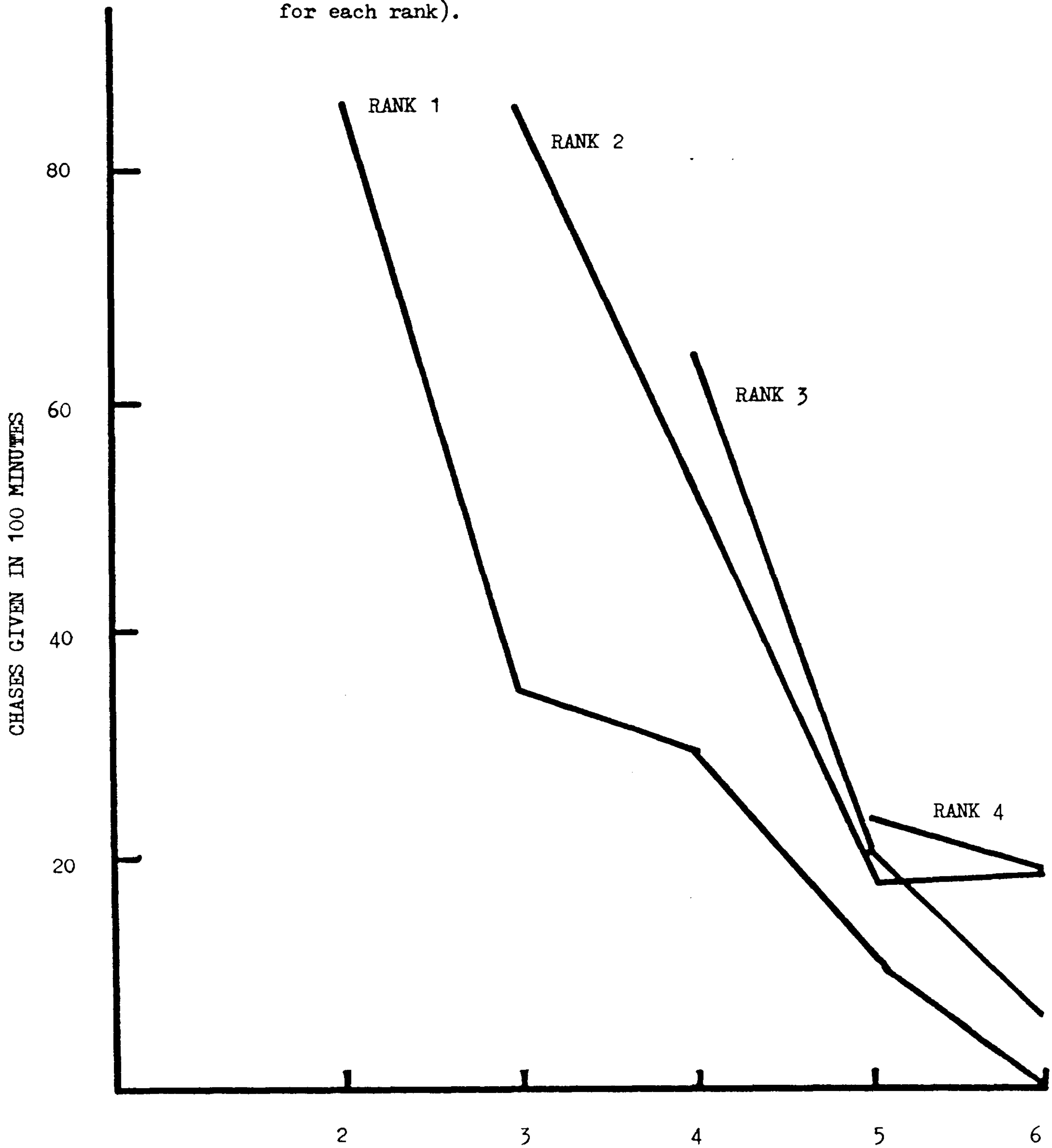
There were initially three possible explanations forwarded to account for an individual fish being a target of aggression. Since the problem is not one of a target individual the explanations involving buffer or releaser individuals are not pertinent here. However, the examination of the individual characteristic of the 'target' fish (the ones removed) may help to explain why it is that fish that at one stage in their life history are virtually ignored by other group members illicit at some later stage aggression from higher ranking fish of their social group.

FIGURE 4

Aggressive activity (in the form of chases) given by each ranked fish in a group to all other ranked fish in the same group.

i.e. Rank 1 chases rank 2 86 times.

(The data are summed accross all six experimental groups for each rank).



All removed fish were within a very narrow size range which is the size range at which this species starts to sexually differentiate. All fish larger than this are mature sexually (unpublished thesis work). The lowest ranking fish therefore are all sexually undifferentiated.

Examination of Fig. 4 shows that the low ranking fish show very little aggressive activity at all. If a statistical analysis is carried out it may be seen that it is only at the higher rank of the removed fish that the number of chases given to other group members is significantly different from zero (Wilcoxon N = 6, T = 0, two-tailed).

In summary, the results show that the low ranking fish in each group elicit very little aggressive activity from other group members: These low ranking fish are all sexually undifferentiated, are all smaller than the size range 2.2 cm - 3.2 cm and their aggressive activity towards other group members appears to be negligible This last point is tentative however as it is based on a very small sample size.

In order to understand when or why a small fish starts to elicit significant intragroup aggression, it is necessary to examine the possible threat that the removed fish pose for those fish above it in rank which lower ranking fish do not pose.

There are three factors which should be considered: a) reproduction; b) food suppl c) space availability.

Reproduction: The importance if intragroup aggression in relation to reproduction is two-fold. Firstly, there is intrasexual selection between males and possibly between females. Schmale (1979) found that there was a positive correlation betwee reproductive success and intragroup aggression in males. A maturing male or female may potentially pose a threat to mature individuals of its own sex so may illicit aggression from these fish. To test whether this is happening, a large group should be selected incorporating several males and females and all interactions between group members monitored. The sex of each group member and the definitive sex of undifferentiated individuals must also be determined.

Secondly, in many species (Allee 1942, Brown 1946, Nagoshi 1967, Shaw 1968, Allen 1972, Borowsky 1973, Wirtz 1974, Fricke and Fricke 1977, Sohn 1977) sexual maturation, differentiation and/or growth in lower ranking individuals of social groups may be inhibited by aggression. Growth and maturation are often linked so that a decrease in growth rate can inhibit maturation. This possibility may be

tested for by isolation experiments in which some undifferentiated fish are isolat
some kept together with mature females and some with mature males. In this way it may be determined whether growth and/or sexual maturation or differentiation are affected by the presence of mature fish.

Food supply: Although this species is a plankton feeder and food as a defendable resource is often excluded in planktivorous species (Myrberg 1972a, Fricke 1975, Thresher 1978, Schmale 1979), the work by Coates (1980) and Jenkins (1969) demonstrate that competition for plankton or at least for optimal feeding position between planktivorous fish does occur. In S partitus the smallest individuals tend to feed on benthic algae and change over to a diet of planktonic algae as they grow (Emery 1973) so the food taken may not be the same for adults and juveniles. However, the size at which changeover from one food type to the other occurs can vary from place to place (Randall 1967, Emery 1973) and I frequently observed large adult fish taking appearing to take algae from the substrate. Emery (loc. ci found large proportions of benthic algae in the stomachs of egg-guarding males which probably feed as close to their nest as possible. Plankton supply can vary considerably close to the substrate (Emery 1968) so that there may be competition for positions which are well supplied with plankton. Food is important for surviva and for reproductive success since larger males and possibly females have a higher reproductive success than smaller ones (Schmale 1979). If competition for food does occur then growing individuals may become incorporated into a hierarchy with mature individuals when they switch their food supply over from benthic to planktonic and thus come into direct competition for food. To determine whether or wher this is important, stomach analyses of developing fish have to be made concomitan with the monitoring of any changes in aggressive activity directed towards or initiated by such developing fish.

Space availability: Space is required for shelter and, in the case of the male, a suitable place in which to guard eggs. Very small fish can hide under rubble but the larger the fish grows, the larger the shelter required. Larger shelters are more scarce so competition is likely to increase for such shelters with increase in fish size. All mature fish hold exclusive territories but very small fish do not defend any specific area and often share the territory of a larger fish until they reach a certain size. At this stage they are excluded either by leaving or by being forced to leave the shared area by the adult fish (unpublished thesis work, Emery 1978). This is also seen in other pomacentrids (Moran and Sale 1977, Ross 1978). The stage at which the smaller fish leaves is critical. Does it at th stage require a territory of its own or does it pose a threat to the larger fish with which it shares, or both?

Detailed work on what happens at the point of leaving the shared territory is necessary to determine why and at what stage it leaves and, with respect to the present study, whether at this stage it becomes incorporated into the social structure of the mature fish of its group.

The final explanation to the question posed by the results of this study could be a combination of all three of the above hypotheses. I believe that chasing behaviour can have various meanings depending on the context of the encounter. To a human observer, a fish has a very limited number of movements which it can perform in communication. Only by detailed study, as in the present work, of intra-group aggression on a single species can a full understanding of the meaning of such behaviour be understood.

In the present study, although the sample size is small it is thought that the trends observed are clear enough to warrant further examination and that the testing of the three proposed hypotheses is justified.

A week is an absolute minimum for a study of this nature. I was fortunate in that I was able to chose a study site during an orientation dive prior to saturation. This saved much time. I also selected two more study groups than the minimum necessary which allowed for unforseen changes in group composition to take place. This enabled me to complete analysis even after having to discard two study groups.

CONCLUSION

1. There is no target individual which receives more aggression from other group members than any other individual thus acting as a releaser or buffer of aggression within each group as originally postulated.

2. Among mature and maturing individuals of each social group there is an inverse straight line relationship between rank and aggression received in the form of chases.

3. Individuals which are low ranking, sexually undifferentiated, are smaller than about 2.2 cm - 3.2 cm and appear to display negligible aggression towards mature fish of their group elicit very little aggression from these mature fish.

the social hierarchy of the mature fish at some stage of their development. This stage may be that at which the developing individuals start to compete with the mature fish for one or more resources for which they had not previously competed. Three hypotheses have been forwarded with the appropriate means of testing them to attempt to explain just when a critical stage is reached:

a) maturing fish pose a potential threat to individuals of their own sex and elicit aggression to prevent their access to mates or to inhibit growth and/or maturation.

b) a changeover in diet at a certain size, stage of development from a benthic to a planktonic diet causes the developing fish to compete for food the planktivorous adults of their group.

c) maturing fish requiring a territory start to compete with the mature fish of their group for space at which point they elicit territorial aggression.

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APPENDIX C. DISSEMINATION OF RESULTS

I feel that the information obtained from this mission represents a significant contribution to the biology of Chromis insolatus and a paper will be submitted to Bulletin of Marine Science or to Copeia shortly.

In addition the data have further relevance with respect to the overall composition and structure of the plankton feeding fishes of St. Croix and will be included in forthcoming publications pertaining to this overall assemblage.

1. EQUIPMENT AND DOCUMENTATION (APPENDIX A)

a). Personnel: Co-PRINCIPAL Investigators:

Ileana E. Clavijo,
Department of Marine Sciences.
University of Puerto Rico.

Yvonne Sadovy,
Department of Zoology,
University of Manchester,
England.

Assistant Investigators:

Kimberley Leighton-Boulon, Humboldt University, California.
Ana Bardales, University of Puerto Rico.

Ileana Clavijo is working on Parrotfish biology, Yvonne Sadovy on fish social behaviour, Kimberley on coral reef ecology and Ana Bardales on reproduction in octocorals.
During the present mission two projects were carried out. One on the dawn and dusk migrations of several species of parrotfish and one on the aggressive behaviour of the damselfish *Stegastes partitus*.

b) Arrival in St. Croix on 6th October 1980. Training, medicals and orientation - 6th- 9th October. Saturation 9th-16th October. Parting from St. Croix 19th October.

c) The pre-saturation orientation dives were particularly useful in saving time once saturated.

d) Nets and quinaldine for capturing fish. The quinaldine has to be made up on the surface but is safely kept on the rack outside the habitat in a large net. The twin aluminium tanks could do with a small metal strip mounted low and to the side for attracting attention of persons without having to use a knife on the tank itself.
The spare regulator hangs freely so when working close to the sand the particles enter. Quick release straps to hold regulators higher would be useful.
Inside the habitat a small formica board close to the trunk would be useful for divers leaving messages but not unsuiting. Another board close to the main porthole on a chain would also be useful. Papers get lost, overlooked or destroyed.

2. DATA TABLES (APPENDIX B)

GROUP A - EXPERIMENTAL GROUP

GROUP SIZE = 7

Figures within the body of the tables refer to the number of chases given by each rank of fish to all the other ranks within its social group.

Pre-removal phase of study

CHASES FROM RANK:

		1	2	3	4	5	6*	Raw Total
TO RANK:	1	/						0
	2	26	/					26
	3	12	21	/				33
	4	6	10	5	/			21
	5	7	2	0	4	/		13
	6*	0	0	0	0	1	/	1

Time spent monitoring group = 115 minutes

Total interactions = 94

Post-removal phase of study - INDIVIDUAL 3 REMOVED

CHASES FROM RANK:

		1	2	4	5	6*	Raw Total
TO RANK:	1	/					0
	2	19	/				19
	4	5	4	/	11		20
	5	11	8	0	/		19
	6*	2	4	0	2	/	8

Time spent monitoring group = 110 minutes

Total interactions = 66

6* refers to two juveniles lumped together

GROUP B - EXPERIMENTAL GROUP

GROUP SIZE = 10

Figures within the body of the tables refer to the number of chases given by each rank of fish to all the other ranks within its social group.

Pre-removal phase of study

CHASES FROM RANK:

		1	2	3	4	5	6*	Raw Total
TO RANK:	1	/	1					1
	2	26	/					26
	3	5	15	/				20
	4	15	16	6	/			37
	5	3	5	9	2	/		19
	6*	1	0	2	12	10	3	28

Time spent monitoring group = 85 minutes

Total interactions = 131

Post-removal phase of study - INDIVIDUAL 4 REMOVED

CHASES FROM RANK:

		1	2	3	5	6	7**	Raw Total
TO RANK:	1	/						0
	2	11	/				20	31
	3	3	9	/			8	20
	5	5	4	7	/		5	21
	6*	0	0	2	7	11	2	22
	7**	15	3	0	0	0	/	18

Time spent monitoring group = 100 minutes

Total interactions = 112

6* refers to four juveniles lumped together.

... Rank 7 which entered after removal

GROUP C - EXPERIMENTAL GROUP

GROUP SIZE = 8

Figures within the body of the tables refer to the number of chases given by each rank of fish to all the other ranks within its social group.

Pre-removal phase of study

CHASES FROM RANK:

		1	2	3	4	5	6	7*	Raw Total
	1	/	1						1
	2	16	/						16
	3	11	19	/					30
TO RANK:	4	0	4	10	/				14
	5	0	3	2	0	/			5
	6	1	6	3	9	0	/		19
	7*	0	1	0	6	3	0	/	10

Time spent monitoring group = 100 minutes

Total interactions = 95

Post-removal phase of study - INDIVIDUAL 3 REMOVED

CHASES FROM RANK:

		1	2	4	5	6	7*	Raw Total
	1	/						0
	2	3	/					3
TO RANK:	4	22	0	/				22
	5	0	14	1	/			15
	6	0	0	1	1	/		2
	7*	2	3	1	1	4	/	11

Time spent monitoring group = 95 minutes

Total interactions = 53

GROUP D - EXPERIMENTAL GROUP

GROUP SIZE = 6

Figures within the body of the tables refer to the number of chases given by each rank of fish to all the other ranks within its social group.

Pre-removal phase of study

CHASES FROM RANK:

		1	2	3	4	5	6	Raw Total
TO RANK:	1	/						0
	2	9	/					9
	3	2	10	/				12
	4	2	3	11	/	1		17
	5	0	0	4	3	/		7
	6	1	13	2	4	0	/	20

Time spent monitoring group = 110 minutes

Total interactions = 65

Post-removal phase of study - INDIVIDUAL 4 REMOVED

CHASES FROM RANK:

		1	2	3	5	6	Raw Total
TO RANK:	1	/					0
	2	5	/				5
	3	2	4	/			6
	5	2	12	22	/		36
	6	2	7	17	3		29

Time spent monitoring group = 105 minutes

Total interactions = 76

GROUP E - CONTROL GROUP WITH REMOVAL

GROUP SIZE = 7

Figures within the body of the tables refer to the number of chases given by each rank of fish to all the other ranks within its social group.

Pre-removal phase of study

CHASES FROM RANK:

		1	2	3	4	5*	Raw Total
	1	/	4				4
	2	4	/	4			8
TO RANK:	3	5	12	/			17
	4	6	4	6	/		16
	5*	0	5	4	4	5	18

Time spent monitoring group = 160 minutes

Total interactions = 105

Post-removal phase of study

CHASES FROM RANK:

		1	2	3	4	5*	Raw Total
	1	/	1				1
	2	6	/	11			17
TO RANK:	3	5	5	/			10
	4	1	8	13	/		22
	5*	0	10	0	2	12	24

Time spent monitoring group = 80 minutes

Total interactions = 74

5* refers to three juveniles lumped together

GROUP F - EXPERIMENTAL GROUP

GROUP SIZE = 6

Figures within the body of the tables refer to the number of chases given by each rank of fish to all the other ranks within its social group.

Pre-removal phase of study

CHASES FROM RANK:

		1	2	3	4	5	6	Raw Total
TO RANK:	1	/		2				2
	2	7	/					7
	3	3	17	/				20
	4	2	18	18	/	1		39
	5	1	5	0	13	/		19
	6	0	0	0	0	0	/	0

Time spent monitoring group = 115 minutes

Total interactions = 87

Post-removal phase of study - INDIVIDUAL 4 REMOVED.

CHASES FROM RANK:

		1	2	3	5	6	RAW TOTAL
TO RANK:	1	/		1			1
	2	11	/				11
	3	20	15	/			35
	5	2	8	13	/		23
	6	0	0	1	0	/	1

Time spent monitoring group = 114 minutes

Total interactions = 71

GROUP G - EXPERIMENTAL GROUP

GROUP SIZE = 6

Figures within the body of the tables refer to the number of chases given by each rank of fish to all the other ranks within its social group.

Pre-removal phase of study

CHASES FROM RANK:

		1	2	3	4	5*	Raw Total
	1	/		1			1
	2	4	/	1			5
TO RANK:	3	4	10	/			14
	4	5	4	25	/		34
	5*	0	1	3	10		14

Time spent monitoring group = 150 minutes

Total interactions = 68

Post-removal phase of study - INDIVIDUAL 4 REMOVED

CHASES FROM RANK:

		1	2	3**	5*	Raw Total
	1	/	1	1		2
TO RANK:	2	4	/	1		5
	3**	1	3	/		4
	5*	0	2	0		2

Time spent monitoring group = 136 minutes

Total interactions = 13

5* refers to two juveniles lumped together

3** this individual was not present most of the time. Because of this these data were not used in the analysis.

GROUP H - CONTROL GROUP WITH NO REMOVALS

GROUP SIZE = 11

Figures within the body of the tables refer to the number of chases given by each rank of fish to all the other ranks within its social group.

Pre-removal phase of study

		CHASES FROM RANK:						
		1	2	3	4	5	6*	Raw Total
TO RANK:	1	/						0
	2	7	/					7
	3	3	2	/				5
	4	0	1	6	/			7
	5	2	7	2	3	/		14
	6*	1	2	22	13	11	23	72

Time spent monitoring group = 120 minutes

Total interactions = 105

Post-removal phase of study

		CHASES FROM RANK:						
		1	2	3	4	5	6*	Raw Total
TO RANK:	1	/						0
	2	8	/					8
	3	3	0	/				3
	4	4	5	6	/			15
	5	3	4	15	1	/		23
	6*	0	2	1	8	3	6	20

Time spent monitoring group = 70 minutes

Total interactions = 69

3. DISSEMINATION OF RESULTS (APPENDIX C)

The results of this study will be incorporated into a PhD thesis on the social behaviour of the damselfish *Stegastes partitus*.

A paper on this work will be submitted to Animal Behaviour or to Copeia for publication.