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Aggressive Behaviour in Tiger Barbs  
(*Barbus tetrazona*)

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Submitted for the degree of M.Sc.

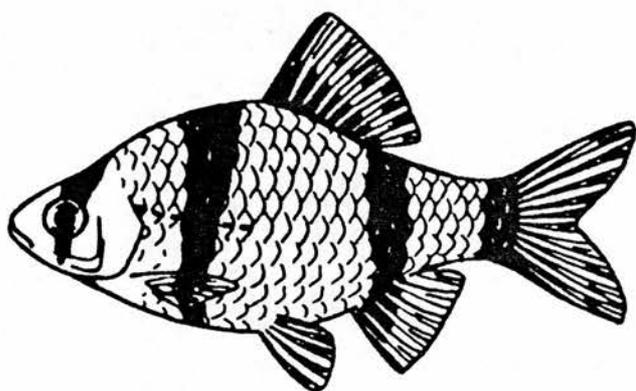
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## Abstract

The aim of this project was to study aggressive behaviour in tiger barbs, *Barbus tetrazona*, and their hierarchy systems and to determine some of the factors which influence them.

The linearity of hierarchies was investigated and it was found that tiger barbs do not form stable linear hierarchies. Nor did the relative weights of fish influence their dominance/subordination relationships.

The effect of the amount of cover on the outcomes of agonistic interactions was examined. A greater amount of cover resulted in earlier terminations of fights due to the loser being more able to hide from its assailant.

The subordinate fish were found to play as important a role in agonistic encounters as the dominant fish.

The effects of group-living on subsequent agonistic interactions was investigated to determine whether prior experience of fish from the same group had any effect on subsequent encounters. This was found not to be the case. The possibility of individual recognition taking place was also examined but was found not to be involved in the outcomes of agonistic encounters. The possibility that each fish had its own individual level of aggression was investigated. This did not appear to be the case, but rather, each individual's level of aggression was affected by the relative fighting abilities of other individuals present. However, the most subordinate fish in a group may have been adopting a different strategy, deterring them from engaging in conflicts. This strategy was possibly maintained by the presence of more dominant fish.

The results obtained lead to the suggestion that the fighting ability of tiger barbs may develop through experience of fighting and differ in rate of development between individual fish.

## DECLARATION

I, Anne Gallagher, hereby certify that this thesis has been composed by myself, that it has not been accepted in partial or complete fulfillment of any other degree of professional qualification.

Anne Gallagher

29 March 1990

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But let me not forget the many tiger barbs, some of which even gave their lives towards the appliance of science!! May those which remain live long, happy and peaceful existences in the company of purely friendly fish!.

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# Chapter 1

## INTRODUCTION

### 1.1 PURPOSE

The aim of this project was to study aggression in tiger barbs, *Barbus tetrazona*, by observing fish in pairs and in larger groups to determine what influences the following factors have on their agonistic interactions: the performance of submissive gestures, isolation prior to encounters, the presence of plant cover in the environment, group-living, prior experience and individual recognition.

These fish have rather stereotyped behavioural actions such as threat displays, chasing, mouth-fighting *etc.*, which are aggressive and flee and ventral roll, which are submissive. Details of these behaviour patterns are examined in Chapter 3 of this thesis and are divided into aggressive and submissive categories with the former being further subdivided into contact and non-contact acts. The importance of these acts in the assessment of fighting ability and thus their reliability in predicting the outcomes of interactions was investigated. The structure of the hierarchies that resulted from paired interactions was examined to determine what factors affected their formation and to determine whether it was affected by the physical characteristics of the fish (such as size) or by environmental characteristics (such as plant cover or whether the animals had normally lived a solitary or a group existence).

In Chapters 4 and 5 the involvement of prior experience in subsequent agonistic interactions was investigated to determine whether the organization of such systems was a consequence of the previous wins and losses for the individuals concerned and also whether recognition between individuals played a part in dominance relations.

As a basis for the whole thesis, in this introduction I discuss the factors which might affect aggression in tiger barbs such as dominance and subordination, hierarchy formation, prior experience and individual recognition in the light of recent applications of games theory models, to the study of aggression, in animals by authors such as Maynard Smith (1982).

## 1.2 AGGRESSIVE BEHAVIOUR IN TIGER BARBS

Aggression can be defined as “The delivery of potentially harmful stimuli to another animal” (Huntingford & Turner 1987) which results in the withdrawal of a rival or opponent (Carthy & Ebling 1964). It is a special case of manipulation in which the desired outcome is brought about by intense displays which can, if required, lead to direct physical conflict and injury and may be accompanied by strong physiological and emotional arousal (Huntingford & Turner 1987).

Scott (1958) and Hall (1965) considered aggressive behaviour as fighting and initiating attack, but fighting has also been regarded as involving ambivalent behaviour, such as threat, defensive behaviour, such as fleeing and submissive behaviour (Barlow 1968). Scott and Fredericson (1951) suggested the term *agonistic behaviour* to include all these aspects of fighting; hence, full scale physical attack is not a necessary component of animal fights (Huntingford & Turner 1987) but rather, conflicts of interest can be resolved by using ritualized threat displays and submissive displays, thus settling fights without serious injury or even physical contact.

This thesis examines the behaviour components involved in agonistic encounters between tiger barbs and whether physical contact is actually the exception rather than the rule in such encounters, these being decided mainly by means of displays and *conventional* fighting, as has been found in many cases (Maynard Smith & Price 1973).

While conflict, at least in higher animals, frequently consists of mainly threatening and bluff (Tinbergen 1951, Lorenz 1952 and 1966), escalation of violence may not just lead to physical damage to the one attacked, but also to the one that is attacking, especially if that attack is unsuccessful (Appleby 1983). Individuals should therefore be expected to assess their opponents and avoid conflicts which they are unlikely to win (Archer 1988). As a result, potentially dangerous fighting should only occur when the outcome is unclear, such as between closely matched opponents (Parker 1974), even after a prolonged assessment (Clutton-Brock *et al.* 1979).

Investigations of agonistic behaviour have recently been invigorated by the application of *games theory* models to the study of animal social behaviour (review in Krebs & Davies 1978 and 1984, Maynard Smith 1982 and Huntingford 1984).

Maynard Smith (1972) was the first to apply games theory to animal contests in order to make predictions about how they evolve and why animals tend to perform complex displays rather than involving direct physical contact in every interaction. Fighting is presumed to be expensive in terms of time, energy and risk of injury (Robertson, 1986). This is regarded as the reason why most animals tend to settle disputes with conventional displays and only rarely fight (Archer 1988). Overt fighting would be expected to occur only when the potential benefits of winning outweigh the likely costs of the fight (Robertson 1986, Maynard Smith & Price 1973, Maynard Smith 1974, Parker 1974, Maynard Smith & Parker 1976) and some form of low cost, non-escalated combat (possibly a low cost display) should therefore persist in the population. It is widely accepted, though as yet no measure of this cost has been made, that one important difference between escalated combat and threat is the cost of the behaviour (review by Caryl 1981).

The assumptions underlying the war of attrition model are that the cost of displaying increases with the length of the contest and that it is the same for both contestants. In practise in fact, to display must cost something, if only because to display for a long time will delay other necessary actions, such as feeding or breeding. It also assumes that the only choice open to an individual is to select a length of time for which he is prepared to play (Maynard Smith 1982).

Bishop and Cannings (1978) point out that the symmetric war of attrition model can be applied in a wide range of contexts provided that:

- (i) No relevant information is received during the contest so that a decision about an action (*ie* persistence time) can, in effect, be made at the start of the contest and, as the opponents are not informed as to how long or how fiercely the other intends to engage in any sort of combat, the behaviour of the eventual winner and loser are consequently expected to be indistinguishable for most of the contests.
- (ii) The winner is the contestant prepared to accept the higher cost.
- (iii) The actual cost to both contestants is equal to the cost acceptable to the loser. This is due to the fact that in symmetrical contests, the expected cost per step will be the same for both opponents before and during the fight (Enquist & Leimar 1983). It is a necessary feature of this model that any injury should not be so great as to prevent a contestant from continuing (Maynard Smith 1982).
- (iv) The range of possible actions must be a continuous one. This means that individuals should display with constant intensity regardless of how much longer they will, in fact, continue (Maynard Smith 1974).

The basis of the war of attrition model is therefore that where contests are symmetrical and contest costs increase with time (*e.g.* if agonistic encounters consist of displays only and longer displays are more costly to perform), the cost an animal is prepared to incur (*e.g.* display time) should be random and unpredictable, showing a negative exponential frequency distribution (Maynard Smith 1974 and 1982, Turner & Huntingford 1986). This theory is applied in Chapter 3 to tiger barb fights to ascertain whether or not their contest lengths followed this pattern.

However, most actual contests are asymmetric (Maynard Smith 1982, Maynard Smith & Parker 1976) in terms of the fighting abilities of the contestants or in terms of the value of the resource contested. Asymmetries in fighting ability affect the probable allocation of contest costs. These are known as asymmetries in *resource holding potential* or RHP. The winner is usually the one with the greater RHP or the greater benefit:cost ratio (Parker 1974). A contest in which there are such differences in fighting ability and in which individuals can vary their cost along a continuum in relation to the value of the

resource is defined as an *asymmetric war of attrition* (Maynard Smith 1982). In most comparative situations, asymmetries play a major role in determining the outcome of contests. Such an asymmetry may be perceived early on in an encounter by the contestants (Archer 1988). If so, it will usually influence the choice of action taken, especially if the asymmetry alters the pay-offs for each individual or affects the likely outcome of an escalated contest. This is explained by Maynard Smith and Parker (1976) who point out that long contests are disadvantageous as they waste time and energy. Consequently, the evolutionarily stable strategy or ESS in asymmetric contests will usually be to permit the asymmetric cue to settle the contest without escalation (Archer 1988). Opponents should therefore base their decisions about whether or not to engage in a contest on relative RHP (Enquist & Leimar 1983, Turner & Huntingford 1986). However, where contestants are evenly matched, the relative RHPs of the opponents are less easily distinguishable and so, escalation of contest cost or risk is more likely to occur (Archer 1988).

Lorenz (1966) found in his studies that some conflicts can be resolved merely by harmless "ritualized" (or symbolic) trials of strength without ever escalating to the point of physical attack. Signals that indicate an intention or readiness to fight are referred to as *threat* signals. Aggressive encounters are often resolved by an exchange of such threat signals (Halliday, 1983) and this agrees with the war of attrition model.

Rand and Rand (1976) described threat displays as tending to be low energy acts which are substituted for and often predict high energy acts such as attack. This would allow an animal to achieve its goal with a lower energy cost. However, actual measurements of energy costs of particular displays and aggressive actions have not been carried out; but an agonistic display may work because it signals the intention to expend more energy if it is unsuccessful. The effectiveness of the display depends on its predictive value and the economy achieved is the difference between the energy used in the display and that of the act which it predicts. Selection will tend to favour exaggeration of cues which are used to assess RHP (Parker 1974). Then selection will favour mechanisms to decode these signals and discover real RHP rather than apparent RHP. In the end, such escalated signals would no longer be deceptive once devaluation by receivers completely compensated for inflation of the signal by senders. Selection would therefore favour costly inflated signals to fall into disuse and be substituted by less costly signals, thus

leading to a new round of escalation and devaluation (Andersson 1982). This would result in animals having a wide repertoire of low cost signals such as threat displays. Consequently, ritualized threat displays could become very complex patterns of signals, as was found by Jenssen (1977) in his analysis of the threat signals of anoline lizards.

Riechert (1988) stated that current evolutionary theory predicts that energy expenditure will be adjusted, in contest situations, to the value of the disputed resource and the probability of winning it. However, Caryl (1981) maintains that threat displays merely carry the message that the sender is aggressive and not how aggressive it is and therefore the energetic quality of the signal should not change.

Many aggressive signals involve the prominent display of offensive weapons such as teeth, claws or horns that are actually or potentially used in fighting (Halliday 1983). A common feature of threat signals is that they involve postural changes that increase the performer's size as perceived by a rival. For instance, Siamese fighting fish (*Betta splendens*) extend their fins and open their opercula to cover their gills (Simpson 1968). Tiger barbs tend to increase their apparent size by raising their dorsal fin and extending their pectoral fins (Kortmulder 1977). Animals can also signal their competitive status by their behaviour patterns rather than necessarily by their anatomical features, such as size or colouration. This could take the form of exaggerated body movements or repeated vocalizations or a combination of both. For instance, male red deer (*Cervus elephas*) signal their territorial status by roaring (Clutton-Brock & Albon 1979). Male frogs and toads also assess each others fighting abilities on the basis of their vocalizations (Robertson 1986, Davies & Halliday 1978).

However, not all displays are aggressive. The behaviour of an animal, once it withdraws from a fight tends to reduce its apparent size (*e.g.* tiger barbs pull their fins in close to their bodies) and/or conceal its weapons or aggressive colours (*e.g.* tiger barbs show their ventral side to their assailant, thus concealing their dark stripes) and this is referred to as submissive behaviour (Halliday 1983, Huntingford & Turner 1987). Unfortunately, the war of attrition model did not predict the evident importance of information about escape in displays (Caryl 1979, Archer 1988). The importance of such information in tiger barb fights is investigated in Chapter 3 of this thesis by determining the effectiveness of submissive displays in terminating agonistic contests.

Maynard Smith (1974 and 1982) used games theory to describe theories for the presence of assessment: if a single asymmetry is present but information about it is uncertain (*e.g.* differences in size or strength), such contests will involve a phase of *assessment*. Assessed asymmetry can settle contests without escalation. Factors favouring assessor as an ESS are:

- (i) Assessment is cheap. Hammerstein (1981) stated that assessment of fighting ability should be unambiguous and without cost.
- (ii) Escalation is potentially dangerous.
- (iii) What is being assessed (*e.g.* size) is a good predictor of victory.

However, even in a population consisting wholly of *assessors*, escalated contests would still occur, such as when the smaller of two contestants erroneously estimates itself to be the larger.

The “rules” for assessment strategy, as put forward by Maynard Smith (1982) are:

- (i) A difference in some property of the contestants is perceived by them and serves to settle the contests without escalation. Animals would be able to minimize the occurrence, severity or duration of competitive interactions by exchanging information about their respective strengths early on in an agonistic encounter. This they can do using forms of displays. An animal that perceives itself to be the weaker of two potential contestants should avoid a competitive encounter, since it will incur the costs involved in that encounter but is unlikely to derive any benefits. Thus:
- (ii) Behaviour during the first phase of a contest enables animals to perceive the difference between themselves.
- (iii) The property should be such that it is expensive in resources to signal a high value, otherwise, assessment strategies would be vulnerable to cheating. So all indicators of RHP should be expensive or impossible to fake. Thus, the criterion of assessment must be a reliable indicator of fighting ability or some individuals might “bluff” and exaggerate their real fighting ability (Maynard Smith & Price 1973, Maynard Smith 1974, Parker 1974, Maynard Smith & Parker 1976, Dawkins

& Krebs 1978). Robertson (1986) also suggested that there is a high metabolic cost to indicators of RHP (such as calling) which prevents weaker individuals from mimicing the signal (see Turner & Huntingford 1986). If it is disadvantageous to fitness to increase actual RHP (*e.g.* by increasing size) or if it is not possible, then selection will favour mechanisms to increase apparent RHP (*e.g.* by raising fins). However, this does not alter the real RHP and animals could then evolve the capacity to distinguish between counterfeit and real RHP. This is likely to limit the extent to which bluff can be employed in animal contests (Maynard Smith & Parker 1976).

(iv) The property should be correlated with fighting success.

Parker and Rubenstein (1981) indicate that information about roles can be acquired only during a contest and at a cost. If costs are high relative to the resource value, or the disparity in fighting ability is large, or the outcome of a single fighting *bout* contains much information about fighting ability, then selection should favour short contests.

Accurate assessment of RHP can often only be obtained after engaging in combat. Contests will be settled entirely peacefully only if reliable estimates of RHP and resource value can be obtained quickly and cheaply. Animals will occasionally make mistakes about their roles which will lead to escalation. Then the animals use the contest itself to increase the information they obtain (Archer 1988). In other words, assessment continues right to the termination of the fight (Enquist & Leimar 1983). Parker (1974) suggested that more reliable measures of RHP might be provided by direct trials of strength between the combatants (*e.g.* pushing and pulling or tail-beating in fish). Very often conventional fighting consists of combinations of *unreliable* displays and *reliable* contests of strength (Parker 1974).

The theoretical withdrawal point in an encounter depends on how much fitness the combatant can afford to lose before retreat becomes the favourable strategy. This assumes that each combatant is playing for the retreat of its opponent. It should therefore be useful for an inferior contestant to give a *surrender* signal (Moynihan 1981). This may be advantageous as it could prevent the loser from incurring unnecessary costs or injury provided that the "winner" takes heed of its signal (Caryl 1979). This should be the only case where a signal should be totally believed without the necessity for

further probing and assessment. This theory is investigated using the displays in tiger barb contests in this thesis.

In Chapter 3 of this thesis, whether or not escalated fights (those including the more dangerous physical contact acts) tended to occur mainly between the more closely matched opponents, is investigated in accordance with Parker's (1974) theory. Games theory was also applied to the tiger barbs' agonistic encounters using the *war of attrition* model to investigate the reason for the occurrence of different behaviour acts by individuals during their agonistic interactions. The theories of Maynard Smith and Parker (1976), referring to asymmetric contests, are investigated, to ascertain whether or not they could be successfully applied to tiger barb contests to predict the form, progression and outcome of encounters. The effectiveness of tiger barb displays is investigated by determining their reliability as predictors of the outcomes of encounters. Parker and Rubenstein's (1981) theory that, due to the cost of passing information about RHP to an opponent, selection should favour short contests, was applied to tiger barb contests. Its validity was investigated by comparing the disparity in behaviour between contestants with the duration of their encounters.

### 1.2.1 DOMINANCE AND SUBORDINATION

Those individuals who show more aggression, all other factors being equal, would be expected to win more fights and become the more dominant members of the society (Lorenz 1966, Brown 1975, Shawcross 1979, Archer 1988). As dominant members, they would gain prior access to disputed resources (Van Kreveld 1970, Barnett 1967, Hinde 1974, Brown 1975). However, this would not be expected if those individuals were not capable of winning. There are many costs involved with being aggressive; such as risk of predation, losses in feeding time, loss of body condition, injury and even mortality (Clutton-Brock *et al.* 1979, Riechert 1988). Therefore, if an individual is less capable of winning, it would be disadvantageous to show aggression, but rather preferable to find alternative strategies to gain resources (Robertson 1986, Kaufmann 1983, Rohwer *et al.* 1981, Barnard & Sibly 1981).

Deag (1977), looking at dyads, found that dominant animals initiated many interactions

with threats and these outnumbered the instances of avoidance shown by the other individual, who is referred to as the subordinate. A dominance/subordination relationship between two individuals is recognized as that in which one animal (the subordinate) defers to the other (the dominant) in contest situations (Kaufmann 1983).

In this thesis such dominance/subordination relationships are examined and particularly the role of the subordinate in the establishment and maintenance of dyadic relations. In these relationships, the behaviour of the persistent loser (the subordinate) can be as important to the outcome of the fight as that of the winner (the dominant) (Hand 1986), as it is often the subordinate who indicates the direction of the asymmetry of the dominance relationship by retiring from the conflict or even avoiding the conflict situation in advance (Wechsler 1988). The dominant is thus allowed to win by default (Hand 1986). In the latter case, the dominant need not direct any overt action towards the subordinate (Rowell 1974, Kaufmann 1983).

It can be advantageous for both individuals to recognize and abide by an established, relatively peaceful, dominance/subordination relationship. This would be affected if the dominant approaches and threatens and the subordinate responds with an *appeasing* gesture. As long as this response remains effective, no fight would then ensue (Hand 1986). In this case, both parties would have achieved their own *priority* in the relationship by using signals as indirect measures of their presumed status, thus indicating which animal would be more likely to win were a conflict to occur (Rohwer *et al.* 1981). These gestures could therefore be used by individuals as a form of mutual assessment of each others likelihood of winning a serious fight and thus enable social dominance relationships to be ascertained without the necessity for overt fighting (Kaufmann 1983). However, such fighting would still ensue should the opponents fail to assess each other or do so incorrectly. Such signals, especially the *appeasing* gestures, would therefore seem to be of great importance in the maintenance of dominance/subordination relationships.

Assessment may also occur by means of recognition of physical differences between opponents, such as asymmetries in their resource holding potential (RHP) (Enquist & Leimar 1983, Turner & Huntingford 1986). For instance, size is a common factor used in RHP assessment and has been found to be an important determinant of winning for

many species of fish (*e.g.* Simpson 1968, Braddock 1945, Frey & Miller 1968 and 1972, Gorlick 1976, Turner & Huntingford, 1986). Size is often an accurate indicator of an animal's strength which in turn indicates its fighting ability (*e.g.* Clutton-Brock *et al.* 1979, Robertson 1986, Davies & Halliday 1978).

Other factors which are also used as indicators of RHP in fish are colouration (*e.g.* Bakker & Sevenster 1983, Ewing & Evans 1973, Kohda & Watanabe 1982 and 1983) and prior residency (*e.g.* Fernö 1987, Bakker & Sevenster 1983, Greenberg 1947, Braddock 1949, Turner & Huntingford 1986). However, these other factors were not investigated in this study, but rather, conditions of residency and age were held constant so as not to interfere with the outcomes of encounters.

Chapter 3 of this thesis examines in detail the results of the performance of *appeasing* gestures in dyadic encounters and also the role of size relations between tiger barbs in the outcome of these encounters.

### 1.2.2 HIERARCHIES

A hierarchy is an arrangement of a group of animals with respect to their dominance/subordination relationships. They are ordered so as to produce a ranking system (which may or may not be linear) which summarizes the patterns of the agonistic relationships within the group (Williams 1966, Wilson 1975, Huntingford & Turner 1987, Kaufmann 1983). In a group that can be arranged in such a hierarchical manner, one individual tends to supplant all other animals whereas another is supplanted by all others. In between these top- and bottom-ranking animals are individuals that supplant some opponents but are, in turn, supplanted by others (Martin & Bateson 1986). The total number of times an animal behaves in a *dominant* way in these interactions could be a useful measure of its hierarchical status and its hierarchical *rank* is therefore a measure of its competitive success (Rowell 1966).

In a linear hierarchy, the highest-ranking individual (A) dominates all others. The second-highest ranking individual (B) dominates all but A, etc., down to the bottom-ranking individual who dominates no other (Chase 1980). This means that in such

a system, all possible triads have a transitive dominance relationship (A beats B, B beats C, A beats C). Linearity requires all the dyadic relationships to be asymmetric and, therefore, these hierarchies tend to be stable (Appleby 1983, Clutton-Brock 1976, Martin & Bateson 1986). This results in stable hierarchies being characterized by linear rank orders (Nelissen 1985). However, Appleby (1983) found that the common method of ranking a group of animals in the closest possible order to a linear one has a surprisingly high probability of producing an apparently linear or near-linear hierarchy by chance when the dominance relationships in the group are, in fact, random. This may explain why many ethologists have found that hierarchies in small groups (of less than about ten members) are frequently linear (review by Chase 1980, and Jackson 1987) but that this is not commonly the case in larger groups of any species (Appleby 1983).

Nevertheless, within a group of animals there is usually some form of dominance hierarchy with its associated threats, supplanting and even physical fights (Huntingford & Turner 1987, Nelissen 1985). In Chapters 3 and 4 of this thesis, the presence and degree of linearity of tiger barb hierarchies and the factors which affected them are examined.

Interactions between two individuals can affect other members of a group. Chase (1980) described hierarchy formation as a developmental process in which the outcomes of previous interactions influence the course of successive ones. He suggested three hypotheses which might affect the formation of a linear or near-linear hierarchy:

- (i) The winner of a dominance contest tends to subsequently engage and dominate other individuals not yet dominated, but not individuals to which it is subordinate.
- (ii) The loser of a dominance contest tends not to attack any bystanders until the individual who has defeated it becomes dominant over the bystanders.
- (iii) One individual will reverse an existing relationship in such a way as to result in a transitive triad ultimately being formed. This hypothesis follows on from the previous two because in an intransitive triad where C originally beat A but A beat B and B beat C, A's win over B, according to hypothesis one, allows it to subsequently dominate other individuals. C, after defeat by B, would, according

to hypothesis two, tend not to attack those who have beaten B. This would consequently lead to A being able to defeat C, thus resulting in a transitive triad.

These hypotheses imply a strong effect of prior-experience of wins and losses for each individual on their subsequent encounters. It would also be useful if the animals were able to recognize individuals they have dominated and those they have not. Chapters 4 and 5 of this thesis examine in detail whether tiger barbs showed any prior experience effects and whether they were capable of individual recognition.

Chase's hypotheses lead him to state that hierarchies emerge from the interactions among group members rather than being generated by any physical differences among these individuals. This supports Landau's (1951) suggestion that social factors must act on animals in groups to promote linearity. However, Appleby (1983) disputes this and consequently puts forward a proposal for hierarchy formation, as he had showed that transitivity in hierarchies was intuitively reasonable if dominance relationships between individuals were related to their competitive abilities. Slater (1986) supported Appleby's idea and suggested that dominance is indeed determined by individual differences between group members. This has been demonstrated to be the case in many species (review by Wilson 1975). In Chapter 6 of this thesis, individual differences between animals are examined to see if they affected the outcomes of interactions which in turn resulted in hierarchy formation.

It has been found that higher hormone levels in some animals influence their aggressive behaviour and rank (Rohwer & Rohwer 1978, Crook & Butterfield 1968, Lazarus & Crook 1973, Shawcross & Slater 1984, Bennett 1940, Wood-Gush 1971). These hormones will result in an animal having its own individual level of aggression which may be unaffected by other factors, such as prior experience of wins and losses or individual recognition of previous opponents (and see Toates & Archer 1978, Archer 1988). Chapter 6 examines whether this is also true of tiger barbs resulting in their own individual levels of aggression being the cause of the outcomes of their interactions.

### 1.2.3 PRIOR EXPERIENCE

Individuals may alter their agonistic behaviour according to their own past history, the losers becoming more submissive and the winners becoming more aggressive. This would be in accordance with Barnard and Burk's (1979) theory for *confidence hierarchies* where, rather than assessment taking place, prior experience determines the behaviour of individuals in subsequent contests.

It has been found in some species that experience of wins and losses can change an individual's willingness to fight and also the probability of its future wins and losses (Scott & Fredericson 1951). Dominance experience is therefore an important determinant of subsequent success in a wide variety of vertebrates ranging from fish (*e.g.* Braddock 1945, McDonald *et al.* 1968, Frey & Miller 1972, Francis 1983) to birds (*e.g.* Collias 1943, Ratner 1961) and mammals (*e.g.* Ginsburg & Allee 1942, Kahn 1951, Bevan *et al.* 1960, Lagerspetz 1979). In these and related studies, there was a significant relationship between the dominance status of the subjects and their dominance histories. In general, the experience of being dominated resulted in reduced success in subsequent dominance encounters (Archer 1976 and 1988), while the experience of being dominant had the opposite (but much weaker) effect (*e.g.* McDonald *et al.* 1968, Frey & Miller 1972, Francis 1980 and 1983, Beacham *et al.* 1987).

In some cases these changes are the result of altered hormonal activity (see Archer 1988). For instance, levels of testosterone in males or luteinizing hormone (LH) in females tend to stay high in victors of contests and fall in losers (Bronson *et al.* 1973, Sachser & Prove 1984, Eberhart *et al.* 1980) so that dominant and subordinate animals differ in hormonal state and the effects of winning and losing a fight on hormone production tend to perpetuate and exaggerate small status imbalances. This effect is also found in the case of androgen levels in some fish species (*e.g.* Hannes *et al.* 1984, Wapler-Leong & Reinboth 1974).

However, this is not the only explanation for the modification of subsequent behaviour following victory or defeat; learning processes may also be involved (Van der Poll *et al.* 1981, Archer 1988). Scott and Fredericson (1951), McDonald *et al.* (1968), Scott (1971) and Ratner (1970) proposed that complex agonistic behaviours conform

to the principal of *association learning* and that dominance and submission can be created through a conditioning process such as the "conditioning of submissive reactions" (Ratner 1970). Several studies of agonistic behaviour in fish pertain to this social conditioning hypothesis (*e.g.* Thines & Heuts 1968, Francis 1983).

Tiger barb hormone levels were not measured in this study. However, Chapters 4 and 5 examined the effects of prior experience on the subsequent behaviour of contestants in encounters to determine whether any alteration in their aggressiveness or willingness to fight was dependent on the outcome of previous contests.

In Chapter 6, the effect of prior experience was investigated by seeing whether submissive individuals (who had previously shown dominance tendencies) remained submissive when put in a group of subordinates due to their conditioning or whether they returned to a more dominant status.

#### **1.2.4 INDIVIDUAL RECOGNITION**

Hierarchies can be formed by animals recognizing other individuals and using cues unrelated to fighting ability, but by adjusting their behaviour according to past experience of wins and losses against that particular individual (Barnard & Burk 1979). This suggests that, as a result of experience with other individuals, an animal learns which it can dominate and which it cannot and this leads to the development of status differences within a group (Kruijt 1964, Huntingford & Turner 1987). Implicit in such an explanation is that individual recognition is involved in the setting up and maintenance of hierarchies. Jenkins (1969) described such hierarchy formation as being based on "learned inhibition of aggression towards certain individuals".

Familiarity of individuals is known to influence the outcome of aggressive interactions in various species (*e.g.* Guhl 1968, Wood-Gush 1971, Beaugrand *et al.* 1984, Gorlick 1976, Zayan 1974 and 1975, Ewer 1971, Rowell 1974). Beaugrand *et al.* (1984) suggested that individual recognition would be responsible for the stability of dominance relations within small groups (but not in large groups where it would be more difficult for an animal to remember its dominance status compared to every other individual). Rowell

(1974) suggested that, in primates, individual recognition of each member of a group by each other member is the basis of their hierarchical organization and therefore their particular hierarchical relationships must be learned.

However, individual recognition may not always be essential for hierarchy formation (*e.g.* Ginsburg & Allee 1942, Shawcross & Slater 1984), but rather a different mechanism for status determination could apply such as prior experience effects.

Chapters 4 and 5 of this thesis investigate whether individual recognition is a factor in determining the dominance/subordination relationships in tiger barbs and whether it effects subsequent encounters between particular individuals.

## Chapter 2

# GENERAL MATERIALS AND METHODS

Mature male tiger barbs, *Barbus tetrazona*, were used for all experiments. The fish were kept eight to a tank in holding tanks of dimensions 60 cm x 30 cm x 40 cm for at least two weeks prior to experimentation. The tanks were aerated, with under-gravel filtration, gravel substrate, and cover consisting of both real and artificial plants. The tanks were screened on two sides to prevent visual contact between them. The experimental tanks were exactly similar to the holding tanks.

The fish were kept in a constant temperature room at 25° C, under an artificial light regime of 16 hours light and 8 hours darkness. They were fed twice a day on dried commercial fish food and sometimes live *Daphnia*.

Fish were transferred to the experimental tanks, using a beaker, the evening prior to experimentation and 30 minutes before darkness. This was to allow them to adjust to their new surroundings and to recover from any distress caused by the transferral process. The fish were always allowed one hour between being fed and the start of observations to allow time to prevent the experiments being influenced by hunger. For contests between pairs of fish, the two fish were placed either side of an opaque partition prior to experimentation. This was to prevent both visual and physical contact before commencement of an observation period. At the start of each recording session, this

partition was removed manually, with minimum disturbance to the fish, and replaced at the end of observation.

Each fish was randomly assigned a letter so that individuals could be identified. The alphabetical ordering of fish in a group had, therefore, no relation to their dominance order. Although fish in different chapters have been assigned the same letter, this was merely for convenience within the individual chapters and cannot be used for cross-referencing of fish as each chapter involved different fish.

Observations were made using a check sheet for both ad libitum sampling and focal animal sampling. The continuous recording method was used in both cases. An Epson portable computer was also used for continuous recording when observing a pair of fish. This was programmed as a real time data recorder.

A problem encountered with the computer was that its memory capacity is only sufficient for up to 90 key presses, after which it is necessary to store the data obtained so far on a cassette. This caused a loss of approximately one minute of recording time up to five times during a set of observations. To overcome this recording gap, observations were recorded during this period on audio-cassette, also recording the time at which audio-recording took place. After the experiments, these recordings were added to the computer data at appropriate times and all the data was transferred to the University's Vax computer.

The fourteen categories of behaviour for each fish that were recorded are:

Follow (fo)	Lateral threat (lt)
Frontal threat (ft)	Head down threat (ht)
Parallel threat swim (ps)	Bite/tap/butt (b)
Attack (at) [b from dist]	Caroussel (ca) [circling+b]
Mouth-fight (mf)	Chase (ch)
Waggle (wg)	Flee (fl)
Dorsal roll (dr)	Ventral roll (vr)

Full descriptions of these acts can be found in the appendix A1.

A fight was recorded as starting as soon as any one of these actions took place, and was scored as finished when the loser was seen to avoid the winner (usually by hiding and keeping still) and the winner was seen to pay no attention to the loser for a period of five minutes.

## Chapter 3

# DOMINANCE RELATIONS AND ENVIRONMENTAL INFLUENCES

### 3.1 INTRODUCTION

This chapter describes two experiments. Both consist of staged contests between pairs of tiger barbs.

The first experiment forms a preliminary survey of the general aggressive behaviour of the fish. The second experiment studies how this general behaviour is altered by a change in the environment. In this case the change is in the form of an increase in plant cover in the experimental tanks. The hypothesis examined by this comparison is that an increase in cover will provide a greater chance for the loser to escape the dominant fish and thus reduce the length of fights.

The following points have been examined in this chapter:

- (i) The difference in general behaviour of dominants and subordinates.
- (ii) Physical and behavioural characteristics of individuals which determine domi-

nance.

- (iii) Whether fish assess an opponent's fighting ability to predict the outcome of an encounter.
- (iv) The effect of an increase in cover in the environment on the above points.

## 3.2 MATERIALS AND METHODS

Eight male tiger barbs were used for the experiments. Different fish were used in experiment two (with additional cover) to those in experiment one to prevent any carrying over of effects from one experiment to the next.

Each fish was kept in an isolation tank (dimensions 30 cm x 20 cm x 15 cm) before and between experiments. Visual contact between fish was prevented while they were separated, so that no interactions could take place which could affect dominance before the experiments were carried out.

The experimental tanks were of the size and conditions as described in Chapter 2.

In experiment one, cover in the tank consisted of two large artificial plastic plants in each tank. In experiment two, cover consisted of two large and two small plastic plants as well as two large real broad-leaved plants in each tank. These were split equally between the two sides of an opaque partition down the centre of each tank so that each fish on either side of the partition had the same amount of cover.

The experiments described here consisted of a round robin tournament, in which all possible pair combinations of fish were tested, to ascertain dominance relations. The order in which the pairs were tested was worked out in a systematic manner; the groups in experiment one being {IvJ, KvM, OvP, QvR}, {IvM, JvK, OvR, PvQ}, {JvM, OvQ, PvR, IvK}, {JvP, IvO, KvQ, MvR}, {IvP, KvR, MvQ, JvO}, {KvP, MvO, IvR, JvQ}, {IvQ, JvR, KvO, MvP} in that order. The groups in experiment two were arranged in a similar manner. Each group of four pairings was tested on the same day after which a two day gap was left before the next round. Preliminary observations ascertained that two days is sufficient for the colour and behaviour to return to normal and to allow

the animals to settle completely after a fight. As all fish fought on the same day and all had the same two day gap between fights, the results could not have been affected by differences between fish in the length of time between fights. Each fish was in a different tank for each fight, eliminating the chance of a prior-residence effect. As a further precaution against effects such as chemical cues, the water in each tank was changed between each round.

Comparisons were made between experiment one and experiment two for each test used to see what changes, if any, occurred due to the increased cover in the tanks.

### 3.2.1 TREATMENT OF RESULTS

#### 3.2.1.1 Linearity of Hierarchy

The data were arranged to place the fish in a dominance hierarchy so as to minimize the number of individuals dominating others above them in apparent rank. This is a common method of showing ranking in a group. It tends to increase the overall impression of linearity by obscuring irregularities such as reversals. This method has thus a high probability of suggesting an apparently linear or near-linear arrangement by chance (Appleby 1983).

A statistical test by Kendall (1970) on paired comparisons is also relevant to a round-robin tournament. Appleby (1983) gives an adaptation of this test to apply it to the calculation of transitivity in dominance; *ie* to examine whether the number of circular triads ( $A > B > C > A$ ) in a proposed hierarchy is less than would be expected by chance. An advantage of this test is that it makes no assumptions about the presence of a hierarchy and treats all relationships within the group in question as equivalent.

The significance of the hierarchy was tested using the procedure given by Appleby (1983) and Landau's method was also used to calculate the index of linearity for the hierarchy (Landau 1951, Martin & Bateson 1986). This gives the value  $f$  which is apparently equivalent to the *coefficient of consistence*,  $K$ , given by Kendall's test.

Appleby's test for the significance of linearity in hierarchies may be calculated as follows:

$$d = \frac{N(N-1)(2N-1)}{12} - \frac{1}{2} \sum (S_i)^2$$

$d$  = number of circular triads.  $N$  = sample size (number of fish).  $S_i$  = number of subordinates for each individual. The degree of linearity of the hierarchy is indicated by the coefficient  $K$ :

$$K = 1 - \frac{24d}{N^3 - 4N}$$

Landau's index of linearity,  $h$ :

$$h = \frac{12}{N^3 - N} \sum_{a=1}^N (V_a - \frac{N-1}{2})^2$$

$V_a$  = number of subordinates for each individual.  $N$  = sample size (number of fish).

### 3.2.1.2 Contest duration: Log-survivorship plot of cumulative persistence times

A log-survivorship plot of persistence times (number of contests still continuing after a certain length of time, logarithmically transformed), against contest length in 10 minute intervals, was drawn. A straight line is predicted by the war of attrition model, as described in Chapter 1, and this would show a negative exponential function. However, this would not necessarily be due to the opponents being evenly matched, but could also be expected under any random conditions.

The best fitting straight line for the data was drawn using the method outlined in Duncan *et al.* (1970). The formula for the best fitting straight line is:

$$n = N(e^{\frac{-X_1}{X_{av}}} - e^{\frac{-X_2}{X_{av}}})$$

$n$  = the expected number of intervals within any class interval  $X_1$  to  $X_2$ .  $N$  = total number of intervals.  $X_{av}$  = average interval (average duration of fights).

The Kolmogorov-Smirnoff one sample test for goodness of fit was used (Siegel 1956) to test the closeness of the actual distribution to the best fitting straight line.

### **3.2.1.3 Comparative sizes of fish**

After the round robin tournament was completed, each fish was weighed by first weighing a beaker of water and then placing the fish (which had excess water removed by blotting) in it, re-weighing and measuring the difference.

For many fish species, ranking is in order of body size. One also might suppose that fights between opponents more evenly matched in size should be of greater duration.

Spearman rank correlations were carried out, using the minitab statistical package, of rank difference with weight difference and each of these measures with fight duration to test whether tiger barb fights are similarly influenced.

### **3.2.1.4 Differences in behaviour of winners and losers**

**Wilcoxon test for differences between winners and losers in the total frequencies of behavioural elements.**

To examine the difference between winners and losers, the total frequencies of discrete and continuous acts which were not of a mutual nature were compared using the Wilcoxon matched-pairs signed-ranks test (Siegel 1956) with the two fish in a contest as the pair. This was carried out using the SPSSX statistical package.

**Determination of the reliability of behavioural elements as predictors of the outcome of fights.**

The reliability of each behavioural element as a predictor of the contest outcome was determined. The prediction is that the frequency of a behavioural element will be greater in winners than in losers. The proportions of winners and losers were graphed using a histogram and also illustrated using a histogram of  $\text{winner}/(\text{winner} + \text{loser})\%$ .

### **The frequencies of behavioural acts across quarters of fights.**

The variance in frequencies of behavioural acts through the four quarters of the fights was examined to quantify the change in frequency of each behaviour across the fights. A nested ANOVA was carried out on each behaviour category, with winners and losers lumped separately, to test for significant variation. The Alice statistical package was used for this purpose.

#### **3.2.1.5 Intensity of fights**

The intensity of fights can be influenced by contest cost or risk (Turner & Huntingford 1986). A possible measure of cost is the number of all behavioural acts per minute, which gives an indication of the relative speeds of action in a contest. A possible measure of risk is the contact:non-contact act ratio, which indicates relative risks by considering the proportion of all acts that were the more dangerous, higher risk contact acts (Turner & Huntingford 1986).

Correlations were carried out, using the MINITAB statistical package, of both these intensity measures with fight duration, rank difference and weight difference to determine whether escalation of contest cost or risk did occur in fights between the tiger barbs which were more evenly matched in rank or body weight. As these measures may not be independent of one another, the *Bonferroni correction factor*, as described in Machlis *et al.* (1985), was used when testing for significance. This is as follows:  $p = \text{significance level}/(\text{number of factors})$ . In this case the number of factors is 5. Therefore  $p < 0.01$  is used as the level of significance instead of  $p < 0.05$ .

The measure of acts per minute will be affected by the number of short breaks in fighting, when one fish temporarily escapes from the other. This should occur more in experiment two as there is more cover into which a fish can escape. To investigate this hypothesis, the frequency of (stops in fighting) per minute was calculated and correlated with fight duration, rank difference and weight difference. A *stop* is defined as a definite break of 15 seconds or more in fighting by the fish when neither are in contact, threatening or approaching the other.

To look for changes in levels of aggression through the tiger barb fights, ANOVA tests were carried out, using the Alice statistical package, on the frequencies of the two intensity measures (acts per minute and contact:non-contact act ratio) across quarters of fights.

### 3.2.1.6 Individual differences in behaviour

It is possible that differences in individuals may affect the frequency with which each carries out certain actions. For instance, a bigger fish may perform lateral display or waggle more, as these show off size and weight. Alternatively, frequency of behavioural acts may vary with the apparent ranking of the fish. To test these hypotheses, correlations were carried out, using the minitab statistical package, of fish body weight with rank and of each of these with behavioural actions.

## 3.3 RESULTS

### 3.3.1 LINEARITY OF HIERARCHY

The dominance relations found are shown in Figures 3.1 and 3.2, with the fish arranged so that there is a minimum number of individuals dominating others above them in the figure.

**Experiment 1:** The significance of the hierarchy was tested using Appleby's (1983) formula. For a group of size  $N = 8$ ,  $d$  must be  $\leq 7$  to be significant. In this hierarchy the number of circular triads ( $d$ ) is 10. This value of  $d$ , according to Appleby (1983), has a probability of occurring in a group of eight of 0.153. It is not therefore significant at  $p < 0.05$ . The degree of linearity of the hierarchy,  $K = 0.5$ , is not significant for  $d = 10$  as  $K$  must be  $\geq 0.65$  for significance in a group of 8.

According to Appleby (1983), a hierarchy in a group of 8 is only significantly different from random if there are less than 3 reversals. There are 4 reversals here and therefore this hierarchy could have occurred by chance with the relationships being actually

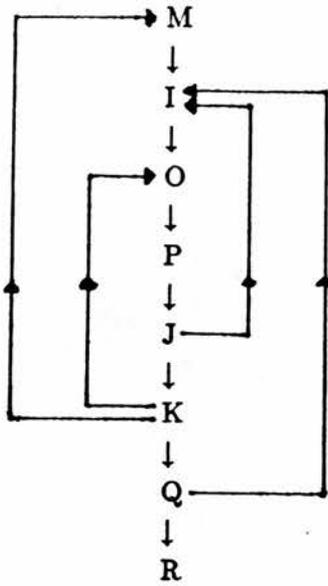


Figure 3.1: Apparent hierarchy: Experiment 1.

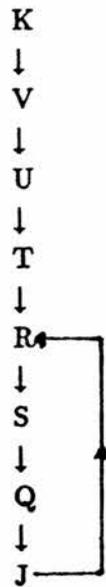


Figure 3.2: Apparent hierarchy: Experiment 2.

Arrows indicate direction of dominance.

random.

For the present data, Landau's index of linearity;  $h = 0.52$ . This value is just significant at  $p < 0.05$ . This index concludes that the linearity of the hierarchy is just significant. It is possible that the two tests carried out disagree, because the latter is a less sensitive test when such a small group is being examined. It may imply that the result is near the border of significance as tests are more likely to disagree if this is the case.

**Experiment 2:** The number of circular triads  $d$  was found to be 6.5. This is significant at  $p < 0.05$  in a group of 8. The degree of linearity ( $K$ ) is 0.68 which is also significant at  $p < 0.05$ . As this apparent hierarchy has only one reversal, it is significantly different from random. Landau's index of linearity ( $h$ ) is 0.91. This value is significant at  $p < 0.01$ .

In some of the following statistical tests the apparent rank order will be used (*e.g.* in correlations) as it is possible that there are other effects determining dominance, such as physical characteristics or motivational state (Wilson 1975, ch 13) which cannot be tested when using such a small group.

### 3.3.2 CONTEST DURATION: Log-survivorship plot of cumulative persistence times

Figures 3.3 and 3.4 show a log-survivorship plot of cumulative persistence times.

**Experiment 1:** For these data;  $N = 28$ ,  $X_{av} = 55$ .  $n(0 - 100) = 23.5$  (total number of intervals from 0 to 100 on  $x$  axis). Therefore when  $x = 0$ ,  $y = 28$ . When  $x = 100$ ,  $y = 4.5$  (a decrease of 23.5). The resulting straight line through these two points was drawn on the log-survivorship plot (Figure 3.3).

The results for the Kolmogorov-Smirnoff goodness of fit test are given in Table 3.1. The calculation of (contests finished)/(contests left) is given in Table 3.2. From this the value  $D$  was calculated.  $D =$  greatest difference between observed and expected.  $D = 20\% = 0.20$ . (At  $p < 0.05$ ,  $D$  must be  $\geq 0.25$  for significance). Thus this value of  $D$  is insignificant and we accept the null hypothesis that there is no difference between

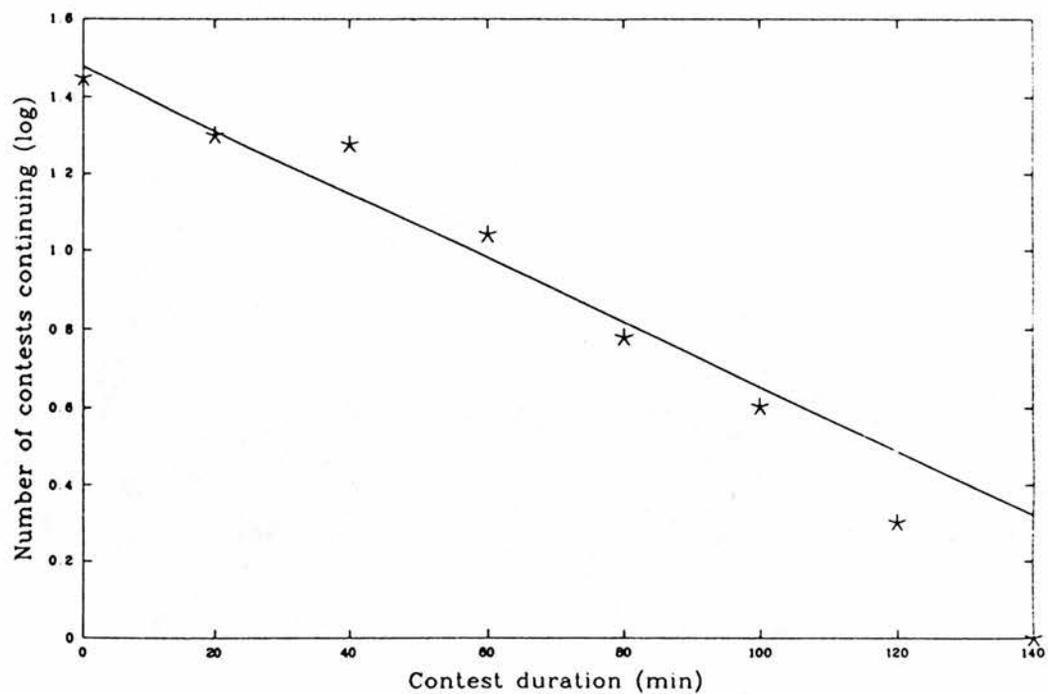


Figure 3.3: Log survivorship plot of cumulative persistence times: Experiment 1

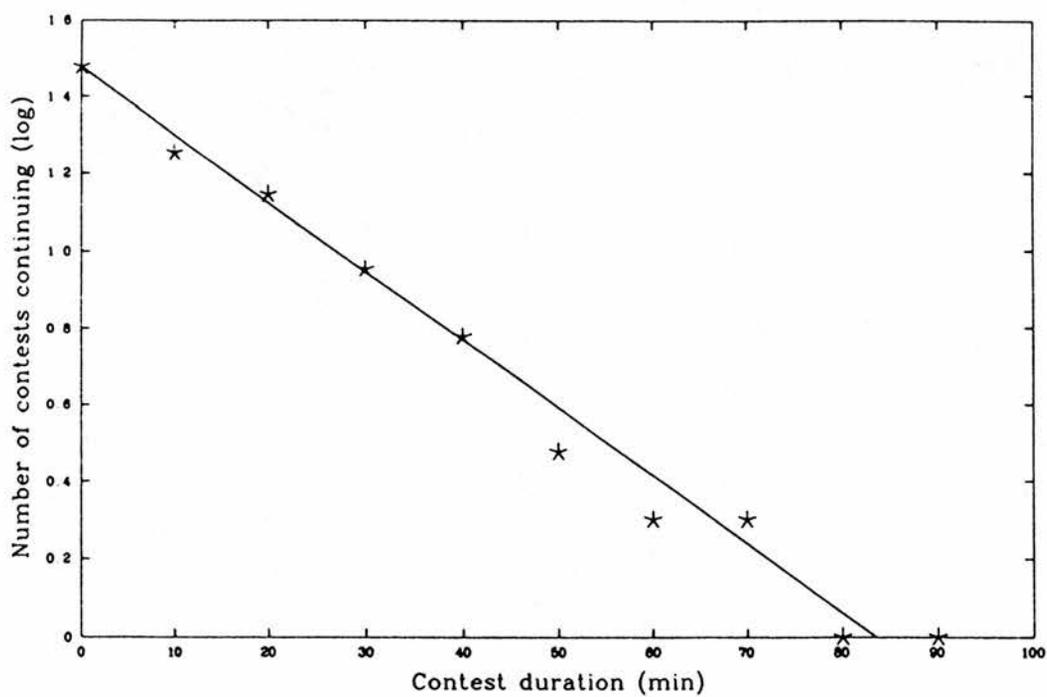


Figure 3.4: Log survivorship plot of cumulative persistence times: Experiment 2

the observed line and the expected line. Therefore, it can be concluded that the data here conform to the negative exponential slope predicted by the war of attrition model.

Table 3.1: Kolmogorov-Smirnoff one sample test: Experiment 1 (Table of readings from Log Survivorship Plot – Figure 3.3).

Interval	Expected†		Observed†	
0	28.0	0.0	28	0
20	19.5	8.5	23	5
40	13.5	14.5	19	9
60	9.4	18.6	11	17
80	6.5	21.5	6	22
100	4.5	23.5	4	24
120	3.2	24.8	2	26
140	2.2	25.8	0	28

†First column under these headings = number of contests left.

Table 3.2: Table of contents finished/contents left: Experiment 1

Expected (%)	Observed (%)	Difference (%)
30	18	12
52	32	20
66	61	5
77	79	2
84	86	2
89	93	4
92	100	8

**Experiment 2:** For these data;  $N = 28, X_{av} = 25. n(0 - 50) = 24$ . The resulting straight line was drawn on the log-survivorship plot ( Figure 3.4). The results for the Kolmogorov-Smirnoff goodness of fit test and (contests finished)/(contests left) are given in Tables 3.3 and 3.4 respectively. In this experiment  $D = 5\% = 0.05$ . This value is also insignificant and the null hypothesis is again accepted.

Table 3.3: Kolmogorov-Smirnoff one sample test: Experiment 2 (Table of readings from Log Survivorship Plot – Figure 3.4).

Interval	Expected†		Observed†	
0	28.0	0.0	28	0
10	18.8	9.2	18	10
20	12.6	15.4	14	14
30	8.4	19.6	9	19
40	5.7	22.3	6	22
50	3.8	24.2	3	25
60	2.5	25.5	2	26
70	1.7	26.3	2	26
80	1.1	26.9	1	27
90	0.8	27.2	1	77
100	0.5	27.5	0	28

†First column under these headings = number of contests left.

Table 3.4: Table of contests finished/contests left: Experiment 2

Expected (%)	Observed (%)	Difference (%)
33	36	3
55	50	5
70	68	2
80	79	1
86	89	3
91	93	2
94	93	1
96	96	0
97	96	1
98	100	2

The average persistence times for experiment one were significantly longer than those for experiment two ( $t = 4.02, d.f. = 48, p < 0.01$ ).

### 3.3.3 COMPARATIVE SIZES OF FISH

Plots of the weights of fish vs. hierarchy position are given in Figures 3.5 and 3.6. Ranking in the tiger barbs was not in order of body size. The correlation (Spearman rank) of rank difference with weight difference was insignificant (Table 3.5). The correlation of both rank difference and weight difference with duration of fight gave insignificant correlations (Table 3.5). However, the insignificant correlations concerning rank, for experiment 1, were inevitable as the rank order itself was not significantly linear.

Table 3.5: Spearman rank correlation: Correlations between rank difference, weight difference and fight duration.

Variables	$N$	$r(s)$	Significance
r,w	28	-0.22	NS
	28	-0.33	NS
r,f	28	-0.27	NS
	28	0.01	NS
w,f	28	-0.03	NS
	28	-0.32	NS

r = rank difference

w = weight difference

f = fight duration

N = number of fights

NS = insignificant

Dominance in tiger barbs was thus not a product of fish weight, nor did the duration of a fight depend on the rank difference between opponents. Therefore, fish who seemed, by their rankings, to be more evenly matched did not have relatively longer or shorter fights.

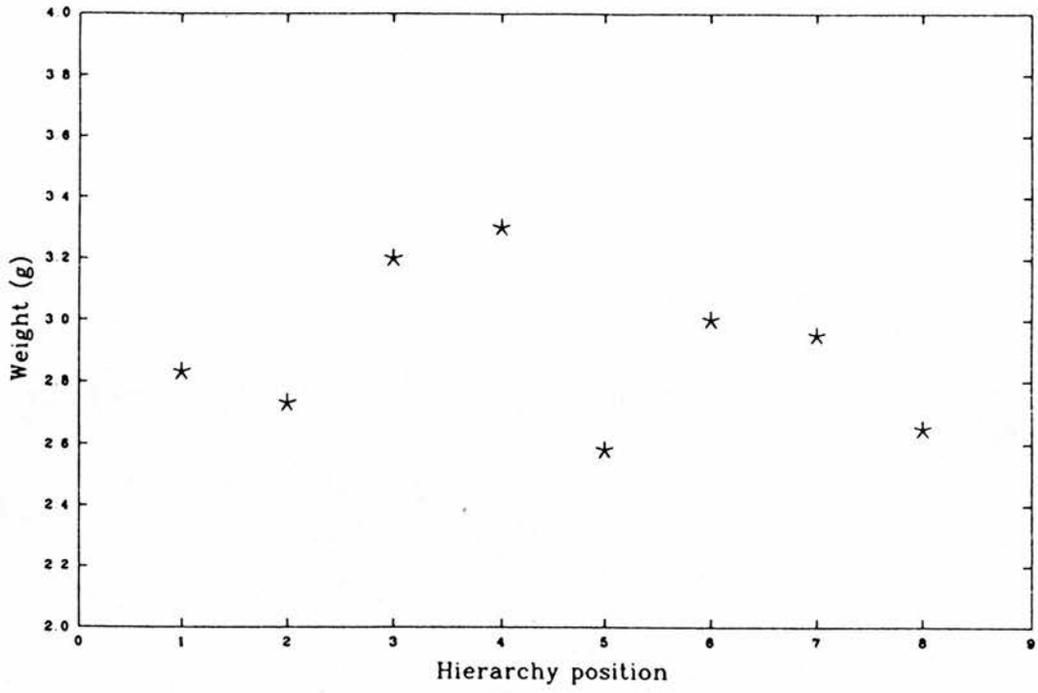


Figure 3.5: Comparative weight of fish v's hierarchy position: Experiment 1.

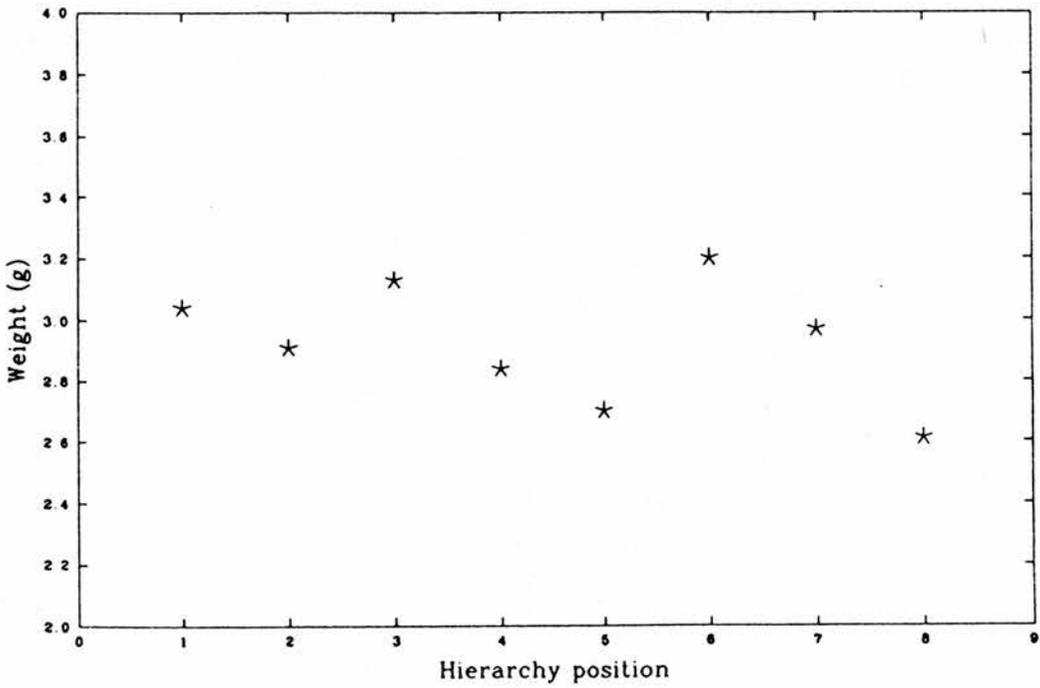


Figure 3.6: Comparative weight of fish v's hierarchy position: Experiment 2.

### 3.3.4 THE BEHAVIOUR OF WINNERS AND LOSERS

#### 3.3.4.1 Wilcoxon test for differences between winners and losers in the total frequencies of behavioural elements.

**Experiment 1:** The results of the Wilcoxon tests, comparing the total frequencies of the behavioural acts between winners and losers, are given in Table 3.6. There was a very significant difference between the frequencies of most behaviour acts of winners and losers ( $p < 0.01$ ). Only waggle was not significantly different, with the winner performing this behaviour most in some fights and the loser performing it more in others. Waggle is a defensive act which protects against being bitten (Kortmulder 1972) and would therefore be useful to both fish, though it would be expected that, as the winner bites more than the loser, the latter would waggle more. This was not so as the loser often performed *flee* in response to being bitten. As waggle was not often performed it will be omitted from the remaining analysis on differences in behaviour.

**Experiment 2:** The results of the Wilcoxon test are given in Table 3.7. There was a very significant difference ( $p < 0.01$ ) for all the behavioural acts in which differences were also found in experiment 1 and additionally for waggle ( $p < 0.05$ ). In this case the loser did waggle more than the winner, as would be expected.

Attack and head-down threat could not be analysed statistically in either experiment one or two as they were absent from most fights.

The results of the Wilcoxon tests for each quarter (by time) of the contests are given in Tables 3.8 to 3.11 for experiment 1 and 3.12 to 3.15 for experiment 2. This was to investigate at what stage, in tiger barb fights, differences in frequencies of behavioural elements between opponents became apparent.

**Experiment 1:** Even in the first quarter, there was a very significant difference in the frequencies of all of the behavioural elements between winner and loser, this great difference being carried through all four quarters of the fights. Thus, the outcome of the contests could be predicted even in the first quarter of the fights.

Table 3.6: Results for Wilcoxon test on differences in frequencies of behaviours in fights:  
Experiment 1.

Behaviour	loser < winner	loser > winner	ties	z value	2 tail p value	Significance
follow	24	2	2	-4.23	<0.01	0.01
bite/butt	22	3	3	-4.09	<0.01	0.01
chase	26	1	1	-4.52	<0.01	0.01
lat. threat	24	3	1	-3.87	<0.01	0.01
front. threat	27	0	1	-4.54	<0.01	0.01
waggle	9	17	2	-1.36	0.17	NS
ventral roll	0	28	0	-4.62	<0.01	0.01
flee	0	28	0	-4.62	<0.01	0.01

Table 3.7: Results for Wilcoxon test on differences in frequencies of behaviours in fights:  
Experiment 2.

Behaviour	loser < winner	loser > winner	ties	z value	2 tail p value	Significance
follow	26	2	0	-4.17	<0.01	0.01
bite/butt	23	0	5	-4.20	<0.01	0.01
chase	20	0	8	-3.92	<0.01	0.01
lat. threat	16	2	10	-3.46	<0.01	0.01
front. threat	17	1	10	-3.31	<0.01	0.01
waggle	2	12	14	-2.51	0.01	0.05
ventral roll	0	24	4	-4.29	<0.01	0.01
flee	1	26 8	1	-4.48	<0.01	0.01

Table 3.8: Results for Wilcoxon test on differences in frequencies of behaviours in first quarter of fights: Experiment 1.

Behaviour	loser < winner	loser > winner	ties	z value	2 tail p value	Significance
follow	17	9	2	-2.32	0.02	0.05
bite/butt	19	6	3	-3.24	<0.01	0.01
chase	21	1	6	-4.01	<0.01	0.01
lat. threat	17	2	9	-3.10	<0.01	0.01
front. threat	22	2	4	-3.91	<0.01	0.01
ventral roll	1	20	7	-3.86	<0.01	0.01
flee	1	22	5	-4.15	<0.01	0.01

Table 3.9: Results for Wilcoxon test on differences in frequencies of behaviours in second quarter of fights: Experiment 1.

Behaviour	loser < winner	loser > winner	ties	z value	2 tail p value	Significance
follow	20	5	3	-3.61	0.02	0.05
bite/butt	23	2	3	-3.85	<0.01	0.01
chase	22	1	5	-4.17	<0.01	0.01
lat. threat	16	1	11	-3.05	<0.01	0.01
front. threat	21	0	7	-4.01	<0.01	0.01
ventral roll	1	22	5	-4.15	<0.01	0.01
flee	1	21	6	-4.01	<0.01	0.01

Table 3.10: Results for Wilcoxon test on differences in frequencies of behaviours in third quarter of fights: Experiment 1.

Behaviour	loser < winner	loser > winner	ties	z value	2 tail p value	Significance
follow	19	2	7	-3.55	0.02	0.05
bite/butt	22	1	5	-4.03	<0.01	0.01
chase	24	3	1	-4.18	<0.01	0.01
lat. threat	15	2	11	-2.67	0.01	0.05
front. threat	24	1	3	-3.78	<0.01	0.01
ventral roll	1	25	2	-3.96	<0.01	0.01
flee	1	25	2	-3.96	<0.01	0.01

Table 3.11: Results for Wilcoxon test on differences in frequencies of behaviours in fourth quarter of fights: Experiment 1.

Behaviour	loser < winner	loser > winner	ties	z value	2 tail p value	Significance
follow	24	1	3	-4.31	<0.01	0.01
bite/butt	20	0	8	-3.92	<0.01	0.01
chase	26	0	2	-4.46	<0.01	0.01
lat. threat	14	2	12	-3.15	<0.01	0.01
front. threat	25	0	3	-4.37	<0.01	0.01
ventral roll	0	26	2	-4.46	<0.01	0.01
flee	0	28	0	-4.62	<0.01	0.01

**Experiment 2:** In the first quarter, the frequencies of lateral threat, frontal threat and ventral roll in winners and losers were not significantly different. Most of this quarter of the fight consisted of apparent assessment in the form of lateral and frontal threats by both fish. Ventral roll was rarely performed which is what would be expected as it is a submissive gesture. Chase, waggle and flee showed a significant difference ( $p < 0.05$ ). Follow and bite, which are performed most in the earlier stages of the fight were significant ( $p < 0.01$ ). In the second quarter, there was a significant difference in the frequencies of all acts between winners and losers. This difference was carried through for the rest of the fights, except in the case of waggle, which was insignificant in the last quarter as it was hardly performed.

Thus, the outcome of the contests could be predicted even in the first quarter of the fights, but less clearly and for fewer categories of behaviour than in experiment one.

### 3.3.4.2 Determination of the reliability of behavioural elements as predictors of the outcome of fights.

The results of the cumulative prediction of contest outcome from behaviours, giving the reliability of each behaviour measure as a predictor of the contest outcome, are given in Figures 3.7 and 3.8. The height of the columns indicates the proportion of positive and negative predictions out of all contests where that action was recorded. Figures 3.9

Table 3.12: Results for Wilcoxon test on differences in frequencies of behaviours in first quarter of fights: Experiment 2.

Behaviour	loser < winner	loser > winner	ties	z value	2 tail p value	Significance
follow	22	3	0	-3.64	<0.01	0.01
bite/butt	13	2	10	-2.73	0.01	0.05
chase	6	0	19	-2.20	0.03	0.05
lat. threat	8	4	13	-0.94	0.35	NS
front. threat	7	1	17	-1.40	0.16	NS
ventral roll	3	9	13	-1.80	0.07	NS
waggle	1	8	16	-2.19	0.03	0.05
flee	2	13	10	-2.13	0.03	0.05

Table 3.13: Results for Wilcoxon test on differences in frequencies of behaviours in second quarter of fights: Experiment 2.

Behaviour	loser < winner	loser > winner	ties	z value	2 tail p value	Significance
follow	16	1	8	-3.24	<0.01	0.01
bite/butt	19	0	6	-3.82	<0.01	0.01
chase	12	0	13	-3.06	<0.01	0.01
lat. threat	13	0	12	-3.18	<0.01	0.01
front. threat	11	0	14	-2.93	<0.01	0.01
ventral roll	0	14	11	-3.29	<0.01	0.01
waggle	0	8	17	-2.52	0.01	0.05
flee	2	20	3	-3.81	<0.01	0.01

Table 3.14: Results for Wilcoxon test on differences in frequencies of behaviours in third quarter of fights: Experiment 2.

Behaviour	loser < winner	loser > winner	ties	z value	2 tail p value	Significance
follow	13	5	7	-2.07	0.04	0.05
bite/butt	18	0	7	-3.72	<0.01	0.01
chase	14	0	11	-3.30	<0.01	0.01
lat. threat	12	1	12	-3.01	<0.01	0.01
front. threat	14	0	11	-3.30	<0.01	0.01
ventral roll	0	17	8	-3.62	<0.01	0.01
waggle	0	7	18	-2.37	0.02	0.05
flee	0	19	6	-3.82	<0.01	0.01

Table 3.15: Results for Wilcoxon test on differences in frequencies of behaviours in fourth quarter of fights: Experiment 2.

Behaviour	loser < winner	loser > winner	ties	z value	2 tail p value	Significant
follow	19	4	2	-3.37	<0.01	0.01
bite/butt	19	0	6	-3.82	<0.01	0.01
chase	20	0	5	-3.92	<0.01	0.01
lat. threat	14	2	9	-3.15	<0.01	0.01
front. threat	13	0	12	-3.18	<0.01	0.01
ventral roll	0	23	2	-4.20	<0.01	0.01
waggle	0	4	21	-1.83	0.07	NS
flee	0	23	2	-4.20	<0.01	0.01

and 3.10 show the calculation of winner/(winner and loser) (%).

**Experiment 1:** It can be seen from the columns in Figure 3.7 that each of these categories could be used as a predictor of the outcome of the contests. Figures 3.9 also takes the ties into consideration, when both fish perform a behaviour to an equal amount. This shows that some categories were much better predictors than others. Chase was apparently a very good predictor of which fish would win as it was hardly ever carried out by the eventual loser, even in the first quarter. Ventral roll also seemed a very good predictor as to which individual would lose and was performed frequently by losers, even in the first quarter of fights. Lateral threat was not a very good predictor, due to the large number of fights in which it was performed with similar frequency by both fish.

Figure 3.7 shows that the reliability of all the good predictors increased progressively through the fights (with the exception of bite/butt which seemed to be a better predictor in the middle of the fight). The level of predictiveness with lateral threat apparently decreased progressively through the fight.

**Experiment 2:** In this case, only follow, bite and chase could be used as good predictors of the outcome of the contests. Unlike experiment one, submissive gestures could not be used as predictors. Flee could be used as a predictor by the second quarter and ventral roll by the third quarter. The predictiveness of all behaviour acts apparently increased as the fights progressed, except for follow. The predictiveness of this seemed to decrease as the fight progressed.

The relevant statistical tests (ANOVA) for these predictions are given Tables 3.16 and 3.19.

#### **3.3.4.3 ANOVA on the frequencies of behavioural acts across quarters of fights.**

The graphs for different behaviour categories, illustrating the significant variation in frequencies of behavioural acts through the four quarters of the fights, are given in Figures 3.11 to 3.16 for experiment 1 and Figures 3.17 and 3.22 for experiment 2.

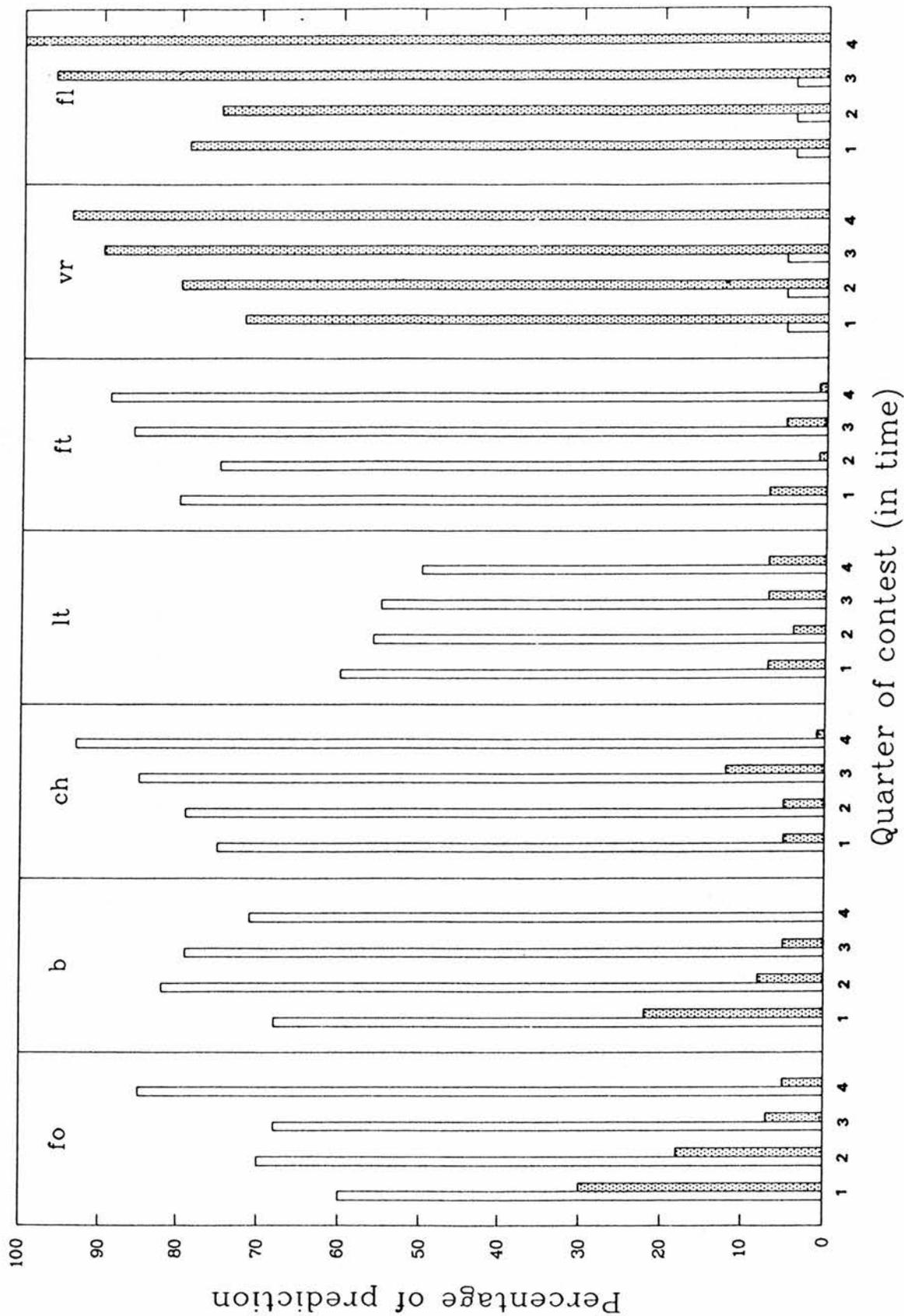


Figure 3.7: Proportion of behaviours performed more by winners or by losers: Experiment 1.

Hatched areas represent loser values.

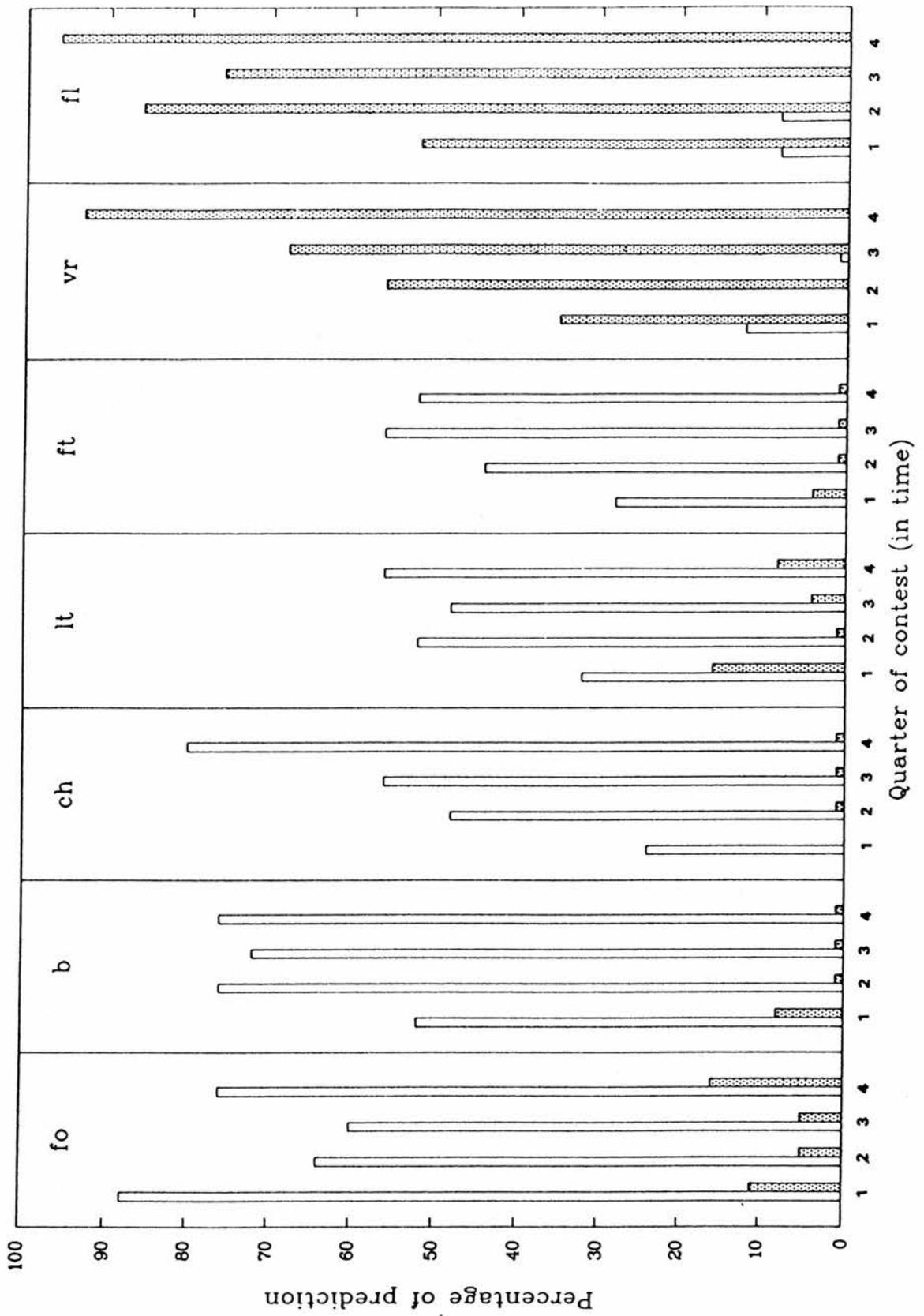


Figure 3.8: Proportion of behaviours performed more by winners or by losers: Experiment 2.

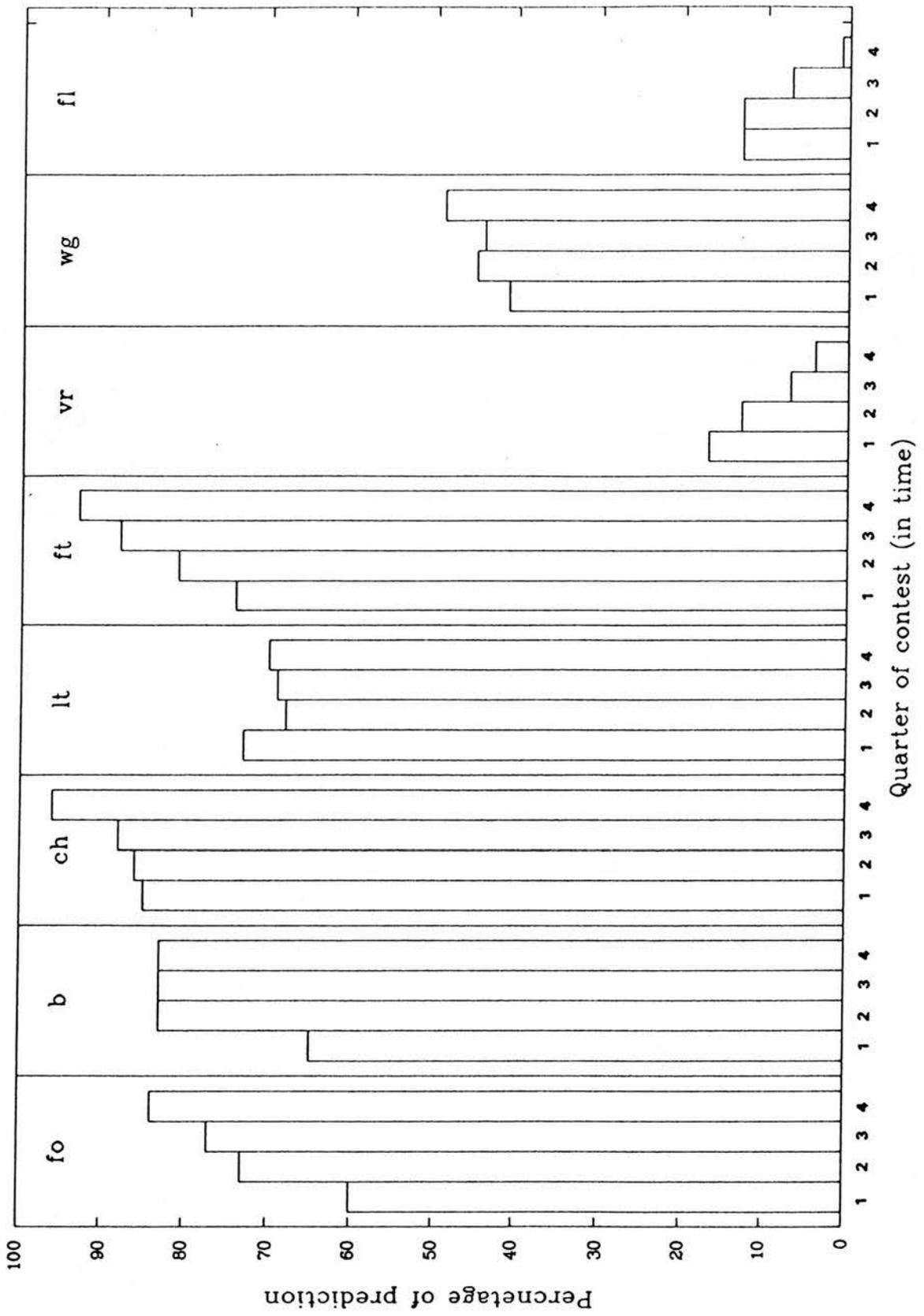


Figure 3.9: Proportion of behaviours performed more by winners: Experiment 1.

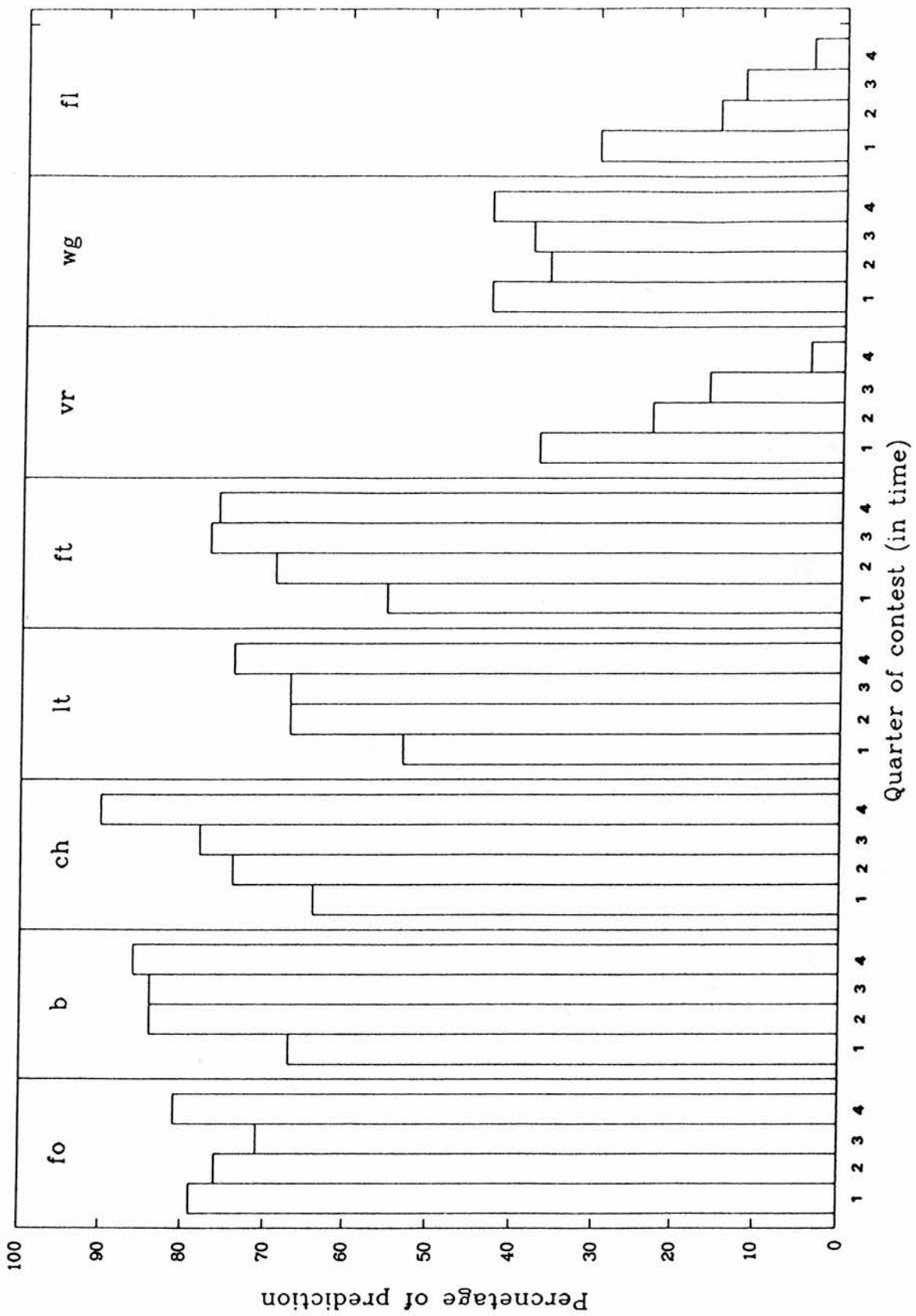


Figure 3.10: Proportion of behaviours performed more by winners: Experiment 2.

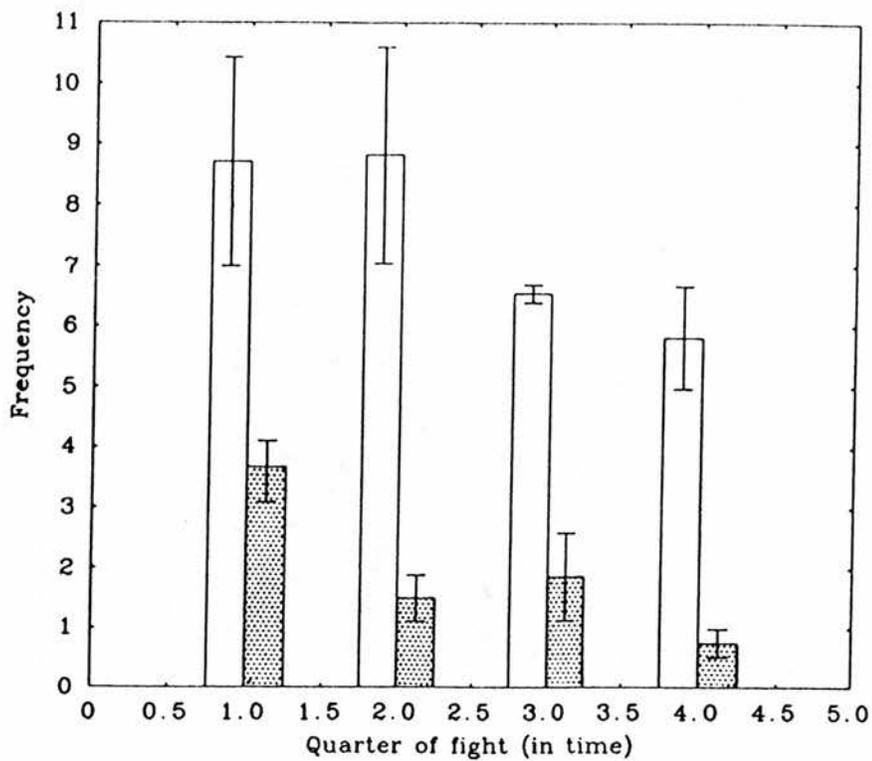


Figure 3.11: Variation in follow by winners and by losers during fights: Experiment 1.

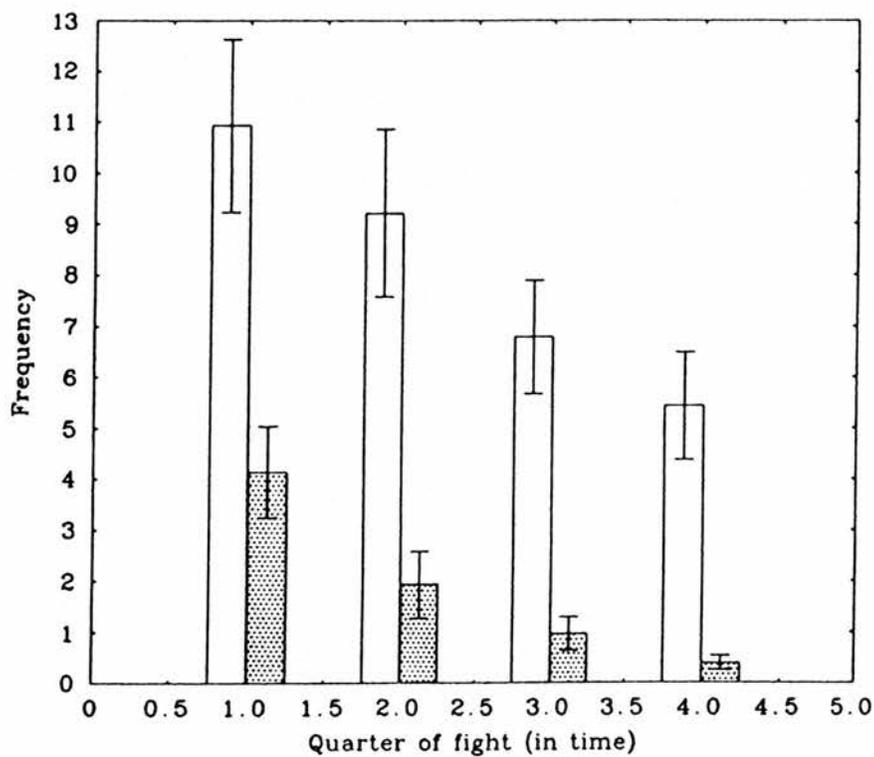


Figure 3.12: Variation in bite/butt by winners and by losers during fights: Experiment 1.

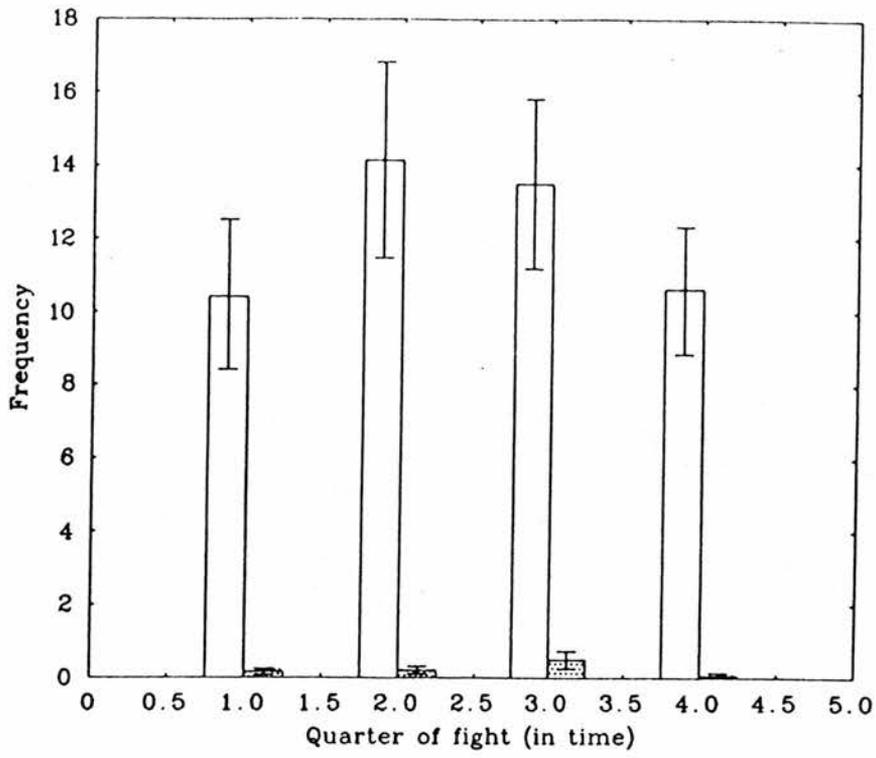


Figure 3.13: Variation in chase by winners and by losers during fights: Experiment 1.

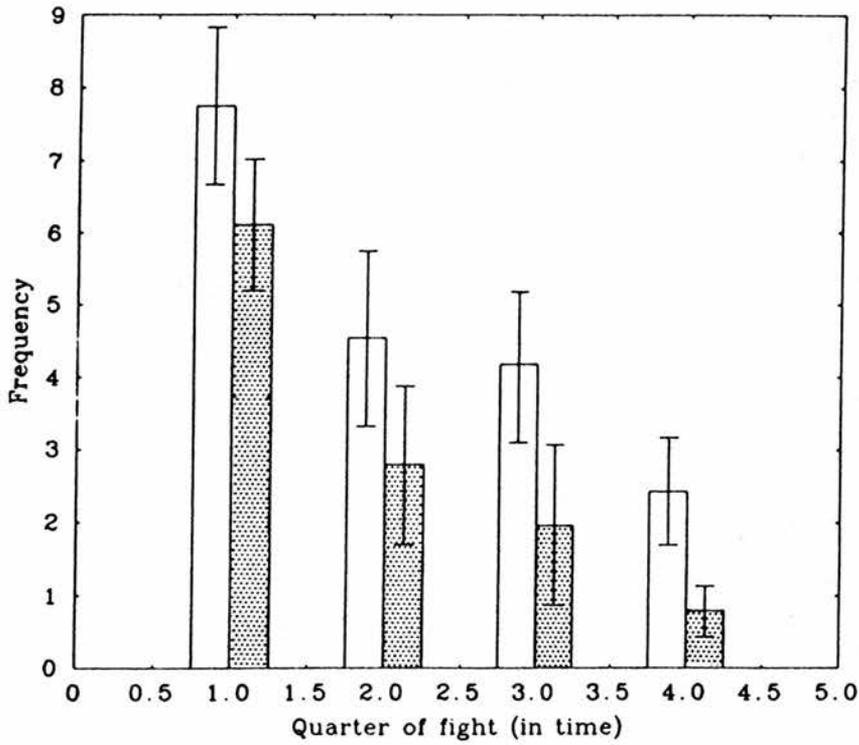


Figure 3.14: Variation in lateral threat by winners and by losers during fights: Experiment 1.

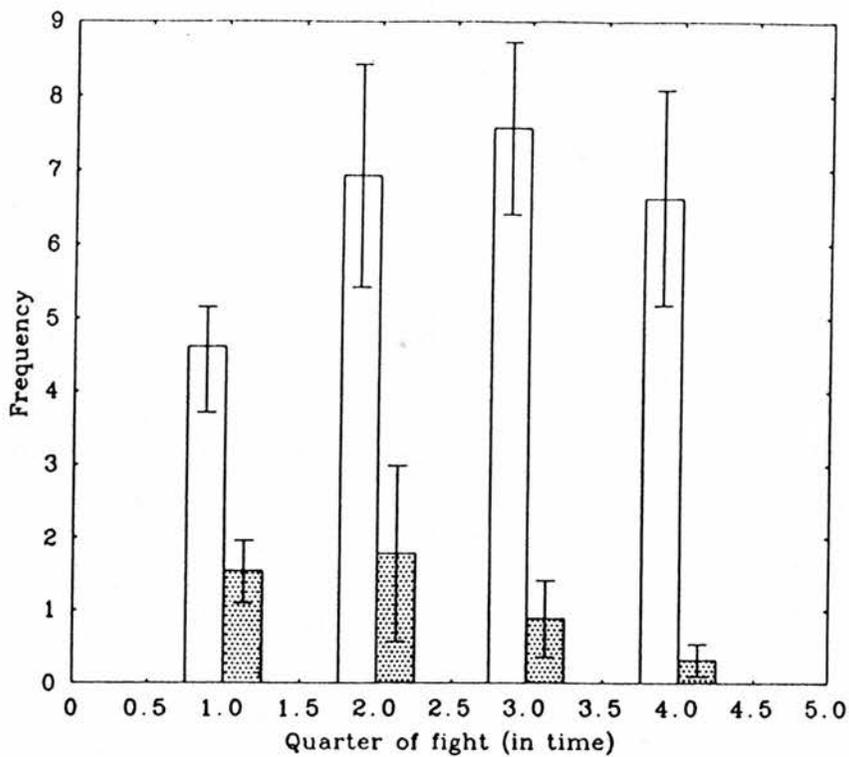


Figure 3.15: Variation in frontal threat by winners and by losers during fights: Experiment 1.

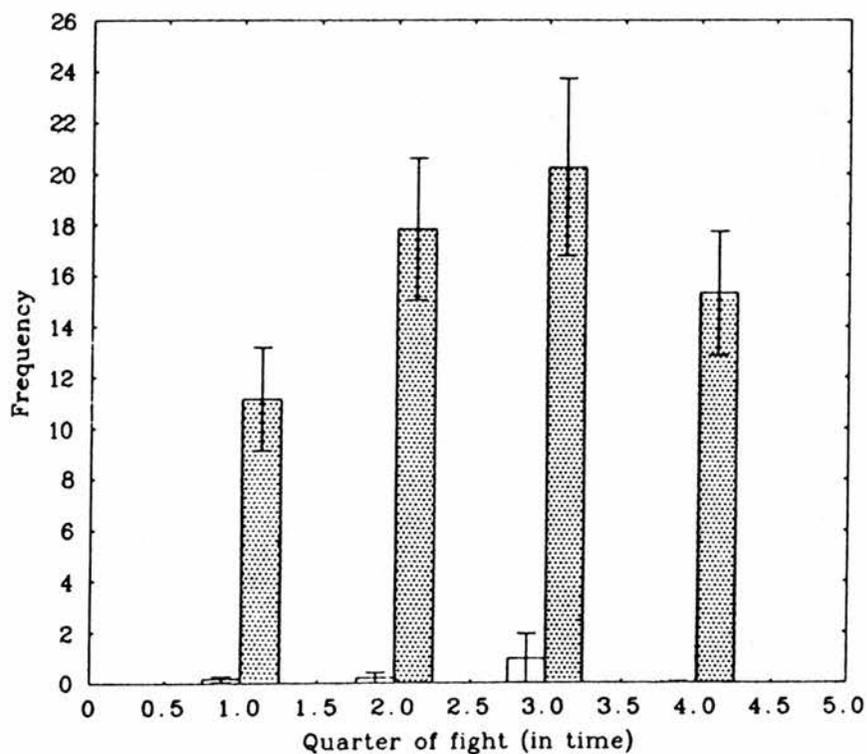


Figure 3.16: Variation in ventral roll by winners and by losers during fights: Experiment 1.

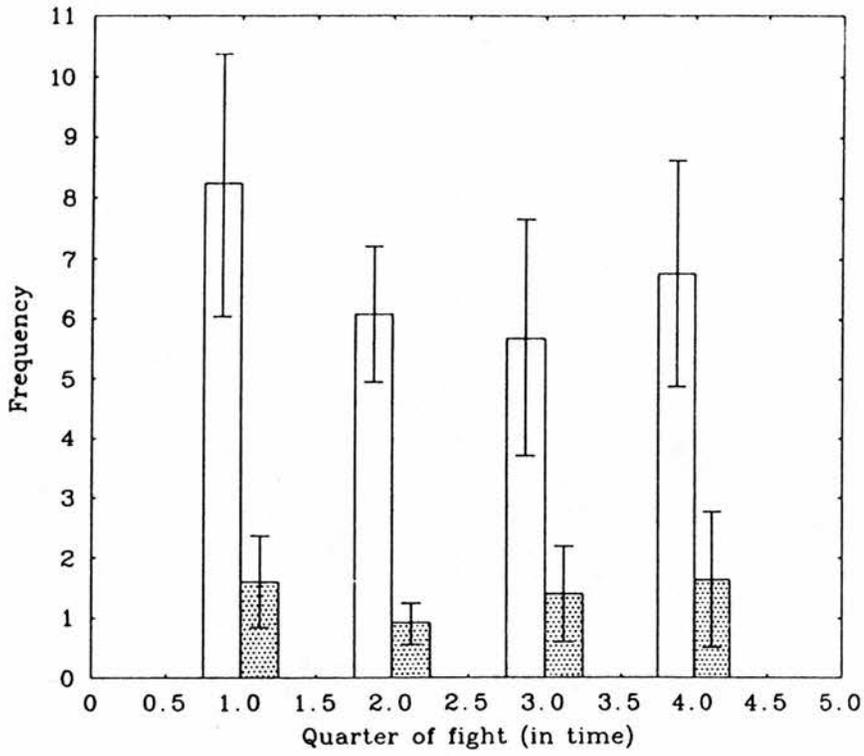


Figure 3.17: Variation in follow by winners and by losers during fights: Experiment 2.

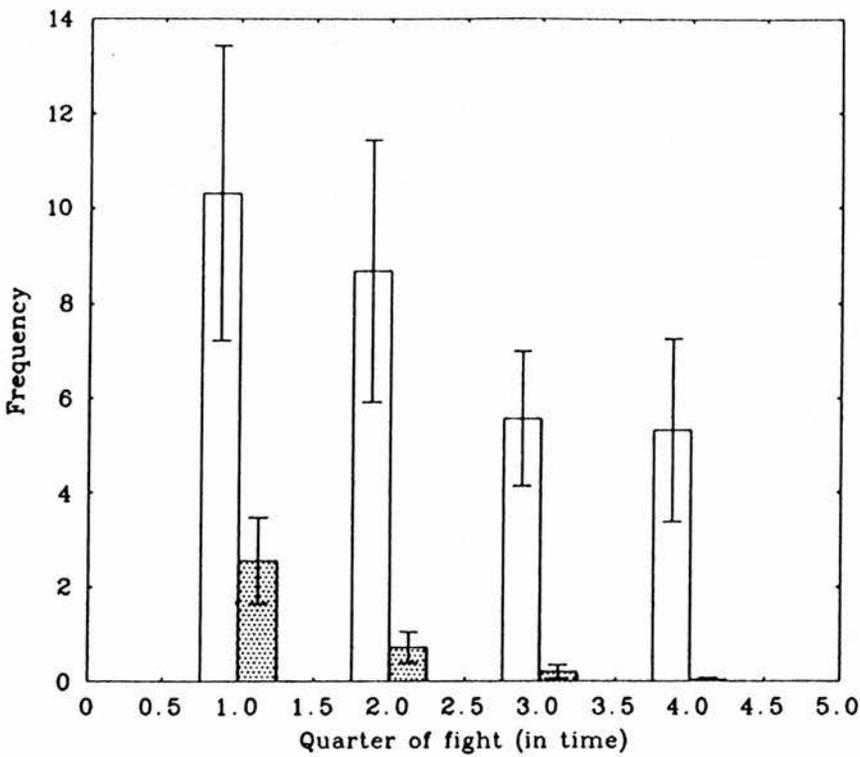


Figure 3.18: Variation in bite/butt by winners and by losers during fights: Experiment 2.

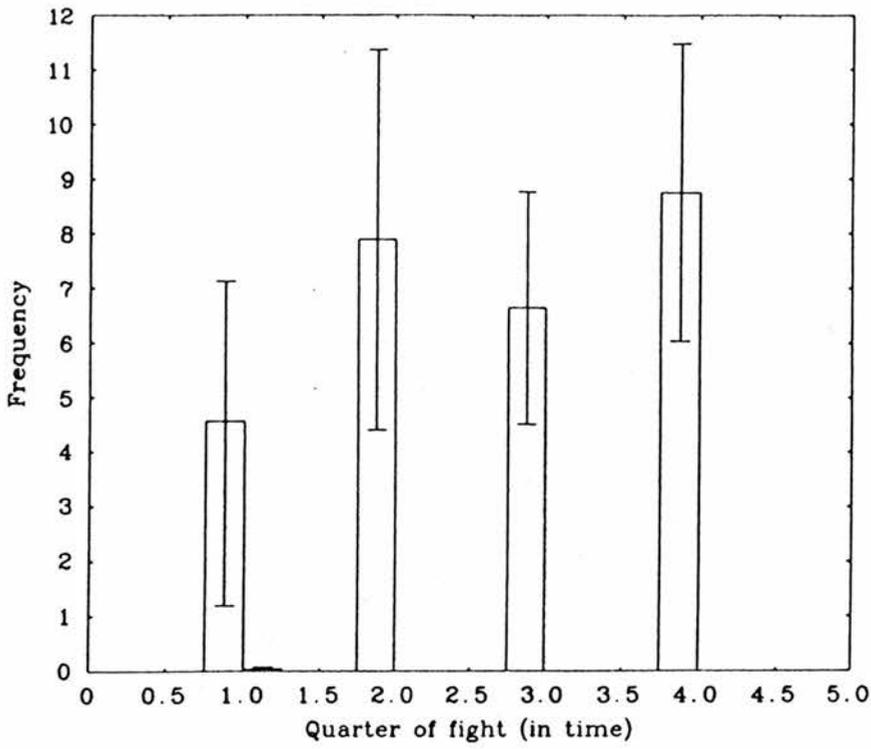


Figure 3.19: Variation in chase by winners and by losers during fights: Experiment 2.

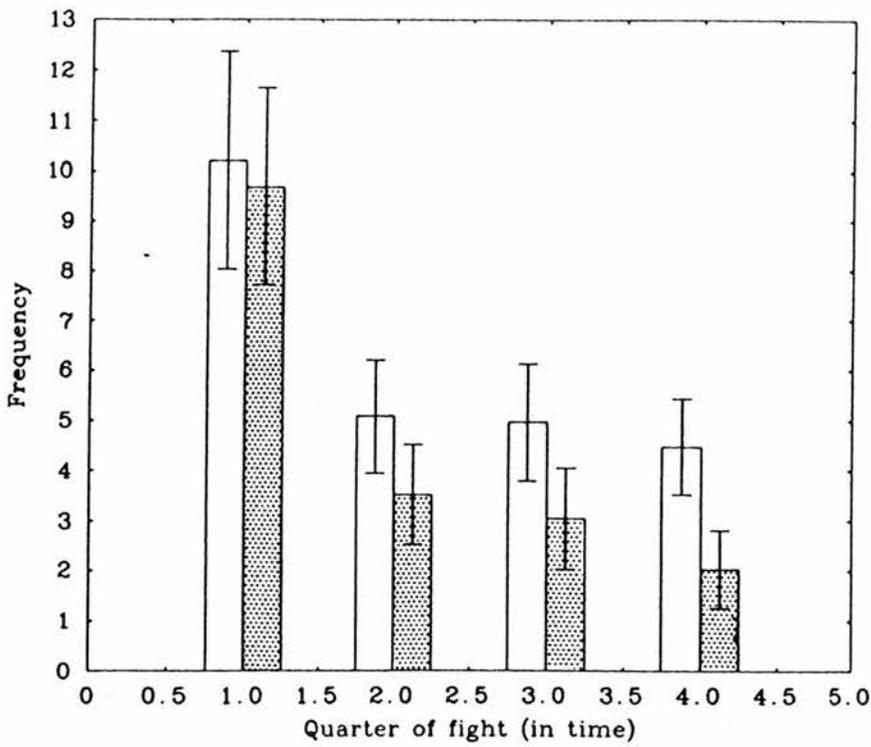


Figure 3.20: Variation in lateral threat by winners and by losers during fights: Experiment 2.

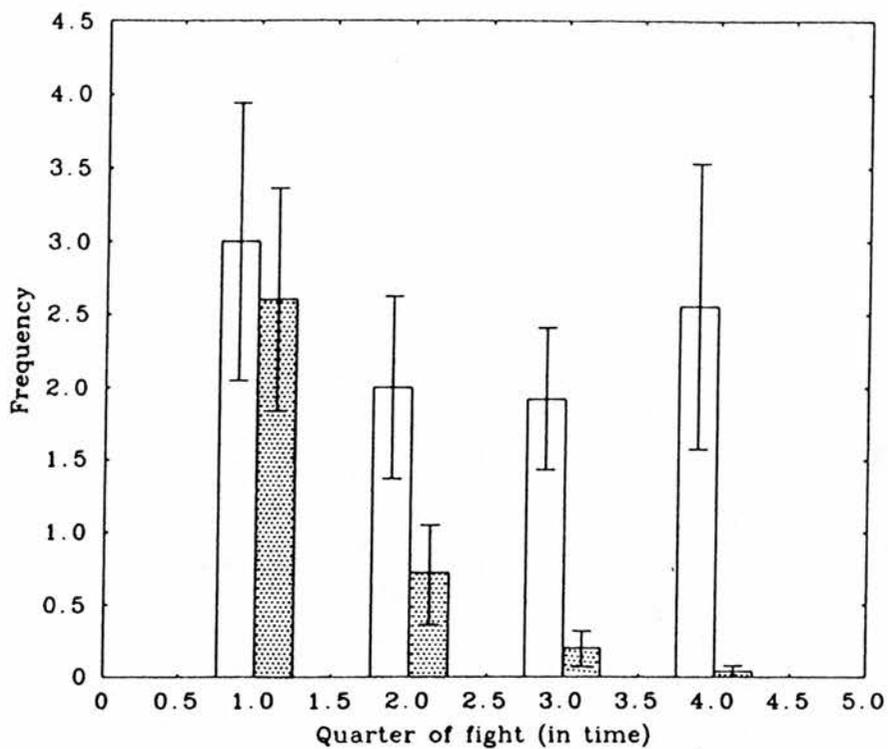


Figure 3.21: Variation in frontal threat by winners and by losers during fights: Experiment 2.

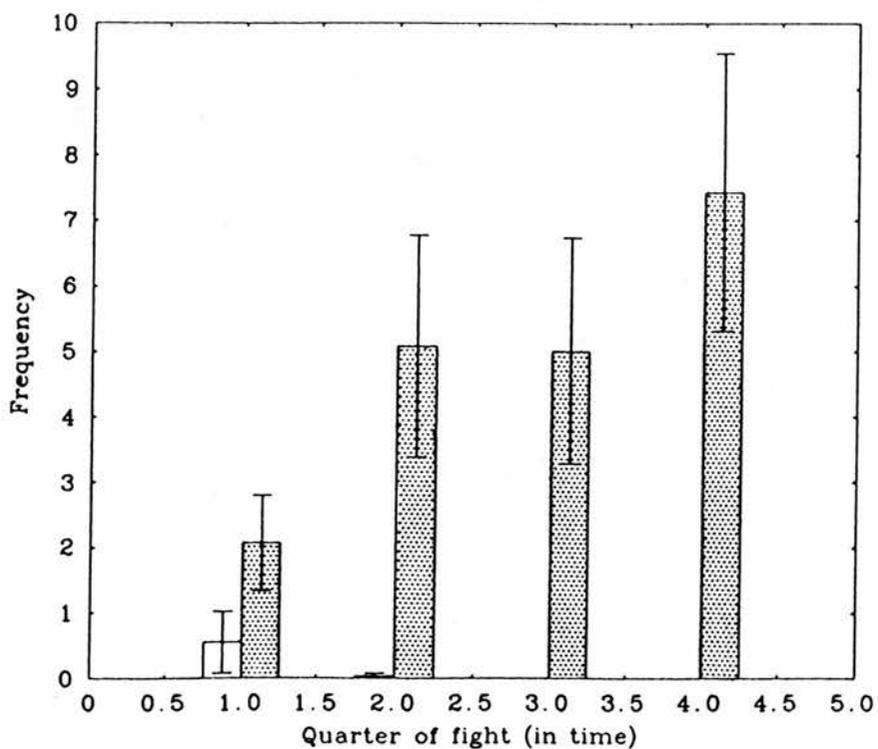


Figure 3.22: Variation in ventral roll by winners and by losers during fights: Experiment 2.

**Experiment 1:** The results of the ANOVA tests on the data show that there was a significant variation across quarters for almost all the behaviour categories tested (Table 3.16). The actions follow, bite/butt, chase (from the second quarter) and lateral threat decreased as a fight progressed. Ventral roll increased as a fight progressed, decreasing again only slightly in the last quarter. Frontal threat increased from the first to the third quarter. However, it gave an insignificant result on the ANOVA due to the closeness in frequencies between the last three quarters, each value being within the confidence limits of the other two (Figure 3.15).

The interaction between winner and loser points was insignificant in each case, except for chase and ventral roll. The significant interaction in the case of chase was due to the marked increase in frequency between the first and second quarters by the winners, whereas for the losers it remained more or less constant and very rarely performed. The significant variation in the case of ventral roll was due to the marked increase in frequency between the first and third quarters by the losers whereas for the winners it remained more or less constant, the only increase being very slight.

A Newman-Keuls post-hoc test was carried out on the ventral roll data (Sokal & Rohlf 1981). This showed an insignificant difference between the frequencies for the winners in the second and third quarters and in the second and fourth quarters. Mean frequencies for each quarter were all insignificantly different from one another for the losers. The results of this test are given in Table 3.17.

**Experiment 2:** There was a significant variation across quarters for all behaviour categories, except for follow. As in experiment one, bite/butt, chase (from the second quarter) and lateral threat decreased as a fight progressed. Ventral roll increased in frequency throughout the fight, unlike experiment one where it decreased in the last quarter. Frontal threat also differed between the two experiments. In this case, it decreased significantly until the last quarter, when its frequency amongst winners increased. The interaction between winner and loser points was again significant in the case of chase and ventral roll, for the same reasons as described in experiment one. The results of this test are given in Table 3.18.

The hypothesis was examined as to whether the difference between the frequencies of

Table 3.16: ANOVA on frequencies of behavioural acts across quarters of fights: Experiment 1 (winners lumped and losers lumped).

Behaviour	Source of variation	<i>f</i> value	<i>d.f</i> <sub>1</sub> / <i>d.f</i> <sub>2</sub>	<i>p</i> value	Significance
follow	winners v losers	20.18	1/54	<0.01	0.01
	fo across quarters	5.49	3/162	<0.01	0.01
	interaction	1.28	3/162	0.28	NS
bite/butt	winners v losers	29.36	1/54	<0.01	0.01
	b across quarters	12.30	3/162	<0.01	0.01
	interaction	0.75	3/162	0.52	NS
chase	winners v losers	37.11	1/54	<0.01	0.01
	ch across quarters	2.73	3/162	0.04	0.05
	interaction	2.15	3/162	0.10	NS
lat. threat	winners v losers	2.23	1/54	0.14	NS
	lt across quarters	33.49	3/162	<0.01	0.01
	interaction	0.12	3/162	0.95	NS
front. threat	winners v losers	27.61	1/54	<0.01	0.01
	ft across quarters	1.10	3/162	0.35	NS
	interaction	1.93	3/162	0.13	NS
waggle	winners v losers	21.55	1/54	<0.01	0.01
	wg across quarters	2.03	3/162	0.17	NS
	interaction	0.66	3/162	0.58	NS
ventral roll	winners v losers	48.70	1/54	<0.01	0.01
	vr across quarters	4.97	3/162	<0.01	0.01
	interaction	3.68	3/162	0.01	0.05
flee	winners v losers	48.27	1/54	<0.01	0.01
	fl across quarters	4.61	3/162	<0.01	0.01
	interaction	4.31	3/162	<0.01	0.01

Table 3.17: Table of results for Newman-Keuls test on ranked means. Matrix of comparisons of observed mean frequencies of ventral roll in quarters of fights.

Quarters	Winner means				Loser means			
	Q <sub>3</sub>	Q <sub>2</sub>	Q <sub>4</sub>	Q <sub>1</sub>	Q <sub>3</sub>	Q <sub>2</sub>	Q <sub>4</sub>	Q <sub>1</sub>
Q <sub>3</sub>	-	NS	0.05	0.01	0.01	0.01	0.01	0.01
Q <sub>2</sub>		-	NS	0.01	0.01	0.01	0.01	0.01
Q <sub>4</sub>			-	0.05	0.01	0.01	0.01	0.01
Q <sub>1</sub>				-	0.01	0.01	0.01	0.01

the behavioural acts of winners and losers would be expected to be much less apparent at the beginning than at the end of the fight. It has already been shown that most of the behaviours shown by tiger barbs could be used as predictors of the outcome, even in the first quarter of fights, and that, at this early stage, there is a difference between the frequencies of acts in eventual winners and losers. To examine whether there was a significant variation in the discrepancy between winners and losers through the fight, ANOVA tests were carried out on the difference in each pair in the frequency of behaviours across quarters of fights (Tables 3.19 and 3.20).

**Experiment 1:** All but ventral roll and flee gave an insignificant result, showing that the contestants in a fight differed as much in the frequency of behaviours at the beginning of fights as they did at the end. The significant result for waggle was because of the marked decrease in frequency of its performance between the first quarter, when it was mostly performed by the winner, and the rest of the fight. The significant result for ventral roll and flee was due to a large increase in frequency between quarters for both behaviours in the losers compared with the tiny fluctuations in the winners.

**Experiment 2:** In this case, only ventral roll and flee gave a significant result, whereas waggle showed an insignificant variation across quarters. The reason for significance in these two behaviours is likely to be the same as in experiment one.

Table 3.18: ANOVA on frequencies of behavioural acts across quarters of fights: Experiment 2 (winners lumped and losers lumped).

Behaviour	Source of variation	$f$ value	$d.f_1/d.f_2$	$p$ value	Significance
follow	winners v losers	19.38	1/48	<0.01	0.01
	fo across quarters	1.79	3/144	0.15	NS
	interaction	0.97	3/144	0.41	NS
bite/butt	winners v losers	9.94	1/48	<0.01	0.01
	b across quarters	5.64	3/144	<0.01	0.01
	interaction	0.98	3/144	0.40	NS
chase	winners v losers	7.06	1/48	0.01	0.05
	ch across quarters	2.96	3/144	0.03	0.05
	interaction	3.07	3/144	0.03	0.05
lat. threat	winners v losers	1.01	1/48	0.32	NS
	lt across quarters	25.27	3/144	<0.01	0.01
	interaction	0.44	3/144	0.73	NS
front. threat	winners v losers	4.30	1/48	0.04	0.05
	ft across quarters	6.36	3/144	<0.01	0.01
	interaction	1.99	3/144	0.12	NS
waggle	winners v losers	3.31	1/48	0.08	NS
	wg across quarters	6.21	3/144	<0.01	0.01
	interaction	0.86	3/144	0.46	NS
ventral roll	winners v losers	10.31	1/48	<0.01	0.01
	vr across quarters	4.80	3/144	<0.01	0.01
	interaction	7.42	3/144	<0.01	0.01
flee	winners v losers	8.27	1/48	0.01	0.05
	fl across quarters	2.61	3/144	0.05	NS
	interaction	4.86	3/144	0.01	0.05

Table 3.19: ANOVA on frequency between each pair of behaviour patterns across quarters of fights: Experiment 1.

Behaviour	Source of variation	$f$ value	$d.f_1/d.f_2$	$p$ value	Significance
follow	diff fo across 1/4's	1.27	3/81	0.29	NS
bite/butt	diff b across 1/4's	1.13	3/81	0.34	NS
chase	diff ch across 1/4's	2.11	3/81	0.34	NS
lat. threat	diff lt across 1/4's	0.30	3/81	0.82	NS
front. threat	diff ft across 1/4's	2.65	3/81	0.06	NS
flee	diff fl across 1/4's	3.41	3/81	0.02	0.05
ventral roll	diff vr across 1/4's	3.51	3/81	0.02	0.05

Table 3.20: ANOVA on frequency between each pair of behaviour patterns across quarters of fights: Experiment 2.

Behaviour	Source of variation	$f$ value	$d.f_1/d.f_2$	$p$ value	Significance
follow	diff fo across 1/4's	1.12	3/72	0.35	NS
bite/butt	diff b across 1/4's	1.44	3/72	0.24	NS
chase	diff ch across 1/4's	1.96	3/72	0.13	NS
lat. threat	diff lt across 1/4's	2.17	3/72	0.10	NS
front. threat	diff ft across 1/4's	2.37	3/72	0.08	NS
ventral roll	diff vr across 1/4's	5.25	3/72	0.003	0.01
flee	diff fl across 1/4's	5.27	3/72	0.002	0.01

### 3.3.5 INTENSITY OF FIGHTS

Results were only regarded as significant at the  $p < 0.01$  due to the application of the Bonferroni correction factor (Machlis 1986).

**Experiment 1:** It was found that total acts per minute (acts/min) was significantly negatively correlated with duration of fight (Table 3.21). However, this was not the case for contact:non-contact act ratio. This indicates that shorter fights contain more threat displays per minute but are not of higher intensity.

Table 3.21: Spearman rank correlation: Correlations between weight difference, rank difference, fight duration and measures of intensity.

Variables	<i>N</i>	$r(s)$	Significance
f,a	28	-0.53	0.01
	25	-0.09	NS
f,c	28	-0.40	0.05
	25	0.33	NS
r,a	28	-0.31	NS
	25	-0.05	NS
r,c	28	-0.05	NS
	25	0.30	NS
w,a	28	-0.34	0.05
	25	-0.37	0.05
w,c	28	-0.07	NS
	25	-0.15	NS

f = fight duration

r = rank difference

w = weight difference

a = acts/min

c = contact:non-contact ratio

N = number of fights

Neither rank difference nor weight difference correlated significantly with either measure. Thus those fish that were more evenly matched in rank or weight did not have a greater likelihood of higher intensity contests.

**Experiment 2:** Each correlation produced an insignificant result. Therefore, in this case, shorter fights did not contain more threat displays per minute.

The results for the tests on the amount of gaps in fighting are given in Table 3.22. Each correlation gave an insignificant result in both experiments. However, in experiment one the fights did contain a greater number of short gaps in fighting (av stops/min=1.89) compared with experiment two (av stops/min=0.77).

Table 3.22: Spearman rank correlation: Correlations between weight difference, rank difference, fight duration and frequency of stops in fighting/min.

Variables	<i>N</i>	<i>r(s)</i>	Significance
r,s	28	-0.24	NS
	25	-0.13	NS
w,s	28	+0.28	NS
	25	+0.06	NS
f,s	28	-0.03	NS
	25	-0.38	0.05

f = fight duration

r = rank difference

s = stops/minute

N = number of fights

The results for the ANOVA tests on the variation in acts/min and contact:non-contact act ratio through the four quarters of the tiger barb fights are summarised in Table 3.23 and graphs for the frequencies of these measures are given in Figures 3.23 and 3.24 for experiment 1 and Figures 3.25 and 3.26 for experiment 2.

**Experiment 1:** There was no significant change in contact:non-contact act ratio, though it did increase somewhat in the third quarter and decrease in the last quarter.

Table 3.23: ANOVA on frequencies of aggression across quarters of fights.

Measure	<i>f</i> value	<i>d. f</i> <sub>1</sub> / <i>d. f</i> <sub>2</sub>	<i>p</i> value	Significance
acts/min across quarters: Experiment 1	5.83	3/81	<0.01	0.01
acts/min across quarters: Experiment 2	2.52	3/72	0.06	NS
cnc across quarters: Experiment 1	1.00	3/81	0.40	NS
cnc across quarters: Experiment 2	1.67	3/72	0.18	NS

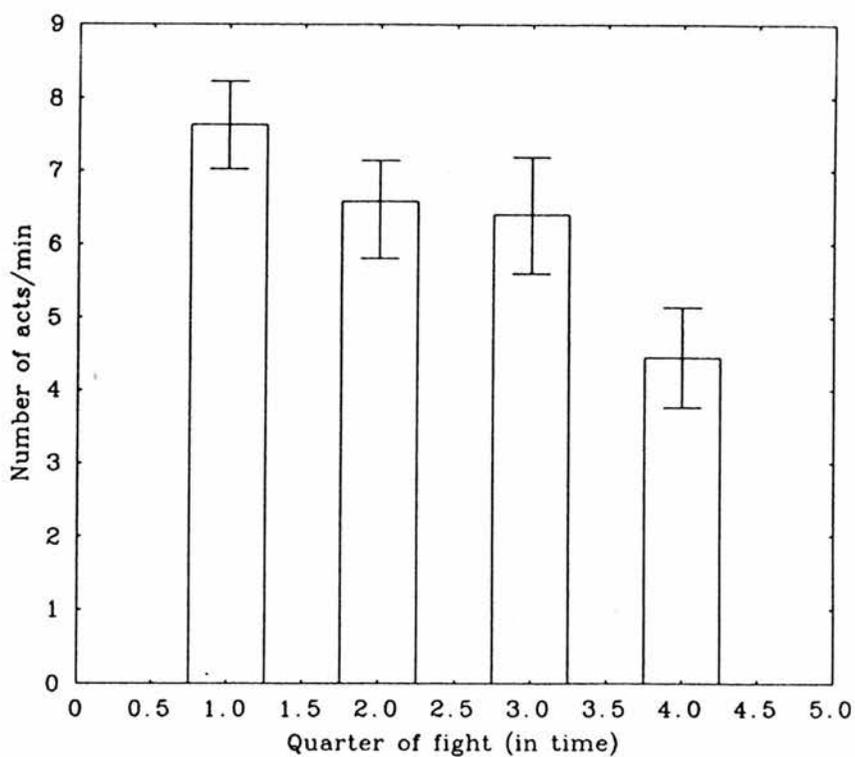


Figure 3.23: Variation in acts/min during fights: Experiment 1.

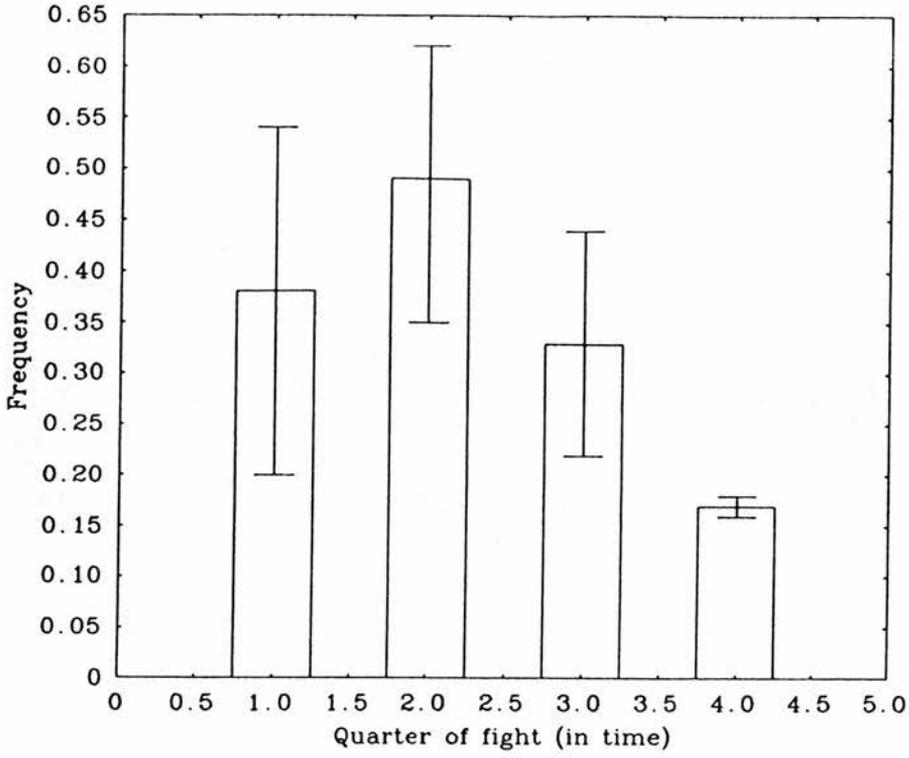


Figure 3.24: Variation in contact:non-contact act ratio during fights: Experiment 1.

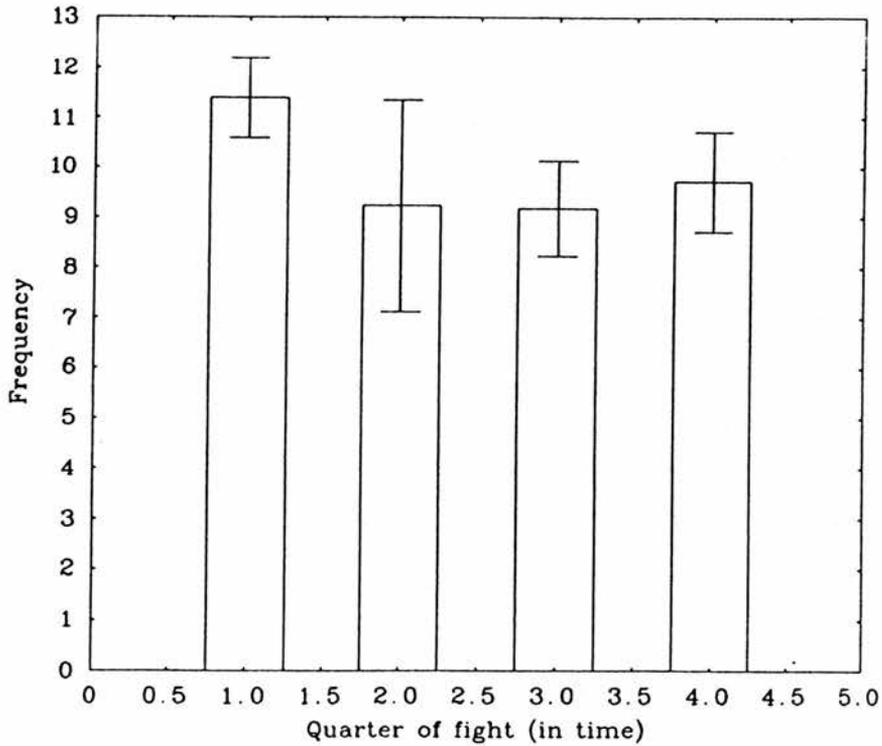


Figure 3.25: Variation in acts/min during fights: Experiment 2.

However, acts/min decreased significantly across quarters, being at its highest in the first quarter. A Newman-Keuls post hoc test (Table 3.24) shows that acts/min did not vary significantly between the first three quarters, but that each of these quarters had significantly more acts/min than the last quarter. There was thus no significant increase in intensity through the fight, but there was a significant decrease at the end of the fight.

Table 3.24: Results for Newman-Keuls test on ranked means. Matrix of comparisons of observed mean frequencies of acts/min in different quarters of fights.

	Q <sub>1</sub>	Q <sub>2</sub>	Q <sub>3</sub>	Q <sub>4</sub>
Q <sub>1</sub>	—			0.01
Q <sub>2</sub>		—		0.05
Q <sub>3</sub>			—	0.01
Q <sub>4</sub>				—

Q<sub>1</sub>...Q<sub>4</sub> represent the various quarters.

Blank squares denote insignificant differences between the two quarters compared.

**Experiment 2:** There was no significant variation in either measure of intensity across the quarters of the fights. This implies that the level of intensity did not vary as the fights progressed.

### 3.3.6 INDIVIDUAL DIFFERENCES IN BEHAVIOUR

It was found in both experiments that weight and rank were not correlated (Tables 3.25 and 3.25) and neither measure correlated with the frequency of any behavioural act. Rank and fight duration were not significantly correlated, indicating that fights were of random duration. Weight did not correlate with either intensity measure.

**Experiment 1:** Both acts/min and contact:non-contact act ratio gave significant correlations with rank (Table 3.25). Therefore higher ranking fish tended to fight at a higher intensity regardless of the rank of the opponents (as already described in section 3.5, where intensity was not significantly correlated with rank difference).

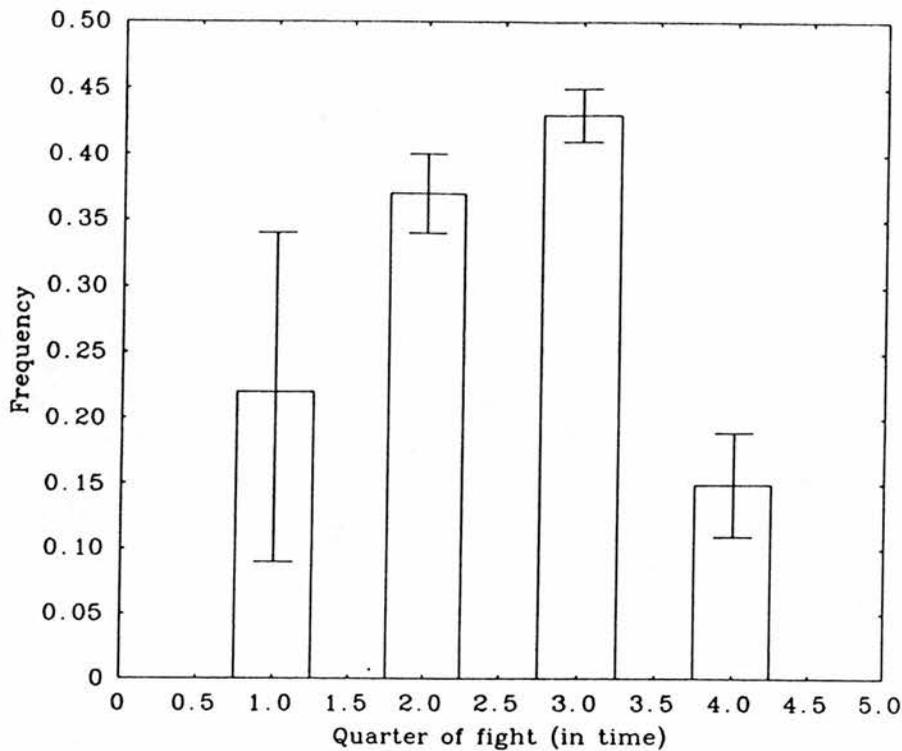


Figure 3.26: Variation in contact:non-contact act ratio during fights: Experiment 2.

Table 3.25: Spearman rank correlations: Experiment 1. Correlations between weight, rank, fight durations, behavioural acts and measures of intensity.

Variables	$N$	$r(s)$	Significance
w,r	8	-0.33	NS
r,a	8	-0.60	NS
r,c	8	+0.91	0.01
w,a	8	+0.60	NS
w,c	8	+0.48	NS
w,d	8	+0.48	NS
r,d	8	+0.43	NS

Table 3.26: Spearman rank correlations: Experiment 2. Correlations between weight, rank, fight durations, and measures of intensity.

Variables	$N$	$r(s)$	Significance
w,r	8	-0.33	NS
r,a	8	-0.66	NS
r,c	8	-0.88	0.05
w,a	8	+0.71	NS
w,c	8	+0.48	NS
w,d	8	+0.57	NS
r,d	8	-0.44	NS

**Experiment 2:** Contact:non-contact act ratio was significantly correlated with rank. However, acts/min was not (Table 3.26). This indicates that higher ranking fish performed more contact acts, but lower ranking fish had a similar rate of acts/min in their contests due, perhaps, to their submissive actions. Neither weight nor rank correlated with duration of fight, indicating that those fish which were heavier or higher in rank did not always persist in the fight for longer, the overall distribution of fights being of random duration.

### 3.4 DISCUSSION

#### 3.4.1 LINEARITY OF HIERARCHY

The results of experiment one show that the tiger barbs could not be arranged in a fashion which was significantly different from random, as there were four reversals present where one fish defeated another apparently higher in rank. Two of these reversals were fish winning against one apparently five ranks higher in the hierarchy, which further increased the randomness of the arrangement. There is, however, the possibility that other factors (*e.g.* motivational state) are playing a part in bringing about such reversals (Wilson 1975). Two of the reversals also occurred in the first round of experiments.

This could be due to the fish being unsettled when meeting an opponent after a long time in isolation. The other two reversals occurred in the last round. No explanation of why this should be the case is obvious. It is possible that experience affects some fish more than others, leading eventually to unexpected defeats. The role of learning due to cumulative fight experience in the outcome of fights is, therefore, investigated in Chapter 4.

In experiment two, only one reversal occurred and, therefore, the hierarchy was significantly linear. This is what would be expected as such defeats should be the exception rather than a common occurrence.

The discrepancy between the two experiments could be due to the fact that, as the loser was able to hide from the dominant, the fight ended. However, in experiment one, the loser could not hide and so the contest continued. As the dominant fish tired from continuous chasing and biting (which may be more energy consuming activities than fleeing) the subordinate may have been able to retaliate, thus resulting in a reversal.

The environment in which the fish fought was a very artificial one. The environment in experiment two would be closer to the wild state, as the fish would be able to hide in the murky waters of their natural environment.

The fish were not ranked by weight, as is the case with many other species. They were possibly ranked by another factor, such as motivational state or hormone levels. Both of these conditions could vary a lot and could therefore explain the lack of linearity. However, these factors were not measured in this study.

### **3.4.2 CONTEST LENGTH (LOG-SURVIVORSHIP CURVE)**

The data for both experiments show that the contest durations follow a negative exponential distribution. This indicates that the durations of fights were random. This is expected when there is no ESS strategy for a fixed time of persistence, but that the one which wins is the one which holds out for the longest time (Mosler 1985). Turner and Huntingford (1986) found a negative exponential distribution of durations also, even though the fights they studied were asymmetric, the winner being determined by size.

This was not the case here. The war of attrition model is based on the assumption that the opponents are evenly matched in fighting ability and that only a difference in persistence times is used to determine the outcome (Turner & Huntingford 1986). It is clear from the results reported here that all fights were not evenly matched. This could, however, be due to a greater strength of some fish and ability to persist for longer, perhaps due to a more excited motivational state. The results, in that case, would fit in with the war of attrition model. These questions cannot be answered as there is no measurement of the strength or motivational state of the fish.

Fights between fish that were closer together in rank were not of a different duration to those further away in rank. It would, however, have been expected that fights between more evenly matched fish would be longer. This might not be expected to be the case if both fish were low in the hierarchy, for instance, and both tended to have relatively short persistence times, which could be the case if persistence times varied according to an individual's strength. However, it was found, when looking at individual differences, that lower ranked fish did not have shorter fights than higher ranked fish, which indicates that all of the fish had similar average persistence times.

The outcome of the analysis of the durations of fights may be due to the fact that, in these small samples of eight fish, all were evenly matched, there being only a slight difference between the fish placed at the top and at the bottom of the hierarchy. If this is the case, it might offer an explanation as to why, in experiment one, a hierarchy that was significantly different from random was not found.

The average duration of fights in experiment two (25 min) was significantly less than in experiment one (55 min). Therefore, providing cover for the loser to escape and hide and thus visually isolating the opponents, leads to an earlier termination of contests.

### **3.4.3 THE BEHAVIOUR OF WINNERS AND LOSERS**

Games theory expects the behaviour of the eventual winner and loser in a fight to be indistinguishable for most of the contests (Turner & Huntingford 1986). According to Dow *et al.* (1976), most functional systems in behaviour, such as aggressive en-

counters, are structured in time, with the frequencies of behavioural elements changing during the course of the encounter, which was the case in their experiments. They also suggested that matching occurs during a fight, with both fish achieving the same level of aggression. This falls abruptly at the end when the actions of one fish signal defeat. Balthazart (1973), on *Tilapia macrochir*, and Turner and Huntingford (1986), on *Oreochromis mossambicus*, divided the fights into quarters and found that the outcomes could be predicted by the end of the first quarter. The remaining period merely accentuated the differences in behaviour of the dominant and subordinate fish apparent at that stage. The data here also show that the outcome of fights could be predicted from the very beginning of the fights, there being great differences in behaviour between winners and losers. These differences continued right through the fight, indicating that matching did not in fact occur. However, in experiment two, it was harder to predict the outcome of fights in the first quarter. This could be due to the fact that, as the end of the fight was extended in experiment one, the quarters contained a different proportion of the behaviours than in experiment two and thus had a greater amount of the actual fight in the first quarter, resulting in easier predictions.

As in the experiments of Ewing and Evans (1973), though the dominants already had the upper hand in a fight, the subordinates continued to display to and follow the dominant, thus apparently inviting attack. The behaviour of the subordinates may represent a continual testing of the relationship. This may explain why, in one case in experiment one, a reversal of dominance occurred during a fight with the fish that appeared initially to be subordinate retaliating and eventually winning the fight. In a natural environment where the fish are not separated after each fight, this testing of relationships could perhaps lead to reversals of the fights that appear to have gone the wrong way, thus leading to the formation of a true linear hierarchy. This testing of relationships inevitably leads to prolonged fights. This may allow time for each fish to learn *its own place* (the position it is able to defend) in the hierarchy, thus reinforcing the relative ranks of the contestants.

As the loser could not easily escape the dominant in experiment one, the fights were more prolonged than in experiment two, resulting in a greater amount of *testing*. This would explain why the loser performs more follow and lateral threat in this case than in experiment two.

Long fights are only adaptive to the fish at an initial disadvantage if it has some chance of winning. If the benefits of winning are sufficiently great or the consequences of losing sufficiently severe, such as a possible reduction in reproductive success, then it is worthwhile fighting for as long as possible, even when the chance of winning is low (Dow *et al.* 1976).

Prolonged fights may be a consequence of the fact that displays or actions which can be used to predict the outcome of fights might not be transmitting information about the intentions of either fish, as Maynard Smith (1982) suggests that they should not. However, it may not be possible for an individual to hide its intentions, or, if RHP assessment is being used, an eventual loser might not be able to disguise its inferiority successfully. Information might be transmitted as a side effect of an action, the advantages of which outweigh the disadvantages of the signal (Krebs & Dawkins 1984, Turner & Huntingford 1986). Examples of this would be probing for information or defensive strategies (such as ventral roll). Actions which have highest frequency at the beginning of the fight and decrease as the fight progresses (such as lateral threat) may be activities that assess the RHP of the opponent. The fact that chase showed an increase in the second quarter, may indicate the use of a more aggressive act to display RHP. However, it may simply indicate that the eventual winner was asserting its dominance over its opponent.

Mosler (1985) suggests that a reason for prolonged fights is that the loser's assessment of its opponent only becomes relevant to it when it becomes aware of a slight tiredness. This Mosler calls the *critical fighting stage*. This is because it is of no advantage to fight to exhaustion as the loser would then become susceptible to disease or to predators. This is very unlikely to be the case. It is more probable that the benefits of winning are great enough to make fighting for as long as possible worthwhile.

What cannot be explained by these suggestions is the fact that, in experiment one, the eventual loser performed obvious submissive behaviour in the first quarter of the fight which tended to stop an attack, but yet the submissive gesture was further ignored and the fight continued for much longer. It would be expected that when one fish indicates by a submissive gesture that it is losing, this act should result in a termination of the fight (Caryl 1979). Submissive or flight behaviour in the early stages of the contest

was also found in the studies of Balthazart (1973), Dow *et al.* (1976) and Turner & Huntingford (1986). However, in experiment two, ventral roll was rarely observed until the third quarter. It therefore did appear, in this experiment, to result in a termination of the fight. It is possible that, had there been more cover present in the tanks in experiment one, many of the fights would have ended sooner. This would have led to proportionately different quarters when the fight was divided and thus much less submissive behaviour occurring in the first quarter. An indication of the subordinates' efforts to concede the victory in experiment one is the large increase in frequency of ventral roll as the contest progressed.

#### 3.4.4 INTENSITY OF FIGHTS

If assessment of RHP is occurring, then it would be expected that contests between more evenly matched opponents should be of greater cost (Turner & Huntingford 1986). The cost of contests can be increased by an increase in the performance of high-cost acts, such as biting or mouth-fighting, an increase in the rate of performance of acts leading to an increase in the cost per unit time, or by fighting for longer. According to Mosler (1985), the contestant must only compare its state with the supposed one of its opponent, seen in its reactions as they test each other in direct, energy costing, physical combat. Otherwise, it might be possible for the inferior individual to feign strength and thereby cheat its opponent. Dow *et al.* (1976) suggest that the intensity of fights should be greatest in the middle, falling precipitously at the end. The data given here did not show an increase in intensity as it was high at the beginning of the fights also. This may be due to the fact that the increase occurred very quickly and that dividing the fight into quarters was not sufficient to reveal the presence of such an increase. However, there was a significant decrease in intensity in the last quarter, which agrees with the predictions of Dow *et al.* . This suggests that in the last quarter of the fight the actions merely consisted of submission by the loser and an assertion of the dominant position (by means of chasing, following and threatening) by the winner. Evidence supporting this can be seen from the results of the Wilcoxon test for the last quarter (Tables 3.11 and 3.15). In experiment one, both acts/min and contact:non-contact act ratio decreased in the last quarter. In experiment two, acts/min did not

decrease. This is due to the fact that the fights ended sooner after submission and did not have as many short breaks in fighting as occurred in experiment one due to the loser's unsuccessful attempts at escape. In experiment two, enough coverage was available to allow escape attempts to be more successful, resulting in fewer gaps in fighting and in shorter contests.

The fact that rank difference did not correlate with intensity would suggest that more evenly matched opponents did not have fights of greater cost. As has already been suggested, this may merely be due to the small sample size and the fact that the fish in the experiments may have been too evenly matched to reveal any such differences in intensity.

### **3.4.5 INDIVIDUAL DIFFERENCES**

It has been found in many species that contests are settled on the basis of size, which is typically a measure of RHP. Turner and Huntingford (1986) found that the larger fish of the cichlid species *Oreochromis mossambicus* won, even when the difference in length was as small as 1 mm. In tiger barbs the relative weights of the fish had no influence on the outcome of the contests. Actions of the fish did not have any relevance to the weights of the fish.

It is likely, therefore, that other factors are determining the outcome of the contests. One possibility is that some fish, due perhaps to their hormonal levels, are naturally more aggressive than others and thus have an advantage in contests. This would explain why the apparently higher ranking fish tended to have more aggressive fights regardless of the rank of their opponents. This was investigated in Chapter 6 by comparing aggression within a group formed out of dominant fish and one formed out of submissive fish. Winning one fight may also increase the aggressiveness of a fish in other fights in the near future (before the excited motivational state returns to its previous level).

## **3.5 CONCLUSION**

- (i) Tiger barbs did not form hierarchies in accordance with their weight.

- (ii) Contests between tiger barbs were of random duration. A greater amount of cover, allowing visual isolation of opponents, resulted in shorter fights.
- (iii) The outcome of contests could be predicted in the early stages of a fight. When enough cover is present to allow escape by the loser, a submissive gesture, such as ventral roll, tended to result in a termination of the fight. If cover was lacking, the dominant continued to pursue the subordinate fish long after it had first signalled defeat.
- (iv) Fights were of similar intensity throughout, until the last quarter. This consisted mainly of submission by the loser and assertion of dominance, in the form of chase and threat, by the winner. More evenly matched fish, according to rank, did not have more intense fights. Lack of cover prevented a successful escape by the loser. Therefore, breaks in fighting were followed by further approach, threat or attack by the dominant fish. Where enough cover was available, breaks in fighting, due to escape by the loser, tended to result in a termination of the fight as the opponents were now visually isolated from each other.
- (v) Fish of different weights did not behave differently in fights. Higher ranking fish fought more intensively regardless of the rank of their opponent.

## Chapter 4

# LIVING IN A GROUP: MEMORY OR RECOGNITION?

### 4.1 INTRODUCTION

One aim of the study described in this Chapter is to ascertain whether fish are more or less aggressive to each other when they have been living in a group as opposed to living in a solitary state, as in Chapter 3. Deag (1977) suggested that studies based on dyadic encounters of otherwise isolated animals may have limited usefulness and stressed the need for observation in intact groups. Fernö (1978) suggested that isolation leads to recovery from habituation of a conspecific and tends to increase the aggressiveness of the isolated fish. Such an increase in aggression, due to isolation, was also found by Dixon and Cade (1986), Huntingford and Turner (1987) and also Davis (1975), who suggests that isolation induces increases in aggression and display readiness could be an expression of the general *psychophysiological response* to a low level of environmental stimulation. However, other authors found that social isolation results in a reduction of aggression levels (Heiligenberg 1964, Gallagher *et al.* 1972).

This Chapter also investigates whether individuals that have previously encountered

each other in groups behave differently towards each other than those that have not. This would only occur if individual recognition was occurring with the individuals remembering which fish were dominant or subordinate to them. If this were the case, it would imply that, within groups, individual recognition is involved in the setting up and maintenance of hierarchies. Each individual would become aware of its rank by learning which fish it could dominate and which it could not. The amount of fighting in the group would thus diminish over time as subordinate fish learnt to avoid encounters with those individuals that had beaten them.

Huntingford and Turner (1987) suggest that animals that have the ability to recognize each other individually may use experience in encounters with specific individuals to gain a direct measure of their relative fighting abilities. Eccles and Shackleton (1986) suggested that individual recognition among members of a group might serve to eliminate the need for many social displays once a hierarchy has been established (see also Beaugrand *et al.* 1984, Zayan 1975).

Beacham *et al.* (1987) found that once a dominance relationship was established in *Lepomis gibbosus*, reversals never occurred and he stated this to be an effect of prior experience. It could, however, have been due to a natural asymmetry in RHP or to experience in interpreting RHP signals and have nothing to do with either prior experience or individual recognition.

According to Ginsburg and Allee (1942), inbred mice do not recognize differences between individual competitors, but respond to characteristic patterns of aggressive behaviour or submissive behaviour performed by their opponents. Van Kreveld (1970) explains the transitivity of dominance, found in hierarchies, by individual differences in motivation and ability. However prior experience, he suggests, could result in a reduction of aggression between group members as a result of mutual acknowledgement of dominance relations. Francis (1983) found that experience of being dominated resulted in reduced success in subsequent encounters (see also Thines & Heuts 1968, Frey & Miller 1972, Goldstein 1975, Cain & Baenninger 1980, Bakker & Sevenster 1983, Dixon & Cade 1986, Archer 1988).

Barnard and Burk (1979) suggest that there are three different types of dominance

hierarchy:

- (i) In *statistical hierarchies* the outcome of encounters depends only on the fighting ability of the contestants, the individuals not adjusting their behaviour in the light of experience or assessing their opponents in any way.
- (ii) In *assessment hierarchies* animals adjust their behaviour according to cues from the opponent that correlate with its fighting ability.
- (iii) In *confidence hierarchies* no assessment would take place, but individuals would alter their behaviour according to their own past history. Those that lose become more apathetic and those that win become more aggressive.

These hierarchies do not necessarily involve recognition. Therefore, if any of these types are the case in tiger barbs, no difference in behaviour should be found between opponents which were familiar with each other, from group experience, and those which were not. If the hierarchy is a confidence hierarchy, the behaviour shown in this Chapter should be different to that shown in Chapter 3, as these fish have prior experience of wins and losses, whereas those in Chapter 3 had remained in a solitary state prior to experimentation.

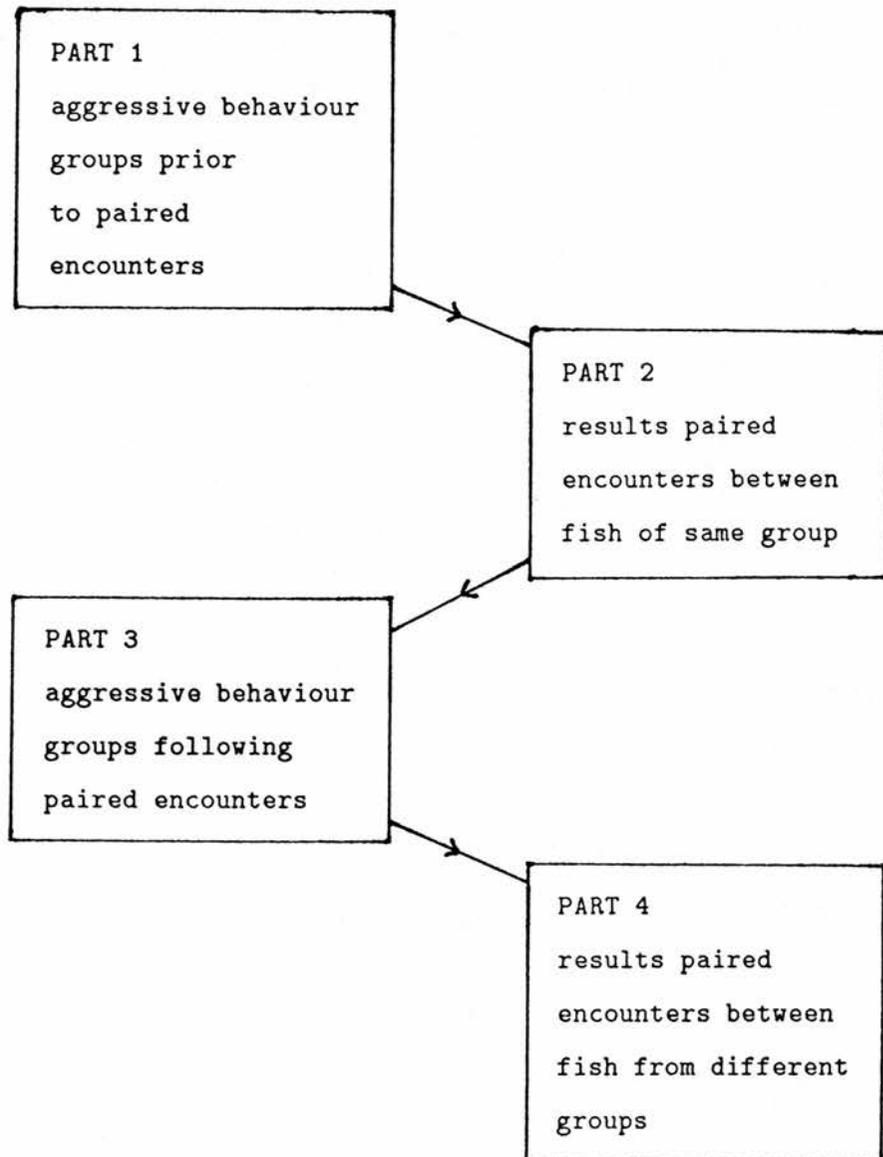
Hierarchies can also be formed by animals recognizing other individuals and using cues unrelated to fighting ability, but adjusting their behaviour according to past experience of wins and losses against that particular individual. If this is the case with tiger barbs, less aggression should be shown by opponents that had previously met within a group situation. Once the fish are returned to their original groups after the pair-fights, the hierarchies should be similar to the original arrangements, each fish recognizing the individuals to which they had been dominant or subordinate.

Shawcross and Slater (1984) found that, although male weaver birds, *Quelea quelea*, formed clear dominance hierarchies, these did not require individual recognition. No difference in fighting could be found in encounters between pairs of birds taken from the same, well established group and pairs taken from different groups. Thus the hierarchy which occurred in settled groups did not appear to depend on past meetings.

This Chapter examines whether a similar situation occurs in groups of tiger barbs which

also form dominance hierarchies. The experiment is carried out in four parts. Parts one and three investigate aggressive behaviour within a group, part one being prior to and part three following paired encounters between fish of the same group. These paired encounters are investigated in part two of the experiment; part four studies paired encounters between fish from the two different groups which have never previously met.

#### Flowchart for experiment



## 4.2 MATERIALS AND METHODS

**Part 1:** This experiment involved two groups of six male tiger barbs each. They were kept in tanks of the same size and conditions as the holding tanks described in Chapter 2, and with the same plant cover as described for the tanks in experiment 2 of Chapter 3. Group 1 was made up of fish *A, B, C, D, E, F* and group 2 was made up of fish *G, H, I, J, K, L*.

The fish were observed for seven days in their respective groups. The method of focal animal sampling, using a check sheet, was used. The behaviour of each fish in a group was continuously recorded for a period of 10 minutes per fish per day. The behaviours recorded were: *Threat* (lateral threat + frontal threat) (*lft*), *Bite/butt* (*b*), *Chase* (*ch*), *Mouth-fight* (*mf*), *Caroussel* (*ca*), *Flee* (*f*) and *Ventral roll* (*vr*).

**Part 2:** The fish then met in paired encounters, each individual meeting another from the same group. The experimental tanks were of the same conditions as those described in part 1, which they were familiar with from their group experience. A round-robin tournament was carried out in which all possible pair combinations of fish from the same group were tested to ascertain dominance relationships. The order in which the pairs were tested was determined in a systematic manner. Each fish fought in a different tank for each contest to eliminate any bias from one fish being more familiar with its surroundings than the other. The fish were transferred from tank to tank, using a beaker, the night before a contest took place. An opaque divider through the centre of the tank separated the two contestants. At the commencement of observations, this divider was removed manually and observations were recorded on the Epson portable computer, as described in Chapter 2.

**Part 3:** The fish were then returned to their original groups and observed for seven days, as in part 1 of this experiment.

**Part 4:** A round-robin tournament of paired encounters was carried out as in part 2, except that each individual in one group met an opponent from the other group.

## 4.3 RESULTS PART 1: GROUP 1 AND GROUP 2

### 4.3.1 HIERARCHIES

The hierarchy for each group was established (Figures 4.1 and 4.2) and the stability of each, over the 7 days observation period, was examined and comparisons were made between the two groups.

In group 1, the hierarchy was not totally stable and originally more submissive fish did improve their position in the hierarchy during the observation period. Challenges to fish higher in rank were a common occurrence.

In group 2, *J* was the dominant fish and was very dominant over the other fish in its group. The other fish in group 2 spent most of the observation period at the sides of the tank and behind the heater and plants. This resulted in far fewer encounters occurring between lower ranked fish than occurred in group 1. At the end of the observation period, individuals *K*, *H* and *L* seemed to have established a territory each, around their hiding places (from *J*), where they remained for most of the observation period, and were dominant to any other fish which entered their territories, except *J*. No territories were observed for any of the fish in group 1.

### 4.3.2 GROUP BEHAVIOUR

The variations in the frequency of threat, bite/butt, chase, ventral roll and contact:non-contact act ratio (*cnc*) over the observation period and between individuals in each group were examined by means of a nested ANOVA (*ALICE statistical package*). The results of these ANOVAS are given in Tables 4.1 and 4.2. Significant variations are illustrated in Figures 4.3 to 4.5 (group 1) and Figures 4.6 to 4.8 (group 2).

In group 1, the frequency of threat displays and chase increased significantly and that of *cnc* decreased significantly towards the end of the observation period. No fish performed any act significantly more than all the other fish.

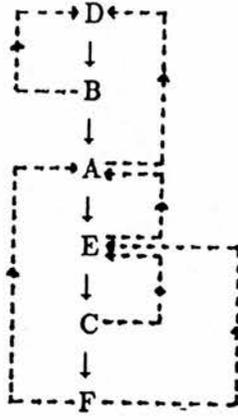


Figure 4.1: Hierarchy: Group 1.

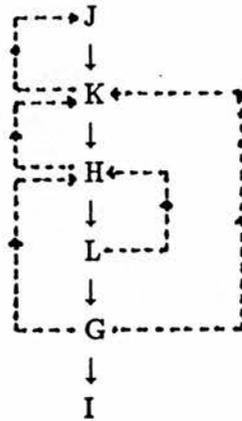


Figure 4.2: Hierarchy: Group 2.

Discontinuous (dotted) arrows indicate direction of aggression shown by a less dominant to more dominant fish.

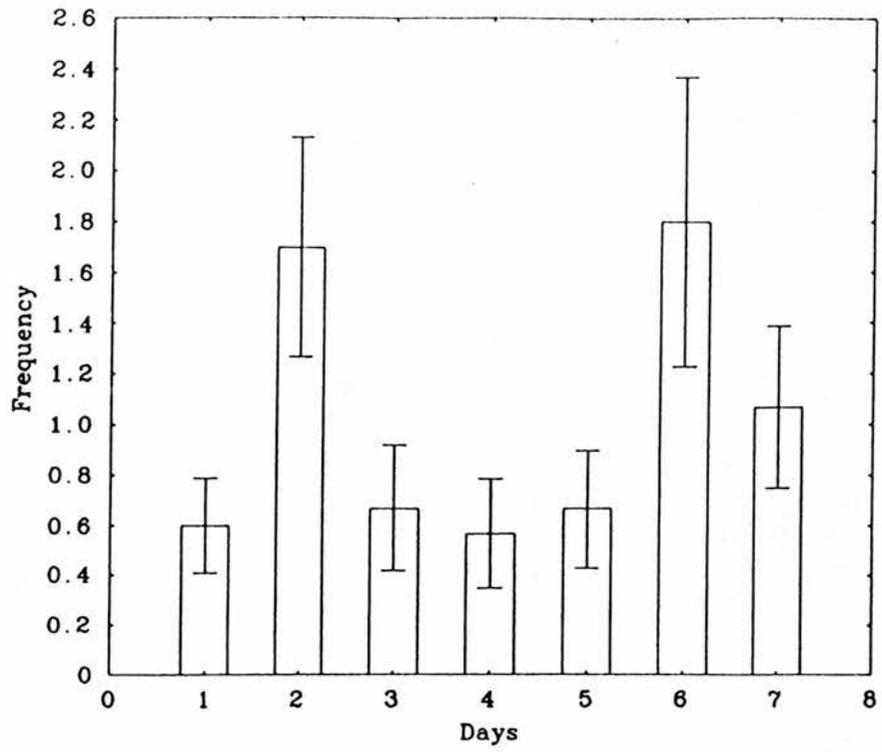


Figure 4.3: Variation in threats over observation period: Group 1.

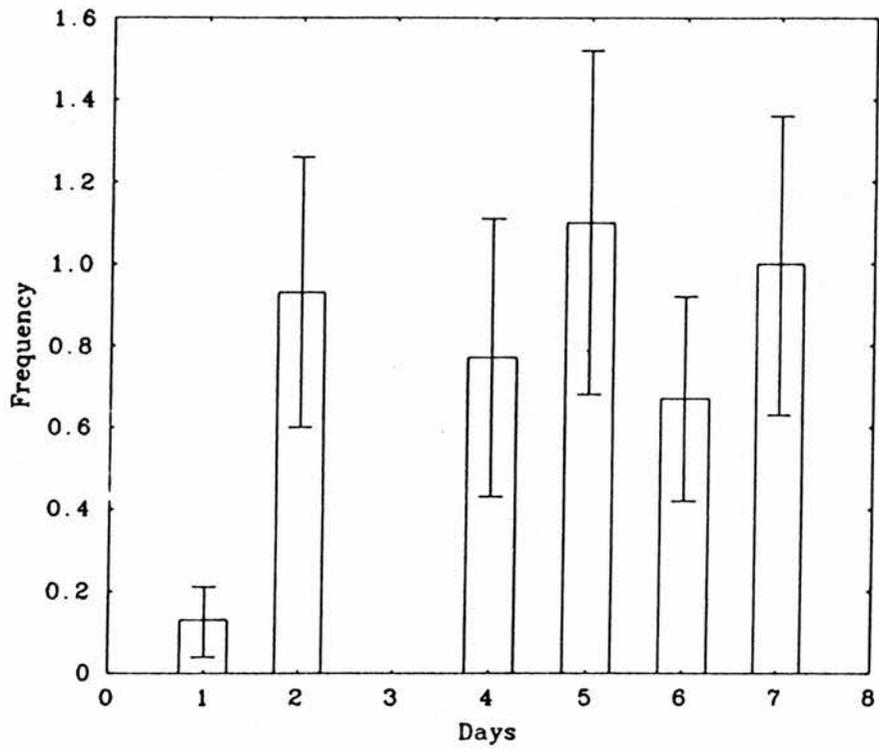


Figure 4.4: Variation in chase over observation period: Group 1.

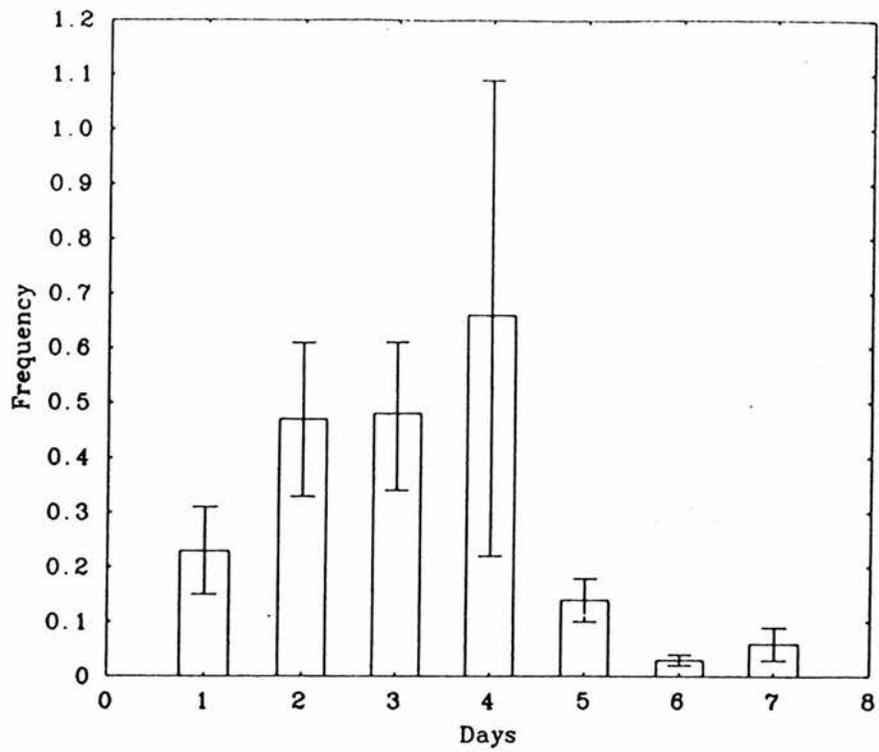


Figure 4.5: Variation in cnc over observation period: Group 1.

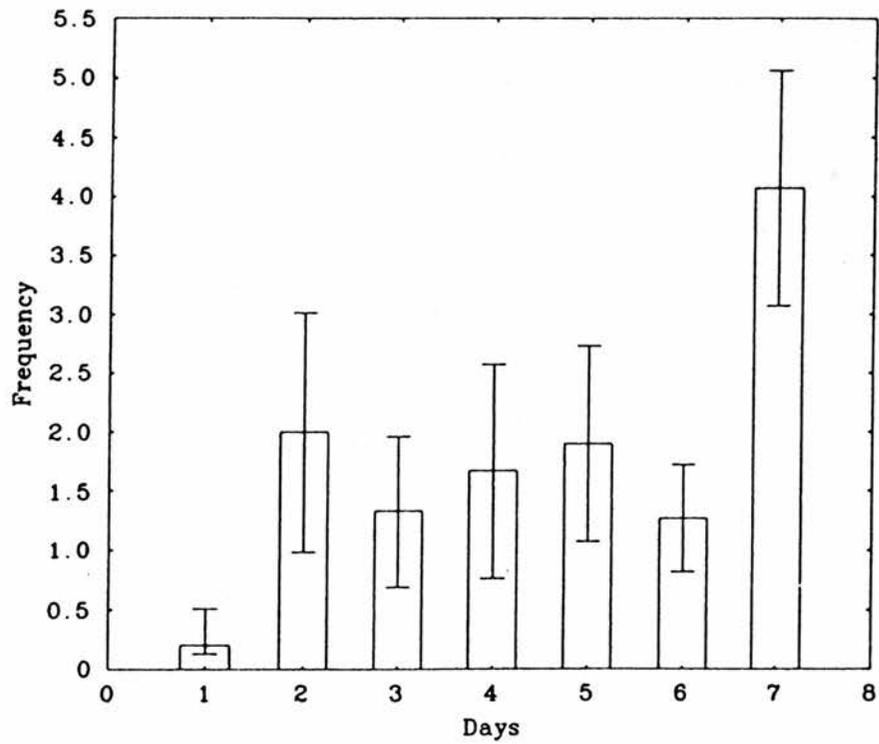


Figure 4.6: Variation in chase over observation period: Group 2.

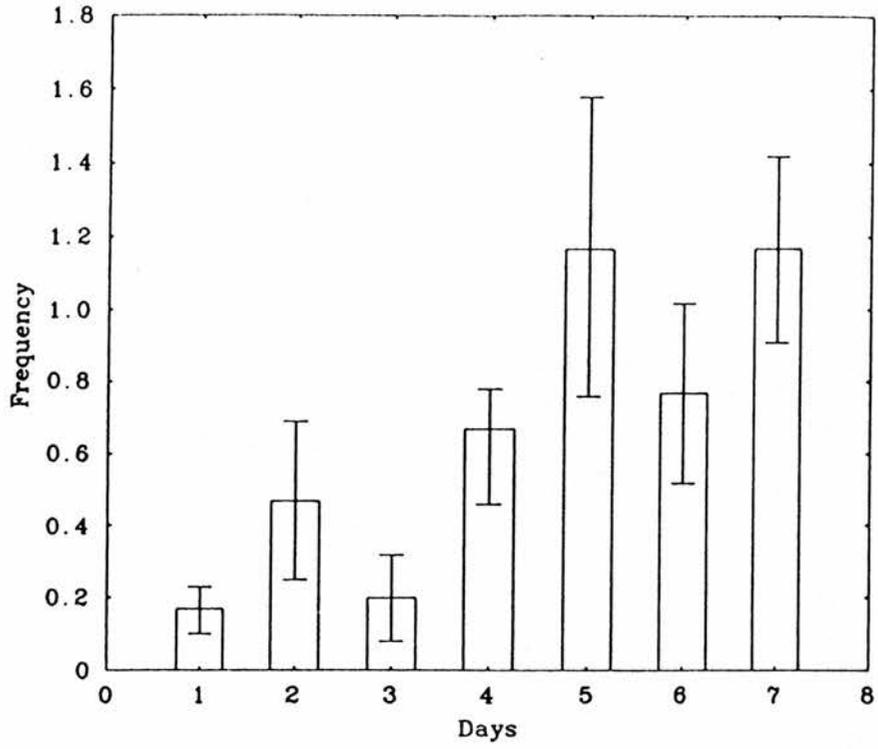


Figure 4.7: Variation in ventral roll over observation period: Group 2.

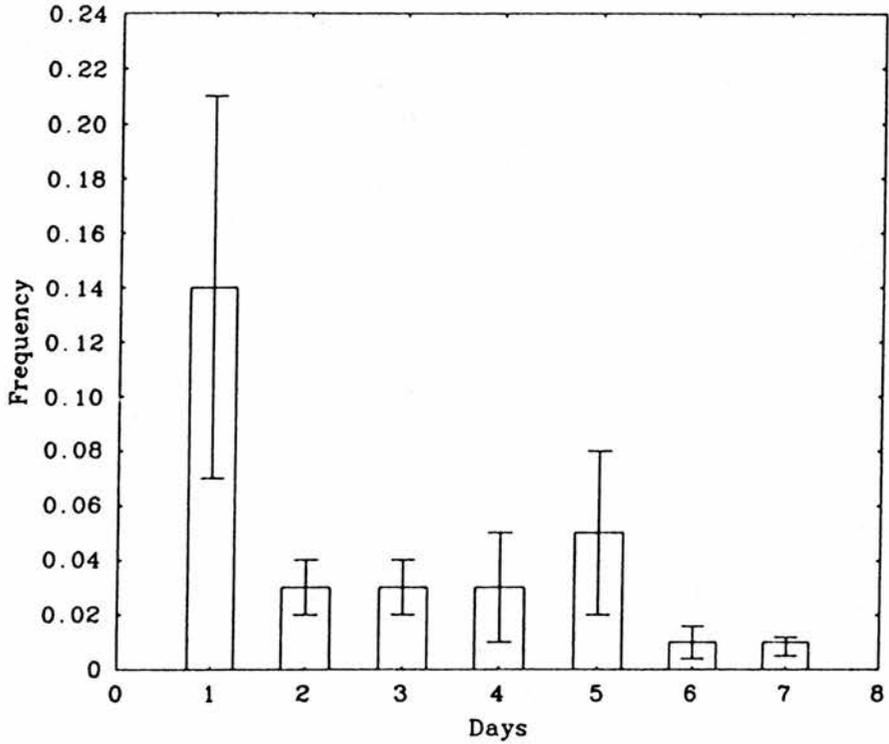


Figure 4.8: Variation in cnc over observation period: Group 2.

Table 4.1: Nested ANOVA results for variation in behaviour Group 1 over 7 days.

Behaviour	Source	$d.f_1/d.f_2$	$f$	$p$ value	Significance
Threat display	variation between fish	4/25	0.73	0.58	NS
	variation across days	6/150	4.01	<0.01	0.01
	interaction	24/150	0.92	0.58	NS
Bite/ Butt	variation between fish	4/25	0.98	0.44	NS
	variation across days	6/150	2.03	0.07	NS
	interaction	24/150	0.90	0.60	NS
Chase	variation between fish	4/25	1.46	0.24	NS
	variation across days	6/150	4.05	<0.01	0.01
	interaction	24/150	1.63	0.04	0.05
Ventral Roll	variation between fish	4/25	0.36	0.84	NS
	variation across days	6/150	1.17	0.33	NS
	interaction	24/150	1.04	0.42	NS
Contact: non-contact Act ratio	variation between fish	4/25	1.57	0.21	NS
	variation across days	6/150	1.77	0.11	NS
	interaction	24/150	1.45	0.05	0.05

Table 4.2: Nested ANOVA results for variation in behaviour Group 2 over 7 days.

Behaviour	Source	$d.f_1/d.f_2$	$f$	$p$ value	Significance
Threat display	variation between fish	4/25	1.61	0.20	NS
	variation across days	6/150	0.83	0.55	NS
	interaction	24/150	1.71	0.03	0.05
Bite/ Butt	variation between fish	4/25	1.69	0.18	NS
	variation across days	6/150	0.70	0.65	NS
	interaction	24/150	0.85	0.67	NS
Chase	variation between fish	4/25	2.39	0.08	NS
	variation across days	6/150	5.83	<0.01	0.01
	interaction	24/150	2.76	<0.01	0.01
Ventral Roll	variation between fish	4/25	0.36	0.84	NS
	variation across days	6/150	3.38	<0.01	0.01
	interaction	24/150	0.61	0.92	NS
Contact: non-contact Act ratio	variation between fish	4/25	2.93	0.04	0.05
	variation across days	6/150	3.40	<0.01	0.01
	interaction	24/150	1.09	0.36	NS

In group 2, the frequencies of chase and ventral roll, but not threat displays, increased towards the end of the observation period. However, the frequency of *cnc* decreased. There was a significant difference between the results for each fish (Table 4.2) for *cnc*. *J* performed significantly more aggressive acts against all other fish than any other individual in the group. It was observed that when two individuals challenged each other, *J* usually chased one or both fish away, thus ending the challenge without any conclusion. There was more ventral roll in this group than in group 1 and most of it was directed towards the most dominant fish.

### 4.3.3 EFFECTS OF RANK ON BEHAVIOUR

Correlations of dominance rank to frequency of threat displays and to *cnc* (Spearman rank) were carried out to ascertain whether the amount of aggression shown was affected by rank.

In group 1, the frequency of neither of these behaviours was related to dominance rank (threat display:  $r_s = 0.77 \Rightarrow \text{NS}$ ; *cnc*:  $r_s = 0.77 \Rightarrow \text{NS}$ ).

In group 2, both the frequency of threat display and *cnc* were positively correlated with dominance rank (threat display:  $r_s = 0.93, p < 0.05$ ; *cnc*:  $r_s = 0.94, p < 0.05$ ). However, this result was merely due to the most dominant fish, *J*, performing most of these aggressive acts. Therefore, when *J* was removed from the calculations, the correlations were found to be insignificant ( $r_s = 0.67$  for both behaviours). However, this result is to be expected, as, with such small numbers of animals as were used in this experiment, it is very hard for correlations to be significant.

## 4.4 RESULTS PART 2: PAIR FIGHTS WITH FISH FROM THE SAME GROUP

### 4.4.1 HIERARCHIES

Apparent hierarchies for the two groups were established, based on the outcome of the paired encounters (Figures 4.9 and 4.10). The linearity of each hierarchy was calculated using the methods of Appleby (1983) and Landau (1951). These tests are outlined in Chapter 3.

The hierarchy of group 1 was not significantly linear. According to Appleby's equation, in this case the degree of linearity,  $K = 0.563$ . This is insignificant as  $K$  would have to be greater or equal to 1.0 for a group of 6. Landau's index of linearity,  $h = 0.529$  for group 1, is also insignificant for a group of 6.

In group 2, no reversals occurred, so the degree of linearity  $K = 1.0$  and the index of linearity  $h = 1.0$  which both signify a perfectly linear hierarchy.

### 4.4.2 CONTEST DURATION

The average duration of contest for each fish was compared between the two groups, using a two-sample  $t$  test; no significant difference was found ( $t = 1.00$ ,  $d.f. = 23.8$ ,  $p = 0.33$ ).

The effect of rank difference on contest duration was examined by means of Spearman rank correlations. These were insignificant for both groups (group 1:  $r_s = 0.12 \Rightarrow$  NS; group 2:  $r_s = 0.34 \Rightarrow$  NS). Therefore, fish which were closer together in rank did not have longer fights.

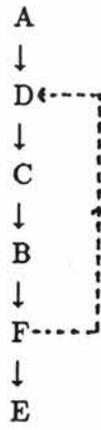


Figure 4.9: Apparent Hierarchy: Group 1.



Figure 4.10: Apparent Hierarchy: Group 2.

#### 4.4.3 COMPARISON OF THE FREQUENCIES OF BEHAVIOURS

A two-sample  $t$  test was used to compare the frequencies of the behaviours  $lt$ ,  $bi$ ,  $ch$ ,  $vr$  observed, between the two groups. The results for each act were insignificant (Table 4.3).

Table 4.3: Comparison of frequency behaviours for Group 1:Group 2 - Two sample  $t$  test.

Behaviour	Ratio of Group 1 average to Group 2 average	$t$	$p$	$d.f.$	Significance
Lateral threat	18.9:24.1	-0.75	0.46	26	NS
Bite/butt	15.3:7.1	1.86	0.07	25	NS
Chase	8.9:8.9	-0.02	0.99	27	NS
Ventral Roll	14.4:13.5	0.16	0.88	21	NS

#### 4.4.4 FIGHT INTENSITY

The acts/sec and the contact:non-contact (cnc) ratio were used to examine the intensity of fights. A two-sample  $t$  test was used to compare the intensity of fights between pairs from group 1 with those between pairs from group 2. It was found that the pair-fights between fish from group 1 contained significantly more physical contact acts (cnc) than group 2 ( $t = 2.23, d.f. = 16, p < 0.05$ ) but not more acts/sec ( $t = 0.49, d.f. = 24 \Rightarrow$  NS).

## 4.5 RESULTS PART 3: FISH RETURNED TO THEIR ORIGINAL GROUPS

### 4.5.1 HIERARCHIES

The hierarchies were examined, as in part 1. The hierarchies ascertained from the observations are given in Figures 4.11 and 4.12.

A Kolmogorov-Smirnoff two-sample test (Siegel 1956) was used to test whether a significant change took place in the relative dominance positions of individuals in each group.

The result for the Kolmogorov-Smirnoff test for group 1 is:  $D = 5\% = 0.05$ . This indicates a significant change in the dominance order between parts 1 and 3 of this experiment. *F* had been the most subordinate fish in the original hierarchy and had only risen one dominance place according to the results of the pair-fights in part 2 (though it had beaten *D* which was originally the dominant member of the group). However, in part 3, it had now risen in rank to become the most dominant fish. As in part 1, challenges to fish apparently higher in rank were common.

In group 2, *J* still remained the most dominant fish. The result for the Kolmogorov-Smirnoff two-sample test is:  $D = 1\% = 0.01$ . This indicates an insignificant change in ranking order. As in part 1, *J* swam about the tank and the rest of the group remained hidden for most of the observation period. Fish *H*, *K* and *L*, once again, seemed to establish a territory each, around their hiding places from *J*. *I* remained the most submissive fish, as it had in part 1, though it had won two of the paired contests in part 2.

### 4.5.2 GROUP BEHAVIOUR

The *t* test for correlated samples (Robson 1973) was used to compare the frequency of threat display and *cnc* performed by each individual fish in parts 1 and 3. This test is not affected by differences in behaviour between the fish. Both measures of behaviour

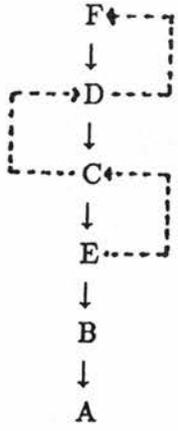


Figure 4.11: Hierarchy: Group 1.

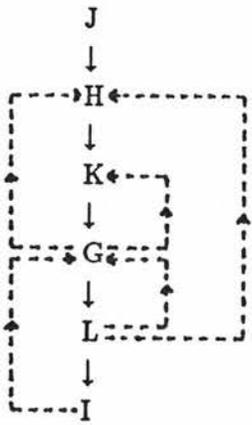


Figure 4.12: Hierarchy: Group 2.

gave an insignificant result (threat display:  $t = 0.20 \Rightarrow$  NS for group 1,  $t = 0.44 \Rightarrow$  NS for group 2; *cnc*:  $t = 1.32 \Rightarrow$  NS for group 1,  $t = 0.70 \Rightarrow$  NS for group 2).

The variation in the frequency of behavioural acts, over the observation period and between the individuals in each group, was examined using nested ANOVAS (Table 4.4 and 4.5). There was a significant increase in the frequency of threat, chase and ventral roll in both groups and of bite/butt in group 1 (Figures 4.13 to 4.16 for group 1 and Figures 4.17 to 4.19 for group 2). There was, however, a significant decrease in the frequency of *cnc* over the observation period, in group 2 (Figure 4.20) but no variation was found for this measure in group 1.

Table 4.4: Nested ANOVA results for variation in behaviour Group 1 over 7 days.

Behaviour	Source	$d.f_1/d.f_2$	$f$	$p$ value	Significance
Threat display	variation between fish	4/25	6.34	<0.01	0.01
	variation across days	6/150	4.87	<0.01	0.01
	interaction	24/150	1.03	0.43	NS
Bite/ Butt	variation between fish	4/25	3.00	0.04	0.05
	variation across days	6/150	4.25	<0.01	0.01
	interaction	24/150	1.07	0.40	NS
Chase	variation between fish	4/25	6.96	<0.01	0.01
	variation across days	6/150	9.26	<0.01	0.01
	interaction	24/150	4.72	<0.01	0.01
Ventral Roll	variation between fish	4/25	0.48	0.75	NS
	variation across days	6/150	5.60	<0.01	0.01
	interaction	24/150	0.66	0.83	NS
Contact: non-contact Act ratio	variation between fish	4/25	0.54	0.70	NS
	variation across days	6/150	2.37	0.06	NS
	interaction	24/150	0.85	0.63	0.05

In group 1, a significant variation was found, between fish, in the frequencies with which they performed the behaviours threat, bite/butt and chase, but there was no significant variation between fish in group 2 for any of these behaviours (because no fish, excepting *J*, showed much aggressive behaviour).

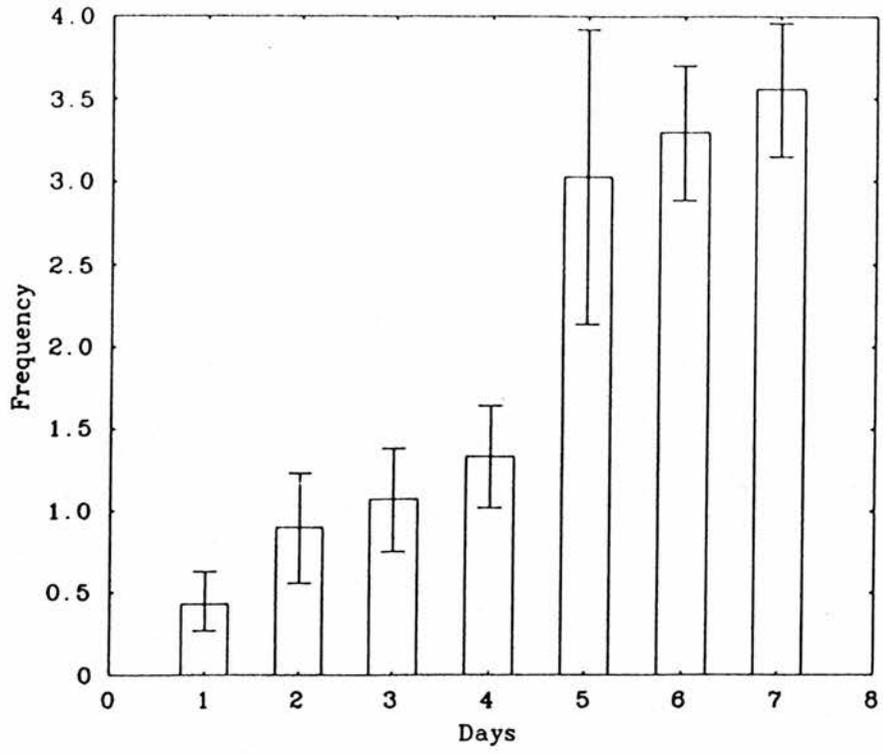


Figure 4.13: Variation in threats during observation period: Group 1.

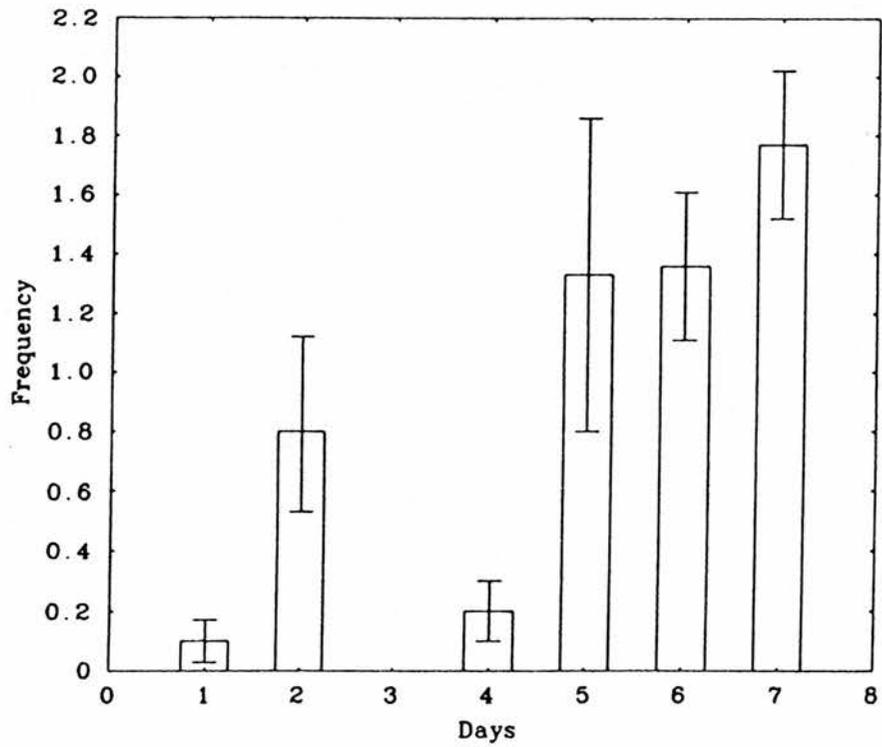


Figure 4.14: Variation in bite/butt during observation period: Group 1.

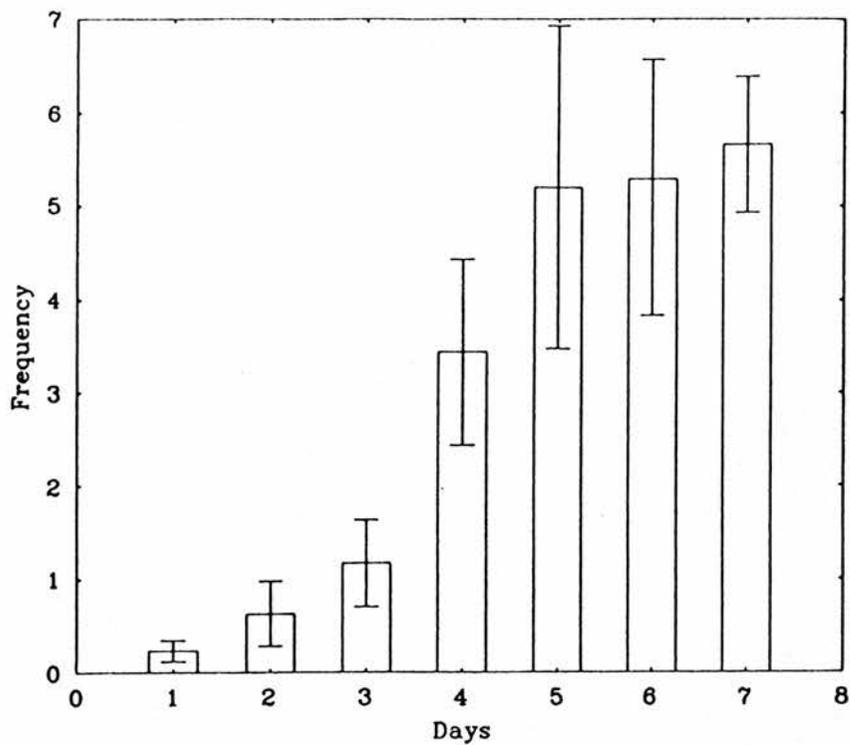


Figure 4.15: Variation in chase during observation period: Group 1.

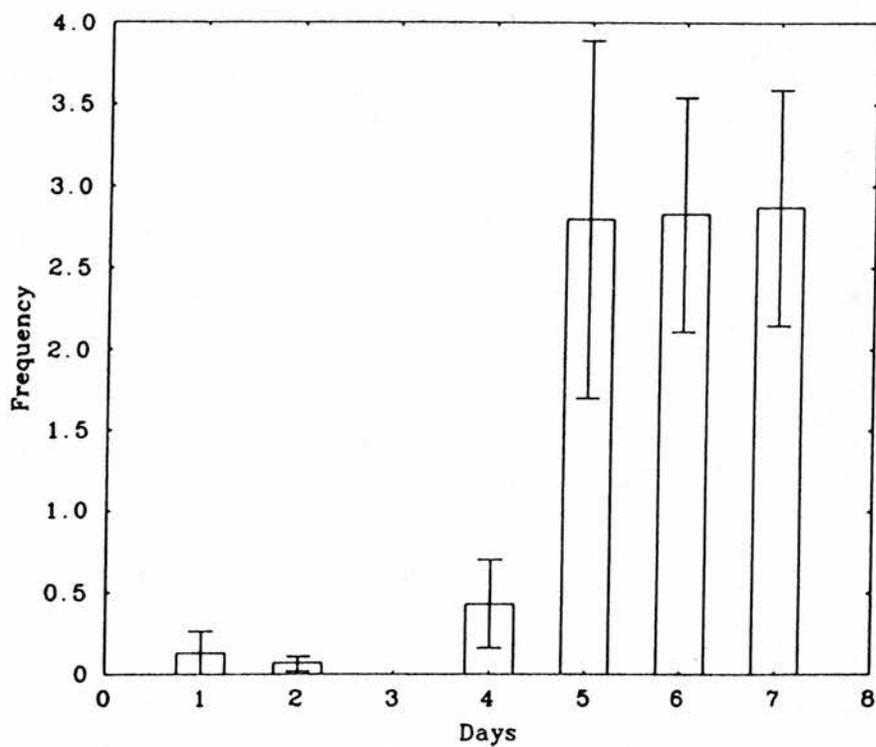


Figure 4.16: Variation in ventral roll during observation period: Group 1.

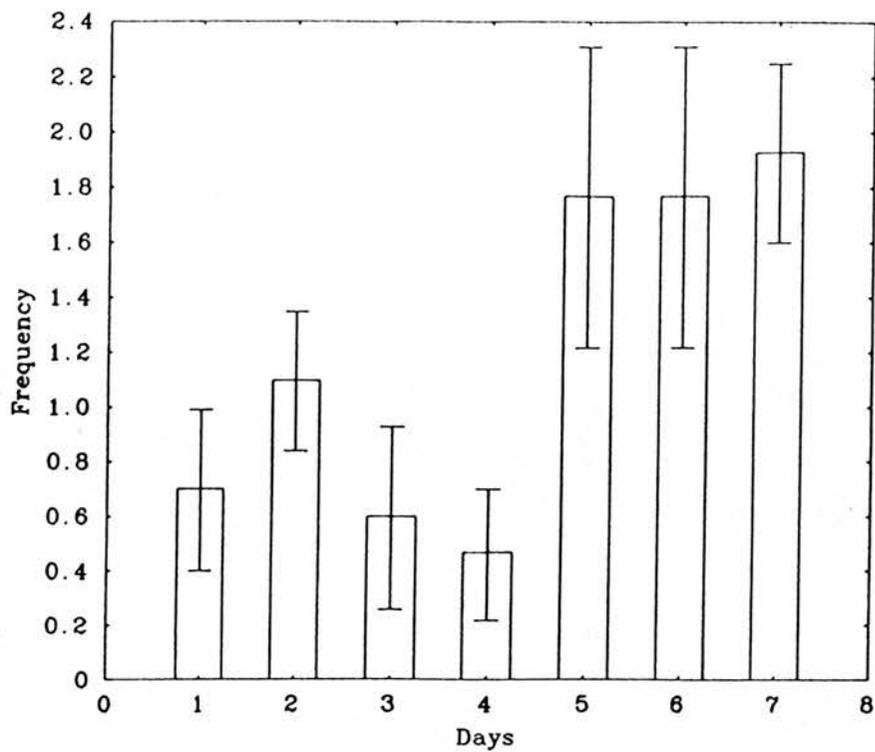


Figure 4.17: Variation in threats during observation period: Group 2.

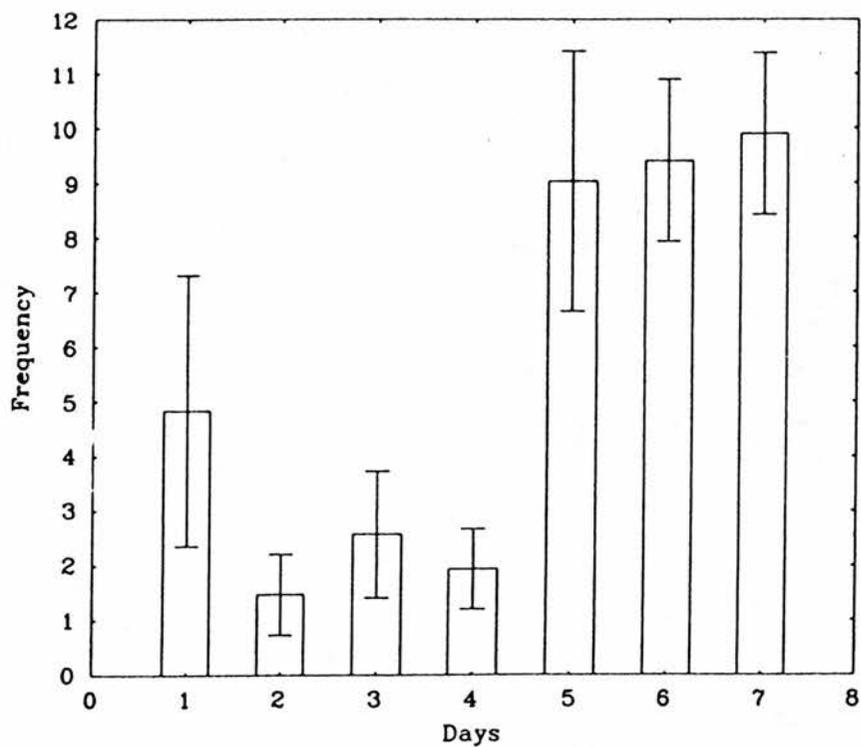


Figure 4.18: Variation in chase during observation period: Group 2.

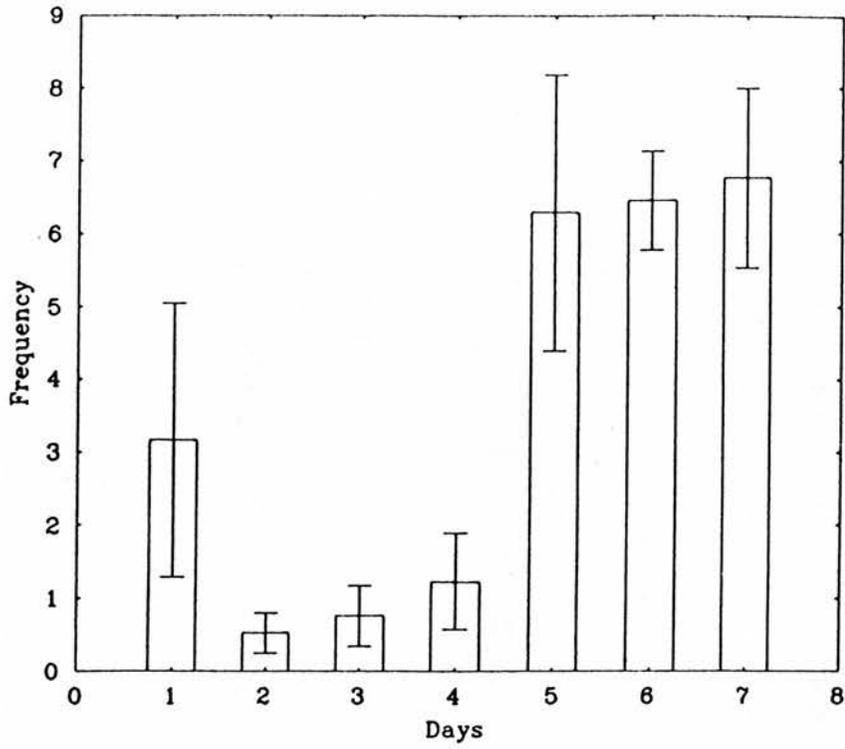


Figure 4.19: Variation in ventral roll during observation period: Group 2.

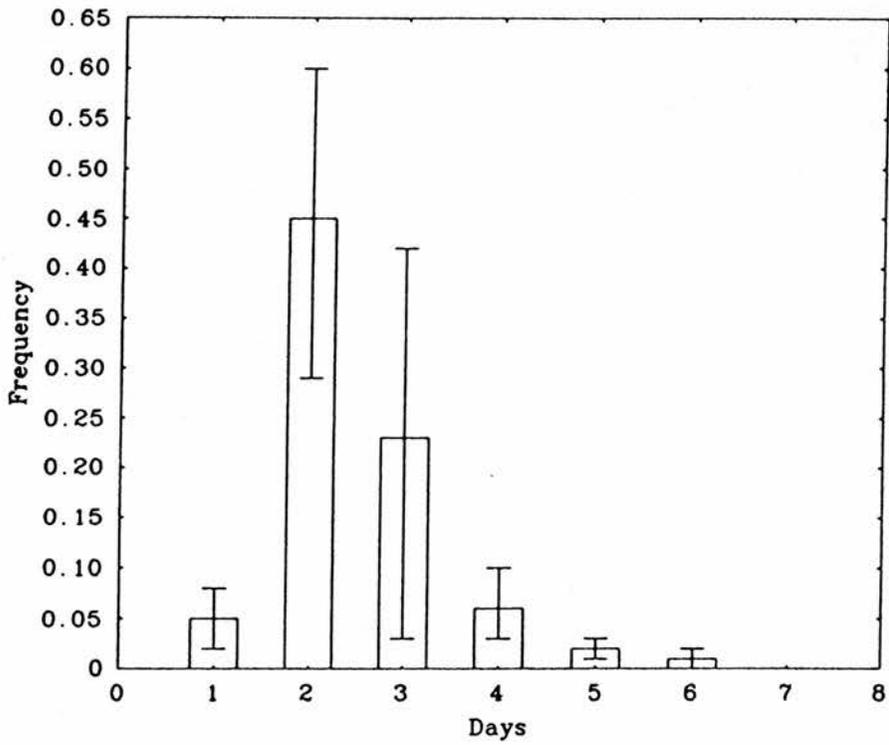


Figure 4.20: Variation in cnc during observation period: Group 2.

Table 4.5: Nested ANOVA results for variation in behaviour for Group 2.

Behaviour	Source	$d.f_1/d.f_2$	$f$	$p$ value	Significance
Threat display	variation between fish	4/25	0.80	0.67	NS
	variation across days	6/150	3.03	0.02	0.05
	interaction	24/150	1.14	0.33	NS
Bite/ Butt	variation between fish	4/25	0.70	0.60	NS
	variation across days	6/150	1.12	0.35	NS
	interaction	24/150	0.86	0.61	NS
Chase	variation between fish	4/25	1.40	0.26	NS
	variation across days	6/150	7.43	<0.01	0.01
	interaction	24/150	0.63	0.85	NS
Ventral Roll	variation between fish	4/25	0.61	0.66	NS
	variation across days	6/150	6.76	<0.01	0.01
	interaction	24/150	2.24	<0.01	0.01
Contact: non-contact Act ratio	variation between fish	4/25	0.93	0.46	NS
	variation across days	6/150	2.60	0.04	0.05
	interaction	24/150	1.39	0.16	NS

For group 1, there was no significant variation in bite/butt or ventral roll in part 1. This implies that more physical aggression and submission was carried out in part 3. In group 2, an increase in the frequency of threat displays over the observation period only occurred in part 3.

### 4.5.3 EFFECTS OF RANK ON BEHAVIOUR

Correlations (Spearman rank) were made of dominance rank with the frequencies of threat display and of physical aggression for each group. A positive correlation for dominance rank and frequency of threat displays was only found in group 1 ( $r_s = 0.94, p < 0.05$  for group 1;  $r_s = 0.58 \Rightarrow$  NS for group 2). Therefore, only in this case did more dominant fish tend to perform more threat displays. *cnc* did not correlate significantly with rank for either group ( $r_s = 0.70 \Rightarrow$  NS for group 1;  $r_s = 0.43 \Rightarrow$  NS for group 2). The frequency of both behaviour measures had been positively correlated to dominance rank in part 1 (threat display:  $r_s = 0.93, p < 0.05$ ; *cnc*;  $r_s = 0.94, p < 0.05$ ).

## 4.6 RESULTS PART 4: PAIR FIGHTS WITH FISH FROM A DIFFERENT GROUP

### 4.6.1 HIERARCHIES

The apparent hierarchies for each group (Figures 4.21 and 4.22) and for the two groups combined (Figure 4.23) were established, based on the outcome of paired encounters between opponents from different groups. The apparent dominance relationships of individuals were compared with those found in the other parts of this Chapter.

It can be seen from this that the groups were mixed together in dominance relations and all the fish in one group did not dominate the other entire group. *G* was apparently the most dominant fish, even though it had been ranked only fourth in its own group in part 3. *F* also dominated *J*, though *J* had been more dominant over the rest of group 2 than *F* had been over the other individuals in group 1. The apparent dominance



Figure 4.21: Apparent Hierarchy: Group 1.



Figure 4.22: Apparent Hierarchy: Group 2.

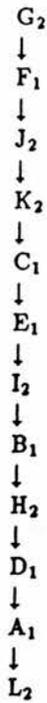


Figure 4.23: Apparent mixed Hierarchy: Group 1 + 2.

arrangement of both groups was different to what it had been in any other part of this experiment.

#### 4.6.2 COMPARISON OF CONTEST DURATIONS

The average contest duration for each individual fish was compared between part 2 and part 4 using the  $t$  test for correlated samples ( $t = -0.81 \Rightarrow \text{NS}$ ). This insignificant result suggests that the length of time each individual fought did not depend on whether it had previously met its opponent in a group situation.

#### 4.6.3 COMPARISON OF THE FREQUENCY OF BEHAVIOURS AND FIGHT INTENSITY

The frequency of the behaviours  $lt$ ,  $bi$ ,  $ch$ ,  $vr$ ,  $acts/sec$ ,  $cnc$ , observed for each individual fish, was compared between part 2 and part 4 using the  $t$  test for correlated samples (Table 4.6). No significant difference was found in the behaviour of each individual towards an opponent it had previous experience of, in a group situation, and a fish which it had never previously met.

Table 4.6: Comparison of individual behaviours Part 2:Part 4  $t$  test for correlated samples.

Behaviour	$t$	$d.f.$	Significance
Lateral threat	0.325	11	NS
Bite/butt	0.909	11	NS
Chase	0.937	11	NS
Ventral roll	0.039	11	NS
Acts/sec	1.390	11	NS
CNC	1.690	11	NS

## 4.7 DISCUSSION

### 4.7.1 HIERARCHIES

In the case of group 1, the hierarchy was not totally stable, as aggression was sometimes shown to individuals apparently higher in rank. Since the hierarchy, based on the outcome of pair-fights, was different to the original hierarchy, the experience that the fish had of each other and their relative dominance positions did not determine the outcome of contests when the fish met again in paired contests in part 2. When the fish were returned to their original group, the hierarchy changed further.  $F$ , which had beaten the originally most dominant  $D$ , but then lost all later pair-fights in part 2, became the most dominant of the group in part 3.  $A$  became the most submissive fish in the hierarchy in part 3, as it had won all its pair-fights in part 2.

The results suggest that individual recognition did not play a part in the outcome of encounters, but that in each part of the experiment, the fish treated their opponents as if they had never previously met. The results might also be because the fish in the group were quite evenly matched and so minor changes in the environmental conditions or motivational state could have led to an individual dominating another which had previously been the dominant. However, this cannot be proved, as such changes were not measured in this Chapter.

In the case of group 2, although the hierarchy was not totally stable, as aggression was directed towards individuals of apparently higher rank, the relative dominance arrangement of the group hardly changed throughout the study.

In part 1, *J* was by far the most dominant individual, the other fish all avoiding encounters with it. This fish dominated all the others from the group when it encountered them in a pair-fight situation in part 2. When the fish were returned to their original group, the other individuals once again avoided encounters with *J*.

Fish *K*, *H* and *L* seemed to establish territories in part 1 and again in part 3. No other fish observed has shown any tendency towards territoriality. The defence of these territories may account for the change in dominance order of these fish from part 1 to part 3 and for the challenges made by *L* to the apparently higher ranked *H*. These three fish could have been quite evenly matched in fighting ability. However, the presence of such territories will have made the dominance relations more difficult to assess accurately.

The perfect linearity of the apparent hierarchy of this group, in part 2, would suggest that the fish were not evenly matched in fighting ability. However, there is no evidence to suggest that the similarity found in hierarchical arrangement through the study was due to individual recognition taking place.

No conclusions can be drawn from the apparent hierarchical arrangements of the groups in part 4, as there is no reason why a fish which was dominant in one group would also be dominant to fish from a different group. The fact that the dominance arrangement was mixed between the two groups would be expected from two groups drawn from the same population.

The results of these observations on the hierarchical arrangements, plus the fact that there was a change in the apparent dominance positions of fish through the study in this Chapter, would suggest that the outcomes of fights depended on the rate of improvement of fighting ability of the contestants, the individuals involved not being able to recognize which opponents had previously dominated them and hence not adjusting their behaviour in the light of experience. Therefore the type of dominance hierarchy

found in tiger barbs may either be a *statistical* or an *assessment* hierarchy according to the theory of Barnard and Burk (1979) as outlined in the introduction to this Chapter.

#### 4.7.2 CONTEST DURATION

In part 2, even though the outcomes of the pair-fights for group 2 were similar to the dominance arrangement observed in part 1, the duration of contests was no shorter than that of opponents from group 1. However, the resultant apparent hierarchy for group 1 was different to that which had been ascertained from the observations in part 1. Neither was the duration of contests for either group affected by the relative dominance ranks of the opponents. These results would also suggest that individual recognition did not play a part in these encounters. Though the fish in group 2 may have been less evenly matched in fighting ability, resulting in the retention of dominance relationships within the group through the experiment, the opponents behaved in each encounter as if they had not previously met and challenged each other until one became the dominant and the other submitted. If this was the case with both groups, it would explain why the average contest durations of the groups were similar, even if the individuals in group 1 were more evenly matched in fighting ability than those in group 2. The fact that the average duration of contests in part 4 between opponents which had never previously met was similar to those of part 2 between fish which had prior experience of each other further supports this explanation and the lack of individual recognition.

#### 4.7.3 BEHAVIOUR WITHIN GROUPS AND DURING PAIRED ENCOUNTERS

In part 1, a significant difference between individual fish was found in group 1 for the frequencies of chase and the measures of physical aggression. Some fish performed these acts more some days than others in the group. This result could be due to the individuals testing dominance relationships and sometimes altering their positions in the hierarchy. When the group settled to its ultimate arrangement at the end of the observation period, *D* (the dominant) performed these acts most. This settlement of the hierarchy into the dominance order could also account for the increase in the frequency

of threat displays and chase towards the end of the observation period. The lack of significant correlation of behaviour with rank and the lack of differences in behaviour, between individuals in the group, would suggest that the fish were quite evenly matched with frequent challenges to those apparently higher in rank.

In part 3, a significant difference was found in the frequencies of behaviours for each fish. This could be due to the continual occurrence of challenges directed towards more dominant fish, thus testing the stability of the hierarchy. *F* now performed chase more often than any other individual in its group. It is possible that its aggressiveness had increased or that its fighting ability had improved since part 1. Higher ranked fish performed more threat displays towards the end of the observation period. This possibly functioned to maintain their dominance positions. Both more aggressive acts by dominants and more submissive acts by subordinates were performed in part 3, as compared with part 1, and there was also more variation between the results for each fish in part 3. This might suggest that the individuals in the group were now less evenly matched, which could have been brought about by an increasing difference between fish in their rate of development of fighting ability during the paired contests in part 2. The difference in behaviour did not seem to be based on experience of wins and losses, as the hierarchy, observed in part 3, bore no resemblance to the outcomes of the pair-fights in part 2. However, it might indicate that individuals were adjusting their behaviour according to cues from their opponent that correlated with its fighting ability. This would conform with the theory of Barnard and Burk (1979) for an *assessment hierarchy*.

In group 2, the frequency of chase and ventral roll increased during the observation periods in both parts 1 and 3, as the group settled down into a more stable hierarchy. A clear difference was obvious between the dominant fish *J* and the rest of the group. In part 1 and in part 3, the frequency of contact acts decreased towards the end of the observation period. This could be due to the fact that the rest of the fish in the group ceased challenging *J* and challenges between other individuals were usually interrupted by *J*, thus preventing any escalation of aggression between the two challengers. It is possible that winning a fight may increase the aggression level of an individual, resulting in the greater likelihood of it winning its next fight. This could ultimately lead to an originally subordinate animal being capable of defeating the most dominant. Therefore, by interrupting a fight and preventing either opponent from winning, *J* may have been

preventing an increase in aggression level of any of its subordinates, thereby helping to maintain its own position as the most dominant member of the group.

In part 1, the most dominant of the group, *J* and *K*, performed more threat displays and chase than the other fish at the end of the observation period as the hierarchy seemed to settle. However, in part 3, there was no difference in the amount of threat behaviour performed by each fish. This may be explained by a decrease in the degree of dominance of *J*, allowing the other individuals more chance to encounter each other. The apparent territorial behaviour shown by *H*, *K* and *L* might also have been involved in causing this increase in frequency. It could also have been the cause of the high frequency of ventral roll performed by the second most dominant fish, *H*, and by the fourth ranked, *L*, as these individuals submitted to each other and to *K*, when in the other animal's territory.

The results of the paired encounters in part 2 and part 4 indicate that all fish behaved similarly whether or not they had prior experience of their opponent. The only exception to this was in the case of bite/butt, as this act was performed more frequently between fish in group 2 than in any other circumstance. This could again be due to the fact that the individuals in group 2 were less evenly matched, resulting in less retaliation occurring and therefore, less need for *J* to assert its dominance by physical aggression. There is no evidence that this result is due to the involvement of individual recognition of opponents from prior experience in the group situation.

A greater frequency of threat displays occurred in paired encounters in this experiment than occurred in experiment 2 of Chapter 3 (though this difference was not statistically verified, as only informal comparisons can be made between these two, totally different, experiments). Therefore group-living might have had an effect on subsequent encounters between individuals. There is no apparent explanation as to why threat displays were the only type of behaviour to be affected by group-living. It is possible that as the fish in a group experienced challenges from other individuals, they became accustomed to assessing opponents by threat displays (which is, perhaps, a less energetic activity than physical aggression) and therefore used the same form of assessment in subsequent paired encounters. Individuals that had been kept in a solitary state would have lacked experience of opponents and thus, perhaps, also of fighting strategies. This may have

led to a tendency to physically challenge an opponent, before first assessing its fighting ability in a ritual fashion.

#### **4.7.4 FIGHT INTENSITY**

There was no difference in fight intensity of paired encounters within group 1 or between the two groups. However, pair-fights between individuals in group 2 did contain less physical contact acts than either of the other circumstances. This result is probably not due to the involvement of individual recognition between fish from group 2. Otherwise, it would also be expected to occur between fish from group 1. It is more likely to be because the individuals in group 2 were less evenly matched than in the other two circumstances and the contests were, therefore, concluded without as great a need for escalated fighting behaviour.

The individuals had similar intensity fights regardless of whether they had prior experience of the opponent and also of whether they had lived in a group or in a solitary state prior to the paired contest (based on an informal comparison with the results of Chapter 3). This implies that no individual recognition was involved, but that the intensity of each fight depended merely on the fighting ability of the contestants. The results also suggest that living in a solitary state may not have resulted in the fish being of a higher aggressive or motivational state. Otherwise the contests between individuals in Chapter 3 would be expected to have been of greater intensity.

#### **4.8 CONCLUSIONS**

- (i) The hierarchies never became totally stable as aggression was also continually directed to apparently higher ranked fish.
- (ii) The experience the fish had of each other in the group, concerning their relative dominance positions, did not determine the outcome of contests when the individuals met again in subsequent paired encounters.
- (iii) Individuals did not adjust their behaviour in the light of their experience of wins and losses; the outcome of each contest may have depended on the relative fighting

abilities of the contestants.

- (iv) The individuals in group 1 were probably quite evenly matched, resulting in a reshuffling of dominance positions throughout the study. However, the fish in group 2 were less well matched, *J* being extremely dominant over the rest of the group; this resulted in very little change occurring in the hierarchical arrangement throughout the study.
- (v) Individuals may have differed in the rate of development of their fighting ability, thus leading to some becoming more aggressive and others more submissive and also to changes in ranking order.
- (vi) Group-living may have affected behaviour in subsequent paired contests. It is possible that it lead to a greater amount of assessment of opponents in the form of threat displays before indulging in physical combat.
- (vii) Individual recognition did not appear to be involved in the outcome of encounters between pairs of tiger barbs.
- (viii) Tiger barbs may form hierarchies of the type *assessment hierarchy*, as described by Barnard and Burk (1979).

## Chapter 5

# PRIOR EXPERIENCE OR INDIVIDUAL RECOGNITION?

### 5.1 INTRODUCTION

The aim of this Chapter is to examine repeated paired encounters between two particular fish from different groups and compare these with multiple encounters between fish from two other groups, each individual meeting a different opponent at each encounter.

If encounters between opponents which have previously met differ from those between new opponents, the involvement of individual recognition in such encounters is implied. Thus, an individual would recognize whether the familiar opponent should be dominant or subordinate to it. This result is not expected here, as the results of Chapter 4 indicated that a second encounter between the same two opponents was not influenced, in the outcome, duration or observed behaviour, by individual recognition.

This study also tests whether individuals alter their behaviour according to their own past history, the losers becoming more submissive and the winners becoming more aggressive. This result would be in accordance with the theory of Barnard and Burk

(1979) for *confidence hierarchies*, as described in the introduction to Chapter 3. If this is the case, individual behaviour should be affected by the outcomes of a tiger barb's previous encounters but not by the familiarity of its opponent. In Chapter 3, the hierarchy did not appear to be of the *confidence hierarchy* type, as opponents behaved in a similar manner to each other regardless of whether they had won or lost their previous fight. However, this result was only based on two encounters between fish. This Chapter tests the theory more thoroughly by examining six encounters between pairs of fish and determining whether any prior experience effect on individual behaviour occurs.

The experiment consists of two parts: in part one, each fish repeatedly met the same opponent from another group. In part two, each fish met a different opponent, again from another group, at each encounter.

If the outcome of fights depends on prior experience rather than on individual recognition, then no difference in behaviour should be found between the two parts of this study. In each part, the individuals which repeatedly win fights should become more aggressive and those which lose should become more apathetic and submissive. Parker (1974) postulates that prior conditioning and experience can be very important in determining the outcome of aggressive disputes. In some cases, it seems likely that successful fighting experience markedly increases the readiness for escalation, which is explicable in terms of experience increasing RHP. Within social groups, RHP disparity seems the main determinant of aggression and dominance rank.

Gorlick (1976) supports the interpretation that hierarchy formation is based on *learned inhibition of aggression* to certain individuals. Thines and Heuts (1968) describe the same effect as *retention of conditioned fear* (see Chapter 2). Therefore, if the outcome of fights is based on individual recognition, then aggression should decrease in frequency during repeat fights in part one, as the individuals learn to recognize which is dominant. No such decrease in aggression should be shown in part two, except possibly for the last fight in the round-robin experiment when each individual meets the same opponent as it had met in the first round of encounters. This last point assumes that tiger barbs have adequate memory, capable of remembering a particular individual over this timespan.

If tiger barbs neither recognize each other nor change their behaviour according to their own past history, then no paired contest will be affected by any encounters that either opponent has previously been involved in.

Other literature, relevant to this Chapter, has been outlined in the introduction to Chapter 4.

## 5.2 MATERIALS AND METHODS

This study involved four groups, each of six tiger barbs. They were kept in holding tanks of the same size and with the same conditions as the holding tanks described in Chapter 2, with the same plant cover as described in experiment 2 of Chapter 3. The experimental tanks used were identical to the holding tanks.

The four groups were made up as follows:

Group 1: *A, B, C, D, E, F*

Group 2: *G, H, I, J, K, L*

Group 3: *M, N, O, P, Q, R*

Group 4: *S, T, U, V, W, X*

The two parts of the study were carried out as follows:

**PART ONE:** Groups 1 and 2 met in paired encounters, every three days, for seven encounters, with each individual meeting the same opponent from the other group at each encounter.

**PART TWO:** Groups 3 and 4 met in paired encounters, every three days, for seven encounters, with each individual meeting a different opponent from the other group at each encounter in a round-robin fashion, but finally being repaired with their original opponent in round seven.

The fish were transferred from tank to tank, using a beaker, the night before experiments were carried out. They were returned to their own original groups between each

round of paired encounters.

At the start of each observation, the opaque divider separating the two fish in each tank, was removed manually and behaviours were recorded on the Epson portable computer, as described in Chapter 2.

## 5.3 RESULTS

### 5.3.1 DOMINANCE RELATIONS

In part one, there was no change in dominance relations for each pair of fish throughout the seven rounds of contests. This is illustrated in Table 5.1.

In part two, 6 of the 12 fish reversed dominance positions in round seven with the opponent that they had originally met in round one. The outcomes of the pair-fights in part two are given in Table 5.2.

It was found that the outcome of contests was not affected by previous fights (binomial test,  $p = 0.43 \Rightarrow \text{NS}$ ; Table D in Siegel 1956). Therefore, a win by an individual in one fight had an equal chance of being followed by a win or a loss by that fish in following fights.

The binomial test was also carried out between round one and round seven to determine whether the outcomes of these contests were affected by the previous outcomes when the opponents had previously met. In this case, 3 fights went the same way as they had in round one and, in the other 3 contests, a reversal of dominance positions occurred. Therefore, the outcomes of contests were not affected in this way (binomial test,  $p = 0.66 \Rightarrow \text{NS}$ ; Table D in Siegel 1956).

Table 5.1: Hierarchies: Outcome of contests, +  $\equiv$  A-F beats G-K, -  $\equiv$  G-K beats A-F.

Fish		Fish					
		A	B	C	D	E	F
G	1	+					
	2	+					
	3	+					
	4	+					
	5	+					
	6	+					
	7	+					
H	1		+				
	2		+				
	3		+				
	4		+				
	5		+				
	6		+				
	7		+				
I	1			-			
	2			-			
	3			-			
	4			-			
	5			-			
	6			-			
	7			-			
J	1				-		
	2				-		
	3				-		
	4				-		
	5				-		
	6				-		
	7				-		
K	1					-	
	2					-	
	3					-	
	4					-	
	5					-	
	6					-	
	7					-	
L	1						+
	2						+
	3						+
	4						+
	5						+
	6						+
	7						+

Table 5.2: Outcome of individual fights.

fish	fish						
	1	2	3	4	5	6	7
M	-†	+	+	+	+	+	+
N	-	-	-	-	+	-	-
O	+	+	-	-	+	-	-
P	+	+	+	-	+	-	+
Q	-	-	-	-	-	-	+
R	-	-	-	-	-	-	-
S	+	+	+	+	-	+	-
T	+	-	+	+	-	+	+
U	-	+	-	+	+	+	+
V	-	-	+	-	+	+	-
W	+	-	+	+	-	+	-
X	+	+	-	+	-	-	+

†-  $\equiv$  loss, +  $\equiv$  win.

### 5.3.2 CONTEST DURATIONS

It was found that there was no significant difference, between parts one and two, either in the total duration of contests (two-sample  $t = -0.03, p = 0.98$ ), or in the length of time until the first submissive act was performed (two-sample  $t = 0.10, p = 0.93$ ). There was also no difference found, in either of these measures, between round one and round seven of part two ( $t_{total} = 0.98, p = 0.51; t_{1stsub} = -1.04, p = 0.49$ ). Therefore, the fights were not terminated sooner after submission by the loser if the opponents had met previously.

No significant change across the seven rounds was found, for either part, in the duration of contests (ANOVA: part one:  $F = 1.56, d.f_1/d.f_2 = 6/30, p = 0.19$ ; part two:  $F = 2.0, d.f_1/d.f_2 = 6/66, p = 0.08$ ). Therefore, contest durations did not decrease, in either case, the more often the fish fought either with the same fish (part one) or with different fish (part two).

### 5.3.3 BEHAVIOUR

The change in the frequency of behaviours across the seven rounds was examined for each fish, using the ANOVA test (Tables 5.3 and 5.4).

Table 5.3: Table of variation across rounds in difference in behaviour between opponents in Part 1.

Behaviour	$f$ value	$p$ value	significance	$d.f_1/d.f_2$
Bite	1.23	0.32	NS	6/30
Chase	2.61	0.04	0.05	6/30
Flee	2.32	0.06	NS	6/30
Ventral roll	2.42	0.05	0.05	6/30
Lateral threat	1.53	0.20	NS	6/30

In part one, only chase (Figure 5.1) and ventral roll (Figure 5.2) showed a significant variation, with each of the two measures increasing over the seven rounds. In part two,

Table 5.4: Table of variation in behaviour across seven rounds in Part 2.

Behaviour	<i>f</i> value	<i>p</i> value	significance	<i>d.f</i> <sub>1</sub> / <i>d.f</i> <sub>2</sub>
Lateral threat	2.38	0.04	0.05	6/30
Chase	2.84	0.02	0.05	6/30
Flee	3.07	0.01	0.05	6/30
Ventral roll	3.69	<0.01	0.01	6/30

all the behaviours, except bite/butt, became significantly more frequent over the seven rounds (Figures 5.3 to 5.6).

#### 5.3.4 INTENSITY

ANOVAS were carried out to ascertain whether the intensity of fights changed over the seven rounds.

For both parts one and two, no significant variation was found in the ratio of contact:non-contact acts (cnc) (part one:  $F = 0.80, d.f_1/d.f_2 = 6/30, p = 0.58$ ; part two:  $F = 1.30, d.f_1/d.f_2 = 6/66, p = 0.17$ ). There was also no variation, in part one, for the frequency of acts/sec ( $F = 0.84, d.f_1/d.f_2 = 6/30, p = 0.55$ ). However, Figure 5.7 illustrates that this frequency did increase significantly over the seven rounds in part two ( $F = 3.37, d.f_1/d.f_2 = 6/66, p < 0.01$ ).

Therefore, fish appeared to increase the rate of action of fights when they had multiple contests against different opponents. However, fights did not decrease in intensity when individuals re-encountered the same opponent.

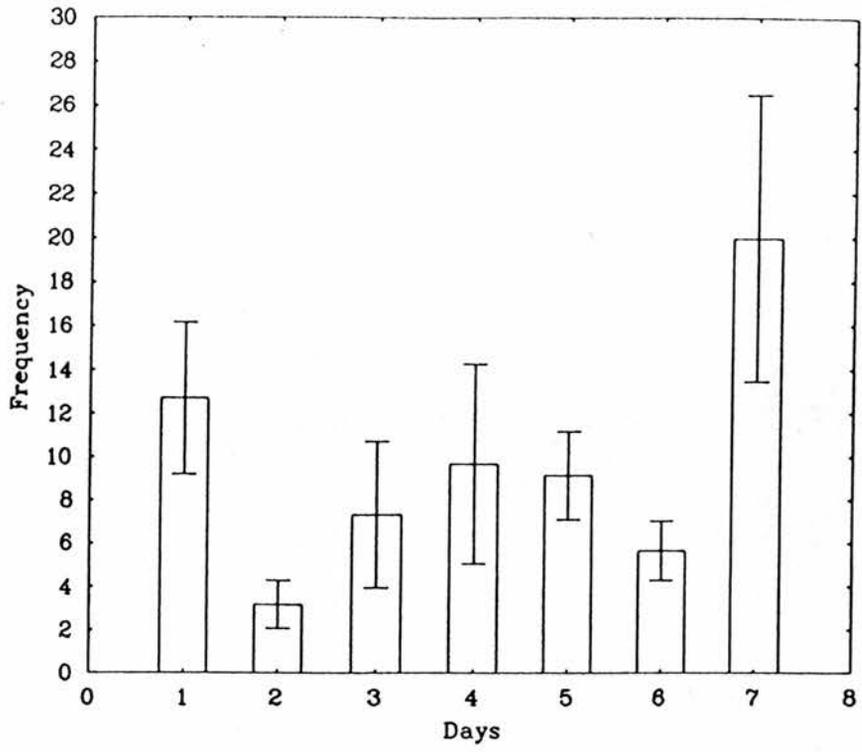


Figure 5.1: Variation in chase during observation period: Part 1.

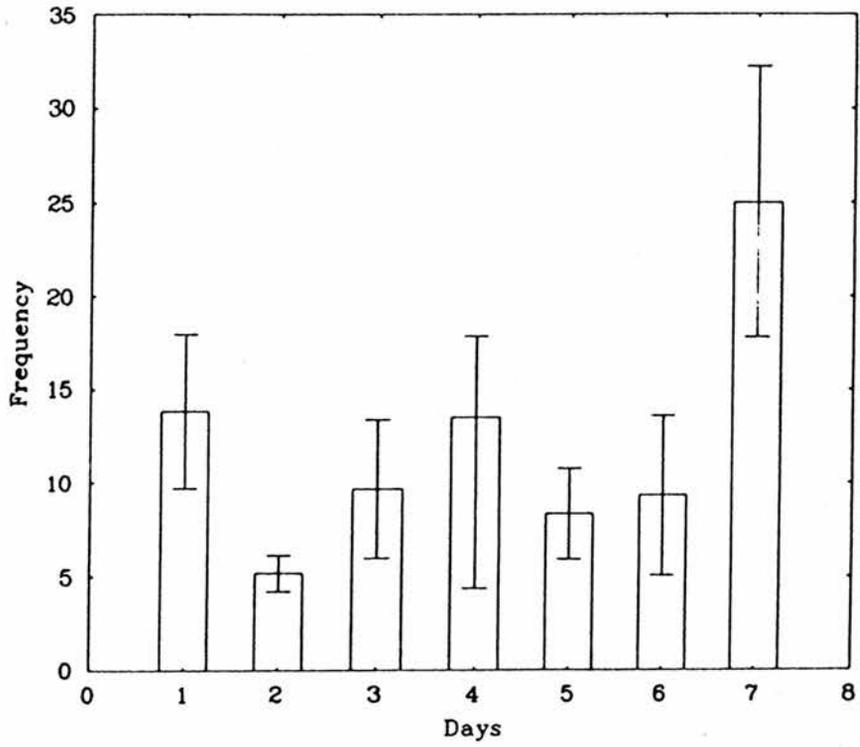


Figure 5.2: Variation in ventral roll during observation period: Part 1.

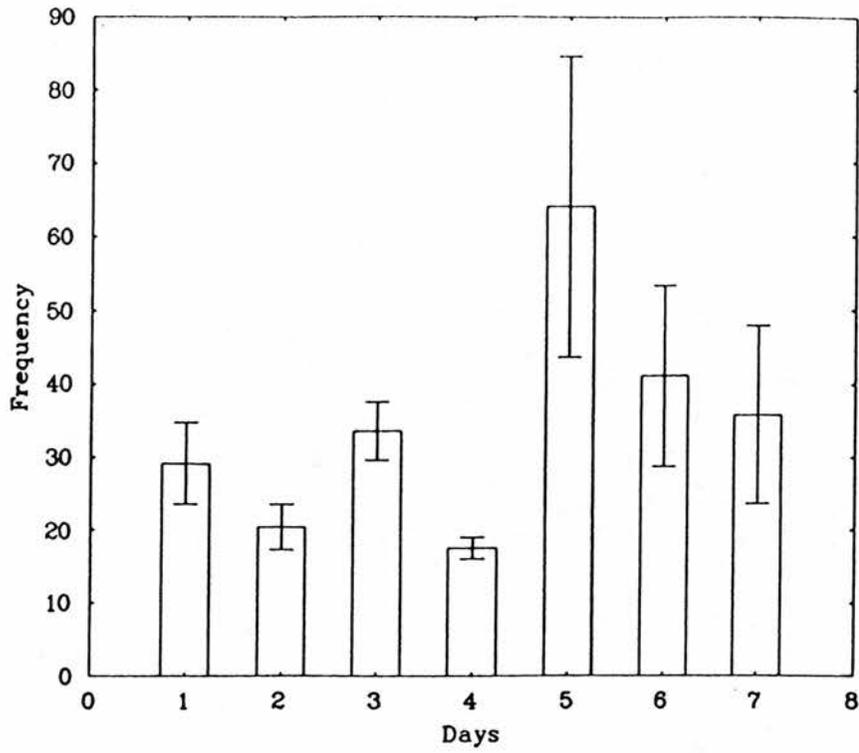


Figure 5.3: Variation in lateral threat during observation period: Part 2.

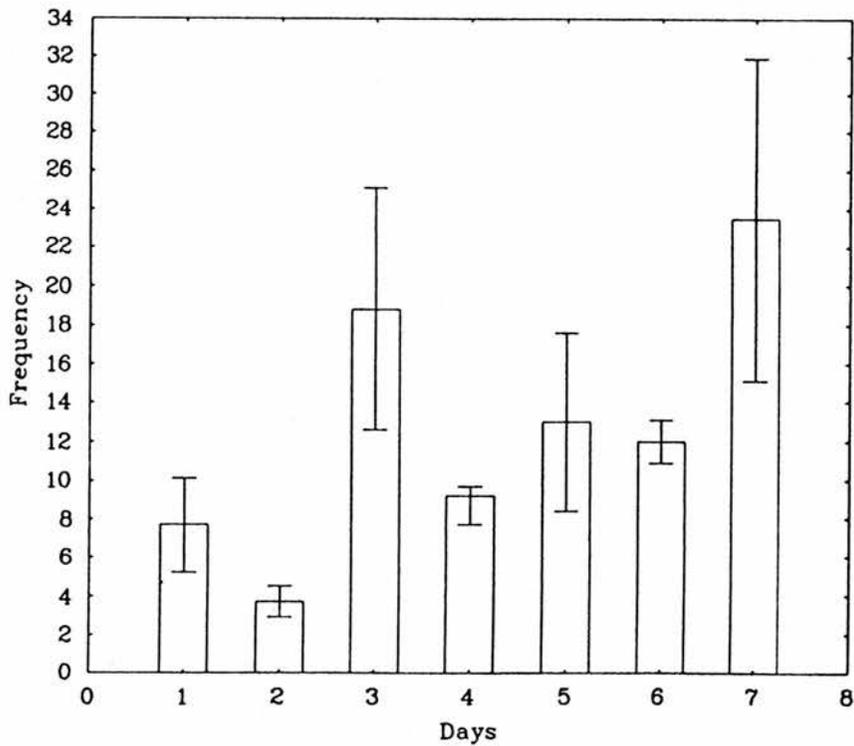


Figure 5.4: Variation in chase during observation period: Part 2.

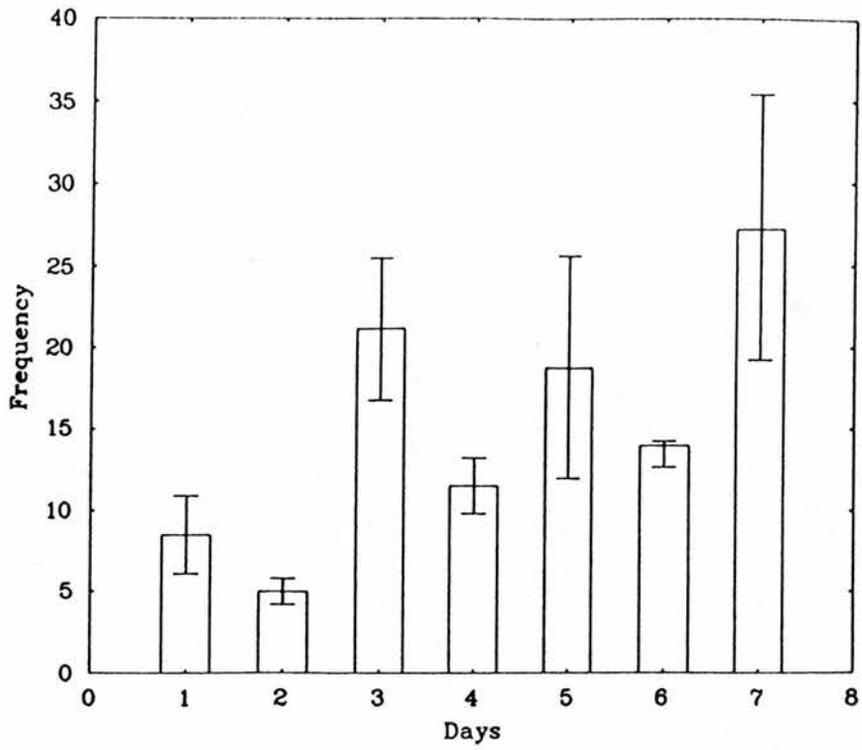


Figure 5.5: Variation in flee during observation period: Part 2.

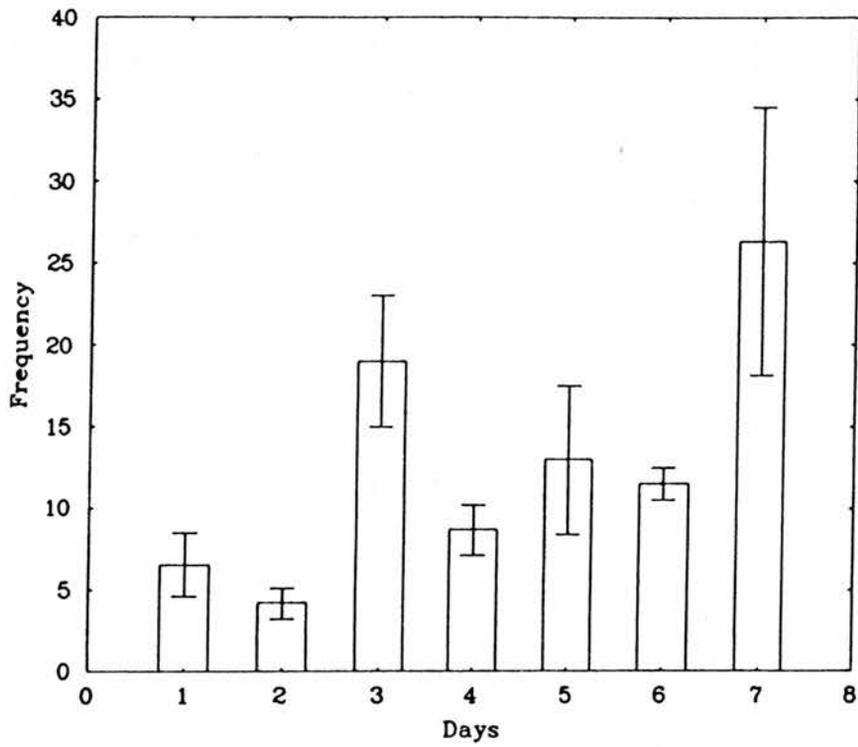


Figure 5.6: Variation in ventral roll during observation period: Part 2.

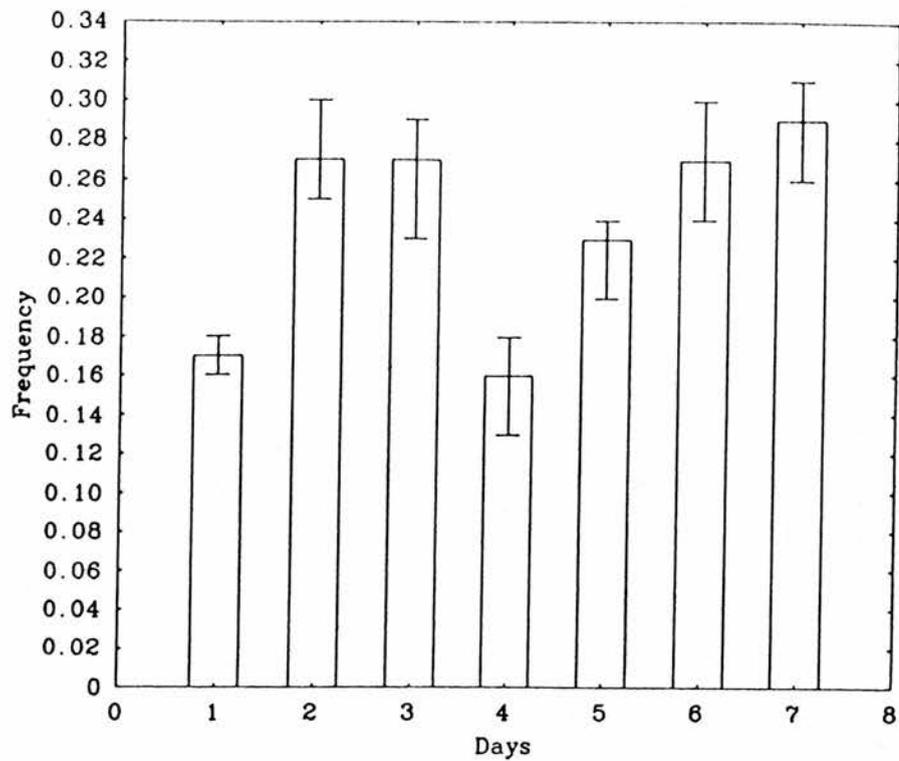


Figure 5.7: Variation in acts/sec during observation period: Part 2.

## 5.4 DISCUSSION

### 5.4.1 HIERARCHIES

In part one, the fact that the same opponent won each pair-fight could have been due to individual recognition or to prior experience of winning fights, but a more probable explanation would be that one opponent in each pair was more capable of winning the fight and, therefore, repeatedly dominated the other fish.

In part two, half of the pair-fights in round seven resulted in a reversal of the original dominance positions between the two contestants. These fish probably did not, therefore, recognize which of the pair had previously been the dominant individual. This result implies that individual recognition was not involved in the outcomes of the fights in round seven. However, it is also possible that the tiger barbs might still use individual recognition, but did not have sufficient memory to allow them to recognize other individuals after the elapse of this length of time.

As the outcomes of pair-fights were not affected by whether an individual had won or lost its previous fights, it can be presumed that prior experience did not affect the

outcomes of subsequent contests. Therefore, the fact that the outcomes of only half the fights in round seven complied with those in round one was probably not caused by the experience of wins or losses by any individual in the interim.

#### **5.4.2 CONTEST DURATION**

The insignificant results found in this section indicate that the fish did not fight for a significantly shorter time or submit significantly sooner when encountering opponents they had previously met than those they had not. This result, and the fact that contests did not decrease in duration the more two particular opponents encountered each other, suggests that no individual recognition was involved in these paired contests.

In part two, if individuals were affected by their previous wins and losses, it would be expected that the fish which were repeatedly defeated would then submit earlier in subsequent contests. Fish which repeatedly dominated their opponents would be expected to engage in longer contests against similarly dominant individuals. Neither of these situations was found to be the case. Therefore, it is probable that prior experience of wins or losses did not affect subsequent encounters.

#### **5.4.3 BEHAVIOUR**

If individual recognition affected the behaviour shown towards an opponent, it would be expected that fish which had previously been defeated by their opponent would increase the amount of submissive behaviour towards that individual when they re-encountered each other. This did in fact occur in the case of ventral roll. However, individuals which met different opponents in each round also showed the same trend. It cannot, therefore, be concluded that individual recognition was the cause of the variation in behaviours observed over the seven rounds.

If the behaviour was affected by prior experience of wins and losses, then the individuals which repeatedly won their fights would be expected to perform more biting and chasing in subsequent contests and the individuals which were repeatedly defeated would perform more flee and ventral roll. This could have been the case in part two, as the

frequencies of these behaviours increased significantly over the seven rounds. However, as no such variation was found in part one, it would suggest that prior experience did not affect behaviour in subsequent paired contests. It is possible that, both in parts one and two, the increase in the frequency of behaviours over the seven rounds was due to the fish gaining experience of fighting itself, rather than of winning and losing, and so performing actions more frequently. The reason that more types of behaviour were found to show an increase in part two might be due to the fact that encountering a different opponent each time gave these individuals better experience of fighting than those which continuously met the same opponent. This may, therefore, have been the cause of an increased use of threatening and fleeing behaviour by the fish in part two of this study.

#### 5.4.4 INTENSITY

If individual recognition took place in part one, then the intensity of fights should have decreased over the seven rounds as the dominant fish became less aggressive to opponents which they recognized to be submissive and as the subordinate fish submitted quicker to individuals which they recognized to be more dominant. However, no variation in intensity was observed, which suggests that the fish did not recognize which individuals they were capable of defeating or which they were likely to be defeated by.

If the behaviour was affected by prior experience, then the most dominant fish, in both parts one and two, should have become more aggressive. However, the number of contact acts showed no significant variation over the seven rounds, so this is also unlikely to be the case. Even though the frequency of acts/sec increased in part two, the results might have been due to the fish gaining in fighting experience, some to a greater extent than others, thus leading to the increases found. This increase was due to a greater number of non-contact acts, such as threat displays, rather than the highly aggressive contact acts. A possible reason for this is that, as the fish became more experienced in fighting, they learnt to conserve energy by increasing the less energetic acts rather than the highly aggressive, possibly more energetic, contact acts. The tiger barbs in part one may not have gained as much experience of fighting and of *different* fighting strategies as those in part two, as they were only paired with the same individual each

time, and so no change occurred in their frequency of acts/sec.

## 5.5 CONCLUSIONS

- (i) Winning a fight did not affect an individual's chance of winning subsequent contests.
- (ii) Fish did not submit sooner to a fish that had previously beaten them in a paired contest or when they were constantly defeated by different opponents.
- (iii) Fish did not alter their behaviour or levels of aggression based on their own past history of wins or losses, or on previous fights with the same particular opponent.
- (iv) Individual recognition is probably not involved in encounters between pairs of tiger barbs.
- (v) Prior experience of wins or losses is probably not involved in encounters between tiger barbs.
- (vi) Tiger barbs may learn, through experience of fighting, to make more use of the behaviours, such as threat displays, which are possibly less energy consuming activities.

## Chapter 6

# HIERARCHY FORMATION AND INDIVIDUAL DIFFERENCES IN AGGRESSIVENESS

### 6.1 INTRODUCTION

The aim of this Chapter is to examine whether more aggression is shown within a group of dominant fish than within a group of subordinate fish. This would indicate that each fish has its own individual level of aggression which may not be affected by whether it wins or loses contests, but rather could be the cause of the outcome of its encounters.

Such clear individual differences in aggression were found in the study on weaver birds, *Quelea quelea*, by Shawcross and Slater (1984). They found that previously subordinate birds were placid and sociable with each other, tending to sit in contact with each other, while the dominants, grouped together, maintained a distance between each other and fought much more. These results on weaver birds suggest that there are differences in the behaviour or appearance of individuals which give the others cues about status and which thus make individual recognition unnecessary for hierarchy formation.

It has already been concluded, from Chapters 4 and 5, that individual recognition was not involved in encounters between tiger barbs and also that individuals did not adjust their behaviour in the light of experience of wins and losses, but rather, the outcome of each contest probably depended on the relative fighting abilities of the contestants. Therefore, it is expected that groups of dominants should show differences in behaviour to groups of subordinates. If this is found to be the case, it then raises the possibility that the individual fish are adopting different strategies which pay in different ways (Rohwer *et al.* 1981, Barnard & Sibly 1981, Kaufmann 1983, Robertson 1986).

Chase (1982, 1985) and Nelissen (1985) both support the *jigsaw puzzle* model for hierarchy formation, the pieces being interaction patterns in component triads of larger groups. This implies that interactions between one pair have important implications for the interactions between other pairs and affect the behaviour of bystanders. This might explain the overall form of group social relationships. Nelissen describes the effects of group factors, such as: a chasing animal will immediately chase another and a chased animal will immediately be chased by another. If this is the case with tiger barb groups, then groups of dominants and groups of subordinates should settle into hierarchies involving similar behaviour patterns.

This Chapter investigates which, if either, of these theories is true of tiger barbs.

## 6.2 MATERIALS AND METHODS

This study involved four groups of four tiger barbs each. They were kept in tanks of the same size and conditions as described in Chapter 4. The four groups were made up as follows :

Group 1: *A, B, D, E*

Group 2: *G, H, I, J*

Group 3: *M, N, Q, R*

Group 4: *S, U, W, X*

The fish were left to settle in these groups for two weeks prior to this study. The study was made up of three parts. In all parts, each group was observed twice a day, using

the system of focal animal sampling, the observations being recorded on check sheets. The behaviour of each individual in a group was continuously recorded for a period of ten minutes per fish in each observation period. The behaviours recorded were *threat* (th) [lt, ft and ps], *bite/butt* (b) [ca and mf inc.], *chase* (ch), *flee* (fl) and *ventral roll* (vr).

In part one, each of the four groups was observed for two days (days 1 and 2) to determine the hierarchies from observations on which fish were threatening, biting and chasing and which were fleeing, submitting and hiding.

In part two, the fish were regrouped in different tanks so that group 5 included the most dominant fish from each original group, groups 6 and 7 included the second and third ranked fish from each group respectively and group 8 was made up of the most subordinate fish from each group. The groups were observed for the first four days (days 3 to 6) after transferral and their behaviours and the resultant hierarchies recorded. A period of ten days was then allowed for the fish to settle into their new groups, after which the fish were observed for another two days (days 7 and 8).

In part three, the fish were again grouped, as in part one, and were observed for another four days (days 9 to 12) to determine whether the hierarchy structures differed from those in part one.

The hierarchies, over the three parts of this study, were compared and the behaviours, recorded in part two, were compared between groups 5 to 8.

## **6.3 RESULTS**

### **6.3.1 HIERARCHIES**

#### **6.3.1.1 Part one : Groups 1 to 4; Observation days 1 to 2**

The dominance orders for each group, determined from the behaviours shown, are as follows:

**Group 1:**  $A > E > D > B$ ; **group 2:**  $J > I > H > G$ ; **group 3:**  $M > Q > R > N$ ;  
**group 4:**  $S > U > W > X$ .

These hierarchies were the same during both days of observation.

#### **6.3.1.2 Part two : Groups 5 to 8; Observation days 3 to 6 and 7 to 8**

The fish were then regrouped according to rank. The dominance orders for the new groups were then determined from the behaviours shown:

**Group 5:**  $M > S > J > A$  (day 3);  $M > S > A > J$  (days 4 to 6);  $M > S > A$  (days 7 to 8).

From day 2,  $S$ ,  $A$  and  $J$  were most often observed to be hiding from  $M$ , the dominant fish.  $M$  frequently attacked  $J$ , which probably caused the death of  $J$  (perhaps weakened by stress) eight days after being placed in this group.

**Group 6:**  $U > Q > I > E$  (days 3 to 8).

No change in dominance positions occurred in this group during part 2 of the study. By day 6,  $Q$ ,  $I$  and  $E$  were most often observed to be hiding from  $U$ .

**Group 7:**  $R > W > H > D$  (day 3);  $W > R > H > D$  (days 4 to 8).

These fish did not hide from the dominant during the first four days of observation. They were, however, most often hiding from  $W$  by day 7.

In group 8 (consisting of the subordinate fish from the original groupings), very few interactions were observed between the fish. Unlike the other three groups, these fish tended to remain in close proximity to each other and swam about the tank together. Even after the ten day settling period, although the fish did interact more, they still remained in close proximity. Submissive behaviour was observed, but none of the fish remained hidden from any of the others in the group. The dominance orders from day 4, given below, for this group show only apparent hierarchies as they are based on so few encounters.

**Group 8:**  $X > N > B > G$  (day 4);  $X > N > G > B$  (day 5);  $X > G > N > B$  (day 6);  $N > X > G > B$  (day 7 to 8).

It can be seen from these results that the hierarchy in group 8 was much less stable than in the other groups, though it did seem to have become more stable by day 7.

### 6.3.1.3 Part three : groups 1 to 4; Observation days 9 to 12.

The dominance orders determined from behaviours in this part are:

**Group 1:**  $A > D > B > E$ ; **group 3:**  $M > N > Q > R$ ; **group 4:**  $X > W > U > X$ .

**Group 2:**  $H > G > I$  (day 9);  $I > G > H$  (day 10);  $G > H > I$  (day 11);  $I > G > H$  (day 12).

The fish,  $J$ , which had originally dominated this group died in part two of this study. The remaining fish in the group did not display much aggression towards each other over this observation period, but rather tended to remain in close proximity to one another, thus behaving in a similar manner to the subordinate group 8 in part 2. The dominance orders, given above, for this group are, therefore, only apparent ones.

## 6.3.2 BEHAVIOURS WITHIN GROUPS OF EQUALLY RANKED FISH

Nested ANOVAS (Alice package) were carried out to compare the differences in behaviours between groups 5 to 8, and also the variation in behaviour in each group, over the observation period.

The variation in the frequency of total acts performed was significant, both between the groups ( $F = 6.50, d.f. = 3/12, p = < 0.01$ ) and over the 6 days for each group ( $F = 3.89, d.f. = 5/60, p = < 0.01$ ). This was only due to the variation in the amount of submissive behaviour shown as the variation in the frequency of aggressive acts was also

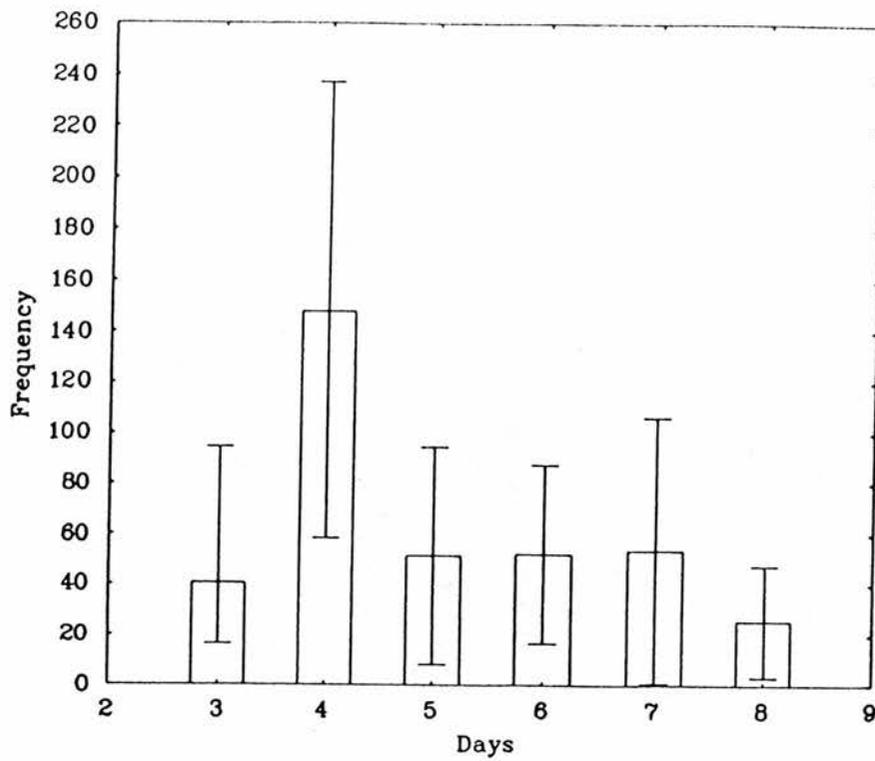


Figure 6.1: Variation in aggressive acts during observation period: Group 5.

found to be insignificant in both cases (between groups:  $F = 0.80, d.f. = 3/12, p = 0.52$ ; over 6 days:  $F = 2.25, d.f. = 5/60, p = 0.06$ ).

Changes in behaviour within each group were further investigated by means of correlations (minitab package) between the frequency of aggressive acts and the number of days of observation. These results differed from the ANOVA results for the variation in aggressive acts. This was due to the frequency of aggressive acts on one day of observation being much greater than on all the other days, when the frequencies were of a similar level (Figures 6.1, 6.2 and 6.5).

It was found that, in both groups 5 and 6 (Figures 6.1 and 6.2, the frequency of aggressive acts decreased significantly over the six observation days (group 5:  $r = -0.71, p < 0.05$ ; group 6:  $r = -0.76, p < 0.05$ ). The significant result for group 5 was due to a significant decrease in the amount of threatening behaviour (Figure 6.3) carried out from day 5 ( $r = -0.71, p < 0.05$ ). The significant result for group 6 was due to a significant decrease in the amount of biting behaviour (Figure 6.4) performed from day 6 ( $r = -0.80, p < 0.05$ ).

It was found, however, that in group 8, the frequency of aggressive acts (Figure 6.5)

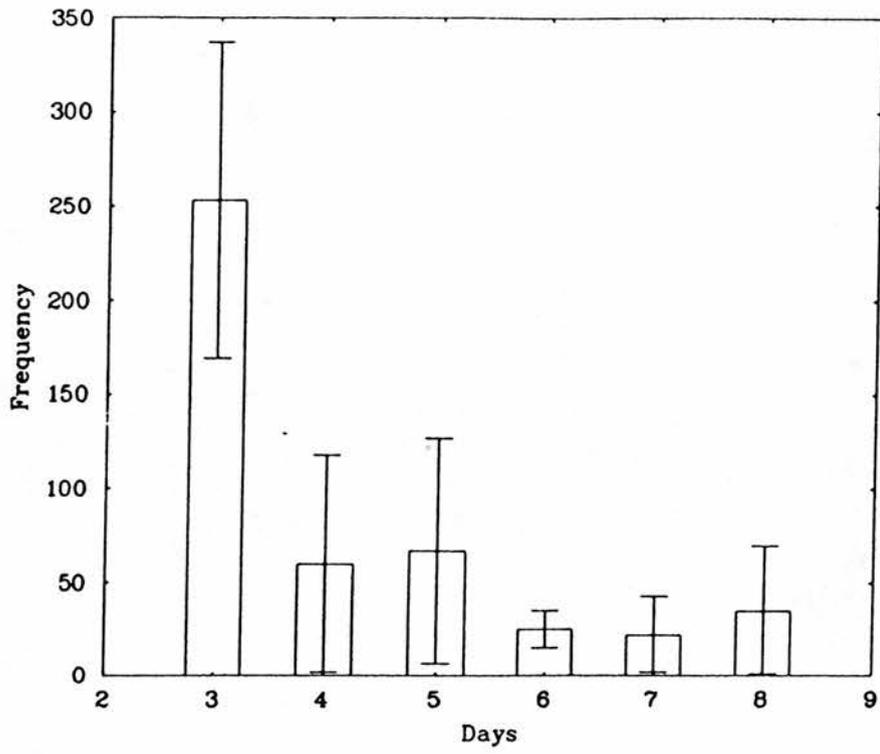


Figure 6.2: Variation in aggressive acts during observation period: Group 6.

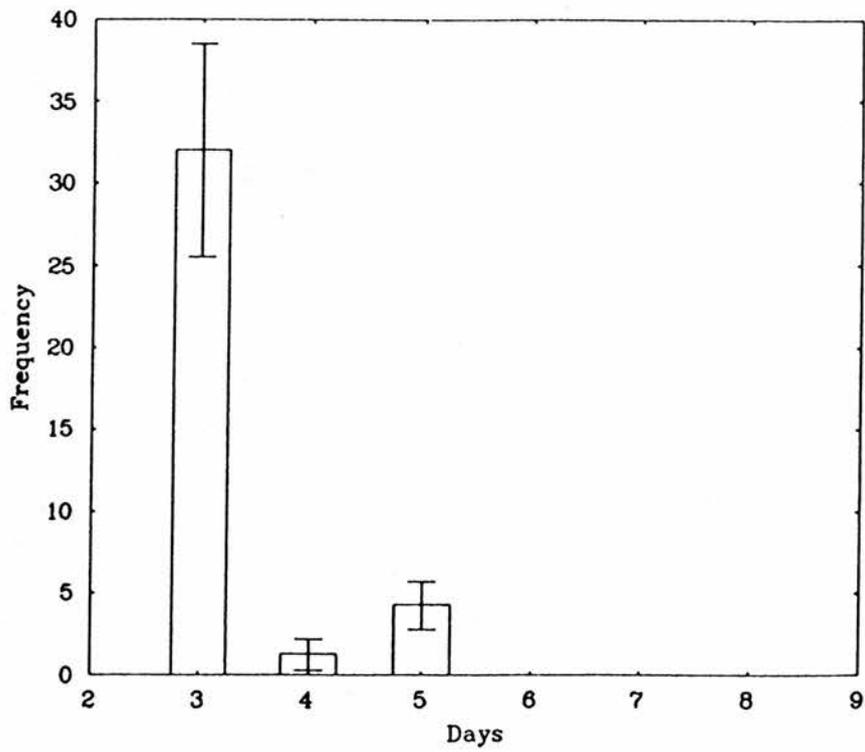


Figure 6.3: Variation in threats during observation period: Group 5.

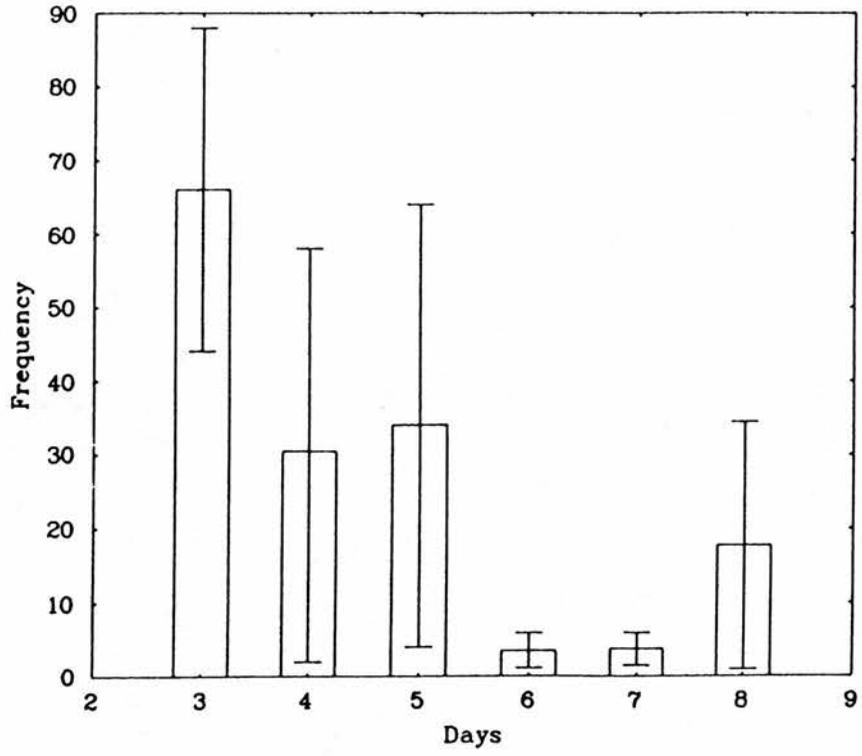


Figure 6.4: Variation in bite/butt during observation period: Group 6.

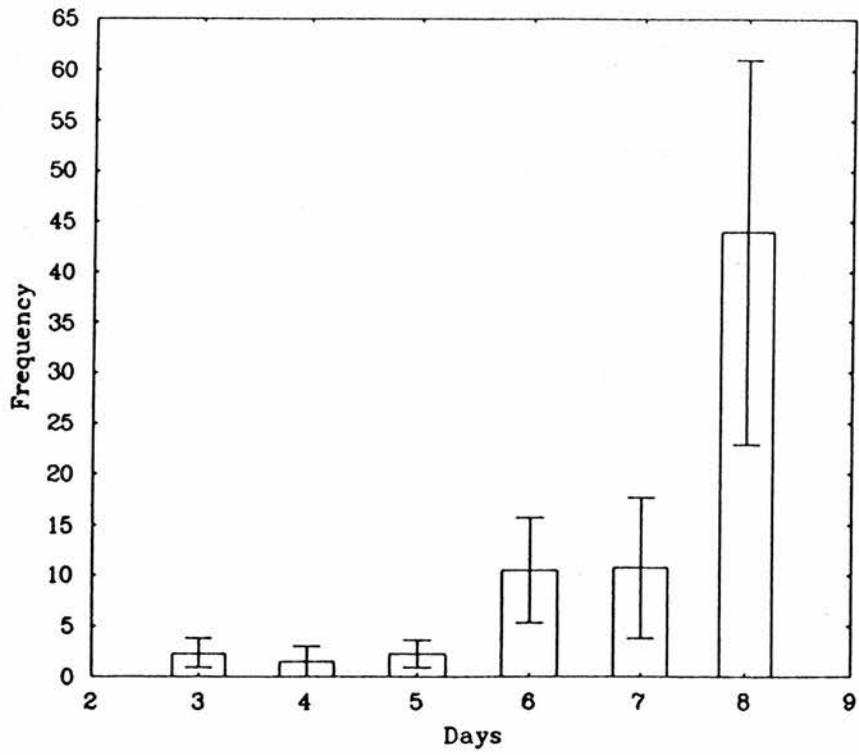


Figure 6.5: Variation in aggressive acts during observation period: Group 8.

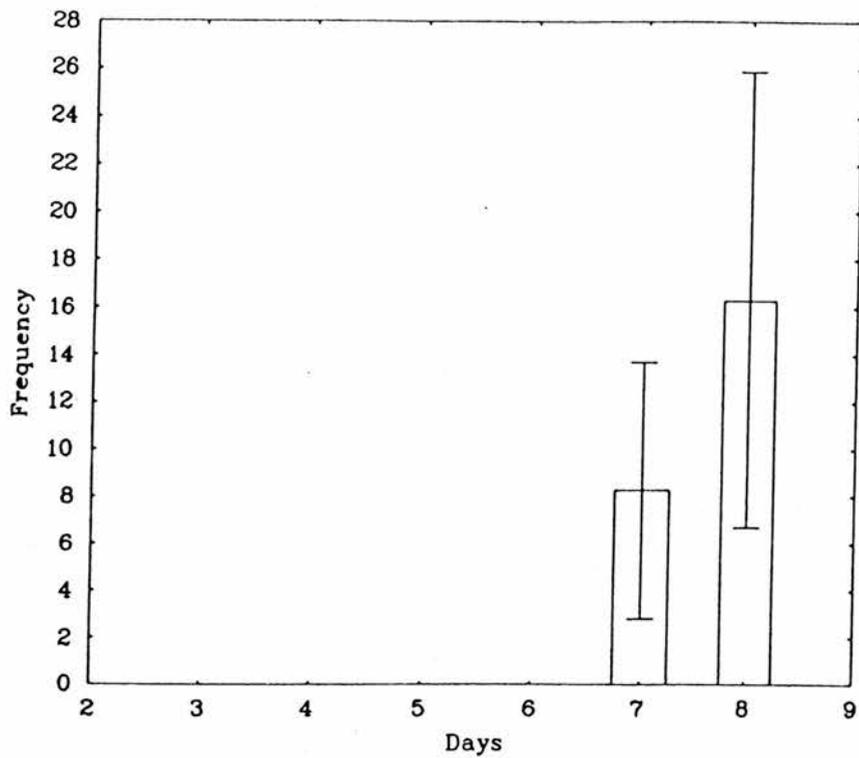


Figure 6.6: Variation in chase during observation period: Group 8.

increased significantly over the six observation days ( $r = +0.80, p < 0.05$ ). This was due to a significant increase in the number of chases (Figure 6.6) performed from day 7 ( $r = +0.83, p < 0.05$ ).

## 6.4 DISCUSSION

### 6.4.1 HIERARCHIES

In part two of this Chapter, it was found that the hierarchies in groups 5 to 7 were established in the first two days after the fish were placed in these groups and remained stable over the rest of part two. The dominance arrangements continually changed in group 8 until day 7, when it seemed to have become more stable. This may be due to the fact that, as the individuals had not been dominated by any other fish over this time, they were able to show more aggressive behaviour. Interactions therefore occurred, resulting in the fish establishing a hierarchy.

When the fish were replaced into their original groups, in part three of this study, the hierarchies were all different to those observed in part one and did not seem to be

closely related to the rankings of the fish in part two.

Individuals *N* and *X* had been ranked first and second respectively in group 8 and had both now improved their original lowest rank placings in their respective original groups. This may be due to the fact that both individuals, when placed solely with other submissive fish, had been able to improve their dominance positions and so had abandoned the submissive strategy and were more inclined to engage in contests. Individual *E* had been ranked third in part one, but had now dropped a place to become the lowest ranked in that hierarchy. This may be due to the fact that it had been the most subordinate fish in group 6.

Group 2, in part three, behaved in a similar manner to group 8 in part two, and also had a very unstable hierarchy. These three fish had each been ranked third in their respective groups in part two. When they were regrouped together, but this time without the originally dominant individual *J* (which had died in part two), these fish were possibly still adopting a submissive strategy and therefore behaved as the group of submissives did, and so did not tend to engage in contests.

The fact that the hierarchies, observed in part three, were not the same as those for the same groups in part one would also suggest that the outcomes of encounters were not based on individual recognition of which opponents were previously more dominant or submissive. There is no obvious explanation as to why the other changes in dominance positions occurred. Different individuals may have been affected by different levels of stress in their respective groups or may have differed in the extent to which they had improved in fighting ability during part two of this study.

#### **6.4.2 BEHAVIOUR IN GROUPS EACH MADE UP OF FISH OF EQUAL RANK.**

It can be seen, from Figures 6.1 and 6.2, that group 6 showed a greater amount of aggression on day 3 than was observed in group 5. This was not expected as the prediction was that a group made up of the most dominant fish should show the most aggression within the group. However, it may be explained by the individual *M*, in

this group, quickly dominating the other individuals, due to its superior fighting ability, and so the rest of the group avoided this fish, thus resulting in fewer encounters. The reason that a similar situation did not occur in group 6 might be because no individual had a much greater fighting ability than the others in the group and so had to engage in more fights to determine which was to be the dominant.

The behaviour observed in group 8 was very different from any of the other three groups. This suggests that these fish may have adopted a different strategy and that this submissive strategy deterred them from engaging in conflict. By day 6 in part two, as no fish was continually asserting its dominance over the others, the individuals began to engage in aggressive encounters with each other. Therefore, the amount of aggressive behaviour performed by each individual in the group increased rapidly. At the end of observations for part two of this study, this group had not yet established a stable hierarchy, though individual *N* had now become the dominant fish, and so interactions had not yet begun to decrease in frequency again.

Another explanation for both the continual assertion of dominance by the highest ranking individual in a group, and also the marked difference in the behaviour shown by the most submissive fish, is that the experience of being continually dominated suppresses the aggressive tendencies of the subordinate, thus resulting in an overall difference in the behaviour shown by the subordinates (Wapler-leong & Reinboth 1974, Hannes *et al.* 1984, and see Chapter 1). When the dominant fish is removed, the levels of aggression in the subordinate animals increase and so they engage in more fights. The fact that fighting did not occur immediately, in the absence of the dominant individual, may have been because the aggressive tendencies of the subordinates had not yet increased to a sufficient level. This explanation would support Chase's (1980) hypothesis that hierarchies emerge from the interactions among group members (Chapter 1). However, the involvement of such effects on aggression could not be proved, as hormonal changes were not examined in this thesis.

This explanation, however, disagrees with the results of both Chapters 4 and 5, where it was found that tiger barbs did not alter their behaviour in the light of experience of previous wins and losses. Therefore, the adoption of an alternative strategy by the subordinate fish is a more likely explanation. This strategy might be maintained

by the presence of a more dominant fish (*e.g.* by preventing the subordinates from engaging in contests by its own intervention). Thus, when the dominant was removed, this intervention would no longer occur and so the number of agonistic interactions between the subordinates could increase, as was found to be the case in this Chapter.

The fact that individuals *N* and *X*, which became the two most dominant fish of the subordinate group, then improved in rank when returned to their original groups, may not just be due to a change in strategy (or an increase in aggression levels), as neither would explain why fish, which had previously defeated them, could not do so again. It could also be due to an improvement in their fighting abilities, resulting from engaging in contests instead of avoiding them. The fact that the hierarchies were not the same in part three as in part one would also suggest this reason.

This would comply with the results of Chapters 4 and 5, which indicate that winning contests does not increase a tiger barb's aggressiveness, but rather the chance of winning increases due to an improved fighting ability, resulting from engaging in a greater number of contests. This would also explain why individuals which were lowest ranked in each hierarchy in part two, were not necessarily the most subordinate when returned to their original groups. This would suggest that losing fights had not made them more submissive or less aggressive. Perhaps these fish had not been bottom of a hierarchy for long enough to result in them employing the submissive strategy.

## 6.5 CONCLUSIONS

- (i) The most subordinate tiger barbs, when placed together in a group, behaved differently towards each other than any of the other more dominant fish.
- (ii) Other than the most subordinate fish, the most dominant fish were not more aggressive to each other, when placed in a group, than any other rank of fish.
- (iii) Subordinate tiger barbs appeared to be adopting a different strategy to the other individuals in a group. Their strategy deterred them from engaging in conflicts, whereas the other members of a group continually performed aggressive behaviours. The adoption of this strategy may have been due to, and then maintained by, the presence of more dominant fish.

- (iv) Individual recognition of opponents did not appear to influence the outcome of encounters.
- (v) Prior experience of wins and losses did not appear to render individuals more aggressive or submissive. However, engaging in more contests could result in an individual improving in fighting ability, thus increasing its chances of winning further contests.
- (vi) Groups of dominants and groups of subordinates eventually settled into hierarchies, involving similar behaviour patterns.

## Chapter 7

# GENERAL CONCLUSIONS

- (i) Tiger barbs form dominance hierarchies, but these are not always linear. Unlike many other animal species, including other fish species (Braddock 1945, Simpson 1968, Frey & Miller 1968, Gorlick 1976, Turner & Huntingford 1986) tiger barbs do not form hierarchies in accordance with their size (measured, in Chapter 3 as weight). These hierarchies are not totally stable (Chapter 4), as aggressive behaviour is continually performed towards higher ranked fish.
- (ii) Environmental factors do affect agonistic interactions. In Chapter 3, a greater amount of plant cover resulted in shorter fights, by allowing the loser of an encounter to escape from the winner.
- (iii) The outcome of a contest can be predicted in the early stages of a fight. This disagrees with games theory's *war of attrition* model (Bishop & Cannings 1978), that the behaviour of the eventual winner and loser should be indistinguishable for most of the contest. However, it agrees with Maynard Smith's (1982) rules for *assessment strategy*; that the behaviour during the first phase of a contest enables animals to perceive the difference between themselves (Chapter 1).
- (iv) Higher ranked fish tend to fight more aggressively, regardless of the rank of their opponents. More evenly matched fish do not have more intense fights. This also disagrees with the *war of attrition* model (Maynard Smith & Parker 1976, Maynard Smith 1982) which states that escalation of contest cost or risk is more likely to occur when contestants are evenly matched.

- (v) Submissive gestures are very important in influencing agonistic interactions, as their performance tends to lead to the termination of a fight. *Appeasing* gestures, such as ventral roll, therefore appear to be of great importance in the maintenance of dominance/subordination relationships.
- (vi) Isolation prior to encounters does appear to have a different influence on subsequent agonistic interactions as compared with when the opponents were previously living in a group. Fighting strategies may be learned by experience of social interactions (Scott & Fredericson 1951, McDonald *et al.* 1968, Scott 1971, Ratner 1970). Tiger barbs may learn, through experience of fights, to make use of the behaviours such as threat displays, which are possibly less energy-consuming activities. It is therefore possible that group-living leads to a greater amount of assessment of opponents, in the form of threat displays, before indulging in physical combat.
- (vii) Dominant fish, when grouped together, do not behave more aggressively than lower ranked fish, grouped together, except in the case of the most subordinate fish. When these were grouped together, they showed very little aggressive behaviour towards each other. However, they eventually settled into a hierarchy involving similar behaviour patterns to those found in the other groups.
- (viii) It is possible that the subordinates may adopt a submissive strategy, which deters them from engaging in conflict. This strategy may be adaptive for those incapable of winning a contest. It may, for instance, result in them avoiding costs associated with being aggressive, such as loss of body condition and injury (Clutton-Brock *et al.* 1979, Riechert 1988, Rohwer *et al.* 1981). The adoption of this strategy may have been maintained by the presence of more dominant fish in the group, possibly by preventing the subordinates from engaging in contests by the continual assertion of their own dominance (*e.g.* by intervening in interactions between two group members, see Chapter 4).
- (ix) Individuals may have differed in the rate of development of their fighting abilities, thus leading to some becoming more aggressive and others more submissive. This could lead to changes in dominance relations between opponents by increasing the chances, for some individuals, of winning further contests.
- (x) Prior experience did not appear to affect tiger barb encounters. Individuals ap-

parently did not adjust their behaviour in the light of wins and losses, but rather the outcome of each contest might have depended on the relative fighting abilities of the contestants.

- (xi) Individual recognition did not appear to be involved in the outcomes of encounters, as fish did not alter their behaviour on the basis of previous fights with the same particular opponent.
- (xii) Tiger barbs may adjust their behaviour according to cues from the opponent that correlate with its fighting ability, thus conforming to the theory of an *assessment hierarchy* (Barnard & Burk 1979).

It is clear from the above conclusions that the behaviour of *both* the dominant and the subordinate fish are of great importance in the establishment and maintenance of tiger barb hierarchies.

# Appendix A1

Explanation of behavioural categories:

*Follow* (fo): One fish moves in the direction of another at a slow or normal pace.

*Lateral threat* (lt): The fish assumes a posture sideways onto its opponent with all fins maximally spread.

*Frontal threat* (ft): The fish faces its opponent with all fins maximally spread.

*Head down threat* (hd): Similar to frontal threat, but the body is at an angle to the opponent with head lower than tail.

*Parallel threat swim* (ps): Both fish swim alongside each other at the same speed with fins maximally spread.

*Bite/tap/butt* (b): The fish hits its opponent on flank or fins. Tap and butt are with the mouth closed. Butt is harder than tap. Bite is when the mouth is open. These actions were grouped as they were too fast to be easily differentiated.

*Attack* (at): The fish approaches its opponent at high speed and bite/taps/butts its flank or fins.

*Carousel* (ca): Both fish circle each other, frequently biting the other's flank. During this behaviour, both descend to bottom of tank.

*Mouth-fight* (mf): Both fish direct bites to the opponents jaws resulting in a "tug of war". Bouts of mouth-fighting occur between bouts of carousseling and take place at

the bottom of the tank.

During mouth-fight and caroussel the flanks of both fish darken to the shade of the tiger barb's stripes. This colouring does not fade until one fish flees. The eventual loser's colouring fades faster than the winner's. This darkening of the flanks also occurs if a fish is moved to a new tank and is thought to be a sign of stress.

*Chase (ch)*: One fish pursues the other at an accelerated pace.

*Waggle (wg)*: The fish performs a high amplitude, low frequency flexing of the body which results in the tail beating in the direction of its opponent. During this action the fins are maximally spread and the body often darkens.

*Flee (fl)*: One fish moves away from its opponent at an accelerated pace.

*Dorsal roll (dr)*: The fish rolls in a horizontal plane until its back is facing the opponent. This usually occurs when it is threatened or chased and is thought to be a submissive gesture.

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