The Functional Analysis of Display.

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Declaration

I hereby declare that the original research cited here was carried out, and the manuscript composed by myself.

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Abstract

The conflict theory has often been invoked to explain causal and functional aspects of agonistic communication. The advent of games theory analysis of the same behaviour has provided models of agonistic behaviour standing in complete contrast to the earlier 'conflict' models. The difference lies in the advocacy of a system conveying differences in intention by the latter approach.

The present study examines, in the light of a number of tests of consistency, the explanatory power of the conflict theory at an empirical level. The methods used followed those previously used to support the 'conflict' view. Lack of consistency leads to the rejection of the 'conflict' view that displays represented varying levels of signaller intention.

Using the same basic method, temporal association, two further analytical techniques are explored. One examines the inter-dependence of display use, the other examines the effect of display, distance, orientation combinations on their recipient. These latter methods suggest that the threat display repertoire of the great skua is more restricted (in terms of component displays) than was previously thought. I suggest that a threat system comprising one display is indicated, bringing it into line with that anticipated by some early games theory models.

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Introduction

'Force, and Fraud, are in war the two cardinal virtues'
Thomas Hobbes.

Disputes between individuals of the same species over resources, e.g. mates, food, territories, occur frequently. To the ethologist interested in such behaviour two things soon became evident. Firstly, the majority of disputes are settled by displays rather than actual combat. Secondly, species members appear to have a number of displays at their disposal.

Whilst accounting for the first of these observations has proved relatively unproblematic, the second has fostered considerable speculation. While a number of attempts have been made to account for the observed displays (e.g. Tinbergen 1959, Cullen 1966), the existence of a number of displays has prompted further theoretical observations ranging from suggesting that the number of displays observed will be insufficient to meet the animals social needs (e.g. Beer 1975, Smith 1977), to suggestions that a range of displays should not evolve to subserve threat by conveying differences in signaller intention. (Maynard Smith 1972).

Many studies concerned with the understanding of displays have concentrated on their role in fulfilling a threat function and it is in this context that the contradiction between the view that displays convey differences in signaller intention, and in particular to attack (Cullen 1966) and those advocating a system whereby differences in such intention should not be conveyed (Maynard Smith 1974) is most evident (Caryl 1979).

Assessing the relative merits of these different viewpoints is hindered by the differing theoretical frameworks upon which each is built, a difference which has its roots in a difference of opinion over the manner in which natural selection works (Caryl, in press). However, an alternative would be to use the predictions of one approach to phrase questions which could be tested in data provided by a different approach (Caryl 1980). This approach has proved fruitful in recent years. By demonstrating the ambiguity present in data previously used to support the possibility of displays forming a series conveying a range of intentional information, Caryl (1979) has paved the way for a more critical analysis of these ideas (and particularly those based on the conflict theory) and the data used to support them. Caryl also emphasised the importance of demonstrating consistency before accepting the general validity of any evidence and it was with providing a test of consistency to data derived by applying the conflict theory to the functional analysis of agonistic behaviour that the present study was concerned.

What is a functional study?

The views outlined above, the ethological and the games theory view, differ in more than the threat system anticipated.

The games theory view is based on the development of models to explain how a theoretical animal should behave to maximise its fitness, and to facilitate comparison between models their outcome has to be expressed in some common currency (McCleery 1978). This is achieved by the use of function in the strict sense of a contribution to fitness (Krebs 1976). The adoption of this view has been criticised by a number of authors. Taylor and Taylor (1979) refer to this approach as the fitness paradigm and suggest that it is more important to consider the advantages of behavioural differences at the individual level since it is only through adopting an appropriate strategy for day to day encounters that an individual will survive to reproduce. A similar conclusion was reached by Caryl (1980), though from a different theoretical perspective. Caryl's view was stimulated by a variance in benefit that accrued over a lifetimes use of the various strategies open to theoretical animals although their mean pay-offs would be similar. This has particular relevance for real animals where it may not be possible to make up for a present poor performance at a later date. It is necessary to shift from considering net benefit over a lifetimes use of a given strategy. Since fitness is a 'lifetime' currency an alternative is needed to compare different strategies on a 'day to day' basis and for this Caryl (1980) proposes an intermediate currency - energy. Davies (1981) has shown how the relationship between energy and strategy can be used to account for the adoption and stability of a given strategy. The use of energy as a currency is more easily related to individual investment in the short term, i.e. through its behaviour. This is more in line with the traditional ethological treatment of function where that consequence that a system appears designed to fulfil has been considered as its function (Beer 1975).

While the ultimate pressure on a system will be in terms of the fitness contribution accruing to an individual adopting a given system, and while dealing with function in these terms is necessary to permit the comparison of different theoretical models, the limitations posed by empirical research necessitate a broader and simpler definition to aid understanding the proximate effect of a system. Function will be used here in terms of the qualities of display behaviour, e.g. the ability of displays to affect an opponent, responsible for the proximal effectiveness of a system.

Within this broad, proximate approach further divisions can be made. If communication is taking place then the system will be maintained by virtue of its effect on a recipient. In a functional study of displays it is important to demonstrate consistency in the manner in which displays exercise their effect. After this has been demonstrated the other functional components of the system can be investigated, e.g. the form of displays and the manner in which this form derives its effectiveness, the area of investigation which has been central to the etholigical approach, and how the system is adaptively maintained, the area which has been of prime concern to the games theorists.

This may seem a rather back to front approach and it is one which has not received widespread acceptance of ethological opinion. For example, Marler (1961) was one of the first ethologists to base an analysis on semiotics. He considered that the area of this approach of most direct interest to animal communication studies was pragmatics and, specifically, how the recipient of a signal should respond. Using the same approach Smith (1969) considered that contextual influences would diminish the effectiveness of Marler's approach and, instead, suggested that analysis should concentrate on the search for the message components of displays. The reasons for basing an analysis on the responses of the recipient are varied and concerned, in the main, with surmounting problems arising from defining displays (and their constituent components in particular) and with the means whereby displays are categorized as fulfilling a threat function using temporal association.

One of the earliest functional questions posed by ethologists studying disputes was why display should replace combat as a means of settling disputes.

Combat versus Display.

The primary reason for the substitution of display for combat is the risk of injury associated with the latter. Combat, serious injury and even death are more common than was earlier believed (Geist 1971) and this, in itself, may be sufficient to provide the adaptive pressure for reducing the costs associated with disputes, costs that arise from the risk of injury involved. However, further complications arise from the difficulty of determining the debilitating effects of injuries not leading immediately to death or which would not even be considered serious, a problem that has only come to light through considering the possibility that an apparantly minor injury may reduce the fecundity of an individual relative to that of other individuals (Clutton-Brock et al. 1979). In this light it is easier to appreciate the adaptive pressure moulding the development of a means other than combat for settling disputes. Fighting does still occur and greater theoretical attention is being given to conditions under which escalation would be advantageous (Caryl 1980).

In answer to the question there seems to be a general consensus that the use of displays arose in response to the risk of injury associated with combat (Tinbergen 1959, Maynard Smith and Price 1973). However, a difference in opinion exists concerning the mechanism underlying the evolution of this system. These differences can be broadly split into an historically 'ethological' view and a more recent 'games theory' view. Although their views regarding this mechanism are more similar today the historical ethological perspective has probably exerted a considerable influence on present day ethological thinking (Caryl, in press).

The early ethological view suggested that the reduction in the risk of injury arose in response to group selection - restrained display fighting evolved to prevent species damage. This functional view (of preventing species damage) channelled thinking of displays as having evolved to make information mutually available (Lorenz 1966). Since it was species survival that was at stake the interests of individuals are in concert and it makes sense within this framework for interactants to make information about their intentions clear and unambiguous (Cullen 1966). Both interactants, according to this view, share the common purpose of ensuring the fittest population.

A contradictory view arose from considering selection acting at the individual level. According to this view the interests of the interactants would be opposed. As such an individual would be expected to gain considerably by attacking an opponent immediately. The reason why restraint, i.e. the use of display, should appear lies with the risk of injury associated with attack and conventional (display) fighting has been shown to be adaptive at the individual level (Maynard Smith 1972).

Further divisions are evident between these views with regard to the dynamic mechanism leading to dispute resolution using display.

The ethological view with its roots in group selection advocates the transmission of intentional information, a view supported by the observation of a number of displays serving ostensibly the same purpose, threat.

The more recent view, basing its argument on individual selection, suggests that displays should not evolve to convey differences in signaller intention.

Basically, the difference between these views lies with the number of displays considered as serving a threat function. It is only when faced with a number of displays apparantly serving the same function that the concept of information need specifically be invoked. The number of displays described has rested on the intuitive sense of the observer and a more exacting definition of displays and the means whereby they are categorized as fulfilling a threat function may illuminate this problem.

Before considering how this problem may be surmounted, what does each of these views offer the study of agonstic communciation and how do the views differ?

Games Individuals Play.

The foundation upon which the games theory view is built is that selection acts at the level of the individual and it was to the question of how individuals should behave in order to maximise their fitness that this approach addressed itself. A corollary of considering selection as acting at the individual level was that, in a dispute, the interests of the interactants would be opposed and this led to a number of intuitive observations.

Each interactant is assumed to be attempting to acquire the disputed resource with minimum cost to itself and since there exists pressure fostering the use of displays rather than combat, differences between individuals will be conveyed symbolically and under such circumstances there exists the possibility that 'bluff' will arise where an individual may signal in excess of its capability in the event of an escalated contest (Maynard Smith 1974). Such a possibility is very likely if displays are used to convey differences in the level of threat intensity and so Maynard Smith suggested that displays should not convey differences in intention and, instead, individuals should display with a constant intensity (Maynard Smith and Parker 1976).

The ethological suggestion that displays would represent motivational differences was well suited to explain the dynamics of an interaction. For this alternative suggestion to have any credibility a means of settling a dispute where only a single intensity display is adopted is necessary.

By considering the interests of the interactants as being opposed it was possible to draw on a branch of mathematics, games theory, to provide theoretical models of how individuals should behave. If individuals use only display to resolve disputes the risk of injury is reduced but an additional cost would be incurred as a result of the time spent displaying, time which could be spent in the execution of other activities. For example, Clutton-Brock and Albon (1979) found that there was a pressure on harem holding red deer stags to resolve disputes as quickly as possible to prevent harem loss through the actions of kleptogamists, subordinate stags who may attempt to steal fertilisations.

Displaying with different costs that an individual is prepared to incur has been ruled out (Maynard Smith 1974) and instead Maynard Smith described the War of Attrition model which suggested that individuals should display with a constant intensity for a duration chosen at random from a negative exponential distribution of persistance times. In so doing the individual would be behaving according to what has become the cornerstone of this approach, the Evolutionarily Stable Strategy (ESS).

The second intuitive observation to emerge from adopting this view was that, in competing for resources, the best choice for an individual was dependent upon what other individuals in the population were doing. Where a resource is relatively abundant and accessible to individuals competition will be relatively rare. However, when a resource becomes limiting in both time and space choice will be restricted and direct competition between individuals will be inevitable, so providing the conditions necessary for the development of the ESS. The ESS is a strategy which, when adopted by the majority of a population, is resistant to invasion by a mutant strategy - no mutant strategy will confer a greater fitness upon its proponent. (Maynard Smith 1972).

Symmetric versus Asymmetric Contests.

The fundamental shift in attention towards considering selection acting at an individual level led to further consideration being given to a number of alternative cues which could serve as a mechanism for resolving disputes.

In the original model proposed by Maynard Smith the contestants were assumed to be equally matched - the contests were symmetrical. In situations where differences between interactants are present, certain appropriate inter-individual differences could be used to resolve disputes. The presence of such differences would result in the contests being asymmetrical (Parker 1974, Maynard Smith and Parker 1976). These authors outlined three broad classes of asymmetry which could provide the cues necessary for settling a dispute.

Firstly, individuals could differ in Resource Holding Power (RHP) (Parker 1974). Information about differences of this nature could be provided directly through variation in size, weaponry, experience (individual recognition) or indirectly via a badge which provides a measure of RHP. It was the possible use of status badges as cues to RHP that led to consideration of 'bluff' as an adaptive pressure acting on communications systems (Maynard Smith 1974). Where such cues are available, what maintains their effectiveness?

A number of species possess morphological enhancements which are considered to provide an indication of the RHP of the holder (e.g. Harris Sparrows, Rohwer 1977; Mountain Sheep, Geist 1971). Presentation of these signals, in the main, is passive and so what prevents them being used as bluff? In the Harris sparrow Rohwer (1977) found that the status of an individual was correlated with the extent of the black bib possessed by that individual. The functional significance of this cue was tested by blackening subordinates to resemble more dominant individuals. In so doing it was found that the blackened individuals were persecuted more (Rohwer 1977). The black bib alone was not sufficient to guarantee success and, further, behavioural cues might also be important; a possibility that was re-inforced by the finding that darkened individuals injected with testosterone, a treatment which brought cue and behaviour into line, experienced greater success against real dominants (Rohwer and Rohwer 1978). In this system 'bluff' is held in check through the necessary matching of both cue and behaviour with a certain level of escalation being used to weed out potential cheats.

Assessment cues need not be limited to visual signals. Clutton-Brock and Albon (1979) proposed a three-tiered assessment system in red deer. The primary component of this system involved roaring contests, RHP being signalled by the rate of roaring. They argued that the considerable energetic cost of roaring resulted in behaviour that could provide a reliable indiciation of RHP differences. Where the roaring rates of each interactant were similar the contest was more likely to develop into an escalated tournament of direct strength and this interplay between display and more overtly agonistic behaviour will act to reduce the possibility of bluff becoming established.

Given that an individual can use such assessment cues, how does that individual develop an awareness of his relative status? Where an individual can perceive a cue with which to asess an opponent, on what basis is the distinction between the opponent being dominant or subordinate made? Geist (1971) was aware of this problem and suggested that a level of overt fighting or tournament (Maynard Smith 1972) was necessary to determine relative status. In mountain sheep horn size is used as a status badge. The size of the horns change as the individual develops and occasional tournaments or trials of strength are necessary to enable the individual to monitor his relative status or RHP. In this way the individual does not monitor his status directly but bases judgement on his performance relative to opponents of differing horn size.

The extistence of an assessment cue is not, in itself, sufficient to order resource access and a level of overt behaviour is necessary to guard against bluff and to permit asessment of relative status or RHP. What is not known is the level of overt behaviour needed for the maintainance of such a system and the form that it should take, e.g. whether it should be in the form of a tournament or of a more directly aggressive nature.

An alternative asymmetric cue may arise from differences in the relative value placed on a resource by each of the interactants. Parker (1974) defined such disputes as those involving differences in Fitness Budget. Fitness was defined in terms of arbitrary units, individuals differing in the number of units they could expend. A situation in which such an asymmetry could arise is where a difference exists in the extent of investment in a resource, e.g. between a territory owner and an intruder. Parker also pointed out that as an influence on decisions of this nature it was less the extent of existing investment but rather the future investment needed to reach a successful conclusion that ordered the manner in which individuals should behave.

The ethological suggestion of displays representing differences in motivation was ideally suited to provide a mechanism for resolving such a dispute - a mechanism whose value has already been criticised (Maynard Smith 1974). An alternative mechanism would be to adopt a display time chosen from the negative exponential distribution described in the War of Attrition model, with differences in the times chosen being correlated with the cost an individual is capable of incurring.

Where the use of asymmetries may be a feature of a contest complications can arise where asymmetries are contradictory.

It is conceivable for a situation to arise where multiple and mutually opposed asymmetries are present e.g. High RHP/Low FB versus Low RHP/High FB, and leads to the question of the mechanism whereby the animal assesses the asymmetries appropriate for the situation or how an individual determines the role it will play in an interaction (Hammerstein 1981). Parker and Ruberstein (1981) term the above an example of a weak role and one which leads to a situation where escalation is likely. If such a situation does lead to an escalated contest they further suggest that the assessment phase will be carried into the direct contest, the latter providing further assessment cues. It is not clear what form such escalation should take.

The third type of asymmetric cue could be one involving an uncorrelated asymmetry (Maynard Smith and Parker 1976). If the resource being disputed is relatively abundant a time saving could be achieved by settling a dispute on the basis of an arbitrary convention. A convention of this nature could take two forms. A 'conventional' strategy would be one where prior ownership would serve as the cue. Davies (1978) demonstrated that prior residence was used by the speckled wood butterfly in settling disputes over possession of sun spots. The alternative strategy is the 'paradoxical', an example of which was observed by Burgess (1976) where, in contests over hiding places in spiders, the intruder was the winner, the incumbent moving off to make way for the intruder.

In the early models of contests involving asymmetries, the asymmetry itself was considered capable of providing the information necessary to resolve a dispute (Parker 1974). More complex models have shown that contradictory interaction between asymmetries is likely to lead to escalation although the escalation itself possibly in the form of a tournament, may be used to furnish further assessment cues (Parker and Rubenstein 1981). However, neither this latter type of model or those concerned with matched individuals provide an explanation for the number and variety of displays generally observed.

Games Theory and multiple display repertoires.

It was the observation of a number of displays all apparently serving a threat function that led to the ethological postulation of a system whereby displays conveyed differences in signaller intention, these differences providing the basis of a mechanism permitting contest resolution with little risk to the interactants. As a result the contradiction between the ethological and games theory views lies not only in the manner in which displays are thought to act but also in the number of displays considered to be used for contest resolution.

The existence of a number of displays has been viewed as problematic to the games theory view (Dawkins and Krebs 1978). The latter authors attempted to integrate the number of observed displays into the games theory framework by suggesting that displays represent a form of gradual escalation. If graded signals are used for assessment they suggest that the use of a high intensity threat display will indicate a high RHP or, more likely, provide an indication of the relative value placed on the resource. The obvious opportunity for bluff thus provided did not go unnoticed and they suggested that displays would differ in the cost associated with their performance with high intensity displays being the most costly and there is evidence to support this, at least for vocal displays (Clutton Brock and Albon 1979). Displays could be used in a sequence with each step revealing an increasing level of cost that the signaller is willing to incur. By working through the repertoire sequentially it should be possible to acquire the resource with the minimum cost. If this were the case, individuals would be expected to work through their repertoire sequentially from low cost to high cost displays. There is a growing body of evidence to support this idea. Caryl (1980) reviews a number of examples where a progressive matching takes place between individuals and a number of information theory based analyses suggest a sequential inter-relatedness in signalling behaviour (e.g. Rubenstein 1981).

If such a system were in existence it might be expected that the immediate use of a high intensity display (i.e. bluff) would tend to be disbelieved. Working on territory establishment in the red-winged blackbird, Yasukawa (1979) found that juvenile individuals in attempting to acquire a territory for the first time would tend to use, predominantly, high intensity displays. Despite this they were less successful against more experienced individuals using less intense variants. Yasukawa suggested that this disbelief of the prompt use of high intensity displays served to prevent the establishment of bluff. This may be indicative of the system anticipated by Dawkins and Krebs (1978).

These findings suggest that it is possible to integrate the variety of observed displays into the games theory framework through suggesting that displays represent different levels of escalation. Before it can be accepted more detailed study is needed on the energetic costs associated with displays and the manner in which this varies between displays. A high energetic cost has been considered as a prerequisite for the prevention of bluff (Clutton Brock and Albon 1979), and it is questionable whether a postural display could ever fulfil this criterion. An explanation in terms of associated cost was proposed by Zahavi (1975) in his 'handicap principal' where cost was related to the magnitude of the handicap suffered by an individual. The adaptive benefit of a system of this nature has been viewed with considerable scepticism (Halliday 1978). A further question which has received little consideration is the extent of the association between assessment signal and overt behaviour. The adaptive maintainance of a system using overt behaviour may reduce the necessity of the cue to mirror RHP or fitness budget (Davies 1981), with the cue becoming an arbitrary sign.

If a sequential display system is in evidence, is an associated and appropriate level of overt behaviour needed at each level of the sequence? If only the top level was subject to bluff checks what might prevent bluff arising at a lower level? The existence of such a system is plausible and may furnish an insight into dispute handling systems. Before it can be accepted a number of questions relating to the manner and extent of energetic interrelatedness needs to be investigated.

It is not possible to account for all multiple display repertoires in this manner. Not all displays occur in the graded or sequential form necessary for the working of this system but rather they occur discretely in interactions of relatively short duration. It is the occurrence of the latter type of behaviour which has most often been cited in support of the idea that displays represent differences in intention (Stokes 1962 ab, Dunham 1966, Andersson 1976).

A second problem that is of interest before any of these theories can be adequately tested concerns the manner in which the display, the central and basic unit, is defined and how it is categorised as fulfilling a threat function. The games theory view has not given consideration to definition of displays but has been concerned with the adaptive maintainance of theoretical systems or strategies and numerous assumptions concerning the units of study are made at the empirical level of applying models and ideas derived therefrom to live interactions, assumptions which may have had a profound influence or the nature of the system thought to be under consideration. For instance, in the sequential analysis presented by Rubenstein (1981) he considered that delivery of the same action pattern at different orientations (relative to the opponent) represented different displays. The question of the contribution of orientation to the communicative function of displays has yet to be fully investigated and it is an area of inquiry which is likely to have particular relevance for postural displays since the visual stimulus presented to the opponent will differ markedly as the relative orientation of the signaller changes.

This criticism can be levelled against the more traditional ethological view but to a lesser extent. In general, the lack of consensus concerning the rigid definition of the units of study will serve to hinder progress towards an understanding of agonistic displays and their function. The problems involved in defining displays and the methods of categorization are important and will be considered in greater detail later.

How have displays been defined by ethologists and what explanations have been offered for the variety of displays observed?

What is a Display?

A formal definition of a display was first suggested by Moynihan (1955), a display being a behaviour pattern that had become ritualised.

> "A behaviour pattern will be considered ritualised if there is evidence that it has a signal function and that it has become specialised in adaptation to that function." (p.21).

The evidence considered appropriate for identifying a display as one fulfilling a threat function was that the display be reliably associated with attack and escape.

It soon became apparant that each species possessed a variety of displays. The criteria outlined by Monyihan (1955) that a display be reliably associated with attack and escape together with the observation that these actions were commonly occurring activities in a population (Tinbergen 1959, Perdeck 1960) led to the variety of displays, related to these actions, being considered as a threat series.

However, there has been little consensus concerning the nature of the series and a number of suggestions have been offered to account for inter-relationships between displays as they relate in fulfilling a threat function.

Why are there so many displays?

Tinbergen (1959) suggested that different displays could be used against different classes of opponent. He suggested the repertoire comprised a long-distance threat, an aggressive and defensive threat for use against casual intruders and an aggressive and defensive threat for use against serious intruders. It is difficult to see the advantage of making a distinction between serious and casual intruders. It is likely that the variant used against a serious intruder would be equally, if not more, effective against casaal intruders (Andersson 1980). As it stands this idea embraces a framework of motivational differences underlying different displays.

Displays used against opponents in different relative spatial positions.

In their study of the display behaviour of Sabines gull, Brown et al. (1967) noted that the display used was in some cases, dependent upon the relative spatial position of the opponent. They were interested in the factors controlling the use of different postural components accompanying the long-call. They found that when the opponent was in the air the oblique variant predominated, but when the opponent was on the ground the upright variant was used. The postural variant used was that which most efficiently directed the call at the opponent. Rather than it being motivational differences underlying the use of different displays, it might have been the relative spatial position of the opponent that ordered the appropriate variant.

Similar suggestions have been made which have incorporated a motivational component with an argument similar to that used above being used to suggest the adaptive pressure moulding the form of different displays. Perdeck (1960) noted that the oblique variant was used against arial opponents by breeding great skuas, with the upright being used against ground opponents. He was also aware of the frequent use of both of these displays in interactions, on the ground, of a subset of the great skua population, the non-breeding 'clubs'. To account for this he argued that an opponent on the ground, by virtue of its greater proximity, constituted a more intense threat than an arial opponent. Any display used against the former, he argued, was likely to be of a more aggressive nature. The spatial relationships between interactants provides the adaptive pressure moulding the form and underlying motivation of a display. The use of both displays in ground interactions thus represent motivational differences in the state of the signaller.

Irrespective of whether a motivational component is invoked or not this explanation could only account for a limited number of displays. The difference in opinion evident between the above studies suggests that interpretation of displays may be influenced by subjective preconceptions. In both these studies, however, an explanation in terms of motivational differences is invoked to account for the remaining displays in the repertoire.

Evolutionary display turnover.

A different view has been taken by a number of authors suggesting that an evolutionary process is at work providing new displays.

The raw material from which displays developed was suggested to have undergone a process of ritualization (Blest 1964) in their development to 'subserve a social signal function' (Moynihan 1955). One proposed component of this ritualization involves a degree of emancipation (Tinbergen 1952) where the display loses its direct relationship with the motivational factors originally underlying it. Baerends (1975) doubted whether complete emancipation could ever occur and suggested that, if it did, the display would become meaningless.

Moynihan (1970), on the other hand, suggests that the emancipation entailed by ritualization will render displays useless as a result of the phylogenetic inertia of decreasing display ambiguity providing the need for a process of dynamic generation of new displays to replace those no longer effective. The adaptive pressure considered as providing the basis for this suggestion is the need for an association between displays and their underlying motivation, a suggestion which implied a direct relationship between display motivation and the information they conveyed (Moynihan 1955).

Andersson (1980) follows up this idea, though from a different theoretical perspective, in a process of display generation that he labels the 'bluff hypothesis'.

A corollary of invoking the idea of mutual benefit to explain the restrained form of fighting characterised by the use of displays was the implication that displays provide a truthful indication of intention (Cullen 1966). If, on the other hand, the individual is considered as the unit upon which selection acts the interest of the interactants, in disputing a resource, are opposed. This means that each individual will be attempting to acquire the resource with the minimum of cost. It was situations of this nature that led to the theoretical consideration of bluff (Maynard Smith 1974). Bluff could be said to occur if an individual signalled with an intensity of threat in excess of its capability in the event of an escalated contest. The use of displays in resource disputes and the possibility of bluff associated with their use led Andersson (1980) to suggest bluff as providing the adaptive setting in which a number of displays might develop.

Originally an unritualized (intention) movement forms an integral part of actual attack and is thus a reliable predictor of attack. Association by an opponent of this action and attack will lead to this action becoming an effective display serving to intimidate and repel an opponent without the need for actual attack. Andersson suggests that with the increasing decoupling from attack associated with this increased efficiency, the pattern will become increasingly open to being used as bluff and this, in turn, will lead to a reduced tendency to be impressed by the display. However, the pattern will never become total bluff as it will occur every time attack occurs.

At this point it is assumed that there is a second pattern sharing a direct association with attack and the above process will be repeated for this second pattern. In this way a repertoire of different displays will be built up as the bluff process renders displays ineffective and it is replaced by a new pattern. With time each of the displays will be equally effective and competition will arise between threat displays and a state of balance might arise due to frequency dependent selection as a result of each display, in turn, becoming less effective at repelling opponents as this display becomes increasingly used as bluff.

An obvious limitation on this proeess, and one realised by Andersson, concerns the availability of suitable source material - attack intention movements. Even the most rigorous breakdown of attack into component intentions fails to provide sufficient raw material for the number of presumed threat displays and the form that they take in the present day.

The above argument rests on the emergence of bluff as attack becomes progressively decoupled from the intention movements, providing the opportunity of signalling an intention removed from the possibility of an overt follow up, a situation which arises from and depends on the recipients association of the display and attack. In the ethological literature, the ritualization of a display and the maintainance of an appropriate response to it have been viewed as progressing simultaneously but independently with no suggestion being offered for the mechanism ensuring appropriate responsiveness (Blest 1964, Hinde 1981). Rather than this dual process, the response of the recipient may maintain a more direct relationship to the development and maintainance of displays. The influence of the recipient in the development of vocalisation pattern, particularly for long-distance communication, has been suggested by Hansen (1979).

In the model proposed by Andersson a display obtains its effectivenss by virtue of its being an integral attack component permitting a reliable association to be made between this pattern and attack by a recipient. This association by the recipient leads to a reduction in the probability that a display will be followed by attack but not, initially, in its effectiveness in repelling an opponent, the effectiveness of a display is maintained by its association with attack by a recipient and a level of overt attack will be necessary to maintain display effectiveness. As the initially high reinforcement schedule (attack) wanes there will be a phase shifted decrease in threat effectiveness with the result that, in a dispute, the opponent will persist for increasingly longer periods of time. In such cases a truthful signaller would be expected to follow through with attack. Rather than having to rely on the production of new displays there would be an oscillating attack probability, the latter being necessary to maintain threat effectiveness. This latter suggestion accounts more readily for the limited range of attack intentions. Support for the maintainance of a threat system by variation in overt attack level comes from work on the maintainance of status signalling devices. Rohwer and Rohwer (1978) found that the status cue in Harris sparrows was supported in limiting bluff by the use of overtly agonistic behaviour.

If such a system is in operation than an alternative explanation will be necessary to account for the remaining displays in the repertoire. The solution to this problem may be found in the method used for categorizing displays as fulfilling a threat function; methods which can be traced to the conflict theory.

The Conflict Theory.'

The approach which has most often led to empirical work was based on an idea originally proposed to account for display phylogeny - the Conflict Theory (Baerends 1975), a theory that was well suited to explain the existance of a number of displays (Cullen 1966, 1972). It has most often been applied to studies of display causation (e.g. Moynihan 1955), but has also been used to furnish functional explanations, usually in terms of the information conveyed (e.g. Andersson 1976).

The theory suggests that the display occurs as an overt expression of an underlying conflict to behave simultaneously in two or more incompatible ways. For threat displays it is suggested that causation is a result of a conflict between simultaneously aroused attack and escape tendencies, expressed as simultaneously occurring intention movements of the appropriate tendencies (Tinbergen 1959).

If displays owed their proximal causation to an interaction of attack/escape tendencies expressed through associated intentions it was logical to assume that it was information about these tendencies that would be conveyed by displays (Moynihan 1955). This functional interpretation was placed on a firm theoretical footing by Cullen (1966) who argued that display variability would be beneficial when it expressed the fluctuating state of the displaying individual and predicted the likelihood of a particular course of action - the form of the displays reflecting the absolute and relative strengths of the contributing tendendies. Such differences could be read by conspecifies permitting appropriate action to be taken in advance with the individual displaying with the lesser intensity moving off.

The conflict theory approach and the possibility of displays conveying differences in signaller attack likelihood has received considerable support (e.g. Andersson 1976) and it is this approach and the results it has produced that stands in direct contradiction to the games theory view (Caryl 1979).

Of the four theories outlined to account for the observed display repertoire the theme central to three of them is that motivational variance underlies their existence and that this state of affairs has arisen to convey intentional differences to an opponent. Only Andersson's (1980) suggestion does not require that displays exist by virtue of differences in motivation, although whether the mechanism he proposed would indeed lead to a number of threat displays is open to question. By eliminating the dynamic variability that might serve to resolve disputes Andersson's suggestion needs a different mechanism that would be capable of providing the information for resolving disputes. In this context Maynard Smith's (1974) War of Attrition model may be relevant.

The conflict theory is that which is most extensively worked out and it is possible, within this framework, to account for the source material from which displays evolved and to offer both causal and functional explanations for presenttday display behaviour.

Displays and Context.

Despite the effort that has been expended in trying to account for the observed range of displays, a number of authors have suggested that this range would be insufficient to cope with the range and variety of situations likely to confront a secial animal during its lifetime (e.g. Smith 1977). Smith suggests that the most obvious feature of social behaviour, the displays, are likely to be only one of a number of information sources available to an opponent and so response is likely to be based on more than the display alone. The circumstances in which a display occurred was used by ethologists in categorizing displays (Tinbergen 1959) but contextual influences are likely to extend beyond the situation in which displays are given.

The influence of contextual features was realised by Smith

(1965). The seeds of Smith's idea lay in the application of Semiotic theory which prompted the distinction between the message of a display from the meaning it had for a recipient. A message is an encoded description of an aspect of the central nervous system of the signalling individual and is identified as that aspect which is common to all situations in which display occurs. Rather than directly releasing responses, displays prime recipients to select from a particular set of responses and the information upon which this situation is based is contextual (Smith 1969a). Application of Semiotic theory to animal communication can thus suggest two possible approaches.

One is to centre analysis on the response shown by the recipient of a display, an approach first advocated by Marler (1961). Smith (1969, 1977) argues for the supplementary importance of contextual features at the pragmatic level of exercising an effect on a recipient together with the possibility of displays exercising a tonic effect (Schleidt 1973) led Smith to concentrate on what he considered to be a less confusing approach centred on the messages conveyed by displays.

Smith (1969b) outlined twelve 'message' classes. However, it is open to question just to what extent the approach suggested for determining messages can escape the contextual influences that led him away from studying the effects of displays on their recipients. The problem arises where the responses shown by the signalling individual are used to delimit messages. In such cases the actions, and thus the presumed message, will be influenced by the same contextual factors since signaller action is likely to be dependent upon the response of the recipient (Hinde 1974, 1981).

To surmount this difficulty Smith suggested that the message could be deduced from the circumstances in which the display was given, the message being the common denominator for each circumstance, a process which is subject to considerable influence from observer preconceptions. This latter approach is unlikely to be of any value for the study of agonistic behaviour where the former method has proved popular.

Before the messgge classes could be verified it would be necessary to identify the contextual features on which a response would be based (the 'meaning') before the message might be deduced through dealing with a standard recipient situation. In so doing it would be more appropriate to concentrate upon the 'meaning' revealed by the response of the recipient (Green and Marler 1979).

Although a number of potential contextual features have been identified, e.g. age, sex, little has been done to assess the qualifying effects of these on the displays that they may accompany. However, Andersson (1976) provided evidence that demonstrated the influence of two contextual factors on the display behaviour of the great skua; mode of approach and status. Contextual features of this nature are important but it would seem premature to outline message categories, particularly of an agonistic nature, until contextual features have been identified and their influence assessed.

A large body of the ethological literature has centred on the behaviour of the signalling individual in categorising displays. This approach has led to considerable speculation regarding the manner in which displays exercise their effect and, particularly, in the information they convey.

The games theory approach has much to offer the functional study of agonistic behaviour. It has brought to light problems that have received little attention, particularly in emphasising the differences between individuals that may serve to resolve disputes and has led to the framing of tighter questions (Hinde 1981). There is a growing body of evidence supporting the role of displays in assessment (Clutton-Brock and Albon 1979, Davies and Halliday 1978, 1979). What of the earlier models? Parker (1972) found that the persistance times of dung-flies at cowpats corresponded to the negative exponential distribution predicted by the war of attrition model (Maynard Smith 1974). Further, the adoption of different persistance times did not affect fitness (measured as mating frequency) so this behaviour corresponded to an E.S.S. However, this behaviour is very different from the display dominated interactions that characterise much agonistic behaviour (Maynard Smith 1976).

Before this view can be properly assessed a number of questions have to be answered. Firstly, to what extent are contests symmetrical? If symmetry can be demonstrated the contradiction between these views rests on the number of displays fulfilling a threat function, a distinction which may be dependent upon the definition of display adopted and the manner in which displays are subsequently categorized as fulfilling this function. If contests are asymmetrical further consideration needs to be given to the manner of display inter-relationships to determine the possibility of sequential relations existing within an increasing cost series (Dawkins and Krebs 1978).

The functional approach embraced by this view with its emphasis on the adaptive maintainance of theoretical systems in terms of fitness, precludes or hinders consideration of areas of traditional ethological concern. It offers no suggestions for the form that displays should adopt. In this respect, Andersson's (1980) account of the conditions prompting the development of a number of displays as a response to prevent the establishment of bluff integrates traditional ethological explanations of the factors moulding display form into a system that is theoretically compatable with Maynard Smith's (1974) suggestion for a system of constant intensity display.

Research in this field has centred largely on mathematical models and simulations of populations whose behavioural options, or strategies, are constrained by the modeler. The arbitrary nature of the strategies and their associated costs and pay-offs limits acceptability, particularly as the number and nature of the strategies provided can alter the outcome. This may be particularly so when it comes to relating models to real-life situations, a difficulty that has recently been realised at both theoretical (Caryl 1980) and empirical (Rubenstein 1981) levels.

As a result an alternative approach to resolving the ethological/games contradiction is needed. One approach would be to apply more rigorous tests of the validity and generality of the intentional views and their theoretical basis, an approach which has already attracted some attention (Caryl 1979, Andersson 1980).

The Information Content.

The conflict theory has provided the framework for a number of causal studies and its use was extended to aid functional analysis by suggesting that if it was a conflict between attack/escape tendencies underlying display causation then it would be information about these tendencies that would be transmitted (Moynihan 1955, Cullen 1966) even if they only did so in a very general way (Stokes 1962a, Hinde 1981).

It has often been suggested that this is a gross over-simplification. Andrew (1972) argues that the conflict is more likely between response classes (i.e. approach and avoidance) rather than more specific tendencies. The idea that intentional information will constitute an important message class is still prevalent (Smith 1969). Despite the emphasis on a conflict between opposing tendendies postulated at a causal level, at the functional level of postulating the information conveyed it has frequently been suggested that it is information about attack that is conveyed (Stokes 1962a, Andersson 1976) and it is this specific suggestion that marks the contrast between the ethological and games theory views. Why this dimension has been singled out has never been stated explicitly, but probably stems from the risk of injury associated with attack making this the information dimension of greatest relevance to an opponent.

This extreme polarisation of information content has been questioned on a number of occasions and even where there is agreement on the information content there has been little consensus on the manner in which displays so constrained would differ.

Monyihan (1955) suggested that different displays were the result of differences in the relative and absolute strengths of the attack/escape tendendies. The fact that when an individual displays it is experiencing a conflict is an idea which has been reiterated on a number of occasions. Hinde (1981) argues that displays result from either an attack/stay or an escape/stay conflict. Stokes (1962a) argues that displays differ in the relative level of attack information they convey, and Andersson (1976) suggests that a display provides an indication of the absolute level of an attack tendency. All are in agreement in accounting for the number of displays by invoking the idea that the displays are the result of different levels of the contributing tendency(s).

There are two main lines of evidence for attack information being conveyed. Firstly, a number of studies have related the varying attack probabilities of the signaller to the escape probabilities of the recipient. Of these, the study providing the most convincing support is Andersson's (1976) study on the great skua, in which he demonstrated a significant and positive correlation between actor Attack probability and subsequent reactor escape probability. A second line of support comes from Blurton-Jones (1968) study of the causation of great tit displays. He isolated stimuli that would elicit attacking, fleeing and feeding and found that threat was only elicited when actual attack was thwarted or was incompatable. In the first instance threat would appear if an attack evoking stimulus was presented to an individual prevented from attacking by wire net. In the second instance threat would occur if an attack and escape evoking stimulus were simultaneously presented. All together there were a number of different ways in which threat could be elicited but the common denominator between them was that an attack evoking stimulus was present but the individual was, in some way, prevented from actually attacking.

The nature of the evidence that has led to the displays being considered as a threat series arose from the use of Moynihan's (1965) definition of a threat display being one for which a reliable attack/escape association could be demonstrated. Subsequently it has been considered sufficient to demonstrate differences between displays in their association with the attack/escape response probabilities to conclude that the displays formed a series varying in the intentional information they conveyed (Stokes 1962a).

In determining these response probabilities one method has predominated, temporal association. Temporal association involves relating displays to certain overt actions; the relation determined in this way being presumed to provide an indication of the level of conflict between tendencies and so of information content. It is important to remember that this method provides a retrospective account of the association and that it is a measure of overt association rather than a direct measure of information about response potentialities.

In using this method the majority of authors have used attack and escape together with the addition of a staying tendency (Stokes 1962a, Blurton-Jones 1968), with which to relate displays and thus it is hardly surprising that these studies have concluded in support of an attack/escape conflict underlying displays. Use of only those responses thought to be important is unlikely to do other than demonstrate that displays maintain the expected association. At this level there is room for doubt about the serial relations of displays. Conclusions were not based solely on evidence of this nature. The finding of a relationship between attack probabilities calculated in this way and an appropriate level of response by the reactor lends credibility to the view that this method did indeed provide a measure of information about attack likelihood and that it was this information that was used by the recipient in guiding response.

On this evidence the two views are incompatible and difficult to reconcile. It was this contrast coupled with the intuitive logic of the games theory view that led Caryl (1979) to re-examine the data used to support the view that displays conveyed attack information and, in doing so, a number of hitherto ignored and concealed inconsistences became apparant.

When attack was singled out as the relevant information dimension it soon became apparent that the attack probabilities were, generally, low. Although this had been noted (Dunham 1966) this finding has generally been ignored. It was in response to this finding that Stout (1969) suggested that, by definition, a threat display should be effective without the need for attack. A high intensity threat display would result in the departure of an opponent without the need for attack and hence low attack probabilities would result if temporal association were used. It has often been suggested that low attack probabilities are an obstacle in the way of accepting conflict theory ideas (Dunham 1966, Caryl 1979, Hinde 1981). This difficulty results from the manner in which the response probabilities are considered, particularly where temporal association is the method used to provide the probabilities.

Temporal association was originally used to provide a quantitative measure of the tendencies contributing to a displays causation. The 'response probabilities' are a measure of the association between the display and the actual occurrence of the chosen overt actions. Rather than being 'response probabilities' these are retrospective 'response actualities'. They do not provide an actual measure of information or likelihood of an action following a display in a direct sense. Instead, it can be assumed that a relatively high attack probability revealed by temporal association indicates a relatively high contribution of an attack tendency for this display. If a display has a high attack probability, calculated using temporal association, this reveals that the display was followed by attack on a large number of occasions rather than indicating that this display was likely to be followed by attack, i.e. a high attack probability means that a display would be a ppor threat display since a high proportion of attack was necessary for this display to exercise its effect. It appears fairly well established that a level of overt attack is necessary within a symbolic dispute settling system to prevent the establishment of bluff (e.g. Clutton Brock and Albon 1979). An area that is certainly worthy of theoretical investigation would be to determine the optimum level of attack necessary within a threat system to prevent bluff, an upper limit on which might be the risk of escalation arising when a display is followed by attack too frequently. This may also have implications for the form of a threat display. A display which maintains close formal links with attack intentions would result in an easier association between this pattern and attack which my, in turn, result in a lower attack frequency being necessary to maintain the threat effectiveness of this pattern than would be the case with a pattern whose links between form and attack capability were less obvious.

The point here is that low attack probabilities by themselves are insufficient to base an argument suggesting that attack information is not conveyed by displays. One way of surmounting this problem may result from using recipient response to a display to categorise displays as fulfilling a threat function.

Following his assertion that low attack probabilities mitigated against the transmission of attack information Caryl (1979) noted that certain displays maintained a higher level of association with escape, the first clue leading to his suggesting the possibility of escape information being transmitted by displays. An argument similar to that applied for low attack probabilities could not be used here. Any situation that warrants giving a high escape probability display would occur at the point where an individual intends breaking off the interaction and so an escape signal is likely to be followed by escape on a large number of occasions. This is in complete contrast to a situation in which an individual is trying to gain an advantage over an opponent. A conclusion based on the magnitude of a response probability is likely to support the use of a display as an escape signal. This initial and basic difference was sufficient to cast doubt on existing interpretations of display information content and further examination of existing data by Caryl (1979) led to a number of interesting findings and further doubts about attack being the information conveyed by displays.

Stokes (1962a) conclusion in favour of displays conveying attack information was based on the finding that a given display was consistently associated with an increase in attack probability when this was measured across seasonal sub-samples. Caryl found a poor correlation in the size of this increase across the sub-samples, a difference for which it would have been expected to result in the use of a different display whose response probability was appropriate. This claim would be countered by arguing that the association between displays and actions gave only a general indication of the threat message (Stokes 1962a), Hinde 1981). A more serious criticism emerged when the probability differences for attack and escape were plotted together. Displays having a high attack probability at the beginning of the season were as likely to be followed by escape at the end of the season. In contrast, displays predicting a high escape likelihood were more consistent in their level of prediction across seasonal sub-samples. Together these two lines of evidence cast a doubt on the validity of suggesting that displays transmit attack likelihood and, in its place, escape was a strong contender for the information transmitted by displays. There remained one stringent test that had to be passed before a conclusion could be reached.

The conclusion of the earlier workers was based not only on the difference in sequelae associated with displays given by the signaller but also on the relation between signaller attack probability and the appropriate recipient response, escape. By demonstrating a significant Actor attack/Reactor escape association, Andersson (1976) has provided the strongest and most convincing support for transmission of varying levels of attack information by displays. The complicated Pitman proceedure used by Andersson was criticised by Caryl on the grounds that the arbitrary scoring system entailed by the use of this method introduced a bias, possibly in the direction of the expected result. Reanalysis by Caryl using a Kendall correlation demonstrated that a better correlation could be obtained between Actor escape probability and Reactor attack probability, a finding which re-informed his suggestion that it was escape information that was encoded by displays and which was used by the recipient in guiding response.

This possibility had been suggested earlier. In his study of the redpoll, Dilger (1960) noted that display was more often associated with thwarted escape than with thwarted attack (cf. Blurton-Jones 1968). He suggested that it would be more advantageous for an animal thwarted in escape to clarify its position to an opponent.

> "An animal not able to flee is likely to avoid further attack if such information is communicated to an opponent: hence, considerable biological advantage is gained."

However, he also suggests that several displays in this species are indicative of a varying readiness to attack. Unfortunately he does not provide any quantitative evidence to support either of these conclusions.

Caryl's reanalysis was prompted by the contradiction between a view which suggested, and supported, the idea that displays conveyed differences in the attack likelihood of the signaller and a view which suggested that such information should not be conveyed. The reanalysis revealed the possibility that displays may convey serial differences in escape likelihood, a possibility which has received little ethological attention in a threat context and only loosely in connection with appeasement displays, and so Caryl would have appeared to have fulfilled his original goal.

This information source was not anticipated by the games theorists but it is less damaging to it than postulating the transmission of attack information (Caryl 1979, Maynard Smith 1979). The reason for this lies with a difference in the opportunity provided for bluff as a result in using each of these information dimensions. Whereas an individual would stand to gain by signalling with an artificially high attack probability since the opponent would experience considerable uncertainty in whether or not to believe the signal. An individual signalling with an artificially high escape probability would be disbelieved if he did not escape, eliminating any uncertainty in the eyes of the opponent.

A number of problems arise when considering escape as the information dimension. While the existence of a display indicating a high escape probability might be adaptive as a means of terminating a dispute, the question remains concerns ing the handling of the dispute by the interactants up until that point when one individual decides to terminate the encounter. The correlation upon which Caryl's conclusion is based still suggests the transmission of intentional differences but with a switch in attention from attack to escape as the important dimension. Where variation in escape likelihood is conveyed, bluff would not arise from signalling a high escape probability but may, instead involve signalling with a low escape probability, i.e.

an individual would signal that he is unlikely to depart. In a system based on the transmission of escape information, signalling with a low escape probability would induce the same uncertainty as signalling a high attack probability in an attack-based system - the signal need not be followed reliably by an action. In an escape-based system it would be the individual signalling with the higher escape probability that would be expected to retreat. Thus a system based on escape might be open to the same type of evolutionary cheating that prompted doubts about transmission of attack information.

Secondly, one of the lines of evidence casting doubt on attack being the information conveyed came from seasonal inconsistency in the association between displays and attack. While a number of displays did reveal consistent escape association in the novel analysis carried out by Caryl, others did not. It is only where a consistent association was demonstrated that the displays can be considered as signalling escape likelihood. For those that did not an inverse logic to that used to test the validity of displays as attack signals can be applied. Displays having an initially low escape probability were as likely to be followed by attack at the end of the season. An increase in escape probability (with its resiliance to bluff) adds support to the possible transmission of escape likelihood but the lack of consistency needs to be explained.

A number of other problems arose from Caryl's (1979) reanalysis concerning the validity of concluding in favour of either attack or escape being the information conveyed, problems of a more methodological nature.

The Method and its problems.

In addition to the criticism levelled against Andersson's (1976) conclusions by Caryl (1979) the validity of his conclusions can be questioned on other grounds.

Andersson demonstrated that mode of approach and status exerted an influence on interaction outcome over and above that of the display they accompanied. The strength of Andersson's conclusion lies in the relationship he demonstrated between actor attack probability and reactor escape probability. The reactor responses used were calculated with the exclusion of those instances when the display (given by the actor) was followed by overt attack, approach or which involved a territorial actor. In this way contextual and overt influences were eliminated and the response of the reactor could be said to be, within limits, due to the display alone. He did not, however, exclude such contextual occasions in calculating actor response probabilities. This means that the populations from which the actor probabilities and subsequent reactor responses were drawn differed and this may have introduced a confounding influence on the result. In his attack category he included those occasions where a display was accompanied by approach. In the great skua approaches are not distributed evenly amongst all the displays. This will have the effect of increasing the attack probabilities associated with a limited number of displays which is divorced from any effect due to the display itself. The inclusion of interactions where contests differ in status is likely to exercise an effect on the actor responses via their effect on a recipient. A territorial actor will increase the likelihood of recipient escape increasing the staying likelihood of the actor which, due to the interrelatedness of all the responses used to categorize displays, will influence the quantitative values of the remaining probabilities.

A further confounding factor arose from the manner in which the reactor responses were calculated, an influence whose implications are greater for the reanalysis than for the original study. The theoretical basis of Andersson's (1976) work suggested the importance of attack information. Assessing the relationship between Actor attack probability and Reactor escape probability could be biased by inclusion of overt attack following a display. As a result Andersson calculated reactor response on to only those occasions where the display was followed by escape or stay. It is the inclusion of actor escape which causes the problem.

The correlation between Actor escape probability and Reactor attack probability found by Caryl (1979) was positive, i.e. the more likely the actor was to escape the greater was the likelihood that he would be attacked. It is unlikely that such a system would confer any selective advantage on the signaller - assuming inappropriately, that the escape probabilities are indeed message components. It would be expected that giving a display indicating escape likelihood would be given in an attempt to prevent attack (Dilger 1960), rather than increasing the probability that the individual would be attacked, a paradox which may be the result of assuming that these probabilities indicate information content rather than the fact that the Probabilities mirror the relationship between displays and actions. The Actor escape probability/ Reactor attack probability correlation may have arisen as a result of an overt association between the overt actions taken by each individual rather than any signal function on the part of the displays, i.e. actor escape is a result of being attacked by the reactor, this direct relationship producing the correlation.

The correlation does suggest that the displays maintain a serial relationship to one another. If the displays lead to differences in the probability that the signaller will be attacked as is suggested by this correlation, then it might be appropriate to consider the nature of the information a display could convey that might prompt attack from the recipient. Rather than it being information about escape likelihood it may even conceivably be information about attack, a relationship which may have remained hidden as a result of a failure to consider interaction.

If actor response is, at least partly, dependent upon the reactor's display (Dunham 1966, Hinde 1981) an Actor escape/ Reactor attack correlation could have arisen even if information is transmitted along only an attack dimension. Hinde argues from the premise originally underlying the conflict theory, namely that displays occur when the animal is in a state of conflict with no clear course of action open to it. In such a situation Hinde suggests that displays are used as a prompt. Within an interactional framework a series of displays varying in associated attack probability act to prompt a display or an action from an opponent and, depending on the display adopted by the opponent, the actor may act in a number of ways. If the display of the opponent is of a higher intensity than that adopted by the actor, the latter is likely to escape. However, it need not always be the case that such an escape would occur in response to the display alone. Where there was a considerable intensity differential between the display adopted by each interactant, the one displaying with the lower intensity might be likely to escape immediately. Where both individuals display with a similar intensity there is a growing body of evidence to suggest that (where individuals are matched) escalation is likely to occur (Kruijt 1964, Rubenstein 1981). In the first instance, where the discrepancy is considerable a series varying in attack likelihood, may lead to a positive Actor attack/Reactor escape association. However, where individuals are closely matched a slight reactor advantage might lead to it being the first to escalate i.e. it would attack the actor, the latter probably escaping resulting in the Actor escape/Reactor attack correlation revealed by Caryl (1979) on reanalysis of Andersson's (1976) data. The point here is that it may be possible to sample from different interaction types, although the information dimension could be the same in both cases. Before this possibility could be accepted further theoretical consideration needs to be given to the intensity differential between interactants that would lead to escalation together with determining the level of overt action necessary to prevent the establishment of bluff. An area of investigation which is of even greater concern where a series of displays is being dealt with.

Interaction may serve to disrupt relations between displays and it will be necessary to account for interaction of this nature before serial relations can be assumed. Since interaction may influence the actions which form the basis of temporal association in a number of ways caution is warranted concerning the emphasis placed on response probabilities calculated in this way as a guide to information content.

Caryl's (1979) reanalysis has underlined the dangers of observer preconception both in design of experiments and in the data interpretation and has revealed the ambiguity present in a large body of data. His reanalysis has also revealed a number of methodological problems which need to be ironed out before any suggestion of the serial transmission of intentional information can be accepted. Finally, he has emphasized the importance of determining response consistency. A measure of consistency is particularly necessary in studies where temporal association is used to throw the conflict theory into relief by adopting Moynihan's (1955) definition of a threat display as one having a reliable association with attack and escape. Where a theory suggests that displays are a result of a conflict between these tendencies and only the actions representative of these tendencies are chosen to categorize displays it would be extremely difficult to do other than conclude in support of the theory. Before the evidence provided by this approach can be used to support the conflict theory as it applies to functional analysis, the displays must be shown to bear a consistent relationship to the limited range of responses. If the displays are to be considered as a series, they mustbbe shown to bear a consistent relationship to one another.

The limitations of many field studies necessitates a simple approach, an approach which thus demands all the more a test for its consistency. Such an approach is described by the conflict theory and temporal association. This raises further questions about the most appropriate method of identifying the threat quality of displays and the inter-relationships between them. This problem embraces such questions as the method chosen to categorize displays as fulfilling a threat function and how a display in itself defined. Both of these questions will be considered in greater detail later.

The central question here concerns the validity of considering displays as maintaining serial relations and which vary in associated intention whether attack or escape, a question for which the evidence in support of displays forming a varying attack series still stands (Andersson 1976), and for the testing of which a number of methodological problems need to be considered. Once this has been done it will be necessary to determine the consistency of predictions.

Andersson's (1976) conclusion, although having been shaken as a result of further analysis of his data on the basis of more stringent questioning (Caryl 1979), still holds and because of this the great skua was chosen as the subject of the present study. To facilitate comparison and to expand upon the questions raised by Caryl's reanalysis, Andersson's methods were adhered to, those changes being made to accommodate methodological problems not anticipated by him.

Chapter 2

2.1. The North Atlantic Great Skua - *Catheracta skua skua* (Brunmich)

Fisher and Lockley (1954) consider the sub-order *Lari* of northern origin and attribute a similar northern origin to the great skua which then colonised the southern hemisphere, there splitting into several distinct taxa, the northern stock becoming extinct. Recolonisation of the northern hemisphere is therefore, geologically speaking, relatively recent. They consider that the differentiations of the great skua superspecies is sufficient to separate it from the three smaller skuas of the genus *Stercorarius*.'

The great skua was first recorded in the British Isles on Shetland in 1774 (Cramp et al. 1974). Their present day distribution within the British Isles is little changed and is restricted to the Northern Isles with a few pairs in Caithness in the north of Scotland and in the Western Isles.

These birds are known locally as bonxies, a name derived from the old norse word "Bonksi" meaning a heap or an untidy, dumpy woman (Furness 1977). They are similar in size to a herring gull, though bulkier.

Bonxies nest on open moorland, usually in the damper areas. Their colonies are characterised by low nesting densities with inter-nest distances of 10-700m averaging at 70m and so are only loosely colonial. They are highly territorial and very aggressive in territory defence. They readily display at or attack ariel intruders and promptly attack any individual landing in their territory.

The adults return to the breeding areas in late March or early

April. The normal clutch is of two eggs laid during May and subsequently incubated for 28-30 days. Foraging and territory defence are split between the sexes, the female being primarily responsible for territory defence, whilst the male forages for both the female and the chicks (Furness 1977). In McCormicks skua this pattern occurs until the chicks hatch, from which time the female forages for herself and the chicks (Spellerberg 1971). This difference probably results from the availability of food within the territories of many McCormick skua colonies where these overlap with penguin rookeries, enabling the females to forage without leaving the chicks unattended. In the bonxie the female would have to leave the colony to forage, an activity that would increase chick mortality through the increased opportunity thus provided for intra-specific predation, an activity which is the chiefccause of chick mortality (Furness 1977).

The chicks fledge at about six or seven weeks. Ringing returns indicate that Shetland birds migrate as a group. There is a degree of migratory variation between different age groups, a stable migration pattern being established when the birds attain maturity at 5-7 years of age. At this age they develop an attachment to a particular colony, virtually all returning to their natal colony. These returning birds from discrete "clubs" (Tinbergen 1953) on traditional sites; these clubs constituting the most distinctive feature of a bonxie colony.

2.1.2. The Club

It has previously been suggested that the clubs are comprised of senile birds, pre-breeders, off-duty breeders and failed breeders (Perry 1948). Observation of colour-ringed birds suggests that the club is comprised mainly of pre-breeders having returned to the club for the first time since they fledged (Furness 1972).

Daily attendance at the club varies, being least in the mornings and highest in the evenings. This pattern is dependent upon the weather, numbers remaining high during bad weather. Seasonal changes also occur. Numbers at the club increase steadily from early May, peaking in early July. This peak corresponds to the return of two year olds. From mid-July numbers start to decline as a result of the departure of birds to sea and the movement of older birds into territories (Furness 1977).

The club is not a homogeneous unit and divisions can be described within it (Perdeck 1960). The central part of the club is comprised of birds relatively closely spaced. Birds here are relatively unresponsibe to over-flying birds and form little attachment to particular parts of the club area. Sexual displays occur often and mating attempts are frequent within this central group. Although birds often make several such attempts, the majority of these interactions are incomplete and short clashes ensue. Perdeck noted that birds that had exhibited sexual behaviour became more territorial or, at least, defended with increasing vigour the area immediately around them. In the periphery, birds paired and formed club territories. These pairs behaved more aggressively towards intruders and displayed frequently at over-flying birds.

The club sites are the most noticeable feature of a bonxie colony and the lush vegetation characteristic of these sites suggests a tradition underlying their use. As a result it is tempting to suggest a functional significance for these sites, a better understanding of which may aid the analysis of the behaviour observed within them and upon which the present analysis is based.

2.1.3. Club Sexual Behaviour

All observers of club skuas have concluded that sexual behaviour is an important interactional component. Perdeck (1960) described such behaviour. The first sexual contacts are made in the central part of the club. Birds failing to make a successful contact may go on to 'propose' to another bird. Repetition of such behaviour by birds that stay together gradually results in territory establishment within the club periphery. These peripheral territories are characterised by birds in various stages of pair formation.

Burton (1968) suggests two broad categories of club behaviour in the brown skua. Firstly, there is the reaction of a bird whose individual space has been violated. Secondly, a bird may approach another in an upright posture which may lead on to Circular Parading, a display similar to the meeting ceremony of mated birds and which is presumed to indicate preliminary mating behaviour (Moynihan 1962).

In McCormick's skua, Spellerberg (1971) noted that birds move about the club showing aggressive behaviour until a male and female meet and behaviour of a more sexual nature ensues. In contrast to Perdeck's findings, Spellerberg did not find any evidence for differences in the extent of pair formation within the club and suggested that a permanent pair-bond was not established until the male lays claim to a breeding territory and attracts a female.

2.1.4. Territory Establishment

Un-paird club birds may have at least three different mating strategies open to them. During the early part of the breeding season single club birds could attempt to mate with single birds occupying breeding territories (e.g. one that may have lost a mate over the winter). Thereis some anecdotal evidence to support this possibility. Club birds were frequently seen to fly over and join single birds in the breeding colony and it was only with the return of the other member of the pair that the intruder was chased off.

Secondly, a male could lay claim to a territory and then display to attract a mate. Spellerberg (1971) suggests that this is the case with McCormick's skua.

Finally, mating could take place within the club, both birds subsequently moving off to claim a breeding territory. This possibility seems the most likely in the bonxie (Perdeck 1960) Furness 1977).

One attempt at territory establishment was observed on Hoy in 1979. A club-pair moved into the breeding colony and settled between two existing pairs. On landing both of the club-pair gave the Oblique/Long Call/Wing Raise display (OLW) an activity which resulted in one of the neighbouring breeding pairs flying over and immediately a fight lasting several minutes involving all four birds ensued. Following this fight the members of both pairs faced each other, all giving OLW for several further minutes. This interaction terminated when both of the breeding pair returned to their territory. Although noticeably uneasy following this interaction, both of the club-pair stayed. In 1980 a pair was seen in the same place and were attempting to breed. This observation provides tentative support for the suggestion that it is pairs formed within the club that are responsible for territory establishment in the bonxie. For the brown skua, Stonehouse (1956) suggests that both members of a pair were necessary for establishing and maintaining a territory in the face of opposition during the early part of the season. Birds who, for whatever reason, were without a mate could not compete and were ousted by intruding birds.

Within the superspecies sexual behaviour is a prominent feature of club life. Despite agreement on the presence of such behaviour no worker has extensively studied the role of displays in the sexual behaviour of this species. Even during the early part of the season when a high proportion of mature birds are present, the number of club-pair birds is small, relative to the number of club birds, suggesting the possibility that pair formation within this species has a competitive basis. This possibility has not gone unnoticed by previous authors.

2.1.5. Competition within the Club.

Perry (1948) described the club as a lek, drawing a comparison between this group structure and the ostensibly similar competitive structure found in a variety of species (e.g. Black grouse; Kruijt and Hogan 1967). Perdeck (1960) argues that a dominance hierarchy is found within the club althuugh he does not provide any evidence upon which to base this conclusion. If such a system were in operation it would be being continually tested as a result of the constant influx of new birds throughout the season, although these two factors combined could account for the observed agonistic behaviour. However, without individually marked birds it would be impossible to detect the existence of such a system. Stonehouse (1956) noted that, in the brown skua colony he studied, two club individuals were dominant and all the others subordinate. He did not consider the possibility of these apparently dominant birds being a club-pair.

These observations provide at least anecdotal evidence suggesting a competitive club structure. There are two possible explanations for these observations.

In the McCormick's skua, Young (1972) removed breeding birds from the colony and found that they were replaced by club birds within 48 hours. Young argued that club birds formed a reserve breeding stock. One tentative explanation for club agonistic behaviour, then, would be that birds are competing for priority of access to breeding sites. From the evidence presented by Spellerberg (1971) on the pair-forming behaviour of this species, a competitive structure would be expected for each sex; the males competing for territory access, the females for male access. In the bonxie removal of breeding birds from their territories resulted in their almost immediate replacement, possibly by club birds (Furness, personal communicatinn). However, no information is available about the possibility of these replacements being existing but peripheral territory holders or, if they were club birds, how successful they were in maintaining the acquired territory. It is unlikely that the agonistic behaviour observed in bonxie clubs is a result of competition for territory access. The evidence presented by Perdeck (1960) and Furness (1977) suggests that territory establishment is perpetrated by pairs who were themselves established in the club. This information could be accommodated if there was a shift in the competitive emphasis onto pair formation within the club.

The most direct suggestion of a sexually competitive club structure comes from the analogy drawn between the club and a lek (Perry 1948). Unlike the normal lek situation where competition is most likely for central position (Davies 1978), the bonxies comprising that club sub-group in which such competition is most likely to occur do not defend particular areas or even settle, as a group, in the same place within the confines of the club area. If a system analogous to a lek is in operation, recognition of the quality of individuals must take place on the basis of relatively subtle cues. In a lek situation display may settle access by members of one sex to position within the lek; position being used as a cue in the assessment of reproductive potential by the other sex. A more direct role is likely to be played by display in the bonxie if the club serves as an arena for mate selection.

In a monogamous species like the bonxie, inter-sexual selection may take place on the basis of a relative assessment facilitated through intra-sexual selection within each sex.

Although both sexes contribute to breeding success, they do so in different ways. The female is primarily responsible for territory defence to prevent intra-specific chick predation and so competition, say, for position within a dominance hierarchy may provide a reliable cue to reproductive potential within this sex. The males' contribution is largely through the provision of food, so a similar form of competition would not necessarily provide as reliable a cue. An alternative cue on which male ability could be assessed, may come from Courtship Feeding, an activity which occurs frequently in the club between un-mated birds and, to a greater extent, between club-pairs. This behaviour is also frequent between breeding birds during the early part of the breeding season.

As a result of the different contributions made by each sex to breeding success, direct agonistic competition within the club may be largely confined to females, and this seems to be the case in McCormick's skua (Spellerberg 1971). Such a system would permit differential access of females to potential mates and provide the opportunity for mate assessment on a more direct basis (possibly through courtship feeding). Birds were often seen to move about randomly, displaying at several birds in succession. On no occasion were any of these encounters seen to proceed directly to courtship feeding, but occasionally these encounters did lead to a behaviour with possible sexual association, circular parading (Moynihan 1962). Interacting with several different individuals may enhance relative assessment. In the gannet, Nelson (1965) reports such a situation. Alternative suggestions have been forwarded to account for this behaviour. Both Perdeck (1960) and Spellerberg (1971) suggest that birds move about in a threatening manner until meeting an opponent who behaves in a submissive or sexual manner. Crook (1964) reports a similar situation in some weaver species (Ploceinae) in which both sexes share in territory defence. When individuals of each sex meet they threaten each other until one responded in a sexual manner.

While not in itself conclusive the available evidence strongly suggests the presence of both functionally sexual and functionally agonistic behaviour. To further complicate matters these categories are unlikely to be discrete with certain behaviour patterns and actions for different categories overlapping, e.g. unsuccessful sexual introductions may end in overt attack (Perdeck)1960). This problem is particularly serious in the present study with its reliance on overt behaviour as a means of categorizing behaviour and hints that caution should be exercised in reaching any conclusion from data obtained from the temporal association of displays and overt actions.

2.2. Location and Description of Colonies.

Bonxies were studied at three colonies in the Northern Isles of Scotland; Hoy, Noss and Fair Isle (Fig 1)

2.2.1.

Hoy, the second largest island in the Orkney archipelago, is the home of the largest breeding reserve of bonxies in Orkney and lies towards the southern edge of their breeding distribution. Bonxies established themselves on Hoy in 1914 and they presently number in excess of 400 pairs (Furness 1977). They are not distributed evenly over the whole island. The present study was restricted to a population on North Hoy situated about 800m south-east of the Old Man of Hoy. The low nesting density and cryptic nature of the birds makes it difficult to assess the number of breeding pairs in this area but a conservative estimate would be 60-70 pairs. The catchment area for the club studied here is unknown.

The club is situated in the centre of the breeding colony and covers an area of about $600m^2$. During the period of study the numbers of birds attending varied from ten to forty individuals, with a mean of twenty-two.

Of the three study sites, the Hoy club was the highest. It is situated at an altitude of 250m (equivalent to 1000m in the Cairngorms). As a result it suffered the most severe weather conditions, a combination of high winds coming in off the North Atlantic and the altitude made it the coldest colony.

2.2.2.

Noss lies about five miles east of Lerwick on the Shetland mainland. It is seperated from the larger island of Bressay by a narrow channel. The colony was established in 1910 and presently supports a breeding population of about 200 pairs. The Island supports two club sites. One of these is presumed to be fairly recent, Andersson (1976) makes no mention of it and the vegetation upon which it is situated does not show the characteristic signs of more established club sites. Attendance at the new site was rather sporadic compared with that at the more traditional site. This traditional site, from which data was collected, covered an area of about $400m^2$ and comprised a population of, on average, 40 individuals, about half the number recorded by Andersson. Of the three clubs, the numbers attending on Noss demonstrated the greatest stability. Furness (1977) notes that the high level of aggression in these birds places density limitations on the club sites. In this case further limits are imposed on the size of this site by the proximity of the breeding population, so any overspill would be forced to find an alternative site. At present it is not known what leads to the choice of a new site or who is forced to take up station there.

2.2.3.

Fair Isle was the third study colony, lying about half way between the other two colonies. This is one of the most recently established colonies (1921) and supports only 30 or so breeding pairs. It differs from the other sites studied in a number of respects. The club population here demonstrated no strong attachment to any particular site and five different sites were used to varying extents. Attendance was not evenly distributed between these sites.

The most commonly attended site was on the island airstrip, the choice of which resulted in considerable disturbance not only from air traffic but also from interaction with arctic skuas, the club being in the centre of the breeding colony of this species. As a result it remains a mystery why an alternative less disturbed site was not utilized.

The second most frequently used site was at Lerness. Although relatively little used in 1979, the Lerness site was attended almost as often as the airstrip site during 1980. Air charter traffic was considerably higher in 1980 and this may have contributed to the altered attendance pattern. Clark (1894 - in Furness 1977) noted that the Foula colony shifted in response to disturbance.

The other three sites, Dronger, Goorn and Busta were used infrequently. The data presented here was gathered from the Airstrip and Lerness sites.

More than at any of the other colonies studied, the number of birds attending the Fair Isle club varied widely. On some days only one or two birds were present at any one site. In contrast the maximum number seen at any one time was sixty plus. The average attendance was 15-22 birds, but the fluctuating attendance raises questions concerning the source of these birds.

2.2.4. Colony Attendance

The study was carried out over a three year period and each colony was visited at least twice, with the exception of Noss which was only visited in 1978. Observation time at each site is given in Table 1.

At each colony, observation was carried out at the same time each day. The duration of each daily observation period varied depending on weather conditions and the number of birds present.

On Hoy, observations were carried out between 14.00 hours and

18.00 hours.

On Noss, observation periods were split in two, one being carried out between 14.00 and 18.00 hours and the other between 20.00 and 22.00 hours.

On Fair Isle, three observation periods were used. The morning period was between 10.00 and 12.00 hours, the afternoon period between 15.00 and 17.00 hours and the evening period between 19.00 and 21.00 hours.

All the data presented was gathered from club interactions. At no site did it prove necessary to use a hide. Generally, the birds took no notice of the observer so long as the approach was slow and steady and, once in position, no sudden movements were made.

On Hoy the club was observed from a distance of 70-100m with the aid of 10x40 binoculars where necessary. On Noss birds were observed from a distance of 20m and binoculars were unnecessary. On Fair Isle the birds were 'jumpier' than at other sites.and the distance from which they were observed varied but was generally between 50-100m.

2.2.5. Inter-Colony Differences.

During the execution of this study a number of inter-colony differences became apparant, which may exert an influence at a behavioural level.

One of the most obvious of these, to the human observer, was the temperature difference between the colonies resulting from differences in altitude, wind and the time of year at which the different colonies were studied. Perry (1948) noticed an increasing lethargy associated with increasing temperature and one possible effect of the temperature differences between colonies may concern levels of activity.

The entire observation period on Hoy in 1979 was characterised by very cold weather with high winds and frequent blizzards. A harsh winter resulted in a late return of the birds. In contrast a mild winter the following year resulted in an earlier return and a considerable number of birds were already present when I arrived in late April. This raised the possibility that the observed activity was drawn from populations differing in the extent to which behaviour had progressed and may have particular relevance to the extent of pair-formation.

May 1980 saw one of the warmest spells that Hoy has seen in many years. In two particularly warm and windless weeks there was a noticeable difference in club attendance, with only club-pair birds being regularly present. Visits of club birds were sporadic and usually ended in interaction with a club-pair with the latter invariably the victor. Although these interactions were excluded from the analysis the possibility exists that such interaction will alter the manner of responsiveness of this club individual in future interactions.

Three things set the Fair Isle club apart from the other two sites. On both Hoy and Noss the club is situated in the centre of the breeding colony whereas on Fair Isle the club is situated a good distances from the nearest breeding birds, reducing the number of interactions between club and breeding birds.

Secondly, the club site is predominantly situated on the Island airstrip and so is subject to considerable disturbance from aircraft. Finally, this site is situated in the centre of the breeding arctic skua population. Interaction between the two species are relatively common with the bonxies usually coming off worst.

At each colony a number of different factors may exert an influence on the level of club activity. For example, the increased disturbance may increase the tendency for birds to withdraw in an interaction, a sort of inverse 'confidence effect' (Scott and Friedericson 1951), or it may alter the distance over which interactions occur.

These various factors may exert an influence which will vary between colonies so altering the levels of activity within colonies and will subsequently raise problems in a study which relies on quantitative comparison where such comparison is made between colonies.

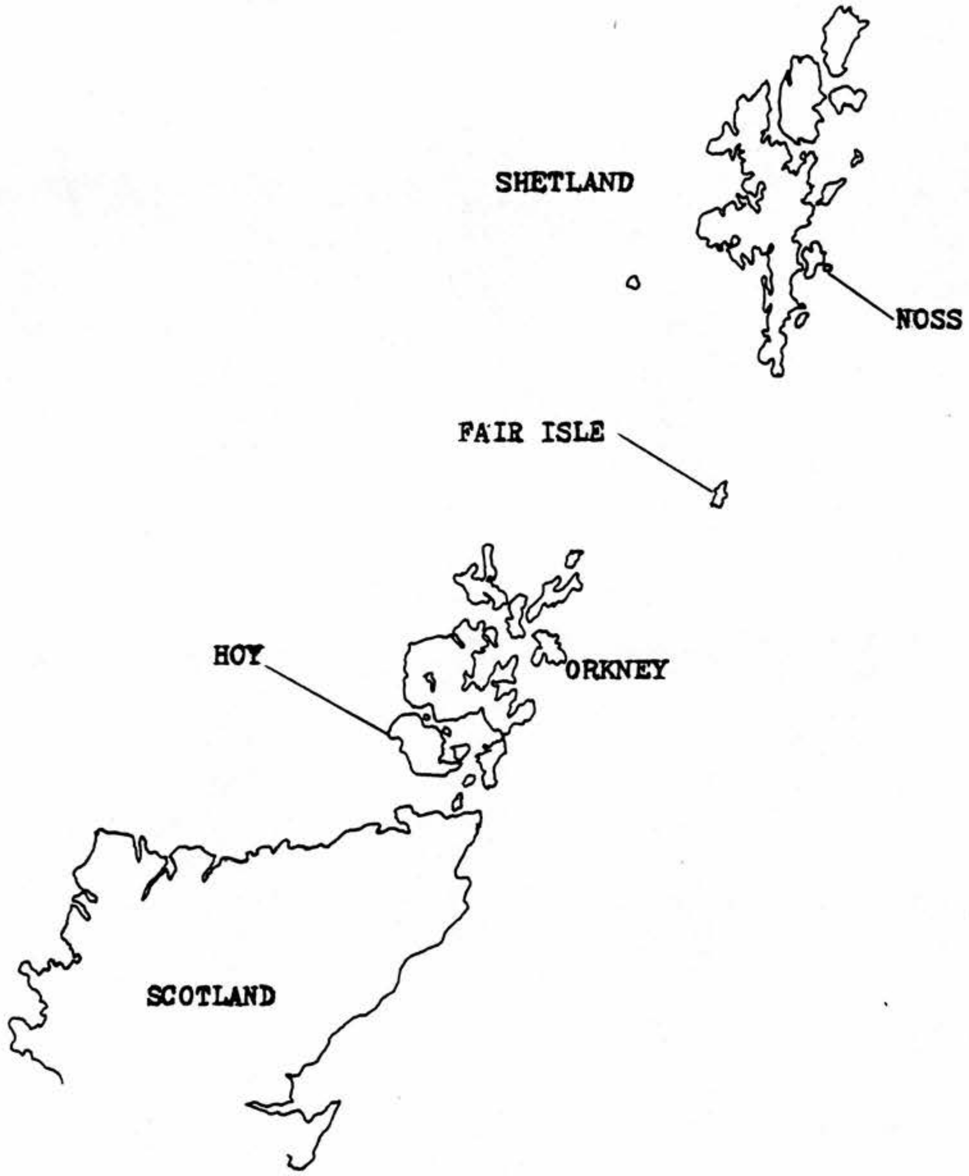


Fig I : The location of the study colonies.

3.1. Displays

The signalling systems existing in the animal world are many and varied and utilize a number of sensory modalities. By far the most extensively used modalities through which such systems operate are visual and auditory (Smith 1977).

While any detectable act by one individual may be informative to another (the mere presence of another individual may constrain future actions (Hazlett 1975), some behaviour, due to its elaborate and conspicuous nature, appears too specialised to be informative and it is these elaborate patterns that have been labelled displays.

Displays can be considered as postural components, as combinations of such components, as distinct morphological features or as combinations of components utilizing different modalities simultaneously. In view of the variety and range of available possibilities it is hardly surprising that definition has been phrased only in very general terms.

In a study concerned with understanding displays it is essential to identify the appropriate units for study. How these units are defined will have implications for the number of displays within a repertoire and for the inter-relationships between patterns, both of which are of interest if the contradiction between the ethological and games theory views (Caryl 1979) is to be resolved.

Moynihan (1955) was the first to formally define a display as a behaviour pattern that had become ritualised. He qualified this by saying that

> "A behaviour pattern will be considered ritualised if there is evidence that it has a signal function and that it has become specialised in adaptation to that function".

He does not describe what constitutes evidence of adaptation, although the evidence he considered appropriate for defining a display as fulfilling a threat function was that it be reliably associated with attack and escape.

The key to Moynihan's definition is ritualisation. While ethologists have outlined a number of changes that behaviour patterns may undergo in the course of ritualisation (Blest 1964, Hinde and Tinbergen 1965), little consideration has been given at the level of the single display to the number or quality of changes that produce a ritualised display, e.g. what adaptive pressures prompt the use of one type of change rather than another or whether different types of change result in displays of differing quality?

The ultimate pressure on displays leading to their ritualisation was the reduction in ambiguity necessary to ensure the accurate rendition of a message (Cullen 1966). The framework suggesting mutual benefit within which much of this work was based fostered the view that individuals should convey truthful information and ritualisation was the adaptive means of ensuring accurate transmission of a distinct level of motivation.

When selection is considered as acting at the individual level the opposite would be the case and it has been suggested that ritualisation would serve to obscure any motivational information that might be present in the display.(Dawkins and Krebs 1978). The pros and cons of ritualisation are an evolutionary concern dealing with the adaptive maintainance of a display. The central theme of the present study is the nature of the present day display irrespective of how it arrived at its present form. Such a distinction is likely to be artificial though making this distinction may illuminate the evolutionary process responsible for display production if it demonstrates the manner in which the present day display is effective.

Displays were considered by the early ethologists to be rigid in form and the term Fixed Action Pattern was coined to describe these functional units. The form of displays has subsequently been found to exhibit a greater degree of plasticity than was earlier thought and more refined recording techniques have demonstrated a variance that led Barlow (1977) to label displays as Modal Action Patterns.

Little attention has been given to the functional relationship or independence of the postural, vocal and morphological components that comprise displays, or how variation of components within each of these classes contributes to the functional quality of a display.

3.1.2. Morphological Characteristics.

In studying the contribution of displays to the social behaviour of animals, one of the features that drew the attention of ethologists was the observation that a number of species possessed distinct morphological features, e.g. distinctive plumage characteristics, whose existence was difficult to explain in terms other than their having a signal function - the "sign stimuli".

Hinde (1970) reviewed the evidence for the effectiveness of sign-stimuli as communicative characters and emphasised the dependence of a response on the physiological state of the recipient. Of more direct interest from the point of view of the present study was the finding that individual variation existed in the stimulus dimension upon which a response was based over and above any preference arising from differences in physiological state.

Most of the work on sign stimuli considered by Hinde involved studying responses to models, a technique which he (Hinde) 1974) considers limiting as a result of the perceptual restriction entailed by the use of models. While the use of a model may accurately present to anoopponent the feature considered important, any subtle interplay between this feature and behaviour would be concealed and any conclusions drawn may be misleading. An alternative approach is to alter the feature in a live individual, an approach which has seen frequent use. Morphological cues may be split into two types. There are those which are continuously present, at least at certain times of year, e.g. the red-breast of the robin. Secondly, there are those that serve to enhance a particular structure.

3.1.3. Morphological Enhancement.

When the wing-patches of McCormick's skua were painted to resemble the rest of the wing, Spellerberg (1971) found that the two females so treated were displaced by intruding females - the 'removal' of these patches resulted in their inability to successfully defend a territory. The effect appeared to be sex specific, the one male similarly treated was not affected. This sex specific effect might have been expected in view of the greater role played by the female in territory defence in this species.

The small sample site used by Spellerberg makes any conclusion tentative. However, a similar experiment was carried out on the red-winged blackbird (Peek 1972). The seventeen territorial males that had their red epaulets 'removed' experienced great difficulty in maintaining their territory.

In both these species badges of territory ownership are revealed by wing-raising and 'removal' of this feature results in an inability to maintain their territory. These examples illustrate one of the problems arising from a conflation of techniques considered appropriate for causal analysis being used for functional analysis. Wing-raising is the component under control of the displaying individual and may be an overt indication of the influence of certain causal factors on the signalling individual. Application of the conflict theory to functional analysis assumed that information would be conveyed by the recipient 'reading' the appropriate components (Moynihan 1955). Painting out the wing-flashes does not alter the causal control of the display or the actions indicative of the influence of certain causal factors. However, the results cited above suggest that signal function is mediated by the wing-flash rather than the component under causal control (wing-raising) that is used by the recipient in guiding the response. In these cases the response to the display would appear to be ritualised and, further, the means whereby this display exercises its effect may have become emancipated from the causal control of the display, at least in the eyes of the recipient.

A number of species possess morphological characters which enhance postural displays e.g. the facial markings of the blue tit enhance displays in which the head is presented to an opponent

(Hinde 1970). It might be appropriate to consider how presentation of this enhancement changes with different displays. If this does not change then perhaps distinction between displays may be artificial in terms of the functional qualifies responsible for exercising effect on a recipient.

The second type of morphological enhancement concerns cues which are continuously present.

3.1.4. Features Continuously Present.

In an investigation of inter-individual distance in the chaffinch, Marler (1956) found a sex difference in distance relationships with males tolerating females at distances far less than they would tolerate other males. A candidate for the feature responsible for this sex difference was the orange breast possessed by the male.

Altering the breast colour of females to resemble that of the males resulted in an alteration of the normal male/female distance in line with that normally shown between males, indicating that distance behaviour in this species is mediated by this sex-specific cue. Marler noted that distance tolerance was also influenced by the display of the individuals concerned. A bird adopting a submissive display being permitted to approach closer than on adopting an aggressive display.

Since altering the female breast colour did not result in a concomitant sex change, the manner in which distance tolerance is thus altered must have arisen from behavioural cues emanating from the male and this behaviour resulted in an alteration of the females perception of herself in relation to the male and, indeed, it also altered the females awareness of herself in relation to other females. These two factors combined suggest that the response shown is the result of a cue-behaviour interplay.

Further evidence for an interdependence between behaviour and morphological cues in communicative behaviour comes from work on status signalling in Harris sparrows. In this species the amount of black plumage on the breast is correlated with rank. Rohwer (1977) took subordinate birds and blackened them to resemble more dominant individuals and found, contrary to what might have been expected, that rather than being more successful in encounters these dyed birds suffered greater persecution.

The work was carried out in a small flock and it is possible that individual recognition occurred, the increased persecution having arisen through dominant's recognition of the dyed birds as deceitful (Ketterson 1979). However, dyed birds were successful when the dyed treatment was accompanied by testosterone injection, a treatment which increased the propensity of individual so treated for overt aggressive behaviour (Rohwer and Rohwer 1978). The status cue was only successful when both cue and behaviour were in accord. As an alternative to persecution having arisen as a result of individual recognition it may have arisen from a cue/behaviour anomoly. In the initial treatment where birds were only dyed they behaved as though they were subordinate. The interdependence between cue and behaviour would serve to prevent the establishment of bluff.

The contribution of a morphological feature need not be the same in each instance where such a feature is present. In the Harris sparrow and chaffinch the morphological features serve as status cues; of rank in the former and sex in the latter. The interdependence of status cue and behaviour, with the dominant role being played by behaviour, suggests that the morphological feature acts in a contextual manner. It does not have a signal function per se but rather qualifies the behaviour of a signaller and may serve to qualify to the recipient the relevence of the information conveyed behaviourally (Smith 1969b).

The examples drawn from McCormick's skua and the red-winged blackbird need an alternative explanation. The morphological feature serves to enhance an action, but from the evidence available it would appear that these morphological features, rather than the actions they enhance, have display status i.e. they appear to be adaptations to fulfil a signal function.

Spellerberg's (1971) findings are of interest here. The evidence he presents suggests that it is the white wing patches that serve a signal function. In the bonxie wing-raising is a component of a number of displays (OLW, BLW, NW). If the signal function of these displays is mediated by the wing-patch the question of the validity of a functional distinction between these displays is raised?

The nature of a morphological feature i.e. whether it be continuously present or revealed by an action, may have different implications for communicative behaviour and the manner in which such features act needs to be defined before the signal function of a display can be understood.

3.1.5. The Contribution of Components.

The above studies illustrate how particular features may be chosen preferentially in guiding response. They have all been concerned with distinctive morphological features whose existence would have been difficult to explain if they did not function as signals. However, there also exists a large number of displays lacking in any morphological enhancement.

The general display definition offered by Moynihan (1955) with its concentration on attack and escape as the end points with which to relate displays led to display description in terms of the information they were assumed to convey or of the causal balance peculiar to that display, e.g. aggressive or intimidated upright (Perdeck 1960). Tinbergen (1959) stated the necessity of describing displays in terms of form characters alone. This treatment brought to light a number of problems that had hitherto received little attention. Components may occur on their own or in combination with different components in a variety of displays. Where displays were considered to mirror a particular motivational state, how did components contribute to the various displays in which they were present? Further, this anatomical approach may lead to components being ascribed a signal function where they may contribute contextually or may simply be effects.

For postural displays there is a limit to the degree of independent movement possible between different parts of the body and many parts have to serve more than one function. A wing can only serve as a display component in as much as its secondary signal function in no way impedes its primary function of enabling flight. Given this interdependence between different parts of the body on what basis should a decision regarding the components actually constituting a display be made, particularly if an effect/function confusion (Otte 1974) is to be avoided.

Identifying a number of components is relatively easy, but the question remains whether all components are of equal importance to an opponent or if particular components are attended to preferentially by an opponent. Preferential attention may be particularly important for agonistic displays where the high arousal likely to exist in a contest and the possible necessity for reaching a prompt decision may lead to a simple categorization of the signallers future actions by the recipient, perhaps through responding to a limited set of cues (Caryl 1979).

The type of problem that could arise can be illustrated with reference to work on Sabines gull (Brown et. al. 1967). In an investigation of the signal function of the displays of this species they found that the use of a number of different displays was correlated with differences in the relative spatial position of an opponent. The two postural components were an oblique and an upright. Both involved the use of the long-call, but the posture accompanying it was that which most efficiently directed the call at an opponent; the oblique against an ariel opponent, the upright against a ground opponent. This raised the possibility that the long-call is the essential component and so, from a functional point of view, perhaps a distinction between the two would be artificial.

Would a bird in the air be able to distinguish the postural variant accompanying the call? If not, then one source of pressure maintaining oblique as a signal component would be missing and its use is likely to be maintained by the efficiency that this component permits for directing the call at an opponent. At least initially the oblique could be said to be an effect rather than a component having signal function.

While it may be the case that the long-call is the relevant component from the point of view of the causal factors impinging on the signaller, from a functional point of view (i.e. that of a recipient who has to reach a decision) this need not be so and the response of the latter may be based on a number of cues.

The vocal component could attract the attention of a number of potential opponents to a given situation. The posture associated with the call could provide further cues, e.g. whether a given receiver is likely to be the intended recipient; is the recipient in a spatially relevant position? Further cues e.g. the relative orientation of the signaler could provide more exact information about whether a given individual is the intended recipient.

In this situation we have a signal component (the long-call) plus a number of additional components-posture, orientation -which may be contextual to the signal and which serve to qualify to a recipient information from the signal, rather than dealing with a composite signal. Stokes (1962a) suggested that information conveyed by certain components of blue tit displays were contextually constrained by accompanying components.

One way of assessing the contribution of components would be by determining the response probabilities associated with different components. Comparison of these probabilities may illustrate the inter-relationship between components and the manner in which a component contributes to the displays in which it is present. Treatment of components in this way has been adopted in a number of studies involving the categorisation of displays by their temporal association with overt behaviour, usually attack and escape.

In the temporal association analysis carried out on bonxie displays, Andersson (1976) analysed both components and commonly occurring combinations in this way. Comparison of response probabilities for components and combinations led Andersson to conclude, following Stokes (1962a), that combinations gave better results i.e. the response probabilities, particularly for attack, were higher for combinations. Neither author raised the question of how components, when combined, may produce this greater responsiveness. Dilger (1960) and Blurton-Jones (1968) suggested that as the level of threat increased different components were added to the display, each component appearing at its particular threshold level of arousal. The nature of component inter-relationships has been receiving increasing theoretical consideration in recent years (Wiley 1975,1976). Until the manner in which an individual component contributes can be specified theoretical or empirical treatment of their combined effects is premature, particularly where the possibility exists that components may act contextually or simply be effects. Does the method proposed and used by Andersson provide an insight into this problem?

The treatment he uses needs careful handling. Components rarely occur in isolation and to permit their treatment individually they have to be abstracted from their occurrence within a combination. Thus the quantitative relationship generally found between components and combinations (Stokes 1962a, Andersson 1976) is hardly surprising since broadly the same behaviour being dealt with in each case. A more serious problem arises from the possibility that the probability associated with one component may reflect the effectiveness of a different component within the same combination. For a variety of reasons, then, assessing the contribution of components in this way is unlikely to reliably illuminate the role of components and an alternative means of determining the manner in which components contribute to a display is needed.

Some work on preferential response to components has been carried out by Stout and his co-workers (Stout and Brass 1969, Galusha and Stout 1977). Using models these authors demonstrated that it was the height of the head above the ground that was the relevant feature, from the recipients point of view, in guiding behaviour rather than it being an interplay between relative body, neck and head angles or head/bill angle as had previously been suggested from observation of behaviour leading to a labelling of displays in terms of the total number of components discernible to the observer (Tinbergen 1959, Moynihan 1962, Andersson 1976). Whether the remaining components have any communicative significance remains to be seen. This work illustrates the problem that may arise from observer labelling of components, a process which may lead to an incorrect description of postural and behavioural inter-relationships at a functional level.

Model experiments do not provide the complex of stimuli associated with a live opponent and caution should be exercised in the interpretation of data so provided. What is needed is a method of determining the contribution of components in live individuals. Model experiments could then be used to elucidate in a more precise manner the nature of the contribution of a component whose functional significance has been suggested from live interactions.

From a functional point of view a display will be maintained as a result of its ability to alter the behavioural probabilities of a recipient in a manner favourable to the signaller (Dawkins and Krebs 1978) and by virtue of a recipients continued response to the display. It might be expected that the recipient will constitute a strong selection pressure on the components of a display responsible for eleciting the effect associated with that display.

An alternative approach for determining component significance involves switching attention from the responses of the signalling individual associated with a given display to the response shown by a recipient and would involve assessing the response to combinations. These combinations could be refined by prior consideration being given to the component stimulus dimensions capable of being perceived by a recipient. The contribution of a given component could be determined by comparing responses to combinations differing in only one component.

A similar logic was expressed by Hansen (1979) as a source of adaptive pressure moulding vocal displays, particularly for long-distance communication. Basically, the song components picked up and mimicked by a recipient would be those that could successfully reach a recipient; a process that would mould the song characteristics to the environment in which they would be used. An analogous process might be responsible for the functional significance of the bonxies white wing patches. This display is used most often in encounters involving territorial individuals and, owing to the cryptic nature of the birds, permits this display to be seen over greater distances than would otherwise have been possible. It is likely that the wing-patch is the only discernible feature over the long-distances arising in a species having a low nesting density, creating a situation constraining responsiveness and leading to this feature adopting the signal function for the display.

3.1.6. Multiple Modality Displays.

So far little attention has been given to displays comprising components which utilize different sensory modalities - concomitant use of both visual and auditory channels is not uncommon. Where different channels are used simultaneously there may either be a high degree of redundancy within the system with similar information being transmitted by each channel or, alternatively, each channel may transmit different classes of information.

One important influence is likely to be environmental 'noise', the level of which will be influenced by the nature of the environment and the distance over which information has to be conveyed. Marler (1968) proposed that environmental noise will constitute a strong adaptive pressure prompting display stereotypy and also for displays to adopt a form utilizing different modalities conveying the same type of information to ensure display effectiveness i.e. multiple modality use entails a high redundancy system.

The song-spread display of the red-winged blackbird contains both vocal and visual components and, although given simultaneously, Pick (1972) found that each component differed in the manner in which it exerted its effect in territory defence. When a territorial individual had its vocal chords anaesthetised the individual was engaged in a significantly greater number of territorial conflicts, a finding which led Peck to suggest that the vocal component served as a long-distance territorial advertisement warning potential intruders off. The individual was still able to maintain his territory, indicating that the visual component, the red-epaulets, served as a second line of defence for closer encounters. When the red epaulets were painted out the individual lost a significant number of close territorial encounters. Here the different components can be said to convey similar information (at least in terms of the signaller being a territorial individual) but each component is specialised for transmission to components in different spatial positions relative to the territory holder.

This distinction may have relevance for the bonxie. A analogy has already been drawn between the red-winged blackbird and the bonxie on the basis of the functional similarity in their use of the morphological enhancement occurring when the wings are raised. The OLW display comprises both vocal and visual components and is used frequently in long-distance and close quarter interactions. If the parallel between these species is extended it implies that the long-call may be the essential component in the long-distance territorial encounters generally between ground and aerial birds (cf Brown et al. 1967) and the visual component may be the effective component in close quarter club interactions (cf Spellerberg 1971).

Both modalities have benefits and drawbacks in their use. For a visual display to be effective it has to be seen by an opponent and may have to be delivered at a specific orientation. An auditory signal is less dependent upon delivery orientation and the signaller need not be seen for a display utilising this modality to be effective.

Topography and other extraneous noise sources pose ecological obstacles that displays will have to surmount to communicate with a recipient and the nature of the obstacle may constrain the modality used and even the nature of the signal within a given modality.

The characteristics of an auditory signal are generally adapted to the nature of the environment within which interactions take place (Wiley and Richards 1978).

Postural components may be better suited to surmount wind noise against which a vocal display would be less effective, particularly where communication is in the horizontal direction (Suthers 1977). Postural components may be effective over a greater range and will convey positional information, whether intended or not. Vocal components may be more effective in awkward typography where vision is impeded or where conveying positional information would be disadvantageous e.g. their use as alarm calls.

More so than with a display utilising a single modality it is important to determine the contribution of components where these utilise different modalities within the same display and where it is possible that one or other component may contribute contextually, redundantly or by conveying different classes of information.

In resolving this problem it may prove useful to consider the suitability of different modalities for conveying diffetent classes of information.

3.1.7. Modalities and their use.

There is a growing body of evidence for individual regognition by voice in seabirds (e.g. Beer 1970, White and White 1970).

At a more direct level problems of a perceptual nature may arise. For postural displays in particular the visual stimulus presented to an opponent will alter with changes in the relative orientation of the signaller. It may be appropriate to consider the visual stimulus presented to the opponent in determining signal function. While the presence of a given component may be indicative of the signallers motivational state, unless that component is visible to an opponent it will have no functional significance.

Concentration on causal analysis has led to a preoccupation with the displays and actions of the signalling individual. From a functional point of view determining the information content and the manner in which a display makes information available should be secondary to determining the consistency of the response shown to the display. Displays are adaptive only by inducing an appropriate response in a recipient and for a functional approach it is appropriate to use the recipient, probably the most important selective pressure on displays as functional signals, to define the display. In this way it is hoped to arrive at a more accurate account of the number of threat displays, threat being defined as the ability of a display to change the escape probability of a recipient, and to provide a guide to the components that are effective. Once the effective components have been identified a starting point will have been provided for studying the potential information content, their evolutionary history and the mechanism responsible for their adaptive maintainance.

The gross units from which a tighter display will be defined still need to be outlined. The displays forming the basis of this study of bonxie displays were those outlined by Andersson (1976). It is this study that has provided the most convincing evidence for serial display relationships conveying variation in attack intensity and, as such, is an appropriate place to investigate the contradiction between the view expressed in this study and the more recent games theory view (Caryl 1979).

Two components not observed by Andersson were noted in the present study. The first of these, Gape, is a common component of the brown skua repertoire (Burton 1968). This component was only noticed during the latter half of the 1980 season and insufficient data was gathered to permit analysis. It usually accompanied the relaxed posture or NB and was invariably performed with the open-bill directed towards the opponent. The differences is likely to convey only gross levels of motivation; more subtle motivational information being conveyed, perhaps, by differences in repetition rate or speed of performance (Morris 1957). Little theoretical attention has been devoted to determining why one system rather than another is likely to be used or why a number of displays should be used where one display varying along a single or multiple parameters might be equally effective. The use of a number of displays has been proposed to eliminate ambiguity but in close-range encounters a number of different theoretical perspectives exist (cf. Cullen 1966 and Marler 1968).

Each modality has a broadly similar signal potential. Where these are combined in a single display it will be difficult to judge, a priori, the functional contribution of each to the display.

Summary.

Previously the number of displays in the repertoire of the species under study has been left to the discretion of the observer, and is usually compiled on the basis of the number of discernible components. This approach stemmed largely from a preoccupation with the causal basis of displays and with the idea that the components contributing to the display provided an indication of the presence and level of motivational tendencies contributing to the display (Moynihan 1955, Dilger 1960).

From a functional point of view individual component assessment is necessary for a number of reasons.

A direct conflation of causal and functional approaches is conceptually dangerous (Purton 1978). The conflict theory has most often been applied in studies of a basically causal nature and its extension to aid functional analysis presumed that the components comprising a display, each of which is related to a level of a contributing tendency, would be read as such by an opponent. While components may indeed mirror the contribution of a tendency, it need not necessarily follow that they would have functional significance to an opponent. An example here would be the ineffectiveness of the wing-raising component, per se, in the red-winged blackbird (Peck 1972). In a function study assumptions of a causation - form - function relationship may be misleading.

A further problem may arise from labelling all components as fulfilling a signal function. Some of these components may be effects rather than contributing any functional quality. Further, some of these components need not be redundant but may contribute in a contextual manner.

For visual displays this facility has been little studied, though Rothblum and Jensen (1978) demonstrated this potential through individual stereotypy of bob pattern in an iguanid lizard.

Both visual and auditory components could convey information about sex and breeding condition through the occurrence of song or the appearance of breeding plumage. Although Yasukawa (1979) presented evidence of age related behavioural differences, on the whole sex, age, identity and breeding condition are likely to be contextual sources of information irrespective of the modality used (Smith 1977, Green and Marler 1979).

Of more direct relevance to the present study is the ability of cues using these modalities to contribute in a directly agonistic manner. In a number of species badges of fighting potential are in evidence e.g. horn size in mountain sheep (Geist 1971). It was the presence of features of this kind that prompted theoretical consideration of 'bluff' (Maymard Smith and Parker 1976), a possibility that is held in check by the maintainance of an appropriate level of overt aggressive behaviour (Rohwer and Rohwer 1978). As a guide to fighting ability vocal cues may have an advantage over visual cues by providing a more accurate picture of relative size (Clutton-Brock and Albon 1979). The active nature of vocalisation incurs an energetic cost that is less open to cheating. Nevertheless, a level of overt aggression is required to maintain the effectiveness of this behaviour as an assessment cue (Clutton-Brock et al. 1979).

Zahavi (1975) proposed a cost incurring basis for the prevention of bluff where postural components are used based on the extent of the handicap imposed on the individual. The theoretical basis for this idea has been subject to considerable criticism (Halliday 1978) and has been considered to be less effective in fulfilling this function than a system where fighting ability is signalled in a more active manner e.g. the roaring of red deer (Dawkins and Krebs 1978).

The traditional explanation for the variety of observed displays was that each display was associated with a particular motivational level (Cullen 1966). Vocal cues have also been attributed with the potential of providing motivation structure (Morton 1977) and so may convey subtle motivational differences between individuals at close range.

Clearly a variety of suggestions exist to account for the signal role played by postural and vocal components and their combined contribution to display quality. Multiple modality displays pose an interesting problem and emphasise the difficulty in defining displays.

For a study of display the basic units of study need to be identified. For the present analysis, its attempt to reconcile the evidence of Andersson (1976) with alternative theories led to the use of the basic displays used by Andersson, but with one reservation.

Andersson labelled the relaxed posture (NN-fig. 3) as a display. Any action following adoption of this posture is perhaps likely to be indicative of a bird unwilling to engage in interaction rather than it having become 'adapted to subserve a social signal function'.

Formal description of displays is the first step in their study and provides a first level insight into their facility to convey serial differences.

The second novel pattern observed in the present study but not by Andersson (1976) was Neck Short/Wings Raised (NSW). This posture occurred sufficiently frequently to permit its inclusion in the analysis. This pattern will be discussed more fully in the next section.

3.2.1. The Displays of the Bonxie.

Previous analyses of skua behaviour have been either descriptive (Perry 1948, Stonehouse 1956) or concerned primarily with display causation (Perdeck 1960, Moynihan 1962, Burton 1968, Spellerberg 1971, Andersson 1976). All have based their causal analysis on the conflict theory using temporal association to provide quantitative data. Most have freely adapted the data generated by temporal association to suggest a measure of the information content, though only two (Burton 1968, Andersson 1976) attempted a functional analysis through determining the effects of different displays on a recipient. In all but the study by Stonehouse (1956) analysis has centred on club behaviour.

The most noticeable difference between these studies lies in the number of displays identified as fulfilling a threat function - from two (Stonehouse 1956) to fifteen (Andersson 1976). Although both authors were interested in threat they studied displays in the breeding colonies and clubs respectively.

In breeding colony interactions, usually over territory boundaries or food, Stonehouse found only two displays to which a threat label could be affixed: the 'Challenge Walk' (corresponding to NB in the present study) and the 'Challenge Display' (corresponding to the long-call complex). In these interactions the source of the dispute, food or territory, was obvious to the observer. In the clubs the nature of the disputes, or at least the frequent interactions, is not at all obvious and Andersson's (1976) description of threat repertoire rests totally on the temporal association between displays and selected overt actions. The difference in the number of displays identified as threat becomes all the more interesting when it is related to possible presence of club sexual behaviour and the differing spatial organisation between club and breeding colony.

Bonxies spend only a relatively small proportion of their lives in the clubs. It is conceivable that most of the selective pressure moulding a threat display repertoire will stem from such activities as chick and territory defence and will arise during their breeding lifetime. Considering the prevailing low nesting densities and correspondingly large territories, what is the likelihood that a complex threat system would evolve? An intruder landing in a territory is likely to do so at some distances from the owner. The latter would thus have to fly over to the intruder and a flying skua is likely to constitute a great threat stimulus than one landing and displaying. Indeed, the normal pattern of dealing with an intruder was for a breeding bird to simply chase the former from its territory. The majority of displaying occurred after such supplanting and invariably involved OLW.

Cullen (1966) relates nesting density, aggression and the size of the display repertoire. As the nesting density increases there will be an increase in aggression as a bird is more likely to come into conflict with its neighbours.and the resulting pressure to reduce overt aggressive behaviour will lead to the development of a number of distinct displays. Burton (1968) suggests that the absence or reduction of ritualization in the Stercoraridae of certain patterns present in the Laridae can be correlated with the increased territory size in the former. A similar conclusion was reached by Moynihan (1962) and Spellerberg (1971). The factors prompting a display repertoire and the nature of display inter-relationships will be considered more fully in the following section.

Of all the studies on skua behaviour only Andersson (1976) outlined an objective criterion for defining displays. He described a number of components on the basis of their typical form and thereafter studied commonly occurring combinations of these components with only those combinations which occurred more than fifteen times during the course of the study being used for analysis.

The evidence presented by Andersson constitutes the strongest support for the view that displays form a threat series. It is this possibility that is going to be under test and so, to facilitate comparison, the displays he indentified and the nomenclature he used for their description was adhered to in the present study. The display repertoire of the bonxie falls into three groups.

3.2.2. The Long-Call Complex. (Fig. 2)

The Long-Call complex comprises two displays: the Oblique/Long Call/Wing Raise display (OLW) and the Bend/Long Call/Wing Raise display (BLW).

Of the two OLW is the most commonly occurring bonxie display. It is a contageous display, particularly during the early part of the breeding season, in both the breeding colony and the club.

OLW is used by breeding birds in a number of situations: as a 'greeting' between the members of a pair; by a breeder landing in its territory; it is given before and, more usually, after expelling intruders from the territory and it is given in response to intruders flying over the territory. An aerial version of the long-call complex is given by breeding birds in the air over their territory in response to an encountered intruder.

The long-call complex is, generally, the most frequently occurring club display; being used predominantly in the course of an interaction but also after repelling an opponent.

The most distinctive feature of this display are the white wing patches that are revealed only when the wings are raised. Due to the cryptic nature of these birds the display is thus made visible over a considerably greater range than would otherwise have been possible. That these wing patches perform a signal function was demonstrated by Spellerberg (1971).

During the pre laying period he took one bird from each of three pairs (one male and two females) and painted their wing patches to resemble the rest of the wing. Within four days both the females were displaced by intruding females, the latter then pairing with the males in each territory. The displaced females remained single for the duration of that breeding season. In contrast, the males experienced no such disturbance.

It seems logical to assume that the wing-raising component with its flashes evolved to surmount the problem of territorial communication over the large distances resulting from the low nesting density. However, other gulls possessing large territories (e.g. Sabines gull) do not have a wing-raising component in their homologous display. These other gulls are predominantly white and so would be visible against their nesting background whereas the bonxie is not. The addition of wing-raising, and the white wing patches with which the movement is enhanced, may have evolved to increase the ease with which an intruder could locate a territorial signaller. Recognition by an intruder of territorial occupance has been shown to be adaptive on energetic grounds (Davies 1981).

The wing-raising component itself may have evolved from an intention movement to fly up, possibly prior to supplanting and intruder. Wing-raising is still a prominent feature of the pre-flight display.

The necessity for cryptic plumage may have arisen in response to the kleptoparasitic habits of these birds (Furness 1979), an idea previously suggested for the smaller arctic skua (Grant 1971).

Tinbergen (1959) treated the Larid long-call complex in an analogous manner to passerine song, its effect being dependent upon the status of the recipient, this arguement being reiterated for the bonxie by Perdeck (1960). Spellerberg (1971) was more specific on this point. The common occurrence of OLW after territory boundary disputes suggested to him that OLW was a display of territory ownership or temporary ownership of an area containing food or a potential mate, serving to attract a mate by virtue of its indicating territory ownership.

Both OLW and BLW occur in similar situations, the most obvious difference between them resting with their frequency of occurrence, the former being eight to fifteen times more common.

Temporal association revealed no significant difference between these displays (Andersson 1976). However, Andersson did find a difference when the use of these displays was considered with respect to the spatial position of the opponent. Whereas BLW was used equally often against both ground and aerial intruders, OLW was used far more frequently against aerial intruders, a finding which prompted the possibility of these displays carrying a similar message but each being adapted for use against opponents in different spatial positions. The evidence upon which Andersson based this conclusion was gathered primarily from interactions involving breeding birds responding to aerial opponents. Andersson did not make any attempt to relate these findings to the common occurrence of these displays in club interaction where the proximity between opponents is greater and where both interactants are on the ground.

Perdeck (1960) used a similar argument to base an explanation for their use in the latter situation on motivational grounds. The relatively greater use of BLW against ground opponents led Perdeck to suggest that the use of this display is representative of a more intense threat on the assumption that a bird on the ground would constitute a stronger threat stimulus than a bird in the air. This difference, he suggests, provides the adaptive medium for the development of displays that subsequently differ in threat intensity and their use in the club reflects this motivational difference.

In his analysis of the brown skua, Stonehouse (1966) suggested that BLW was used more against subordinate birds. His arguement for the common use of both OLW and BLW was still framed in motivational terms but his argument ran counter to that of Perdeck and he suggested that BLW was the less intense variant. The subjective nature of the incidental information upon which each of these conclusions was based leaves the question of the difference in the use of these two variants open.

Andersson's (1976) conclusion was based on combined club/ breeder data. For breeding skuas interaction is most frequently between ground and aerial birds whereas, in the club OLW is used five to six times more frequently against ground birds than it is against aerial birds, and so an explanation in terms of a differential response between birds in different relative spatial positions may be too simple.

The available evidence does suggest that OLW has evolved as a distance display and this may provide a clue to the essential feature of this display when used in club interactions. When used at the relatively much shorter inter-individual distances characteristic of club interactions wing-raising, with its enhancement for effect over distance, may be redundant.

3.2.3. The Uprights. (Fig 3).

The second and most extensive group into which bonxie can be split is the Upright group.

In a relaxed, resting skua the neck is withdrawn (Fig. 3a). Maximal extension of the neck in the vertical direction qualifies a posture for inclusion in the Upright group.

The number of divisions that have been made within this group varies between authors. Perdeck (1960) and Moynihan (1962) split the group in two, labelling the displays as an aggressive and an intimated upright. Andersson (1976) split the group into three, identifying the three displays as forming a core from which a number of displays could be defined. The core group he identified were as follows: Neck Forward/Bill Straight (NFB); Neck Straight/Bill Straight (NB) (these two displays together comprising what had previously been labelled the Aggressive Upright) and finally Neck Back/Bill Up (NbBp) (corresponding to the Intimidated Upright). (Fig 3 b,c,d). Of these three NB is the most commonly occurring, accounting for 65-90% of all upright occurrence.

Further divisions can be made within this group as a result of the availability and appearance of a few more labile components acting as postural suffixes. Although NfB tends to occur on its own, both NB and NbBp may be accompanied by additional components. NB may be accompanied by either the Long-call or tail raising and, on occasions, both. NbBp is occasionally accompanied by the long call. As a result of these additions each of the ensuing combinations is labelled as a separate display. It is the presence of components such as these, i.e. those occurring in combination with a variety of different components, which constitutes a major problem for the identification of displays, their number and the nature of the contribution of the components themselves.

Perdeck (1960) and Spellerberg (1971) noted that, in addition to its clear threat function, there was an association between sexual behaviour and the aggressive upright. They suggested that the aggressive upright was used to determine whether another bird was a potential opponent or sex partner. In this respect, the uprights were examined for their association with circling, a component of early pairing and pre-copulatory behaviour (Moynihan 1962). When this was done it was found that circling was not associated to each upright display to the same extent. On average over four tests (Table 2) 33% of the occurrence of NbBp was in association with circling. Of the other two displays comprising the Upright core there was only, on average, a 8% association for NB and even less for NfB. However, the level of association for NB increased markedly when it was accompanied by tail-raising; the association is increased from an average of 4% to an average of 20%.

In terms of their evolution to subserve a threat function the uprights appear to have undergone little in the way of ritualisation (Button 1968), their form having remained very similar to that of the intention movements from which they are assumed to have evolved.

In attack a bonxie pecks at an opponent and both NfB and NB bear a considerable similarity to the intention to attack. Perdeck (1960) suggested that NbBp was an intention movement of withdrawal. In a number of interactions he noticed that the reaction to an opponents approach involved drawing the neck backwards, the extent of the backward movement increasing in proportion to the increasing proximity of the opponent. If this is the case then NbBp could be said to have undergone little ritualisation.

The association between NbBp and circling has already been mentioned. Hinde (1970) suggests that such circling is the result of an approach-avoidance conflict. As conflict of this nature is likely to exist in the early stages of pair-formation in a species where little sexual dimorphism exists and where both sexes are likely to be highly aggressive, circling may have evolved from such a situation of conflict into a pair-formation display. This may explain the common occurrence of NbBp with circling and if this explanation is correct this might be one display where causal emancipation underlies its use in the behavioural repertoire.

3.2.4. Neck Short (NS) and Neck Short/Wing Raise (NSW). (Fig 4)

The third group into which bonxie displays can be split comprises a basic Neck Short component where the neck is extended maximally in the horizontal direction. This component occurs either on its own or in combination with Wing-Raising.

Perdeck (1960) suggested that this compenent served as a pre take-off intention. A similar pattern emerged in the present study, though by far the most common pre take-off posture was NSW (Fig.4) As a result of this association Andersson (1976) labelled this posture as an escape signal which presumably evolved from the intention movement of taking off.

Both Neck Short and the wing-raising compenent may be comfort movements. Frequently, a bird that had been sitting for a considerable length of time would stretch its body and neck into the neck short posture and/or stretch its wings either upwards (wings raised) or to the side (Fig. 4). Only an upward movement of the wings ever preceeded take-off or escape.

3.2.5. (Bend (Fig 4).

In addition to its occurrence as a compenent in BLW, a bird may Bend its neck forward until the bill touched its chest.

Two compenents were found to be relatively labile in that they were not consistently associated in a fixed manner with other components.

3.2.6. Tail-Raising

On a number of occasions the tail was raised making an angle of about 45° to the body. This component occurred most frequently with either NB or Bend. It appears causally related to a sexual tendency (Andersson 1976), though he found analysis difficult as a result of the varied association of this compenent.

3.2.7. The Long Call.

Not to be confused with the long-call complex, the long call was a component frequently associated with a number of postural components. Though possessing a number of vocalisations only one occurred sufficiently often to permit analysis, the long call (sound spectrograph, Andersson 1973).

Perdeck (1960) and Spellerberg (1971) both suggest that differences in the rate of long-calling are correlated with different situations. An attempt was made to quantify this by recording the long-call frequency of a breeding bird to different situations which were presumed to differ in stimulus strength; the presence of an intruder over the territory. It was only possible to gather data from one bird. It was assumed that a bird passing low and immediately over a breeding bird on its territory would consistute the strongest threat, then in decreasing order of stimulus strength, a bird passing high overhead and, finally, one passing well away. The results (Table 2b), which give the mean long-call frequency, provide a small measure of support for this possibility that the frequency with which the long-call units are delivered is related to stimulus strength and so the long call may be capable of conveying motivation structure (Morton 1977).

3.2.8. Conclusion

On the basis of form alone the displays of the bonxie can be split into three broad groups; the long-call complex, the Uprights and the Neck Short group. This distinction suggests that caution should be exercised before concluding in favour of these displays forming a unitary threat series. The need for caution is reinforced when the different roles played by each group is considered.

Circling, with its sexual association, is restricted to the Uprights, the neck short group may be attributed with fulfilling a comfort movement and pre take-off function and most authors have concluded in favour of a territorial/advertising function for the long-call complex.

On the basis of form variation, the Uprights, as a group, are the most likely candidates for representing a unitary series. Closer examination suggests further caution is necessary before accepting this possibility. In the first instance NB accounts for 65-90% of all Uprights used in interactions. Whilst circling is restricted to this group its distribution within the group is uneven. Relative to the other actions with which it may be associated NbBp has a circling probability, on average over the four tests, of 35%. This is many times higher than that for the other core uprights (Table 2).

A number of incidental sources of information cast a doubt on displays forming a unitary series and suggests that care should be taken in determining the method with which displays should be classified functionally, i.e. as fulfilling a threat or sexual function.

3.3. Categorization.

Having outlined the displays upon which analysis will be based we are then faced with the problem of how they are defined as subserving threat. Until this is done we cannot proceed with the analysis. The importance of this task cannot be underestimated. This is an area which may hold the key to resolving the games/conflict theory contradiction. The method chosen to categorize displays will determine what constitutes a threat display by providing the criteria a display will have to fulfill to be considered as performing a threat function. The method will determine whether displays mirror the intentions of the signaller This problem is of particular interest here. The present thesis is concerned with resolving the games/conflict theory contradiction. Following Caryl (1979,1980) the method chosen to achieve this involves setting questions derived from games theory predictions. The answers will be sought in data provided by ethological methods. Attention will be centred on that area of ethological theory and method where the contrast between these opposing theoretical views is most evidence- the conflict theory with its emphasis on a motivational basis for animal communication.

In reviewing the ethological literature on the display behaviour of the Larids, Tinbergen (1959) summarised a number of methods developed for the study of displays within a conflict/ motivational framework. It is important to ask to what extent these methods will reveal a motivational basis.

3.3.2. A Motivational Framework for Categorizing Displays - Methods.

(1) Form Analysis

One of the earliest analytical tools employed was form analysis.

Satisfactory use of this method requires a thorough understanding and knowledge of the overt motor patterns of the species under study (Tinbergen 1959). Basically, this method involves assessing the similarity between display form and the performance of a particular action e.g. between display form and attack. Usually individual postural components were investigated for association. From this approach the evolutionary significance of intention movements was suggested.

This method is open to subjective interpretation, not so much from relating displays to the intention movements from which they were assumed to have evolved, but more in determining functional similarities or differences between displays e.g. whether different displays can be considered as part of a functionally homogeneous threat series.

The type of problem that could arise can be illustrated with reference to a number of studies on bonxie agonistic behaviour. Darwin (1872) noticed how displays which were functionally opposite, e.g. aggressive and appeasement displays, maintained a similar relationship in their respective form - one would be the antithesis of the other. This type of relationship has subsequently been used to support interpretation of display function. For instance, it has been used to identify the displays at either end of a threat series.

Perdeck (1960) described two bonxie displays, BLW and NbBp (see fig.2&3) as maintaining an antithetical relationship. The former was considered the aggressive and the latter the appeasement display. Andersson (1976) also sought antithetical relationships in bonxie displays. The two displays he described as maintaining such a relationship were NfB and NS (see fig 3&4). Thus two authors working on the same species and looking for the same kind of relationship can come to very different conclusions.

At the root of this difference are different methods of quantifying threat function. The point here is that form analysis was used in a subjective manner to support each authors quantitative display classification. This example illustrates the difficulty of describing antithetical relations on the basis of form in an objective manner. It is possible for an observer to superimpose a functional description on the basisof a subjective interpretation of form.

One important contraversial area to arise from games theory concerned the evolutionary instability of a threat series (Maynard Smith 1974). It is clear from the above example that form analysis is an unsuitable base from which to suggest that displays do indeed form a series as has often been suggested in the ethological literature (e.g. Cullen 1966).

(2) Situation Analysis.

An alternative method of classifying behaviour involved assigning functional relations to displays on the basis of the situation in which they occur. The conflict theory suggested that display was only likely to occur when an individual experienced uncertainty in choosing a course of action. One situation in which ncertainty might arise would be at a territory boundary. In conflict terms this would be a situation in which both attack and escape tendencies would be simultaneously activated. When this method is used there is again a risk involved. It is within the observers discretion to define the nature of the conflict and so to define the type of display e.g. a territorial display rather than a sexual display. Problems may arise using this approach when threat displays are under investigation owing to the variety of resource situations where the use of such displays would be necessary. Under such circumstances description of the nature of the conflict assumed to underlie the display would be left to the subjective discretion of the observer.

(3) Temporal Association.

Of the analytical methods developed within a conflict/motivational framework the one that has enjoyed the most extensive use has been temporal association.

This method involves examining the extent of the association between displays and selected overt actions. These actions are chosen on the assumption that they are representative of the tendencies underlying the displays causation.

The logic underlying this method is as follows. The uncertainty in our understanding of the causal basis of a display can be reduced by recording the temporal association between a display and behaviour patterns of more certain causation. For threat the actions chosen to relate displays were usually attack and escape. This approach is built on the assumption that an animal does not change from one motivational state to another when the environment is unchanging; a state of affairs which may be difficult to assess. Further, it assumes that the extent to which a given action follows a display reflects the level of the contribution of a given tendency to a display.

Close ties exist between this approach and form analysis. Although used predominantly to furnish causal explanations of display behaviour this approach has also been used to offer explanation in functional terms. The underlying causal influences were considered to constrain the form of displays. Each contributing tendency lead to the appearance of an appropriate intention movement. The form taken then provides the recipient with a view of the signallers motivational state. Temporal association was considered to reveal a quantified picture of information conveyed. In this way causation, form and function (ability to convey information are linked (Moynihan 1965).

Ritualization; where a display loses its exact relationship to the motivational factors originally underlying it (Tinbergen 1952), poses a problem for the explanatory power of temporal association. Baerends (1975) suggests that the motivational amancipation entailed by ritualization will undermine the value of this technique. Tinbergen (1959) argued in favour of the continued use of temporal association on the grounds that the behaviour patterns, as they appear in the present day, are still followed most frequently by attack and escape. Baerend's criticism applies more to the use of this technique for determining the motivation of the pattern from which the display evolved.

Of the three methods outlined here; form, situation and temporal analysis, the latter provides the most objective analytical tool to emerge from a motivationally based view of animal communication. Consequently its use has been widespread. All methods are something of a compromise and temporal association is no exception. What are the methodological pitfalls inherent in this approach and to what extent do they undermine its value?

3.3.3. Temporal Association - its applicability and limitations.

The strongest supporting evidence for a motivationally based communication system comes from Andersson's (1976) study of the bonxie. It is his finding of a significant Actor Attack Probability/ Reactor escape probability correlation that most convincingly marks the contrast between the existence of a motivational system and the suggestion that such a system would be lacking in evolutionary stability (Maynard Smith 1974). Caryl (1979) demonstrated how Andersson's data was open to interpretation in more ways than had been envisaged by the original author. In so doing Caryl revealed that the conflict and games theory views might not be as divergent as they at first seem. However, neither Andersson's original conclusion or Caryl's alternative, i.e. whether displays revealed information about attack or escape, could be demonstrated with complete satisfaction. Clearly further data of the sort used previously is needed if this difference in opinion is to be resolved.

In order to do this and, more particularly, to facilitate comparison with Andersson's findings the latter authors methods adhered to as far as possible. This was particularly so for the method used to categorize displays as fulfilling a threat function. To this end the main analytical tool used by Andersson, both for causal analysis and for determining the level of information in a display, was temporal association.

The value of temporal association rests with its ability to accurately reflect the contribution of different tendencies. As an analytical tool temporal association can be split into a number of areas, e.g. choice of time units, behavioural categories etc., each of which will have implications for the type of behaviour thought to be under consideration. Little attention has been given in the past to the methodological problems inherent in this approach. These problem areas have to be identified. Once this had been done it will be possible to determine the value of temporal association in display analysis and its suitability for a study of bonxie displays.

3.3.4. Time Units

Temporal association involves looking for relations between displays and selected overt actions within time units of fixed duration. Any correlation between a display and an overt response will be dependent on the length of this time interval. The longer this is the more likely a correlation is to arise. Further, the direction of the correlation may change with differences in interval length (Andersson 1976). Decreasing the interval length will increase the resolving power of this method though practical considerations will place limits on this.

Andersson (1976) chose an interval of 10s and recorded whether a display did or did not occur within this interval. Common causation was attributed to those displays and overt responses if both occurred within the same or immediately following 10s interval.

Anderson did not explain his choosing an interval of this length. The same interval was used in the present study. 10s was the minimum time interval within which all details of the interaction could be recorded.

3.3.5. The stationarity of the situation.

The most important condition to be fulfilled for this method to have any credibility concerns the necessity for stationarity in the situation. Non-stationarity can be influenced in a number of ways. The two most important determinants are the duration of interactions and the action of the interactants.

Increasing the length of the time interval within which relations are sought increases the likelihood that circumstances will change and with it the motivational influences impinging upon an individual. Having chosen an interval of 10s it is assumed that this provides a measure of stationarity. However, this will only be the case if the majority of interactions take place within this time interval.

All observed interactions were of short duration. 85% of interactions occurred within one 10s interval. Temporally the situation provides sufficient stationarity to warrant the use of temporal association.

A more important source of non-stationarity arises from the actions taken by each interactant (Dunham 1966, Hinde 1981). A display by A may lead to a display by B which may lead to an overt action by A or to further displaying. An overt response by A may have been made in response to B's display rather than being an overt expression of the tendencies underlying A's display. Information theory analyses have shown that displays do influence the behaviour of an opponent (Hazlett and Bossert 1965) even in interactions of very short duration (Bossemma and Burglar 1980).

Blurton-Jones (1968) suggested that this interactional problem could be partly surmounted by scoring only those interactions where the recipient did not display. In the bonxie this would account for 60% plus of interactions, i.e. those involving a displaying actor whose response occurred to an opponent who maintained the relaxed posture (NN-fig 3).

Of the 40% of interactions in which the reactor did display 74% of these (30% of the total) were decided on the basis of only one display be each interactant. This latter situation is similar to that envisaged by the conflict theorists. Each interactant could be thought of an indicating a relative motivational level, the dispute being resolved by the difference between them. Thus a situation has arisen which is completely opposite to that anticipated by the games theorists. Since it is the resolving of the contradiction between these views that is central to the present study the bonxie is, in this respect, an interesting species for study.

Together the short duration and limited display use in bonxie interactions will serve to reduce interactional effects. They can never be eliminated and this should be borne in mind when analysing data provided using temporal association.

An additional confounding factor which may arise involves what Cullen (1972) called the "Church Clock Fallacy'. Although event A may reliably be followed by B both may share common causation with an earlier event. A problem of this type could arise if behaviour is related to an event external to the interaction under direct observation. The highly territorial nature of the bonxie is such that birds will often break off an activity (e.g. copulation) and respond to an external, ostensibly unrelated event (e.g. an ariel intruder). Where temporal association was used behaviour appropriate to dealing with an aerial intruder would be scored as part of the species sexual behaviour. To reduce the possibility of such misclassification a record of external events was kept. If any occurred in conjunction with an interaction, that interaction was excluded from the analysis.

This type of influence could be exerted in a subtle manner. It might prove difficult to determine the extent of the influence of previous interactions on the likelihood of further actions. Scott and Friedericson (1952) found a 'confidence effect' whereby a winner in and interaction had an increased chance of winning in future interactions. The result of previous encounters is likely to shape future patterns of responsiveness.

On the basis of these observations the bonxie is reasonably well suited as a subject for temporal association analysis. How should the overt behaviour used for categorization be determined?

3.3.6. Categorization - the chosen responses.

Where the threat relations of displays have been under consideration a number of authors (e.g. Stokes 1962, Andersson 1976) have based their analyses on Moynihan's (1955) definition of a threat display as being one which is reliably followed by attack and escape. Although the term 'reliably' was included in the definition, criteria for reliability were never stated explicitly. Often it was considered sufficient to observe differences between displays in the extent of their association with the chosen overttactions to conclude in favour of the existence of a threat series (Stokes 1962a).

The choice and number of overt actions has a number of important implications.

3.3.7. The number of responses.

One area in which ethological concern has arisen as a result of using temporal association involves the magnitude of the response probabilities (Dunham 1966, Caryl 1979, Hinde 1981). This concern was particularly evident where attack probabilities were being studied.

Attack probabilities have been found to be low. If displays conveyed serial differences in the attack likelihood of the signaller the attack probabilities, for at least a few displays, would be expected to be high. In fact these are rarely above average. The failure of these probabilities to attain the heights expected of them probably results from a misinterpretation of the nature of the data provided using temporal association.

Using temporal association the 'probabilities' mirror the relative frequency of the actions chosen to categorize displays. Obviously the number of overt actions used for categorization will influence the size of the individual response "probabilities'. Generally, the greater the number of overt actions used for categorization the smaller the individual probabilities are likely to be. For example, if three actions are used and responses are distributed equally between all three, the response probability for each will be 33%. If four actions are used, an equal distribution will result in each having a probability of 25%.

The size of an individual probability needs to be considered in this light before being used as the basis for accepting or rejecting the possible transfer of a given type of information. Instead analysis should be based on the relative size of the response probabilities in relation to those for the remaining displays making up the threat series.

3.3.8. <u>The nature of the overt responses chosen for categorization.</u>

The number of overt responses and their nature can determine the type of display, e.g. whether a threat or a sexual display, thought to be under consideration. The confusion that could arise can be illustrated with reference to Andersson's (1976) work on the bonxie.

The overt actions chosen for categorization represent the tendencies presummed to contribute to a displays causation. A bonxie colony can be split into two parts. Observation of individuals in the breeding colony and the non-breeding club area can provide the observer with different expectations. For example, breeding behaviour is expected in the colony but not in the clubs. Andersson's causal analysis involved both club and breeding birds. The tendencies he chose for analysis were Attack, Escape, Copulation, Grass Throw, Nest Build. Inclusion of breeding birds led to behavioural expectations which were mirrored in the choice of the overt behaviour chosen for categorization.

For the analysis of threat function attention was centred on club birds. Here the influence of Moynihan's (1955) definition was evident and Attack, Escape,and Stay were used. This latter restriction was applied irrespective of any relations revealed in the earlier causal analysis. One very important relationship which this shift in attention may have obscured was between displays and sexual motivation.

Andersson's causal analysis revealed a significant association between Tail-Raising and the behaviour he chose as representative of a sexual tendency; copulation. This part of the analysis involved breeding birds on whose part sexual behaviour would be expected. The influence of a sexual tendency (as a possible information dimension) on Tail-Raising was neglected in the later club analysis where displays were analysed only for their association with attack, escape and stay. There are two possible explanations for this. Firstly, since the club is comprised of non-breeding birds sexual behaviour would not be expected. Secondly, the overt behaviour Andersson chose as indicative of the presence of a sexual tendency, copulation, is rare in the club situation. It could be argued that the infrequent occurrence of this behaviour suggests that sexually motivated behaviour is an unimportant influence on club bonxie display behaviour. Be this as it may the same could not be said for the behaviour for which a prior and significant sexual association had been demonstrated - tail-raising. This neglect could have important consequences for a temporal association analysis.

The primary reason for Andersson's neglect of any contributing sexual motivation was that his functional analysis was concerned with determining threat relations for displays. To this end he was influenced by Moynihan's (1955) threat definition and sought temporal relations between displays and three overt responses; attack, escape and stay.

At a basic level of threat display might be expected to exert an influence by repelling an opponent (Moynihan 1955, Brown 1975). If all displays were designed to achieve this then the use of temporal association might reveal threat relations for displays since the same variables will be acting on the response shown. However, where a sexual display is used co-operation is sought between the signaller and an opponent. If temporal relations are sought without consideration for a sexual influence, an influence which will affect the response expected from an opponent, temporal association is likely to prove unsuccessful in revealing consistent association since different variables will be acting on the responses likely after a display. For example, after a threat display the recipient would be expected to escape, after a sexual display it would be expected to stay. This disruptive effect would be heightened if sexual responses were not distributed equally amonst all displays.

The influence of tendencies other than attack, escape and stay have rarely been considered in the search for agonistic relations. Where a tendency has the potential to influence an overt response this influence and the extent of its influence on all displays must be determined. If this is not done the variety of confounding influences will obscure temporal relations making it difficult for a method relying on overt relationships to produce a consistent picture.

3.3.9. An appropriate response.

How do we chose the overt response that reveals the presence of a given tendency? The difficulty that could arise can be illustrated in the bonxie with reference to the influence of a sexual tendency.

In analysing club behaviour an association between tail-raising and an underlying sexual tendency could have been missed through the chosen response, copulation, being inappropriate. For copulation to occur it might be expected that the pair involved would be fairly well established. Pair formation is not an instant phenomena. Choice of copulation as an overt response ignores the earlier stages of pair formation. Instead it might be more appropriate to look for behaviour indicative of these earlier stages, the occurrence of which would be expected in the club.

The most prominent of these is Circular Parading (Moynihan 1962). This behaviour was chosen as a more representative indicator of club sexual behaviour.

Using this behaviour an association between tail raising and an underlying sexual tendency was again evident (Table 2).

Neglect of a sexual tendency may have obscured the true nature of another display, NbBp (fig. 3). In his causal analysis Andersson (1976) concluded that NbBp was highly indicative of an escape tendency. There was no relation between this display and copulation. If circular parading is substituted for copulation a different picture emerges. Up to 40% of NbBp occurs in association with this overt response. The extent of this association may have important functional implications for this display. A difference in response would be expected form NbBp as an escape display and NbBp as a sexual display.

These examples demonstrate the importance of choosing an appropriate response for categorizing a display. Failure to do so may lead to an inappropriate label being afixed to a display. Further, it illustrates the possibility that displays may bear an association with different parts of the same system.

In the bonzie, NbBp may be a display representative of the earlier stages of pair formation judging from the extent of its association with circular parading. Further support for this possibility comes from the extensive use of this display by established pairs during the early breeding season when pairs have newly returned to the colony. NbBp did not maintain any association with copulation. Tail-raising, on the other hand, did.

Copulation is only likely to occure in a fairly well established pair. The use of tail-raising may indicate a higher level of association with a sexual tendency. The former being used to initiate pair-formation the latter being used to initiate the higher level act of copulation. If this is so then the choice of overt response must be appropriate to that level within a system being considered.

A final problem concerns the choice of action that is included within a response. In his bonxie study Andersson (1976) demonstrated an important influence for the mode of approach of the signaller, an influence which superceded that of the accompanying display in terms of its effect on a recipient. A moving actor constituted a stronger threat stimulus than a stationary actor. However, he included a display accompanied by either walking or running in his attack category. Not all displays are accompanied by locomotion of any sort, The majority are delivered from a stationary position. Lack of a uniform distribution of approaches will result in an artificial inflation of attack probabilities for a limited number of displays. This would have the effect of increasing the range of attack probabilities associated with displays, re-inforcing the impression that displays form a series. In order that a display comparison will have any credibility responses should be measured for a 'statinnary' display, eliminating any influence of locomotion.

3.3.10. Summary and Conclusion.

Temporal association is built on the assumption that an overt response following a display occurs because of the causal influence of a tendency represented by an action, e.g. attack or escape. Because of this reliance on overt responses care must be taken to ensure that any external influences on response can be controlled or, at the least, that their influence be noted.

More importantly all tendencies contributing to a display need to be identified. This is necessary to obtain an accurate picture of display function and an accurate level of the influence of each tendency. Limiting classification to the extent of association with overt attack, escape and stay illustrates the catch-22 nature of this approach. If displays are assumed to owe their causation to an attack/escape conflict and only those actions are used to categorize displays it would be difficult to do anything other than conclude in favour of the theory.

As an analytical tool temporal association may prove useful as long as its limitations are borne in mind. Considerable care is needed in choosing response categories and assigning actions to these categories. Most importantly some measure of consistency is needed before any findings can be generally accepted.

3.4 Proceedure

The description, form and name of the displays used followed those suggested by Andersson (1976). Short code names were then devised for each display. The list of displays, their code names and the recording technique were finalised after the first field season (1978).(Appendix 1 and 2). Check Sheet.

During each observation period (Chapter 2; Table 1) the birds were observed using binoculars (Swift Trilyte: 10x40) where necessary. The details of the interactions were recorded on a microcassette recorder (Olympus Pearlcorder).

Andersson kept a continuous record of an individual, recording from all the interactions in which this individual was involved from its arrival in the club until it departed. This method was adopted during the 1978 field season. However, the bird chosen was invariably the least active and this method of continuous recording was subsequently abandoned in favour of recording interactions in an opportunistic manner. Using this method it was found that interactions were fairly evenly distributed throughout the club population. This method increased the number of observed interactions.

Neither this method or that used by Andersson enabled recording of an individuals behaviour throughout the season although within a given observation period it was possible to keep track of a number of individuals either through plumage differences or by the presence of colour rings (the latter enabled a record of behaviour to be kept throughout the season for only a small number of birds). The single greatest fault of the present study lay in its inability to record the behaviour of individual birds throughout the season. An attempt was made to capture club birds on Fair Isle without success. The Fair Isle birds are rather nomadic, not forming any strong attachment to particular sites and demonstrating considerable freedom of movement within a given site. Setting up a phht net resulted either in a movement of the birds to an alternative site or in the birds settling just outwith the range of the net.

Only dyadic interactions were recorded. Within each dyad two classes of interactant were delimited. Firstly, the Actor was the individual initiating the interaction and was identified by being the first to display or to move towards another individual. For landing interactions the first bird to display, whether being the landing or the ground bird, was labelled the Actor. If neither bird displayed then the landing bird was labelled the Actor. The other bird in the dyad was labelled the Reactor.

When an interaction occurred certain information was recorded from both individuals during successive ten second intervals until the interaction had terminated. The majority of interactions occurred within a single ten second interval. The interaction was said to have terminated when one individual escaped and no further action on the part of either individual occurred during the time interval following that in which the last action took place. If an interaction did not involve escape by one individual it was said to have terminated if no further action occurred during the time interval immediately following that in which the last action took place. This usually involved both birds adopting the relaxed posture.

The time intervals were delimited using an electronic timer which delivered an audible signal every ten seconds; to the observer via an earpiece and simultaneously into the tape-recorder used for recording the interactions. This method was unsuitable for determining fine temporal relations within the signalling system. The timer was designed and built in the Electronics workshop of the Psychology Department, Edinburgh University.

The information recorded during each interaction was as follows:

1. The displays adopted by the Actor and Reactor (see 3.2) and;
2. The overt actions taken by each individual following a display. These were selected from walking; running; attack; escape; stay; circle and copulation.

In adddtion to these a number of non-display factors were also recorded.

3.4.2. Mode of Locomotion: In addition to recording the manner of approach, the mode of escape for either individual was recorded as walking, running or taking-off.

3.4.3. Status: Not all club skuas are of equal status. Pair formation is likely to take place within the club and this behaviour, undertaken during the early stages of the breeding season, may result in these birds establishing territories on the club periphery (Perdeck 1960). These birds actively defend such territories against intruders and are generally more aggressive (as a result of an increase in, and greater definition of their inter-individual distance preference). In interactions between these birds and non-territorial club birds, the former invariably won. The status i.e. whether territorial or non-territorial, of the interactants were recorded.

It was not possible to split the club into age/sex classes. Sex could be transiently indentified from behavioural evidence. The occurrence of such behaviour was too infrequent to distinguish sex during sufficient interactions to permit analysis. Age data was available from year-ringed birds on Fair Isle. In 1980 the age range was from two to twelve years. Again, there was insufficient data from different age classes to analyse for behavioural differences.

3.4.4. Inter-Individual Distance: A number of distance measures were recorded for each interaction. Where the actor walked or ran towards the reactor, the distance at which escape was evoked in the reactor was recorded. Where both birds were stationary the distance between them was recorded.

Measuring the distance between individuals proved difficult using conventional measurements, particularly when observing birds through binoculars. To surmount this problem distances were measured in bird-lengths (B.L). Since the basic unit of measurement was always present this proved to be a more reliable yardstick and, as a unit of measurement, it may have some biological relevance to the birds in their assessment of distance. The inter-individual distance was measured from a point between the legs of each interactant.

3.4.5. Relative Inter-Individual Orientation: The orientation of each of the interacting individuals, in the horizontal plane, was recorded relative to the other.

Initially five different orientation classes were distinguished. There were 0^{o} (facing), 45^{o}, 90^{o}, 135^{o}, 180^{o} measured as the relative angle of the body of the signaller to the opponent. Of these five, 90% plus occurred at either 0° or 90° and the relative orientations were subsequently recorded as either 'facing' (0°) or 'Not Facing'. The orientation of each individual was recorded independently of the opponent. (See Fig. 5)

3.4.6. The <u>relative spatial positions</u> of the birds were noted i.e. whether they were on the ground or in the air.

3.4.7. <u>Additional Notes</u>: In addition notes were made on tape to accompany the above details of any events external to the interaction but which may have had a hearing on it, e.g. a bird passing overhead or a display by a bird other than one of the interacting dyad simultaneously displaying. Any other events which proved difficult to condense into a form that enabled easy recording were also noted in this way.

After each observation period the taped data was transcribed onto checksheets, examples of which can be found in the appendix.

3.4.8. <u>Calculation of Response Probabilities</u>: The response probabilities associated with each display were calculated on the basis of the temporal association of each display with each of the overt categories. The response probabilities are a retrospective measure of the percentage occurrence of each of these actions following any given display. To facilitate comparison with Andersson (1976) the response probabilities determined followed those used by him. These were attack, escape and stay.

Those distances of display occurrence associated with one or other of the sexual categories, circling or copulation, were excluded from the analysis irrespective of whether they were subsequently followed by attack, escape or stay. In so doing it was hoped to reduce as much as possible any combined influence of functionally different behaviour.

In the study of the effect of orientation it emerged that the outcome of a number of different interactions were decided on the basis of a change in orientation. These interactions were excluded from the computation of response probabilities.

Andersson (1976) demonstrated the importance of mode of approach and status on interaction outcome over and above that of the display used. For this reason interactions whose outcome was the result of overt movement by one individual towards another and those involving club-pair birds were excluded from the data used in calculating the response probabilities.

The analysis was thus carried out using data from dyadic interactions where both participants were initially stationary and were non-territorial in status.

		Colony Observation Hours	
		May	June/July
Noss	I978	-	I70
Hoy	I978	56	-
	I979	75	-
	I980	80	-
Fair Isle	I979	-	240
	I980	-	3I0

Table I a: A seasonal breakdown of observation hours at each colony.

	Observation Periods		
	Morning	Afternoon	Evening
Hoy	-	I4.00-I8.00	-
Noss	-	I4.00-I6.00	20.00-22.00
Fair Isle	I0.00-I2.00	I5.00-I7.00	I9.00-2I.00

Table I b: Colony by colony breakdown of daily observation periods.

%

	FI 1979	FI 1980	HOY 1979	HOY 1980	$\bar{X}$
NbBp	41	40	33	17	33
NBT	31	21	24	24	25
NbBpL	22	2	30	3	14
NB	10	4	11	8	8
NfB	5	-	6	-	3
NBL	3	1	4	4	3

Circling Probability

	FI 1979	FI 1980	HOY 1979	HOY 1980
FI 1979	1·00	0·9*	0·942	0·6
FI 1980		1·00	0·7	0·8
HOY 1979			1·00	0·2
HOY 1980				1·00

Table 2 : The Probability of Circling.

Circling probabilities were calculated in the same way as the other response probabilities. They represent the relative frequency with which each display was followed by circling, expressed as a percentage of total occurence.

The circling probabilities of displays in each test were ranked and compared. In only one instance did a significant correlation appear (p 0.05), ruling out the possibility that displays form a 'sexual' series.

	Low Near	High Near	Away
Mean	2.55	2.25	2.03
S.D.	0.359	0.305	0.03
N.	I8	6	2

Table 2b: The mean long - call frequency given by a breeding bird on its mound to ariel opponents in different relative spatial positions. (Long-Call units/second).

Low near, when the opponent passed within two metres of the breeding bird, was considered to represent the most intense stimulus. High near, when the opponent passed over the breeding bird at a height of more than two metres, was ranked next. All other interactions which elicited a response were classed as the least intense stimulus, Away.

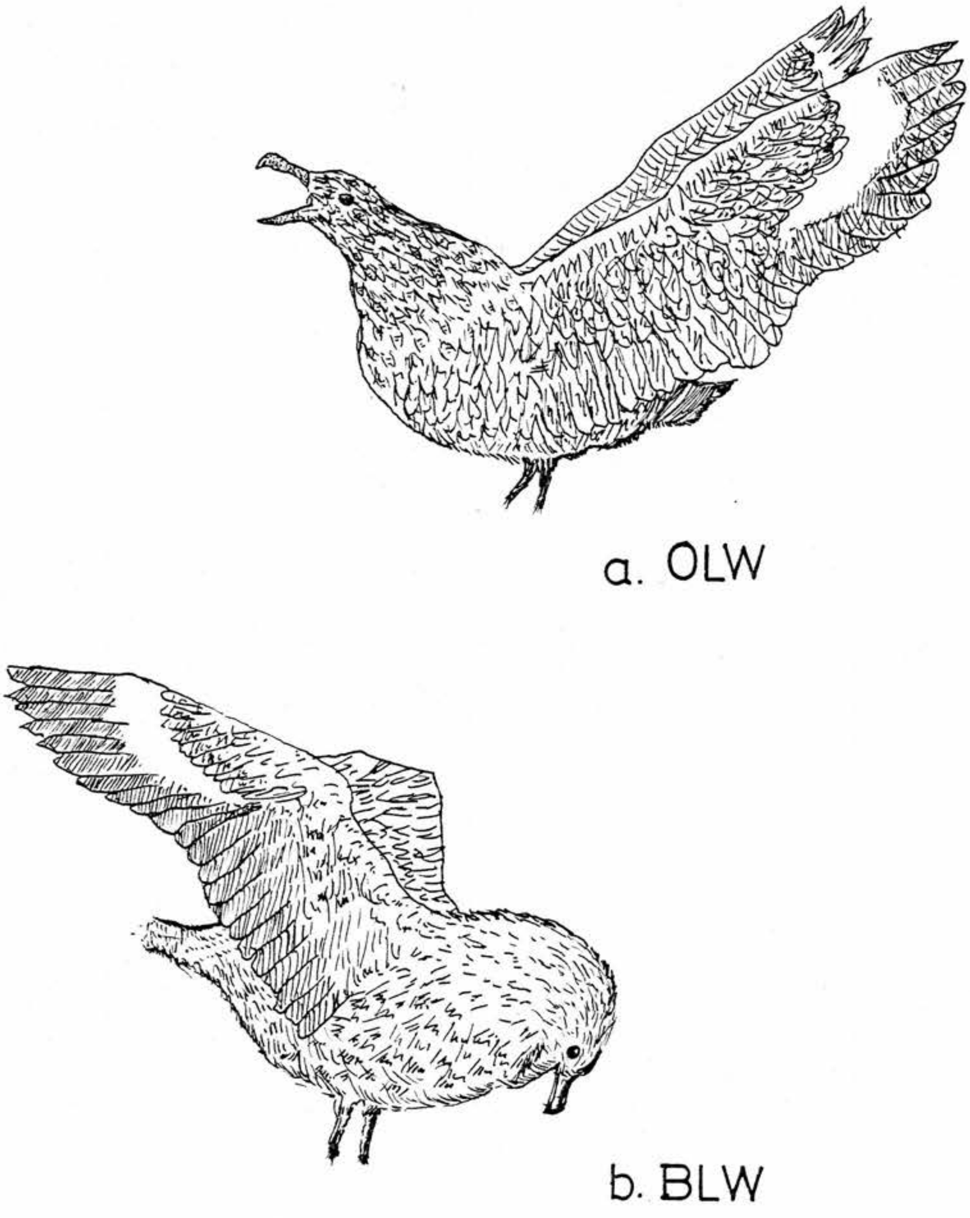
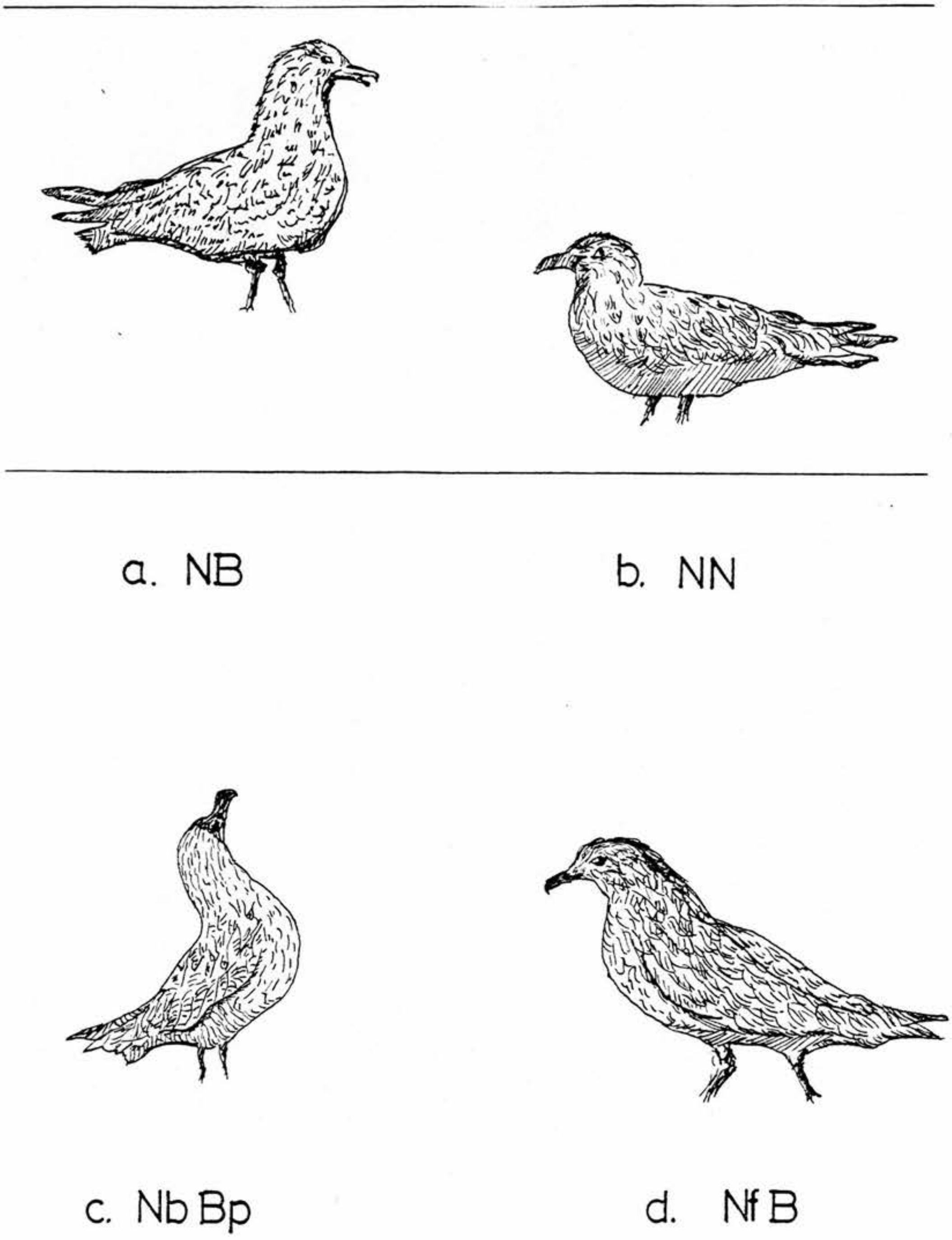


Fig 2 : The Long-Call Complex.

a. Oblique/Long Call/Wings Raised (OLW)

b. Bend/Long Call/Wings Raised (BLW)



a. NB

b. NN

c. NbBp

d. NfB

Fig 3 : The Uprights.

a. Neck Straight/Bill Straight (NB)
b. Neck Normal (NN) (Relaxed)
c. Neck Back/Bill Up (NbBp)
d. Neck Forward/Bill Straight (NfB)

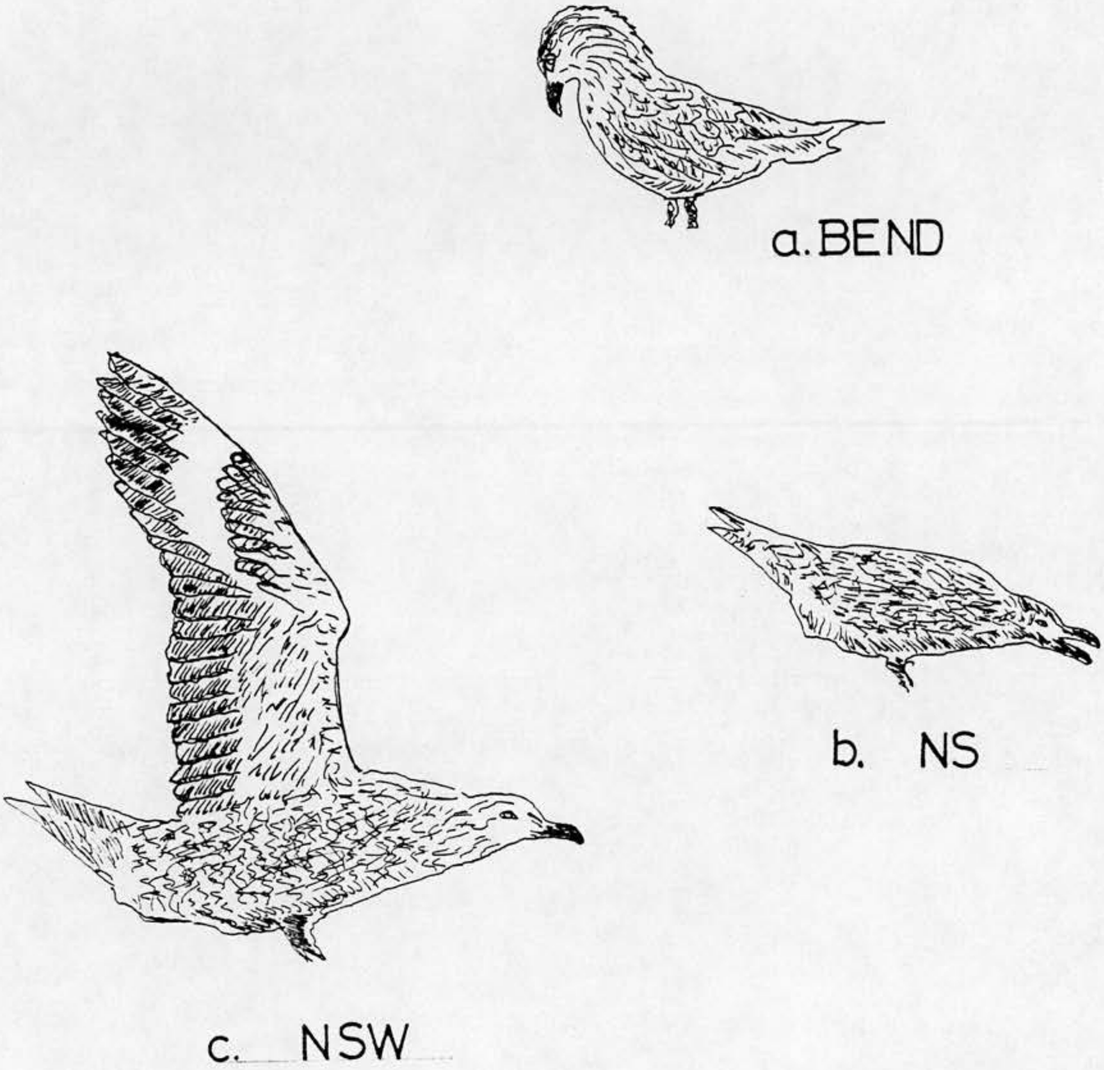


Fig 4 : Bend and the Neck Short group.

a. Bend

b. Neck Short (NS)

c. Neck Short/Wings Raised (NSW)

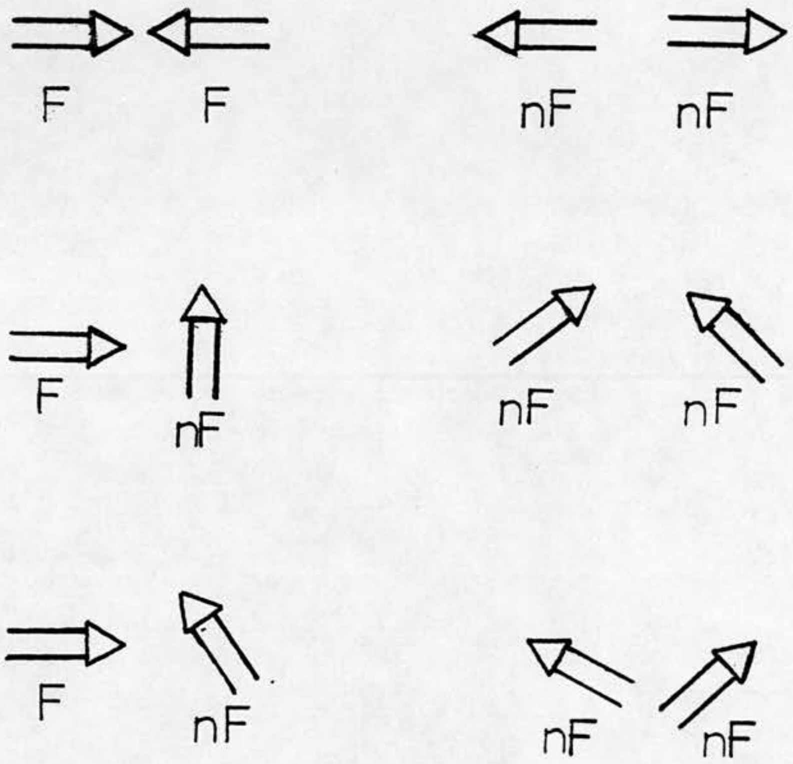


Fig 5 : Orientation classification.

The relative orientations of the interactants were divided into two classes, Facing (F) and Not Facing (nF).

The head of the arrow represents the the head of a bird. Where one individual faced an opponent directly its orientation was scored as 'Facing'. All other orientations were scored as 'Not Facing'.

Chapter Four

4.1 1. The Conflict Theory and displays as signals of intent.

The conflict theory has exercised a prominent influence on the study of agonistic communication. Of the methods considered appropriate for revealing the nature and extent of this conflict, temporal association (Tinbergen 1959) has proved popular. In applying this method annumber of studies (e.g. Stokes 1962, Andersson 1976) have followed Moynihan (1955) in using, predominantly, attack and escape as the end points with which to categorize displays as fulfilling a threat function. Differences in the extent of the association between these actions and displays was considered sufficient to indicate that the range of observed displays served the same function, i.e. threat.

The variety of displays was absorbed into the conflict framework by suggesting that each display was associated with a particular level of attack/escape conflict. The varying level of conflict associated with different displays formed the basis of a; system for conveying signaller intention (Moynihan 1965, Cullen 1966).

This approach has been critisised for its simplicity (Orians and Christman 1968) and because it cannot deal with the full range of information potentially available from a display (Andrew 1972). Despite these criticisms it has been suggested that intentional information, based on an attack/escape conflict, will make an important contribution to the potential information repertoire of a display (Smith 1969,1977).

Approaching a system of this nature from an intuitive games theotetic point of view a number of inherent problems became apparent. Firstly, the existence of a range of displays conveying intentional information would provide a ready opportunity for the establishment of bluff (Maynard Smith 1972,1974). A second problem concerns the accuracy with which a display could convey intentional information (Caryl 1979). Caryl's re-analysis of a number of 'conflict' studies demonstrated the range of conclusions possible from a single set of data. In so doing he demonstrated that the gulf between the games and conflict theory views may be less than might at first appear.

The logic originally underlying the use of temporal association was as follows. If displays do provide intentional information, recording the extent of the association between displays and overt attack and escape would provide a quantitative measure of the conflict. It was assumed that each display was associated with a particular absolute and relative level of attack/escape conflict (Moynihan 1955). According to this view the response probabilities associated with a display is akin to a signature characteristic of that display. If using temporal association is a valid method of determining the threat quality of a display, consistency would be expected in the distribution of the responses associated with a display.

The consistency of this association has never been tested and so is remains to be seen whether it exists. If consistency in the distribution of responses is not in evidence a doubt would be cast on the validity of using temporal association as a tool for the analysis of communication.

The method adopted here to answer this question involved comparing the response probabilities for each display when it was given by the actor and by the reactor.

Dyadic interactions have formed the basis of previous studies using temporal association to determine the threat relations of displays. However, the data upon which the subsequent analyses were based was gathered from the actor alone (Andersson 1976) or else responses given by each interactant were combined (Stokes 1962). The latter method assumes that a display does indeed maintain a consistent response association, a state of affairs which has never been demonstrated.

If response sequelae are characteristic of a display then a similarity would be expected between these sequelae for a given display when given by the actor and when given by the reactor.

4.1.2. Comparison of Actor and Reactor.

Response probabilities were calculated for each display for both the actor and reactor. For each display the number of times each of attack, escape and stay occurred following a display was recorded. The probabilities (expressed as a percentage of total display occurrence) represent the relative frequency of each action. Although each interaction involved both an actor and a reactor for the purposes of the present analysis, each was treated independently. It need not be the case that both interactants adopted the same display. Differences between the actor and reactor were tested for using a chi-squared test for the independent samples (Siegel 1956). This would determine whether the distribution of response probabilities for actor and reactor could be said to have been drawn from the same population. The displays, their associated response probabilities and chi-squared scores for each colony can be found in tables 3 to 7.

For the majority of displays within each colony significant differences are revealed by these actor/reactor comparisons, i.e. the probabilities do not appear to be drawn from the same population. Where no difference is revealed (a possible indication of a reliable association) this similarity is not present in each test. For example, when comparing the actor/reactor responses following NbBpL on Fair Isle (1980. Table 7) the chi-squared result suggests that these responses could have been drawn from the same population. However, this pattern is not evident in any other test.

Taken together this data (Tables 3 – 7) does not support the suggestion that the response probabilities, measured by the temporal association of displays and selected overt actions, are as characteristic of displays as has previously been assumed (e.g. Moynihan 1955).

If the manner in which the actor/reactor responses differ are examined a consistent pattern emerges. This pattern can be seen for each display but is more readily apparant when the responses, within each colony, are summed (Table 8). Generally, the actor is twice as likely to attack or stay as the reactor. The reactor is two to three times more likely to escape.

Since the response probabilities represent a measure of the relative frequency with which a particular action occurred throughout a test an individual who is more likely to have attacked or stayed can, generally, be said to have a greater likelihood of winning an encounter. An individual showing a high escape probability has a greater likelihood of being the loser. It would appear that an outcome asymmetry exists that is independent of the display used. This asymmetry is in favour of the initiator of an interaction, i.e. the actor is more likely to win an encounter.

The emergence of significant differences between each class of interactant in the sequelae associated with displays reveals that the use of temporal association, without consideration for more contextual influences (in this case signaller status), is not a reliable method for determining the extent of contribution of the various tendencies presumed to underlie a threat display. By implication the data resulting from the use of this method cannot be assumed to accurately reflect the level of signaller intention.

The failure to find consistency have supports Caryl's (1979) contention that displays do not accurately transmit information. This result is in accord with the games theory prediction that displays should not convey signaller intention. Before this conclusion can be accepted, however, a number of other lines of investigation need to be pursued.

4.1.3. Temporal Association and Information accuracy.

Whether temporal association will accurately reveal either the contribution of a tendency or the information conveyed is, in itself, a contentious point (Hinde 1981).

Stokes (1962a) was aware of a number of inconsistencies in his findings e.g. the generally low level of attack probabilities. He suggested that displays provide only a general picture of signaller intent. He still maintained that displays serve as a threat series. It is the latter suggestion that most clearly marks the contrast between the conflict and games theory views.

To account for the existence of the observed range of displays, all of which appeared to serve the same function, the conflict view suggested that the displays formed a threat series. Although criticising this possibility on the grounds of evolutionary instability (Maynard Smith 1972) a games theory explanation for the number of displays was not forthcoming. One suggestion that has arisen from this more recent school of thought suggests that displays represent different levels of escalation (Dawkins and Krebs 1978). For this suggestion to have any practical application it would be necessary for individuals to work through their display repertoire sequentially from the less to the more intense displays. If displays were used discretely the emergence of bluff would be more likely since it would be possible for an individual to use an intense variant immediately. In the bonxie, the display repertoire is not worked through sequentially in the course of an interaction. The fact that the bonxie has a sizeable display repertoire and the fact that these displays are used predominantly in a discrete manner makes this an interesting species to study in the light of the conflict/games theory contradiction. The system apparant in the bonxie possesses all the components anticipated by the conflict theory and completely counter to the system anticipated by the games theorists. Analysis is further complicated by the failure of the latter to provide an explanation phrased in terms of the feature originally responsible for prompting the conflict view, namely, the existence of a range of displays.

The conflict model, applied to the bonxie, is not without support (Andersson 1976) so evidence obtained from this species counter to the predictions of the conflict model will be particularly damaging to the latter view and would lay the way open for the investigation of alternative models.

Functional studies using temporal association have incorporated a shift in emphasis away from the conflict of incompatable tendencies responsible for causation towards suggesting that displays convey information about attack likelihood (Cullen 1966). Although this shift occurs frequently in the conflict literature the reasons underlying it have never been stated explicitly. This condentration probably stemmed from an awareness of the risk of injury associated with overt attack making information about attack of greatest relevance to an opponent. It is the transmission of varying levels of attack in a threat series that provides the principle bone of contention between the games and conflict theory models.

The strongest support for the conflict view comes from Andersson's (1976) demonstration of a significant positive correlation between Actor attack probability and reactor escape probability. This, he claimed, supported the view that displays conveyed attack information and that the level of intention could be detected using temporal association.

The nature of the information conveyed is by no means beyond doubt. Caryl (1979), on re-analysis of the date ased by Andersson, came to a different conclusion and one which offered a possible reconcilliation of the games theory views with the observation of a range of displays ostensibly serving a threat function. Conveying attack information was considered open to bluff because on receipt of a display indicating a high attack likelihood the recipient would be uncertain about whether or not to believe it. Caryl's re-analysis suggested that displays convey information about escape. If an individual signalled escape and did not subsequently do so this bluff would be easily detected. Transmission of escape information was easier to reconcile with the games theory models (Maynard Smith 1979).

Two possibilities exist with respect to the information conveyed by displays and both have been supported empirically. More importantly both conclusions were generated by the same set of data. Evidence for either on the basis of response magnitude is in doubt (section 4.1.2.). The relative magnitude of response probabilities were breadly dependent upon signaller status (table 8). Since the pattern of this response asymmetry was broadly similar for all displays more general serial relations between displays may have been obscured. The question now shifts to considering whether displays represent a series conveying threat information and whether this information concerns the likelihood of the signaller to attack or escape.

It is broadly accepted that displays will provide a general indicator of actor intent (Stokes 1962a, Dunham 1966). It is assumed that a display indicative of a high intensity motivation will manifest itself as an appropriate level of the overt behaviour characteristic of the underlying motivational influence.

The popularity of the conflict theory at an empirical level lay, in part, with the ease with which it lent itself to field recording. This very simplicity demands some measure of the consistency of its results. Where a theory suggests that the causation of a display results from a conflict between attack and escape and only those overt actions are used to categorize displays it would be difficult to do other than support the theory. It would not be sufficient to reveal quantitative differences in the extent to which displays are followed by attack and escape. Rather consistency must be demonstrated in the order of displays ranked according to their respective response probabilities - a display must consistently appear in the same place within the series.

Display inter-relatedness could be tested in a number of ways. Three basic measures were used here. Within each colony the response probabilities for both the actor and the reactor were ranked and compared. Secondly, ranked actor probabilities within each colony were compared over different seasons. Finally, a comparison of ranked actor response probabilities was made between colonies.

4.1.4. Actor/Reactor Comparison.

Within each colony the displays of the actor and reactor were ranked according to the probability that each was followed by attack and escape. Each class of interactant was treated seperately. The ranked probabilities were then compared using a Spearman rank correlation co-efficient (Siegel 1956). The probabilities were taken from tables 3 -7 . The correlation co-efficients for each colony are given in table 9 .

Attack

In the main, conflict studies suggest that the attack probabilities reveal differences in the likelihood of the signaller to attack.(e.g. Stokes 1962a, Andersson 1976). If this is so, a positive correlation would be expected between the order of displays ranked according to their attack probabilities in the actor and reactor.

Of the five tests in which this comparison was undertaken in only two does a significant and positive correlation emerge - Fair Isle 1979 and 1980 (table 9). The remainder are all in the expected direction.

Treatment of the response probabilities in this way reveals that the extent of the association for displays ranked according to theiraattack probabilities is less than would be expected if temporal association provided a reliable measure of information transfer in the manner anticipated by the conflict model.

Escape.

In an attempt to reconcile the number of observed displays with the predictions of the early games theory models, Caryl (1979) suggested escape as a candidate for information transfer. Is there any greater consistency in actor/reactor relations for displays ranked according to their escape probabilities?

The correlation co-efficients appropriate for this comparison do not support this possibility (table 9). One correlation (that for Hoy 1980) only just fails to reach significance. The remainder all exhibit an appropriate positive relationship but the extent of this association is less than that revealed for attack.

If temporal association reveals information content then on the basis of the evidence presented here the displays of the bonxie do not appear to convey escape information.

Of the two candidates describing the nature of the information transmitted by displays no overwhelming evidence is available to suggest that either offer a real possibility. The limited support tentatively suggests a trend between displays and a varying likelihood to attack. At this stage this supports the original conflict view in favour of transmitting attack information.

In an attempt to clarify this uncertain state of affairs further comparisons were made.

4.1.5. Actor Comparison.

The displays of the actor within each colony were ranked according to the extent of their association with attack, escape and stay. These probabilities were taken from tables 3 to 7 .

Using this data two further types of comparison were made. The first of theses involved comparing data gathered from a single colony but from different seasons. The second of these involved comparing data between colonies.

Firstly, data was collected at each colony over two seasons. The Hoy and Fair Isle data was collected by myself during 1979 and 1980. For the Noss comparison data collected by myself was compared with that collected from the same colony by Andersson (1976). This made it possible to compare ranked responsiveness in each colony over two different seasons. The date from each colony was collected at the same time of year.

The actor was chosen for comparison as his behaviour was considered likely to provide a more representative picture of any association between displays and overt actions. Bonxie interactions are of short duration. Further, over 60% of interactions are settled without display by the reactor. Where the reactor does display, the interaction is generally resolved on the basis of only one display per individual. This 'one-display' nature of the interactions is taken to suggest that any motivational information associated with a display would be more apparent when a display is given by the actor. The display response of the actor might indicate the relative value of a resource to the signaller. This approach makes no attempt to control for interactional influence. This will be dealt with more fully in a later section.

The point here is that the displays of the actor have, in the past, been credited with the ability of conveying motivational differences. This ability provided the framework of a dispute settling system. We are concerned with testing the validity of this assumption, an assumption that runs counter to the games theory ideas on communication. Further, this validity will be tested using data derived from methods previously used to <u>support</u> the conflict view. The presence of absence of consistency is a crucial first step towards resolving the games/conflict contradiction.

The within and between colony comparisons were made using a Spearman correlation co-efficient. (Siegel 1965). The results are presented in the form of a correlation matrix (Table I0). The data was presented in this form for two reasons. Firstly, the criterion for the inclusion of a display for analysis was that it should occur on a minimum of ten occasions. This meant that a number of displays were included in some tests but not in others. The correlation co-efficients represent a comparison of the same displays but the displays used to calculate the co-efficients may differ between colonies. As a result each correlation was calculated separately. Secondly, the data was presented in this way to aid the detection of subtle colony differences or similarities. A number of extrinsic colony differences were noted during the study. These arose in response to, for example, differences in prevailing temperature. Separate treatment of test comparisons may reveal whether such variables are influential and, if so, whether this is consistent.

When the responses were ranked and compared in this way support for displays forming a series by virtue of differences in the extent of an association between displays and selected overt action diminishes.

It proved more convenient to treat the data in terms of the correlation matrix. The within-and between-colony comparisons will be dealt with at the same time.

Firstly, do displays exhibit consistent attack relations?

Attack (Table I0a)

Comparing actor responses over different seasons reveals only one significant result (Fair Isle 1979/1980 - table I0a). The Noss correlation (1972/1978) only just fails to reach significance. At this juncture a trend similar to that found in the previous actor/reactor comparison is evident and support for an attack series is good. However, this picture, and with it the main support for an "attack' series, is rudely shattered on Hoy. Comparing the Hoy tests (1979/1980 - table I0a) reveals a co-effieient which is both low and negative - the opposite of what would have been expected. This inverse relationship reveals that a display having a high attack probability one year is associated with a low attack probability the following year.

Even if non-significant a positive correlation could be taken as providing a measure of support for an 'attack' series. It is not possible for the latter to absorb this negative finding.

On extension of this comparison across colonies the picture becomes even clearer. In only one case does a significant correlation emerge. (Hoy 1980/Fair Isle 1980 - table I0a).

Within this broad comparison only two out of fifteen comparisons reveal the significant support that would be expected had these displays formed an attack series. The remaining coefficients are low. The temporal association of displays and overt attack does not provide a reliable insight into the nature of the information conveyed by displays.

It was evidence produced by the above methods that formed the cornerstone of the conflict theory. Without any test for consistency their conclusions are unfounded. When their consistency has been tested it is evident that the displays of the bonxie do not form an attack series. This finding is in accord with games theory predictions. If temporal association does provide an insight into information content it may lie with esaape, a dimension which satisfies a number of criticisms (Caryl 1979).

Escape

Actor displays were ranked according to their respective escape probabilities. Comparing these ranks between seasons on each colony reveals only one significant and positive result (Fair Isle 1979/1980 - table 10 b). While the Hoy 1979/1980 correlation isrrelatively high, that for Noss 1972/1978 reveals an almost random association.

At this level there is little to suggest that these displays form an escape series, a view that is re-inforced when comparison is extended between colonies.

When this was done only one further significant relationship is evident (Hoy 1980/Fair Isle 1979 table 10 b).

As for attack only two of fifteeen correlations revealed the level of association that would be expected of a species specific 'escape' series. This conclusion is re-informed by the prevailing low level of the reamining co-efficients together with the finding that one is negative, the opposite of what would be expected.

Form this evidence temporal association does not reveal whether displays convey the level of impending signaller escape,

4.1.6. Conclusion

Using temporal association to provide the raw data both Andersson (1976) and Caryl (1979) presented evidence that the displays of the bonxie formed an 'attack' and an 'escape' series respectively. The simple nature of the method warranted a test of consistency - whichever of the above suggestions provided an appropriate level of consistency could be said to be a prime candidate for type of information conveyed by agonistic displays.

When data gathered in a similar fashion was tested for its consistency both of the above suggestions appeared to be without foundation.

Early games theory models (e.g. Maynard Smith 1974) criticised the possibility of transmitting variations in attack intention. Conflict support for this view was obtained using temporal association and the failure of a similar approach here to reveal a consistent picture suggests that Maynard Smiths criticisms were justified.

Games theorists have been slow to forward models incorporating an explanation for the observed range of displays, an explanation for which is all the more necessary now that earlier conflict explanations can be discounted. One such attempt at integration was offered by Caryl (1979). His suggestion that displays convey escape information was not supported.

A state of affairs now exists where a range of displays can still be said to fulfil a threat function but, irrespective of theoretical orientation, no model exists which might provide an explanation.

However, the above conclusion should be viewed with caution. The results presented here suggest that the conclusions of earlier conflict studies were based on inadequate data but not that displays do not convey intention. The method adopted here may not be appropriate for detecting intentional variation. In this vein two further conflict models based upon the framework adopted above have been suggested. The first of these suggests that information is conveyed in a relative manner and the second with information in the strict sense of a conflict between opposing tendencies. Each of these will now be tested in an attempt to illuminate the tricky functional problem concerned with the nature of the information conveyed and whether this is conveyed in a serial manner.

4.2.1. Relative Information Transfer : responses in the presence and absence of displays.

The conflict theory, applied empirically using temporal association, has formed the basis of a number of hypotheses aimed at explaining the causal and functional significance of displays.

In the previous section data obtained using temporal association was treated in an absolute manner. The frequency with which each action followed a display was assumed to provide an absolute measure of the level of information conveyed by a display. This line of thinking may be inappropriate.

Instead, information may be conveyed relative to an appropriate baseline. This suggests an alternative baseline. This suggests an alternative method of analysis. This would involve comparing the response probabilities associated with giving a display to a baseline level provided by the response probabilities expected when that display is not given. According to this new definition of information it would be the difference between these two measures that is characteristic of a display.

Stokes (1962a) conclusion in favour of displays conveying attack information was based on his finding an increase in attack probability when a display was given compared with the likelihood of this response in the absence of the display across a number of seasonal subsamples. The basis of this conclusion was the fact that an increase occurred in each subsample,, This is one of the few studies where a test of consistency was made. Closer examination of this date, however, revealed that this consistency was limited (Caryl 1979).

Firstly, displays ranked according to the size of this increase for attack revealed little consistency in their ranking when seasonal sub-samples were compared. Secondly, when the seasonal attack and escape probabilities wereeplotted together an anomaly appeared. Displays initially associated with a high attack probability were equally likely to be followed by escape by the end of the season. In contrast, displays having an initially high escape association revealed far higher seasonal consistency in the extent of this association.

Two conclusions can be drawn here. Firstly, the consistency revealed for escape suggests that this relative method of treating the data may be more viable than the earlier 'absolute' approach. Secondly, it would appear that escape offers greater possibilities as the type of information conveyed by displays.

It now remains to be seen whether the displays of the bonxie exercise their threat function by conveying information in this relative manner.

4.2.2. Calculating the presence and absence probabilities.

How are the baseline 'absence' probabilities calculated? The 'absence' probabilities for each display are determined by summing the responses occurring following every display other than that under immediate consideration. A single set of probabilities are calculated from this summed data. Absence probabilities are thus calculated for each display separately. The summed probabilities are then compared with the probabilities for their complimentary display. (i.e. the probabilities associated with the use of each display (from Table 3-7). The relative response value thought to be characteristic of a display is the difference between the presence and absence sequelae.

This approach has been used frequently (e.g. Andersson 1976), Stokes 1962, Dunham 1966). Where it has been used finding a difference between the presence and absence probabilities was considered sufficient to demonstrate a threat function for displays when attack, escape and stay responses were used.

The summing of responses used to calculate the absence probabilities calls into question the validity of this means of determining the baseline. The absence probabilities are the sum of responses from a variety of displays. Any difference that does arise from a comparison of presence/absence probabilities need not be due to any effect of the display under immediate consideration but may result from a display that is contributing to the absence probabilities. For example, if an individual display had a high attack probability and was included in the calculation of the absence probabilities the combined attack probability would be inflated. This may influence the magnitude and direction of the probability change for the display being considered directly. If the display being included in the 'absence' response was a very intense threat display and the display for which a relative probability was being calculated was of a lesser intensity the presence/absence comparison would indicate a decrease in attack likelihood. In effect, though, it is only a decrease in relation to this intense display. Where a display of high intensity is included in the absence probabilities all other display may appear to show a decrease. Using this method it is questionable whether any realistic impression of information is revealed.since the base level with which a display is conveyed is not arbitrary and is different for every display.

However, the consistency that emerged for escape information in Caryl's (1979) reanalysis suggests that an analysis of this type might be worth pursuing.

4.2.3. Presence and Absence comparison.

In view of the criticism offered above it is insufficient to base a conclusion on finding a difference between the probability associated with a display and that expected when it is not given. Demonstrating a significant difference is important but as Caryl pointed out the consistency of this difference must be determined.

Firstly, the nature of the difference between the 'presence' and''absence' probabilities has to be determined. The 'presence' probabilities were taken directly from tables 3 to 7 . The 'absence' probabilities were calculated from summing the same data.

When the probabilities associated with each actor display are calculated in this manner the ensuing picture regarding the insight into information transfer by display is ambiguous.

a. Noss 1978 (Table II)

A significant difference is evidenccfor all but three displays (table II). For almost 50% of the display repertoire there is no evidence for any response difference i.e. for these displays information would not appear to be conveyed in this relative manner.

b. Hoy (Tables I2 & I3.

A similar picture is evident on Hoy 1979 (table I2). Four out of nine displays appear to ineffective transmitter of relative information, there being no significant difference between the presence and absence of responses. These displays are NB, NBL, NBT, NfB. In the following year, Hoy 1980 (table I3), a similar proportion of display are lacking in effectiveness (NBL, NbBpL, NSWand OLW). It is interesting to note that there is little consistency over the two seasons in thos displays lacking in effect. Only one display (NBL) appears in both years;;

c. Fair Isle (Tables I4 & I5).

On Fair Isle 1979 (table I4) only three out of ten displays lack effect (NBL,NbBp, NbBpL). In 1980 (table I5) the number lacking effect is reduced to two (NBL and NbBpL).

Here, not only is there a higher proportion of displays which can be considered as effective relative information transmitters, but there is also greater consistency in the displays for which no significant differences are evident.

Overall, though, the picture is not very encouraging. In three of the tests (Noss 1979 and Hoy 1979/80) almost half of this displays comprising the testable repertoire fail to reveal the difference expected if displays conveyed information in this relative manner. The remaining two tests (Fair Isle 1979/1980) offer only marginally greater support. All together, over the five tests, a total of nine different displays have at one time failed to demonstrate a difference between the presence and absence sequelae.

On the basis of this evidence displays do not appear to maintain a consistent relationship to the relative levels of the tendencies presummed to underlie their causation and about which they are assummed to convey information.

4.2.4. Relative information along a single dimension.

In the previous section it was suggested that a display might be followed by attack, escape and stay even if they actually functioned by transmitting information along only one of these dimensions. This might obscure any threat relationship if evidence for this relationship were sought through a comparison of all possible responses. A 'relative' relationship might be more evident when comparison is restricted to a single dimension. The available evidence (Stokes 1962a, Caryl 1979) suggests two possibilities, attack and escape respectively.

At the most basic level it is pertinent to ask how consistent the direction (i.e. whether an increase or a decrease) and magnitude of the presence/absence probabilities are. To determine the consistency of this relationship the change in response (from tables I1-I5) was scored as a presence/absence different (PAD). These are presented in table I6 . The data presented here is for displays delivered by the actor.

4.2.5. <u>The size of the difference.</u>

The most basic measure that could be taken here is the magnitude of the difference. Comparison of these size differences (irrespective of direction) reveals immediately that considerable differences exist for a single display when compared across tests (table I6). Quantitative differences of this nature could arise as a result of a number of extraneous influences. For example, it was suggested earlier that temperature differences at the time of testing may affect the activity levels of the birds, and influence which may be empirically manifest as colony differences similar to those found in table I6 .

Obviously a quantitative comparison of this sort is likely to be of little value. A better idea of the consistency of the relative response association would be expected from a comparison of the direction change associated with a display. A display would always be expected to be followed by either an increase or a decrease irrespective of the size of the change.

The attack and escape RAD were treated independently. The directional change associated with each display were compared within each colony over consecutive years and, more generally, by a comparison between colonies.

a. Attack

Comparison of the direction of the change in the attack response on Hoy 1979/1980 (table I6) reveals that for five of the eight displays considered the direction change is inconsistent an increase one year but a decrease the next.

For Fair Isle 1979/1980 (table I6) far greater consistency is evident. Eight out of nine displays demonstrate a consistent direction change.

The difference between these colonies in the picture ensuing from this comparison prohibits forwarding even a tentative conclusion. This view is reinforced when comparison is extended between the colonies (table I6). The picture from this inter-colony comparison is a negative one. Only two out of nine displays maintain a consistent change in direction - NfB a consistent increase and NS a consistent decrease. The direction associated with these two displays is in accord with their anticipated functional roles, NfB being an aggressive display and NS being an appeasement display (Andersson 1976).

Overall the failure of such a large proportion of displays (seven out of nine, table I6) to demonstrate consistency in the direction taken by the difference between the attack response probability in the present and absence of a display does not support the possibility of attack information transfer in this manner.

b. Escape.

Comparison the direction change of the escape probability associated with display between Hoy 1979/1980 (table 16) reveals a consistent direction for seven of eight displays. Only NbBp provides an anomolous result. This is surprising since NbBp has generally been considered as a display representing a high escape likelihood (Perdeck 1960) Andersson 1976) and so would have been expected to demonstrate a sizeable increase in escape likelihood.

A similar comparison on Fair Isle 1979/1980 also reveals a relatively high consistency. Seven out of nine displays demonstrate a consistent escape direction change. The two displays failing to do so are NfB and NS. NfB has been labelled an aggressive display (Perdeck 1960, Andersson 1976) and, as a result, it is not surprising to find any escape component for this display. The failure of NS to do so is unexpected. Both the above authors labelled this display as one highly indicative of an escape tendency. It would thus be expected to maintain an association with an increased escape probability.

Within each colony the relative greater consistency (compared to attack) raises the possibility an association between displays and a relative escape level. This finding supports Caryl's (1979) view that displays transmit relative escape information.

However, two lines of evidence suggest caution before reaching a conclusion. Firstly, comparing the results for each colony (table I6) reveals a difference in the display which fail to reveal consistency. Secondly, in each colony the display which fails to reveal a consistent direction change is one considdred to fulfill the function of conveying a high escape likelihood. Contrary to what was actually found these two displays, NbBp and NS, wouldhave been expected to reveal a high and consistent association with an increase in escape probability.

Despite this consistent within-colony association the level of consistency decreased when a between-colony comparison is made. Only four out of eight displays maintain consistency in the direction of their relative escape probabilities (OLW, BLW,NB,NBL-table I6 - data for Hoy/Fair Isle). Extension of this inter-colony comparison to include Noss 1978 (table I6) the number of displays maintaining a consistent direction change is reduced to three (OLW,BLW,NB).

If a conclusion is based on comparison within each colony the evidence points to escape being the medium through which displays exercise their effect. If a conclusion is based on an overall comparison the limited directional consistency for attack and the only marginally greater consistency for escape is insufficient to suggest that displays maintain an association with either of these actions nor does this method appear to offer an insight into the possibility of displays conveying information in a relative manner.

4.2.6. Relative information in serial form.

Displays treated in isolation fail to reveal consistency in their relative association with a response. The within colony consistency evidence for escape warrants one final test. The 'conflict' explanation for the range of observed displays was that they served to convey differences in signaller intentions. It remains to be seen whether displays and their associated relative probabilities maintain the consistent relationship to one another that would suggest that they form a threat series.

To determine this possibility it is necessary to determine the consistency of serial display relations. The PAD's associated with the displays were ranked from a high increase in PAD to a high decrease in PAD. The PADs were taken from table I6 . Spearman correlation coefficients (Siegel 1956) were used to determine relations. Correlation coefficients were sought within colonies (between seasons) and also between colonies.

a. Attack (Table I7 a)

Within-colony comparison of ranked PAD's for attack reveals a significant correlation between Fair Isle 1979/1980. On Hoy (1979/1980) however, the distribution of ranked responses is almost random. The anomoly between these results is weighed in favour of there being no serial relationship between attack PADs by the generally low value of the correlations revealed by a wider inter-colony comparison. While the majority of these are positive they fail to reach significance. On the basis of this comparison there is no evidence to suggest that the displays of the bonxie form a series of displays of differing relative attack intensity.

b. Escape. (Table I7a)

Comparison of ranked PAD's for escape over different seasons on Fair Isle and Hoy reveals of similar picture to that found for attack. Fair Isle 1979/1980 reveals a significant and positive correlation, that for Hoy 1979/1980.

A more extensive inter-colony comparison reveals more support for escape than for attack. With only 30% of the correlations reaching significant support is weak.

4.2.7. Summary and Conclusion.

Do displays convey the relative likelihood of the signaller executing a partioular response? From the above comparisons, both where displays were treated individually as conveying information about attack, escape and stay (Tables I6) and where serial relations were sought for attack (Table I7a) and escape (table I7b), the answer is no! The displays of the bonxie do not convey the relative likelihood of signaller response.

The data used to examine this possibility was provided by the-temporal association between displays and a number of chosen overt actions. Where this 'relative' approach has been used previously to support the possible transfer of intentional information the analyses were also based on temporal association (e.g. Stokes 1962a, Dunham 1966), Further, the presence and absence probabilities were calculated in the same manner as in the present study.

The validity of Stokes' conclusion has already been criticised by Caryl (1979). In addition to these criticisms the inconsistency evident from the present study suggests that some measure of consistency should be applied to existing studies before accepting their conclusions.

This conclusion has to be qualified. If only applied to the above method of determining the presence and absence probabilities and thus the pattern of responses used for comparison. The absence probabilities represent the summed responses for every display other than that under immediate study. Any difference may result from an influence arising from a display contributing to the absence probabilities. We may in fact be dealing with the response probability relative to another display rather than to an objective baseline. If an appropriate and objective baseline could be determined it is still possible that this method may provide an insight into the functional role played by displays.

Until such a baseline could be determined there are no grounds for concluding in favour of this method providing an insight into the potential for displays to convey variation in intentions. This failure is in accord with predictions derived from games theory analyses (e.g. Maynard Smith 1972) that intentional information should hot be conveyed. It is not possible at present to provide an alternative explanation. This explanation may be found by a return to the idea originally underlying the conflict theory; namely, displays convey information about the state of conflict being experienced by an individual.

4.3.1. Displays and the transmission of conflict information.

Where temporal association has been used to illustrate conflict relations for threat displays three tendencies have predominated; attack, escape and stay. Comparison of the extent to which displays are associated with these responses failed to reveal any support for this approach providing an insight into the information content of displays (Tab3-7). Rather than looking at all three tendencies attention was switched to looking at only one (either attack or escape). This approach also failed to reveal any consistent display association. An additional problem was also revealed. The individual response probabilities were found to be low, a finding which has caused some ethological concern (Dunham 1966, Caryl 1979, Hinde 1981). Use of this latter method resulted in a shift in attention away from the original conflict framework. For a state of conflict to exist at least two opposing tendencies must be present simultaneously.

An awareness of these two problems led Hinde (1981) to suggest that displays may convey the conflicting likelihood of a signaller to perform two incompatable actions. In particular he suggested that display may signal that an individual is going to attack/stay or escape/stay. For example, in the former the signaller could be considered as saying perhaps; 'I am going to stay and feed but will attack if provoked.'

This suggestion was offered to fulfil two aims. Firstly, it was aimed at increasing the numerical value of the response probabilities, the magnitude being assumed to be a measure of signal reliability. Secondly, it aimed to provide an insight into the nature of the information content of displays.

4.3.2. The magnitude of the probabilities.

Since we are dealing in the first place with only three different responses summing two of these will inevitably increase the numerical value of the probability. Basically, combining responses offers a solution to one of the earlier problems. The magnitude of the responses is now high enough to be considered as having a threat function (Hinde 1981). Examples of the magnitude if the summed probabilities can be found in table I8 .

A closer examination of the individual response probabilities contributing to the summed values reveals that 'staying' makes the largest contribution irrespective of other contributing responses. The theoretical implication of this for a dispute settling system will be discussed later.

Owing to the limited number of responses available as source material simply generating higher response probabilities from summing certain individual probabilities does not provide sufficient basis for concluding in favour of this approach revealing an insight into the information content of displays. Before any such conclusion could be accepted the consistency of any dual association needs to be determined.

4.3.3. The Information Content.

Hinde (1981) suggested two possibilities for the nature of the information conveyed by displays. Displays could convey either attack plus stay information or escape plus stay information. He further suggested that the greater the magnitude of the combined probabilities the more reliable the insight into the potential of a display to transmit information. From table I8 it is obvious that the probabilities are large and that differences exist between displays. A combination of these suggests a test for the consistency provided by this approach.

If size of probability is important then it is logical to look for the combination that produces the highest probability. If this approach does provide a reliable insight then each display would be expected to maintain a consistent association with a particular combination, i.e. attack + stay or escape + stay. The consistency could be tested by comparing the pattern of the association for displays given by the actor and those given by the reactor.

Basing this analysis on the size of the probabilities the individual responses for each display were summed for stay plus whichever of attack or escape yielded the highest probability. These probabilities were taken from tables 3 to 7 .

Do displays maintain a consistent association with a probability combination? Comparing the pattern of combinations between actor and reactor (table I8) reveals that this is not so. For the actor the general picture is one where association is between attack and stay. For the reactor the highest responses are for escape plus stay. The extent of this difference can be seen more clearly in table I8 . Here the results are summarized for the actor and the reactor according to whether attack plus stay was most likely, whether escape plus stay was likely and where both responses were equally likely. This was done on the basis of the magnitude of the probabilities. For the actor 55% of displays revealed a highest probability from summing attack plus stay whereas only 34% maintained a higher escape plus stay probability. For the reactor, on the other hand, the majority of displays (93%) maintain a highest association with escape plus stay.

On this evidence there are no grounds for concluding that this method provides an insight into the information potentially available from displays. The asymmetry in the pattern of the association between the actor and reactor is hardly surprising. The above data was compiled from individual probabilities for which a difference in response likelihood was evident (table 3–7). The greater likelihood of reactor escape is mirrored in the above date.

This method, at this level of analysis, is no more effective than previous methods which dealt with single responses. The result is dependent upon the status of the interactant i.e. whether the actor or the reactor.

The consistency of the actor/reactor asymmetry means that a more general relationship may have been hidden. A more general test of consistency would involve comparing the pattern of response, summing for the actor alone. (Table I8).

The highest combined actor responses were compared over consecutive seasons on Hoy (1979/1980, Table I8). Only three of seven displays (OLW, BLW, NB) maintain a consistent summed association (the numerical value of the sum was ignored). For three (NBL, NBT, NbBpL) an equal likelihood of both responses is evident. For the remaining display, NfB, Hoy 1979 reveals an Escape + Stay advantage but an Attack + Stay advantage in 1980. This finding is all the more surprising since NfB is considered to be the most aggressive bonxie display (Andersson 1976). It would thus be expected to provide attack information and not to provide escape information.

On Fair Isle (1979/1980, Table I8) the picture shows a slight improvement. Five of the nine displays studied reveal a consistent association (OLW, NBL, NBT, NfB, NS). For one (BLW) there is an equal response likelihood in 1980. For the remaining three a mixed responsiveness is evident - Attack + Stay one year and Escape + Stay the next.

Within each colony there is less consistency in summed association than would have been expected if this approach provided a more reliable insight into information transfer. In an attempt to clarify this situation comparison was extended across all colonies (Table I8). Rather than clarifying the situation this extension serves to further confuse the issue. Now only two actor displays maintain a consistent summed association (OLW, NS).

If analysis is based on the magnitude of a summed response there is little to commend the possible transmission of conflict information whether this is in the form of attack + stay or escape + stay information.

4.3.4. Serial relations between summed probabilities.

When single responses were being considered the consistency with which the response asymmetry appeared for each display (see tables 3-7) suggested that a more general relationship may have been hidden. This asymmetry was carried over into the investigation of summed probabilities (tables I8). Perhaps a more appropriate line of investigation would be to look for serial relations between displays. This line of investigation is in accord with the conflict theory suggestion that displays convey differences in the response likelihood of the signaller. When the individual responses are summed differences in the extent of the summed probabilities are evident. Before this can be accepted as evidence of serial threat relations, the consistency of the differences between displays needs to be determined.

To assess the possibility of the existence of a conflict system of this nature a combined attack plus stay and a combined escape plus stay probability was calculated foreeach display. The combined probabilities were calculated from table 3 to 7 .

a. Attack + Stay. (Table I9)

Displays were ranked as an attack + stay series. Comparison was made within each colony over two consecutive seasons followed by a broader between - colony comparison. A Spearman ranked correlation co-efficient (Siegel 1956) was used to determine display relationships. The number of displays for which sufficient data was available to permit analysis differed between colonies. Because of this the correlation co-efficients for each comparison were calculated separately. The attack + stay correlations are given in table I9 .

Comparison of the ranked attack + stay probabilities on Hoy (1979/1980) reveals that, although failing to reach significance the co-efficient is high and in the expected direction. If displays functioned in this manner a positive correlation would be expected between ranked displays.

However, a similar comparison on Fair Isle (1979/1980) does not provide support to the same extent. Although positive the correlation is low.

From a within-colony comparison support for the possibility of displays forming a threat series by virtue of displays differing consistently in their level of association with attack + stay probabilities is not forthcoming.

Does a more general inter-colony comparison provide any greater support? No, only one inter-colony correlation reaches significance (Hoy 1980/Fair Isle 1979, table I9). The remaining co-efficients are low and, further, two of three are negative. This latter result is the opposite of the result expected if displays formed a series.

When actor displays are ranked according to their summed attack + stay probability a comparison of these probabilities fails to provide any conclusive evidence that the displays of the bonxie are a result of varying levels of an attack/stay conflict.

Caryl (1979) proposed an alternative information dimension - Escape. Do displays form a series according to their Escape + Stay probabilities? This was the alternative system proposed by Hinde (1981).

b. Escape + Stay (Table 20)

Escape plus stay probabilities were calculated for each display (from tables 3 -7)). Displays within each colony were then ranked according to their escape + stay probability. Within and between colony comparison were made using a Spearman correlation co-efficient (Siegel 1965). As before each comparison was dealt with separately to facilitate comparison of the varying number of displays comprising the repertoire within each colony.

A summed escape plus stay probability comparison on Fair Isle 1979/1980) (table 20) reveals the significant and positive correlation that would be expected of an 'escape + stay' threat series. On Hoy, however, a very different picture emerges. While failing to reach significance the 1979/1980 co-efficient is very high. The surprising thing is that it is negative, i.e. a display with a high escape + stay association one year is associated with a low escape + stay probability the next. This is contrary to the picture expected of an 'escape + stay' threat series and is even more surprising considering the very positive and supporting result from Fair Isle.

In an attempt to resolve this contradiction attention was turned to a broader inter-colony comparison (table 20). This comparison did not provide further support for a conflict series. Thecco-efficients are generally low and an additional negative correlation is found (Noss 1978/Hoy 1979).

When the displays of the actor are ranked according to their escape plus stay probabilities and compared there is no basis for concluding that the displays of the bonxie result from varying levels of escape/stay conflict when the levels of these combined probabilities are determined using temporal association.

4.3.5. Discussion and conclusion.

Earlier analyses bases on temporal association presented two problems which prevented acceptance of a threat communication system effected by transmission of intentional information. These concerned the magnitude of the probabilities and the nature of information transfer (Caryl 1979). In response to these criticisms Hinde (1981) reasserted the conflict view that displays owed their causation to the simultaneous arousal of conflicting tendencies. It was thus possible that a threat system would be based on transfer of this conflict information.

Hinde's suggestion does provide higher response probabilities (Table I8, I9, 20). However, the number of responses that an animal is methodologically capable of is limited. Displays were categorixed according to the likelihood of their being followed by attack, escape and stay. As a result combining any two of these separate probabilities is bound to produce a considerable increase in the magnitude of a probability. Although differences in the extent of this summed association are evident the finding that their is little consistency in the summed probability for a display relative to the other displays comprising the repertoire undermines the validity of using this method to reveal the information available from a display.

At a theoretical level further criticisms can be levelled against this approach. The displays of the bonxie are being examined for their ability to subserve threat. It is generally agreed that threat displays serve to oust an opponent from a disputed resource without recourse to actual attack (Brown 1975, Dawkins and Krebs 1978). If we look at the individual probabilities in tables 3 -7 it is evident that the major contribution to the combined probabilities comes from 'staying'. If it is assumed that this response constitutes a message component its threat contribution has to be considered carefully. There would appear to be little point in conveying such a large proportion of staying information if the signaller is trying to oust an opponent. To signal with a high staying likelihood implies that the proponent is already in possession of the resource. A threat system of this nature is likely to develop only where individuals are defending resources, e.g. a display indicating territorial ownership.

What sort of display would an individual use (in terms of information content) when trying to gain access to a resource over an opponent? Would conveying conflict information (e.g. attack + stay or escape + stay) provide a viable medium for the handling of such disputes?

The conflict theory explained the variety of displays by suggesting that displays differed in the extent of the causal contribution of conflicting tendencies. How would these 'conflict' displays differ? A causal explanation for displays could be offered in terms of different levels of contributing tendencies, i.e. differences in the extent of the attack/stay conflict. At the functional level of the evolutionary pressures impinging on displays moulding the information they convey, a pressure arising primarily from the recipients propensity to respond, this might not be so.

If dipplays were a product of, say, an attack/stay conflict, the conflict theory assumes that information about both of these tendencies is available to an opponent (Moynihan 1955). Would both types of information be attended to equally by an opponent? Caryl (1979) argues that the high arousal likely during a dispute will lead to decisions being made on a basis permitting rapid and simple categorization of the future actions of an opponent. Where two individuals are both trying to acquire a resource the information of greatest relevance to one individual is likely to concern the attack probability of an opponent. Attack information will be given preferential attention and the expense of staying information. As a source of selective pressure on the functional ability of a display to convey information the recipient will act to anhance the ability of displays to convey attack information. In ethological terms emancipation could be said to have occurred. We are now back where we started with a system, basdd on the transmission of varying levels of attack intention,which was criticised theoretically on the grounds of evolutionary instability (Maynard-Smith 1979). Evidence for the existence of such a system has subsequently been shown to be lacking (Caryl 1979 and the present study-tables 3 -7 & I0a and chapter 4.I).

A system based on the transmission of attack plus stay information would be viable where an acquired resource was being defended. Data for the present study was gathered from non-breeding bonxie club birds. Any territorial individuals were excluded from the analysis. Conveying the high proportion of stay information. implied by the present study would appear to have limited functional application. It seems unlikely that the disputes occurring in the clubs are for the acquisition of a resource rather than its defence.

An escape/stay system is unlikely to offer stability. Hinde (1981) argued that displays were used to prompt an opponent so reducing the uncertainty necessitating the use of a display in the first place. If an individual prompted with a display signalling escape/stay information an opponent would have little to lose by attacking. The signaller is saying "I want to stay but will escape if provoked". A system of this sort would have little viability as the basis of a means of settling disputed access to a resource.

Signalling a likelihood of staying has little value in settling disputed access to a resource. The high staying probabilities, which provide the major contribution to the summed probabilities, is somewhat paradoxical when the nature of the club bonxie interactions are considered. The staying respones may be an artefact of the method rather than constituting an information component. The probabilities are a measure of the relative frequency of a given action. Staying could result from using a successful threat. The signaller would stay because his opponent has departed. Ascribing information potential to this behavioural component may not be justified.

In addition to the above theoretical criticisms there is no clear empirical support for the displays of the bonxie forming a conflict system (Hinde 1981) when the data used to determine its existence was derived using temporal association. The original suggestion of such a system was based on data derived using temporal association (Hinde 1981).

It now remains to be seen whether temporal association is itself a viable method for determining threat relationships for displays.

4.4.1. The Conflict Theory - Summary and Discussion.

Attack and escape are frequently observed components of the social behaviour of animals. Close examination of the situations in which such actions occurred, e.g. at territory boundaries, and the form of displays preceeding these actions prompted the suggestion that the displays were an overt sign of an underlying conflict to behave in incompatable ways (Moynihan 1955, Tinbergen 1959). Temporally relating displays and these actions formed the basis of a method for quantifying underlying influences on displays and served as a model explaining how disputes were settled using displays. This was the conflict theory. It is the explanatory power of this model that was tested here.

Finding differences in the extent of the association between displays and actions was considered sufficient to support the conflict view that displays represented differences in the motivational state of the signaller (Stokes 1962a). However, if threat displays are defined in terms of an association with overt attack and escape and only these actions are used in the field it would be difficult to do other than support the theory. A recent shift in theoretical perspective has suggested that displays should not convey intentional information since doing so would be evolutionarily unstable (Maynard Smith 1974). Together these observations suggest that 'conflict' data should be subjected to stringent tests for consistency. It was to the latter end that the present study of orientated.

The first problem to be tackled concerned the consistency with which each display was associated with attack, escape and stay. This was done by comparing the response probabilities of displays given by the actor and by the reactor (Ch. 4 , tables 3 -7 & 8). Significant differenees were revealed in the distribution of responses between actor and reactor although greater consistency was evident between displays in the pattern of this response asymmetry. The reactor was generally two to three times more likely to escape than the actor. In other words the initiater of an interaction was more likely to win. Interactional status (whether actor or reactor) was an important determinant of success irrespective of the display adopted. While status has been shown to be important in bonxie interactions involving territorial birds (Andersson 1976) the above result shows that more subtle and dynamic status differences can also be important.

This finding also suggests that the level of association between displays and a number of overt actions is an unreliable indicator of information content. The accuracy with which information could be transferred is one area in which conflict and games theory ideas contradict (Caryl 1979). What are the implications of the above findings for this question?

4.4.2. The Information Content.

It is generally accepted that the adaptive pressure prompting the use of displays to settle disputes results from the risk of injury associated with overt combat (Tinbergen 1959, Maynard-Smith 1973). This has been used to suggest that displays convey information about differences in intention to attack (e.g. Cullen 1966, Andersson 1976). However, it has generally been found that attack probabilities are low, a finding which has formed the basis of an argument against displays transmitting attack information (Caryl 1979).

Should attack probabilities, measured by temporal association, be high? This is doubtful. The attack probabilities are a measure of the relative frequency with which displays are followed by attack. If attack information was conveyed the 'probabilities' might be expected to be low. A high attack probability means that the display was actually followed by attack on a large number of occasions. The necessity for such action is counter to the display being an efficient threat. If a display was effective it would result in the departure of its opponent without attack being necessary. Stout (1975) explained thellow attack probabilities in terms of this interactional argument. This argument was questioned by Caryl (1981) in terms of Stout's own findings. If a display possessed the facility of repelling opponents per se, escalation would be expected when the opponent did not depart. Using dummy opponents, lack of either the use of a more intense display or attack against a staying opponent prompted Caryl's rejection of the argument. It would appear that irrespective of the magnitude of the overt attack response, displays do not convey attack likelihood.

Although a system conveying differences in attack intention is open to bluff (Maynard Smith 1974),a system based on escape information is less so (Caryl 1979, Maynard Smith 1979). It was the higher escape probabilities in the conflict studies he re-analysed that provided Caryl with a possible means of reconilling the games and conflict theory views. If this line of argument is to be supported it must be demonstrated that escape probabilities are considerably higher than attack probabilities and that any differences are consistent.

With respect to attack probabilities the present study provides considerable support for Caryl's argument (tables 3 - 7). On only one occasion does a display reveal a greater than average association with attack (NfB(72%); Fair Isle 1980,(table 7). This result is an exception and is inconsistent with the data from the remaining tests (tables 3 - 6) and low attack probabilities are the norm.

However, it is also the case that actor escape probabilities are below average (tables 3-7), a finding which runs counter to Caryl's argument. In only one test (Hoy 1979, table 4) are the ~~attack~~ escape probabilities consistently higher than those for attack.

Caryl's argument rested heavily on two displays (NN and NS, fig. 3 & 4) which, in Andersson 1976), revealed a particularly clear association with escape.

NN is the posture adopted by a resting skua and inclusion of this as a display (i.e. as adapted to fulfil a signal function) is questionable. The high probability of its being followed by escape may indicate an unwillingness to engage in dispute. Despite this it is not associated with high escape probabilities here. In the present study actor escape probability for NN ranges from 37% (Hoy 1980, table 5) to 51% (Fair Isle 1980, table 7) with an average of 44%.

NS is frequently seen as a pre-flight intention and so is a more likely candidate for a display indicative of impending escape. Nevertheless the extent of the association between this display and escape is less than might be expected, ranging from 20% (Fair Isle 1979, table) 6) to 50% (Hoy 1979, table 4) with an average of 33%.

When given by the actor the magnitude of the association between displays and either attack or escape is insufficient to consider information transfer being along either of these dimensions.

A higher level of association is evident when the displays are given by the reactor. For NS the escape probabilities range from 53% -83% with a mean of 65%. For NN the range is between 51%-67% with a mean of 61%. For attack, reactor probabilities are low. From the point of view of displays delivered by the reactor the consistently high escape probabilities supports Caryl's argument. However, the higher level of this association may be the result of a general response asymmetry rather than an indication of information context.

The contradiction between the above findings and those of Caryl's re-analysis are all the more interesting since his conclusion embraced data from a number of species. An explanation for this contradiction may lie with the methods used to provide the data upon which re-analysis was based.

In the present study it was found that only the reactor exhibited a higher than average escape probability. A similare state of affairs in the blue tit may explain the higher escape association found by Stokes (1962a). Stokes combined data for both actor and reactor to provide the probabilities used for his anaylis. Reactor escape probabilities inflated in a manner similar to that found in the bonxie could, in such combined probabilities, give the impression of a higher level of escape.

Andersson (1976) did not combine his data in this manner. An explanation for his higher escape probabilities may lie with his use of interactions involving individuals of a mixed status.

In this same study Andersson demonstrated that club territory holding individuals would win an interaction irrespective of whether they were actor or reactor and irrespective of the display adopted. He did not exclude this influence in determining response probabilities. The important thing is that in these mixed interactions the non-territorial individual was very likely to lose. Andersson's study was carried out during the early part of the season during which time club-pair birds are involved in claiming club territories. The interactions revolving around this activity are frequently of a mixed nature. Further, these mixed interactions are equally, if not more, likely to be initiated by the non-territorial individual (personal observation). Thus by virtue of their non-territorial status such actors are likely to lose a high proportion of interactions, and the escape probabilities associated with actor displays will be higher.

It is possible that the higher escape probabilities found by Stokes (1962a) and Andersson (1976) mya have resulted from the method used to score interactions rather than providing an insight into information content.

At this level Caryl's (1979) attempt to reconcile the gamesaand conflict theory views is without support. In an attempt to further elucidate upon this problem attention was switched to the second area within the conflict model which prompted games theoretic concern, namely, whether displays conveyed a range of intentional information.

The response asymmetry revealed in tables 3 - 7 may have served to obscure qualitative relations between displays. To provide a realistic model bringing the conflict/games theories together Caryl's suggestion would have to reveal that displays ranked according to their escape probabilities provided more consistent serial relations than a series. based on attack.

Displays were ranked according to the probability that they would be followed by attack and escape and a number of comparisons of this ranked data were made (tables 9 and10). These comparisons revealed that no support was forthcoming for either suggestion - as defined by temporal association the displays of the bonxie did not form a threat series. The importance of this finding lies with the fact that methods developed from and subsequently used to support the conflict theory do not reveal sufficient consistency in the data they generate to provide this model with any explanatory power.

At this point the criticisms and doubts of the games theorists appear justified - at this level displays do not convey intentional differences. This verification brings with it an old problem, namely, how do we explain the variety of threat displays. Caryl (1979) provided a plausible explanation for a range of displays within a games framework, but with the lack of support for this alternative the problem remains. One area of ethological doubt concerns the failure of games theorists to adequately explain a range of threat displays and this problem must be tackled if ethological and games theory views are to be satisfactorally reconciled.

At this point in the analysis this conclusion must be set in perspective. Because of the inadequacies of temporal association as it has been used so far it is not possible to reject the idea that displays convey differences in signaller intention.

Temporal association relies upon two assumptions. Firstly, it assumes that the number and choice of overt behavioural responses reflects the tendencies thought to underlie the display causally.

Secondly, it relies on the relationship between cause, display and action being insulated from any influence external to the immediate situation i.e. it assumes that the motivational level revealed by the extent of a response is not influenced by, say, the response of an opponent. It is unlikely whether either of these conditions have been fulfilled.

A whole range of responses could arise if displays conveyed only one type of information. Assume for the moment that displays conveyed varying levels of attack intention. A might attack B if the latter's display was less intense but might escape if B adopted a more intense varient. The influence of such interaction will be considered more fully in a later section.

Further, it is possible that the same response could occur to displays of a functionally different nature. 'Escape' could occur to an opponent adopting a threat of a relatively higher intensity but it might also arise when the actor has adopted a sexual display. Perdeck (1960) found that, in the bonxie, a sexually displaying individual may display at a number of individuals in succession. The implications of a failure to separate functionally threatening and functionally sexual behaviour are considerable where temporal association is used. If threat is defined in terms of attack or escape then the sexually behaving bonxie moving off to display at another individual would be scored as 'escape' leading to the inappropriate categorization of this display as a threat.

The influences on the response shown after a display are many and varied. It is perhaps not surprising that if displays did form a threat series temporal association of actors display and subsequent action would fail to reveal its presence. The games/conflict contradiction may be further illuminated by adopting a more sophisticated analysis - one which will involve integrating the behaviour shown by both actor and reactor.

TABLES

Actor and Reactor Response Probabilities

Tables 3 to 7 record the actor and reactor response probabilities. Any instance of circling following display was excluded from the sample before each response was calculated. Each response probability represents the relative frequency with which each display was followed by attack, escape and stay.

Differences between the distributions of actor (A) and reactor (R) response probabilities were tested using a Chi - squared test. The levels of significance are denoted as follows:

NS	Not Significant
**	$p < 0.025$
***	$p < 0.001$

			%			
		Attack	Escape	Stay	Chi^2	N
OLW	A.	31	15	54	1·108	61
	R.	13	27	60	**	48
BLW	A.	21	14	65	12·972	14
	R.	25	33	42	***	12
NB	A.	13	30	57	38·973	92
	R.	6	74	20	***	154
NBL	A.	11	33	56	11·983	9
	R.	0	33	67	***	6
NBT	A.	27	12	62	58·339	26
	R.	9	64	27	***	11
NfB	A.	45	19	36	4·236	11
	R.	33	17	50	NS	6
NbBpL	A.	18	6	76	14·019	17
	R.	17	25	58	***	12
NbBp	A.	75	0	25	96·316	4
	R.	0	30	70	***	10

Table 3 : Noss I978 Actor and Reactor response probabilities.

		Attack	Escape	Stay	Chi^2	N
OLW	A.	15	12	73	7·17	96
	R.	11	28	61	*	47
BLW	A.	21	0	79	38·683	19
	R.	11	32	57	***	19
NB	A.	13	23	64	27·198	47
	R.	9	59	32	***	44
NBL	A.	13	13	74	1·016	15
	R.	10	10	80	NS	10
NBT	A.	6	31	63	8·58	16
	R.	0	23	77	*	13
NbBp	A.	0	55	45	13·846	9
	R.	12	55	33	***	9
NbBpL	A.	0	38	62	12·644	13
	R.	7	21	72	***	14
NfB	A.	17	22	61	27·174	18
	R.	14	57	29	***	14
NS	A.	0	50	50	25·437	12
	R.	0	83	17	***	24

Table 4 : Hoy 1979 Actor and Reactor response probabilities.

		Attack	Escape	Stay	Chi^2	N
OLW	A.	10	8	82	11·357	288
	R.	4	23	73	**	113
BLW	A.	7	0	93	70·42	15
	R.	0	50	50	***	4
NB	A.	11	22	67	17·132	186
	R.	11	49	40	***	178
NBL	A.	22	9	69	11·384	45
	R.	11	22	67	**	27
NBT	A.	22	22	56	14·54	39
	R.	11	53	36	***	19
NbBp	A.	0	0	100	56·929	5
	R.	0	44	56	***	25
NbBpL	A.	17	17	66	7·156	24
	R.	8	28	64	*	39
NfB	A.	37	25	38	13·338	8
	R.	25	50	25	***	4
NSW	A.	14	14	72	78·58	7
	R.	0	75	25	***	8
NN	A.	18	37	45	24·03	73
	R.	2	67	31	***	454

Table 5 : Hoy 1980 Actor and Reactor response probabilities.

		Attack	Escape	Stay	Chi^2	N
OLW	A.	9	8	83	11·961	327
	R.	5	26	69	***	131
BLW	A.	9	0	91	32·00	43
	R.	0	22	78	***	9
NB	A.	21	25	54	12·524	344
	R.	10	48	41	***	343
NBL	A.	13	9	78	11·521	95
	R.	6	26	68	***	65
NBT	A.	41	12	47	23·70	17
	R.	13	31	56	***	16
NbBp	A.	18	23	59	1·289	39
	R.	13	21	66	NS	29
NbBpL	A.	9	13	78	5·91	54
	R.	7	28	65	*	41
NfB	A.	26	24	50	0·363	58
	R.	29	21	50	NS	14
NS	A.	4	20	76	24·09	141
	R.	1	53	46	***	75
BEND	A.	9	9	82	0·13	11
	R.	10	10	80	NS	10
NN	A.	7	45	48	3·163	137
	R.	2	51	47	NS	712

Table 6 : Fair Isle 1979 Actor and Reactor response probabilities.

		Attack	Escape	Stay	Chi^2	N
OLW	A.	10	9	81	13·103	581
	R.	9	29	62	***	204
BLW	A.	11	11	78	22·834	36
	R.	0	33	67	***	6
NB	A.	39	23	38	16·761	417
	R.	18	48	34	***	274
NBL	A.	27	7	66	13·11	145
	R.	22	26	52	***	69
NBT	A.	49	8	43	11·121	39
	R.	33	24	43	***	21
NbBp	A.	38	25	38	53·501	8
	R.	0	20	80	***	10
NbBpL	A.	16	10	74	2·968	51
	R.	12	18	70	NS	33
NfB	A.	72	14	14		14
	R.	-	-	-		
NS	A.	0	30	70	23·177	51
	R.	3	60	37	***	40
NSW	A.	0	30	70	120·998	16
	R.	0	100	0	***	11
NN	A.	10	51	39	6·149	364
	R.	3	65	32	***	1334

Table7 : Fair Isle 1980 Actor and Reactor response probabilities.

			Attack	Escape	Stay	Chi^2	N
HOY	1978	A.	19	11	69	46·72	119
		R.	5	56	39	***	128
HOY	1979	A.	11	23	66	6·772	245
		R.	8	40	52	*	194
HOY	1980	A.	16	15	69	23·020	690
		R.	8	46	46	***	871
NOSS	1978	A.	26	16	58	18·197	234
		R.	12	42	46	***	259
FI	1979	A.	15	17	69	6·075	1266
		R.	9	31	61	*	1445
FI	1980	A.	25	19	56	15·716	1722
		R.	10	42	48	***	2002

Table 8 : Mean actor and reactor response probabilities.

The response probabilities within each colony were summed and mean probabilities calculated. Mean actor and reactor response probabilities wre compared using a Chi - squared test. The significance levels are denoted as follows;

* $p < 0.05$

*** $p < 0.00I$

		REACTOR		
		A	E	S
ACTOR	A	0·548		
	E		0·3	
	S			0·4

HOY 1979

		REACTOR		
		A	E	S
ACTOR	A	0·688		
	E		0·872	
	S			0·9*

HOY 1980

		REACTOR		
		A	E	S
ACTOR	A	0·82**		
	E		0·204	
	S			0·784**

FAIR ISLE 1979

		REACTOR		
		A	E	S
ACTOR	A	0·612*		
	E		0·51	
	S			0·058

FAIR ISLE 1980

		REACTOR		
		A	E	S
ACTOR	A	0·2		
	E		0·216	
	S			0·285

NOSS 1978

Table 9 : Ranked actor and reactor comparison

Displays were ranked according to the probability that they were followed by each of attack, escape and stay. Within colony comparisons of response rankings were made using a Spearman rank correlation coefficient. The significance levels of the coefficients are denoted as follows;

* $p < 0.05$ ** $p < 0.0I$

	NOSS 1972	NOSS 1978	HOY 1979	HOY 1980	FI 1979	FI 1980
NOSS 1972	1·00	0·6	0·4	0·142	0·25	0·19
NOSS 1978		1·00	0·428	0·144	0·28	0·142
HOY 1979			1·00	-0·299	0·047	0·152
HOY 1980				1·00	0·63	0·828*
FI 1979					1·00	0·966**

a. ATTACK

	NOSS 1972	NOSS 1978	HOY 1979	HOY 1980	FI 1979	FI 1980
NOSS 1972	1·00	0·08	0·64	0·347	0·6	0·619
NOSS 1978		1·00	-0·5	0·108	0·178	0·07
HOY 1979			1·00	0·666	0·583	0·552
HOY 1980				1·00	0·882*	0·342
FI 1979					1·00	0·633*

b. ESCAPE

	NOSS 1972	NOSS 1978	HOY 1979	HOY 1980	FI 1979	FI 1980
NOSS 1972	1·00	0·486	0·571	0·085	0·176	0·083
NOSS 1979		1·00	0·143	0·178	0·143	0·321
HOY 1979			1·00	0·714*	0·7*	0·51
HOY 1980				1·00	0·982**	0·785*
FI 1979					1·00	0·848**

c. Stay

Table I6 : Correlation coefficient (Spearman) matrix from inter – test comparison of ranked actor response probabilities.

* p< 0.05   ** p< 0.0I

		Actor	Response (%)			
		Attack	Escape	Stay	Chi^2	N
OLW	+	31	15	54	5·354	
	-	18	23	59	NS	169
BLW	+	21	14	65	1·947	
	-	22	21	57	NS	216
NB	+	13	30	57	11·314	
	-	28	14	58	**	138
NBL	+	11	33	56	6·859	
	-	22	20	57	*	221
NBT	+	27	12	62	3·896	
	-	21	22	57	NS	204
NfB	+	45	19	36	13·688	
	-	21	21	58	**	219
NbBpL	+	18	6	76	12·573	
	-	22	22	56	**	213

Table II : Noss I978 - Actor response probabilities
in the presence(+) and Absence (-)
of displays.

* $p < 0.05$ ** $p < 0.0I$ *** $p < 0.00I$

		Actor Response (%)				
		Attack	Escape	Stay	Chi^2	N
OLW	+	15	12	73	6·359	96
	–	11	26	64	*	149
BLW	+	21	0	79	25·62	19
	–	12	22	66	***	226
NB	+	13	23	64	0·37	47
	–	12	20	68	NS	198
NBL	+	13	13	74	2·269	15
	–	12	21	67	NS	230
NBT	+	6	31	63	5·074	16
	–	13	20	67	NS	229
NbBp	+	0	55	45	35·190	9
	–	13	19	68	***	236
NbBpL	+	0	38	62	19·610	13
	–	13	19	68	***	232
NfB	+	17	22	61	1·34	18
	–	12	20	68	NS	227
NS	+	0	50	50	29·67	12
	–	13	19	68	***	233

TableI2 : Hoy I979 – Actor response probabilities
In the presence (+) and absence(–)
of displays.

* $p < 0.05$ ** $p < 0.0I$ *** $p < 0.00I$

		Actor Response (%)				
		Attack	Escape	Stay	Chi^2	N
OLW	+	10	8	84	5·819	288
	-	14	18	68	NS	324
BLW	+	7	0	93	16·244	15
	-	12	13	75	***	597
NB	+	11	22	67	6·481	185
	-	12	9	79	*	427
NBL	+	22	9	69	4·731	45
	-	11	13	76	NS	567
NBT	+	22	22	56	9·923	37
	-	11	12	77	*	575
NbBp	+	0	0	100	25·852	5
	-	12	13	75	***	607
NbBpL	+	14	14	72	0·25	24
	-	12	13	75	NS	590
NfB	+	37	25	38	30·539	8
	-	11	13	76	***	604
NSW	+	14	14	72	0·252	7
	-	12	13	75	NS	605

Table I3: Hoy I980 - Actor response probabilities in the presence(+) and absence (-) of displays.

* $p<0.05$ ** $p < 0.0I$ ***$p < 0.00I$

		Actor Response (%)				
		Attack	Escape	Stay	Chi^2	N
OLW	+	9	8	83	11·799	327
	-	15	23	62	**	939
BLW	+	9	0	91	24·70	43
	-	13	20	66	***	1223
NB	+	21	25	54	7·99	344
	-	10	17	72	*	922
NBL	+	13	9	78	5·167	95
	-	13	20	68	NS	1171
NBT	+	41	12	47	20·027	17
	-	13	20	68	***	1249
NbBp	+	18	23	59	1·825	39
	-	13	19	68	NS	1227
NbBpL	+	9	13	78	3·046	54
	-	13	20	67	NS	1212
NfB	+	26	24	50	7·66	58
	-	13	19	68	*	1208
NS	+	4	20	76	6·259	141
	-	14	20	66	*	1125
BEND	+	9	9	82	6·401	11
	-	13	20	67	*	1255

Table I4 : Fair Isle I979 - Actor response probabilities in the presence(+) and absence (-) of displays.

* p < 0.05 ** p < 0.0I *** p < 0.00I

		Actor Response (%)				
		Attack	Escape	Stay	Chi^2	N
OLW	+	10	9	81	21·859	581
	-	32	18	50	**	776
BLW	+	11	11	78	6·191	35
	-	23	14	63	*	1322
NB	+	39	23	38	26·473	417
	-	15	11	74	***	940
NBL	+	27	7	66	3·489	145
	-	22	15	63	NS	1212
NBT	+	49	8	43	16·171	39
	-	22	15	63	***	1318
NbBp	+	38	25	38	12·950	8
	-	22	15	64	***	1349
NbBpL	+	16	10	74	3·134	51
	-	23	15	63	NS	1306
NfB	+	72	14	14	58·647	14
	-	22	14	64	***	1343
NS	+	0	30	70	29·186	51
	-	23	14	63	***	1306
NSW	+	0	25	75	27·146	16
	-	23	14	63	***	1341

Table I5: Fair Isle I980 – Actor response probabilities in the presence(+) and absence (-) of displays.

* $p < 0.05$ ** $p < 0.0I$ *** $p < 0.00I$

		HOY 1979	HOY 1980	NOSS 1978	FI 1979	FI 1980
OLW	A	+4	-4	+13	-22	-6
	E	-14	-10	-8	-9	-15
	S	+9	+14	-5	+31	+21
BLW	A	+9	-5	-1	-12	-4
	E	-22	-13	-7	-3	-20
	S	+13	+18	+8	+15	+24
NB	A	-1	-1	-15	+24	+11
	E	-3	+13	+16	+12	+8
	S	-4	-12	-1	-36	-18
NBL	A	+1	+11	-11	+5	0
	E	-8	-4	+13	-8	-11
	S	+7	-15	-1	+3	+12
NBT	A	-7	+11	+6	+17	+28
	E	+11	+10	-10	-7	-8
	S	-4	-21	+5	-21	-20
NbBp	A	-13	-12	--	+16	+5
	E	+19	-13	--	+10	+4
	S	-6	+25	--	-25	-9
NbBpl	A	-13	+2	-3	-7	-4
	E	+19	+1	-16	-5	-7
	S	-6	-3	+20	+11	+11
NfB	A	+5	+26	+24	+50	+13
	E	+2	+12	-2	0	+5
	S	-7	-38	-22	-50	-18
NS	A	-13	--	--	-23	-10
	E	+31	--	--	+16	0
	S	-18	--	--	-7	+10

Table I6: Colony by colony breakdown of the direction and size of the change in actor response probabilities in the presence and absence of displays.

\+ increase

\- decrease

	HOY 1979	HOY 1980	FI1979	FI1980
NOSS 1978	0·414	0·234	0·054	-0·035
HOY 1979	1·00	0·09	0·128	-0·108
HOY 1980		1·00	0·518	0·526
FI 1979			1·00	0·845**

a. Attack

	HOY 1979	HOY 1980	FI 1979	FI 1980
NOSS 1978	-0·357	0·321	0·286	0·428
HOY 1979	1·00	0·247	0·6*	0·371
HOY 1980		1·00	0·682*	0·263
FI 1979			1·00	0·716*

b. Escape

	HOY 1979	HOY 1980	FI 1979	FI 1980
NOSS 1978	0·126	0·450	0·136	0·360
HOY 1979	1·00	0·349	0·567	0·734*
HOY 1980		1·00	0·610	0·5
FI 1979			1·00	0·828*

c. Stay

Table I7 : Correlation coefficient (Spearman) matrix from inter - test comparison of ranked presence/absence probability differences. (from table)

* $p < 0.05$ **$p < 0.0I$

		NOSS 1978	HOY 1979	HOY 1980	FI 1979	FI 1980
OLW	A.	A/S 85	A/S 88	A/S 92	A/S 92	A/S 91
	R.	E/S 87	E/S 89	E/S 96	E/S 95	E/S 91
BLW	A.	A/S 86	A/S 100	A/S 100	A/S 100	A(E)/S 89
	R.	E/S 75	E/S 89	—	E/S 100	--
NB	A.	E/S 87	E/S 87	E/S 89	E/S 79	A/S 77
	R.	E/S 94	E/S 91	E/S 89	E/S 90	E/S 82
NBL	A.	E/S 89	A(E)/S 87	A/S 91	A/S 91	A/S 93
	R.	E/S 89	E/S 90	E/S 92	E/S 94	E/S 78
NBT	A.	A/S 89	E/S 94	A(E)/S 78	A/S 88	A/S 92
	R.	E/S 91	E/S 100	E/S 89	E/S 87	A/S 76
NbBp	A.	A/S 100	E/S 100	--	E/S 82	A/S 76
	R.	E/S 100	E/S 88	E/S 100	E/S 87	E/S 100
NbBpL	A.	A/S 94	E/S 100	A(E)/S 83	E/S 91	A/S 90
	R.	E/S 83	E/S 93	E/S 92	E/S 93	E/S 88
NfB	A.	A/S 81	E/S 83	A/S 75	A/S 76	A/S 86
	R.	A/S 83	E/S 86	--	A/S 79	--
NS	A.	--	E/S 100	--	E/S 96	E/S 100
	R.	—	E/S 100	—	E/S 99	E/S 97
NSW	A.	--	--	A(E)/S 86	--	E/S 100
	R.	--	--	E/S 100	--	E/S 100

Table I8: Response probability combinations (A/S - attack + stay; E/S - escape +stay) providing maximum response value.

	NOSS 1978	HOY 1979	HOY 1980	FI 1979	FI 1980
OLW	85	88	92	92	91
BLW	86	100	100	100	89
NB	70	77	78	75	77
NBL	67	87	91	91	93
NBT	89	69	78	88	92
NbBp	--	45	--	77	--
NbBpL	94	62	83	87	90
NfB	81	78	--	76	86
NS	--	--	--	80	7o

Actor Attack plus Stay Probabilities

	HOY 1979	HOY 1980	FI 1979	FI 1980
NOSS 1978	-0·392	-0·116	0·178	0·071
HOY 1979	1·00	0·811	0·619	0·035
HOY 1980		1·00	0·898*	0·029
FI 1979			1·00	0·429

Table 19: Correlation coefficient (Spearman) matrix from inter - test comparison of ranked actor attack + stay (see above) probabilities.

	NOSS 1978	HOY 1979	HOY 1980	FI 1979	FI 1980
OLW	69	85	90	91	90
BLW	79	79	93	91	89
NB	87	87	89	79	61
NBL	89	87	78	87	73
NBT	74	94	78	59	51
NbBp	--	--	--	82	--
NbBpL	82	100	83	91	84
NfB	55	83	--	74	82
NS	--	100	--	96	100

Actor Escape plus Stay Probabilities

	HOY 1979	HOY 1980	FI 1979	FI 1980
NOSS 1978	0·414	-0·492	0·185	0·143
HOY 1979	1·00	-0·812	0·209	0·192
HOY 1980		1·00	0·646	0·724
FI 1979			1·00	0·951**

Table 20 : Correlation coefficient (Spearman) matrix from inter - test comparison of ranked escape + stay (see above) probabilities.

Chapter 5

5.1.1. The Response of the Reactor.

That displays exert an adaptive benefit on the signaller, i.e. a display acts to elicit a response from the recipient that is, at least statistically, advantageous to the signaller, is central to a number of definitions of communication (e.g. Moynihan 1955, Brown 1975, Dawkins and Krebs 1978).

The methods employed so far have followed those used in studies investigating the emotional basis of agonistic communication. These studies (e.g. Moynihan 1955) have been concerned primarily with display causation. Causal influences constrained the form of displays through 'releasing' appropriate intention movements permitting the recipient to perceive the emotional state of the signaller. In this way causal and functional explanations were linked within the same framework. Working from the causal point of view attention has centred on displays and the signalling individual and has tended to shift attention from the important function of a signalling system - the ability of this system to influence a recipient (Marler 1961, Green and Marler 1979).

Before concluding that temporal association does not provide an insight into the communicative nature of displays one final test has to be applied. This involves comparing the varying levels of agonistic information suggested by temporal association to be conveyed by displays and the responses shown by the reactor. This approach is neither new nor has it been free of criticism.

This approach stems from applying semistic theory to the analysis of animal communication. In so doing Marler (1961) was one of the first to deal with the pragmatics of a system and to stress the importance of studying the effects of displays on a recipient. Ironically, criticism of this approach has stemmed from adopting a semiotic approach. Smith (1977) argued that tonic influences (Schleidt 1973) will undermine the value of this approach. He suggested that a display by one individual may not immediately alter the behaviour of a recipient but rather alter or prime a future response. For threat displays such influences should be minimal. Threat displays and their effects usually occur in close temporal proximity.

Since Marler first used this approach a number of authors have followed suit. In his study of the brown skua Burton (1968) compared the responses given by the reactor to various actor displays. On finding no significant difference between the responses shown by the reactor he concluded that the existence of a range of threat displays was superfluous *and* that responsiveness was poorly developed on the receiving side. This conclusion exemplifies the ethological distinction made between pressures moulding display development and those guiding responses to them (Blest 1964). This view would have been untenable if the recipient itself was considered as a source of selection pressure, a view which is becoming increasingly popular (e.g. Hanson 1979). In concluding in favour of these diplays forming a threat series Burton was heavily influenced by his expectation that a series existed because Moynihan's (1955) definition was fulfilled......the displays were 'reliably' followed by attack and escape. Further, the response sequelae for the displays differed. According to the actor/reactor comparison, though, one of the major pressures moulding and maintaining such a system did not appear to be doing so. The reactor did not make the distinction (on the basis of the response shown) between displays that would have been expected if the displays represented differences in threat quality. In the face of a contradiction between what the actor did and how the reactor responded Burton concluded in favour of what he expected to find, namely that the only plausible explanation for there being a variety of displays was that they represented differences in threat.

A number of other studies have used the response shown by the reactor to reinforce claims made about the information content of displays. Stokes (1962) and Andersson (1976) concluded that the displays of the blue tit and the bonxie, respectively, formed a threat series since the sequelae associated with each display differed. The extent of reactor escape responses was used to support their suggestion that information about attack was conveyed by displays and used by the recipient in guiding response. Of these studies only Andersson (1976) dealt with the matter statistically. No effort was made to determine the consistency of the association. Any inconsistencies that have appeared have largely been ignored. For example, rarely has it been the actor display associated with the highest attack probability that induces the highest reactor escape probability (Caryl 1979).

It now remains to be seen whether the reactor shows a response appropriate to the information assumed to be conveyed by the actor's display when the latter is determined using temporal association.

5.1.2. The relationship between actor and reactor behaviour

The response shown by the reactor on receipt of a display has often been used to support claims made concerning the information content of displays, particularly about attack information. In only one case has this comparison received statistical verification. Andersson (1976) found a positive and significant association between ranked actor attack probability and subsequent reactor escape probability. As a result he suggested that the probabilities associated with the actor's displays did provide a measure of the signaller's attack likelihood. Further, it was this information that was used by the recipient in guiding response. This result most clearly marks the contrast between the 'conflict' view suggesting transmission of a range of attack information (e.g. Cullen 1966) and the games theory view which suggests that variation in signaller intention should not be conveyed (e.g. Maynard Smith 1972).

The ensuing contradiction prompted Caryl's (1979) re-analysis. Caryl suggested that escape information was conveyed by displays. Support for this idea came from a number of sources. The most convincing was a significant and positive correlation between ranked actor escape probability and subsequent reactor attack probability. This correlation was obtained using the same data upon which Andersson (1976) claimed that attack information was conveyed. From the same set of date a choice is evident concerning the nature of the information conveyed.

Which one of these views is correct? Before this qeustion can be answered a number of methodological problems need to be ironed out. The most important of these concerns the manner in which the response probabilities are viewed. The probabilities calculated using temporal association represent a retrospective indicator of the relative frequency of each possible response (the number of responses being constrained by the observer). It is assumed that this level of activity mirrors the contribution of a tendency. If the probabilities are considered to indicate a level of information rather than a measure of activity the positive correlation found by Caryl is something of a paradox. The direction of this correlation means that signalling with a high escape probability increased the likelihood of the signaller being attacked. This state of affairs would appear to have little adaptive value. Dilger (1960) suggested that escape signals would be used to <u>prevent</u> attack.

A possible explanation lies in the manner in which Andersson (1976) calculated the reactor responses. The same data was used by Caryl (1979). The theoretical basis of Andersson's study suggested that attack information was important. He quite rightly excluded those occasions when a display was followed by overt attack in calculating reactor response to remove the possibility of this introducing a bias into the result. He did not exclude overt actor escape. Overt actor attack was excluded because it may have induced reactor escape. If the same logic is applied to the reactor it is possible that a sizeable proportion of actor escape resulted from the latter being overtly attacked by the reactor. This could have been responsible for the positive correlation found by Caryl - this arising as a result of overt behaviour shown by each interactant rather than from a more subtle transfer of information. If information transfer did take place it might be more appropriate to ask what type of information would be transmitted by the actors display to prompt attack from a recipient? Before the relative merits of the conclusions set out by Andersson (1976) and Caryl (1979) can be assessed overt interaction of this nature must be controlled. This could be done by measuring reactor response to displays when the actor stays after displaying. Reactor response could thus be assumed to be in response to the display alone.

When this has been done any remaining relationship between actor response probabilities and an appropriate reactor response would suggest that temporal association is a valid means of providing a quantitative measure of the information conveyed.

Before proceeding with this analysis one further question needs to be asked. How might we expect the behaviour of the interactants to be related? The definition of threat being adopted here is that the threat quality of a display would manifest itself as an appropriate change in the escape probability of the recipient. A high intensity threat leading to a high recipient escape probability, a low intensity threat producing a low recipient escape probability. If displays represented differences in signaller attack probability a positive correlation would be expected between displays ranked according to their attack probabilities and ranked recipient escape probabilities. A correlation of this nature was found by Andersson (1976).

Caryl's (1979) re-analysis raised the possibility of displays conveying serial escape differences on the basis of a relationship between actor escape and recipient attack. An 'escape" display should act to inhibit attack (Dilger 1960). A display indicating a high escape probability would be associated with an appropriately low attack probability in the recipient. Since temporal association provides a measure of actual behaviour this relationship is all the more likely. An inverse relationship would be expected between ranked actor escape and subsequent reactor attack.

Threat displays are being presumed, here, to function by permitting the signaller to gain an advantage over an opponent. As a result the threat definition being used is a measure of the escape probability of the recipient. In this case transmission of escape information in the signaller's display would be evidenced by an inverse correlation between actor escape probability and subsequent recipient escape. A high escape probability by the signaller being associated with a low escape probability by the recipient.

Both the above authors demonstrated a significant association to support their claim. Although, important, this is not sufficient evidence upon which to base a conclusion, a possibility which is made all the more difficult in view of the conflicting findings. Before accepting or rejecting these findings it is necessary to determine the consistency of each association.

Reactor responses were calculated for each display when the actor stayed after signalling. The attack, escape and stay probabilities for the reactor were calculated in this manner. Each of these responses were ranked. Comparison was made of each ranked actor response (from tables 3-7) with the ranked responses of the reactor. A Spearman ranked correlation coefficient (Siegel 1955) was used for the comparison. The results of these comparisons were calculated for each colony (tables 2I - 25).

5.1.3. Results.

In the results tables (2I - 25) the three columns on the left list the actor response probabilities (obtained from tables 3 - 7) determined using temporal association. The three columns to the right list the response probability shown by the reactor to each actor display when the actor stayed.

Noss 1978 (Table 2I)

1. Response to actor attack probability. Although positive the actor attack/reactor escape correlation is low and fails to reach significance.(table 2Ib). This result does not support the possibility that the reactor bases a response on varying levels of attack information gleaned from the actor's display.

2. Response to actor escape probability. Table 2Ib reveals a significant and negative correlation between ranked actor escape probability and ranked reactor attack. The greater the likelihood of actor esaape the less likely is the actor to be attacked. This supports the possibility of the recipient using information about varying levels of escape information in the actors display.

However, in terms of the threat criterion used here, where a threat display should produce an appropriate escape response from the recipient, the picture adopts a more complex appearance. Although failing to reach significance the actor escape/reactor escape correlation (table 2Ib) has a high value and is positive. The greater the likelihood of escape signalled by the actor the greater, also, is the reactors. Since the data from which this correlation is derived represents overt action on the part of each interactant the pattern suggests that both individuals exhibit an equal likelihood of fleeing in an interaction. This does not suggest any threat validity for displays since the signaller does not gain any advantage from his behaviour.

For Noss (1978) a number of contradictory lines of evidence prohibit any conclusion regarding the information conveyed by displays.

<u>Hoy 1979</u> (Table 22)

1. Response to actor attack. The actor attack/reactor escape correlation reaches significance but is in the wrong direction (table 22b). This inverse relationship suggests that the greater the likelihood of actor attack, the <u>less</u> likely is the reactor to escape. In threat terms this state of affairs has little adaptive value. The reactor is not using information about future actor attack probability to guide response.

2. Response to actor escape. The actor escape/reactor attack correlation is significant and in the expected direction (negative) (Table 22b). This supports the possible use of actor escape information by the reactor in guiding response.

Again, however, an anomaly appears when this question is addressed to the alternative correlation; that between actor escape/reactor escape. Though failing to reach significance the high and positive nature of this correlation (table 22b) is contrary to expectations if the level of escape information provided the display with its threat quality.

Once again the overall conflict in the pattern of correlations prohibits any firm conclusion.

Hoy 1980 (Table 23).

1. Response to actor attack. The actor attack/reactor escape correlation is low and negative (Table 23b). This pattern does not support the use of attack information by the reactor in guiding response.

2. Response to actor escape. The actor escape/reactor attack correlation is low and **positive** (table 23b). The pattern of this correlation is the opposite to what would be expected if actor escape information were used by the reactor in guiding response.

However, the actor escape/reactor escape is high and negative (table 23b). This provides limited support for displays having a threat quality by virtue of the transmission of varying levels of escape information.

Overall, the inconsistency in the patterns of the correlations does not permit any conclusion to be drawn.

Fair Isle (1979) (Table 24)

1. Response to actor attack. The actor attack/reactor escape is positive and, though failing to reach significance to reach significance (table 24b) provides very limited support for the reactor using information about actor attack likelihood as a guide to future response.

2. Response to actor escape. The actor escape/reactor attack correlation is both significant and positive (Table 24b). Caryl (1979) based his conclusion in favour of displays conveying escape

information on a correlation which followed this pattern. I previously suggested that a correlation of this nature may have resulted from overt behaviour shown by the interactants. A similar argument could not be used here since reactor response was recorded to each display when the actor stayed, ruling out such overt interaction. The situation becomes even more paradoxical when it is considered that, despite being attacked, the actor stayed. If a display conveyed escape information its expected effect would be to prevent attack (Dilger 1960). In this light the above pattern has little adaptive value and is difficult to reconcile if displays do indeed convey escape information.

Turning to the alternative threat definition no clearer picture is evident. The actor/reactor escape correlation is very low (table 24b).

Conflicting evidence prevents answering any question regarding the nature of the information conveyed by displays.

Fair Isle 1980 (Table 25)

1. Response to actor attack. The actor attack/reactor escape correlation is significant and in the direction expected if the threat quality of displays was attributable to their transmitting the varying likelihood of the signaller to attack. (Table 25b).

2. Response to actor escape. The actor escape/reactor attack correlation is low and positive (table 25b). For the same reasons outlined for Fair Isle (1979) this does not support the possible transmission of escape information.

The actor escape/reactor escape correlation just fails to reach significance and reveals the inverse relationship expected if a threat response was based on the reception of varying levels of escape information.

5.1.4. Discussion & Conclusion.

The most convincing support for displays acting in threat by conveying attack information comes from Andersson's (1976) finding of a positive and significant Actor attack/Reactor escape correlation in the bonxie. In the present study, relating these variables revealed only limited support for this possibility. Of five tests only two correlations reached significance.. For one of these (Fair Isle 1980, table 25) the positive correlation revealed supports the argument that the displays convey variation in the level of attack information and that it is subsequently used by the recipient in guiding response. However, although reaching significance the Hoy 1979 correlation (table 22) is negative - the opposite of what would be expected if displays derived their threat quality by virtue of transmitting attack information. This suggests that the greater the likelihood of attack the less likely the recipient is to escape.

Over five different test periods the ensuing picture does not accord with the result expected of a series conveying attack likelihood. The inefficiency with which these displays serve threat, with respect to conveying attack information, is further indicated in a more general comparison. Caryl (1979) pointed out that it was rarely the display having the highest attack probability that resulted in the highest recipient escape probability.

On Noss 1978 (table 2Ia) displays associated with both the highest and lowest actor attack probabilities (OLW and NB respectively) produce the same reactor escape probability. This finding is difficult to explain if response is based on receiving attack information.

On Hoy 1979 (table 22a) a rather paradoxical situation is evident where a display having a zero actor attack probability (NbBpL) results in the highest reactor escape probability and the display associated with the highest actor attack probability results in the least reactor escape probability (BLW). Hoy 1980 (table 23a) also reveals a situation where a display associated with the lowest actor attack probability (BLW) results in the highest reactor escape likelihood. It is interesting to note that over tho seasons on Hoy one display (BLW) is associated with both the highest and the lowest actor attack probabilities (tables 23a & 24a).

Fair Isle 1979/1980 tables 24a, 25a) also reveals a number of anomalies in the general patterns of relations between actor attack and reactor escape probabilities.

Where temporal association is used to quantify the information assumed to be conveyed by displays the evidence obtained from relating actor attack probabilities to the escape response shown by a recipient (tables 21 -25) is contrary to that expected if the information conveyed was constrained in this manner.

If displays maintain serial relations by virtue of a variation in the level of information conveyed Caryl (1979) suggested escape as an alternative. Evidence for this was sought by comparing Actor escape and Reactor attack probabilities. Appropriate evidence would take the form of an inverse relationship between these variables on the assumption that 'escape' displays function to prevent attack (Dilger 1960).

A supplementary definition was also adopted. This was built on the premise that threat displays will be used to gain access to a disputed resource and so permit the signaller to gain an advantage over an opponent. It is also assumed that in such disputes there can only be one winner. In this case it was considered appropriate evidence of displays deriving their threat effectiveness by conveying escape information through relating actor escape and reactor escape probabilities. A display signalling an intense threat would be one indicating a low subsequent escape likelihood. Evidence of displays acting in this way would be revealed as an inverse relationship between these two variables.

Firstly, what of the actor escape/reactor attack likelihood? Of the five tests (tables 2I -25), two reveal an inverse and three a positive relationship. Of the latter only one reaches significance (Fair Isle 1979, table 24b). Although a relationship of this nature was suggested by Caryl (1979) to support the transmission of escape information, the validity of this conclusion was questioned on the grounds that little adaptive value is conferred on an animal signalling in a manner likely to increase the probability that the animal will be attacked.

However, two tests (Noss 1978, table 2Ib ; Hoy 1979 table 22b) reveal a relationship of the type expected of a display signalling escape, i.e. the greater the likelihood of signaller escape the less likely that individual is to be attacked.

So, two tests reveal that relationship expected, the remaining three the opposite. This lack of consistency warrants against concluding in favour of displays acting in this manner.

The date in tables **21a-25a** reveals very low reactor attack probabilities. In each colony a sizeable proportion of displays do not **elecit** *any* attack from their recipient. The responses of the recipient were measured in response to a *staying* actor. If displays conveyed escape information this means that the actor, after signalling escape did not in fact do so. "Attack' displays were laid open to bluff since their recipient would be uncertain about future signaller intentions. Escape signals were considered to have greater evolutionary stability because bluff would be more easily detected (Caryl 1979, Maynard Smith 1979). If an individual signalled escape and did not subsequently do so its bluff would be called. There is a growing body of evidence that bluff is relatively easily detected and is immediately persecuted by real attack (e.g. Rohwer 1977, Rohwer and Rohwer 1978).

In the present situation the signaller stays after displaying. If the displays signal escape the actor, by staying is, in effect, bluffing. The low reactor attack probabilities suggests that such bluff is not punished. The lack of retaliation can be interpreted either by suggesting that the bonxie can be easily fooled or that escape information is not being conveyed.

Alternatively it could be argued on the basis of the above evidence that escape signals are being used simply to prevent attack. In suggesting this it is difficult to see the advantage of having a number of displays acting in this manner or what the nature of the resource might be that would permit the loser to remain. Adopting the former line of thought there is no evidence to suggest that any one display is particularly good at inhibiting attack. From tables 2Ia-25a it is evident that the display associated with the highest actor escape probability is often that producing the least reactor attack probability, i.e. it serves to inhibit attack. It is equally true that displays associated with only half that escape probability are equally effective in preventing attack.

Where a relationship between Actor escape and reactor attack is sought it is logical to assume that the displays serve to prevent attack. From this point of view, though, an explanation for the existence of either a single display or the range of displays is not forthcoming. An alternative suggestion would be that the displays serve to gain an advantage over an opponent. To determine whether such a mechanism is in existence an alternative relationship between the interactants must be sought.

Evidence for displays acting in this way would be gleaned from an inverse relationship between Actor escape and Reactor escape probabilities.

No clear pattern was evident. Of the five tests one (Fair Isle 1979, table 24b) reveals an almost random association between these variables. Two (Hoy 1980, table 23b ; Fair Isle 1980 table 25b) indicate a relatively high inverse relationship that provides a measure of support for displays acting in threat via transmitting escape information, i.e. the greater the escape likelihood signalled the less likely the recipient is to escape. In such a series a display with a low escape probability has a high threat quality.

However, the remaining two tests suggest the opposite. Both Noss 1978 (table 2Ib) and Hoy 1979 (table 22b) reveal a positive association between the relevant variables. In effect, the greater the escape likelihood signalled the greater is the likelihood that the recipient will also escape.

In all four of these tests irrespective of the direction of the correlations they are all of a breadly similar magnitude. Thus the evidence for the transmission of escape information is equally divided between relationships supporting and those opposing the possible transmission of varying levels of escape information in a manner serving to gain an advantage over an opponent

5.1.5 Analytical Problems

The present analysis was concerned with testing two contrary propositions. One suggested that displays derived their threat effectiveness from their ability to transmit variation in attack likelihood (e.g. Andersson 1976). The other suggested that effect came from transmission of escape information (e.g. Caryl 1979). Both assumed that the level of information could be determined by temporal association. Threat is about the ability of one individual to gain an advantage over another through display. The acid test for threat efficiency is to determine the extent to which the information conveyed (in the present case this is constrained by the use of temporal assooiation) can influence the recipient to respond in a manner adaptively favourable to the signaller.

When actor and reactor responses were compared the inconsistency in the pattern of response association, irrespective of the information dimension considered, does not warrant concluding that displays convey differences in intention in a manner that is species specific. This conclusion is in accord with games theory predictions that displays should not convey intentions.

The conclusions of a number of existing studies were based on relationships obtained in the above manner. The date upon which these conclusions were based were generally gathered from a single season andffew attempts were made to test the consistency of the result. Where inconsistencies were revealed these have generally been ignored (e.g. Burton 1968). In the present study a significant level of support for each proposition could be drawn from isolated tests but when the general consistency of the data were tested via comparison of data gathered over different years and in different colonies the only conclusion possible was that, within the limits imposed by the method, neither propostion provided a reliable indicator of display function.

For future studies an important area of convern will be in determining the consistency of a result. A conclusions based on an isolated test will have only limited value.

It should be borne in mind that the above conclusion is based on the assumption that the probabilities upon which the analysis was based reflect the level and nature of the information conveyed by displays. If temporal association does not provide a quantitative measure of information content then the above conclusion will need qualification At this peint it is appropriate to reflect on the validity of temporal association as a mechanism to explain the manner in which information is constrained.

The value of temporal association as an analytical tool in the study of agonistic behaviour depends on; 1) identifying the tendencies contributing to a display, 2) that the extent of the overt association between tendency and display mirrors the causal and functional contribution of a display to the series, 3) using appropriate behavioural measures to detect the influence of a given tendency. An inadequacy in any of these areas will hinder detection of information.

The concept of a 'tendency' is vague. In the study of social behaviour two tendencies have enjoyed universal popularity; attack and escape. A variety of other tendencies have also been used. Crook (1964) employed a social and an advertising tendency. Andersson (1976) employed a grass-throwing tendency. The choice of tendency has tended to mirror observer preconception and the choice of overt behaviour has been limited.to what was available and which could be ascribed a recognisable function fairly easily. Serial relations of the type suggested in the conflict literature between actor displays would not be expected to appear until each contributing tendency had been identified and its influence considered. The probabilities are a relative measure and so are dependent upon the number of tendencies involved. If all contributing tendencies are not identified then it is unlikely that consistent serial relations would be evident.

In this respect the neglect of a sexual tendency could have serious implication for a study based on temporal association and how responses could arise in particular. In an attempt to limit a confounding influence on response those occasions where a display was followed by overt sexual behaviour were excluded from the data used to calculate the attack/escape/stay probabilities. Not all sexual approaches are successful (Perdeck 1960). In some interactions displays influenced by a sexual tendency will not be followed by an action that would identify it to the observer as such. A confounding sexual influence on response cannot be eliminated.

If all displays were the result of a conflict between the same incompatible tendencies neglect of one, e.g. the sexual tendency might not pose too serious a problem since the same relative levels of sexual influence is being exerted on the displays each time they occur. But is it the case that all displays share the same causal factors? In the bonxie this is doubtful. In the analysis of display sexual relations (table 2) it was found that, in the club, overt sexual behaviour had a limited association with one display group, the Uprights. Within the limited categorizing mechanism used here the Uprights could be said to result from varying levels of attack/escape/stay/sex conflict. In contrast, the long-call complex (OLW, BLW) and the neck short complex (NS,NSW) resulted from only an attack/escape/stay conflict. With the predominance of attack/escape it is relatively easy to ascribe threat relations to the latter groups. The addition of a sexual tendency to the former group raised a conceptual problem in ascribing any straightforward functional relations. This difference raises the question of whether all the bonxie displays can all be considered together. Bonxie displays may not be functionally homogeneous.

Until the manner in which tendencies interact to produce a given display (and thus the information conveyed) can be specified temporal association will have only a limited value for describing the information potentially available from displays.

In the light of these criticisms the previous failure to find an association between actor displays and the response shown by the reactor may have been due not to the inability of displays to convey serial threat differences but to the inability of the method to detect these differences in the actors display. Heterogenous influences on the responses shown by the actor will disrupt the appearance of the expected relations between actor and reactor behaviour. For example, no attempt was made to determine the number of tendencies contributing to displays. The limited association of a sexual tendency to the upright group was not taken into consideration. These omissions introduce an influence which is difficult to eliminate. Further, they are likely to have prevented the method from revealing display information content. As a result the earlier conclusion that displays do not convey intentional differences must be viewed with caution. Further analysis is needed to determine whether intentional differences exist. Attacking the problem from a different perspective may surmount the above problems.

If differences in threat are transmitted by displays then, irrespective of the causal mechanism producing these differences or the range of information that a display might potentially transmit, evidence for displays conveying intentional differences might come from determining whether the range of responses shown by the recipient are appropriate. The problem in the previous approach is that two components of the threat system were being investigated simultaneously. The information assumed conveyed was given priority, the response shown by the recipient was considered secondary (Burton 1968 in particular). There has been a shift from the functional aspect of communication of prime importance ; the ability of a signal to influence its recipient, to one concerned with the nature of the information conveyed. The conceptual problems involved in defining the latter restrict this approach. It is important for a study of animal communication to concern itself firstly with determining whether a recipient responds consistently to a given behaviour. Only after this has been done can the behaviour be ascribed with having a signal function. A functional analysis can then be expanded to investigate the nature of the information conveyed.

With this basic approach the first problem to be surmounted concerns defining the type of response to be investigated. The present study is concerned with determining whether displays serve a threat function and, in particular, whether a threat series exists to convey differences in intentional information. How would the recipient be expected to respond on receiving a threat? Marler (1961) suggested that a threat display be defined as one which would produce a change in the escape probability of the recipient. This definition will be used here. Differences in the level of threat conveyed by displays would produce appropriate differences in the escape probability of their recipient.

5.1.6 The Response shown by the Reactor.

If displays differ in threat quality then irrespective of the causal mechanisms underlying the differences or the range of information they may contain, differences in threat would manifest themselves as a consistent serial relationship between displays measured as the escape probability induced in the recipient.

For this analysis the response of the recipient was assessed independently of the response probabilities (and thus the assumptions about information conveyed) associated with the use of the display when given by the signaller. Response was measured for those situations where the signaller stays. Response could then be assumed to be in response to the display alone, eliminating any possible influence of overt signaller behaviour.

There are a number of ways in which the consistency of the response shown can be tested.

5.1.7. The Actor and Reactor.

The most basic comparison is one between the actor and reactor within each test period. To facilitate this comparison the actor and reactor were treated independently. Response probabilities were calculated for the Reactor when receiving displays for a staying actor. Response probabilities were also calculated for the Actor when receiving a display from a staying reactor. In this way response on reception was calculated for two distinct classes of interactant. As before three responses were scored; attack, escape and stay. The response probabilities are the relative frequency of each response.

Of central interest here is the escape response shown by the recipient of a display, whether the actor or reactor.

For analysis the response probabilities were ranked. The ranked probabilities for each response were then compared, the data being obtained from within each test period. The extent of the statistical association between ranked actor/reactor responses were determined using a Spearman Ranked Correlation co-efficient (Siegel 1956). If the displays of the bonxie form a threat series then, from the point of view of recipient response, the series would manifest itself as a positive correlation between the responses shown by the recipient. The results of the comparison in the four tests for which sufficient data was available are given in table 26 &27.

For both 'attack' and 'stay' there is no supporting evidence to suggest the existence of serial threat relations. The correlations are low and two are negative.

Of the three responses permitted by the method the escape response is the one most likely to reveal that displays fulfil a threat function. It is this response that provides the most direct indication that the signaller is gaining an advantage over the recipient.

For tables 26&27 it is evident that only the Fair Isle 1979 comparison reveals a significant and positive association. However, the remaining correlations are all high and are in the expected direction. Only a small sample was available for analysis, primarily due to the relative infrequence of reactor displaying. This hinders reaching a firm conclusion. The distinct underlying trend suggests that further examination of a possible serial display function is warranted.

5.8.8. Reactor Comparison.

Further investigation necessitates a different approach.

A broader comparison is facilitated by comparing the ranked responses of the reactor on receiving a display given by a staying actor. This was done, in the first instance, within each colony over consecutive seasons. A Spearman correlation was used for the comparison.

If displays act by conveying serial threat differences this would manifest itself in the present analysis as significant and positive correlations between the ranked responses over successive seasons. The response probabilities listed in tables are those of the recipient of a display.

Hoy 1979/1980 (table 28) Reactor responses from tables 22/23

For all three possible responses no comparison yields a significant result. For the response of greatest relevance for detecting threat function, escape, the correlation is negative. A display which induced a high escape probability one year tended to produce a low probability the following year. This is the opposite of what would be expected and so does not support the possibility that bonxie displays form a threat series.

Fair Isle 1979/1980 (table 28) Reactor responses from table 24/25

In contrast to the above finding a similar comparison on Fair Isle revealed significant and positive correlations for all three responses. In view of the low probabilities and the high number of ties associated with attack the signficant result here is of limited consequentce. The significant and positive association between the escape responses over the two years supports the possibility of displays representing a threat series in the eyess of the recipient.

In the latter comparison the displays fulfil the most important functional criterion necessary to consider the displays as forming a threat series, i.e. they consistently influence the recipient in an appropriate manner. However, the force of this conclusion must be tempered by the failure to find this consistency in both colonies. The Hoy correlation (table 28) does not even suggest a trend in the inter-year relationship. In view of this it is not possible to conclude in favour of the displays forming a threat series. The available evidence does warrant further investigation.

To this end there remains one further means of comparison. The responses shown by the reactor on receipt of a display from a staying actor were ranked and a comparison between colonies was carried out. The correlations were calculated using a Spearman correlation co-efficient. The co-efficients are presented in table 28 . These were presented in this form to account for differences in the number of displays used in each colony for the comparisons.

(a) Escape (table 28b). Reactor responses from tables 2I-25

When a general comparison of this nature is made support for the view that display maintain serial threat relations, by virtue of their ability to induce appropriate differences in the escape probabilities of the recipient, diminishes. Only one correlation reaches significance in the appropriate directions (Fair Isle 1979/ 1980). Since this result is from a single colony there is no evidence to support the existence of a between-colony association. This conclusion is re-inforced by the finding that half the correlations are negative and two of these only just fail to reach significance (Noss 1978/ Hoy 1979 and Hoy 1980/Fair Isle 1980).

The low value of the majority of the correlations and the high proportion of negative correlations reveals an overall picture that is contrary to what would be expected if the displays of the bonxie formed a species-specific threat series.

(b) Attack (table 28a). Reactor responses from tables 2I-25

Displays were ranked according to the probability that they induce attack from a recipient. Such a situation might arise if displays were used to convey escape in a manner serving to prevent the signaller being attacked. In looking for a relationship between induced attack a similar picture to that revealed for escape is evident. Of the inter-colony correlations almost half are negative. Three of these only just fail to reach significance. On the basis of this finding bonxie displays do not form a species-specific series acting to influence the attack responses of the recipient.

5.1.9. Discussion.

Three levels of comparison have been used here. There has been a decrease in the extent of the association as the number of variables embraced by the comparison increases. A relatively high degree of consistency is revealed when comparison takes place within a single season (tables 26&27). This descends to a situation where no consistency is present when the comparison is carried out between different colonies. (Table 28)

In the latter case the prevailing low level of correlations and the high proportion of negative correlations, irrespective of the response given, suggests that these displays do not form a general species-specific code. Overall the bonxie does not respond to displays in a manner consistent enough to permit ascribing a signal function to displays.

However, within a single colony during each season there is a strong underlying trend suggesting that displays form a series. The co-efficients in tables 26 & 27 are all high and in the appropriate direction although only one reaches significance. Failure to reach significance may have resulted from the observer's failure to account for all the variables impinging on the response shown. For example, no provision was made to account for the display adopted by the recipient and how this may influence response.

The Fair Isle studies were carried out during the latter half of the season so it is feasible that a display code could have developed during the earlier part of the season. This would account for the consistency of response to the displays. A similar argument could not be used on Hoy. The study here took place during the early part of the season while the non-breeding birds were returning from their migration. There would be no time to develop a code. Club birds spend, on average, two to three years in the club (Furness 1977). A colony specific code could develop and be transmitted culturally from year to year with new arrivals learning the code from birds already present. Support for the suggestion that the codes are culturally transmitted diminishes with the finding that there is very poor inter-colony consistency. The bonxie does not appear to have a species specific and innate display code. If this suggestion holds true then, in addition to the high actor/reactor consistency there should be a relatively high correlation within a colony over consecutive seasons.

Fair Isle shows this consistency both within (table 27) and between (table 28) seasons fairly dlearly. Hoy does not. Between 1979/1980 there is no consistency in response (table 28). No explanation for Hoy's single season consistency (tables 26) is readily available. A more extensive comparison involving marked individuals and over a greater number of seasons may prove illuminating.

The failure of the Hoy data to reveal the consistency evidence on Fair Isle may be due to the small sample sizes in the former colony. The consistency shown on Fair Isle (tables 27 & 28), with its higher display and observation totals suggests that the question of inter-colony threat display effectiveness warrants more detailed analysis. If displays tend to be colony-specific and culturally transmitted rather than species-specific with an innate threat code an interesting question regarding the nature of the information conveyed and the manner of its transmission is raised.

	ACTOR			REACTOR Response		
	A	E	S	A	E	S
OLW	31	15	54	0	70	30
BLW	21	14	65	0	77	23
NB	13	30	57	0	70	30
NBT	27	12	62	13	69	18
NbBpL	18	6	76	15	31	54

a.

		REACTOR		
		A	E	S
	A	−0·112	0·102	−0·41
ACTOR	E	−0·894*	0·667	−0·051
	S	0·671	−0·359	0·154

b.

Table 2I: Noss I978

a. Actor response probabilities and subsequent reactor response on receipt of each display given by a staying actor.

b. Correlation coefficient (Spearman) matrix from comparison of ranked actor and reactor probabilities. (from a.).

* $p < 0.05$ ** $p < 0.0I$

	ACTOR			REACTOR Response		
	A	E	S	A	E	S
OLW	16	13	71	1	58	41
BLW	21	0	79	7	20	73
NB	13	23	64	6	64	30
NBL	13	13	74	10	60	30
NBT	6	31	63	0	50	50
NbBpL	0	38	62	0	88	12
NfB	17	22	61	0	50	50

a.

		REACTOR		
		A	E	S
	A	0·374	-0·709*	0·705*
ACTOR	E	-0·724*	0·563	-0·523
	S	0·889*	-0·252	0·218

b.

Table 22: Hoy I979

a. Actor response probabilities and subsequent reactor response on receipt of each display given by a staying actor.

b. Correlation coefficient (Spearman) matrix from comparison of ranked actor and reactor probabilities. (from a.).

* $p < 0.05$ **$p < 0.0I$

	ACTOR			REACTOR Response		
	A	E	S	A	E	S
OLW	10	6	84	0	43	57
BLW	7	0	93	0	57	43
NB	11	22	67	5	42	53
NBL	22	9	69	4	48	48
NBT	22	22	56	0	43	57
NbBpL	14	14	72	6	50	44

a.

		REACTOR		
		A	E	S
ACTOR	A	0·191	−0·221	0·406
	E	0·338	−0·662	0·551
	S	−0·116	0·667	−0·567

b.

Table 23: Hoy I980

a. Actor response probabilities and subsequent reactor response on receipt of each display given by a staying actor.

b. Correlation coefficient (Spearman) matrix from comparison of ranked actor and reactor probabilities. (from a.)

* $p < 0.05$ ** $p < 0.0I$

	ACTOR			REACTOR Response		
	A	E	S	A	E	S
OLW	9	8	83	1	45	54
BLW	9	0	91	0	51	49
NB	21	25	54	3	52	45
NBL	13	9	78	1	54	45
NBT	41	12	47	0	38	62
NbBp	18	23	59	13	34	53
NbBpL	9	13	78	0	40	60
NfB	26	24	50	4	65	31
NS	4	20	76	1	12	87

a.

Table24: a. Actor response probabilities and subsequent reactor response on receipt of each display given by a staying actor.

		REACTOR		
		A	E	S
	A	0·342	0·367	-0·435
ACTOR	E	$0{\cdot}69^{*}$	0·033	-0·251
	S	-0·345	0·067	0·016

b.

Table 24 : Fair Isle I979

b. Correlation coefficient (Spearman) matrix from comparison of ranked actor and reactor probabilities. (from a.)

* $p < 0.05$ ** $p < 0.0I$

	ACTOR			REACTOR Response		
	A	E	S	A	E	S
OLW	10	9	81	1	52	47
BLW	11	11	78	0	48	52
NB	39	23	38	3	58	39
NBL	27	7	66	1	56	43
NBT	49	8	43	0	53	47
NbBpL	16	10	74	0	32	68
NS	0	30	70	3	3	94
NSW	0	25	75	0	17	83

a.

		REACTOR		
		A	E	S
ACTOR	A	-0·065	0·826*	-0·698
	E	0·257	-0·619	0·491
	S	-0·360	-0·523	0·359

b.

Table 25: Fair Isle I980

a. Actor response probabilities and subsequent reactor response on receiptof each display given by a staying actor.

b. Correlation coefficient (Spearman) matrix from comparison of ranked actor and reactor probabilities. (from a.).

* $p < 0.05$ ** $p < 0.0I$

	Actor Stay/Reactor Response			Reactor Stay/Actor Response		
	Att.	Esc.	Stay	Att.	Esc.	Stay
OLW	1	58	41	0	41	59
NB	6	64	30	0	50	50
NBT	0	50	50	0	30	70
NbBp	0	88	12	0	33	67
BLW	7	20	73	27	9	64

		Reactor		
		A	E	S
	A	0·725		
Actor	E		0·76	
	S			0·2

a. Hoy 1979

	Actor Stay/Reactor Response			Reactor Stay/Actor Response		
	Att.	Esc.	Stay	Att.	Esc.	Stay
OLW	1	43	56	1	26	73
NB	5	42	53	3	22	75
NBL	4	48	48	11	39	50
NbBpL	6	50	44	0	36	64

		Reactor		
		A	E	S
	A	– 0·4		
Actor	E		0·812	
	S			–0·4

b. Hoy 1980

	Actor Stay/Reactor Response			Reactor Stay/Actor Response		
	Att.	Esc.	Stay	Att.	Esc.	Stay
OLW	1	52	47	4	31	65
NB	3	58	39	3	39	58
NBL	1	56	43	6	36	58
NBT	0	53	47	0	44	56
NbBpL	0	32	68	0	35	65
NS	3	3	94	0	0	100

		Reactor		
		A	E	S
	A	0·254		
Actor	E		0·77	
	S			0·701

a. Fair Isle 1980

	Actor stay/Reactor Response			Reactor Stay/Actor Response		
	Att.	Esc.	Stay	Att.	Esc.	Stay
OLW	1	45	54	2	42	56
NB	3	52	45	6	28	66
NBL	1	54	45	7	45	48
NbBp	13	34	53	0	18	82
NbBpL	0	40	60	0	22	78
NS	1	12	87	3	21	76

		Reactor		
		A	E	S
	A	0·061		
Actor	E		0·885 *	
	S			0·371

b. Fair Isle 1979

	NOSS 1978	HOY 1979	HOY 1980	FI 1979	FI 1980
NOSS 1972		-0·8		0·657	
NOSS 1978	1·00	-0·86	0·344	-0·335	-0·625
HOY 1979		1·00	-0·102	-0·019	0·438
HOY 1980			1·00	0·370	0·158
FI 1979				1·00	0·938*

a. ATTACK

	NOSS 1978	HOY 1979	HOY 1980	FI 1979	FI 1980
NOSS 1972		-0·8		0·485	
NOSS 1978	1·00	-0·447	0·131	0·782	0·205
HOY 1979		1·00	-0·231	-0·072	0·085
HOY 1980			1·00	-0·085	-0·8
FI 1979				1·00	0·75*

b. ESCAPE

	NOSS 1978	HOY 1979	HOY 1980	FI 1979	FI 1980
NOSS 1972		0·2		-0·257	
NOSS 1979	1·00	-0·899	-0·359	-0·3	0·289
HOY 1979		1·00	0·115	0·054	0·028
HOY 1980			1·00	0·371	-0·6
FI 1979				1·00	0·78*

c. STAY

Table 28: Correlation coefficient (Spearman) matrix from inter - test comparison of ranked reactor response on receipt of displays given by a staying actor.

* $p < 0.05$ ** $p < 0.0I$.

Chapter Six

6.1.1. Interaction

The principle criticism that can be levelled against the conflict model as it has been applied here concerns the extent to which the test situation provides the necessary stationarity. Although bonxie interactions are of short duration and involve only limited display use (with respect to the number of displays used per interaction), the fact that individuals may act in concert constitutes an important source of non-stationarity and so may influence the responses shown. Such influence will be particularly disruptive where the response shown is considered to provide an indication of information conveyed - the approach which forms the basis of temporal association.

The ensuing interaction could take two forms. Firstly, an overt action e.g. attack or walking towards, could influence opponent response over and above that of the accompanying display. For this reason the response of recipients in chapter five were calculated for 'staying' signallers, eliminating any overt influence on response. The second influence concerns the display adopted by an opponent.

In studies using temporal association few attempts have been made to control this more overt form of interaction, either because of the short duration of interactions (Stokes 1962a) or because reactor display was infrequent (Andersson 1976). However, Bossemma and Burglar (1980) demonstrated that even in interactions of very short duration the actions of the actor were not independent of the display or actions of the reactor. Time is a variable which must be considered irrespective of its relative duration in our eyes. Although many bonxie interactions are settled without reactor display, the latter does occur.

The possible disruptive influence of interaction has not gone unnoticed in 'conflict' studies. Using temporal association the magnitude of a probability has been thought an important aid in revealing information content. The low attack probabilities prevailing with the use of this method has fostered concern. Dunham (1966) suggested that this could have arisen, in part, to the unknown influence of the reactors motivational state, though he follows Stokes (1962a) in concluding that displays provide a general indicator of actor intent. The influence of the opponents motivational state is an area in which theoretical interest has recently been rekindled.

Hinde (1981) reasserts the premise originally underlying the conflict theory. Displays are the result of a state of conflict arising when no clear course of action is open to the signaller. He suggests that this hesitance is due primarily to an uncertainty about the opponents motivational state. By displaying, the actor uses his signal to prompt an opponent either to respond overtly or to reveal his intentions by the use of an appropriate display. The relative magnitude of the respective displays provides the mechanism whereby the dispute is resolved. It is assumed that the individual displaying with the less intense variant would move off. Hence a response by the actor will be a function not only of his signal but also of the display adopted by the opponent. Recording the responses of one individual in isolation from the display or actions of the opponent will provide a misleading impression of possible information content. In this light the failure to find consistency in Chapter four is hardly surprising.

It was the use of displays as prompts representing intentional differences that led to Maynard Smith's (1974) criticisms. Where an individual signals he is revealing uncertainty. What is to stop an opponent either attacking or bluffing by signalling with a display of higher intensity? This problem was seen in the light of a 'conflict' approach by Orians and Christman (1968) though they offered no solution. In such a situation a single display indicating 'I am in dispute' as suggested by Caryl (1979) would be sufficient to prompt a response from an opponent and would be less open to bluff (Maynard Smith 1979).

Before the predictions of the conflict model can be accepted or rejected it will be necessary to determine how interaction influences outcome. It is in this respect that clash between the games and conflict models is most readily apparant. If, after controlling for interaction, there is no evidence for displays forming a series then the explanatory power of the conflict model would be severly limited and the way would be open to investigate alternative models.

6.1.2. A stationary test situation.

One of thepprinciple problems encountered in studying displays concerns the difficulty of finding a standard or baseline against which to assess their effect. If was in response to this problem that work was carried out using models. The latter approach raises problems and has often been criticised for its failure to mirror the complexity of real interactions. Where displays comprise distinct morphological features it is often possible to alter this feature and assess its relevance as a signal component in live individuals (e.g. Marler 1956, Peek 1972). Where a display does not permit such cosmetic alteration the problem remains.

Blurton-Jones (1968) suggested that displays could be studied only where the opponent does not display. Care should be taken if this approach is adopted. Even such nil-responses can be influential (Hazlett and Bossert 1965). Alternatively a nil response may indicate an unwillingness to engage in dispute and even if signals differ in intensity they all may have an equal likelihood of eliciting the response following a lack of display.

Where both individuals display a standard situation could be provided by holding the display of one interactant constant and recording the extent of the response shown by this individual to the various displays adopted by an opponent. For example, hold OLW constant and record the responses given when the opponent adopts OLW, NB, NBL etc.

By framing the analysis in these terms it is easy to see the inadquacies of the earlier approach which assumed that each display wouldhave only one set of specific response probabilities. Applied to the present situation the logic of the conflict theory dictates that a given display will have a set of response probabilities specific to <u>each</u> display that an opponent may give i.e. to each of the displays comprising the repertoire. For example, if OLW is adopted then a specific set of response probabilities will exist for the state of affairs dictated by use of NB by an opponent but these will be different from the response probabilities dictated by an opponent adopting NS.

Using this method a set of specific responseeprobabilities will be revealed for each standard situation, the latter being defined in terms of the actor display held constant. If the displays form a series then the extent of the responses shown to each display should be consistent. Each display should elicit a response which bears a consistent relative relationship to every other display in the repertoire. In no way can these probabilities be considered to reveal the absolute level of information conveyed but rather they will provide a measure of relative threat efficiency.

The manner in which the responses are scored is important. To facilitate comparison with the earlier methods attack, escape and stay responses were scored. The actor display was held constant. Attack was scored irrespective of the action taken by the reactor though most commonly the latter escaped. Where the actor escaped or stayed such responses were only scored when the Reactor stayed after displaying to ensure that the response shown by the actor was to the display alone.

Since the actor display was held constant we are, in effect, looking at the actor as the recipient of a variety of displays. From the point of view of determining threat relations the response of greatest relevance is escape. On receipt of displays varying in threat intensity a display having a high threat intensity would produce a high escape probability and a display having a low threat intensity, a low escape probability. Attention is still centred on one functional aspect, namely, the ability of displays to consistently elicit a response. In this

rein attack

vein attack responses were also studied. The ability of displays to consistently elicit either of these overt responses may provide a starting point to investigate another functional compnennt, the information conveyed.

The attack and escape probabilities were treated separately. The probabilities were ranked and a Spearman rank correlation co-efficient (Siegel 1956) was used to determine the consistency of seriel relations both within and between colonies.

6.1.3. Results.

a) OLW

1) Attack.

A comparison of ranked attack probabilities was made on Fair Isle from data gathered in 1979 and 1980. Table 29a reveals that no significant association was evident. The lack of consistency in the relative order in which displays elicited attack is further evident when comparison is extended to cover Hoy and Fair Isle.

Table 29a reveals that the Hoy 1980/Fair Isle 1980 correlation has a very low value. More damaging evidence comes from the Hoy 1980/Fair Isle 1979 comparison. Here the correlation is negative, the opposite of what would be expected (table 29a). Hence a display likely to elicit a relatively high attack response in one colony is more likely to achieve the opposite in another.

The stationary situation here comprised the actor adopting OLW. The attack probability likely on receipt of a number of displays was measured. The results (table 29a) provide no support for the possibility that displays act in a serial threat manner by virtue of their eliciting consistent but varying levels of attack.

2) Escape

From the point of view of determining a threat function for displays more direct evidence of such a system will come from looking at the ability of displays to consistently elicit escape in a recipient. Actor escape was only scored when the reactor stayed after displaying to ensure that escape was elicited in response to the display alone. If a threat series did exist a positive correlation would be expected between displays ranked according to the magnitude of the escape response they elicited.

A similar picture to that revealed for attack is evident. Comparing data gathered on Fair Isle over 1979/1980 reveals the correlation to have a low value (table 29b). The results of the inter-colony comparison are mixed. While that for Hoy 1980/ Fair Isle 1980 (table 29b) is low, that between Hoy 1980/Fair Isle 1979 only just fails to reach significance.

Despite this latter result the overall picture ensuing from a comparison of ranked escape probabilities does not conform to the pattern expected if displays formed a threat series.

Where stationarity is provided by the actor constantly displaying with OLW it would appear that the earlier failure to find serial consistency between bonxie displays cannot be attributed to the disruptive influence of interaction.

There also proved to be sufficient data to test one other display in this manner, NB.

b. NB

1) Attack

Comparison of displays ranked according to the extent to which they elicit attack on Fair Isle over 1979/1980 fails to reveal a significant association between displays (Table 30a).

However, extension of this comparison between Hoy and Fair Isle does support the possibility of serial relations between displays (table 30a). In both the Hoy 1980/Fair Isle 1979 and Hoy 1980/ Fair Isle 1980 comparisons, a significant and positive association between displays ranked according to their ability to elicit attack is revealed. This raises the possibility that the displays of the bonxie act as a series by virtue of the transmission of information which elicits varying levels of attack from an opponent. Evidence that displays elicited attack prompted Caryl (1979) to suggest that displays conveyed information about signaller escape likelihood.

2) Escape

It is assumed that a more accurate measure of threat quality would be revealed by the ability of displays to consistently elicit escape.

Comparison of ranked escape probabilities on Fair Isle over 1979/1980 (table 30b) fails to reveal the pattern expected and the co-efficient is low. The inter-colony results are again mixed. Between Hoy 1980/Fair Isle 1980 (table 30b) a low co-efficient is evident. Between Hoy 1980/Fair Isle 1979, though the co-efficient only just fails to reach significance.

Overall the evidence does not support the possibility of the displays of the bonxie forming a threat series, nor does it suggest that the previous failure to reveal consistent escape responses was due to a failure to consider interaction.

6.1.4. Discussion.

Before considering the implications of this result two criticisms must be discussed. Firstly, the sample sizes were small. Sufficient data was available to test only two displays in this manner. Further, the number of observations from which the probabilities were calculated were, with the exception of OLW, NB and NN, very small (table 31). This state of affairs may in itself be informative. Threat was defined via an association of displays and overt attack and escape. The predominance of OLW and NB revealed by this association perhaps suggests that these displays may fulfil an agonistic function but the remaining displays comprising the repertoire do not.

A second note of caution is prompted by the relatively higher level of consistent association with attack revealed for NB (table 30a). Following the previous arguement it might be suggested that only NB is worthy of being labelled a threat. However, a closer examination of the data used to furnish these correlations suggests an alternative explanation. It was only the inter-colony comparisons that yielded significant results. The distribution of attack responses on Hoy 1980 (table 30a) is very limited and only two displays actually elicited attack. Hence there were a large number of tied scores associated with this test, a state of affairs which might have produced the significant correlation. In such a small sample four out of six observations (displays which did <u>not</u> elicit any attack) being tied would introduce a high degree of linearity when Hoy 1980 was compared with data from another test. The result would revealed for NB attack may be an artefact rather than a reliable indicator of an association.

Bearing in mind the above criticisms what are the implications of this result for the present thesis?

Considered together the results for both OLW and NB, irrespective of the overt response measured, do not suggest that the displays of the bonxie can be considered as a threat series.

A state of affairs has been created here which mirrors the theoretical dispute resolving system anticipated by the conflict theory. It is now possible, within the limits of the present analysis, to reject the conflict theory and the use of signalling intentional differences to resolve disputes as having any emphirical explanatory power. Previous failure to find consistent serial relations (e.g. tables26 - 28)cannot be attributed to a failure to control the influence of covert interaction.

That, as is now evident, displays should not convey intentional differences was anticipated by the games theorists (e.g. Maynard Smith 1974). Verification at an empirical level of one of their predictions adds weight to their argument. However, this support also resurrects an old and familiar problem. The conflict theory provided a convenient explanation for the existence of a variety of threat displays. With rejection of the latter model we are left with having to offer an explanation for a threat series. Two arguments presented within a games theory framework (Dawkins and Krebs 1978, Caryl 1979) were considered but neither was applicable to the bonxie. Until an explanatory model of a range of displays is offered within its framework the games theory approach will have limited use as an aid to understanding this widespread aspect of agonistic behaviour.

The problem may lie not so much in any inadequacy on the part of the games theorists models but rather in their critical concentration on only certain aspects of existing ethological display theory. They have tended to ignore problems relating to the definition of a display and the manner in which they are described in functional terms. However, earlier ethological work can be said to be guilty on the same count. The remaining part of the present study is an attempt to come to terms with these problem areas.

6.2.1. An alternative approach to interaction.

As it stands the present analysis has not offered any evidence to suggest that displays function in threat. The observation that displays enjoy frequent use implies that they have some functional significance.

The above approach to interaction, in terms of defining response probabilities, was adopted to facilitate comparison with the earlier conflict models.

An alternative approach would be to ignore quantitative response values and concentrate instead upon whether the use of a display by one individual influenced the display adopted by an opponent with respect of a particular action. The previous approach attempted to account for two variables simultaneously. Responses were measured relative to the other possible responses *and* relative to each possible display. For this alternative approach each response will be considered in isolation.

A standard situation is provided by holding the display of one individual constant and measuring (with respect to an overt action, e.g. Escape) the relative frequency with which this response is elicited by the various displays that the opponent may adopt. This represents a departure from the traditional conflict approach so it will not be possible to compare these results with those obtained earlier.

Restricting the scope of the study in this respect increases its scope in another respect. It will now be possible, by virtue of the increased samples permitted, to compare actor and reactor. Sufficient data was available to test only OLW and NB in this manner.

For the actor analysis the actor display was held constant and the proportion of each response was calculated relative to the display adopted by the reactor. For reactor analysis, reactor display was held constant and the proportion of responses were calculated relative to the displays adopted by the actor. The analysis itself was simple, involving averaging the relative frequencies from all colonies to determine whether the choice of displays is in any way constrained by the display adopted by the initiator.

6.2.2. Actor Responses (Table 32&34).

The most striking feature to emerge from adopting this approach is the skewed distribution of responses. When the actor display is held constant it appears that, irrespective of the display adopted, attack had the highest frequency of occurrence when the reactor adopted NN. From table 32a the average attack frequency after actor OLW/reactor NN was 42%. For actor NB/reactor NN the average attack frequency was 58% (table 34a). The propensity for actor attack appears not to be equally distributed between all displays but is more likely to occur when the reactor maintains NN.

The escape frequencies are listed in tables 32&34. Contrary to the finding for attack, actor escape is more likely to occur when both individuals adopt the same display. When the actor adopts OLW (table 32b) 54% of escapes occurred when the reactor also adopted OLW (cf. 13%NB; 14%NN). When the actor adopted NB (table 34b) on average 44% of escapes occurred when the reactor also adopted NB (cf. 23% OLW; 5% NN). There is also a fair measure of consistency between each test for this pattern. This is all the more interesting since it is the propensity to escape that is considered most indicative of the existence of a threat function.

The distribution of staying responses does not exhibit the same degree of inter-display consistency. For OLW 41% of all staying responses resulted when the reactor adopted NN (table 32c). This finding is surprising considering that attack was also most likely to be elicited under similar circumstances. For actor NB adoption by the reactor of either NB or NN had equal likelihood of producing actor staying. (Table 34c). Again it is paradoxical that a posture eliciting the maximum attack frequency could also elicit a relatively high staying response.

It is evident for both the displays considered here that a large majority of the overt responses that are considered relevant are elicited by a very limited variety of display combinations.

While it is interesting that a single posture of dubious 'display' quality, NN, should be responsible for eliciting the majority of attacking and staying responses it is even more interesting, from the point of view of determining the mechanism whereby displays are used to resolve disputes, that escape is most likely to occur, not in response to a display which might indicate a higher threat intensity, but rather when both individuals adopt the same display. This state of affairs arises because the reactor chooses to mimic the display adopted by the actor, and occurs irrespective of the display initially chosen by the actor. This finding runs counter to conflict theory logic but it brings the extent of bonxie display behaviour more into line with the type of system anticipated in early games theory models where contests were considered to be symmetrical and settled by display alone (Maynard Smith 1974). The implications of this finding will be discussed later.

Blurton-Johes (1968) suggested that interactional influences could be controlled in live interactions by studying only these interactions where the reactor did not display. In the bonxie this would entail studying those interactions where the reactor maintained NN. From the data presented here (tables32,34) it is unlikeky that this would provide an unbiased insight into the nature of the information content if temporal association were used. It would lead to an inflated picture of attack and stay probabilities relative to escape probabilities.

Before going on to discuss this tentative conclusion the consistency of these inter-display relations must be determined. It provided possible to do this by carrying out the same analysis from the point of view of the reactor, i.e. the reactors display was held constant and the relative frequency if each response was measured to displays adopted by the actor.

6.2.3. <u>Reactor Response</u> (Table 33&35).

When reactor behaviour was analysed in this manner it was immediately apparant that certain differences were to be found between the actor and reactor.

Contrary to the relationship found for the actor where attack was most likely to occur in response to opponent NN, in the reactor it is evident that irrespective of the display held constant attack is most likely after both individuals have adopted the same display.

When reactor OLW is held constant 38% of attack occurred when the actor had given OLW (table 33a ; cf NN-13%). If reactor NB is held constant 61% of attacks followed actor NB (table 35a ; cf NN-14%). Clearly there is a substantial differences between the conditions likely to provoke actor attack and those likely to elicit attack by the reactor.

For escape there is greater consistency between actor and reactor. From table 33b it is evident that when reactor OLW is maintained 73% of escape responses occur following actor OLW. Likewise for NB the majority of escape responses are elicited in response to actor NB-41% (table 35b). Since the actor stayed the choice of reactor display and subsequent response were to the actors display alone.

Turning to 'stay' a difference is again evident between actor and reactor. On average 60% of staying following OLW occurs when both individuals adopt the same display (table 33c). The picture for NB is not as clear cut and, following reactor NB, staying is equally likely after adoption by the actor of either OLW or NB.

There exist both similarities and differences within and between the pattern of display inter-relationships for the actor and reactor. In the actor, irrespective of the display adopted, both attack and stay are most likely to result from use of NN by the opponent. In the reactor each of these responses is most likely after both individuals have used the same display.

The response considered here to be the most indicative of a threat function being fulfilled in escape. In this respect it is assumed that after a display is held constant recording the extent to which opponent displays elicit escape will provide an insight into the mechanism by which displays are used to settle disputes. It is interesting to note the greater consistency evident between actor and reactor (tables 32-35). Escape is most likely to occur when both individuals adopt the same display. Of the two displays considered here this is most clearly illustrated with OLW. It is less evident for reactor NB. The greater similarity between OLW and NB in the frequency with which they elicit escape overall is counter-balanced by the greater consistency between each test. For NB (reactor) OLW has a standard deviation of 6.79 but NB is only 3.09. This greater inter-test consistency reinforces the view that escape is most likely following the use of the same display by each individual rather than using displays of differing intensity.

It is further evident that the number of displays used in agonistic interactions is rather more restricted than was previously thought given the number of displays which could be used.

6.2.4. Discussion.

What can this limited body of evidence say about the nature of the communicative process and the conflict/games theory contradiction.

The result partly supports the suspicions of Dunham (1966), Hinde (1981) and the conclusions of Bossema and Burglar (1980). The display adopted and the overt response shown are less an indication of intrinsic display information and more a consequence of the display adopted by an opponent. The result does not support the view that displays convey a range of agonistic information. Rather a very limited number of displays assumes responsibility for a disproportionately large number of agonistic interactions. The predominant use of OLW and NB in this context suggests that only these displays can really be considered to fulfil an agonistic function.

Is it possible that these two displays could indicate intentional differences? Tinbergen (1959) anticipated a system comprising a display for use against serious intruders and one for use against casual intruders. Could these displays represent actions ritualized to fulfil these different ends? This seems unlikely. Assuming that recording the incidence of escape is a viable means of defining threat effect then, irrespective of the display held constant, the maximum escape frequency would always occur in response to the same display. This is not the case (tables 32-35). Escape is most likely after both individuals have adopted the same display rather than to a display indicating a higher threat insensity. Thus it does not appear as if the dynamic mechanism for resolving disputes can be ascribed to the 'conflict' view based on displays conveying differences in intention.

Having rejected the conflict view, what can be put in its place? Is any support forthcoming for the games theorists views on agonistic behaviour?

The Games theorists criticism of signalling a range of intimations intentions led to their proposing a system which was very much more limited in terms of displays used than that considered by the conflict theorists. The latter theory was attempting to embrace the observed existence of a number of agonistic displays. The present analysis suggests that the basis of their analysis may have been inappropriate for detecting threat displays and, at least for the bonxie, the number of displays fulfilling a threat function is limited. However, it is the finding that individuals tend to match displays in disputes that brings the threat display system of the bonxie into line with that anticipated by the games theorists. Since those interactions terminating in escape were settled by display alone the way is open to investigate, and indeed it is necessary to find, alternative mechanisms of dispute resolution.

The situation is complicated by there being two threat displays. The matching found rules out their being used to convey intentional differences. Instead the occurrence of each of these displays may be representative of different types of contest. There is at least anecdotal evidence to support this possibility.

OLW and NB adopt very different forms (fig. 2 & 3 which suggests differences in the manner in which they might exercise their effect.

OLW is by far the most frequently used display in the breeding colonies. Here its form, and the white wing patches in particular, make it well suited for communication over the large distances between pairs and against the background against which they nest. In addition to the manner of its use as analysed here, OLW is frequently given by the victor after an opponent has fled. As a result bonxie workers have generally concluded in favour of a territorial function for this display (e.g. Moynihan 1962, Andersson 1976), Perdeck (1960) noted how club birds become increasingly territorial during their stay. It is possible that OLW represents conflicts of a territorial nature. Interactions involving territorial individuals were excluded from the analysis so if the above supposition is correct such contests might involve normal club birds attempting to acquire a territory. Spellerberg (1971) suggested that OLW also served to attract a mate. OLW may serve to preserve an area free from competitors within which to attract a mate.

NB, on the other hand, could be representative of contests of a more directly agonistic nature as evidenced by the similarity between the form adopted by this display and the actions associated with overt attack.

A more exact understanding of any distinction is hindered by the nature of the disputes being far from obvious to the observer. Without more detailed information about club dynamics from individually ringed birds the above suggestions remain purely speculative. Two conclusions are possible.

a) The threat repertoire of the bonxie is very much more restricted than had previously been thought. Within the limits of the present analysis only NB and OLW can be considered to fulfil this function. There are no grounds for considering all the displays of the bonxie as being functionally homogeneous. More detailed analyses of display behaviour are revealing functional differences between displays previously lumped together (e.g. Orians and Christman, 1968, Mock 1979). The simple nature and, more specifically, failure to determine consistency in previous 'conflict' studies is thus likely to have revealed a misleading picture of the compenents of the threat system.

b) Where interaction actually takes place i.e. where the reactor responds to an actor display by adopting a display, a matching of displays is revealed suggesting that each of OLW and NB is representative of different types of dispute.

By suggesting that this analysis provides a more realistic insight into the components and mode of operation of the threat system with respect to display it should now prove possible to investigate the manner in which displays are used to furnish the information on which disputes are settled. Unfortunately the scope of the present study did not extend to this but the results could be used to assess the explanatory power of existing models.

It was evident that a differences in display relations existed which depended upon whether the analysis was based on actor or reactor displays. (cf. tables 32 & 33.

In a bonxie club before an interaction all the birds are sitting or standing relaxed. An interaction commences when the actor adopts a display either after approaching or while in the vicinity of a chosen opponent. It is assumed at this point that the actor is signalling intention to dispute and that he is aware of the value, to himself, of the disputed resource. The reactor has more information at its disposal. The latter is likely to be aware of the nature and the extent to which it values the disputed resource but not the relative value placed on this resource. At all times whether or not the resource is actually disputed rests with the reactor. Only when the latter actively displays can a dispute be said to be in progress.

Maintainance of a relaxed posture (NN) is likely to indicate a reluctance on the part of the reactor to enter into dispute. This might be perceived by the actor as a situation in which he has little to lose by attacking and seeing his opponent off. Complications arise in the form of the high staying frequency also evident in response to maintainance of NN by the reactor (table 32,34). Hinde (1981) suggested that display would be used where the actor was uncertain about a future course of action. If display acts as a prompt in this manner such a nil-response may not provide the necessary reduction in uncertainty to permit action. This state of affairs is more likely to occur where the signaller is relatively inexperienced. The constant influx of new birds into the club throughout the season (Furness 1979) may result in such an eventuality being fairly common.

An alternative variable which may be instrumental in determining the response shown is the distance between individuals. Attack may be more likely between individuals close together.

For both actor stay and attack such responses are most likely in response to a non-displaying reactor i.e. it could be argued that the resource is not being disputed. For the remaining response, escape, the reactor is more likely to display hence the resource is being disputed. Further, such disputes exhibit a high degree of display matching (OLW - 54%, NB - 43%;tables32,34). The implications of this finding for the mechanism used to resolve disputes will be discussed in conjunction with data from reactor displays. For the present the significance of this finding rests with the fact that, considering the actor instigates an interaction, its decision to terminate the interaction is made predominantly from information received (or elicited) after the reactor has adopted the <u>same</u> display.

Interaction only really takes place when the reactor displays. It must be borne in mind that the reactor is responding to a display that has already been given by the actor. The highly skewed distribution of displays seen in table 33&35 provides the strongest evidence that the bonxie threat repertoire is likely to be restricted to OLW and NB.

Since the actor initiates the interaction he has choice of display. Hence the high level of display matching by the reactor in response to displays already adopted by the actor provides the strongest support for the suggestion that use of each display represents disputes which differ in their respective natures.

After reactor display all three responses are most likely after display matching.

For both actor andrreactor escape response was measured when the opponent stayed after displaying. So, generally, the contest was settled by display alone and only a single intensity of display was used. Th~~i~~us a number of the criteria outlined in the War of Attrition model (Maynard Smith 1974) are fulfilled. Although the present analysis did not permit it, it might prove fruitful to investigate the termporal course of bonxie interactions to determine whether disputes are settled on the basis of persistance times.

While the War of attrition model has the potential to explain disputes settled by display alone it doesnnot have the facility to explain why contests which are similar, in respect of the displays used, may end in attack. Here it is likely to be this overt action which terminates the dispute though information gleaned from the display stage may underly this response.

Parker and Rubenstein (1981) suggest that displays may furnish information about Resource Holding Potential (RHP) or Resource Value (RV) and so convey the role played by each interactant. Where information about either of these asymmetries is clear this would be used to settle the dispute. In the present analysis such a process may explain those interactions which were terminated using display alone. They also realised that the situation is bound to arise where such information is not related perfectly. A number of possible situations were outlined. Firstly, the respective roles played may be weak because information about RHP and RV is weak and will be undetectable in short contests. Under such circumstances escalation is likely to provide more reliable assessment information. The second possibility is that asymmetry information may be ambiguous leaving each individual uncertain about which asymmetry to respond to. Again it is suggested that escalation will be used to resolve the contradictory information from the display process. Finally, escalation is likely where both individuals are evenly matched. In this respect empirical evidence is available to support this possibility

(Kruijt 1964, Rubenstein 1981). Where individuals are evenly matched conventional means of resolving the dispute will be inadequate. Presumably escalation will provide information about individual differences in RHP or RV in finer detail than would be available from display alone. Parker and Rubenstein suggest that escalation is an integral part of the assessment process.

An obvious but essentially ignored problem is raised here. How fine can an individual resolve asymmetric information from a display and to what extent must the assessment cues differ between individuals for them to be used in the above manner?

With respect to the bonxie it remains to be seen whether OLW or NB can be credited with the facility of conveying information which may serve to communicate differences in RHP or RV. Before any of these questions can be answered the basic units of study must be identified. Only then can the nature of the information and its use be determined.

In the bonxie the situation is further complicated by the finding that both interactants show a propensity to stay following display matching. Further, staying is the most commonly observed outcome. If it is assumed that threat is used to determine which of two individuals will have access to a limited resource this outcome is indeed puzzling. It is doubtful whether a solution will be evident until a more precise understanding of the nature of the disputes is found.

The application of games theory to the theoretical analysis of agonistic behaviour has provided a number of interesting models. However, a gulf is evident between the theory and its empirical application. The present study had as a starting point an attempt to assess games theory models in the light of data gathered to prove a completely different theoretical system (Caryl 1979). The contradiction between these two theoretical perspectives would appear to have resulted from a failure by both approaches to adequately define threat displays and to provide methods for their detection. Although the present analysis is simple this confers upon it ease of application in the field. While still being based on temporal association it reveals how a slight shift in emphasis can put an entirely different complexion on the nature of the display system under consideration. Only after the components have been identified with consideration for reliability will it be possible to assess the relative merits of various theoretical constructs. In so doing the theoretical and empirical sides of the study will be brought together permitting co-operation and introducing a greater sense of future realism.

Reactor Display

	OLW	NB	NBL	NN	NbBpL
HOY 1980	7	27	40	13	8
FI 1979	21	17	13	20	0
FI 1980	13	24	11	23	0

	HOY 1980	FI 1979	FI 1980
HOY 1980	1·00	-0·4	0·2
FI 1979		1·00	0·6
FI 1980			1·00

a. Interactional Attack Probabilities

	OLW	NB	NBL	NN	NbBpL
HOY 1980	23	3	20	15	17
FI 1979	26	14	38	6	20
FI 1980	24	19	16	5	17

	HOY 1980	FI 1979	FI 1980
HOY 1980	1·00	0·8	0·3
FI 1979		1·00	0·3
FI 1980			1·00

b. Interactional Escape Probabilities

Table 29 : Interactional response probabilities. Actor OLW is held constant and response probability following each reactor display is measured. Correlation coefficient (Spearman) matrices are given for an inter-test comparison of ranked responses.

	Reactor Display					
	OLW	NB	NBL	NN	NbBp	NbBpL
HOY 1980	0	16	0	47	0	0
FI 1979	5	49	9	59	25	25
FI 1980	28	53	36	83	20	14

	HOY 1980	FI 1979	FI 1980
HOY 1980	1·00	0·857*	0·845*
FI 1979		1·00	0·521
FI 1980			1·00

a. Interactional Attack Probabilities.

	Reactor Display					
	OLW	NB	NBL	NN	NbBp	NbBpL
HOY 1980	47	38	60	9	17	57
FI 1979	35	22	55	0	0	25
FI 1980	36	25	50	3	60	29

	HOY 1980	FI 1979	FI 1980
HOY 1980	1·00	0·811	0·371
FI 1979		1·00	0·232
FI 1980			1·00

b. Interactional Escape Probabilities.

Table 30. Interactional response probabilities. Actor NB is held constant and the response probability following each reactor display is measured. Correlation coefficient matrices are given for an inter-test comparison of ranked responses.

Actor OLW	Reactor Display OLW	NB	NBL	NN	NbBpL
Attack	4	8	2	7	I
Escape	I2	I	I	3	2
Stay	36	20	2	4I	9
N.	52	29	5	5I	I2

a. Hoy I980

Actor OLW	OLW	NB	NBL	NN	NbBpL
Attack	I0	6	I	I3	0
Escape	I2	5	3	4	I
Stay	26	26	4	5I	4
N.	48	37	8	64	5

b. Fair Isle I979

Actor OLW	OLW	NB	NBL	NN	NbBpL
Attack	I2	9	0	38	0
Escape	2I	7	3	7	2
Stay	57	2I	I5	I07	4
N.	90	37	I8	I52	6

c. Fair Isle I980

Table 3Ia: The number of observations used to calculate the interactional response probabilities on receipt of actor OLW.

Reactor Display

Actor NB	OLW	NB	NBL	NN	NbBp	NbBpL
Attack	0	8	0	I6	0	0
Escape	9	I9	6	3	I	3
Stay	I0	23	4	I5	5	3
N.	I9	50	I0	34	6	6

a. Hoy I980

Actor NB	OLW	NB	NBL	NN	NbBp	NbBpL
Attack	I	34	I	29	I	I
Escape	6	I5	6	0	0	I
Stay	I3	20	4	20	3	2
N.	20	69	II	49	4	4

b. Fair Isle I979

Actor NB	OLW	NB	NBL	NN	NbBp	NbBpL
Attack	I0	39	3	I06	2	2
Escape	I3	I8	4	4	3	2
Stay	I3	I6	I	I8	I	4
N.	36	73	8	I28	6	8

c. Fair Isle I980

Table 3Ib: The number of observations used to calculate the interactional response probabilities on receipt of actor NB.

Reactor Display

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1979	50	7	0	36	0	7	0	0	14
HOY 1980	17	33	8	29	8	4	0	0	24
FI 1979	31	19	3	41	0	0	6	0	32
FI 1980	21	16	0	60	0	0	0	0	57

a. Frequency distribution of actor attack responses

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1979	56	11	0	11	0	11	11	0	9
HOY 1980	60	5	5	15	0	10	5	0	20
FI 1979	48	20	12	16	0	4	0	0	26
FI 1980	52	17	7	17	0	4	2	0	41

b. Frequency distribution of actor escape responses

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1979	31	12	7	31	0	4	7	7	26
HOY 1980	32	18	2	36	1	8	1	0	113
FI 1979	23	23	4	46	1	4	0	3	111
FI 1980	27	10	7	51	0	2	1	1	210

c. Frequency distribution of actor stay responses

Table 32: The interdependence of display use. Actor OLW is held constant and the relative frequency with which the reactor adopts a given display is measured. This was done for each response (attack, escape and stay) independently.

Actor Display

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1980	50	33	17	0	0	0	0	0	6
FI 1979	43	14	14	28	0	0	0	0	7
FI 1980	21	47	16	11	0	5	0	0	19

a. Frequency distribution of reactor attack responses

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1980	86	5	5	0	0	0	5	0	22
FI 1979	65	25	15	0	0	0	0	0	20
FI 1980	67	10	10	0	0	3	10	0	30

b. Frequency distribution of reactor escape responses

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1980	67	20	4	4	0	0	2	2	46
FI 1979	49	20	2	7	2	5	5	5	41
FI 1980	66	13	5	1	0	8	0	7	76

c. Frequency distribution of reactor escape responses

Table 33: The interdependence of display use. Reactor OLW is held constant and the relative frequency with which the actor adopts a given display is measured. This was done for each response (attack, escape and stay) independently.

Reactor Display

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1980	0	33	0	66	0	0	0	0	24
FI 1979	1	48	1	41	1	1	1	4	71
FI 1980	6	24	2	66	1	1	1	0	161

a. Frequency distribution of actor attack responses

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1980	20	43	14	7	2	7	5	0	44
FI 1979	19	48	19	0	0	3	0	3	32
FI 1980	28	39	9	9	6	4	4	0	46

b. Frequency distribution of actor escape responses

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1980	17	38	7	25	8	5	0	0	60
FI 1979	18	29	6	29	4	3	0	10	68
FI 1980	24	29	2	32	2	7	2	2	55

c. Frequency distribution of actor Stay responses

Table 34 : The interdependence of display use. Actor NB is held constant and the relative frequency with which the reactor adopts a given display is measured. This is done for each response (attack, escape and stay) independently.

Actor Display

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1980	20	60	0	10	0	5	5	0	20
FI 1979	12	61	9	12	3	0	3	0	33
FI 1980	12	62	0	20	0	0	4	2	50

a. Frequency distribution of reactor attack responses

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1980	41	45	0	0	0	7	7	0	29
FI 1979	25	38	16	11	4	2	0	5	56
FI 1980	37	39	9	5	0	5	12	0	43

b. Frequency distribution of reactor escape responses

	OLW	NB	NBL	NN	NbBp	NbBpL	NBT	NS	N.
HOY 1980	38	48	4	0	0	4	4	2	48
FI 1979	35	29	8	8	2	2	2	15	63
FI 1980	34	32	5	7	0	7	5	9	44

c. Frequency distribution of reactor stay responses

Table 35 : The interdependence of display use. Reactor NB is held constant and the relative frequency with which the actor adopts a given display is measured. This was done for each response (attack, escape and stay) independently.

Chapter Seven.

Non-Display Influences.

Analysis so far has concentrated on explaining the role of the most obvious feature of avian social behaviour, the displays. As behavioural units displays are gross features comprising a number and variety of components. Towards the latter little attention has been directed. Recently, increased attention has been given to the less obvious features of the communication process. Bossema and Burglar (1980) demonstrated how subtle display features (e.g. whether the recipient was fixed with binocular or monocular gaze) could influence response. It has been suggested that ignorance of the influence of more subtle actions renders any display concept meaningless (van Rhijn 1980).

The analysis of chapter six revealed that gross displays did elicit a consistent response and so are worthy of further study. It is also true that this latter analysis provides little insight into how the process works or into the subtle interplay between display components. However, once a gross action, a display, has been shown to elicit a consistent response it might prove possible to resolve the influence of individual components. To do this the analysis must switch to a different tack.

The scope of the analysis was broadened by bringing into play a number of variables intrinsic to the situation in which displays occur; variables which have largely been ignored as influences on display effects. That more than displays had an interactional role had not gone entirely unnoticed.

In his study of the bonxie Andersson (1976) realised that two non-display factors affected outcome over and above the influence of the accompanying display - mode of approach and status. Irrespective of the display used a running bird constituted a stronger threat stimulus than a walking bird which, in turn, constituted a stronger stimulus than a stationary bird. The second factor concerned the relative status of the interactants. Within a skua club not all individuals enjoy equal status. Perdeck (1960) noted that birds forming club pairs become increasingly territorial. In interactions involving territorial and non-territorial individuals the former was invariably the victor. For these reasons the interactions analysed in the present study involved stationary, non-territorial birds.

In the present study two further influential variables emerged - the relative orientation and distance between interactants.

7.1.2. Inter-Individual Distance (I.D.).

Hediger (1950) described two broad categories of intra-specific dispersion. Firstly, there were those species whose members spent considerable time in close proximity to one another, the 'contact species'. Secondly, there were the 'distance-species'- those where individuals possessed an area around them within which transgression by another would elicit attack or escape.

Early studies concluded that this distance was a reflection of the degree to which individuals would tolerate crowding, its size being determined by the distance a bird could strike from a stationary position (Emlen 1952). However, more detailed examinations of I.D. revealed greater flexibility than had earlier been thought.

Marler's (1956) classic study was one of these. In the chaffinch he found a gradual decrease in aggressiveness with increasing I.D. rather than there being a sudden cut-off in aggressiveness. Although the chaffinch does not exhibit an I.D. preference per se, Marler was able to quantify and compare distance preference by employing the concept of the 50% distance. This was the distance at which there was a 50% likelihood of aggressive behaviour. Using this approach a number of interesting observations emerged.

A sex difference was evident in that the 50% distance for females was less than that for males. Males were also more tolerant of females than they were of other males. A similar sex difference was also found in the redpoll (Dilger 1960).

Of particular interest from the point of view of the present study was the finding of a display/distance interaction. The 50% distance was smaller with submissive than with aggressive displays.

More recent studies have revealed the variable nature of I.D. and the many factors that impinge upon it.

Spatial complexity can increase I.D. (Marler 1965). Patterson (1975) concluded that the increase in agonistic activity in rooks foraging in the snow arose from the increased proximity resulting from foraging in such conditions. Hazlett (1979) found that the conditions under which individuals are held can exert a strong influence on the distance at which social behaviour is executed.

Dominance relations can result in I.D. differences (Gibson 1968). Even where dominance is not influential, interaction with others can produce I.D. differences (Crook 1961) Huang and Hazlett 1972) and may be correlated with the frequency of agonistic encounters (Balph 1977).

It had previously been assumed that I.D. formed a radius of fixed dimensions around an individual (Lorenz 1966) though this need not always be the case. McBride et al (1963) found that, in the domestic hen, the preferred distance was greater in front of the animal than behind. The distance at which different responses are elicited may vary. Hazlett (1975) noted that the distance at which attack was evoked need not coincide with the distance at which escape was evoked.

Huang and Hazlett (1972) found that I.D. preference was not dependent upon the relative or absolute size of an individual. This, together with finding that the distance at which social behaviour was executed did not vary proportionally with the size of the individual led Hazlett (1975) to suggest that animals have set distances for the delivery of different behaviour patterns and that these set points can be altered by experience. Hazlett also noted that variance in the distance at which various patterns were shown could be accounted for by considering the behaviour pattern shown by an opponent.

Blurton-Jones (1968) raised the possibility of display use in the great tit being distance dependent. In this species the horizontal display was given at a closer range than the head-up display. Each display was associated with different types of overt attack behaviour. Head-up was a frequently used threat in territorial encounters where, with its associated flying attack, it was suited to the distances involved in such circumstances. In contrast, horizontal may be more adaptive as threat in the close encounters of the food disputes kind; its running, jabbing form of attack being better suited to close range disputes.

I.D. is obviously going to be an important agonistic influence. The relationship between distance and display use has received little detailed study. The possibility of their interacting prompted Hazlett (1975) to suggest that displays should be defined in terms of probability distributions. This approach will be adopted here.

7.1.3. I.D. in the bonxie.

Before display-distance interaction can be studied it must first be determined whether the bonxie is aware of distance. Do bonxies show an I.D. preference?

The non-territorial bonxies in the central part of the club do not form an attachment to any particular area within the club and are mobile in their use of available space. However, the distribution of individuals is not haphazard. The first birds to land following a disturbance select a position within the club and later landing birds congregate around the former. Burton (1968) stated that club birds exercised a distance preference and that this influenced club agonistic behaviour. He did not discuss the role played by distance in any detail.

Whether distance exercises its influence in a discrete (e.g. McBride et al 1963) or a continuous manner (e.g. Marler 1956) will have implications for the manner in which the displays might be effective and which must be considered in any analysis. For example, if I.D. is discrete inclusion, for analysis, of displays occurring outwith this distance will cloud the perceived nature of display effect. At such distances display effectiveness would be reduced due to a counter influence arising from the recipients perception of the inter-individual distance being at a level which might not require any response.

Firstly, any distance preference in the bonxie must be determined in a manner free from display influences. Determination of a basic I.D. preference would prove a useful baseline against which to assess/display/distance interaction.

Crook (1961) outlined two methods of determining distance preference. Firstly, there was the 'arrival distance' - the distance separating two birds following the landing of one of the dyad. Secondly, recording the distance after adjustments had taken place provided a measure of the 'settled distance'.

Measuring the distance between resting skuas (those adopting NN) did not prove to be a very reliable method for detecting a distance preference. Where birds had previously been involved in interactions prior to measurement the distance was found to be highly variable. The distance moved off was dependent upon whether a bird escaped in response to a display, to being attacked and was particularly dependent upon the status of the signaller. The number of variables influencing distance measured using this approach seriously reduced its effectiveness in determining an I.D. preference. Instead the 'arrival distance' was used.

The distance separating two birds immediately after one landed was measured only where neither of the dyad displayed (i.e. both maintained NN) <u>and</u> where both individuals stayed. Where a bird landed in a group only one distance was taken; that between the lander and its nearest neighbour. Recording distance in this way will provide a passive measure. Any response (e.g. an increase in distance after landing) would arise because of a bird's perception of its proximity to an opponent and not through any overt behaviour on the part of the latter. If the bonxie has a preferred I.D. then most staying NN landings should occur at this distance.

Distances were measured in bird lengths (BL), measured as the length of the bird with the neck in the upright position, i.e. from chest to tail. Distances were measured from a point between the legs of each interactant. This proved to be a more reliable distance measure when observing birds through binoculars, the frame of distance reference being present irrespective of the location of the birds.

7.1.4. Results.

The number of non-display landings were plotted at each I.D. and the results are presented in figs. 6 and7 . It is immediately apparent that such landings are not evenly distributed at all distances. The peak at 10BL is artificial in as much as it records the summed data for all landings at 10BL and over.

The heights of each column record the total number of landings at each I.D. The figures at the head of each column represent the percentage of total landings at each I.D. In each test the number of landings peaks at 3BL and there is a high degree of consistency between each of the tests with only Fair Isle 1980 (fig. 7) showing a particularly high landing frequency (37%). It would appear that the bonxie does have an individual distance preference of 3-4BL (approx 2m).

The bonxie does not make use of all the available club space but tends to exhibit a non-random distribution with respect to available club space and relative to other individuals. This non-random distribution suggests there being a competitive structure to the club.

This baseline I.D. preference will prove useful in assessing how distance and displays interact.

7.1.5. Inter-Individual Orientation.

The second non-display factor to emerge was the relative orientation of interactants in the horizontal plane. Evidence for its importance came from the observation that the outcome of a number of interactions were decided on the basis of a change in orientation by one individual towards another when both display and distance remained constant. All interactions of this nature resulted in opponent escape.

In tables 36 the vertical totals column records the relative frequency of this type of interaction for each display. The predominance of NB is hardly surprising in view of the support for this display fulfilling a threat function (Chapter 6). Of particular interest, with regard to display effectiveness, is that the second most commonly occurring posture revealed by this analysis is that adopped by resting bonxies (NN-FAir Isle 1979, 20% Fair Isle 1980, I9%). This posture cannot be considered a display in the accepted sense, i.e. one that has become specialised in evolution to subserve a signal function. Because of this considerable importance is suggested for the interactional role played by relative orientation.

The horizontally listed totals in tables 36 records the relative frequency of this type of interaction at each I.D. It reveals that the majority of such interactions tend to occur at distances up to and including 3BL (Fair Isle 1979 83% ; Fair Isle 1980 87%). This is likely a reflection of the influence of an I.D. preference and suggests a propensity for interaction and for display effectiveness to occur within this distance but less so at distances greater than 3BL.

This type of interaction may be widespread in the avian world. It has been recorded in the glaucous-winged gull (Hayward et al. 1977) in juncos (Balph 1977) and in redpolls (Dilger 1960). In the latter two species orientation away from an opponent served as appeasement. Dilger also noted grades of orientation change; from a simple turning of the head towards an opponent to a turning of the whole body. The use of orientation has also been observed in domestic hens (McBride et al.1963), in jays (Bossema and Burglar 1980) and sheep (Geist 1971).

It had occurred to ethologists that if displays evolved to fulfill a signal function orientation will have been an important component (Smith 1966). This would be particularly so for visual display components where the stimulus presented to an opponent will alter with changes in orientation with respect to that opponent. In determining the signal function of displays the influence of orientation has been overlooked unless it formed an integral part of the display i.e. one component of its ritualization involved delivery at a particular orientation with respect to an opponent. The 'facing-away' displays characteristic of many gull appeasement displays are a good example. The relative orientation often serves to conceal the potentially offensive elements of the display, thus 'cutting off' the threat (Chance 1962). Orientation has received little attention where it has been highly variable (Smith 1977).

The reason for overlooking the functional significance of changes in delivery orientation probably lies with the causal emphasis of many studies. The ethological distinction between discrete and continuous signals centres on differences in the quality of the motivataonal information conveyed. While continuous signals may reflect subtle changes in signaller motivation, discrete signals trade this facility for a decrease in ambiguity (Cullen 1966). The trade off is not complete and alternative means of conveying subtle motivational differences may have accompanied the evolution of discrete signals. Differences could be conveyed by changes in the frequency of performance (Morris 1956, Cullen 1966), through changes in inter-individual distance (Sparks 1964), through contextual sources (Smith 1969) or orientation. Moynihan (1955) noted the variation in delivery orientation of a number of Black headed gull displays and concluded that these corresponded to changes in the strength of the attack/escape conflict, permitting an increase in the subtlety of the motivational information transmitted.

While it is possible that the causal basis of an orientation change lies with changes in underlying motivation, the change in orientation raises problem at a functional level. The problem centres on the fact that the change in orientation will result in changes in the stimulus form presented to an opponent and concerns the exact nature of the stimulus properties considered to 'release' a response.

The importance of orientation in this respect can be illustrated with reference to the NBT display in the bonxie. This display is almost identical to NB (fig. 3-) differing only in that for NBT the tail is raised at an angle of about 45^o relative to the body axis. Irrespective of any causal significance attributed to tail-raising it can only have functional significance, i.e. have the potential of transmitting information and influencing the response of a recipient if it can be seen by the recipient. If the signaller directly faced the recipient the body of the signaller effectively obscures the raised tail. At the relative orientation the recipient does not have visual access to this information source and so will not have the information at its disposal. In such cases inclusion of the tail raised component in the analysis is likely to cloud the nature of its effect in the eyes of the observer. It is interesting to note that NBT had a relatively high association with circling (table 2). Here its delivery involved standing parallel and head to tail with another bird and so the 'tail-raised' component would be optimally displayed. In this case the recipient would have access to any information that might be conveyed by this component.

In future it might prove beneficial for the observer to record the details of an interaction from the point of view of the participants rather than from his own subjective viewpoint.

Both inter-individual distance and the relative orientation of individuals are likely to influence the outcome of a dispute. There existence as such raises an interesting question with respect of the central theme of the present study, namely whether the dynamic mechanism used for resolving disputes involves transmission of differences in intention. The findings of chapter six ruled out the use of a large number of different displays in this respect. However, both I.D. and orientation have been attributed with serving such a purpose (Sparks 1964, Moynihan 1955) respectively). It remains to be seen whether such a state of affairs exists in the bonxie, a species where both features exert a strong presence.

7.1.6. Distance and Orientation as signals of intentional differences

It is one thing to suggest that a variable has a causal basis and another to suggest that it could provide a mechanism for resolving disputes. The dynamic mechanism for dispute resolution anticipated by the conflict theory concerned the use of relative motivational differences signalled by the use of an appropriate display by each interactant. The individual displaying at the lesser intensity would retreat. Would the use of either distance or orientation provide the conditions for relative information transfer?

With distance as a cue the interactive process would be absent. There can only be one distance between individuals and this is determined by only one individual, usually the actor. While distance may provide a measure of actor intent it would not provide a measure of reactor intent should the latter decide to dispute. Distance would not provide a relative indication of intent and so would not provide sufficient relative information to resolve a dispute.

The range of orientations that each individual could adopt enjoys greater independence and so, in theory, could provide subtle differences in relative motivation which could be used to resolve a dispute.

When this component was introduced to the analysis six orientation grades were considered. These were measured as the angle of the body of one individual relative to a plane perpendicular the an imaginary line drawn between each interactant. They were measured in 30° intervals with 0° (Facing) being the angle when the signaller faced his opponent.

It soon became apparent that the number of relative delivery orientations was quite restricted. The large majority of interactions involved delivery either where the signaller faced an opponent (0°) or where parallel to an opponent (90°) with relatively few at any other angle. For analysis only two orientation classes were considered. 'Facing' and 'No Facing' (see fig 5). In the bonxie relative orientation is not used to furnish information about subtle motivational differences. At best only gross differences could be transmitted.

7.2.1. The inter-relationship between displays, distance and orientation - the functional consequences of their interaction

Two non-display influences have been identified here which have implications at a behavioural level. Both have been shown to be influential in relative isolation. In practice they always occur in combination. A display is always given at a certain relative orientation and distance from an opponent. The inter-relationship between these factors is highly variable. While it was possible to isolate displays from the non-display factors identified by Andersson (1976), those being studied here must be considered together.

Functional emphasis is being placed on determining the consistency with which displays elicit appropriate behaviour from a recipient. The communicative consequences of behaviour will have greatest relevance to their recipient and so the latter was considered here to be the most objective determinant of what constitutes threatening behaviour. Disputes are considered to be over limited resources where only one individual can assume possession. The other must depart. Hence if displays exercise a threat function then the appropriate behaviour to measure is the escape response of the recipient. Only after the extent of the threat repertoire has been identified do we possess the basic material with which to answer other functional questions, e.g. the information conveyed. Thus the functional consequences under examination concerns the manner in which display, distance and orientation combinations influence the likelihood of recipient escape.

7.2.2. The Actor

Before commencing the functional analysis the scene will be set by considering the actors use of distance and orientation in conjunction with display. For analysis data from all tests were summed.

Although the ensuing picture provides a measure of the relative frequency of actor display at each orientation and distance to have any significance the actors choice of each variable must be under his control and this is not always the case.

Approximately half of the interactions included in the present study involved one individual landing in the vicinity of another. The first bird to display was labelled the actor but the actor was rarely the landing bird. Under these circumstances the landing bird determines the relative distance and orientation rather than these variables being actor controlled. Using these variables to provide an insight into actor motivation would be misleading. Although summing the data mayppartially smooth out the ensuing variance the inadequacies of this approach should be born in mind. It was for this reason that this approach was not included directly in the analysis of display function but was used to set the scene for the analysis of the effect of displays on their recipient.

Each display was considered in terms of its delivery orientation. The relative frequency of delivery orientation was recorded as was the relative frequency of occurrence at each I.D.

1) <u>OLW</u> (Table 37 , fig. 8).

Within each orientation class there is a relatively even distribution of display occurrence from 1-3 BL. In both there is a peak at 2BL and a sudden drop in frequency at 4BL. This drop probably reflects the influence of an I.D. preference.(cf. figs 6 & 7).. It has been suggested that OLW served a 'territorial' function (Perdeck 1960, Andersson 1976). Its predominant use within 3BL, the extent of the I.D. preference, reinforces this view and suggests that the display serves to ward off personal space intrusions. Discrete use of space in this manner has important implications for a behavioural study. Interactions involved OLW but occurring outwith 3BL will be subject to influences differing from those occurring within 3BL.

While this even distribution probably reflects a distance function the display is not delivered with equal frequency at each orientation. 68% occur with actor'Not Facing', i.e. when the actor is perpendicular to the opponent. Perdeck (1960) noted a similar frequency of distribution and offered two explanations. Firstly, the distribution may have arisen from the habit of birds standing facing into the wind resulting in their adopting a parallel stance. Alternatively, the higher 'not facing' frequency may reflect a signal function. The most distinctive feature of this display are the white wing patches which have been demonstrated to have a signal function (Spellerberg 1971). Perdeck suggested that this feature would be best displayed at this orientation. In this respect it will be interesting to see how a recipient responeds to this display.

2) <u>NB</u> (table 38 , fig 9).

For this display differences in the frequency of occurrence are evident both within and between each orientation dlass. For 'Facing' delivery an inverse relationship is evident between frequency of occurrence and distance. 51% occurred at an I.D. of 1BL. This is consistent with a postulated role of a more directly agonistic function for NB. At this distance an attack would be easy to press through since the opponent was within striking distance. Further 67% of the occurrence of this display was at this orientation, a finding which further suggests this display/orientation as having a signal function.

For 'Not Facing' the frequency distribution is very different from the 'Facing' distribution (fig 9) and instead, mirrors that for OLW with an even distribution from 1-3 BL and a sharp decrease at 4BL. With OLW this distribution was used to support previous suggestions for its fulfilling a 'territorial' role. It is difficult to adopt a similar argument with NB.

3) <u>NBL</u> (table 39 , fig. 10)

The distributions associated with the actors use of this display effectively mirrors those found for NB.

Despite the crudeness of this introductory analysis an inter-dependence between displays, distance and orientation is evident. For all three displays a preferred delivery orientation exists; 'Not Facing' for OLW and 'Facing' for both NB and NBL. This preference may have implications for the manner in which the respective displays exercise their effect and the difference supports the conclusion of Chapter six that each display represents different types of dispute. This conclusion is further re-inforced when the spatial relations of a number of display/orientation combinations are considered. These can be broadly split into two groups; those exhibiting a discrete distribution for 1-3BL with a marked decrease at 4BL (probably reflecting an I.D. preference) and those exhibiting a continuous distribution in the form of an inverse relationship between frequency and distance.

The presence of differences between displays might be expected in view of the postulated differences in function. What is surprising is that differences in spatial relations can exist for the same display. For both NB and NBL this suggests that their treatment as homogeneous display units without regard for orientation may not be valid. This finding is consistent with the suggestions that displays are effective at a specific orientation with respect to a restricted set of stimuli.

Do these displays have functional significance?

7.2.3. The response of the recipient.

Approaching the analysis from the actors point of view was criticised because the values adopted by each variable were very often outwith the latters control. Approaching the problem from the recipients point of view surmounts a number of difficulties.

On receipt of a display the recipient has a number of potential information sources at its disposal. Firstly, it is in a position to perceive the display. Secondly, it can perceive the relative orientation of the signaller and the distance between them. If the latter variables have functional significance then consistent relations would be expected for each display for the manner in which they interact. If they fulfill a threat function then this interaction would be thrown into relief a consistent escape pattern being shown by the recipient.

Table 36 revealed considerable support for the importance of orientation by virtue of the popularity of NN with orientation-change interactions. The present analysis was built around display/orientation combinations. Further, orientation was a restricted variable occurring in only two forms. Hence, this combination seemed the most appropriate base.

Probability distributions were calculated for each display/orientation combination. To do this the escape probabilities of the recipient were calculated at each I.D., the latter being measured in bird lengths (BL). At each I.D. whether the recipient attacked, escaped or stayed was recorded. The escape probability was the relative frequency of escape at each I.D. In all cases the actor stayed after displaying to ensure as far as possible that recipient response was to a particular display/distance/orientation combination and not to any overt action. In this way a range of escape probabilities were determined for each display when delivered at each orientation. For each display the escape probabilities were plotted against distance and their respective regression lines drawn. These regression lines represent the probability distributions.

A functional significance could be attributed to a combin-ation of variables if they exhibited a consistent probability distribution. The regression lines could differ in two different ways. Firstly, the distributions could be parallel, differing only in height. Where differences of this nature were evident their signifiaance was tested using an analysis of covariance (Armitage 1975). Alternatively, the distributions could differ in their respective gradients. Differences of this nature were tested using an F ratio test for non-parallelism (Armitage 1975).

There proved to be sufficient data to test three displays (OLW, NB, NBL) in this manner. The first question to be asked concerns the consistency of evoked probability distributions. This consistency was tested in a number of ways. Within each colony actor generated probability distributions were compared with those generated by the reactor. In the former actor display was held constant and the probability distribution was that of the reactor as recipient. In the latter, reactor display was held constant and the actor was treated as the recipient. On Fair Isle is proved possible to compare probability distributions from 1979 and 1980. Finally, colonies were compared.

7.2.4. Results.

OLW

The probability distributions were dealt with separately in the first instance.

1) 'Not Facing'

Although in itself a rather gross analysis it was suggested that the frequency distributions of the actors use of displays (table 37 , fig. 8).would provide a baseline from which to consider the pattern of recipient response. At this level spatial distribution mirrored an I.D. preference. Its use might thus be expected to indicate to an opponent that I.D. had been infringed. If escape was evoked would **its** probability mirror this awareness of I.D. preference as an even distribution of escape probability?

The escape probabilities were calculated (tables 40-44) and the probability distributions were plotted (figs II - I6). It is immediately evident that an inverse relationship exists between escape probability and distance.

To be considered as fulfilling a signal function it is necessary to demonstrate that this pattern of response is consistent.

(a) Actor/Reactor comparison

The escape probabilities for actor and reactor OLW ('Not Facing') were calculated (tables 40 - 44) and plotted as probability distributions (figs. I7a-I9a). There were subsequently compared using an analysis of covariance. The results are given in table 45a . In all three colonies no significant differences are evident and so a very similar response is elicited in each colony. The consistency of the probability distribution elicited by OLW ('Not Facing') raises the possibility that this display/orientation combination constitutes threat.

The extent of this consistency was further tested by comparing probability distributions within Fair Isle over different seasons.

b) <u>Fair Isle Inter-year comparison.</u>

The OLW 'not facing' probability distributions were calculated and plotted (tables 40-44 , figs. 2Ia) and compared using an analysis of covariance. The results are recorded in table.45b. Once again no significant differences are evident.

Fianlly, a comparison was made between Hoy 1980 and each of Fair Isle 1979 and 1980 (tables 40 - 44 , figs. 2Ia). The results of the analysis of covariance are given in table 45b . This inter-colony comparison re-inforces the previous results and no significant differences are evident.

A number of tests have been made of the consistency of escape probability distributions following OLW-'Not Facing'. In all cases the use of this display/orientation combination results in an inverse relationship appearing between distance and escape probability. The consistency of elicited response suggests that the information upon which a recipient response decision is made is the same in each case and that this display/orientation combination performs a threat function.

This finding is consistent with finding a higher frequency of OLW occurrence at 'not facing' then at 'facing' (table 37). It is also in accord with Perdeck's (1960) suggestion that parallel delivery of this display would fulfill a signal function as a result of the effectiveness with which the white wing patches were displayed at this relative orientation.

OLW is not delivered solely at this orientation. If Perdeck was correct then delivery at a different orientation would be expected to be less effective as a threat.

2) 'Facing'

When OLW is delivered at the 'facing' orientation the white wing patches are effectively hidden. It is conceivable that it be able to fulfil a threat function less effectively. This is supported by the earlier finding that OLW is less likely to be delivered at this orientation (table 37).

To test this it was first necessary to determine whether OLW 'facing' elicits probability distributions with sufficient consistency to confer upon it any functional significance.

The escape probabilities were calculated at each I.D. (tables 40-44). These were plotted together to give the probability distributions (figs II - I6). As with the 'not facing' delivery of this display an inverse relationship is evident between distance and escape probability.

a) Actor/Reactor Comparison.

The probability distributions generated by the actor and reactor were calculated (tables 40 -44) plotted together (figs. I8a&I9a) and the differences in the heights of the probability distributions were measured using an analysis of co-variance. The results are recorded in table 46a. In both Fair Isle 1979 and 1980 data no significant differences emerge.

b) Fair Isle - Inter Year Comparison.

The probability distributions elicited by actor delivery of OLW 'facing' were calculated (tables 4I,43 fig. 2Ib) and compared using an analysis of co-variance (see table 46b). No significant differences were in evidence.

This comparison was extended to include Hoy 1980 data. The latter probability distribution was calculated in table 40a . The inter-colony comparison was based on an analysis of co-variance, the results of which are given in table 46b . No significant difference is evident between Hoy 1980/Fair Isle 1980 although a significant difference in height is evident between Hoy 1980/Fair Isle 1979 (fig. 21b, table 46b).

On the whole the available evidence reveals sufficient consistency to warrant considering OLW 'facing' as having a threat function. In only one case was a significant difference evident. The nature of this difference raises an interesting question. The tests differ only in the heights of the probability distributions. The parallel nature of the distributions suggests that the recipient is acting on qualitatively similar information, the difference resting with a higher general likelyhood of escape on Fair Isle 1979. Since the magnitude of response at each I.D. is similarly effective it is unlikely that this difference is due to information of a qualitatively different nature being conveyed on Fair Isle (1979).

7.2.5. Probability Distributions - Orientations compared.

Delivery of OLW at both the 'facing and 'not facing' orientations revealed sufficient consistency in the escape probability distribution elicited in a recipient to warrant both being considered as fulfilling a threat signal function. Further, the probability distributions at each orientation appear to be qualitatively similar - for both an inverse relationship between distance and escape probability was evident. It remains to be seen whether they exhibit quantitative similarity.

OLW is the most visually elaborate of the bonxie displays and, as such, might be expected to be heavily dependent upon delivery orientation for effect. The visual stimulus presented to an opponent will alter markedly with changes in relative orientation to that oponent.

Perdeck (1960) argued along similar lines and suggested that the more frequent use of OLW parallel to an opponent (see table 37) best displayed a feature of this display subsequently demonstrated to have a signal function, the white wing patches (Spellerberg 1971). Although both delivery orientations elicit qualitatively similar probability distributions, quantitative differences would be expected. The more effective portrayal of the wing patches with 'not facing' leads to the expectation of a greater effectiveness being likely at this orientation. In other words, the greater perceptual deprivation with respect of visual stimuli entailed by a 'facing' delivery would suggest this delivery to be less effective in eliciting a response.

To test this actor generated probability distribution at each relative orientation was calculated (tables 40-44) and plotted (figs. II,I5,I6). An analysis of co-variance was used to test the significance of any height differences.

When this was done the opposite state of affairs to that was expected was found. The results of the comparison are given in table 47. Although only one colony revealed this difference to be significant (Fair Isle 1979) it is evident from figs. II-I6 that the greater probability distributions are always generated by actor 'facing'.

The parallel responsiveness revealed by comparison of the probability distributions (figs. II-I6) for both orientations suggests that the nature of the information extracted and upon which an escape response decision is made is the same at each delivery orientation.

In the m in the probability distributions at each orientation exhibit both qualitative and quantitative similarity with a consistency that suggests that OLW can be considered in a homogeneous fashion with respect to orientation - the relative orientation of its delivery does not affect the response likely to be elicited. The recipient is not basing its ensuing response on information gleaned from delivery orientation. In this respect orientation cannot be considered to convey motivational information which is likely to significantly affect the response shown.

Distance, on the other hand, does exercise a qualifying effect on the response likely from a recipient. The greater the distance separating the interactants the less likely was the recipient to escape.

It is interesting to reflect that the use of this display with respect of distance by the actor was constrained in a discrete manner which mirrored the existence of an I.D. preference (table 37 7). The response shown by the reactor did not and to the latter distance was influential in a continuous manner.

Only one orientation comparison revealed a significant difference (fig. I5a , table 47 7),but a trend was evident in that the higher level of probability distribution always followed a 'facing'delivery. The parallel responsiveness does not suggest that this arose as a result of differences in the information conveyed. The difference may lie on a more contextual basis. When 'facing' the actor is in a better position to press home an attack. This may be read by an opponent resulting in a general and consistent increase in the likelihood of escape.

The independence of elicited probability distribution from orientation raises another functional problem, namely what what components are responsible for eliciting the response. The white wing patches have been demonstrated to have a signal function (Spellerberg 1971). While the latter are visible with a 'not facing' delivery they are effectively concealed with a 'facing' delivery. If OLW was dependent on these flashes for effect then a 'not facing' delivery would have elicited a greater response. This was not the case (figs. 11,15,16) and so an alternative component must have been responsible. There is one component of this display which remains perceptually constant irrespective of relative orientation, the long-call. This may be the important functional component in the interactions comprising the club situation.

Displays incorporating components utilizing different modalities present an interesting functional problem. Does each modality communicate the same or different types of information? It has usually been assumed that the display as a whole serves an agonistic function. However, unless the contribution of components, particularly where different modalities are used, can be defined little progress is likely to be made towards understanding how this function is fulfilled. It is certainly possible that components exericse different effects.

In the red-winged blackbird, Peek (1972) found a display, the song-spread, which comprised both a morphologically enhanced visual component and a vocal component. This display, as a whole, functional in territorial defence but each component was specialised to be effective against opponents in different spatial positions relative to the signaller. The components, although delivered simultaneously, were not necessarily effective simultaneously and could only be understood when considered in relation to the spatial position of the opponent.

Drawing a direct analogy between this species and the bonxie suggests the long-call as the long distance component. However, the results of the present analysis suggest that the long-call is the effective component in close club encounters. This state of affairs may be adaptive. Owing to the cryptic nature of the birds the white wing patches make this display visible over the large distances resulting from their adopting a low breeding density. This component is thus suited as a distance component. The vocal component, due to the excessive wind noise prevailing in bonxie colonies, experiences a greater restriction in effective range and so may be better suited to close-quarter communication. If this were the case then adaptive pressure on this display would have come from both breeding colony and club.

This explanation is consistent with the present findings but not entirely with those of Spellerberg (1971). In painting out the wing patches Spellerberg in no way impeded vocalisation. The effective loss of the patches would have resulted in an increase in the number of close encounters since the component warding off intruders at a distance was absent. If the vocal component was specialised for closer encounters it is difficult to see why intruders were not repelled by this second line of defence.

The situation is further complicated by Spellerberg's finding that this effect was restricted to females. For the present it is possible only to suggest that the vocal component of OLW serves as a close quarter signal but this must be viewed speculatively until a greater understanding of bonxie natural history is reached. An additional problem is, as we shall see (7.3.I) raised by the response pattern elicited by other displays. The problems raised by OLW will be discussed later.

We shall now return to defining the nature of the influence exerted on a recipient by NB and NHL.

NB

7.2.6. NB - the response of the recipient.

The actors use of this display with respect of distances revealed an interesting phenomenon. The spatial distribution was dependent upon delivery orientation (table 38). For 'facing' the distribution reflected an inverse relationship between frequency of occurrence and distance. For 'Not Facing" the distribution mirrored that shown for OLW (table 37).exhibiting a relatively uniform distribution from 1 - 3 BL and a marked decrease at 4BL. This difference begs the question of whether NB, when considered in isolation from the orientation of its delivery, can be considered as a homogeneous display unit. A first step towards answering this question involves determining whether the recipient makes an orientation dependent distinction and if so, whether this difference is consistent enough to confer it with a functional significance.

1) <u>'Not Facing'</u>

The similarity in actors frequency distribution between NB (not facing) and OLW (table 37 & 38) suggests a similarity in probability distribution. The escape probability at each I.D.

was calculated for this display/orientation combination (tables 40 – 44) and the escape probability distributions were plotted (figs. IIb–I6b). It is evident that this is the case and a similar inverse relationship between escape probability and distance is apparant. Does it exhibit a similar consistency?

a) Actor/Reactor Comparison

The escape probabilities at each I.D. were calculated and plotted to form probability distributions (tables 40 –44 ; figs I7c – I9c). These were subsequently compared using an analysis of co-variance. The results are recorded in table 48a . In only one test (Fair Isle 1980) does the actor/reactor difference fail to reach significant proportions. On both Hoy 1980 and Fair Isle 1979 the actor is significantly more likely to elicit escape in the reactor than the other way about.

However, the parallel nature of the respective probability distributions reveals that the recipient is acting in qualifatively the same manner in each case. This suggests that the information upon which a response decision is made is the same in both cases. The quantitative difference in the magnitude of the elicited response must lie with an information source extrinsic to the display. The reason may lie with a general response asymmetry between initiator and reactor in which, by virtue of deciding to dispute, the former has a greater change of success. It probably reflects contests which the reactor has decided not to dispute.

When delivered at the 'not facing' orientation the escape response elicited in a recipient following NB exhibits sufficient consistency to warrant suggesting that this display/orientation combination fulfills a threat signal function.

This contention was further tested by comparing probability distributions both within and between colonies.

b) Inter-Test comparison

This was first done on Fair Isle over 1979 and 1980. The probability distributions were calculated (tables 40 - 44) and plotted (figs. 21c). They were subsequently compared using an analysis of co-variance, the results being recorded in table 48b .

Significant quantitative differences are evident between the respective probability distributions. The nature of the difference suggests that general response levels differed over the two years. One possible explanation lies with temperature differences between each season. Perry (1948) noticed an increasing lethargy in the bonxie associated with increasing temperature. The milder 1980 season would result in less active birds being manifest as an increase in response threshold with birds being generally less likely to respond.

Comparison of the Hoy and Fair Isle probability distributions re-inforces this view. Only one such comparison revealed a significant difference (Hoy 1980/Fair Isle 1979 : Fig 21c , table 48b). This could also be explained on the basis of a temperature dependent difference in response threshold. Greater consistency in prevailing temperature between Hoy 1980 and Fair Isle 1980 would lead to the expectation of greater consistency in responsiveness. This was revealed by the similarity evident in their probability distributions (fig. 21c table 48b). The temperature difference between Hoy 1980 and Fair Isle 1979 (fig. 21c , table 48b) would result in the different response levels.

Until a greater understanding of the inter-relationship between behaviour and external variables like temperature the above suggestion must remain in the realms of speculation.

The escape probability distributions for NB 'not facing' reveal sufficient qualitative consistency to warrant considering this display/orientation combination as fulfilling a threat signal function. The parallel nature of the probability distributions indicate that the information upon which the recipient makes a response decision is the same in all cases. The quantitative differences may result from differences in response threshold determined by variables outwith the immediate display situation (defined in terms of a given display/orientation/distance combination), e.g. interactant asymmetry in willingness to dispute or temperature. If their influence can be verified the wildely differing nature of the variables suggests that the scope of any analysis of displays must be broadened to reach a reliable picture of the nature of a display and the manner in which it is effective.

The inverse relationship evident between distance and escape probability suggests that response is highly distance dependent. Further, the considerable similarity between NB 'not facing' and OLW raises a question regarding the functional integrity of each of these patterns, but this will be discussed later. For the moment, NB 'not facing' was guilty of greater variance in the magnitude of elicited response than was the case with OLW. This greater sensitivity to external variables reveals some grounds for differentiating these two patterns. The greater consistency evident for OLW (table 45) may be associated with a greater specificity.

1) '<u>Facing</u>'

Of the two delivery orientations this was the one most commonly adopted by the actor (table 38). More importantly, the spatial distribution at this orientation was very different from that associated with a 'not facing' delivery. This difference may have its roots in a functional differences between each delivery orientation arising from a differences in the releasing stimulus presented to an opponent.

Actor NB 'facing' exhibited an inverse association between delivery frequency and distance. Finding over 50% of NB 'facing' at one BL re-inforced the possibility of it having a more directly agonistic nature, At this distance an attack would be easy to press home. The close relationship between NB and distance suggests that the recipient would be most likely to escape at 1BL and to show a decreasing escape likelihood as I.D. increases as the recipient moves further out of range of a possible attack.

Escape probabilities were calculated at each I.D. (tables 40-44) and the probability distributions were plotted (figs. II-I6). It is immediately evident that the above logic is at fault and, instead, a relatively similar escape probability is elicited at each I.D. The recipient was as likely to escape at 3BL as it was at 1BL. The greater independence between distance and escape produces a probability distribution very different from those previously found.

Before this display/orientation combination can be considered to fulfil a threat function the consistency of this elicited response must be determined.

a) Actor/Reactor Comparison.

The escape probabilities at each I.D. were calculated (tables 40 – 44) and used to plot probability distributions (figs. 17d– 19d). Because of the greater angular variation between actor and reactor the scope of the analysis was extended to test for both differences in height and gradient. An analysis of co-variance was used for the former and a test for non-parallelism for the latter (Armitage 1975).

The gradients were compared and the results are recorded in table 49a . In no case was any difference of 'significant proportions.

When the respective heights of the probabilities were compared (table 49a) a significant difference is revealed for only one test (Fair Isle 1980). This is most likely an illustration of a difference in response threshold. In the remaining tests (Hoy 1980, fig 17 ; Fair Isle 1979 fig 18) the actor generally elicits an escape probability distribution of greater magnitude than the reactor but the nature of this difference is really obscured by the variety of the probability distributions. Generally, though, sufficient quantitative similarity is evident between these distributions to warrant conferring a signal function on NB 'facing'. This possibility was further tested by an inter-test comparison.

b) Inter-test Comparison.

The probability gradients of actor NB 'facing' for Fair Isle 1979 and 1980 were calculated (tables 40 – 44) and plotted (figs. 21d). The gradients were compared using a test for non-parallelism and the results are recorded in table 49b . No significant gradient differences were evident. Comparison of their respective heights also failed to reveal any significant differences (table 49b).

This comparison was then extended to include Hoy 1980. The gradients of all three probability distributions were tested simultaneously (table 49b). No significant gradient differences were apparent. The similarity of the respective probability distributions extends to their heights. An analysis of co-variance failed to reveal any significant differences (table 49b).

Taking all these results together (tables 49a,b), the high level of the consistency with which NB 'facing' elicits escape in its recipient suggests that this display/orientation combination fulfills a threat signal function.

Thus both 'facing' and 'not facing' NB delivery satisfy one signal criterion - they both elicit consistent responses in their recipient. The interesting thing is that they do so in different ways. With a 'not facing' delivery the response is heavily distance dependent (figs. 21c,d) but with a 'facing' delivery the escape response appears to be largely independent of distance and a similar escape probability is likely irrespective of the distance between interactants. This difference is made all the more interesting by a difference existing in the actors use of NB with respect to distance which was also dependent on delivery orientation.

For the present it remains to be seen whether any significant quantitative differences between these probability distributions exists.

7.2.7. NB - Delivery orientation compared.

For each test the actor generated probability distributions were calculated (for each orientation (tables 40 - 44) and subsequently plotted (figs. II,I5,I6). Each orientation combination was tested for differences in height and in gradient. The results are recorded in table 50 .

In each test the probability distributions reveal significant differences existing that are dependent upon delivery orientation but the nature of the differences is not absolutely consistent.

From table 50 it is evident that for only Fair Isle 1980 do the differences arise with respect to differences in height, but not in gradient. In Hoy 1980 and Fair Isle 1979 the opposite is the case and for both significant differences emerge between the gradients with no difference in height. Although Fair Isle 1980 fails to reveal a significant gradient differences a similar trend is evident in as much as the respective slopes are divergent rather than being parallel. In all cases the 'facing' delivery is more threatening and although the evidence is not conclusive it appears that significant qualitative differences exist which are dependent on delivery orientation. NB 'facing' is the more 'threatening' of the two variants. The response it elicits is largely independent of I.D. and is as likely to result in opponent escape at 3BL as it is at 1BL. NB 'not facing' does not offer a similar threat quality. Response to this variant is not to the display alone but is also influenced by I.D. i.e. response is distance dependent.

The probability distributions elicited by each relative orientation differ in a qualitative manner which suggests that the information upon which a response decision is based is, in the eyes of the recipient, different at each relative orientation.

From the point of view of the different visual stimuli presented to an opponent by adopting different delivery orientations this finding is not surprising. There are a number of additional lines of evidence which support NB 'facing' being the threat display.

Only when delivered at the 'facing' orientation does NB correspond to the intention movement for attack from which the display presumably evolved. This is also the only orientation from which attack can actually occur. Hence the response elicited is to be expected. Further, the actor's use of this display with respect to orientation (table 38) revealed a greater likelihood of occurrence at the 'facing' orientation which perhaps reflects both signaller and recipient using and perceiving this display/ orientation combination in a specific threat manner.

The difference between the actors use of NB 'facing' with respect to distance and the extent of the reactors escape response with respect to the same variable provides an interesting problem. In the former, frequency of occurrence decreases with distance but in the latter escape probability is independent of I.D. (cf. table 38 and tables 40,41,43). Since the actor can only physically attack when within about 1BL of an opponent it might have been expected that as I.D. increased the recipient would have been less likely to have escaped. That this is not so suggests that NB 'facing' can be considered to be a ritualised threat display. The recipient is responding to the visual stimuli it perceives and not to any other variable e.g. distance. The ritualisation involves a fixation of response rather than a gross exaggeration of any aspect of the posture. Why this should be so will be discussed in more detail latter.

For the present it seems reasonable to conclude that the qualitative difference in elicited escape provides sufficient grounds for suggesting that NB, per se, cannot be considered as a homogeneous display unit. The associated orientation has important functional implications for the nature of the behavioural influence on a recipient and for the nature of the information conveyed. Indeed it may be possible to ascribe a threat signal function to NB 'facing' alone.

NBL

7.2.8. NBL - the response of the recipient.

There proved to be sufficient data to test one further display in this manner, NBL. The form of this display is identical to NB, differing only in the addition of a vocal component, the long call. There are grounds for considering that this similarity extends to a behavioural level. From table 39 it is evident that the actor's use of NBL with respect to both orientation and distance mirrors that shown by NB. As a result it might be expected to see the similarity extend to the manner in which a recipient is influenced.

1) 'Not Facing'

The escape probabilities at each I.D. were calculated (tables 41 - 44) and probability distributions were subsequently plotted (figs. 13 - 16). The above logic appears sound and, like NB, NBL 'not facing' elicits a probability distribution characterised by an inverse relationship between escape probability and distance. How consistent is this response?

a) Actor/Reactor Comparison.

Actor and Reactor generated probability distributions were calculated (tables 4I - 44) and plotted (figs. I3 - I6). The extent of differences in height and gradient were determined using an analysis of co-variance and a test for non-parallelism respectively (Armitage 1975). (See table 5Ia).

From figs. 20a, c it is evident that the actor generated probability distributions exhibit a higher level of escape though in only one case is this difference significant (Fair Isle 1979; fig. 20a ; table 5Ia). No significant differences are revealed in their respective gradients (table 5Ia).

The parallel nature of respective probability gradients suggests that the nature of the information upon which response is based is the same in each case. The difference in the overall level of responsiveness, while not generally reaching significant proportions, may be attributed to an actor/reactor asymmetry and probably reflects the incidence of contests in which the reactor was reluctant to dispute the resource.

b) Inter-test Comparison.

Actor generated distributions over two seasons on Fair Isle were calculated (tables 4I-44), plotted together and compared (figs 22a , table 5Ib). Once again a significant difference is evident for the general level of responsiveness but not in the nature of the response. The parallel nature of the probability distributions suggests that the information upon a response decision is reached is the same in both cases. The manner in which the probability distributions differ is consistent with the pattern found for NB 'Not facing', each having a higher response level in 1979.

this was explained in terms of temperature dependent response thresholds.

Once again a display/orientation combination exhibits sufficient consistency of escape response in a recipient to warrant labelling it as a threat signal.

2) 'Facing'

The actors use of NBL with respect of orientation mirrored that for NB (table 38,39). This similarity was also shown for its use with respect to distance. 'Facing' delivery was the most common and it was used less frequently as I.D. increased (table 39). It seems reasonable to assume that this similarity would extend to cover the response elicited in an opponent.

The escape probabilities at each I.D. were calculated (tables 4I-44) and used to plot probability distributions (figs. I3-I6). The latter are rather more independent of distance than was the case for 'not facing' and a strong resemblance to those elicited by NB 'facing' (figs. I3 -I6) is evident.

How consistent is the response?

a) Actor/Reactor Comparison.

Sufficient data was available to compare actor and reactor generated probability distributions on Fair Isle 1979. (Table4I,42, fig. 20b). The probability distributions were tested for differences in height and gradient using an analysis of co-variance and test for non-parallelism respectively (Armitage 1975).

In neither case did any significant differences emerge (table 52a).

b) Inter-Test Comparison.

Actor generated probability distributions were calculated on

Fair Isle on 1979 and 1980 (tables 4I,43-), plotted (figs 27b) and compared (table 52b).

No significant differences in height or gradient were evident.

When NBL is delivered at the 'Facing' orientation sufficient consistency is evident for the elicited escape response of a recipient to warrant labelling this display/orientation as one fulfilling a threat signal function.

Differences are also apparent between each delivery orientation. Do these differences assume significant proportions?

7.2.9. NBL - Orientations compared.

The 'facing' and 'not facing' probability distributions were plotted together (tables 4I,43 ; figs. I5,I6). These were subsequently examined for differences in their respective heights and gradients. The results are recorded in table 53 .

With a comparison of this nature the similarity of orientation dependent probability distribution between NB and NBL is obvious (cf. figs. I5b,c). In both tests significant differences exist in the gradients of the probability distributions. For 'facing' the response shown is largely independent of distance. For 'not facing' a highly distance dependent response is elicited. This qualitative difference suggests that the information upon which an escape response decision is made is different at each orientation.

Considering the difference in the stimulus pattern presented to an opponent a difference would be expected. This difference is consistent with 'facing' delivery being the most threatening aspect by virtue of the ease of a following attack. Formally, NBL is indistinguishable from NB. Thus NBL has changed little from the original attack intention from which it presumably evolved.

This display is made more interesting than NB by the addition of a vocal component, the long-call. When orientation changes the visual stimulus pattern changes considerably. Vocal components are not so constrained and presumably present a stimulus which is independent of relative orientation. The significant difference between the probability distributions (figs. 15 & 16 , table 53) is likely to have arisen from a change in stimulus parameters. Thus the response of the recipient following NBL is likely to be dependent upon the visual components since only they changed. The vocal component is perhaps redundant with respect to threat quality.

This conclusion is made all the more interesting when compared to that offered for OLW suggesting that only the vocal component was responsible for threat quality. Further light will be thrown on this problem when displays are compared.

For the present it is evident that orientation is an important determinant of recipient response following NBL. If no consideration is given to this variable it is impossible to treat NBL as a homogeneous display unit.

7.3.1. Display Comparison.

So far the criterion that each display/orientation combinations has had to fulfill to be considered having a threat function was to demonstrate that they induced a consistent escape probability distribution in a recipient. Each (OLW,NB,NBL) has fulfilled this criterion and so can, within the limits set by the present analysis be considered as threat signals.

The data upon which this conclusion was based were gathered in the club situation. If displays are to be credited with fulfilling a signal function then consistent differences between each display would be expected with respect to the response they elicit from a recipient. Failure to elicit consistent differences would call into question any functional distinction between these behaviour patterns.

Displays were compared within each colony using actor generated probability distributions. Comparison was based on the delivery orientation.

7.3.2. 'Not Facing'

Within each colony the probability distributions were calculated for all three displays (tables 40 - 44) and plotted together (figs.23b - 25b) The ensuing probability distributions were tested for differences in height and gradient using an analysis of co-variance andaa test for non-parallelism respectively (Armitage 1975). The results are recorded in table 54.

Displays were analysed in dyads. Each display was compared with only one other display at any time. The principle reason for adopting this approach was to enhance the likelihood of detecting and isolating the influence exerted by individual components. For example, NB and NBL differ only in addition of long-call in the latter. Any difference between these displays in the pattern of responsiveness elicited in an opponent could be attributed to this single component. OLW and NBL differ in the visual but not in auditory components. Any ensuing differences could be attributed to differences in the visual stimulus presented. In this way it might prove possible to build up a picture not only of how the display exercises its effect but also about how individual components contribute to this overall effect. Isolating component influence might be an important tool for future analysis of the nature of the information conveyed.

From table 54 it is evident that when each of these displays is delivered at the 'not facing' orientation any differences in either height or gradient fail to reach significant proportions. This is true for each test.

On the basis of this high prevailing degree of similarity existing between the escape probability distributions of OLW, NB, NBL when delivered at the 'not facing' orientation. The recipient does not make any distinction between these patterns and so it is assumed that the information upon which a response is based is the same in each case. At this relative orientation evidence for a functional distinction between these patterns is lacking and labelling each of OLW, NB and NBL as distinct threat signals is not justified. Considering the variation in form embraced by these patterns this finding is rather surprising.

7.2.3. 'Facing'

The escape probability distributions were calculated (tables 41 - 44), plotted (figs. 23a-25a) and examined for differences in height and gradient. The colony by colony results of these comparisons are recorded in table 55 .

To facilitate the detection of differences in the contribution of various components display dyads were compared. The results will be discussed dyad by dyad.

a) NB/NBL

Both of these displays employ the same physical form (see fig. 3) and differ only in the vocal addition to NBL. Because of this formal similarity any emergent difference in response could be attributed to the effect of this vocal component.

Differences in height were examined first. (figs. 24a, 25a; table 55). In both the Fair Isle tests (1979 and 1980) no significant differnnces in height were evident. In both tests NB and NBL elicited very similar response levels.

The consistency of response extends to their respective gradients. A test for non-parallelism failed to reveal any significant gradient differences. Table 55.

Each of these display, NB and NBL, elicit a similar level and similar pattern of recipient response which is characterised by a relatively constant escape probability at each inter-individual distance.

When NB and NBL are given at the 'Facing' orientation the overall similarity of the recipients response suggests that the information upon which this response is made is the same for each of these behaviour patterns, and attributing each with a distince signal function is not warranted.

b) <u>OLW/NBL.</u>

In contrast to the two displays considered above both OLW and NBL share a common vocal component, the long call, but differ widely in physical form (cf. figs. 2 & 3). Any difference in the pattern of recipient response could be attributed to this formal difference.

Firstly, the heights of the distributions were compared (table 55). no significant differences were evident (figs. 24a, 25a). When attention was switched to their respective gradients a more complicated picture emerged (figs. 24a, 25a, table 55). On Fair Isle in 1979 a significant gradient difference is evident and the probability distributions are perpendicular to one another. In 1980, though, a similar comparison fails to reveal a significant difference, although a similar trend is evident and the probability distributions are distinctly divergent.

Although the data does not present itself in a totally conclusive form it seems likely that the information base responsible for eliciting a response following OLW is different from that for NBL. Both displays share a common vocal component hence the difference in recipient response is likely to have arisen from a difference in the visual stimulus of each display as presented to an opponent.

The response elicited by OLW is largely distance dependent while that following receipt of NBL exhibits a greater degree of independence from distance. On the basis of this result labelling OLW and NBL (when delivered at the 'facing' orientation) can be considered as distinct threat signals.

c) <u>OLW/NB</u>.

Of the three displays analysed here this combination represents the extreme - they have no components in common (cf. fig. 2 & 3), Hence differences would be expected between them.

Within each colony actor 'facing' probability distributions were calculated (tables 41 -44), plotted (figs. 23a-25a) and examined for differences in height and gradient. The results are recorded in table 55.

The difference in the heights of the respective probability distributions failed to reach significant proportion (table 55).

Comparison of their gradients revealed a different picture with two out of three tests offering significant differences (Hoy 1880, Fair Isle 1979; table 55). Although a significant difference is not forthcoming from the remaining test (Fair Isle 1980, table 55) a trend approximating to that shown in the other tests is apparent. The probability distributions for these displays are divergent and no hint of their following a parallel course is evident.

This latter result blunts the force of the argument but despite this the available evidence suggests that the information extracted by the recipient upon which an escape response is based differs for each of OLW and NB. When delivered at the 'facing' orientation the escape probability distributions of NB and OLW differ with sufficient consistency to support the view that these display/orientation combinations are distinct threat signals.

7.4.1. Conclusion.

On studying threat the present analysis rests on a number of assumptions:-

1) Threat displays are used where access to a limited resource is disputed and ownership can only pass into the hands of one of the contestants. It is thus logical to assume the fulfillment of a threat function will be revealed by determining the consistency with which a given action pattern elicits escape in a recipient.
2) Where escape is measured in terms of probability distributions differences in their respective

gradients represent differences in threat quality.

3) If displays are to be considered to fulfill a signal funttion each must elicit a consistent response and one which differs from each other display.

Two non-display influences were identified here, distance and orientation. The importance of the latter was suggested by the finding that a number of interactions were settled on the basis of an orientation change. Further, these exhibited a relatively high degree of independence from I.D. (table 36). The importance of orientation led to display being dealt with largely in terms of differences in their delivery orientation. They could be delivered at either a 'facing' or 'not facing' orientation.

Both distance and orientation are important non-display influences. However, they cannot be regarded solely in such terms. The influence of each of these variables was not the aame for each display. The response shown to OLW was qualitatively similar at each delivery orientation. The recipient ignored the presented form of OLW. However, the response shown was highly distance dependent (figs. II-I6).

For both NB and NBL both variables were influential in guiding response (figs. II - I6). The difference centred on the influence of distance. Response on receipt of a 'not facing' delivery was highly distance dependent, whereas that following a 'facing' delivery exhibited a relatively high independence of distance.

Faced with a number of displays, all of which, when considered independently elicit a consistent response, they must fulfil one further criterion to warrant being labelled as independent signals - the response to each display must be specific to that display.

Displays were treated in terms of their delivery orientation. The probability distributions elicited by OLW, NB and NBL following a 'Not Facing' delivery were indistinguishable in terms of their respective gradients.and so could not be considered to differ in threat quality. The recipient, according to the display criteria defined, did not distinguish between these behaviour patterns and the existence of a range of (threat) displays would appear to be superfluous. This is surprising in view of range of forms encompassed by these displays. This, together with the highly distance dependent nature of the response elicited by each pattern (each interactant being less likely to escape as I.D. increases) suggests that the posture is ignored and response is based on the perception of the distance between individuals.

The same behaviour patterns viewed from a different orientational perspective revealed a different picture in some respects (figs. 23 - 25).

When delivered at the 'Facing' orientation the lack of any significant gradient differences between NB and NBL (figs. 24 & 25 table 55) suggested that the information upon which recipient response was based was the same in each case. The patterns are formally similar and differ only in the addition of the long-call to NBL. It is on the basis of this addition that a distinction is made between these patterns by a human observer. Failure to find an appropriate difference in their respective probability distributions suggest that the recipient (the individual to whom the display is likely to be of greatest relevance) fails to make a similar distinction. In future studies of display behaviour it might prove fruitful to place the analysis in a relevant framework e.g. viewing the interaction from the point of view of its participants, rather than as an external observer.

In terms of the definition of threat adopted here there are no grounds for labelling these patterns as separate threat signals. There are grounds for considering both NB and NBL together as a single threat display. In the first place they both utilise the same formal characteristics (fig. 3). Secondly, they elicit the same response in a recipient. (figs. 24 &25, table 54). Further this response is relatively independent of distance and so response is more likely to the display and not some extraneous variable like distance.

If NB/NBL is treated as a single display unit then the significant differences between this and OLW (figs 24 -26a, table 55) warrant concluding that OLW (when delivered at the 'facing' orientation) can also be considered as a threat signal.

So, when displays are viewed from the point of view of their delivery orientation two different views emerge. When delivered at the 'not facing' orientation the displays of the bonxie cannot be considered to act as distinct threat signals and the highly distance dependent nature of associated response (fig. 23b - 25b) suggests a greater importance for the latter variable in determining response.

When delivered at the 'facing' orientation two threat displays are evident. NB,NBL and OLW demonstrated considerable consistency in the response they elicited when considered independently (e.g. figs 11 - 16 , tables 45 - 53). Comparison of each display revealed that NB/NBL must be considered as a single display which, because of significant differences in the gradient of the elicited probability distributions (figs. 24,25 tables 55), was distinct from OLW in executing a threat function.

The dependence of displays on orientation for their effectiveness (as defined in the present analysis) is consistent with the suggestion that for a specific response to be elicited a specific 'releasing' stimulus must be presented to an opponent. The displays considered here are predominantly visual. Any change in orientation will result in a marked change in the visual stimulus presented to an opponent. In terms of a signal function evolution would appear to have acted on a single stimulus pattern.

Up until this point displays have been recorded simply because the observer noted their occurrence. This is likely to have produced a confused picture of display effect. For NB in particular the delivery orientation was a very important determinant of recipient response and the stimuli it considered relevant. For 'not facing' distance was an important cue, whereas, with 'facing' the display itself was important. In future these variables, at least, must be considered and their influence determined before any display can be identified as such. The most appropriate means of achieving this end is to view the interaction from the point of view of its participants.

Viewed from an orientational perspective displays can be considered as such, i.e. specialised to convey information, when delivered at the 'facing' orientation. However, even at this orientation complications arise because of the distance dependent nature of the elicited OLW 'facing' response (figs. II–I6). Analysis of OLW in isolation from the remaining displays revealed a probability distribution that was independent of orientation. Delivery at 'facing' resulted in a similar distribution to that elicited by 'not facing' (figs II – I6). In this light 'facing' delivery does not confer any threat quality on OLW. The inter-display 'not facing' comparison (figs. 23–25, table 54) also failed to reveal any qualitative differences between patterns as divergent in form as OLW and NB and a threat label could not be attributed to these patterns. By implication the OLW 'facing' distribution is not different from that given to OLW, NB and NBL when the latter adopt a 'not facing' delivery (e.g. figs. II–I6).

The singular nature of the elicited probability distributions for each of these pattern/orientation combinations suggests that the information upon which recipient response is based is the same in each case. Hence, OLW 'facing' cannot be attributed with fulfilling a signal function. As in the remaining cases the OLW 'facing' distribution is heavily distance dependent (e.g. fig II) with escape probability being inversely proportional to distance The similarity between all four posture/orientation combinations opens up the possibility that distance is a more important determinant of recipient response than the pattern itself.

The 'display' behaviour of the bonxie can, in terms of the present analysis, be split into two;

1) A distance dependent group comprising OLW ('facing' and 'not

facing') and NB and NBL ('not facing').

2) A distance independent group comprising NB and NBL ('facing').

Of these two groups only the latter can be considered as a threat signal. Both the constituent behaviour patterns are identical in form and so might be expected to elicit a similar response. Further, and more importantly, their ability to elicit an escape probability in a recipient which is insulated from the influence of external factors, e.g. distance, exemplifies the response expected from a threat display - it is the behaviour pattern itself and not some extrinsic factor which the recipient is responding to.

In the former group the opposite is the case. Not only is the response highly distance dependent but it is thus despite the variety of physical forms, morphological enhancement and modalities which are responsible for their elicitation.

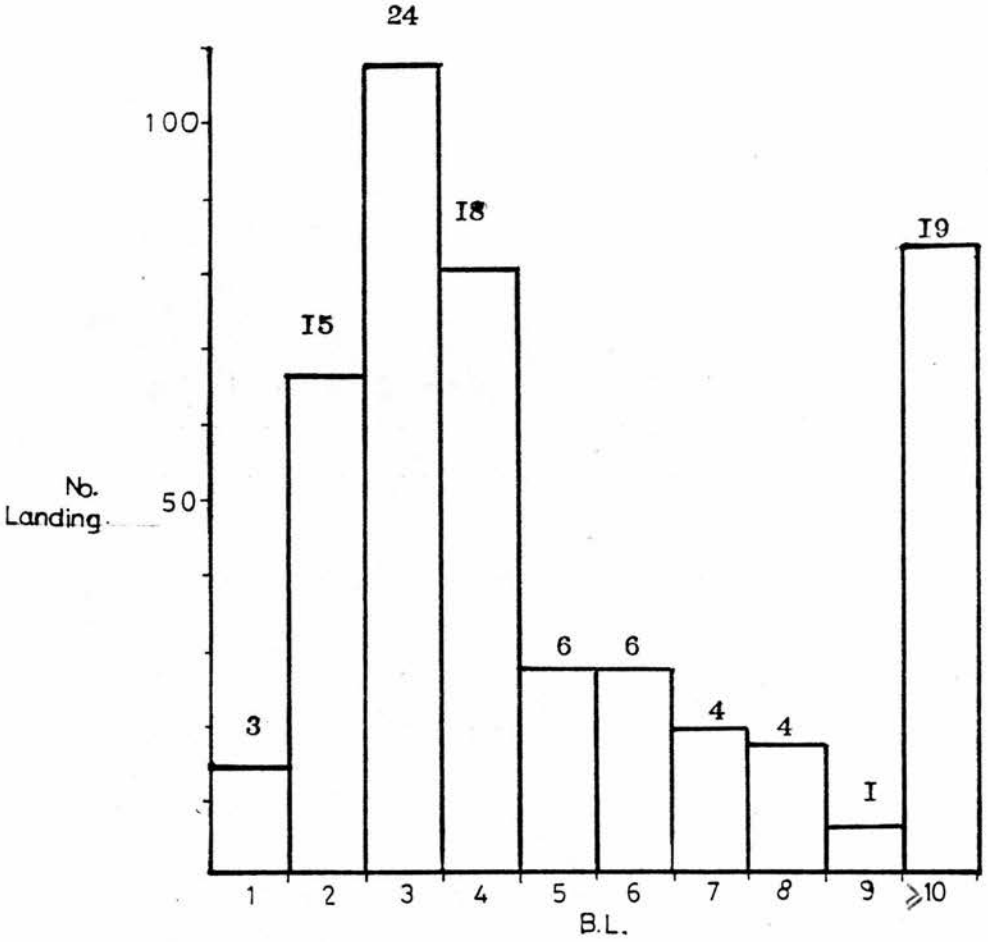
Within the limits of the present analysis it would appear that the bonxie display repertoire comprises only one display serving a threat function. This eliminates the problem of having to explain the existence of a range of displays but raises a further problem. What role does this display play in the mechanism used for resolving disputes? The scope of the present analysis does not extend this far. Display behaviour has been brought into line with more recent theoretical work (e.g. Maynard Smith 1974). The way is open to investigate this and other theoretical models. This empirical demonstration of the extent of the threat repertoire will provide a more realistic point not only for the investigation of existing theoretical models but also for the development of existing and new models.

The stimulus for the present study was a contradiction between a view arguing that display behaviour conveyed intentional differences and one suggesting the opposite. NB/NBL is delivered at two distinct orientations. Could this serve to convey gross motivational differences? The answer to this is likely to be no! The gradient differences between NB/NBL 'facing' and 'not facing' (figs. I3 - I6) could form the basis of an argument suggesting that the 'not facing' distribution is a less intense response than that shown to 'facing' and so is consistent with the possibility that relative orientation conveys motivational differences and are read as such by the recipient. The counter argument rests on the finding that NB 'not facing' elicits distributions almost identical to OLW 'not facing' despite the many differences that exist between these patterns. Because the birds tend to sit parallel to one another the initial stages of any interaction are bound to involve birds adopting 'not facing'. A bird neighbouring one who adopts NB and who is unwilling to dispute may depart before engaging in dispute. In such cases it is not unlikely that the distance separating them would be used as a basis for response. Response to NB 'not facing' may not reflect receiption of a low intensity threat but simply reflect the actions of birds unwilling to engage in dispute. This argument receives further support from the popularity of NB in orientation-change interactions (tables 36) and the fact that response is to the change. For 'not facing' to have any motivational significance adoption of this stance must be under actor control. Because birds sit facing into the wind adoption of this stance is inevitable and so cannot be assumed to have any signal function.

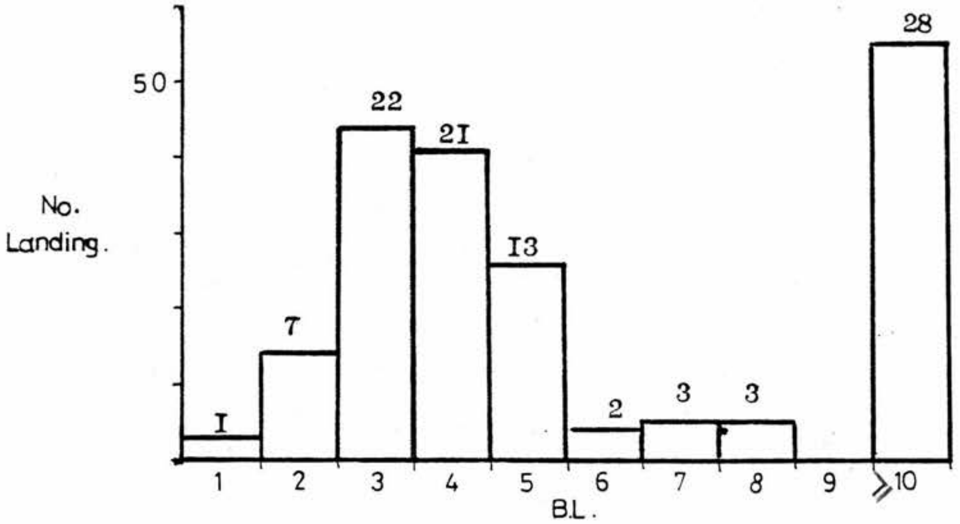
It seems likely that the bonxie possesses only one threat signal, NB/NBL 'facing', and may do little more than signal, as suggested by Caryl (1979), that the signaller is in dispute.

A number of other problems remain to be considered. In spite of the elaborate nature of OLW it does not appear to have a threat function. Indeed it may not fulfill such a function and so the method used to define its function may have been inappropriate to aid understanding of OLW.

Secondly, the long-call component of NBL did not appear to exercise an effect and so itss inclusion remains a mystery. It is feasible that the method may have been inappropriate to detect the nature of its influence. Both of these problems will be discussed in the next chapter.

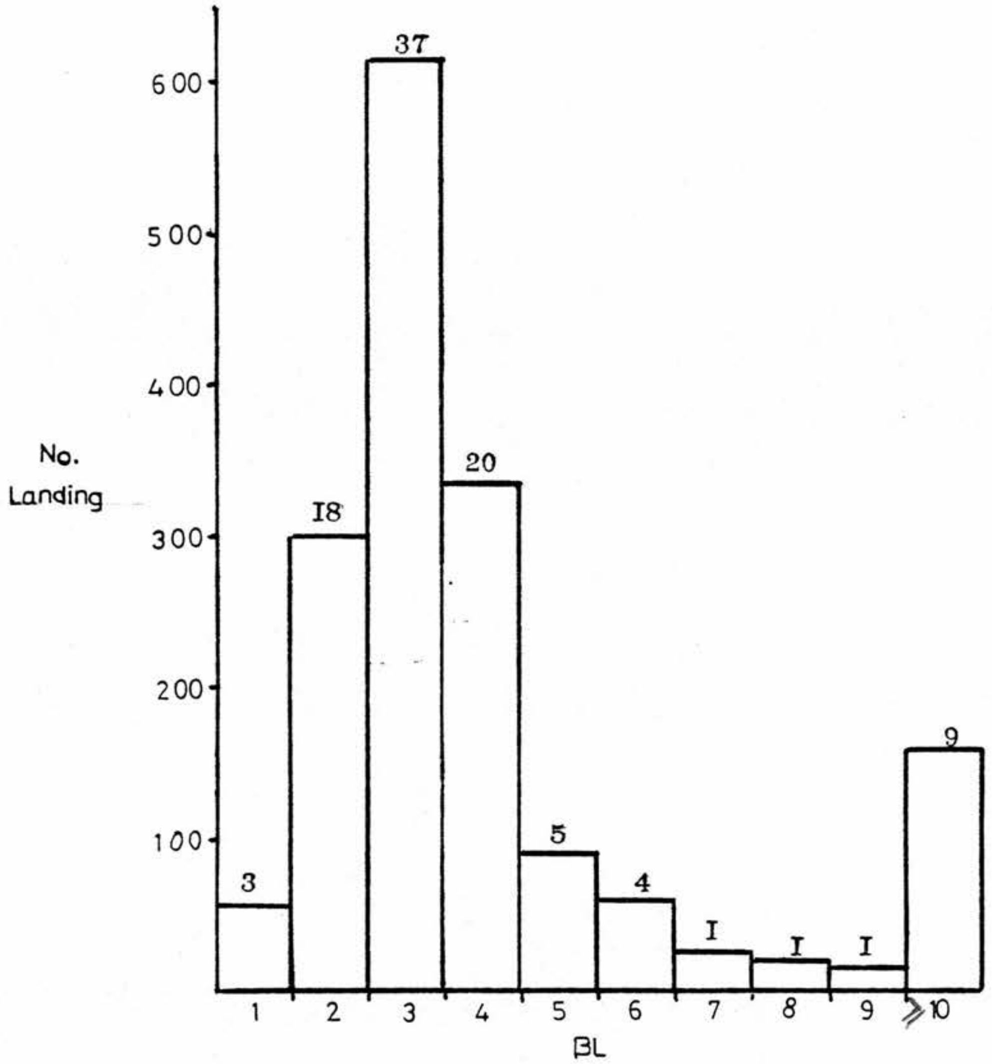


a. hoy 1980

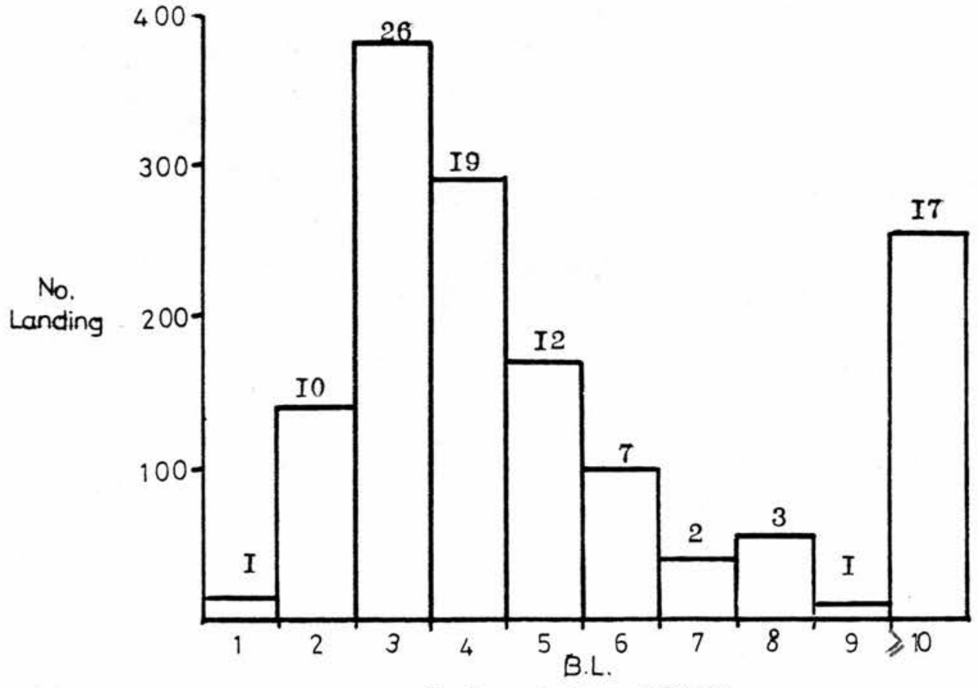


b. hoy 1979

Fig 6.



a. fair isle 1980



b. fair isle 1979

Actor Display	Inter - individual distance.							(total)
	I	2	3	4	5	6	N	%
NB		I2	I3	3	3	I	32	47
NN	I	5	4	I	I	I	I3	20
NfB		2	4	I	I		8	I2
OLW	2	2	I				5	7
NBL		2	2				4	6
BLW		2					2	2
NS	I		I				2	2
NbBpL		2					2	2
NBT		I	I				2	2
N.	4	28	26	5	5	2	70	
%(total)	6	40	37	7	7	3		I00

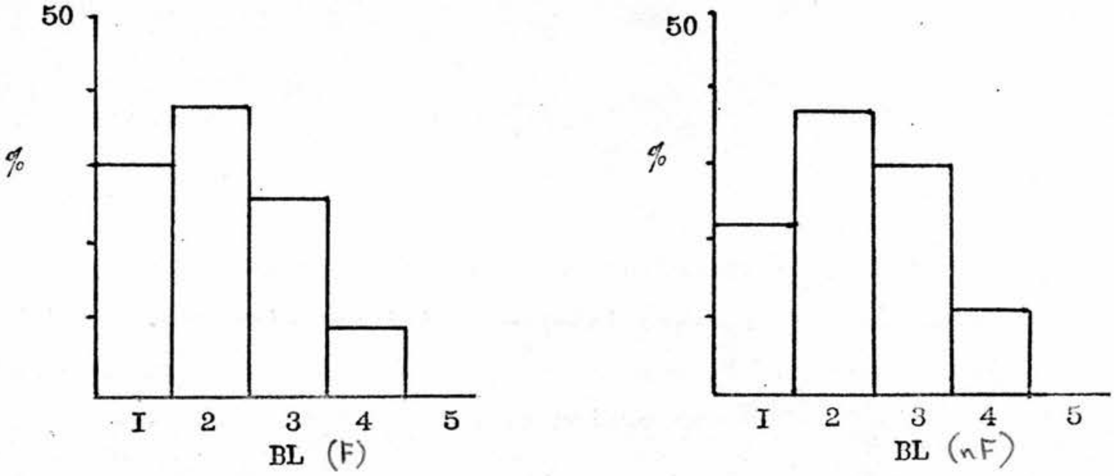
a. Fair Isle I979

Actor Display	Inter - individual distance							(total)
	I	2	3	4	5	6	N	%
NB	I5	38	I8	I3	I		85	59
NN	5	I7	4	2			28	I9
NBL	4	2	2	I			9	6
NBT	5	I	I	I			8	6
OLW	2	I	3	I			7	5
NbBpL	3		2				5	3
NfB	I						I	I
Bend			I				I	I
N.	35	59	3I	I8	I		I44	
%(total)	24	4I	22	I2	I			I00

b. Fair Isle I980.

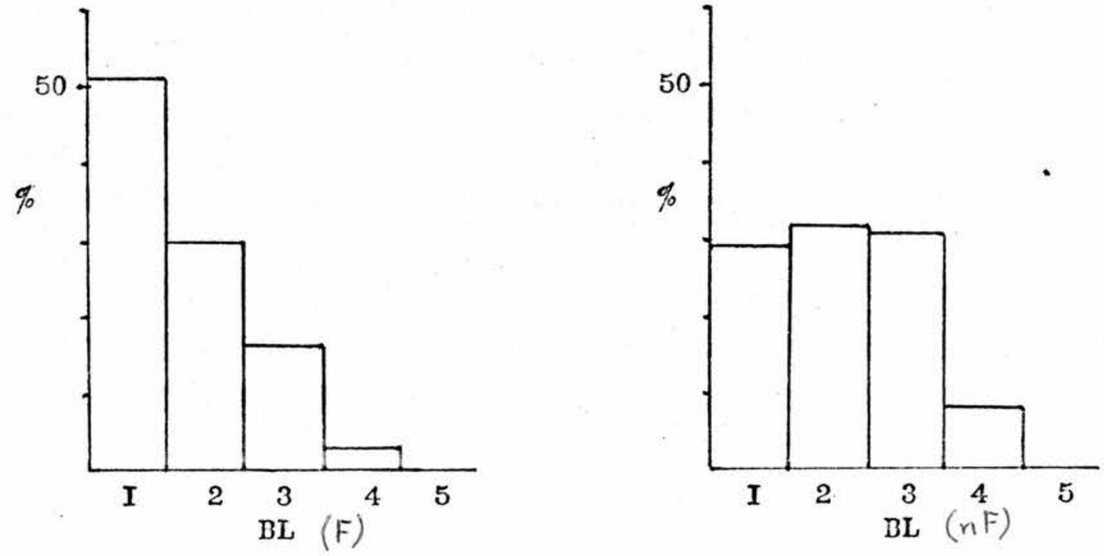
Table 36: The number of orientation change interactions, resulting in reactor escape, at each I.D.

	% per I.D.						
	I	2	3	4	5	N	%
Facing:	30	38	26	6	–	279	32
Not Facing:	22	37	30	II	–	589	68



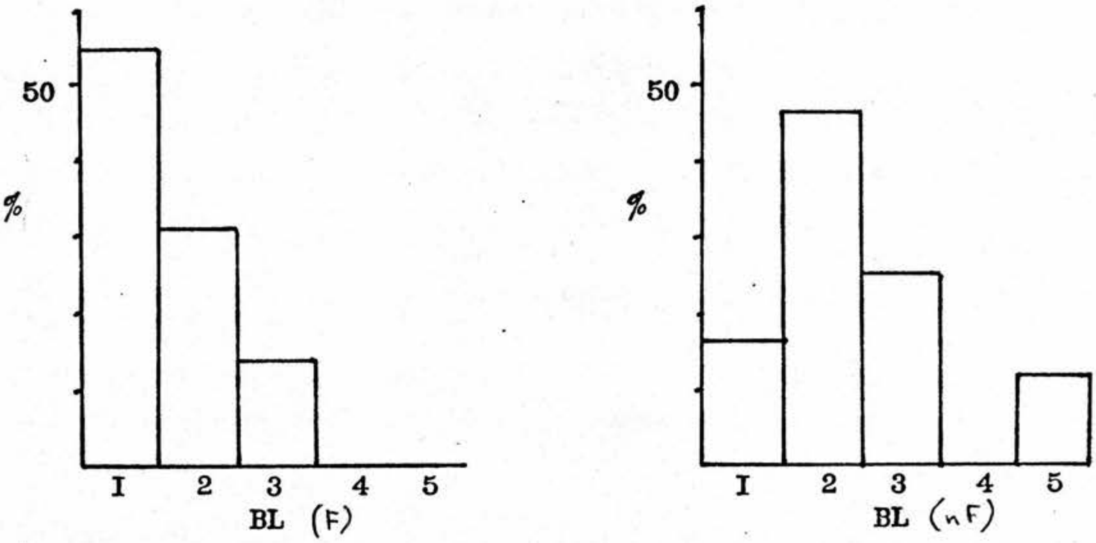
a. Proportion of actor display at each I.D. after OLW

	% per I.D.						
	I	2	3	4	5	N	%
Facing:	5I	30	I6	3	–	287	67
Not Facing:	29	32	3I	8	–	I39	33



b. Proportion of actor displays at each I.D. after NB.

	% per I.D.						
	I	2	3	4	5	N	%
Facing:	55	3I	I4	–	–	II0	6I
Not Facing:	I7	46	25	–	I2	69	39



c. Proportion of actor displays at each I.D. after NBL.

ACTOR OLW

	Inter-individual distance									
	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	81	16	54	35	48	28				
Not Facing	67	36	46	45	28	42	7	15	25	8

ACTOR NB

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	53	45	64	25	54	13	66	9		
Not Facing	50	12	46	12	25	8				

a. Actor

REACTOR OLW

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	–		–		–		–		–	
Not Facing	50	20	32	19	13	15	0	17		

REACTOR NB

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	50	10	57	7	50	6				
Not Facing	28	18	6	15	1	10				

b. Reactor.

Table 40: Hoy 1980 - Actor and reactor response probabilities These were calculated as the relative escape frequency at each I.D. shown by the recipient of the display.

ACTOR OLW. Inter-individual distance

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing			89	18	75	16	60	10		
Not Facing	79	14	61	64	45	66	17	23	33	27

ACTOR NB

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	64	25	65	31	67	21	44	9		
Not Facing			69	29	58	26	50	12		

ACTOR NBL

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	65	20	65	17	75	4				
Not Facing			71	17	56	9			22	8

ACTOR BLW

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	–		–		–		–		–	
Not Facing			75	16	64	11	33	9		

Table 4I: Fair Isle I979 - Actor response probabilities. These were calculated as the relative frequency of escape at each I.D. shown by the recipient.

REACTOR OLW

Inter-individual distance

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing			88	8			60	5		
Not Facing	60	5	67	21	44	16	11	9	0	11

REACTOR NB

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	30	10	58	12	62	8				
Not Facing	40	15	20	25	38	29	0	10		

REACTOR NBL

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	57	7			66	9				
Not Facing			43	11			20	6		

Table 42: Fair Isle 1979 - Reactor response probabilities. These were calculated as the relative escape shown by the recipient at each I.D.

Inter-individual distance

ACTOR OLW	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	87	67	64	58	31	32	42	7		
Not Facing	71	78	45	108	25	70	21	28	8	12

ACTOR NB	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	70	76	73	30	66	12				
Not Facing	46	28	14	7	22	9				

ACTOR NBL	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	71	41	65	17	64	11				
Not Facing	67	12	46	15	13	8				

Table 43: Fair Isle 1980 - Actor response probabilities. These were calculated as the relative escape frequency shown by the recipient at each I.D.

REACTOR OLW

Inter-individual distance

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	55	20	50	8	25	12				
Not Facing	42	26	31	26	14	21	18	13		

REACTOR NB

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	55	20	50	18	50	4				
Not Facing	43	28	15	20	17	6				

REACTOR NBL

	1		2		3		4		5	
	pE	N	pE	N	pE	N	pE	N	pE	N
Facing	–		–		–		–		–	
Not Facing	50	12	38	11	0	6				

Table 44: Fair Isle 1980 - Reactor response probabilities. These were calculated as the relative escape frequency shown by a recipient at each I.D.

Fig II : Hoy 1980. The escape probabilities shown by the reactor at each ID on receipt of a) OLW and b) NB when given by a staying actor (from table 40a). The probability distributions are shown at each delivery orientation.

X— — — —X Facing

O————O Not Facing

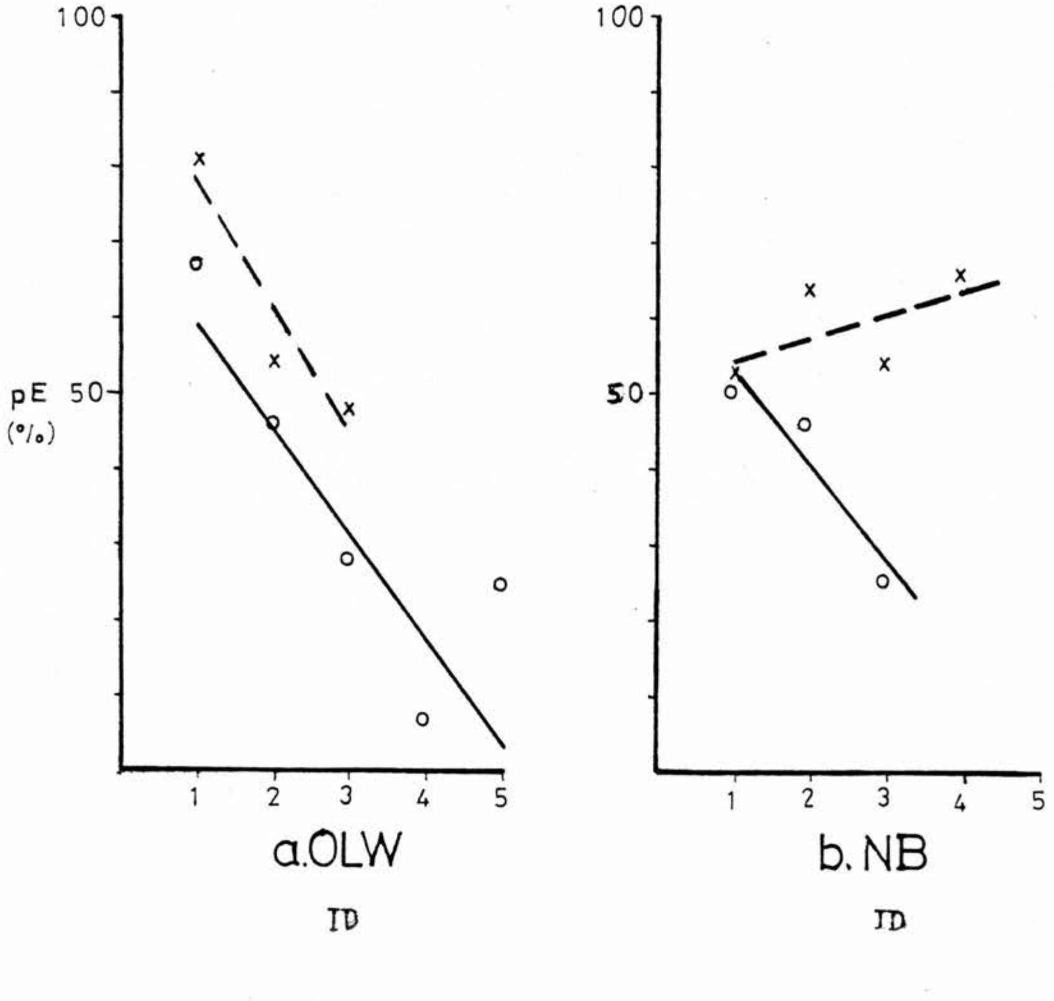
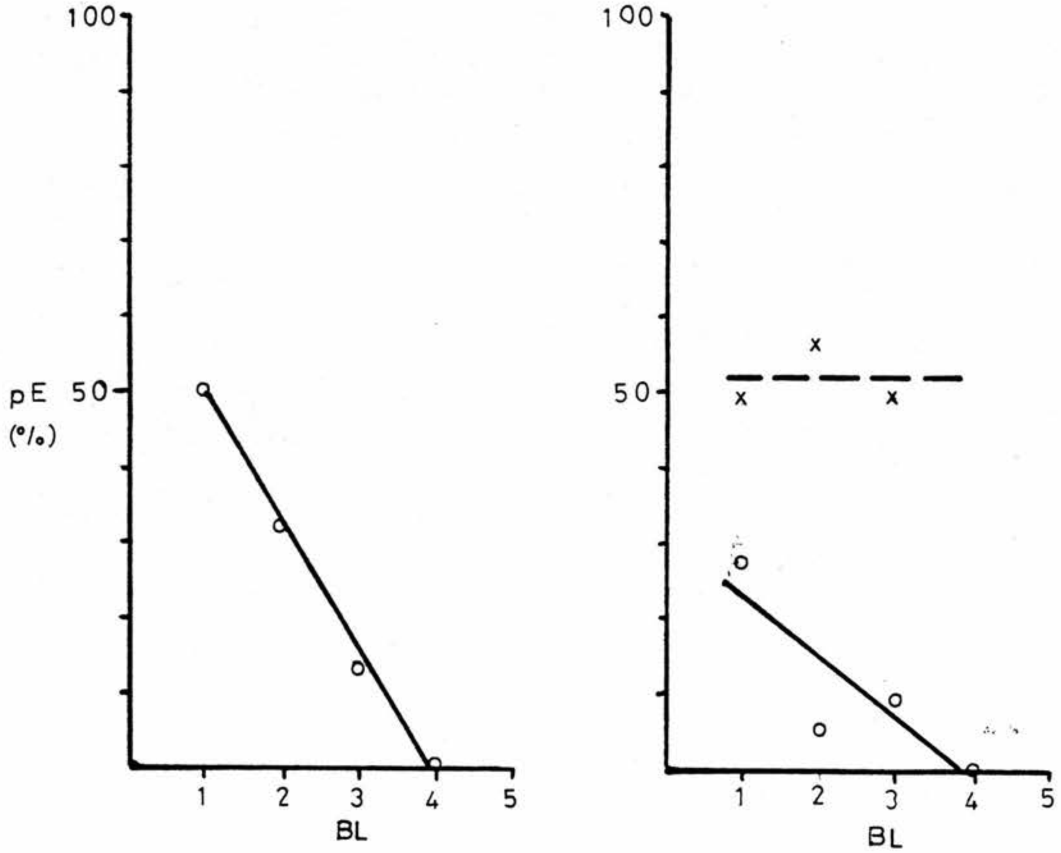


Fig 12 : Hoy 1980. The escape probabilities shown by the actor at each ID on receipt of a) OLW and b)NB when given by a staying reactor. The The probability distributions are shown as regression lines for each delivery orientation.

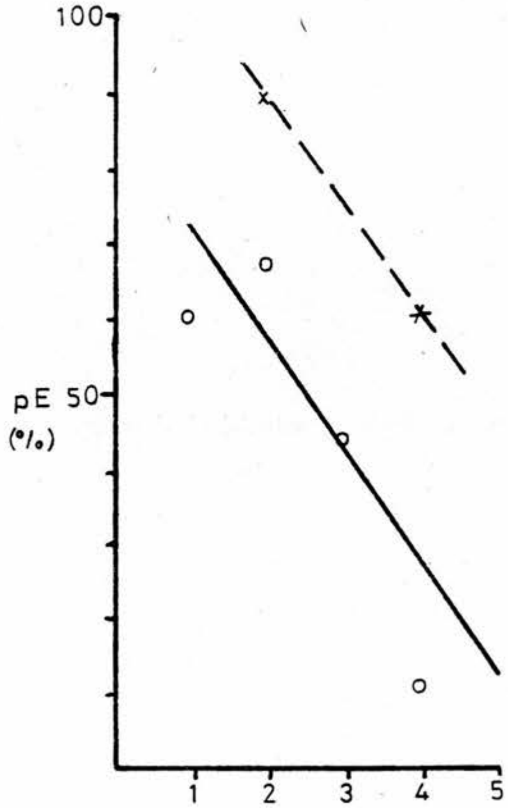
X- - - - - -X Facing

0———————0 Not Facing

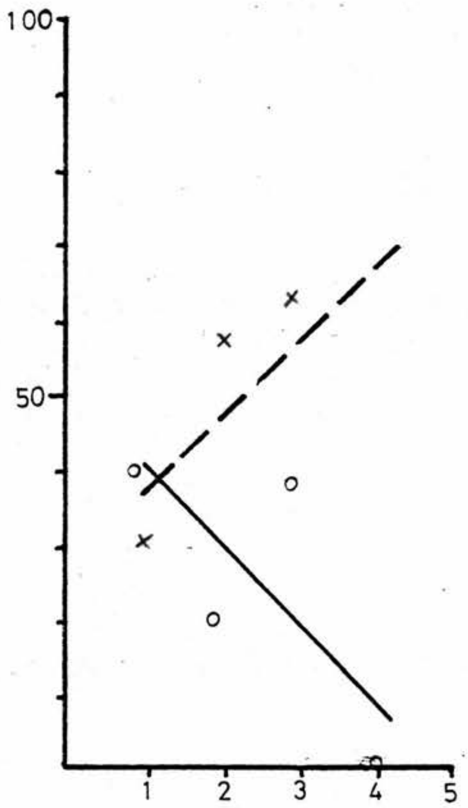


a. OLW

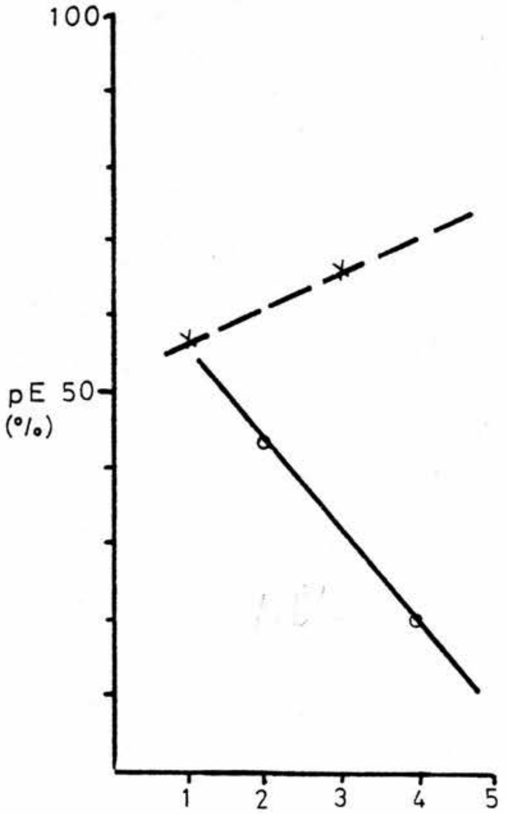
b. NB



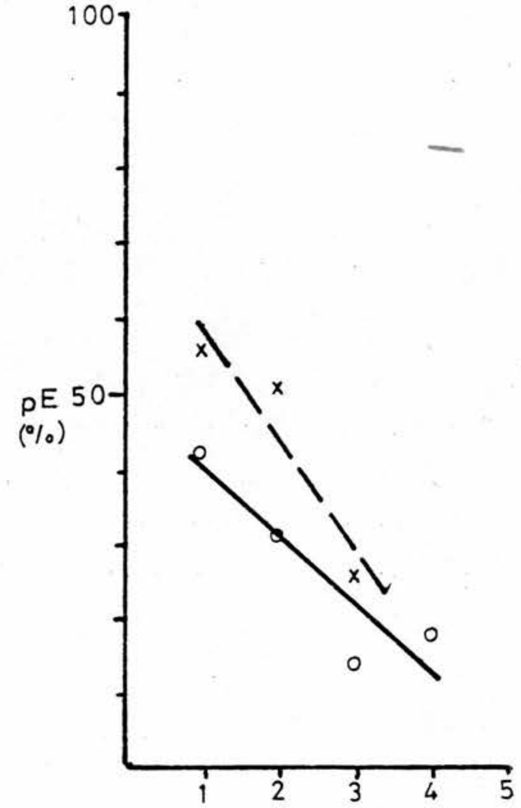
a. OLW



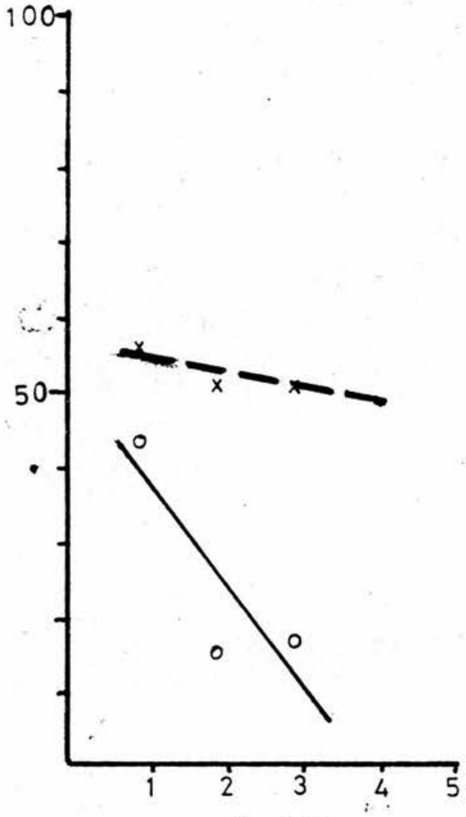
b. NB



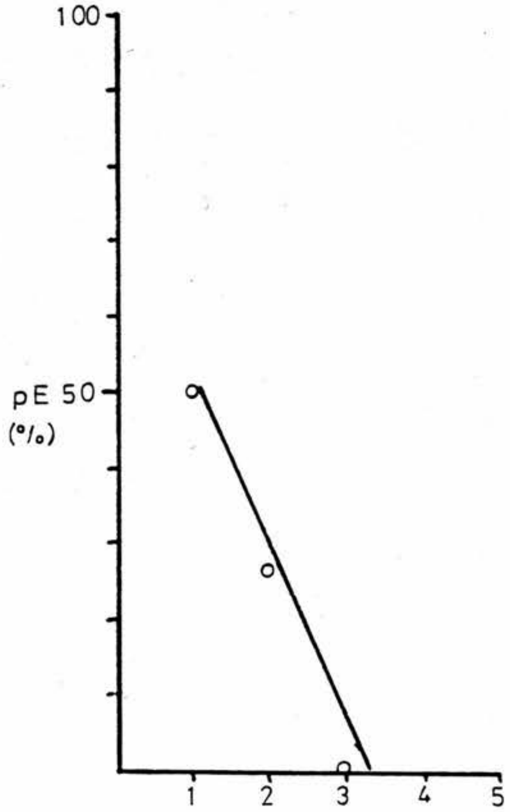
c. NBL



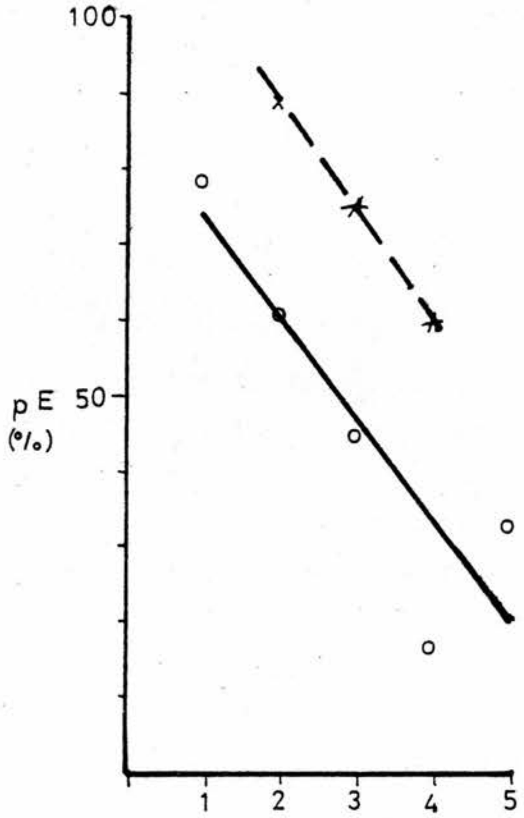
a. OLW



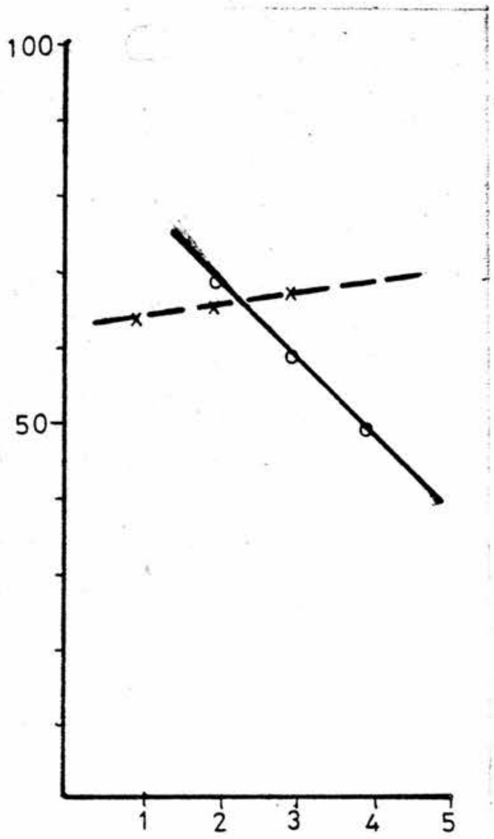
b. NB



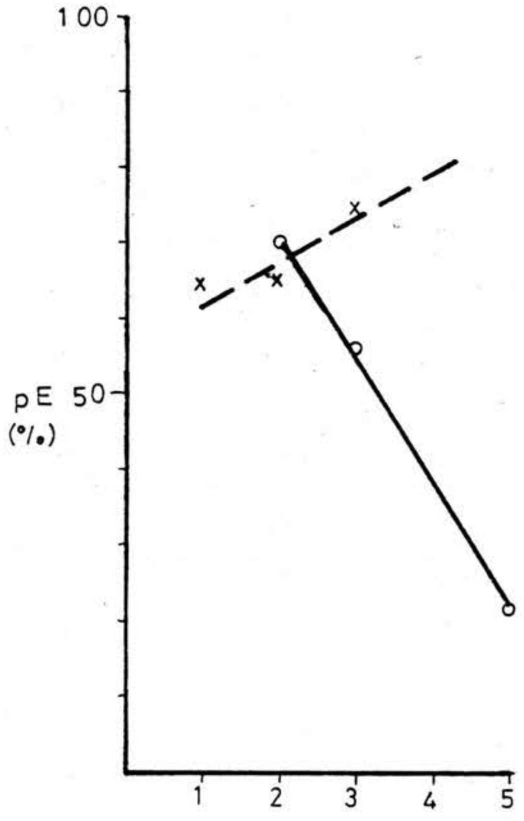
c. NBL



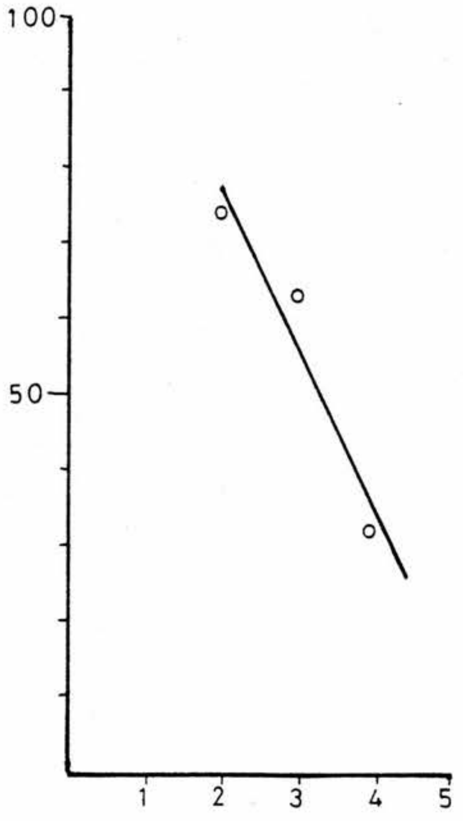
a.OLW



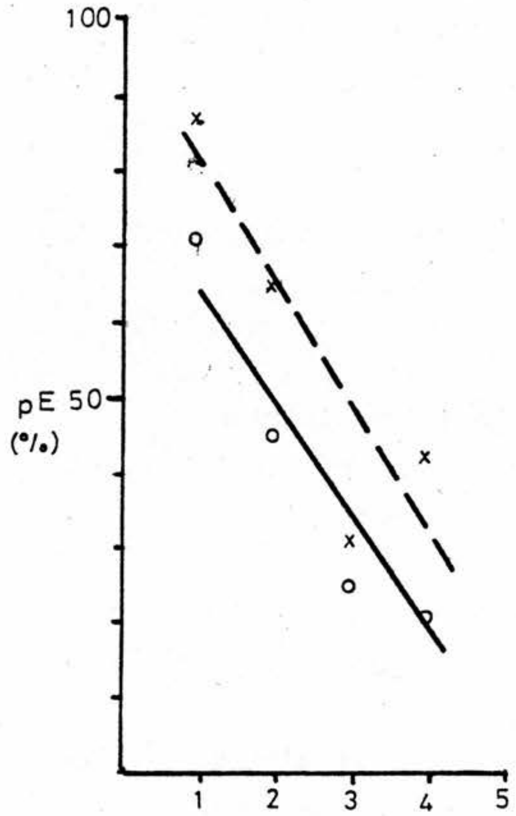
b. NB



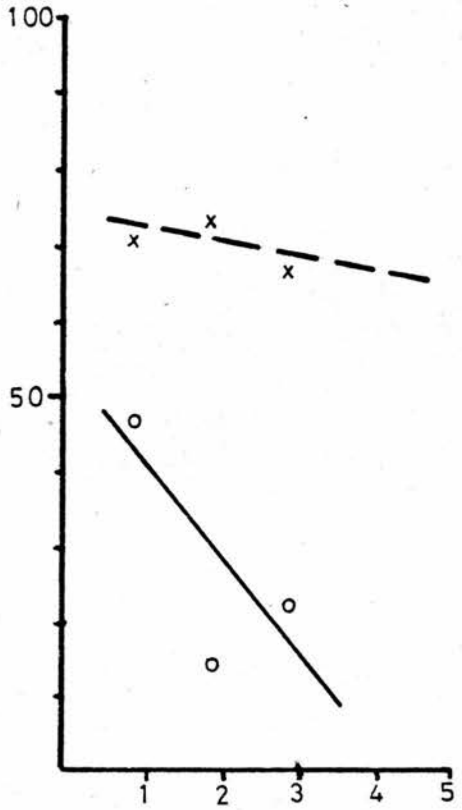
c.NBL



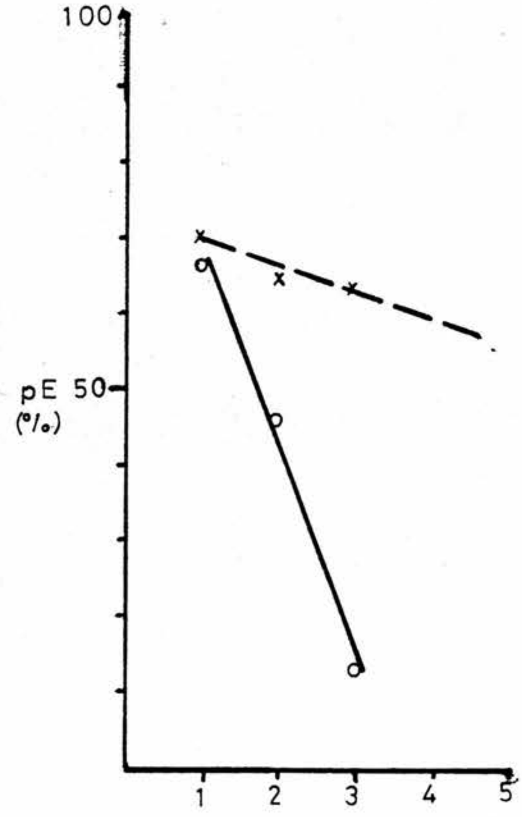
d.BLW



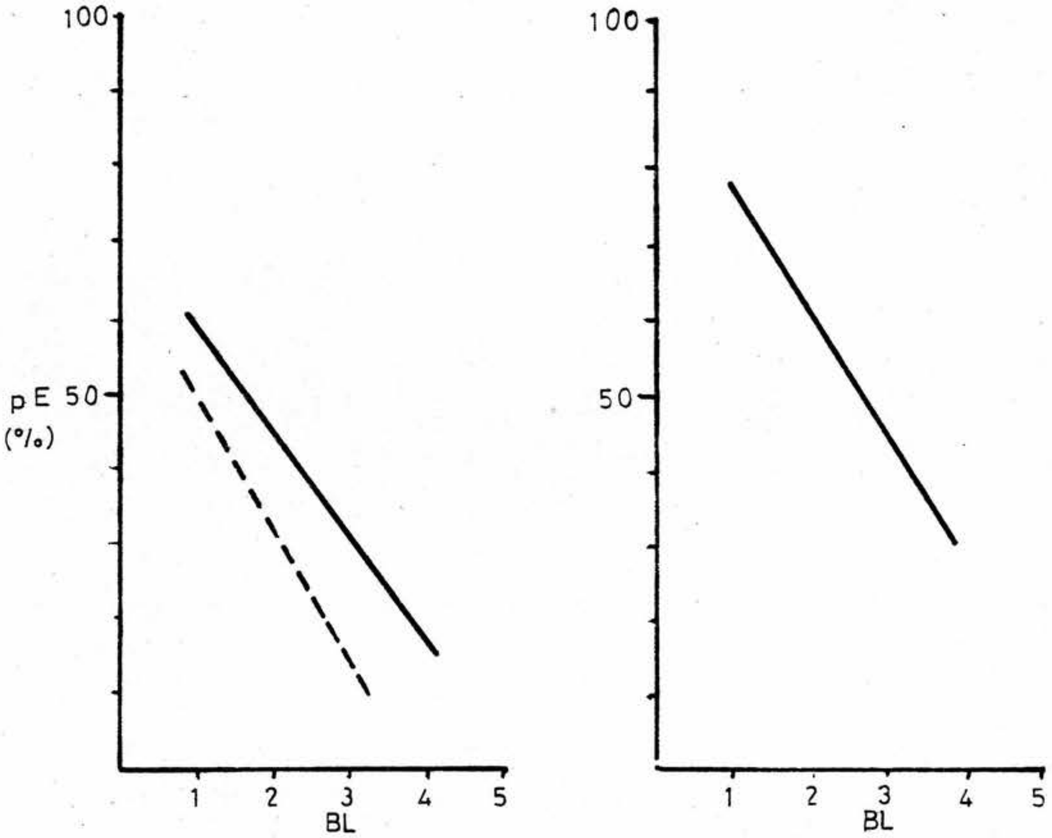
a.OLW



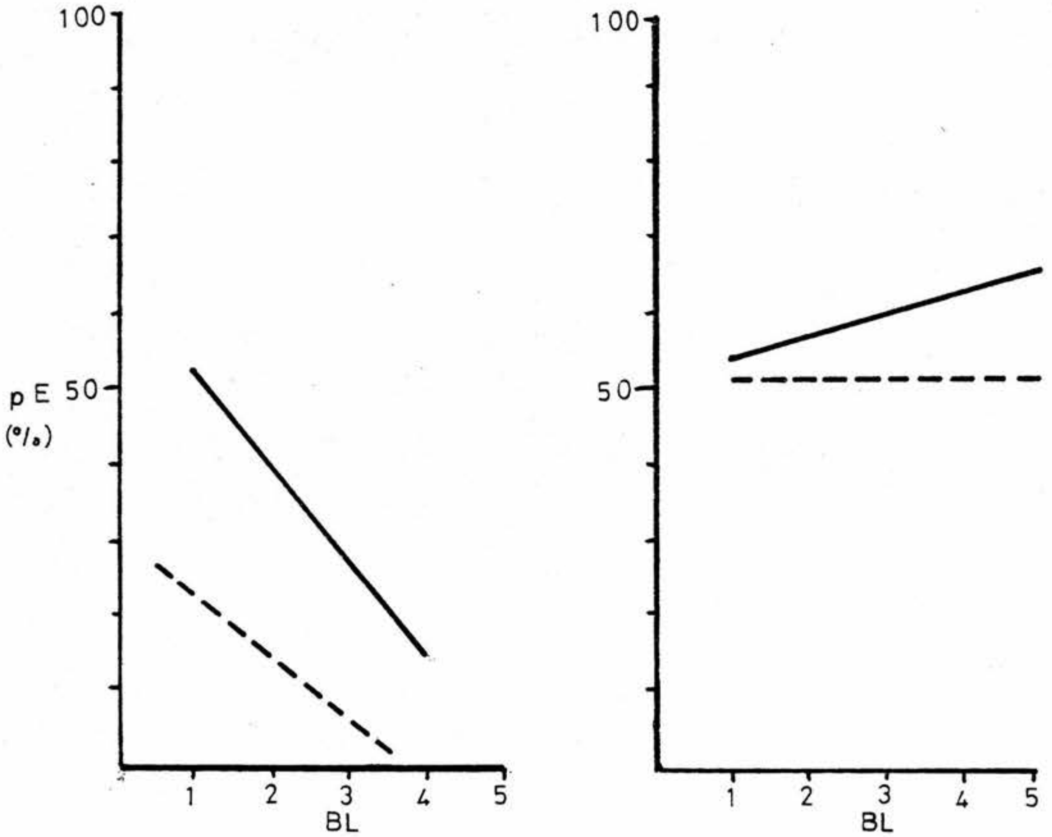
b.NB



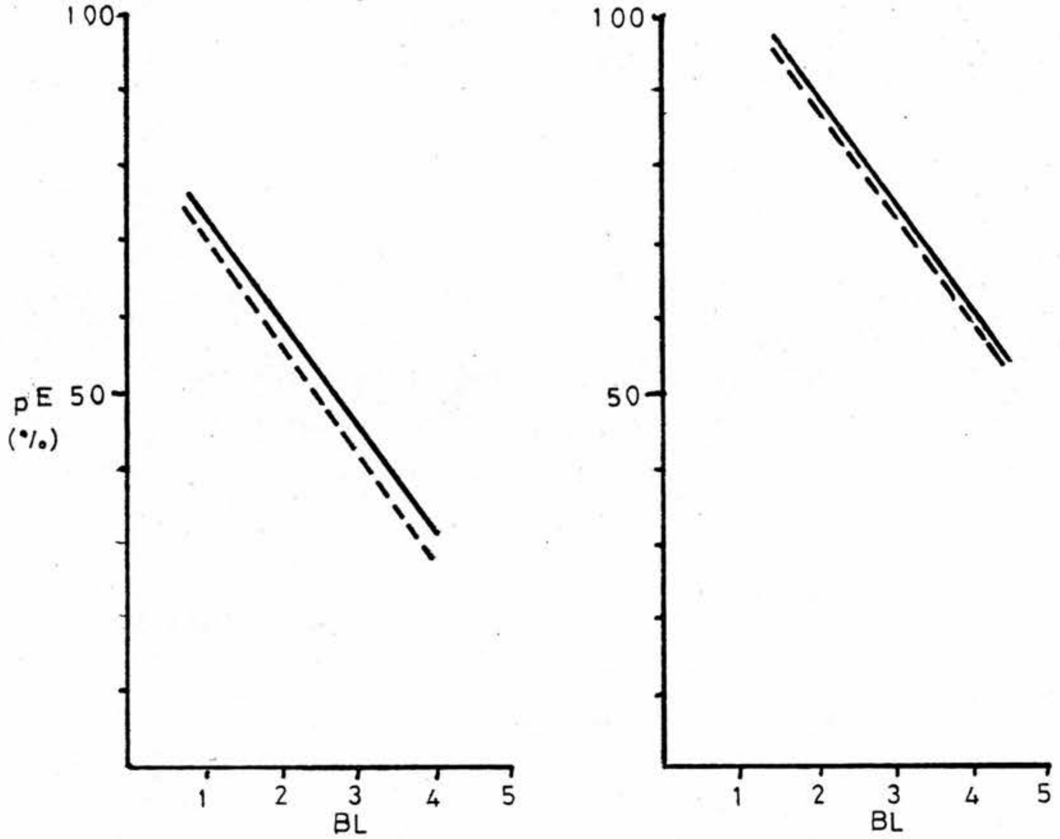
c.NBL



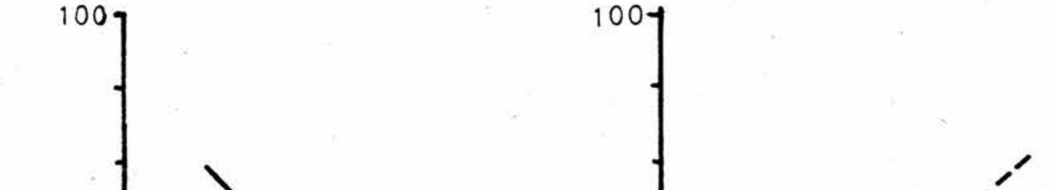
a. nF OLW b. F



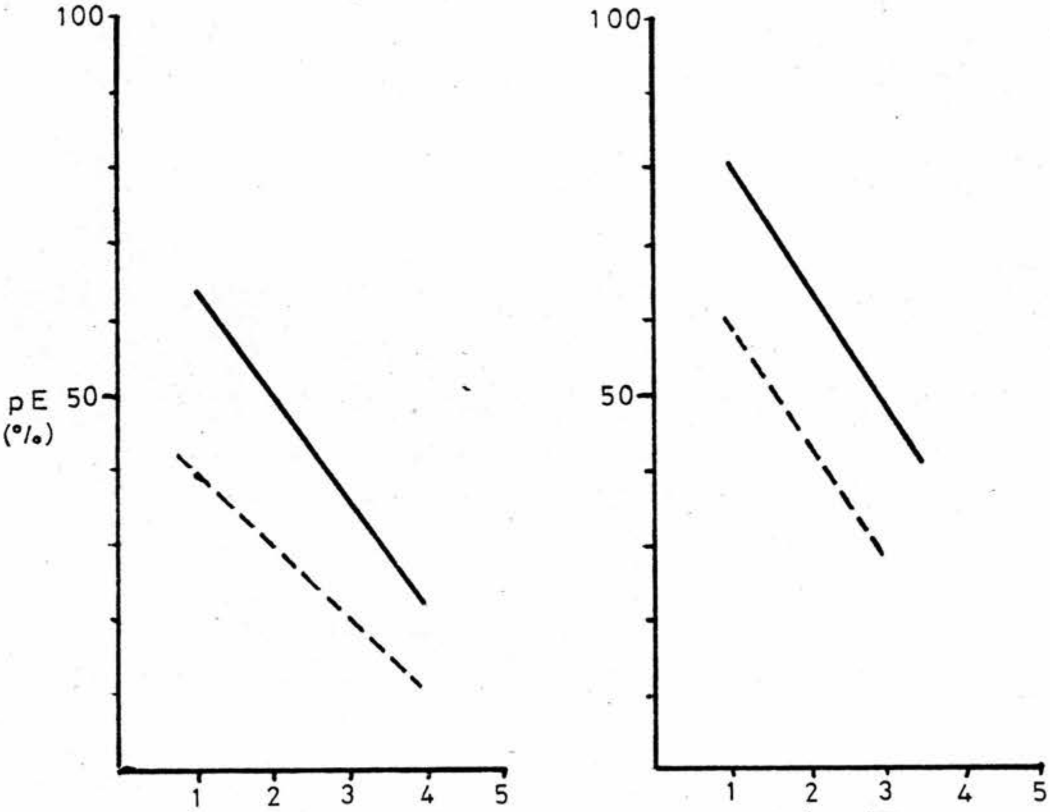
c. nF NB d. F



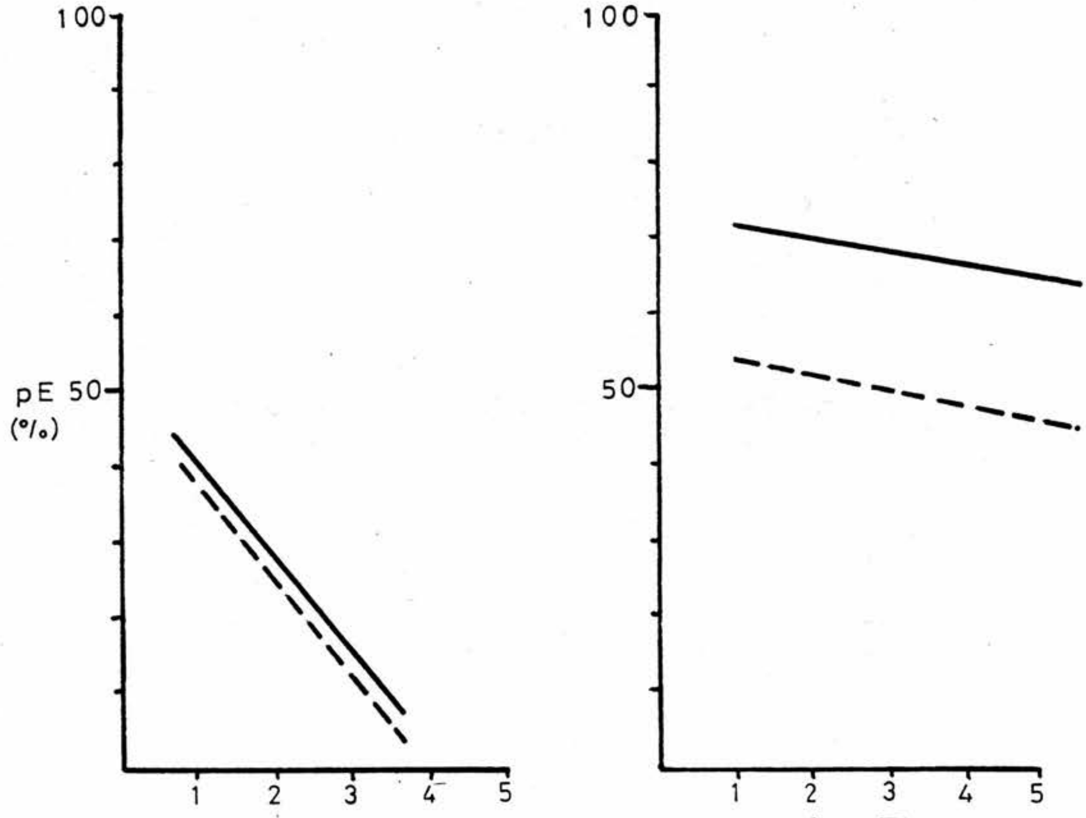
a. nF OLW b. F



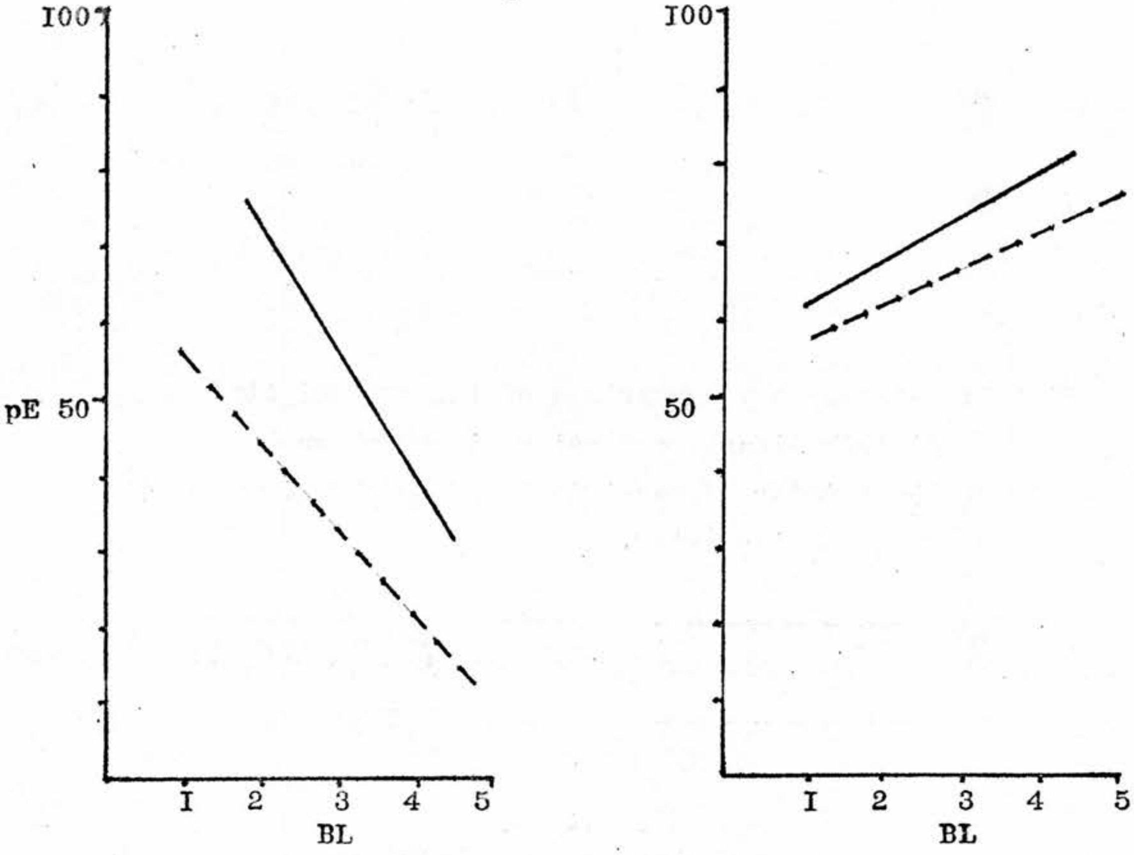
a. nF NB



a. nF OLW b. F



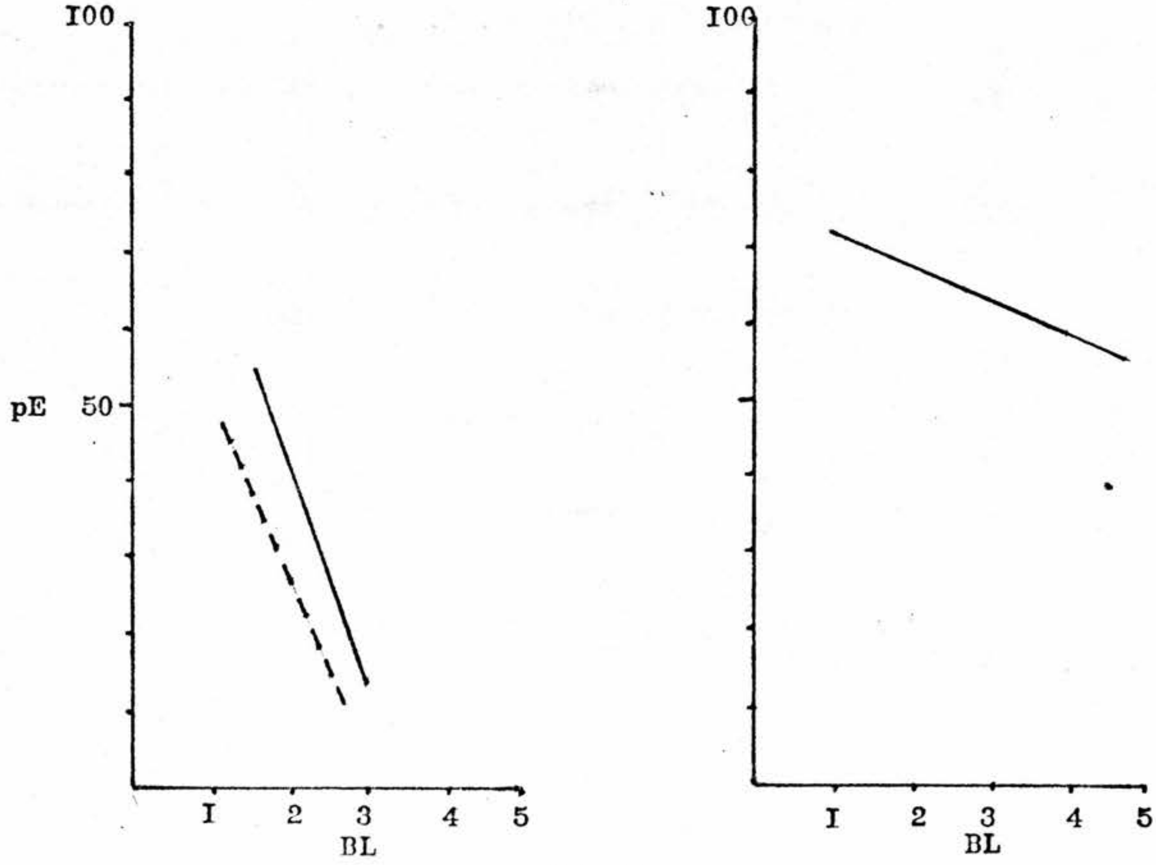
c. nF NB d. F



NBL I979

a. nF

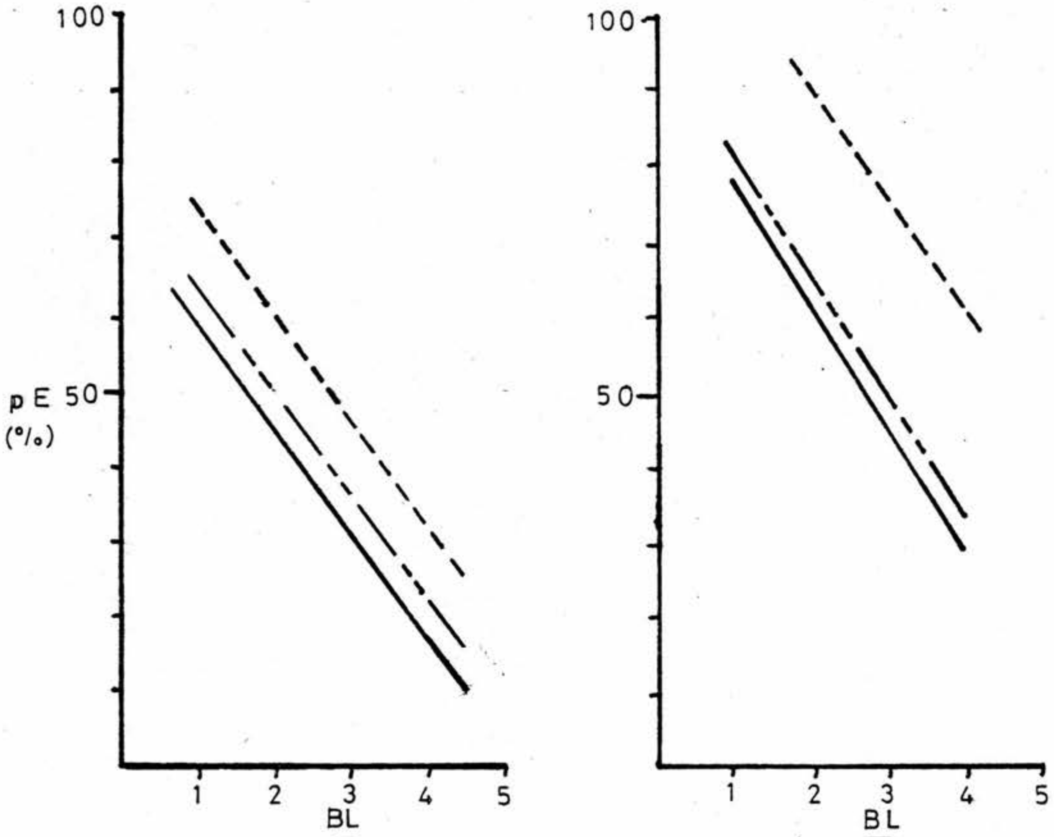
b. F



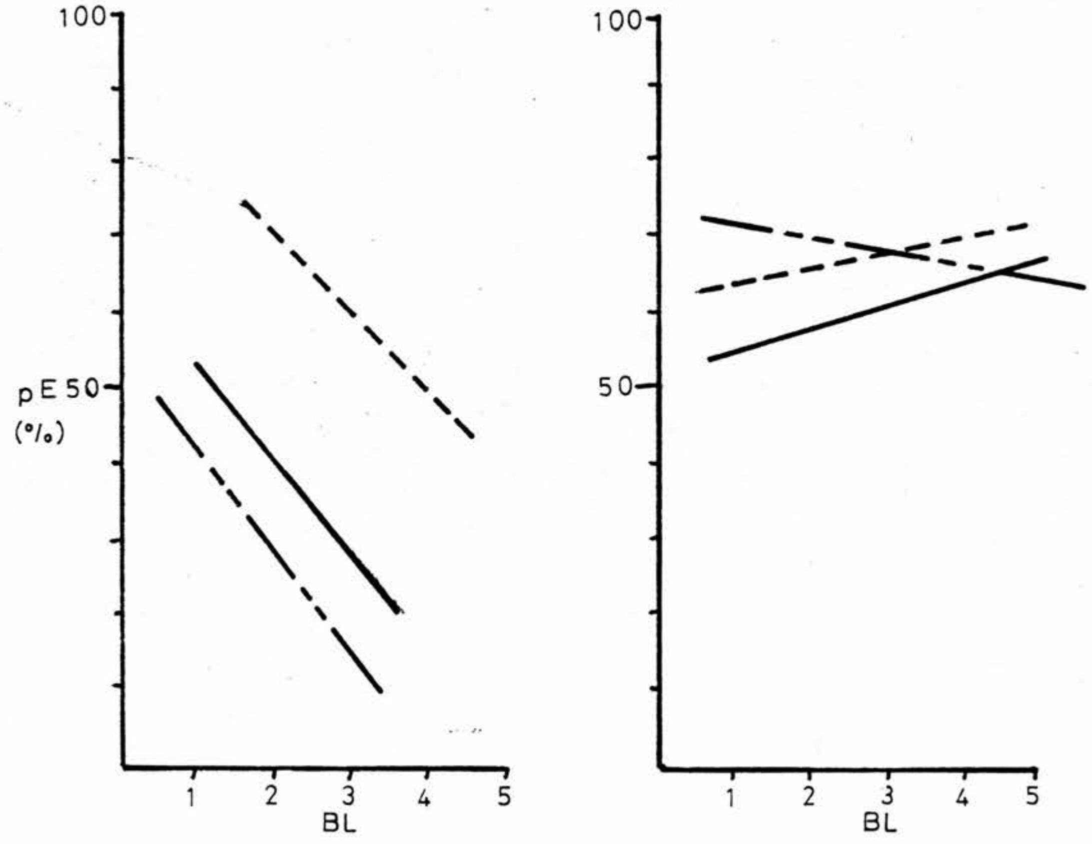
NBL I980

c. nF

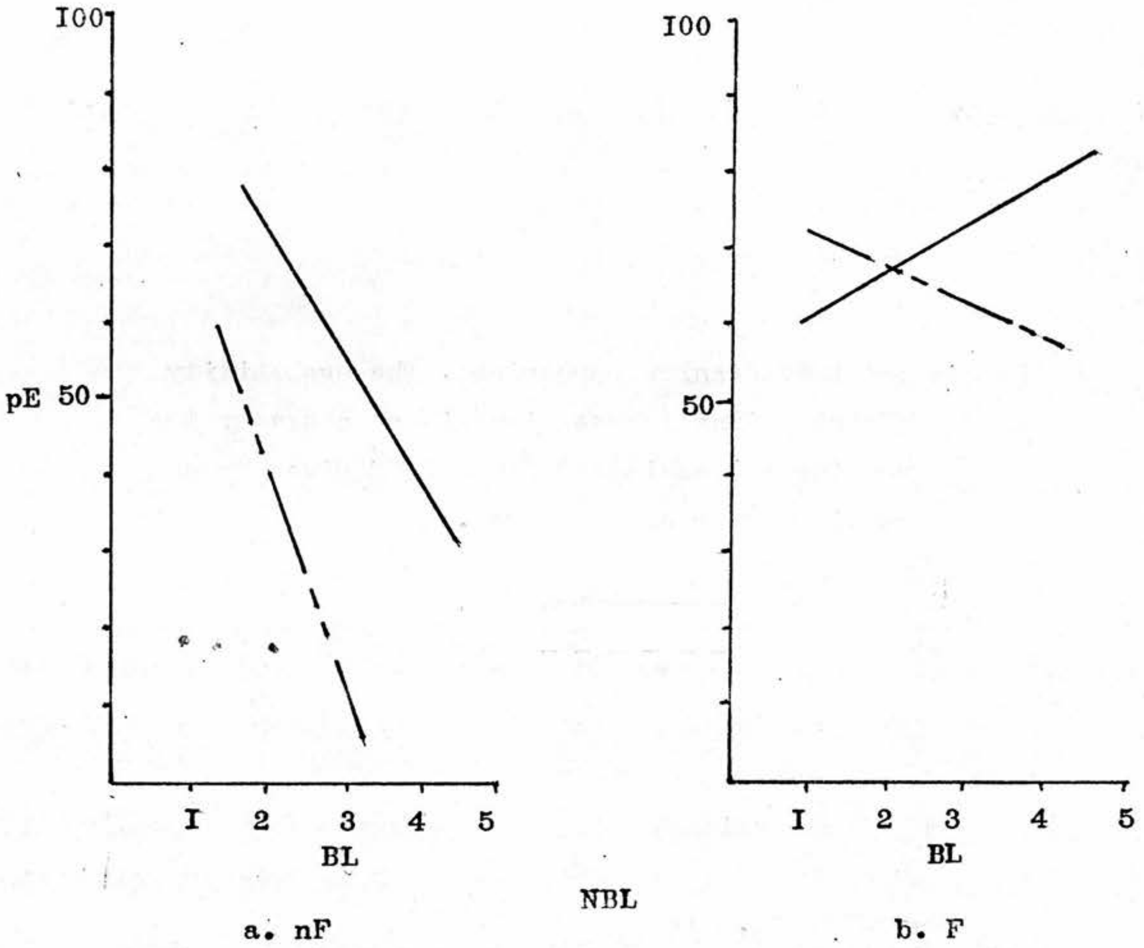
d.F



a. nF OLW b. F



c. nF NB d. F



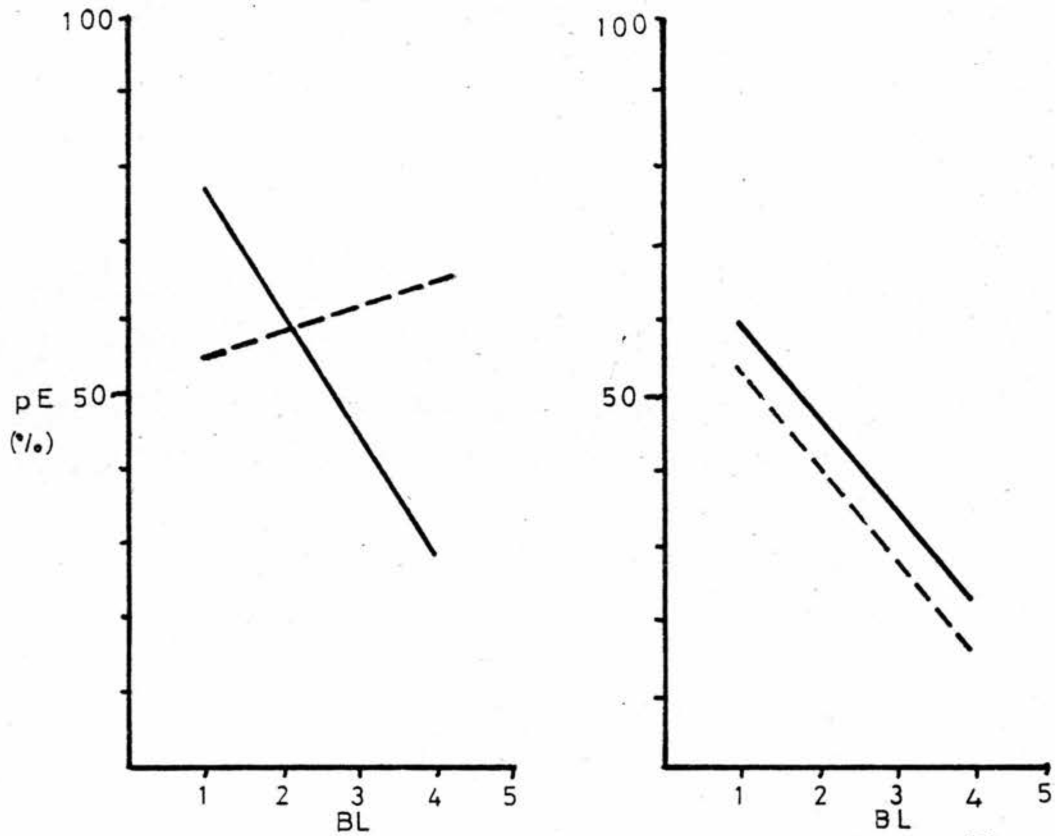
a. nF

b. F

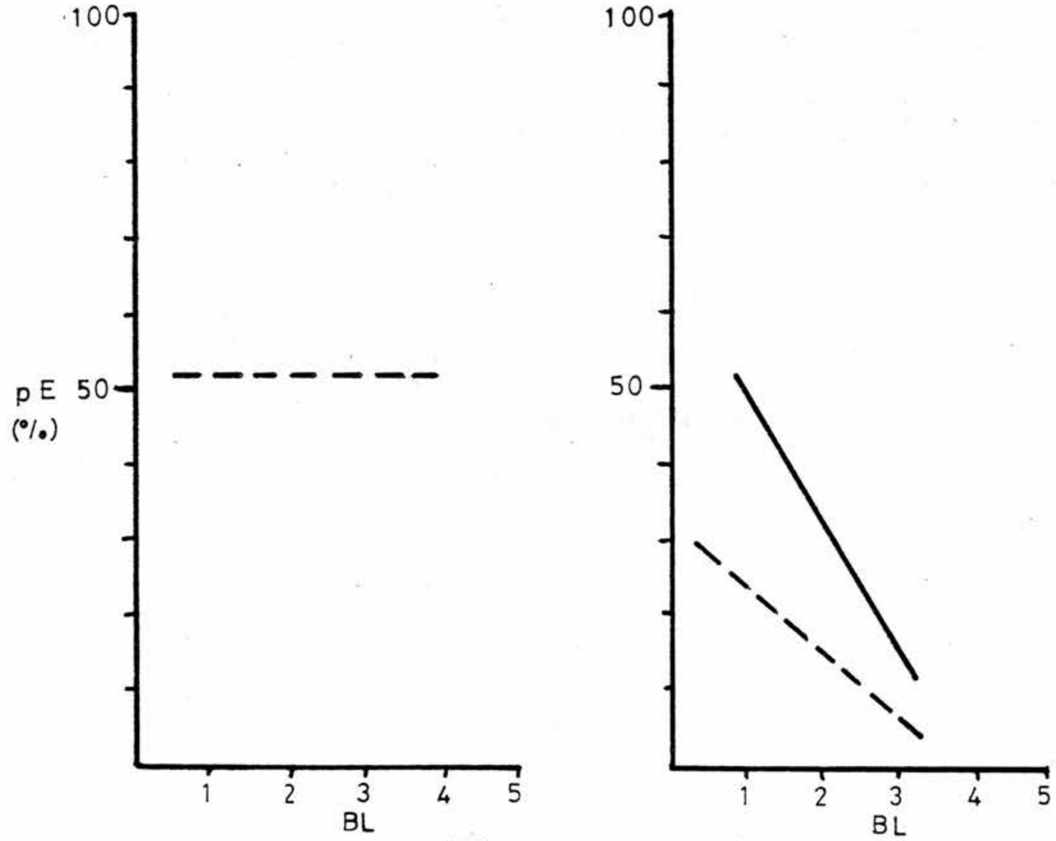
Fig. 22: Comparison (by delivery orientation) of the probability distributions shown by the reactor on receipt of NBL given by a staying actor. **Probability** distributions taken from tables 4I & 43. See also figs I5 & I6 .

— — - - — — Fair Isle I980

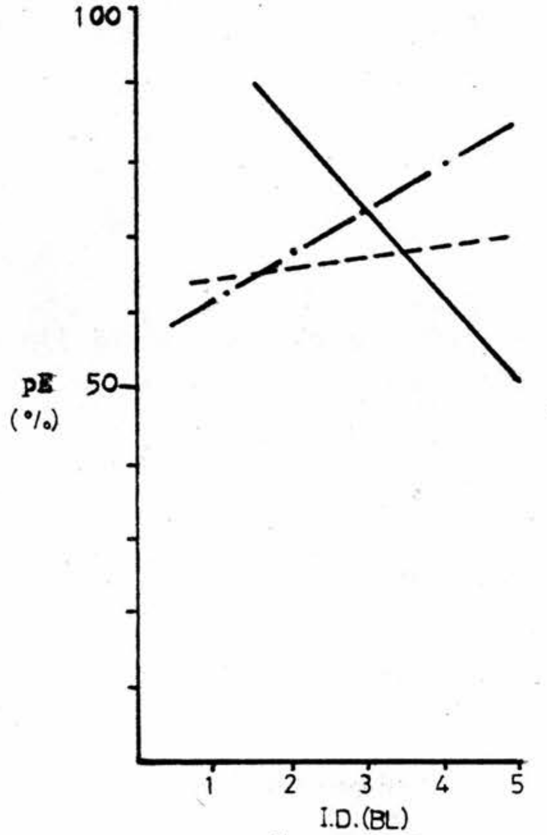
———————— Fair Isle I979



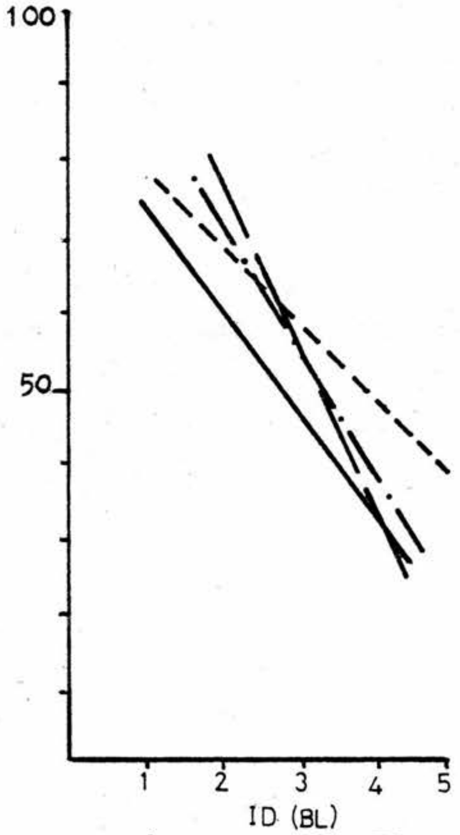
a. actor F b. actor nF



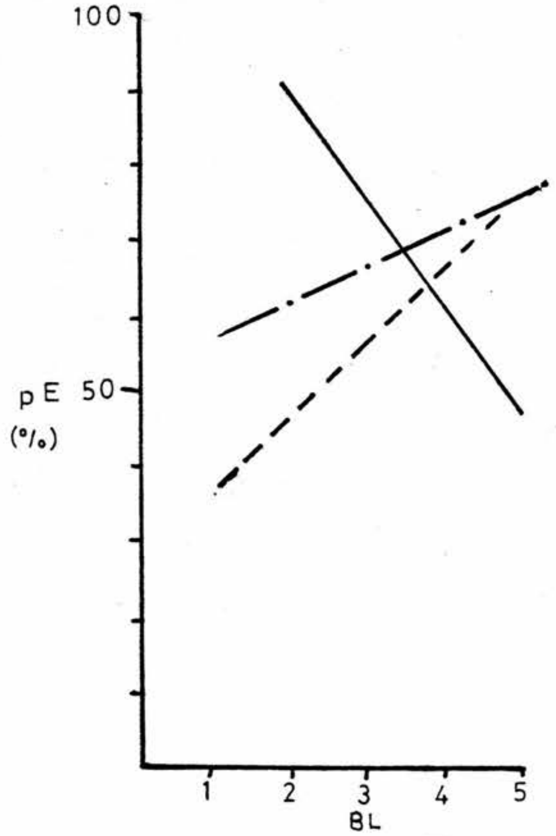
c. reactor F d. reactor nF



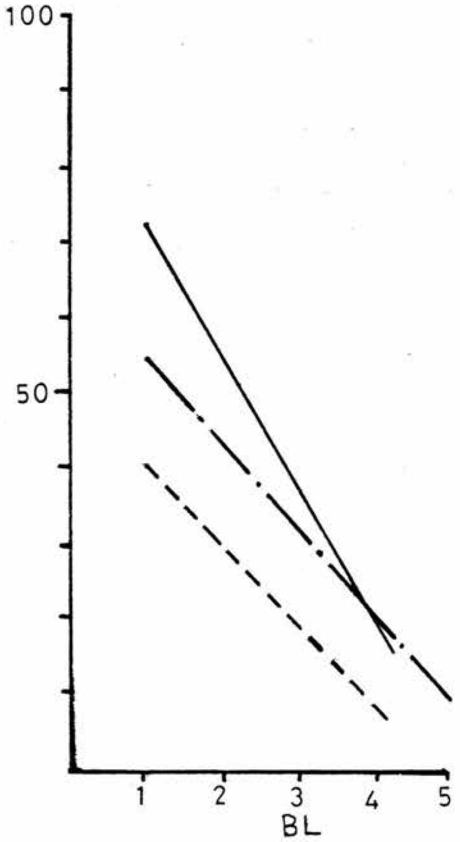
a. actor F



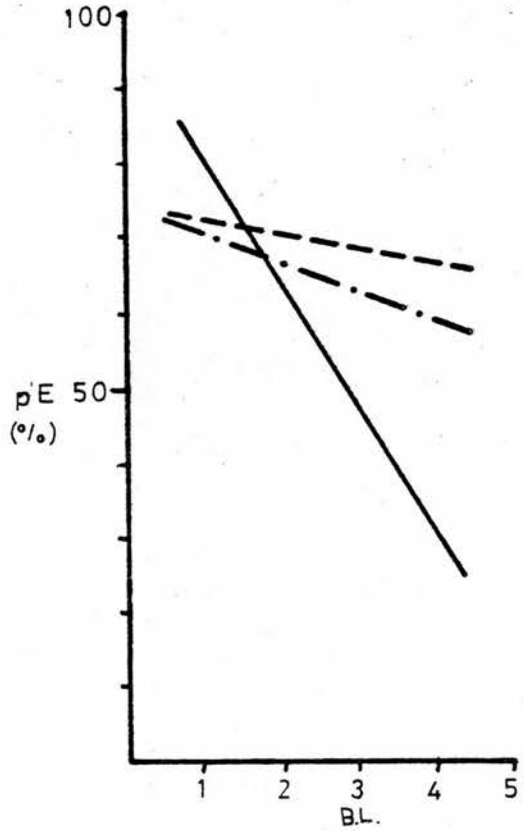
b. actor nF.



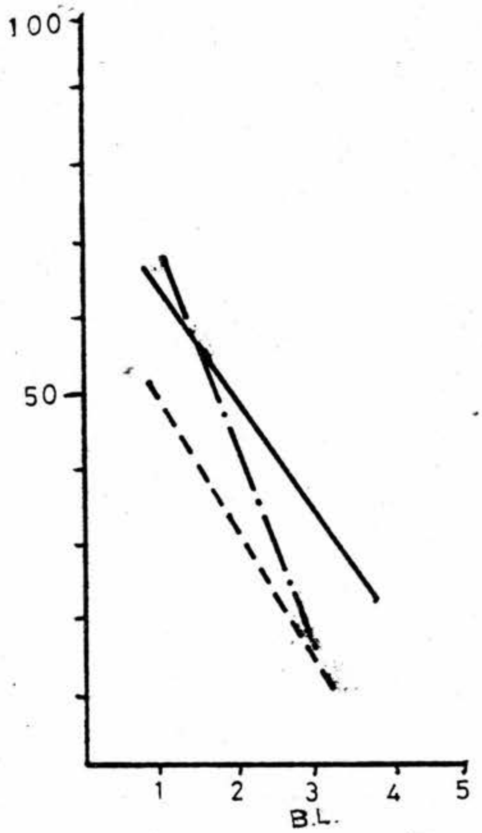
c. reactor F



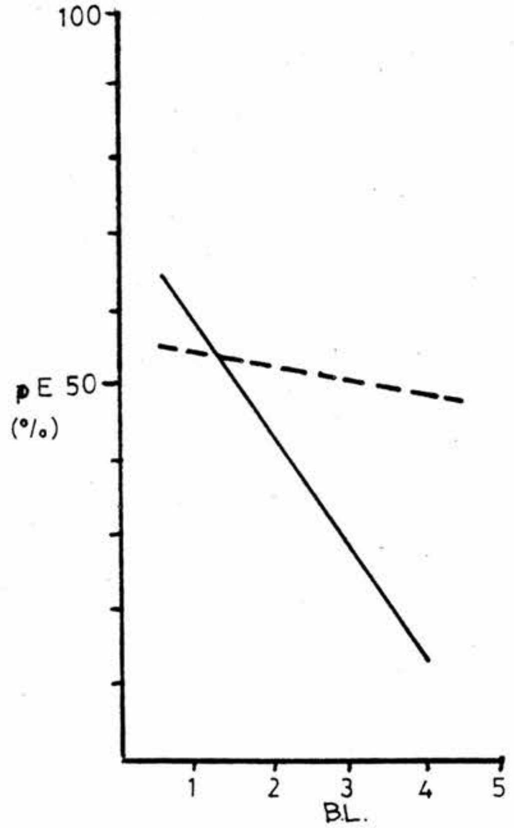
d. reactor nF



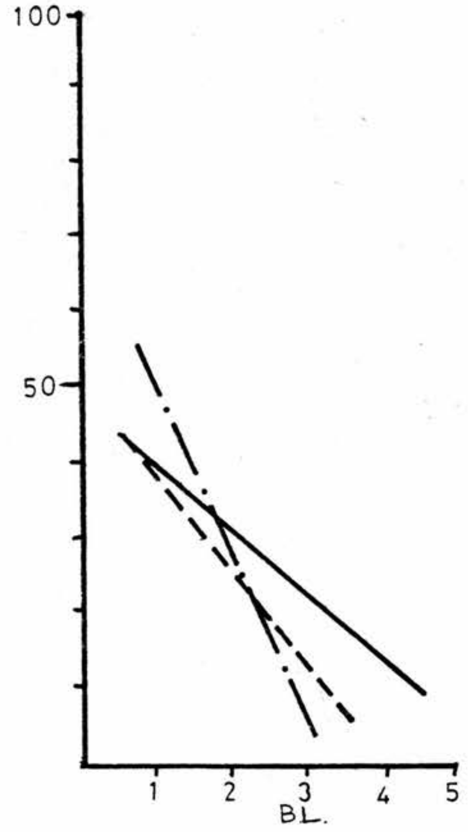
a. actor F



b. actor nF



c. reactor F



d. reactor nF

OLW Not Facing (d.f.)

	Hoy I980	Fair Isle I979	Fair Isle I980
't'	2.3I (6)	I.42 (7)	2.34 (6)

a. Analysis of covariance (t score) results from comparison of actor and reactor generated probability distributions.

OLW Not Facing (d.f.)

	Fair Isle I979/ Fair Isle I980	Fair Isle I979/ Hoy I980	Fair Isle I980/ Hoy I980
't'	0.79 (7)	I.42 (7)	0.743 (7)

b. Analysis of covariance (t score) results from comparison of the probability distributions shown on receipt of OLW not-facing when given by a staying actor.

Table 45: Analysis of covariance results for OLW Not Facing.

OLW Facing (d.f.)

	Hoy 1980	Fair Isle 1979	Fair Isle 1980
't'	-	2.2 (2)	2.37 (4)

a. Analysis of covariance (t score) results from comparison of actor and rector generated probability distributions.

	Fair Isle 1979/ Fair Isle 1980	Fair Isle 1979/ Hoy 1980	Fair Isle 1980/ Hoy 1980
't'	2.67 (4)	5.85* (3)	0.368 (4)

b. Analysis of covariance (t score) results from comparison of the probability distributions shown on receipt of OLW facing when given by a staying actor.

Table 46: Analysis of covariance results for OLW Facing.

$* \ p < 0.01$

	Hoy 1980	Fair Isle 1979	Fair Isle 1980
't'	2.34 (5)	8.506 ** (5)	2.2 (5)

Table 47: Analysis of covariance results from comparison of probability distributions at each delivery orientation.

$** \ p < 0.001$

NB Not Facing

	Hoy I980	Fair Isle I979	Fair Isle I980
't'	6.37 ** (3)	4.796 *** (4)	0.I7 (3)

a. Analysis of covariance (t score) results from comparison of actor and reactor generated probability distributions.

	Fair Isle I979/ Fair Isle I980	Fair Isle I979/ Hoy I980	Fair Isle I980/ Hoy I980
't'	4.64 * (3)	4.36* (3)	2.37 (3)

b. Analysis of covariance (t score) results from comparison of the probability distributions shown on receipt of NB not-facing when given by a staying actor.

Table 48: Analysis of covariance results for NB Not - Facing

* $p < 0.025$ ** $p < 0.005$ *** $p < 0.00I$

	Hoy I980	Fair Isle I979	Fair Isle I980
't'	I.243 (4)	I.866 (4)	8.37 ** (3)
F	0.087	2.686	0.0I2

a. Analysis of covariance (t score) and test for non-parallelism (F score) results of actor and reactor generated probability distributions. (NB Facing).

	Fair Isle I979/ Fair Isle I980.	Fair Isle I979/ Hoy I980	Fair Isle I980/ Hoy I980
't'	2.23 (4)	0.79 (5)	I.08 (4)
F	0.0I4	0.4II	0.4II

b. Analysis of covariance (t score) and test for non - parallelism (F score) results from comparison of the probability distributions shown on receipt of NB Facing.

Table 49: Analysis of covariance and test of non - parallelism results for NB Facing.

** $p < 0.005$

	Hoy I980	Fair Isle I979	Fair Isle I980
't'	2.95 (4)	0.38I (4)	4.6I * (3)
F	I7.89*	72.672*	2.89

Table 50: Analysis of covariance and test of non - parallelism comparison of probability distributions at each delivery orientation on receipt of actor NB

* $p < 0.025$

NBL Not Facing

	Hoy I980	Fair Isle I979	Fair Isle I980
't'	-	6.45 * (2)	2.28
F	-	0.003	0.029

a. Analysis of covariance (t score) and test of non - parallelism (F score) results of actor and reactor generated probability distributions. (NBL Not Facing)

	Fair Isle I979/ Fair Isle I980
't'	4.65 ** (3)
F	0.39

b. Analysis of covariance (t score) and test of non - parallelism (F score) results from comparison of the probability distributions shown on receipt of actor NBL Not Facing.

Table 5I: Analysis of covariance and test of non - parallelism results for NBL Not Facing.

$* \ p < 0.05 \quad ** \ p < 0.025$

NBL Facing

	Hoy 1980	Fair Isle 1979	Fair Isle 1980
't'	-	2.57 (2)	-
F	-	0.014	-

a. Analysis of covariance (t score) and test for non - parallelism (F score) results of actor and reactor generated probability distributions. (NBL Facing)

	Fair Isle 1979/ Fair Isle 1980
't'	0.366 (3)
F	3.359

b. Analysis of covariance (t score) and test of non - parallelism (F score) results from comparison of the probability distributions shown on receipt of actor NBL Facing.

Table 52: Analysis of covariance and test of non - parallelism results. NBL Facing.

	Fair Isle 1979	Fair Isle 1980
't'	0.390 (3)	2.18 (3)
F	37.37 **	19.606 *

Table 53: Analysis of covariance and test of non - parallelism results from a comparison of probability distributions at each delivery orientation on receipt of actor NBL.

* $p < 0.05$ ** $p < 0.025$

NB/NBL	't' (d.f.)	F
Hoy I980	–	–
Fair Isle I979	I.307 (3)	0.36I
Fair Isle I980	I.377 (3)	0.775
OLW/NBL		
Hoy I980	–	–
Fair Isle I979	0.577 (5)	0.054
Fair Isle I980	0.873 (5)	I.263
OLW/NB		
Hoy I980	0.856 (5)	0.006
Fair Isle I979	I.648 (5)	0.06
Fair Isle I980	I.962 (5)	0.03

Table 54: Analysis of covariance (t score) and test of non - parallelism (F score) results from a comparison of the probability distributions shown to displays delivered at the 'Not Facing' orientation.

NBL/NB	't'	F
Fair Isle I979	I.I85 (4)	0.729
Fair Isle I980	I.086 (3)	0.I08
OLW/NBL		
Fair Isle I979	I.007 (3)	I9.557*
Fair Isle I980	0.305 (5)	2.575
OLW/NB		
Hoy I980	0.247 (4)	I2.840*
Fair Isle I979	I.786 (4)	86.480**
Fair Isle I980	I.780 (5)	2.643

Table 55: Analysis of covariance (t score) and test of non-parallelism (F score) results from a comparison of the probability distributions shown to displays delivered at the 'Facing' orientation.

* $p < 0.05$ ** $p < 0.025$

Chapter 8

The story so far - A summary and discussion.

By far the most obvious feature of avian social behaviour are the displays used to administer such activities as mating, dispute solving etc. It soon became apparant that each species possessed a variety of displays. The frequent occurrence of overt attack and escape in conjunction with these displays led to the assumptinn that they served a similar purpose-threat. It has been generally agreed that overt attack as a means of securing a limited resource involves risk (Tinbergen 1959, Maynard Smith 1974) primarily through uncertainty about an opponents abilities. Hence, some means of acquiring this knowledge would be adaptive. Displays were obvious candidates for this facility although divergent biological views have emerged concerning how such ends would best be met.

It is always interesting to compare divergent theories and doubly so when they appear totally contradictory. Such a state of affairs has arisen recently through the advent of games theory analyses of agonistic communication. The display centred dispute resolving system anticipated by the latter school evolves around the prevention of bluff and stands in almost complete contradiction to an earlier model in which a range of displays were considered to subserve threat through conveying differences in signaller intention.

The games theorists consider the latter view untenable as a result of the evolutionary instability of such a system arising from the ease with which it could be invaded by bluff (Maynard-Smith 1974). The contradiction was made all the more interesting by the conflict theory's grounding in offering an explanation for a behavioural fact of life - the existence of a range of displays.

The difference in opinion between each of these views can be reduced to the following question - do all the observed displays perform a threat function?

The 'conflict' view had a sizeable body of empirical evidence to support its claims (e.g. Stokes 1962, Dunham 1966, Andersson 1976). Of these three the latter provides particularly convincing support. Up to this point the balance lay in favour of the conflict view.

The hawk was really set amongst the doves in a re-analysis by Caryl (1979) in which he demonstrated that the previous authors conclusions could be refuted using their own data. This study provided the first chink in the conflict theory armour and suggested the need for a more detailed study of species displays and the methods used to study them. Specifically, the present study set out to resolve the contradiction between the 'conflict' and 'games' views.

The highly theoretical basis of the games theory approach and its failure to offer a satisfactory explanation for the observed range of displays makes trying to understand this feature of avian behaviour difficulty to tackle from this theoretical perspective. The 'conflict' view did offer an explanation for the range of displays but it remained to be seen, particularly in the light of Caryl's (1979) findings, how well it accomplished this task. It seemed appropriate to carry out such an investigation on the species previously providing the strongest support for the 'conflict' view, the bonxie.

8.1.2. The Conflict Theory and Temporal Association.

In chapters four to six a number of methods derived from a basic conflict theory approach, thrown into relief using temporal association, were adopted to test the hypothesis that displays conveyed intentional information and that the latter mirrored the motivation underlying the display, i.e. did the displays form a threat series? The simple nature of these methods necessitated testing the consistency of the ensuing result before any one approach could be credited with the facility of providing an insight into the nature of display inter-relatedness and the information conveyed.

In it simplest and more direct form the conflict theory suggested that a display will exhibit an association with a number of overt actions, attack, escape and stay in this case, in a manner which is peculiar to that display (Moynihan 1955). The extent of association was though to mirror the causal contribution of a given tendency and, via a causal association between motivation and intention movements, to convey this information to an opponent.

The validity of this assumption was tested in chapter four by comparing the probabilities associated with each display when given by the actor and by the reactor. The signficant differences to emerge for the majority of displays (tables 3 - 8) revealed that this approach did not accurately reveal the extent of the information conveyed. The higher reactor escape probability after each display suggested that an outcome asymmetry existed whereby the initiator was more likely to win an encounter and did so irrespective of the display used.

This response asymmetry outlawed the use of temporal association as an accurate guide to information content but its consistency meant that perhaps a more general serial relationship between displays and motivational information may have been obscured.

This possibility was examined by ranking the displays according to the probability that they were followed by each of attack and escape. This analysis mirrored the most commonly adopted 'conflict' analysis. Using this Andersson (1976) argued that displays conveyed information about signaller attack likelihood. Treatment of the displays in this manner also provided the first opportunity to test Caryl's (1979) games theory oriented alternative that escape information was conveyed.

An extensive investigation involving a number of comparisons for each ranked sequence (tables 9 & 10) failed to provide support for either of these possibilities. The displays of the bonxie could not be said, at this level, to form a threat series constrained in such a way as to convey either attack or escape information as had previously been assumed (e.g. Andersson 1976, Caryl 1979).

The second basic approach involved quantifying displays, still in terms of attack/escape tendencies, but this time their 'threat value' was calculated as the difference between the probability of an action when a display was given compared with the probability of that same action when that display was not given. Methodological problems aside (see section 4.2.2) the use of this approach did reveal significant differences in the presence/absence probabilities for a majority of displays (tables 11 - 15). That for the result was consistent with a system acting in such a manner. Problems arose when the direction and magnitude of the ensuing differences were compared (table I6). Further, a failure to find any consistency between the displays when ranked as a series according to these differences ruled out this model as an explanation for the manner in which displays might exercise their effect.

A final approach entailed adopting a system more closely embracing the original conflict idea, i.e. that displays conveyed information about the extent of the signallers conflict and so involve simultaneous transmission of more than one type of information. Hinde (1981) noted the high proportion of staying responses associated with displays (see tables 3 - 7) and suggested that displays conveyed the likelihood of a signaller to either Attack/Stay or Escape/Stay. In section 4.3.I displays were ranked according to the extent of their association with each of these response combinations. Tables I8-20 revealed insufficient consistency in the order of displays so ranked and condemned this approach - it could not adequately account for the range of (assumed) threat displays.

In addition to emerging from a basic 'conflict' framework, these analyses had in common the fact that each attempted to define the information content of displays. They did so by assuming that the extent of the association between displays and Attack/escape provided, if only generally, a quantitative picture of information without giving any consideration to the variety of situations which might result in these behavioural end-points (see section 4.4.I). The different conclusions drawn by Andersson (1976) and Caryl (1979) from the same body of data illustrated the conceptual difficulties involved in postulating information content on the basis of association between displays and overt actions. The failure of displays to exhibit a consistent attack or escape ranking negated the conclusions of both authors. However, the problem of explaining why so many displays should be used remains. The conceptual problems accompanying temporal association (e.g. stay response could result when an opponent departs or where a 'sexual' display was used) limit the usefulness of this technique to define information content and so the above results did not provide sufficient grounds for rejecting the possibility that displays convey intentional differences. Detection of this facility would need a very different approach.

This entailed shifting the functional emphasis away from defining threat displays in terms of possible information content and towards looking at their ability to elicit an appropriate response in a recipient. It was assumed that irrespective of the information on which it was based a system transmitting intentional differences would produce an appropriate range of responses in their recipient. Threat was assumed to be used to settle disputed access to a resource and so recipient escape was an appropriate response to measure. The analysis was carried out only where the signaller stayed, ensuring that response was to the display and not the result of some overt action. Displays were ranked according to the attack and escape probabilities they elicited.

As tables 2I - 28 revealed there was insufficient consistency of elicited response to suggest that the displays formed a threat series.

Although overt interaction had been controlled by only measuring response to a staying signaller no provision had been made to account for a more subtle form of interaction arising via the display used by the reactor. Essential to the 'conflict' view of display conveying motivational differences was the idea that disputes be resolved by virtue of the relative difference in the intensity of display adopted by each interactant. Failure to consider reactor display may have concealed serial relations.

To surmount this problem the display of the actor was held constant. Attack and escape responses were measured to a number of displays, the latter being given by the reactor. The reactor displays relatively infrequently. The ensuing small sample sizes should be borne in mind when considering the result. Consistent with the earlier analyses tables 29 & 30 revealed no association between ranked attack and escape responses from a number of comparisons.

The latter analysis most closely resembles the dispute resolving system anticipated by the conflict theory and so it is this analysis which condemns to failure its ability to account for the manner in which displays are used in agonistic contests. Previous conclusions in favour of this view, when based on temporal association (e.g. Stokes 1962, Andersson 1976) should thus be viewed with caution. Any future use of this method must incorporate numerous tests for consistency before accepting any result.

Under the conditions imposed by the conflict theory the bonxie would appear to behave according to Harvard's Law;

> "Given ideal conditions of pressure, temperature, volume, humidity and other variables the

organism will do as it damn well pleases."

8.1.2. Limited Threat Group.

Up to this point the analysis had been, in the main, negative and had offered little to aid understanding of how a display-based communication system might work. Moreover, the feature at the centre of the 'games conflict' contradiction, the variety of apparant threat displays, was still very much in evidence. The only model coming close to explaining this behavioural feature had just been rejected. Did the range of displays serve any purpose?

A further shift in analytical emphasis away from a 'conflict' based view did reveal a consistent interdependent relationship between the displays adopted by the interactants and so conferred upon displays some functional capacity as signals. Tables 32 & 33 revealed, although not conclusively, that the interactants would match displays when a dispute was actively disputed (i.e. where the reactor also displayed.)

So, if displays are used to settle disputes, and it appears as if they do, then the dynamic mechanism for achieving this end will be very much more subtle than that anticipated by the conflict theory. Since both individuals use, predominantly, the same display it is extremely unlikely that intentional differences were used. The scope of the analysis did not extend to investigating the exact mechanism used but the relationship between these results and a number of relevant theoretical models were discussed (section 6.2.4).

This latter analysis also furnished a further interesting observation. Throughout the study it has been becoming increasingly more apparant that the majority of agonistic interactions (those terminating in attack or escape) concerned only a limited proportion of the potential display repertoire, namely OLW and NB. This is only true where attack and escape are the chosen end points used to define display function as threat. Where this function was being examined this was a reasonable choice. The predominance of OLW and NB suggests that only these displays can be considered representative of a threat system. The importance of relating displays to an appropriate overt behaviour was re-inforced through study of an alternative behaviour.

'Circling' has frequently been suggested as a component of bonxie sexual behaviour (Perdeck 1960, Moynihan 1962). The association between this response and only a limited number of displays has been noted (table 2). OLW is never associated with this overt response and NB reveals, on average, only a 9% association. The ease with which sexual behaviour can be observed enhances the observers ability to understand the functional significance of circling. Lack of any association between OLW and circling and the minimal association between NB and this response (and the fact that since circling occurs with birds standing parallel, the type of response elicited by NB is very different from its effect at a 'facing' delivery) prompts the suggestion that these displays play no functional part in bonxie sexual behaviour. In the same vein, the limited association between NBT, NbBp etc. and attack/escape leads to the possibility that these displays do not fulfill an agonistic function though they could be labelled as such since escape, stay and even attack could occur in encounters of a sexual nature.

For example, Perdeck (1960) noted the escape was a frequent end-point in sexual encounters.

If temporal association is used to illuminate the functional characteristics of displays, a number of factors must be considered before reaching a conclusion. An appropriate response must be chosen for categorization. There will be an obvious difficulty in knowing, a priori, what is appropriate. One possible solution would be to relate displays to a number of overt responses and choosing as appropriate, on a display by display basis, that giving a consistent and relatively high association.

It would appear that the failure to find any serial consistency for bonxie displays was due to treating functionally heterogenous displays in a homogeneous manner. That displays occurring under broadly similar conditions can serve different functional ends is becoming increasingly more apparant (e.g. Orians and Christman 1968, Mock 1979).

8.1.3. An Effect Paradox.

The interdependence revealed in the use of displays in chapter **six** (tables 32 - 35) indicated that displays (OLW and NB) did play a functional role in interaction. It was considered an appropriate first step towards deepening understanding of display function **to** identify how individual components exercised an effect. This was attempted using display/distance/orientation composites and revealed a number of interesting observations.

Displays delivered at a 'not facing' orientation, by virtue of the nature and consistency of the response elicited (figs.23 -25 tables 54) could not be attributed with fulfilling a threat function. When delivered at a 'facing' orientation consistent and significant differences between two displays, OLW and NB/NBL (figs. 23 - 25 , table 55), lead to their being labelled as threat displays. This result emphasised the dependence of displays on presenting a specific visual stimulus to elicit an effect.

Complications arose from the similarity between OLW 'facing' probability distributions and those elicited by all three (OLW, NB,NBL) at the 'not facing' orientation, a finding which cast a specific threat function for OLW in doubt. Since OLW is the most elaborate of the bonxie's displays this finding is surprising and this feeling is enhanced when the results of chapters six and seven are compared.

The problem arose from the highly distance dependent nature of the response elicited by OLW 'facing' (figs. 11 - 16). The similarity between the characteristics of this response and a number of other displays (e.g. figs. 23 -25), the latter being given at 'not facing', raised the possibility that the recipient ignored display form and instead response was guided by the distance between interactants. The fact that a number of displays of widely differing form elicited the same type of response and the dependence of the latter on distance cast into doubt the possibility of labelling OLW 'facing' a threat signal.

However, quite the opposite conclusion was reached in chapter six. Analysis had centred on the interdependence of display use. From tables 32 - 35 it was apparant that where the reactor disputed a resource it did so by adopting the same display as the actor. This was particularly evident for OLW (tables 32 & 33 and, in particular, tables 33b). From this it certainly appeared that OLW had a meaning for the recipient and that outcome was achieved by an interplay, of an as yet, unknown nature, associated with the joint use of OLW.

The paradox is that the conclusion drawn is completely dependent upon the type of analysis used. The interactional emphasis of the latter analysis together with the fact that the reactor actively displays before an outcome is reached leads to attributing greater credence to this analysis, i.e. OLW does have a functional signal capacity.

The display matching found in chapter six formed the basis of a suggestion that OLW and NB were used in different types of contest. In chapter seven threat was defined in terms of repelling an opponent. Such a definition may have been inappropriate for a display not specifically designed to repel opponents but may function,to, say, maintain territorial integrity. Such a function has frequently been postulated for OLW (Perdeck 1960, Spellerberg 1971, Andersson 1976). For the latter, display may serve to indicate possession.

Support for this and the possibility that NB may serve in disputes where acquisition of a resource is sought can be drawn from tables 32 - 35. Display matching was more evident with OLW. If this display were used to signal possession than in the event of a dispute (where both interactants display) it is likely that both are laying claim to the same resource and hence the propensity to adopt the same display (tables 32&33).

Display matching with NB is not so clear. From table 34

41% (on average) of interaction terminated following display matching (i.e. Actor NB/Reactor NB) and 34% involved Actor NB/ Reactor OLW. An actor initiating a dispute by adopting NB could find itself involved in two types of interaction. Firstly, the opponent could be in a similar position and be attempting to acquire a disputed resource. In such cases both individuals might use NB and dispute resolution would be achieved by a subtle interplay of an indeterminate nature. Alternatively, the disputes could be mixed. Here an individual attempting to acquire a resource may come up against opponents already perceiving themselves in possession. The latter would enter the dispute using OLW and so interaction involving mixed displays would be observed.

That OLW is a signal is thus highly plausible. Why should the response elicited by OLW be so similar to those elicited by a number of other displays and so militate against considering it as a threat signal? If it is accepted that OLW and NB represent different types of dispute it is unlikely that a demonstration of the nature of their influence will emerge from the use of one technique. If OLW is not 'designed' specifically to repel opponents evidence for its effect is unlikely to come from measuring the escape probability of a recipient. If OLW signalled possession of a definite area the loser will be concerned only with moving out of range of the eventual winner and may even be a neighbour. This is even more likely if OLW serves to defend an area and attract a mate (Spellerberg 1971). The stimulus evoking a response might well be distance and hence the highly distance dependent nature of ensuing response. If NB is used as an active threat for resource acquisition the loser will have to search elsewhere and so constant escape probability might be expected. A strong threat effect for NB was further evidenced by the frequency of its use in orientation-change interactions (table 36).

Probably the main lesson to be learned here is that it is not sufficient to demonstrate a consistent response. Each display must be tested using a variety of techniques and if a consistent and appropriate response emerges from each then a conclusion regarding the functional consequences of that display should be possible.

What constitutes an appropriate response will be a matter for discussion. For the present, measuring escape probability seems an appropriate response where threat is under study. In terms of the threat criteria outlined here it is possible to conclude that, of the extensive display repertoire of the bonxie, only one, NB, can be considered to subserve threat.

8.1.4. Evolutionary Considerations.

The concept of ritualization is normally associated with an elaboration of display form. The consistancy of the response (and its immunity from external influences) associated with NB suggests that ritualization may have entailed a fixation of response.

The elaboration entailed by ritualization was suggested as a mechanism to prevent signal ambiguity (Cullen 1966). Such elaboration would only be necessary where a number of displays existed to convey different levels of qualitatively similar information. This would be unnecessary where only one display fulfilled a specific threat function. Maintainance of this signal would entail, not elaboration of form, but rather a level of attack to counter the establishment of bluff.

It was suggested earlier that the recipient of a display will exert an important influence on display form. The most commonly postulated source of raw material from which present day displays evolved were intention movements (Tinbergen 1952) or Serviceable Habits (Darwin 1872). The closer association between an attack intention movement and actual attack would lead to an initially reliable association between this behaviour pattern and attack. This pattern would become a display if it was effective in repelling opponents without resource to actual attack. If so, its effectiveness would arise from the ease of its association with attack; an effectiveness which is initially produced and subsequently maintained by the recipient. The close the form/function relation the easier will the association be made in the eyes of the recipient.

However, as the pattern and overt attack become increasingly decoupled (a corollary of its initial effectiveness) the possibility of bluff arises. This possibility led Andersson (1980) to suggest that a new pattern would develop. An animal suffers severe restriction in the manner open to it to attack an opponent and this will limit the sources of raw material capable of developing to signal components. As a result, if Andersson's bluff hypothesis led to display development the form of the latter would be increasingly disociated from a form permitting attack. This would lead to a greater frequency of overt attack following each each of these patterns to ensure an association between pattern and attack in the eyes of the recipient. The necessity for a higher attack frequency may increase the likelihood of escalation, a possibility that runs counter to the use of display in the first place.

Thus a threat display would be expected to retain a strong resemblence to the intention movement from which it evolved. The primary adaptive pressure here would be the recipients perception of components and the ease with which they could be associated with overt attack. To counter bluff a degree of overt attack must follow the display. The level of attack necessary to counter the establishment of bluff may be determined in a frequency dependent manner.

The above display moulding process would be similar for each individual with the result that in a dispute between individuals trying to acquire a resource the same display would be adopted. In the bonxie this could be NB. By removing the possible use of display mediated intention differences to resolve disputes an alternative mechanism must be responsible. By providing a more concrete understanding of the nature of display systems it should prove possible to investigate the explanatory power of a number of existing theoretical models.

The central theme of this study has been to resolve the 'conflict-games' theory contradiction, a contradiction which rested on the number of displays thought to subserve threat. The conflict view was founded on the assumption that the observed displays all subserved threat. If a range of threat displays did exist the 'conflict' view would certainly have a certain credence. In the bonxie, at least, conclusions in favour of the displays forming a threat series appear to have been founded on data gathered through use of inappropriate methods. A change in emphasis reveals that the threat repertoire is comprised of a single display and, hence, it is not necessary to invoke a 'conflict' explanation, The single display to emerge that fulfills all the criteria expected of a threat signal brings the threat system of the bonxie into line with that anticipated by the games theorists. A background has now been set against which their theories can be tested.

In addition to illuminating the 'conflict-games' contradiction a number of additional points were brought to light.

8.1.5. Non-display influences.

It has become increasingly clear that interaction outcome may be settled on more than information emanating from the use of displays. Interactants have a number of additional information sources at their disposal.

In his study of the bonxie, Andersson (1976) demonstrated that status and mode of approach exercised a powerful, influence on outcome over and above any display influence. The response asymmetry apparant in chapter four (tables 3 - 8), which was independent of display, revealed that success was weighed in favour of the actor. Analysis framed in terms of probability distributions revealed that while this actor/reactor asymmetry was present for NB (tables 48) it was not for OLW, the latter exhibiting greater consistency (tables 46). This may be an overt sign of OLWs signal nature.

Van Rhijn (1980) suggested that individual recognition would influence outcome. In the present study there is certainly anecdotal evidence to support the occurrence of individual recognition from interactions between territorial and non-territorial club birds. It was frequently observed that a non-territorial individual would move away from club territorial individuals without any display or overt response on the part of the latter. Bearing in mind the small size of bonxie clubs, individual recognition may be an influential variable. However, there is a constant influx of new birds to the club throughout the season (Furness 1977). This would serve to reduce the influence of this variable.

Whether recognition does or does not take place will have implications for the course of an interaction. For example, contest length may be influenced. If the individuals are unknown to each other a more careful and prolonged assessment period might be expected.

The dynamics of bonxie interactions are influenced by more than display alone. Status and mode of approach have already been mentioned. Distance and relative orientation are determinants of recipient escape response in their own right (i.e. judging by the recipients response in landing and orientation change interactions where the actor maintains NN). There effect is even more marked when used in conjunction with displays. For example, the role played by distance in conjunction with NB is heavily dependent upon delivery orientation (figs.II - I6)

Taken together these findings suggest that of the information sources available to a recipient and upon which a response is based, the display itself may enjoy a low priority. The recipient may even rank the cues.

A territorial signaller was invariably victorious suggesting that status may be the information source of primary importance to a recipient. Locomotion towards an opponent also resulted in a greater than average escape response but not to the extent shown between birds of differing status. It was certainly more important than the accompanying display. The response difference between NB 'facing' and 'not facing' (e.g. fig. I5) demonstrated the importance of delivery orientation. The distance dependent nature of the response elicited by the remaining patterns suggested a preferential importance for distance over the accompanying posture.

The use of models to explain contest behaviour will have to incorporate the facility to account for a number of variables, the extent and nature of whose influence may be difficult to determine.

Could these cues be considered contextual? Smith (1965) argued that the basic behaviour patterns upon which animal social behaviour is based are modified in response to shifts in circumstances. He suggested that 'displays do not release reponses per se but rather they prime recipients to select from a particular set of responses and the information upon which the response is based is contextual'.

To be considered as such the variables examined here must be shown to qualify the response shown to a display. It is doubtful whether status and mode of approach could be considered contextual since, in terms of their effect on recipient response, they over-ride the effect of any accompnaying display.

The dependence of displays on distance and orientation for effect results in a different state of affairs. For OLW 'facing' and 'not facing' and NB/NBL 'not facing', the similarity in elicited response despite considerable differences in form suggests that distance over-rides accompanying posture and cannot be considered contextual. In these cases distance is a cue in its own right. Similarly, orientation is not contextual with OLW. For NB, on the other hand, orientation does qualify the response to this display and so only in this case can it be considered contextual.

It is interesting to note that contextual influence is not universal but only appears in certain circumstances. This problem has already been anticipated (Green and Marler 1979).

8.1.6. Components or combinations.

In functional studies of communication one of the basis problems which must be surmounted concerns indentifying the components responsible for eliciting a given response. Since these provide the communicative link between the interactants a true understanding of the nature of display behaviour can only be reached by identifying these components.

Since Tinbergen (1959) laid the foundations the majority of studies have followed his example and described displays in terms of form characters rather than employing labels embodying more subjective descriptions. Simply because a number of components can be identified does not mean that they will necessarily all contribute to the signal quality of the display.

The work of Brown et al (1967) raised the possibility that certain components may be effects rather than being functional. They suggested that the posture accompanying the long-call in sabines gull was that which most effectively directed the vocal component at opponents in different relative spatial positions. The vocal cue seemed to be the important one with posture providing, at best, contextual information (see section I).

Stout and Brass (1969) also presented evidence that display effect was mediated by only a limited portion of the possible stimulus matrix presented to an opponent. They suggested that the opponent responded to the height of the head above the ground.

The study of components can be split into two parts. A means is needed to determine the divisions into which a display can be split. Secondly, a means of determining which components contribute to the signal function is needed.

Andersson (1976) was probably the first to adopt a statistical definition of display in terms of components. He identified a number of basic postural and vocal components. A display was described as a composite that occurred together more than ten times during the course of the study. He did not attempt to differentiate between components in terms of their effectiveness.

This approach has been pursued by Van Rhijn (1981). Using video tape analysis of black headed gull displays he identified a number of components. A frequency criterion was used to define individual displays. In terms of basic components, 240 'displays' were deemed possible. Of these, 114 occurred at least once, 49 at least 10 times and 17 at least 50 times. Cluster analysis was used to define combinations and 17 displays were subsequently revealed.

An objective approach of this nature is necessary if a reliable estimate of components possibly contributing to signal function is to be built up. At the same time it may be misleading to accept as a display a given composite. A means is needed for determining objectively the components actually making a functional contribution.

The simplest appoaach that could be adopted here is to consider the interaction from the point of view of the interactants. What aspects of an opponents display would an individual be able to see? A case in point here is the NBT display of the bonxie. When a signaller faces an opponent the tail-raised component is effectively hidden. Irrespective of what this says about the signallers motivational state, if the recipient is denied visual access to this component it will have no functional significance.

Once a number of relevant components had been identified how could their individual contribution be assessed? In the present study the recipient was used as the judge of signal quality. Andersson's (1976) component definition was followed. Although defining components in only crude terms a number of interesting observations were made.

For this method to be of value each display must elicit a consistent response from a recipient. Only then will display comparison be valid. In chapter seven consistent responses were demonstrated for a number of displays. The ensuing comparison provided sufficient grounds for suggesting that response was, in terms of stimulus characters, limited.

The qualitative orientation dependent response differences associated with NB (figs. 11,15,16 tables 50) revealed that the bonxie was tuned to the stimulus properties presented to it. What of the components?

The similarity of the probability distributions elicited by OLW at both delivery orientations (e.g. fig. 15,16) suggested that response could not be mediated by visual components. It was suggested that if the display elicited the response it must have been induced by a component whose stimulus parameters did not change concomitantly with orientation. One component fitted the bill-the long-call. It was further suggested that this state of affairs was an adaptive response to opponents in a specific relative spatial position. The work of Peek (1972) was cited in support. In the bonxie vocal communication over the long-distances imposed by low breeding density would be inefficient due to competition from extraneous noise sources, e.g. wind. The wing-raised component with attendant white patches was suited to distance communication and does appear to have a signal function (Spellerberg 1971). It seems odd that wings-raised was not used in close encounters since they would be equally obvious to an opponent irrespective of distance and it was in close encounters that Spellerberg revealed that they did exercise an effect. The situation is further complicated by doubts about the appropriateness of the analysis when used with OLW.

Discussion of how OLW mediates its effect must wait until the role of OLW and role of the club in bonxie natural history are better understood. Notwithstanding, multiple modality displays pose an interesting problem and one worthy of more detailed work. The work of Peck (1972) suggests that tackling the problem in the light of the ecological obstacles to be surmounted may prove fruitful.

Uncertainty about the role of the vocal component resurfaced when NB and NBL were compared. Before that, though, the qualitative difference in the response elicited by NBL at each delivery orientation cast a doubt on attributing responsibility for response to the vocal component. The change in response (e.g. fig. 15) is more likely to have resulted from a change in stimulus, pointing to the visual components as likely candidates. A lack of vocal contribution was further suggested by the failure to find any significant differences between NB and NBL at the orientation at which they could be said to be executing a threat function, 'facing' (figs. 24 & 25 , table 55). It is possible to conclude from this that, in terms of the escape response elicited, the long-call does not alter the threat quality of NB.

However, a different approach may have led to a different or qualified conclusion. The above analysis only measured the relative frequency of escape. It is feasible that, on receipt of the long-call, an opponent might have moved off a greater distance than would have been likely in the absence of that component. Bearing in mind the relatively small size of the bonxie's inter-individual distance (I.D.) the distance moved off may be immaterial as long as the I.D. was evacuated.

Long-calling is a frequently occurring component, an observation which suggests that it does have functional significance. There exist a number of possible explanations for its use.

There is a growing body of evidence for individual recognition by voice in seabirds (e.g. Beer 1970, White and White 1970). One possibility is that long-calling is used to furnish identity information. Assuming that there is no justification for distinguishing between NB and NBL an obvious problem is raised by its selective use.

In an agonistic context a number of studies have attributed vocalisation with the facility of conveying Resource Holding Potential (RHP - Parker 1974). In the red deer, Blutton-Brock and Albon (1979) suggested that the high energetic costs of 'roaring' in this species would provide a reliable indicator of size and so of RHP. Could a similar mechanism in the bonxie explain the selective use of the long-call?

Where display is used for assessment a variety of situations could be anticipated which might need different handling. Throughout the season there is a constant influx of new birds into the club. Birds may encounter both known and unknown opponents. NB, on its own, may be used where the signaller is in a position to assess opponent status, perhaps through individual recognition and having had prior encounters, a likely eventuality in such small groups. Where opponents are unknown to each other assessment by this means may not prove sufficiently reliable and a more accurate form of assessment would be needed. Long-calling may provide more subtle assessment information.

In the interactions studies by Clutton-Brock, roaring was considered a reliable cue to RHP because it was energetically costly. The long-calling occurring during bonxie interactions is generally of 3-5 seconds duration. Birds have been observed long-calling for 25-30 minutes continuously (Stonehouse 1956). The short duration of its club delivery is unlikely to be of sufficient energetic cost to confer sufficient reliability as an assessment cue.

If call duration were not responsible some other intrinsic feature may have been. The auditory frequency could be used with, for example, a low frequency being associated with a large individual, A cue system acting in this way was reported by Davies and Halliday (1978) in the common toad where depth of broak was correlated with size. Incidently, a similar system is used by a number of American frogs with additional adverse conequences (Tuttle, 1982). Frog eating bats home in on this same cue to select frogs which are of a suitable size for eating.

So far discussing of long-calling has centred on its occassional accompanyment of NB. This component is always present in OLW. It s use as an assessment cue is in keeping with the postulated territorial role of OLW. In conflicts fortemporal space over which both individuals lay claim a subtle and reliable form of assessment would be expected. Long-calling may provide this capacity. Bearing in mind the relationship between this display and space, a decision to withdraw would be made on the basis of information gleaned from the assessment cue but the extent of the ensuing response might be guided by the distance between the interactants.

Even if Long-calling did not act as a reliable RHP guide on the basis of certain intrinsic features it still may act in this manner. It has already been suggested that a level of overt attack will be used to maintain the integrity of NB as an assessment threat. If the establishment of bluff is held in check in this way it may not be necessary for the assessment cue to provide more than simply a symbolic representation of RHP. A similar argument was proposed by Davies (1981) to account for the discrepancy between the vocal cues used in territorial defence and their ability to indicate RHP in the pied wagtail.

One final use to which long-calling could be used in an agonistic context is motivational. Club interactions occur at very close range. Under such circumstances Morton (1977) proposed that vocalisation could convey motivation structure. Again it is difficult to adapt this explanation to fit in with the selective use of long-calling with NB and its failure to elicit any more than a distance dependent response in OLW is at odds with a system conveying motivational information, if the latter were used to resolve disputes.

The occurrence of long-calling with a variety of postural components poses an interesting problem. Of the explanations offered above, its use as an assessment cue is, subjectively, the most appropriate and is a line of investigation with pursuing.

The suggestions made in this chapter regarding the nature of bonxie agonistic communication remain speculative until a greater understanding of the role played by the club in bonxie natural history is reached.

Conclusions

1) Temporal association formed the basis of this study and it is evident that the ensuing data can be adapted to suit a variety of analyses, each of which generates a different picture of the threat dipslay repertoire of the bonxie. Its earlier use was restricted to defining response probabilities with a view to quantifying the information made available by agonistic displays. The theoretical basis of this work derived from the conflict theory. However, recent in-depth theoretical exploration of this aspect of display behaviour cast doubts on earlier conclusions and prompted more detailed analyses both within and outwith a 'conflict' framework.

Where only a single hypo-thesis is under study the analytical approach is bound to be constrained in a manner likely to bias interpretation. Nowhere is this illustrated with greater clarity than in the conclusions of the 'conflict' studies concerned with defining information content and explaining the range of (assumed) threat displays. Where displays are defined in terms of an attack/escape conflict and the occurrence of these actions in conjunction with displays was used to define them as threat, the study is likely to do little other than support the original theory.

Clearly a wealth of theoretical constructs are necessary to stimulate analysis of a single body of data in a variety of ways, or, at least, to instil in the observer an awareness of possible alternatives.

2) Where simple methods, like temporal association are used conclusions should be based on consistent results. Earlier suggestions that displays formed a series conveying attack or

escape information could be confirmed on the basis of data drawn from different, isolated tests (e.g. tables 25 & 21). When the body of data was, as a whole, compared the variation in the pattern and the extent of the association between actor and reactor responses negated previous conclusions that displays formed a series constrained to convey variations in threat intensity and emphasised the importance of determining result consistency.

In the present study chapters six and seven adopted two different methods of analysis, both of which revealed relatively consistent results. However, the conclusion drawn was dependent upon the type of analysis used. In chapter six the inter-dependence of display use was considered while in chapter seven the escape probability elicited in a recipient was examined.

From studying the inter-dependence of display use functional display significance was conferred upon OLW. When examined in terms of the escape response elicited it did not appear to have independent threat signal status.

This finding suggests that it is important to determine consistency not only within a given method but also between methods. The latter is important to ensure that a method appropriate to the investigation is being used.

It is also important to define the consequences of the behaviour system (e.g. threat) anticipated, a task that is conceptually easier to understand from the point of view of the behaviour elicited from a recipient rather than postulating, for example, the type of information that may be conveyed. This will be particularly important where anylysis is based on the overt responses shown by the interactants.

3) Finally, the present study was specifically addressed to resolving the contradiction between the conflict theory view which proposed a system of dispute resolution acting via displays conveying serial differences in intention and a basic games theory view suggesting that a single intensity display be used.

The failure of methods previously used to support the conflict view cast in doubt its validity as an explanatory concept. As a result of this failure the contradiction was phrased in terms of the number of displays which could be considered to subserve threat.

While still adopting temporal association to provide the data for analysis a shift in emphasis revealed a different picture of how displays might act. Instead of there being a range of threat displays a number of lines of evidence suggested a limited threat system. Only one display, NB, fulfilled all the criteria outlined for a threat display and brought the bonxies threat repertoire into line with that anticipated by the games theorists.

Within the limits of the present analysis the contradiction appears to have been resolved. The same basic method, temporal association, and the same species, the great skua, was used to furnish supporting evidence for both points of view. The contradiction thus had its roots in the conceptual deprivation existing at the time in which the earlier studies were carried out.

The games theory approach with its firmer theoretical footing and the ease with which it can provide theoretical scenarios should ease the above problem. However, this approach also needs to widen its sphere of interest to encompass a number of areas of interest to more traditional ethological studies, e.g. the form adopted by displays and by developing the means of defining displays in functional terms.

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Appendix I

Scientific names of species cited.

Redpoll	Acanthis flammea
Red winged blackbird	Agelaius phoneceus.
Great skua	Catheracta skua skua.
Brown skua	Catheracta skua lonnbergi.
McCormick's skua	Catheracta skua macormicki.
Chaffinch	Fringilla coclebs.
Jay	Garrilus glandarius.
Herring Gull	Larus argentatus.
Black-headed gull.	Larus ridibundus.
Glaucous-winged gull.	Larus glaucesens.
Blue tit.	Parus caeruleus.
Great tit.	Parus major.
Grosbeak	Pheuticus Ludovicianus.
Arctic skua	Stercorarius skua.
Black grouse	Tetrao tetrix.
Sabines Gull	Xema sabini.
Harris' sparrow	Zonatrichia querula.
Pied wagtail.	Motacilla abba.
Red deer.	Cervus elaphius.
Common Toad.	Bufo bufo.
Pygmy sunfish.	Elassoma evergladei.
Speckled Wood Butterfly.	Parage aegeria.

Appendix II

For field recording each display component was given an abbreviated code name. The form adopted by each component can be seen in the appropriate combinations (figs. 2 to 4). The combinations and the code used where they are referred to in the text are also given.

Component	Field Code	Fig
Neck Forward	Nif	3
Neck Straight	Nis	3
Neck Back	Nib	3
Bill Down	Bid	
Bill Up	Bup	3
Bill Straight	Bis	3
Oblique	Ob	2
Bend	Bend	4
Wing Raise	Wir	2
Tail Raise	Tar	
Neck Short	Net	4
Neck Low	Nel	
Carpals Raised	Car	
Long Call	Loc	
Squeak Call	Squk	
Staccato Call	Stac	
Circling	Circ	
Neck Normal	Rel	3

Combination	Text Code	Fig
Neck Forward/Bill Straight	NfB	3
Neck Straight/Bill Straight	NB	3
Neck Back/Bill Up	NbBp	3
Oblique/Long Call/Wing Raise	OLW	2
Bend/Long Call/Wing Raise	BLW	2
Neck Straight/Bill Straight/ Long Call	NBL	
Neck Straight/Bill Straight/ Tail Raise	NBT	
Neck Back/Bill Up/Long Call	NbBpL	
Neck Short	NS	4
Neck Short/Wing Raise	NSW	4
Neck Normal	NN	3
Bend	Bend	4

Appendix III

The Check Sheet

Following each observation period essential features of the recorded interactions were transcribed on to check sheets.

On these sheets each Actor/Reactor (A/R) block represents one ten second time interval. In this way the temporal course of the interaction was recorded.

Subsequent analysis was carried out on the basis of information taken from the check sheets.

R	A	R	A	R	A	R	A	R	A	R	A	R	A	R	A	R	A	R	A	R	A	R	A	R	A	
																										UP
																										NIF
																										NIS
																										NIB
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																										SQUK
																										STAC
																										CIRC
																										REL
																										RUN
																										WALK
																										STOP
																										ATTAC
																										ESCAP
																										STAY
																										TERRI
																										N.TERR
																										GRND.
																										ARIEL
																										LAND
																										T.O.
																										B
																										C