SOCIAL SPACING IN DOMESTIC FOWL

LINDA JANE KEELING

A thesis submitted for the degree of Doctor of Philosophy.

Edinburgh University

1987

EX BIBL. UNIV. EDINBURGH

DECLARATION

I declare that this thesis has been composed by me and that the work described is my own.

AKNOWLEDGEMENTS

I would like to express my sincere thanks to my supervisors; Dr. Ian Duncan, for his continued encouragement and advise, and Dr. John Deag, especially for his help regarding the presentation of the thesis.

My thanks are also due to the members of the Ethology Department at the Poultry Research Centre and the Animal Behaviour Group at the Edinburgh School of Agriculture. The help and patience of the Statistics Department, in particular Mr. David Sales, were also much appreciated.

Finally, I am indebted to Dr. David Shannon and Dr. Rene Zayan for the provision of laboratory facilities and to the Agricultural and Food Research Council for financial support.

ABSTRACT

This study investigated spacing behaviour in adult laying hens. A previous hypothesis, that birds possess a personal space which they try and keep free of conspecifics, formed the starting point of the study.

There was no clear evidence of a critical interindividual distance when heart rate and feeding behaviour were recorded at different interindividual distances. Subsequent experiments, therefore, investigated factors which influenced the distances between birds with a view to proposing an alternative hypothesis. Using overhead photography, size of enclosure, position in the aggressive dominance hierarchy and orientation were all found to have a significant effect on interindividual distances. In another experiment the effect of activity was significant.

Comparisons of observed and expected interindividual distances indicated attraction was as important a component of spacing behaviour as repulsion. A significant relationship was demonstrated between approach/withdrawal of birds and activity transitions and it was suggested that distances between birds represent an equilibrium between the tendency to approach (A) and the tendency to withdraw (W). Using one-way and two-way partitions to investigate which individual of a pair is responsible for controlling the distance between them suggested that each bird positioned itself in relation to another.

CONTENTS

PAGE

CHAPTER 1

GENERAL INTRODUCTION

1:1 Spacing 1

1:2 Methods To Demonstrate Spatial Organization Within Groups Of Individuals 4

1:3 Classifications Of Spatial Organization 7

1:4 Personal Space And Individual Distance 12

1:5 Long And Short-Term Variation In The Spatial Organization Of Animals 17

1:6 The Roles Of Aggression, Submission And Avoidance In Spacing Behaviour 21

1:7 The Role Of Dominance In Spacing Behaviour 25

1:8 The Role Of Attraction In Spacing Behaviour 30

1:9 An Alternative Mechanism Of Spacing Based On The Tendency Of Conspecifics To Approach And Withdraw From Each Other 32

1:10 Assessing Spatial Requirements Of Domestic Fowl In Intensive Systems 43

1:10:1 Mortality and Production 43

1:10:2 Behavioural Measures 44

1:10:3 Physiological Measures 49

1:10:4 Preference Tests And Operant Conditioning 50

PAGE

CHAPTER 2

THE EFFECTS OF INTERINDIVIDUAL DISTANCE ON THE FEEDING BEHAVIOUR AND HEART RATE OF LAYING HENS

2:1 Introduction 53

2:2 Method 56

2:3 Results 64

2:3:1 Behaviour 65

2:3:2 Heart Rate 70

2:4 Additional Analysis 74

2:4:1 Treatment 75

2:4:2 Trolley Position 75

2:4:3 Bird.Treatment Interaction 75

2:4:4 Test Occasion 76

2:5 Conclusion 77

CHAPTER 3

INTERINDIVIDUAL DISTANCES AND ORIENTATION IN LAYING HENS HOUSED IN GROUPS OF THREE IN TWO DIFFERENT SIZED ENCLOSURES

3:1 Introduction 86

3:2 Method 88

3:2:1 Distribution Of Bird Locations Within The Pen 90

3:2:2 Interindividual Distances 90

3:2:3 Comparision Of Observed And Expected Interindividual Distances 91

PAGE

Experiment 2

4:5 Introduction 142

4:6 Method 144

4:7 Results 145

4:8 Conclusion 151

CHAPTER 5

AN INVESTIGATION TO DETERMINE WHICH INDIVIDUAL OF A PAIR IS RESPONSIBLE FOR THE DISTANCE BETWEEN THEM

5:1 Introduction 153

5:2 Method 158

5:3 Results 163

5:3:1 Nearest Distance 165

5:3:2 Mean Distance 167

5:3:3 Orientation 169

5.4 Conclusion 171

CHAPTER 6

GENERAL DISCUSSION 174

6:2 Attraction-Repulsion Hypothesis 180

6:3 Variation In Attraction And Repulsion To Account For The Variation In Interindividual Distance 182

6:4 Assessing Spatial Requirements 194

REFERENCES 202

GLOSSARY 222

APPENDIX 225

CHAPTER 1

GENERAL INTRODUCTION

1:1 SPACING

In studies of animal social organization, the term 'spacing' is used in many different ways. It can be used to refer to the distribution of animals in relation to each other and also to refer to the distribution of animals in their habitat.

Ultimately, the distribution of animals in their habitat and in relation to each other will have been determined by evolution to maximize their inclusive fitness. However in the short-term, or proximate sense, the distribution is determined by causal factors such as the distribution of food, the presence of predators and the occurrence of threats from conspecifics. Of course this does not imply two separate influences on spacing since the short-term causal mechanisms will have evolved.

In this thesis the term "spacing" is used to refer to the distribution of animals in relation to each other. Nonetheless, it is realized the spacing between animals will be affected by the way in which they distribute themselves in their habitat. Consequently, attempts were made in the experiments in this thesis to minimize these

effects. In addition, I have chosen to concentrate on these short-term causal effects and also to focus on spacing between animals of the same species, same sex and of the same group. Spacing between solitary or non-group living animals will only be considered where relevant to the discussion. The reader is referred to Brown and Orians (1970) or Syme and Syme (1979) for reviews of these aspects of spacing.

In order to investigate spacing behaviour, it is first necessary to demonstrate that there is a spatial organization. Methods to determine whether or not spacing between individuals is random are discussed in the first part of this chapter (1:2).

Once the presence of a spatial organization has been established, it can be viewed at different organizational levels and so classified in a variety of ways. Two possible classifications are discussed in the next section

(1:3). Discrepencies in the terminology used by authors in the past when referring to spacing are also highlighted in this part. To avoid any confusion in the terminology used in this thesis, a precise definition is given each time a new term is used. These definitions are summarized in the glossary. Some time is spent in section 1:4 discussing personal space and individual distance, concepts frequently used in spacing behaviour and the ones most relevant to this thesis.

In the next section of the introduction (1:5), long and short-term variations in the spatial organization of animals are discussed. There then follows sections on the role of aggression (1:6) and the role of dominance (1:7) on spacing behaviour. It is appreciated that these two sections will be interrelated. A short section on attraction between individuals (1:8) comments on the fact that most work on spacing behaviour has concentrated on those factors keeping individuals apart, rather than factors keeping them together. The next section (1:9) develops this further, discussing the hypothesis that spacing between individuals is a balance between the tendency to approach and the tendency to move away from conspecifics.

The previous sections have concentrated on describing and investigating spacing behaviour ie. the mechanism by which one individual positions itself in relation to another. The final section (1:10), concentrates on the spatial

requirements of domestic fowl ie. the amount of space domestic fowl require in order to space themselves in relation to one another. This is an applied question which has arisen in light of the current controversey over how much space should be allocated to laying hens in battery cages. Throughout this section I present my own views on why assessing spatial requirements has proved so difficult and conclude with the proposition that scientists will be unable to answer the second question of how much space birds require until the first question, of identifying the mechanism underlying spacing behaviour, has been answered.

1:2 METHODS TO DEMONSTRATE SPATIAL ORGANIZATION WITHIN GROUPS OF INDIVIDUALS

If there is no spatial organisation in a group then it would be expected that the group members would be randomly distributed. Evidence of a non-random distribution, therefore, is the first step towards demonstrating the presence of, and then investigating, spacing behaviour. In fact, the minimum definition of an animal society according to McBride (1964) is that the animals are spaced non-randomly in physical space as a result of their spacing behaviour to conspecifics. The presence of a non-random distribution of individuals in itself, nevertheless, is insufficient to prove some form of spatial organization. Individuals may independently respond to the same causal stimulus in the environment.

Absence of non-random distribution, however, makes any spatial organization very unlikely.

A simple measurement of the degree to which the distribution of individuals in a population deviates from random was proposed by Clark and Evans (1954). They calculated a ratio of the mean observed distance to the nearest neighbour, to the distance between nearest neighbours expected in a randomly distributed population. The resulting R-value represented a continuum from 0 which represented extreme clumping, through 1 which indicated a random distribution, to a maximum of 2.15 indicating that the individuals were as evenly distributed as possible.

This method can also be used to determine whether different groups of individuals are randomly spaced with respect to each other. In this case, the location of each group or flock is treated as one observation and the R-value calculated in the same way. R-values are frequently calculated in studies of spacing patterns (Katz, Potel and Wassersug, 1981; Miller and Stephen,1966). This method will not work for territorial individuals or groups.

Alternative methods to that proposed by Clark and Evans (1954) have been used to demonstrate spatial organization. Crofton (1958) investigated the distribution of sheep in a field and based his test on the assumption that points which were equidistant between neighbouring individuals would form a polehedral pattern if they were

joined together. If the individuals were regularly spaced then the polyhedra would be hexagons and any deviation from regular hexagons would indicate uneven spacing. Pielou (1969) described a series of tests to investigate spatial patterns. Although mainly dealing with plants, many tests are applicable to groups of animals. It is also possible, rather than comparing only distances to nearest neighbours with those expected by chance, to extend this comparison to include distances to 2nd, 3rd, 4th etc. nearest neighbours. This method has been demonstrated theoretically by Thompson (1956) and used on a wide variety of species by Burgess (1979).

Once the spacing pattern of a population has been shown to deviate significantly from random it is possible to put forward ideas as to the cause or function of the distribution. For example, a regular, or a uniform distribution often suggests some form of aggression or competition between individuals which is keeping them apart. A clumped distribution often suggests cooperation between individuals, or some advantage, such as a decreased risk of predation to any individual in the group which is keeping them together. Nevertheless, proof that the animals are clumped or dispersed in response to social pressures and not in response to the distribution of resources can only come from observations of how the animals interact with one another. Therefore, a description of the spacing pattern alone is insufficient

to draw conclusions about the causation or function of the spacing behaviour of a species.

1:3 CLASSIFICATIONS OF SPATIAL ORGANIZATION

If the spacing pattern of a group is shown to differ significantly from random, then it should be described in more detail so different species can be compared. The classification of spacing patterns depends on how animals use and distribute their time in the space available. Two classifications will be reviewed in this section.

a) The most frequently used classification is based on the area occupied by animals. Total ranges, home ranges and territories can be applied to both individuals and groups. These categories are discussed in detail elsewhere (Wilson, 1975 and Deag, 1980).

Personal space is the final category in this classification. There is still some debate as to whether this is a distinct category or a particular spacing pattern demonstrated by individuals with very small territories, literally just around the animal itself. Rather than using the term personal space when referring to this phenomenon, other people eg. Wilson (1975) have used the term individual distance. But since the terms total range, home range and territory all refer to areas, I think it is better to use the term personal space rather than individual distance for this final category. As the

names suggest, one term refers to area and the other to distance. Nevertheless, this interchanging has led to considerable confusion about the terms personal space and individual distance. To avoid any confusion when using the terms in this thesis, and because the question of whether or not domestic fowl possess a personal space was the starting point of this research, section 1:4 is directed towards discussing personal space and individual distance in more detail. It is also for reasons such as this that a large part of this chapter will be concerned with clarifing terminology. To avoid any misunderstanding of other terms used in this thesis, the reader is referred to the glossary.

b) An alternative classification of spacing patterns has been proposed by Waser and Wiley (1979). This is based on specifying individuals' activity, isolation and aggression fields. Their terminology refers either to individuals or to cohesive groups which behave in a similar manner to that of individuals of more solitary species. They do not specifically discuss spacing within groups although I have commented on the relevance of their work to this question later in this section.

They have overcome some of the difficulties of distinguishing between the categories in the previous classification in certain species by expressing spacing in terms of the exclusiveness with which an individual

uses an area. For example, bicoloured antbirds (Gymnopithy bicolor) overlap in their movements, but each bird has clear dominance over intruders within its territory. Tree sparrows (Spizella arborea), however, occupy totally exclusive territories. Both species therefore show territorial behaviour, but they differ in the degree of isolation they maintain from their neighbours.

In their paper, Waser and Wiley try to describe spacing behaviour in terms of an individual's activity, its degree of isolation, and its aggression. The area over which an individual spends its time is called its 'activity field' and the value of an individual's activity field at any particular location is the proportion of its time spent there in all activities. This activity field can also be used to refer to one particular activity, for example, the time spent feeding at a specified location. In this way it is possible to identify feeding areas, roosting areas etc.

The degree of exclusiveness an individual maintains, or which occurs in a particular area, determines an individual's 'isolation field'. The value of an individual's isolation field at any location is the ratio of the time spent by the subject at a location, to the time spent by all other individuals, including the subject, at the location. The ratio varies from 1, where the subject has exclusive use of a location to 0, where other individuals but not the subject utilize the area.

The specification of an individual's activity and isolation fields therefore describes the area an individual uses and how many other individuals use the same area. When this information is combined with data from other individuals and with the distribution of resources it is possible to describe the pattern of spacing for the population and to what extent each individual monopolizes the resources.

The above information only describes the spacing pattern, it does not show what determines the distribution, nor does it show how the distribution is maintained. For this, Waser and Wiley have specified an 'aggression field', the value of which is the probability of attack or retreat by an individual at any particular location. Unfortunately, as Waser and Wiley point out, the measurement of the frequency of aggressive encounters at a location is not necessarily a good indicator of the aggressive tendency of an individual . An individual may not detect another animal's presence, or there may be avoidance by the two individuals and so no obvious encounter. These occurrences would have the effect of lowering the value of the aggressive field.

Nevertheless, this classification of spacing pattern according to activity, isolation and aggression fields can be used instead of, or in conjunction with, the home range, territory and personal space classification proposed earlier. It is possible to describe at least some

of the latter phenomenon in terms of the former. For example, overlapping home ranges would occur where the values for the activity field were high, but the isolation and aggressive field's values were low, as other individuals are not excluded. A defended territory, on the other hand, would have a high isolation field value as the area would be used exclusively by one individual or social group. The value of the activity field would depend on the type of territory under consideration eg.general purpose, breeding or nesting territories.

Unfortunately, Waser and Wiley give no indication of how their theory could be used with respect to personal space. One might expect 'fields' to be described as a function of distance from the individual rather than of geographical location. The isolation field would therefore be the proportion of time spent at different distances from the subject and as such would be expected to vary with the context. The value of the isolation field would determine whether or not there was an area around an individual free of conspecifics. The aggression field, or distance from the subject which elicited an aggressive encounter, would determine whether aggression was important in the maintenance of this exclusive area. Although this would not take into consideration that an individual can maintain an area around itself free of conspecifics by moving away every time it was approached. An aggression/avoidance field might be more appropriate.

The activity field cannot be expressed in terms of distance from the individual as the value would always be zero. Nevertheless, it would be important to specify the subject animal's activity as in Waser and Wiley's original description of spacing behaviour in relation to location, the dimensions of the isolation and aggressive fields varied with activity.

1:4 PERSONAL SPACE AND INDIVIDUAL DISTANCE

As discussed previously (1:3a), most of the inconsistencies concerning spacing arise from the terminology. It appears that the confusion lies in the distinction between terms referring to an area around an individual (personal space, personal field, personal area, intolerance space and social space) and terms referring to a particular distance from an individual (individual distance, personal distance, minimum approach distance, social distance and flight distance).

McBride (1968) suggested that animals occupy two types of space, the physical space taken up by the animal itself and a personal space around it. He likened this personal space to a 'portable territory' which the animal keeps other conspecifics from entering. Although using the word territory implies exclusive use of the personal space, it is confusing because territory is usually used to refer to a geographical location. It is possible, according to

Marler (1956), for a territory to centre around something that moves eg. a mate or offspring and he suggests that that the only obvious difference between this type of territory and personal space is that the latter is centred on the individual itself rather than some external object. However, I think such arguments are open to misinterpretation, so even though personal space is frequently referred to as a portable territory (McBride, 1968; McBride, James and Shoffner, 1963; McCort and Graves,1982), it will not be described as such here. Another way of describing personal space is Hall's (1966) analogy of a portable 'bubble' of space which is transported by the animal.

It is suggested that the personal space, sometimes referred to as the personal field or personal area, is not necessarily spherical. Nevertheless the perimeter represents the minimum distance the animal will allow a conspecific to approach in a particular direction before there is a response. Theoretically, this response by the subject could be either aggressive, so deterring the conspecific from approaching any closer, or avoidance. Either way the personal space is kept free of conspecifics. Hence another name for personal space is intolerance space.

The distance from the animal to the perimeter of the personal space is referred to as the personal distance or more commonly the individual distance. There should

therefore be a distinction between personal space and individual distance. However, there are considerable discrepencies in the terms used by various authors. Condor (1949) has incorrectly used the term individual distance to describe the area around an animal. Broom (1981) in his book says " Individual distance might be regarded as a form of territory, in that it is a defended area ". By definition a distance cannot have area and I feel both Condor and Broom are referring to the concept of personal space. These examples demonstrate the two terms being used interchangably and are typical of the present confusion concerning individual distance and personal space.

Individual distance has been defined by Hediger (1942) as the distance at which another individual of the same species provokes aggression or avoidance in the focal animal. It should not be confused with flight distance which is the distance an animal will allow a predator to approach before moving away (Hediger,1950). It is for this reason that this review is limited to spacing between individuals of the same species.

Hediger (1942) also suggested that animals can be classified into two types according to the value of their individual distance. In contact species the individual distance is zero in that animals e.g. the long-tailed titmouse (Aegithalos caudatus) will tolerate contact with individuals of the same species (Hinde,1952). Distance

species on the other hand rarely, if ever, come into contact e.g. the chaffinch (Fringilla coelebs) (Marler,1952). This division, however, seems rather simplistic as whether or not animals come into contact will vary with the behavioural context and the season. Consequently, the classification of animals into distance and contact species is probably false, since some species, such as domestic fowl, (Gallus gallus domesticus) may come into contact for some activities such as roosting, but not for others.

The concept of individual distance can only really be applied to individuals that are non-territorial since the distance between two neighbouring territorial individuals would change as they moved around in their respective areas. Where there are a group of animals, such as a male and several females, then distances can be measured within the group but not between groups.

Broom (1981) has suggested five possible advantages of maintaining individual distance. These include 1) less damage due to any body contact, 2) less interference and competition whilst feeding, 3) less impedence when starting to flee, 4) reduced disease or parasite transmission and finally 5) less chance of rape. Another possible advantage of maintaining an individual distance, although not discussed by Broom, is that of priority of access to resources. It may be possible for an individual to position itself sufficiently close to a resource so

that any other individual which wishes to use the resource must approach within the individual distance of the first bird. At this point, individual distance becomes linked with social dominance. This is discussd in more detail in section 1:7. There is even the possibility that space itself, rather than something in that space such as food and water, is the true resource (McCort and Graves,1982).

Until now, I have been using the term individual distance since this term was used in the early studies. But, as individual distance is the distance an individual will allow a conspecific to approach before responding, it is in fact the distance between two individuals and should be referred to as the interindividual distance. From now on, the term individual distance will not be used in the thesis. However, to avoid confusion between interindividual distance, referring to any distance between two individuals, and the particular interindividual distance which provokes aggression or avoidance, this latter distance will be called the "critical interindividual distance". Thus the critical interindividual distance is synonymous with the individual distance throughout this thesis.

To summarize this section, the critical interindividual distance is the distance at which another individual of the same species provokes aggression or avoidance in the subject animal. The subject can therefore maintain an

area around itself (the personal space) free of conspecifics either, by responding aggressively to the approach of a conspecific and so deterring the other individual from approaching any closer or, by responding submissively to the approaching individual and moving away itself. Whether an individual is dominant to or subordinate to the one approaching it will influence whether it responds aggressively or submissively.

Further discussions of a mechanism underlying spacing behaviour based on the theory of personal space (with individuals maintaining critical interindividual distances) are presented in the following sections. It has been taken as the starting point that animals do possess a personal space, then arguments against this are presented in the appropriate sections. As discussed previously, McBride (1968) postulated that personal space was like a 'portable territory' from which conspecifics are excluded. It is this extreme view that is tested in the first part of this thesis.

1:5 LONG AND SHORT TERM VARIATION IN THE SPATIAL ORGANIZATION OF ANIMALS

It might be postulated that although distances between individuals ie. interindividual distances may vary, the critical interindividual distance according to the personal space theory should remain constant. The fact that attempts to measure the critical interindividual distance have, at best, resulted in a range of distances now casts serious doubt on this assumption. These experiments are discussed in sections 1:6 and 1:7. It is because variation in the dimensions of the personal space

is not an inherent part of the theory that provisos have often been included to allow for experimental results. These provisos are that the dimensions of the personal space, and hence the critical interindividual distance, vary according to the orientation and the activity of the individual.

As described in the previous section, personal space is not thought to be spherical. McBride (1971) suggested that personal space may only occur in front of the animal and not extend to the sides or back. If this were the case then there would be no critical interindividual distance at the side or back, and so individuals might come into contact, for example, by lying side by side or back to back, but they would not lie directly facing another individual. If personal space extends around the animal, then they will not come into contact at all. McBride proposed these variations in the shape of the personal space to explain why some animals are contact species and why others are distance species, but it also suggests that the orientation of one individual towards another may be important in determining interindividual distances.

Despite the frequent theoretical discussions stressing the importance of activity on spacing there have been few studies which take account of the animal's activity. Fuchs (1980) showed experimentally that guinea pigs (*Cavia aperea porcellus*) actively maintain proximity during

feeding and Faure (1985) reported the same effect in domestic fowl. Walther (1977) demonstrated that preferred distances between adjacent Thomson's gazelles (*Gazella thomsoni*) were greater when grazing than when resting or moving. In fact it has been stated that "scientists interested in animal social organization frequently need to ask questions concerning the interindividual spacing relations among members of a group but often omit consideration of the ways in which interindividual spatial relations and individual activity patterns are related to one another" (Berkoff and Corcoran, 1975).

Gregarious species will by definition have a tendency to come together. The only constraint on this tendency would be the increased probability of aggression or avoidance between individuals which approach closer than the critical interindividual distance. As a result, it would be advantageous for individuals to position themselves not at this critical distance, where any approach would elicit some response, but at slightly greater interindividual distances. These distances would then be more flexible, allowing some approach if neccessary. However, because of this increased flexibility, they would also be more likely to be influenced by such variables as activity, age, and sex. It may be that experiments (section 1:6) attempting to measure the critical interindividual distance have, in fact, measured these other distances which are slightly greater than the critical distance and so have also

recorded the variation in distances between individuals. Therefore, although the results of these experiments cast doubt on the personal space theory, there is still the possibility that it is the techniques used to measure it which are inappropriate, rather than the theory itself.

In addition to the short-term variations in spacing due to changes in activity or orientation, long term variations have also been suggested. An obvious example is the change in spacing behaviour associated with changes in social organization during the breeding season. Hall (1978) has demonstrated that interindividual distances in horses show seasonal variation and Mech and Knick (1978) have shown that sleeping distances in wolves (*Canis luppus*) vary with time in the breeding season. As discussed in the previous paragraph, however, it may be that only the distribution of observed interindividual distances change as they form breeding pairs, or come together in breeding colonies. The critical interindividual distance may remain constant throughout the year.

Even though I have stated that the critical interindividual distance must remain constant to avoid invalidating the personal space theory, there is obviously one exception. The critical interindividual distance cannot be maintained during copulation. It has been suggested (Bastock,1967) that the complex courtship rituals enacted by some species, many of which involve submissive gestures or postures, are a method of reducing

aggression so enabling individuals to approach closer than the critical distance in order to mate. McBride, Parer and Foenander (1968) have also suggested that submissive gestures or postures may allow individuals to approach closer than the critical interindividual distance without eliciting an aggressive response. Whilst mating must be an obvious exception, if too many exceptions are allowed to the rule of maintaining a critical interindividual distance there is again the danger of the term critical interindividual distance becoming meaningless.

1:6 THE ROLES OF AGGRESSION, SUBMISSION AND AVOIDANCE IN SPACING BEHAVIOUR

It is generally accepted that whatever the mechanism underlying spacing behaviour, aggression, submission and avoidance are important. These behaviours act to keep individuals apart. The role of behaviour which acts to bring individual together, such as attraction and approach will be discussed later (section 1:8). It is not possible, however, to say whether it is the spacing or the behaviour which is causal. The distances between individuals may serve to regulate their behaviour (aggressive, submissive or avoidance behaviour), or these behaviours may serve to regulate spacing. Most likely there are interactions both ways with some form of feedback loop.

Aggression may be overt in the form of direct attack, or

formalized into threats. The importance of aggression in spacing is commonly emphasized, but it is possible for the subject animal to retreat or show avoidance when its personal space is invaded by another. There have, however, been few studies of avoidance behaviour to maintain the personal space. Attempts to determine the dimensions of the personal space by measuring the critical interindividual distance have concentrated on measuring aggression between individuals at different interindividual distances. The main experiments which have tried to measure the critical interindividual distance are outlined below.

Marler (1956) investigated the link between interindividual distance and aggression in non-reproductive chaffinches (*Fringilla coelebs*) by measuring the actual distance one bird must approach another before a fight occurs. He looked for evidence of a critical interindividual distance by varying the distances between perches positioned along side a feed trough and recording the occurrences of agonistic encounters. A ratio was then calculated of the number of non-agonistic encounters over the total number of encounters. A score of 0.5 therefore, represented an equal probability of aggression, and Marler called this the 50% interindividual distance. It was hoped that by plotting this ratio against the distance between the individuals, a distinct region would be apparent where the level of aggression suddenly increased. This would

then represent the edge of the personal space. Unfortunately, this was not the case, although Marler did find an interindividual distance, where there was an equal probability of an aggressive or non-aggressive encounter, of 7cm in females and 21-25cm in males. It was found that a female could approach a male to about half the male-male distance and in some cases closer than to another female before fighting developed. This is in keeping with the idea that males are more tolerant of a female in close proximity than another male (McBride,1971).

Another experiment, based on the experiments by Marler, was carried out by Lill (1969). He investigated interactions during feeding and roosting in domestic fowl. Like Marler, he calculated the 50% interindividual distances when birds were feeding. These distances were found to vary greatly and he could make no estimate of the critical interindividual distance when birds were feeding or when they were roosting. Clumping was common and seemed independent of social status, although significant differences were found between pairs of birds. One slight criticism of Lill's work is that he used raised food hoppers which may have affected the results as both hens and cockerels are known to be less aggressive while perching (Faure and Jones,1982). Modern strains of poultry show low levels of aggression compared to their ancestors so measures of overt aggression to study spacing are perhaps inappropriate in the domestic fowl.

Grubb (1974) determined the position at which gulls (Larus argentatus) landed on a floating log in relation to other birds already settled. The majority of birds landed between 30 and 100cm away from another bird. Aggression was frequently observed at landing distances of less than 30cm but rarely at distances of greater than 40cm. Grubb gave this as an example of a 'narrow-tolerance-threshold', since the boundary below which aggression occurred was very sharply defined. This is unlike the results of Marler and Lill which suggest a zone over which the probability of attack increases. However, Grubb's results can also be explained by considering the amount of free space required for a bird to land. It may be physically impossible for a bird to land less than 30cm from another bird without interferring with it in a way that might cause aggression. The interesting point of these results is not that aggression occurred if a bird landed closer than 30cm from another individual, but that birds rarely landed at distances greater than 100cm.

A final experiment, again specifically designed to measure the critical interindividual distance, has been decribed by Meunier-Salaun and Faure (1984). It involved measuring the level of aggression between three birds feeding from a feed trough. The trough was covered over except for three (5cm x 5cm) holes through which only one bird at a time could gain access to the grain below. These three holes were either 0cm, 5cm, 15cm or 35cm apart. A different

arrangement of holes was used on each test occasion. Observations of the birds at the feed trough indicated that the number of aggressive acts was not influenced by the distances between the feed holes. In fact as the distance between the feed holes increased, the association between the birds increased and they were more likely to feed out of the same hole. This result is contrary to that predicted by the personal space theory. One would have expected aggression between birds to be greater at small interindividual distances and for birds to avoid feeding out of the same hole unless one of the pair adopted a submissive posture. It implied that social attraction rather than aggression was the main factor influencing spacing behaviour in these circumstances.

In summary, specifically designed experiments measuring the level of aggression between birds at different interindividual distances have been unsuccessful in determining the dimensions of the personal space. Experiments relating the level of aggression between birds in battery cages to the stocking density will be discussed in section 1:9.

1:7 THE ROLE OF DOMINANCE IN SPACING BEHAVIOUR

Dominance is closely correlated with aggression/submission. In fact, observations of who pecks whom are frequently used as the basis of the dominance

hierarchy (Syme,1983). Dominance is, however, considered as a separate section in this introduction in view of the acknowledged importance of rank on social behaviour and the importance of social behaviour on spacing behaviour. I have selected only those experiments directly relevant to spacing for discussion.

Dominance has been defined by Wilson (1975) as "assertion of one member of the group over another". In other work (Banks, Wood-Gush, Hughes, and Mankovich, 1979; McBride, 1971) dominance is simply described as priority of access to resources. McCort and Graves (1982) suggest that space per se can be included in this list of resources, and that social dominance is a way by which space may be differentially allocated to group members. This point has been discussed further by Gartlan (1964) and Rowell (1974). It has also been stated that spatial organization based on territories shifts to spatial organization based on dominance hierarchies at higher densities (Wilson, 1975; Hedeen, 1982).

If space is regarded as a resource then it implies there will be competition for space in confined conditions in the same way as there would be competition for food if food were limited, with the dominant individual getting priority. Therefore, any evidence of competition for space, or indeed any defence of space, would suggest that space was a resource and would support the personal space hypothesis. At present there is little evidence of

competition for space in confined conditions and Doyen and Zayan (1984a) even suggest, from their observations in battery cages, that there is cooperation rather than competition for space.

Generally speaking, there would be no need for a low ranking individual to invade the personal space of a high ranking individual. If the personal space of a low ranking individual were to be invaded by a high ranking individual, then the lower ranking of the pair would move away to avoid its personal space being invaded. Alternatively, the lower ranking might turn away from the higher ranking intruder thus presenting the smaller personal space at its sides and rear to the intruder and effectively removing it from its personal space. In this situation, the distance between the two individuals remains the same. This behaviour may also be interpreted by the higher ranking as a submissive gesture and so reduce aggression. Thus as McBride (1971) says, "each bird moves so as to avoid the personal fields of dominant neighbours. "

Wiley and Hartnett (1980) studied captive male juncos (Junco spp.) in an attempt to investigate the mechanism regulating spacing of individuals. They found that an individual's tendency to displace, approach or withdraw from an opponent feeding on a nearby perch depended on the dominance relationship of the two birds and on the

distance between them. For example, a bird was more likely to withdraw from a dominant in encounters at close range than at greater distances. Also, subordinates were less likely to approach a solitary dominant animal. Experiments such as this suggest that the relative ranks of individuals are important in spacing behaviour.

A very early paper, although not referred to by McBride, is directly related to the problem of spacing between individuals. Murchison was an American psychologist who worked on social interactions in humans but used chickens as a model (Murchison, 1935). He studied the tendency of a pair of familiar cockerels to approach each other when released from opposite ends of a 6m runway. This was repeated for all pair combinations. He noted the approach speed of each bird and the distance covered by each bird before they met in the runway. He called this a measure of Social Reflex No.1 and plotted it either as the distance moved by the bird before meeting the other bird of the pair, the time before the two birds met, or a measure of the speed with which the bird moved down the runway. His second measurement, which he called Social Reflex No.2, referred to two individuals fighting each other to a decision. This second measurement therefore ranked the individuals. He showed that the higher the rank of a bird the faster it travelled in the runway, and the greater the total distance covered. Murchison plotted Social Reflex No.1 against Social Reflex No.2 and obtained

a perfect linear function. There is no indication of the relative difference in social rank between cockerels which are allowed to fight, even when the outcome is obvious, only that one bird is dominant to the other. He suggested, therefore, that a bird moving towards another (Social Reflex No.1), which can be quantified, might be a better measure of social rank than fighting.

These results in turn suggest that spacing is influenced by social rank. Murchison's results may have been a consequence of lower ranking individuals being more attractive and so approached more quickly or, of higher ranking individuals being avoided and so in effect approached more slowly or not approached at all.

King (1965) suggested a third factor, peck frequency, to link Social Reflex No.1 (two individuals moving towards each other along a runway) and Social Relex No.2 (two individuals fighting to a decision). He noted the inter-animal peck frequency of a group of hens and a group of cockerels and then selected the four most aggressive and the four least aggressive birds from each group. Then, in an experiment similar to Murchison's, he tethered one bird at one end of the runway and released the other bird into the opposite end and recorded the distance the free bird moved towards the fixed bird within a set time. He tested all combinations of birds with high and low peck frequencies and found a significant relationship between peck frequency and minimum approach distance. However,

when the birds were deprived of food for 3h prior to the start of the experiment, and a dish of food was placed close to the tethered bird, all features of the minimum approach distance disappeared. This showed that the relationship between the minimum approach distance and aggressive behaviour may be modified in the presence of a competing motive such as hunger. So, not only is rank (or perhaps more directly, aggression) important in spacing, but also the motivational state of the animal.

The relationship of rank or aggression and distances between individuals has therefore been tackled in two ways. Murchison (1935) and King (1965) related observed interindividual distances to known ranks or levels of aggression whereas Marler (1956) and Lill (1969) related observed levels of aggression to known interindividual distances.

1:8 THE ROLE OF ATTRACTION IN SPACING BEHAVIOUR

The role of attraction in spacing behaviour has frequently been neglected in favour of studies of aggression (1:6). Only when grouping of animals is extremely obvious, such as fish schools, tadpole aggregations and flocks of birds have there been studies of social attraction (Breder, Lum and Wassersug, 1982; Beiswenger, 1975; Katz, Potel and Wassersug, 1981).

Often this high level of attraction is characteristic of

the species, but it has been shown that repeated exposure of an individual to a given stimulus is sufficient to enhance the individual's attraction towards it. This applies whether the stimulus object is a member of the same species, a different species or an inanimate object. A review of attraction, affiliation and attachment is presented by Zajonc (1969).

Behavioural interaction with the stimulus has also been shown to strengthen social attraction. Werner and Latane (1974) showed that rats became more attracted to a human hand after prehandling sessions when the rats were stroked and fondled and the attraction, measured as percentage of time in contact with the hand, increased over test occasions. It has also been demonstrated that the average distances between pairs of rats in an open field test decreased over test sessions (Latane,1969). In both cases this was attributed to an increase in attraction, but how the change in attraction was mediated by a corresponding reduction in fear of the stimulus was not discussed.

Zayan released a pair of birds from either end of a runway and recorded a series of spatial measures eg. time elapsed before the birds approached to within 25cm of each other, total distance moved in the runway, number of stops etc. (Zayan,1985). He found significant differences between unfamiliar and familiar birds indicative of greater coordination, cohesion (and hence attraction)

between familiar individuals.

In this section I have suggested that attraction of one individual towards another, especially in gregarious species, is the main factor preventing individual moving too far away from each other. Yet in a previous section (1:6), I suggested that aggression of one individual towards another was the main factor preventing individual from approaching too close. I stressed that this aggression was not necessarily overt and that an individual may learn by negative reinforcement not to approach a conspecific too closely. Avoidance, therefore, may be the usual expression of this tendency to withdraw. A balance between the tendency to approach and the tendency to withdraw may be a better explanation of spacing behaviour than the personal space theory.

1:9 AN ALTERNATIVE MECHANISM OF SPACING BASED ON THE TENDENCIES OF CONSPECIFICS TO APPROACH AND WITHDRAW FROM EACH OTHER

So far this chapter has dealt with McBride's view of spacing within a group of conspecifics in terms of a personal space, and Waser's and Wiley's view of spacing in terms of isolation, aggression and activity fields. Finally, an outline will be given of Schneirla's point of view. Schneirla (1959) proposed an approach/withdraw theory to account for the observed pattern of spacing in animals. He suggested that animals show differences in

behaviour in response to stimulation at different intensities. Schneirla claimed (but cited no reference) that it had been shown that weak stimuli cause approach towards the source of stimulation and strong stimuli cause withdrawal from the source. He suggested that this negative-positive response could be attributed to the differential arousal of the excitation reaction systems. He described two spacing vectors, a tendency to approach (the A vector), and a tendency to withdraw (the W vector); the A vector increases with increasing distance from the stimulus, while the W vector decreases.

The theory that spacing between individuals is a balance between the tendency to approach and the tendency to withdraw has since been proposed frequently, for example by Atkins (1981), Zajonc (1969), Kummer (1969) and Bischoff (1975). Breder (1954) even used Coulomb's law of magnetism and electrostatics to help formulate mathematical equations to represent the balance between attraction and repulsion in groups of tadpoles.

McBride (1971) criticized this use of A and W vectors saying it failed to explain the wide range of spacing behaviour. This would indeed be true if the vectors were always constant, but, as Schneirla himself stated variations occur between individuals and according to the circumstances. One would expect, therefore, the equilibrium point at which the tendency to approach is

equal to the tendency to withdraw to vary, and so there to be a wide range of interindividual distances in different situations.

Our present knowledge of these A and W vectors is so small that the whole theory is as yet untested. The only quantative evidence for the existance of a mechanism involving such vectors is from work on motivation.

Brown (1942,1948) measured the gradients of approach and avoidance responses in relation to stimuli of differing intensities. Brown uses the terms 'approach' and 'avoidance' even though Schneirla argued against these, preferring to use' approach' and 'withdrawal' instead. However, the meaning is the same in both cases. Brown (1948) used four groups of rats in his experiments. A group of hungry rats were trained to approach one end of an alley for food whereas another group were trained to avoid one end of the alley using strong electric shocks. The other two groups, whose hunger motivation was weak, or who had received weaker electric shocks were also tested. The strengths of the resulting approach or avoidance tendencies in response to the strong and weak stimuli were tested at two points along the alley. The force with which an animal would pull either towards or away from the source of stimulation was used, although other measures, such as speed of locomotion have been employed in the past (Hull,1938). The mean pull, in grams, away from the stimulus (avoidance) was found to be much greater when the

animal was close to the source of reinforcement than when it was further away. The tendency to approach was also stronger when the animal was close to the source of reinforcement compared to when it was further away.

This does not agree with Schneirla's suggestion that the tendency to approach increases with distance from the stimulus, although the response to food might be expected to differ from that of other stimuli. Nevertheless, the gradient of the avoidance response falls off more rapidly with distance from the source of reinforcement than does the approach response. Therefore, despite the fact that both responses slope in the same direction there is, as in Schneirla's theoretical model, an equilibrium point where the two gradients cross. As might be expected, the mean pull of the animals in response to the weak electric shock or when they were only weakly motivated to feed, was less than when they were strongly motivated at the two distance points from the stimulus. This would suggest that the relative strengths of the forces of attraction or repulsion can be modified according to previous experience of the source of reinforcement

It may be that an individual positions itself in relation to conspecifics in the same way as to any other stimulus. That is to say, at a position where the tendency to approach the stimulus animal is balanced by the tendency to withdraw. The relative strengths of these forces would

be modified by the motivational state of the animal and by its previous experience of the conspecific. A tendency to perform two behaviours at the same time, in this case approach and withdraw, are frequently discussed with respect to conflict theory. Conflict has been reviewed by Baerends (1975) and discussed by McFarland (1985).

If the personal space theory to explain spacing behaviour is correct, then two birds would require, at minimum, sufficient space for each member to maintain its own personal space free of the other. I have also discussed the possibility that spacing behaviour is not based on maintaining personal space, but on birds positioning themselves at a particular interindividual distance where there is neither the tendency to approach nor the tendency to withdraw from the other bird. In this situation, two birds would require, at minimum, sufficient space for them to position themselves at that interindividual distance. The space required to do this, consequently, is a function of both birds and so the term social space is used, as opposed to the term personal space which is a function of only one individual.

Like personal space, the term social space has been used by different authors to have different meanings (Wiepkema,1985). In the course of this thesis, social space will refer to the total space required by a group of birds and social spacing to the mechanism by which the group spaces itself. This group size can be as small as

two birds, but single birds cannot possess social space or carry out social spacing. Since I have chosen to use the term spacing behaviour to refer to spacing between individuals of the same species and within the same group and not to spacing of animals in relation to their habitat, the terms spacing behaviour and social spacing are interchangable.

1:10 ASSESSING SPATIAL REQUIREMENTS OF DOMESTIC FOWL IN INTENSIVE SYSTEMS

In 1965 a Technical Committee was set up by the British Government to inquire into the welfare of animals kept under intensive husbandry systems. With regard to domestic fowl, one of the main factors under consideration was the amount of space that should be given to each individual. The Brambell Committee in their report (Brambell,1965) made recommendations for a floor area of 730cm^2 per bird in battery cages containing three individuals, 880cm^2 per bird in cages containing two individuals, and 1300cm^2 for birds housed in single cages. Six years later the Codes of Recommendation for the Welfare of Livestock, Code No.3, Domestic Fowl (MAFF,1971), suggested a minimum of only 450cm^2 per bird. Neither report described how these figures were derived. Since few objective measures of the requirements of birds in battery cages were available at the time, these recommendations can have little scientific basis. Recently the stocking densities have been revised

(EEC,1986 and MAFF, 1987), but the floor area allowance is still only 450cm^2 per bird in cages containing four or more birds.

A bird cannot be housed in a cage or enclosure which offers less space than the bird itself occupies. This is called the physical space requirement and is the volume of air displaced by an individual. But, in practice, the term is used to refer to the floor space occupied by the bird. The requirement for space in the third dimension i.e. height has been investigated by Dawkins (1985) and Nicol (1986) and is not discussed in this thesis. In a study to investigate physical (floor space) requirements (Freeman, 1983), mature Rhode Island Red females were found to occupy between 395 and 637cm^2 depending on their conformation and feather cover. Freeman's measurements were based on birds which were standing.

It has been stated (MAFF, 1971 and MAFF, 1987) that "irrespective of the type of enclosure or system of management used, all domestic fowls should have sufficient freedom of movement to be able, without difficulty to stand normally, turn around and stretch their wings. They should have sufficient space to be able to perch or sit down without interference from other birds". Naturally, some activities require more space to perform than others. Bogner, Pesche, Seda, and Popp (1979) estimated the area occupied by hens performing different activities. They used a different strain to Freeman, but presented a range

between 424 and 536cm^2 per bird. Baxter and Schwaller (1983) have investigated the minimum space requirement for sows in confinement in a similar way. They subdivided the term physical space into static space, to represent the space required for a stationary individual, and dynamic space, as the space required by an individual which is moving e.g. standing up or lying down.

In commercial situations, the majority of birds are housed in groups. Although each bird in a group may be allowed the same area as a bird in a single cage, the group housed birds are in a larger enclosure which, as a result, is less physically restricting. Elmslie, Jones and Knight (1966) defined a curve of "physically impossible restriction" with 580cm^2 per bird as the minimum area with only one bird per cage, 465cm^2 per bird with two birds per cage, and 300cm^2 per bird with ten birds per cage. Nevertheless, these measures only represent the physical space required by birds to perform essential activities.

As discussed previously, individuals within groups do not distribute themselves randomly. Individuals have a requirement for adequate space in which to position themselves in relation to other group members, and to interact with, or to avoid interaction with them. Therefore, in addition to a static and dynamic physical space requirement, a group of birds will have a social space requirement. Inadequate social space may result in

reduced welfare of the individuals concerned (Dantzer and Raab,1985; Duncan,1981).

Unfortunately, as yet, there is no adequate theory of social spacing. Most investigations have been restricted to looking at the responses of individuals housed at different densities in an attempt to determine whether a particular group, in a particular housing system, has sufficient social space. Differences in behaviour have been attributed to density in a post hoc manner and large differences have been attributed to inadequate social space. Apart from its logical weakness, the main disadvantage of this approach is that it can never lead to a general theory of social spacing as the trials need to be repeated for each change in the housing system, group size etc.

It is worthwhile here making the distinction between density and crowding. Density, is a physical condition that can be described in terms of spatial parameters such as number of birds in a given area. Crowding however, is a state involving perception of space by the individual bird and so is an interaction of spatial, social, and internal factors (Desor, 1972; Stokols,1972). Although a particular density may appear restrictive to an outside human observer, it will not inevitably be inadequate for the occupants of the space. The reverse situation is also true. It is the bird's perception of the density that is important. We should be careful not to impose our own

subjective views on whether or not individuals are crowded. Social interference, in the form of competition or difficulty in coordinating activities, is one of the major factors influencing whether an individual perceives an area as crowded. There is even the potential for a particular density to be experienced as crowded by one individual in the group but not by others. On occasions when the individual cannot leave the crowded situation there may be behavioural changes to try to alleviate the sensation of retricted space. If this is unsuccessful, attempts to cope with crowding may be accompanied by behavioural or physiological changes indicative of stress (Mashaly, Webb, Youtz, Roush and Graves, 1984; Siegel, 1960; Dantzer and Raab, 1985; Warnier and Zayan, 1985; Bessei,1982).

The previous paragraph outlined the responses of animals unable to cope with the particular densities at which they were maintained. Animals do to a certain extent, however, seem able to adapt their spacing behaviour. It has been shown in the jewel fish Hemichromis bimaculatus (Coss and Burgess, 1981) and the intertidal hermit crabs (Clibanarius tricolor and Clibanarius antillensis) (Hazlett, 1975) that subsequent spacing behaviour can be modified by the stocking density at which the animals were reared.

Coss and Burgess (1981) found that whereas jewel fish

reared in uncrowded conditions dispersed at between 80-140 days of age to form territories, jewel fish reared in crowded conditions retained the juvenile schooling pattern. They suggested that this difference in behaviour was due to the individuals in the crowded conditions being unable to develop normal social behaviour, particularly the decision of whether to approach or withdraw from a conspecific.

The effect of crowding on movements towards and away from conspecifics has been investigated in more detail by Hazlett (1975). He identified seven different behaviour patterns, including approach and withdrawal, and the interindividual distances at which they occurred in two different species of intertidal crab. He found that crabs kept at low densities attacked, but also retreated from other individuals at larger interindividual distances than did crabs kept at high densities. As a result, low density crabs were more likely to lose an encounter with a high density individual. Hazlett concluded that the crabs had responded to the high density by modifying the distances at which different behaviour patterns occurred. The idea that crabs may posses interindividual distances which trigger off particular behaviour ie. one distance eliciting approach and the other retreat, is in keeping with Schneirla's (1959) approach/withdraw theory discussed earlier (1:9). Such experiments have not been carried out with domestic fowl, so we do not know whether birds modify

their spacing requirements depending on the conditions in which they are maintained.

There are four main ways in which the spatial requirements of domestic fowl can be investigated. These are (1) recording mortality and production levels at different floor areas per bird; (2) comparing the behaviour of birds kept at different densities; (3) using physiological measures, which are thought to be indicators of welfare, to determine whether individuals are stressed by a particular space allocation; (4) asking the bird to choose between environments in a preference test, or to modify its present environment using operant conditioning.

These methods are briefly discussed below. A full review will be given in the following experimental chapters whenever a particular technique is used. The aim here is to indicate the wide range of techniques which can be used to investigate spatial requirements and to highlight the advantages and the disadvantages of the different methods. Consequently, only a few specific examples have been chosen in each section. I have been critical of some methods and have tried to suggest possible directions for future work.

1) Mortality and Production

Unfortunately, there have been very few studies to measure the effects of area per bird on production, or mortality, which have not been confounded with group size. In battery

cages, where group size and area per bird have been varied independently (Hill and Binns, 1973; Wells, 1973; Bessei,1985) certain trends are apparent. In general, increased colony size and decreased area per bird depress egg production and increase mortality, although single birds in cages do not follow this pattern. There is no evidence of a sudden change in production or mortality as area per bird decreases as would be expected if birds could not maintain critical interindividual distances. Nevertheless, having said that, production and mortality are very crude measures on which to base assessments of an animal's requirement for space. A hen's welfare will be reduced long before it ceases to lay an acceptable number of eggs, and certainly before it dies.

2) Behavioural Measures

Although there have been studies of the behaviour of birds kept at different densities they have usually involved comparisons of pens and cages, or extensive and intensive systems. In these situations, variations in the behaviour of the birds cannot be attributed to any single factor in the two conditions, such as density, but to any one of a number of differences between the two environments.

In general, experiments which have varied density while keeping other factors constant, have concentrated on measuring the level of aggression between birds. It was expected that when the amount of space available to each

bird in the group was decreased, the level of aggression would increase since the individuals would not be able to maintain their personal spaces free of conspecifics. Alternatively, the individuals would become frustrated in the confined conditions and this would lead to an increase in agonistic behaviour (Duncan and Wood-Gush,1971). However, quite the reverse has been found to be true. Craig and Bhagwat (1974) found high levels of aggression in less crowded floor pens compared to birds kept in the same conditions but at a higher density. Polley, Craig and Bhagwat (1974) found that at high densities, although the percentage of agonistic encounters which were severe increased, the absolute frequency of aggression decreased. They proposed a curvilinear relationship with an initial increase in the number of aggressive social interactions as the density was increased, followed by a sharp decline as area per bird was reduced further. As only two density levels were compared within each experiment, the evidence of curvilinearity was not direct but obtained by combining the results from each experiment. Unfortunately, Polley et al (1974) made comparisons between colony cages and pens which, for reasons discussed earlier, may not be valid. Also, birds of differing ages, and a wide range of flock sizes were used for each experiment which may have affected the results.

Hughes and Wood-Gush (1977), who did control for housing condition and group size in their experiment, proposed

three possible explanations for the decrease in aggression at high densities. Firstly, they suggested that since birds require quite a considerable area to perform threat displays, aggression is limited because of physical constraint when birds are maintained in small areas.

The second explanation for this phenomenon was that a middle ranking hen's aggressive behaviour towards a low ranking hen may be inhibited by the closeness of a third, high ranking hen. The overiding effect of high ranking individuals on those of lower ranks has been shown (Ylander and Craig, 1980). Therefore, one might suppose that as density is increased birds are forced closer together and so are more likely to be influenced by higher ranking hens. The percentage of agonistic interactions attributable to middle ranking hens towards low ranking hens would decrease as a result. This has been shown to be significant (Hughes and Wood-gush, 1977) in cages, but whether this is sufficient to explain the overall reduction in number of aggressive acts within groups of birds in cages compared to pens was not made clear.

The level of aggression in pens and cages has been investigated further by Hughes and Black (1978). This experiment involved transfering birds from pens to cages and vice versa. The evidence seemed to suggest that there was an effect of high ranking birds on low ranking

birds which reduced aggression, but only once a hierarchy was established. For example, when a group of unfamilar birds was first placed in a battery cage there was a high level of aggression, but this soon decreased. On the other hand, when a group of unfamilar birds were placed in a litter pen, the level of aggression decreased much more slowly. However, if birds which had been previously housed in pens, where there was a high level of aggression but where a dominance hierarchy had become established, were transferred to cages then there was a sudden decrease in the level of aggression. This suggested that it was the close proximity of the other individuals which reduced the level of aggression. Unfortunately, this experiment did not exclude the possibility that there was some effect of the cage itself, other than the reduction in available space, which triggered off the response. It would perhaps have been more informative to transfer birds from a pen of one size to another pen of a different size or, to use only cages of differing sizes to answer this question.

The third explanation of Hughes and Wood-Gush (1977) to explain the decrease in aggression at high densities was that agonistic encounters only occur when the personal space is invaded and not by continuous proximity. Habituation to the continuing presence of a conspecific within the personal space to explain the reduced level of aggression would seem incorrect. Such a mechanism would be maladaptive and any advantages of a personal space

(proposed earlier) would be lost. The only possible explanation for a reduced level of aggression when a conspecific is within the personal space would be that of learned helplessness (Seligman, 1972).

There is certainly no evidence from the studies of aggression, of a critical threshold below which aggression suddenly increases, as would be expected if there was a critical interindividual distance. These results, therefore, lend no support the notion of a clearly defined boundary to the personal space.

There has been very little work to assess spatial requirements of birds in battery cages that has recorded behaviour patterns other than those normally associated with aggression. Studies which have recorded other behaviour patterns eg. preening, feeding behaviour and comfort behaviours (Tind,1985), pushing (Doyen and Zayan, 1984a,b; Zayan and Doyen, 1985), a full ethogram of behaviour (Nicol, 1985) are difficult to interpret directly. In the majority of cases, we do not know whether or not an increase in the frequency of a particular behaviour pattern at one density compared to another indicates a benefit to the bird. Such studies, however, can point the direction for further work by highlighting differences which can then be investigated further. Rather than determining time budgets of birds in battery cages, studies of the sequences of behaviour by an individual, or the coordination between group members to investigate

whether or not birds hinder or interfere with the behaviour of others (a criterion for crowding) may prove helpful.

3) Physiological Measures

Physiological responses, for example, increased heart rate, and the release of hormones such as adrenaline and noradrenaline, occur when the animal is confronted with a noxious stimulus. This has been called the "emergency reaction" (Selye,1951) and, under natural conditions, these responses would prepare the animal to fight with, or flee from the stimulus. However, the animal may be prevented from behaving in a manner appropriate to the situation when it is kept in confined conditions.

There is also a more long-term response in which the anterior pituitary gland secretes adrenocorticotrophic hormone which, in turn, induces the adrenal glands to produce coricosteroids. The presence of corticosteroids in the blood is indicative of the "General Adaptation Syndrome" (Selye, 1951) and, more long-term stress. Poultry kept at high densities sometimes show enlarged adrenal glands (Siegel and Siegel, 1969). This has led to the suggestion that overcrowding causes the animals to suffer even when they appear to be physically healthy (Dawkins,1980).

A combination of physiological and behavioural studies is

often recommended (Dantzer and Mormede,1981; Duncan,1982).

4) Preference Tests and Operant Conditioning

An alternative to measuring the responses of an animal to an enforced environment would be to let the animal select its own conditions using preference tests. These tests can be used to measure preferences for features of the physical environment or, social environment. Hughes (1975) and Dawkins (1981) have shown that battery-kept hens show a preference for a large cage over a small cage although, this preference is reversed if the small cage contains litter (Dawkins,1981). This may suggest that the dimensions of the space are less important to a bird than what the space contains, in this case litter. An area is unlikely to be totally empty of objects or resources and questions about the interaction between this so-called furniture and space may be more relevant when assessing spatial requirements than questions about space per se.

Dawkins (1982) and Hughes (1977) also measured preferences for familiar birds, unfamiliar birds, empty cages and for groups of different sizes.

There have been criticisms of preference tests (Duncan,1978) because of the difficulties of interpreting the results. A choice between two environments only indicates the relative properties of the conditions, not their absolute properties. Also, only rarely is there a

hundred percent choice for one condition over another. Partial preferences may indicate a preferred distribution of time between the two conditions or, alternatively, only a slight preference for one condition over the other. Some of these criticisms can be overcome by presenting a series of choices, varying only one environmental variable at a time. However, this approach to pre-existing husbandry systems is extremely inefficient as all possible combinations would need to be compared against all others.

My own opinion is that preference tests would be better used to investigate an animal's perception of space. Preference tests could be used to determine what it is about the area that is important to the animal (Thinus-Blanc and Buhot-Averseng, 1985). Comparisons could include keeping the volume of an enclosure constant, but varying the floor area and vice versa. Also, the ratio of area to periphery could be investigated using enclosures of different shapes. The use of partitions to divide an area or the distribution of resources to maximize effective space could also be investigated in this manner.

Operant conditioning involves training an individual to perform a specific task in order to gain a reward. In this case the reward would be a change in some feature of the environment. The difficulty of the task can be altered to measure how hard the individual will work to bring about this change in its environment. Unfortunately, the results obtained with one individual may not predict the results

EX BIBL. UNIV. EDINBURGH

obtained in groups. This may be especially true when some feature of the environment, such as available space, is being considered.

Meunier-Salaun and Faure (1984) have used operant conditioning to investigate the preferences of hens for different cage and feeder sizes. Such experiments are still in the initial stages, but this technique could help assess the importance of space to individuals. By combining these studies with behavioural observations, it might be possible to determine why an individual will work to increase the area available to it. This could be carried out by recording the behaviour before, and then after, it has performed the operant conditioning task.

The above sections demonstrate different approaches to assessing the spatial requirements of domestic fowl. Each technique has advantages and disadvantages, and probably a multidisciplinary approach offers the greatest chance of solving the problem. Of course, as well as reaching a short-term solution of how much space birds require in existing intensive husbandry systems, in the long-term it is important to understand the mechanism underlying spacing behaviour, so that new, alternative housing systems can be designed.

CHAPTER 2

THE EFFECT OF INTERINDIVIDUAL DISTANCE ON THE FEEDING BEHAVIOUR AND HEART RATE OF LAYING HENS

2:1 INTRODUCTION

If the domestic fowl possesses a personal space then presumably its behaviour should change dramatically when this personal space is invaded. It might be possible to get some idea of the dimensions of the personal space by measuring the distances at which this change of behaviour occurs when birds are moved together artificially. McBride (1968) referred to such a distance as the "personal distance" but for reasons already discussed in Chapter 1, it will be referred to as the "critical interindividual distance" throughout this thesis.

Previous experiments, designed to measure the critical interindividual distance, have resulted in such a wide range of values that it has been impossible to propose any dimensions of the personal space. Both Marler (1956) using chaffinches and Lill (1969) using domestic fowl recorded the level of aggression between birds at different interindividual distances, on the assumption that aggressive interactions would be more frequent at distances less than the critical interindividual distance. However, they found no obvious lower limit below which aggression suddenly increased. As a compromise, therefore,

both scientists calculated the interindividual distance at which there was a 50% chance of an aggressive encounter. In domestic fowl (Lill,1969) the low level of observed aggression made even this measure unreliable. The difficulty in determining any threshold may have been a consequence of the experimental design. In these experiments, because individuals were given the freedom of whether or not to approach a conspecific, one would not have expected them to approach closer than the critical interindividual distance and so invade the personal space of their neighbour. As a result, there would be few distance-related aggressive interactions.

The present experiment was also designed to determine whether or not there is a critical interindividual distance in chickens. But, to avoid the bias of birds rarely approaching closer than the critical interindividual distance, it was decided to control the distances between the birds. This was achieved by placing each bird in a cage situated on a wheeled trolley. The birds could then be moved together, or apart, according to a predetermined routine (Figure 2.1). Evidence of a critical interindividual distance would support the theory of personal space and would represent the distance from the bird to the edge of its personal space.

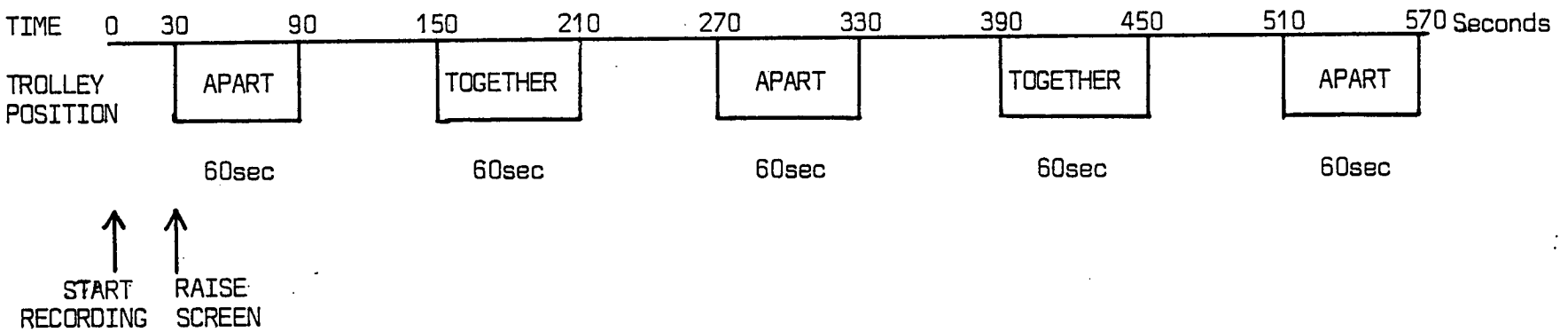


FIGURE 2.1 Experimental Sequence Of Trolley Movements

In addition to recording changes in behaviour as the birds were moved together and apart, it was decided to monitor a physiological parameter, heart rate, since this might be a more sensitive measure of disturbance. It has been shown previously that heart rate can be a useful complimentary measure to behavioural changes in studies in the domestic fowl (Duncan and Filshie, 1980; Jones et al,1981; Candland et al 1969; Mills et al,1985) and in other species (MacArthur and Geist,1982; MacArthur, Geist and Johnson,1983; Candland et al,1970; Cherkovich and Tatoyan,1973; Tatoyan and Cherkovich,1972).

1:2 METHOD

Twenty S-line (a light body-weight strain, predominantly White Leghorn in origin) aged between 30 and 50 weeks were used in this experiment. The birds had been reared in brooders until 4 weeks of age, then kept in group rearing cages. The birds were transferred to individual battery cages at 16 weeks and at 26 weeks to pens where they were maintained, in two groups of 10 birds each, throughout the experimental period.

Four individuals were selected at random from each pen and given an intramuscular injection of 1ml/kg xylazine (Rompun, Bayer). A radiotelemetry device designed to transmit electrocardiogram (ECG) signals (Filshie, Duncan,

and Clark,1980) was then implanted subcutaneously over the right pectoral muscle. (For a more detailed description of the operation see Appendix. After surgery each bird was left for at least two days before observations were started.

The experimental apparatus consisted of two cages directly facing each other. Each cage was situated on a moveable trolley and the two trolleys were connected by a pulley system (Figure 2.2). The cages measured 90x56x50cm (lxbxh) and so were sufficiently large to allow the bird some freedom of movement. The anterior end of the cage was V-shaped, with an opening through which the bird could place its head (Figure 2.3). A shallow feed trough (2cm deep) was placed on the trolley, just in front of the cage, so that the bird could feed by placing its head through the opening. In this way, the bird was always orientated towards the opposite trolley when it was feeding, or when it was standing with its head and neck through the opening. Body orientation has been shown to be important in communication between animals (Hayward, Gillet and Stout,1976; Breden, Lum and Wassersug,1982). In addition, proponents of the personal space theory have suggested that the space is not spherical, but larger in front of than to the side of or behind the head. For these reasons, it was important that the orientation of the birds towards each other was consistent. The feed trough was shallow so that the bird had a clear view of the second trolley even

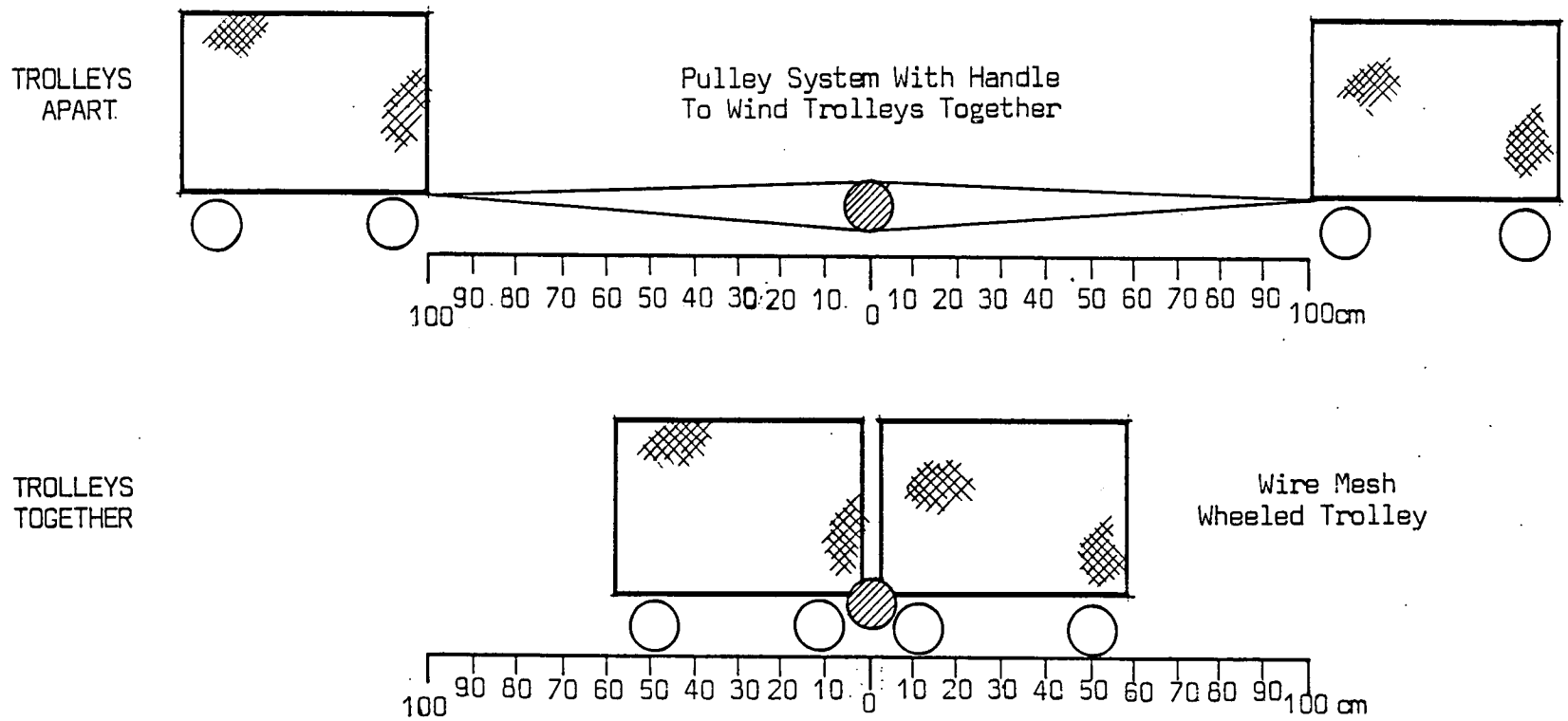


FIGURE 2.2 Side View Of Trolleys When Apart And Together

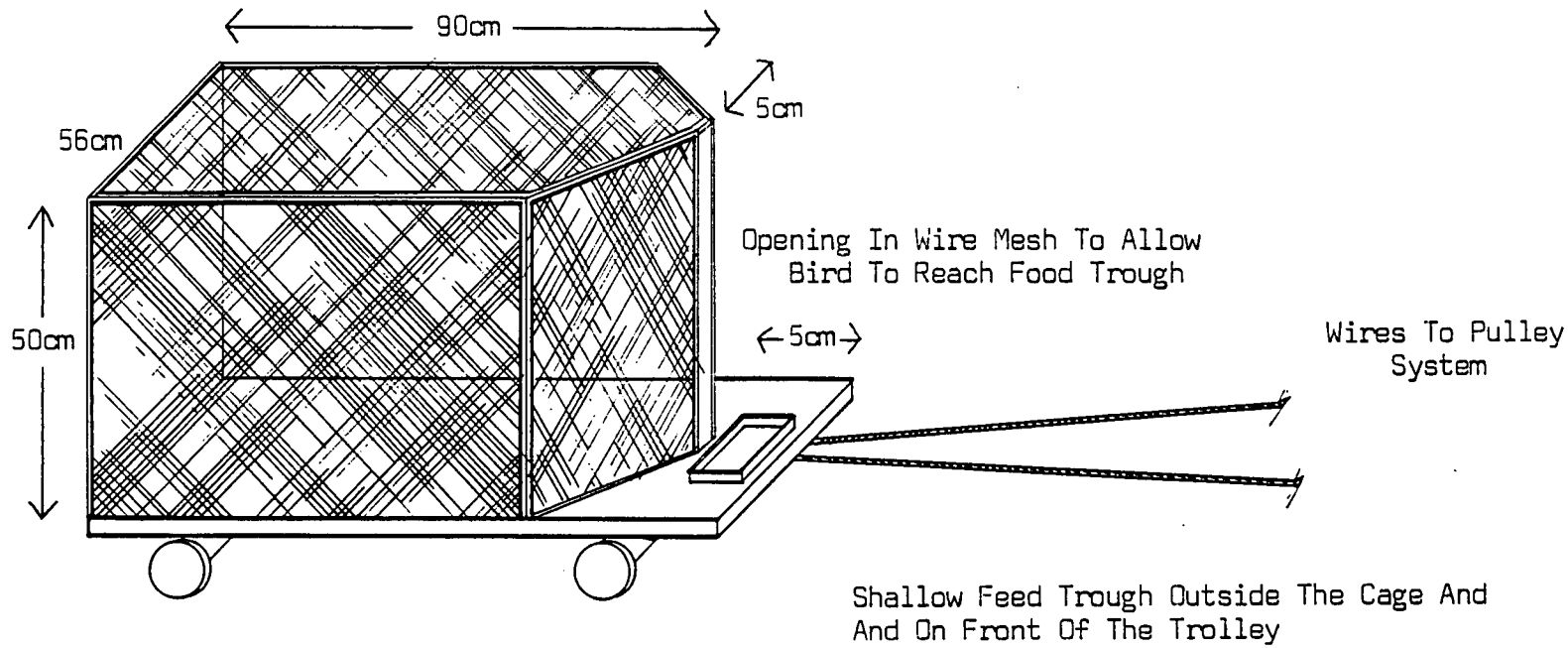


FIGURE 2.3 Diagram Of Trolley

when it was feeding.

The distance between the two trolleys was 200cm when they were apart, and 0cm when they were together. They could be moved by turning a handle connected to a pulley. Precautions were taken, such as having large rubber wheels fitted with rubber tyres and only moving the trolley slowly, to ensure as smooth a movement as possible. All birds were accustomed to being handled, placed in the cages, and to the movement of the trolleys.

Control treatments, with the bird moving towards an empty trolley, provided an important baseline indicating the usual heart rate variations of the birds. They were also intended to check that the movement of the trolley itself did not cause a response and to eliminate the possibility that the subject bird was responding to the approach of the other trolley, rather than the approach of the bird inside the other trolley.

The signal from the transmitter was picked up by a v.h.f. receiver, through a dipole aerial located on the cage. It was then relayed to an oscilloscope which displayed the ECG trace. The signal, along with a sound commentary, was stored on magnetic tape for later analysis. The ECG traces were analysed on a computer. The QRS complex was used to trip a Schmitt Trigger and the time lapse until the next QRS wave was measured. The mean heart rate was then calculated for ten second time periods and the sequences

of mean heart rates for the duration of the test printed out. Using the sound commentary, the behaviour, distance between the two birds and the mean heart rate of the transmitter bird could be synchronized.

Two birds, one from each pen and one of which had a telemetry device implanted, were selected at random. Although the birds were sometimes tested more than once, they were always paired with an unfamiliar individual. Birds interact differently according to whether or not they are familiar to each other, with agonistic interactions more likely between unfamiliar birds (Siegel, 1976; Hughes and Black, 1978; Lee and Craig, 1981; Zayan,1985). By using unfamilar birds it was intended to increase the probability of producing a change in heart rate or behaviour as the two birds approached.

To increase the probability of identifying a critical interindividual distance, factors thought to influence spacing were kept as consistent as possible between tests. The orientation of the birds was always the same. Also as discussed in Chapter 1, behavioural activity is thought to be important in influencing the distances between individuals. It was decided, therefore, that both birds should be performing the same activity for as much of the test period as possible. Consequently, the two subject birds were placed in individual battery cages, without food, one hour prior to the experiment. This deprivation was selected so the birds were motivated to feed during

the experiment, but not so hungry that they would feed to the exclusion of other stimuli, such as the presence of another bird in the opposite trolley.

Feeding behaviour is one of the most easily manipulated behaviour patterns and was used by Lill (1969), Marler(1956) and Wiley and Hartnett (1980) when investigating interindividual distances. In other experiments, roosting (Lill, 1969) and distances between birds landing and taking off (Grubb,1974) have also been studied. Cessation of feeding was found by Jones et al (1981) to be the most reliable behaviour pattern when assessing fear in hens exposed to a looming human stimulus. For all these reasons, cessation of feeding was thought to be the the most suitable behavioural measure for this experiment.

Changes from feeding behaviour could be compared in the experimental and the control conditions and when the trolleys were apart compared to when they were together. The probability of birds feeding would be expected to decrease over the course of the test due to satiation. But, one might also predict that birds would spend less time feeding in the experimental than in the control situation, due to the presence of a conspecific, and when the trolleys are together compared to when they are apart.

The birds, having been deprived of food for 1hr, were taken from the battery cages to the experimental room and

one bird was placed in each of the trolley cages. The two birds could hear each other, but there was a screen between the two cages so there was no visual contact. The birds were allowed two minutes to settle and then layers mash was placed in the food troughs. One minute later the tape recorder was switched on to record the ECG trace. If either individual had not started to feed within fifteen seconds of introducing the food, the test was abandoned. Layers mash, rather than pellets was used in the experiment to slow down the rate at which food was consumed (Savory,1974) and so delay satiation.

Thirty seconds after starting to record, the screen between the two birds was raised. The two trolleys were always the maximum distance apart at the start of the experiment. After 60s in this position, the trolleys were slowly brought together. The trolleys were together for 60s before being moved out again. The birds were moved as smoothly as possible, usually taking 60s to go from one position to the other. After one movement (in and out) the trolleys were kept apart for 60s and then there was a second movement (in and out). The behaviour of the transmitter bird was recorded from the time the recorder was switched on to monitor the ECG trace, until the end of the test period. This was usually between 9 and 10 minutes and recording stopped when the two trolleys were apart at the end of the second movement. In the experimental situations, when both trolleys contained a bird, the

behaviour of the second bird was also recorded, but in much less detail than the transmitter bird.

Birds were replaced in their original pens at the end of the experiment. Each individual was only tested once each day. Experimental and control treatments were carried out in a random order using a different order for each individual. Consequently, the number of times an individual was tested ultimately depended on the number of days the transmitter continued to function.

2:3 RESULTS

The heart rate of the birds was expressed in beats per minute and the behaviour as the proportion of time spent feeding. The time spent feeding was originally recorded in seconds and then later calculated as a proportion of the total time at that interindividual distance. Although recordings were made throughout the test, it was decided to concentrate initially only on those time periods when the trolleys were stationary and apart, and stationary and together. Thus, the portion of time the transmitter bird was feeding and the mean heart rate were calculated for the times when the trolleys were apart at the start of the experiment (A_1), together for the first time (T_1), apart for the second time (A_2) and together for the second time (T_2). The A and T positions represented the maximum (2.0m) and the minimum (0.0m) distances between the two trolleys

and hence, when there was a bird in each trolley, the maximum and minimum interindividual distances. Only if significant differences were found between these two positions would the heart rate and behaviour at intermediate interindividual distances be examined for evidence of a more specific interindividual distance at which the changes occurred. Reasons why this second analysis was not performed are discussed later (2:5).

The behaviour and heart rate data were analysed separately.

1) BEHAVIOUR

The data on the proportion of time spent feeding were analysed in two ways. Firstly, a non-parametric test was used as the data were not normally distributed, having too many occasions when the bird did not feed at all (0.0) and too many occasions when the bird fed continuously (1.0). Transforming the data did not improve the normality of the data because the distribution was asymmetrical. In the second analysis a non-parametric test was carried out. It was appreciated that a parametric analysis may not be entirely valid, but the data were not so extreme in their distribution to make the analysis misleading and it was thought important to give some consideration to possible interactions between variables. It was not possible to test for such interactions using a non-parametric test.

The non-parametric tests were only intended as a preliminary analysis. The results and interpretations

corroborate those of the parametric analysis and since the non-parametric tests were the more superficial they are only discussed briefly. Rather I have chosen to use this preliminary analysis to justify the later parametric analysis.

NON-PARAMETRIC ANALYSIS - For this analysis, only the first control recording and the first experimental recording for each bird were included in the analysis. Since bird 194 had no control recording, only 7 out of the initial 8 birds were included in the analysis.

To test for differences between the control and experimental teatments, the proportion of time spent feeding was averaged across the A_1, T_1, A_2 and the T_2 positions and then the mean proportion of time spent feeding in the control teatment subtracted from the mean proportion of time spent feeding in the experimental treatment (E-C). This was repeated so each individual was matched for its experimental and control. The resulting 7 values (E-C) could be either positive, if the birds spent less time feeding in the control than in the experimental treatments or negative, if birds spent more time feeding in the control treatment. Using a Wilcoxon Signed Rank Test, birds were found to spend less time feeding in the experimental condition than in the control (Wilcoxon Statistic 0.0; N=7; P=0.04).

To test for differences when the trolleys were together

compared to when they were apart, a similar analysis was carried out. The proportion of time spent feeding was averaged across the experimental and control treatment for each individual and then the mean proportion of time spent feeding when the trolleys were apart ($A_1 + A_2$) subtracted from the mean proportion of time spent feeding when the trolleys were together ($T_1 + T_2$). The resulting 7 values ($(T_1 + T_2) - (A_1 + A_2)$) could be either positive, if birds spent less time feeding when the trolleys were apart compared to when they were together or negative, if birds spent more time feeding when the trolleys were apart. Using a Wilcoxon Signed Rank Test, the birds were found to spend less time feeding when the trolleys were together compared to when they were together (Wilcoxon Statistic 0.0; N=7; P=0.02).

PARAMETRIC ANALYSIS - For this analysis, again only the first control and the first experimental recording were included. An Analysis of Variance was carried out on the proportion of time spent feeding. The variables included in the analysis were:

1 Treatment - experimental or control
2 Trolley position - apart or together
3 Trolleys movement - first or second
4 Bird - seven birds in total

The results from the ANOVA are presented in Table 2:1.

2:1 Analysis of Variance of the proportion of time spent feeding

VARIABLE	DF	F-VALUE
Bird	6	6.82 ***
Treatment	1	29.43 ***
Position	1	34.99 ***
Movement	1	40.22 ***
Bird.Treatment	6	2.78 *
Bird.Position	6	0.62
Treatment.Position	1	1.34
Bird.Movement	6	1.56
Treatment.movement	1	1.22
Position.Movement	1	9.313 **
Bird.Treatment.Position	6	1.40
Bird.treatment.Movement	6	1.84
Bird.position.movement	6	0.78
Treatment.position.movement	1	10.49 **
residual	6	mean square = 425.9
Total	55	

*** P<0.001 ** P<0.01 * P<0.05 This notation is used throughout the thesis.

There were significant differences between birds in the proportion of time they spent feeding (P<0.001). This could have been due to the differences in the hunger of the birds at the start of the experiment. Although all birds were deprived of food for 1hr, there may have been

differences in the actual time since their last feed. Alternatively, birds may vary in the degree to which they were disturbed by being placed in the trolley, irrespective of whether it was an experimental or a control treatment. This point is discussed in more detail later in this section (2iv) when the effect of heart rate is investigated.

Trolley position and treatment independently affected the proportion of time spent feeding in a similar way to that found in the non-parametric analysis. But, these variables were part of the interaction between Treatment, Position and Movement and were not therefore considered indepedently. This result is represented in Table 2.2.

TABLE 2.2 Proportion of Time Spent Feeding Averaged Across The Seven Birds

MOVEMENT	FIRST		SECOND	
POSITION	APART(A_1)	TOGETHER(T_1)	APART(A_2)	TOGETHER(T_2)
TREATMENT				
Experimental	0.95	0.19	0.17	0.12
Control	0.95	0.69	0.66	0.38

Standard error of the difference 0.14

One would expect all birds to spend more time feeding in position A_1 than in any of the other positions as this was one of the criteria for the experiment to continue. If a

bird did not start feeding within 15sec of the food being presented then that particular test was abandoned. It would also be expected that the amount of time spent feeding would decrease as each test progressed and the bird became satiated. These results are interesting because the proportion of time spent feeding decreased much more rapidly in the experimental situation than in the control. The largest decrease occurred when the transmitter bird approached another bird for the first time.

The standard error of difference of the means is 0.14 for this interaction. Consequently, the significant decreases in time spent feeding are between A_1 and T_1 in the experimental treatment and between A_1 and T_1, and between A_2 and T_2 in the control treatment.

2) HEART RATE

The heart rate was monitored throughout the test. A computer programme on the departmental PDP 11 microcomputer was then used to calculate the average heart rate over successive ten second time intervals. These averages were combined manually, using the voice track to synchronise trolley position and heart rate, to give the mean heart rate for an individual when the trolleys were stationary and apart, and stationary and together for both the first and the second movements of the trolleys. Only the mean heart rates from positions A_1, T_1, A_2 and T_2 were included in the analysis.

Different techniques have been used when analysing heart rate data to allow for the large minute to minute fluctuations in heart rate, even when an animal appears to an observer to be resting undisturbed. MacArthur et al (1982) determined the usual variation in the basal heart rate of sheep (expressed as an average over 10sec) which would account for 90% of the observed variation. This was found to be within 12bt/min of the mean. Consequently, a change in heart rate of greater than 12bt/min in response to a particular procedure was taken to represent a genuine heart rate response under their experimental conditions. Mills et al (1985) in addition to comparing mean heart rates also tried to compensate for the individual variability in heart rate by comparing the variation in heart rate about the mean in the period before and the period after oviposition.

For the analysis of this experiment it was decided to use the mean heart rate from each trolley position in an Analysis of Variance. The mean was calculated over 60sec and so should be a better representation of the situation, and less subject to fluctuations, than 10sec averages. The data were sufficiently normally distributed to make an Analysis of Variance appropriate. The variables included in the analysis were the same as those in the behavioural study (2:3:1) and only the first experimental recording and the first control recording for each

individual were included. Consequently, heart rates for only 7 birds were analysed and these were from the same test occasions as the behavioural data in the previous analysis. The results of the ANOVA are presented in Table 2:3

Table 2:3 Analysis of Variance of Heart rate

VARIABLE	DF	F-VALUE
Bird	6	2.94 *
Treatment	1	2.21
Position	1	0.18
Movement	1	0.73
Bird.Treatment	6	3.50 **
Bird.Position	6	0.95
Treatment.Position	1	1.02
Bird.Movement	6	0.46
Treatment.movement	1	0.13
Position.Movement	1	0.68
Bird.Treatment.Position	6	0.51
Bird.treatment.Movement	6	0.96
Bird.position.movement	6	0.27
Treatment.position.movement	1	0.01
residual	6	mean square = 916.8
Total	55	

The heart rates of the birds were significantly different ($P<0.05$). There was also a significant interaction between bird and treatment ($P<0.01$). This latter point is discussed in more detail in section 2:4:3. The

Treatment.Position.Movement interaction, important in the behavioural analysis, was not significant where heart rate was concerned (Table 2.4).

Table 2.4 Heart Rate (Beats per minute) Averaged Across The Seven Birds

MOVEMENT	FIRST		SECOND	
POSITION	APART(A_1)	TOGETHER(T_1)	APART(A_2)	TOGETHER(T_2)
TREATMENT				
Experimental	311	308	292	303
Control	311	315	310	326

Standard error of the deviation 16.18bt/min.

In the above analysis of heart rate, to ensure a balanced design, only one experimental and one control recording from each bird were included in the Analysis of Variance. Nevertheless, birds were usually recorded more than once to ensure that at least one recording would be suitable for analysis. In one case, when the transmitter in a bird worked for a particularly long period of time, a bird was recorded on 7 different occasions. All of which were analysed. In these situations, only the first recording of the bird in the experimental situation and the first recording of the bird in the control were included in the initial Analysis of Variance. To make use of this additional data to reduce the variation within a particular bird and investigate whether or not birds responded differently on subsequent test occasions, a

second Analysis of Variance was carried out. The results of this analysis are presented in section 2:4.

2:4 ADDITIONAL ANALYSIS

In addition to the four variables in the previous analysis, a fifth variable; test occasion was included in this analysis. An additional bird (194) which, due to problems with the transmitter, was only recorded in the experimental situation, was also included.

To make it possible for all the available data to be included in the analysis, a statistical package (available on the Prime Computer) able to carry out an Analysis of Variance on designs which are not completely balanced was used. Variables were nested to allow all interactions to be investigated.

The overall results of this analysis were similar to the first so I have not presented the full table of results. The bird.treatment interaction was not quite significant in this analysis unlike previously ($F=2.04$; D.F.=6,104; NS - $F=2.10$ required for significance level $p<0.05$). The differences between birds were nevertheless significant ($F=2.3$; D.F.=7,104; $P<0.05$). In addition, however, this analysis demonstrated very significant differences between birds in how they responded in subsequent test occasions ($F=5.84$; D.F.=25,104; $P<0.001$). This is discussed in more detail in section 2:4:4.

The main points of the analysis of heart rate in this experiment are summarized below. Mean values are from the second analysis, using all the data.

1) THE EFFECT OF TREATMENT

There was no difference in the mean heart rate of birds in the experimental and the control treatments (F=0.69; D.F.=1,97; NS)

TREATMENT	HEART RATE (mean±SE)	N
CONTROL	314 ± 7.5	59
EXPERIMENTAL	310 ± 5.8	95

2) TROLLEY POSITION

Neither was there a significant difference between the heart rate of birds when the trolleys were together compared to when they they were apart.

POSITION	HEARTRATE (mean±SE)	N
APART	312 ± 6.7	75
TOGETHER	311 ± 6.8	76

3) BIRD.TREATMENT INTERACTION

As stated previously this interaction was significant in the first analysis of variance but only approached significance when more than one recording of each bird was used. Nevertheless it is probably fair to say that birds

varied in how they responded to whether the second trolley was empty or contained a conspecific. For example, the heart rate of bird 192 was 77bt/min higher when there was another individual in the second trolley than when it was empty. However, bird 181 showed the reverse pattern, as the heart rate was 67bt/min lower when there was a conspecific in the second trolley.

	TREATMENT			
BIRD	CONTROL	N	EXPERIMENTAL	N
181	356 ± 15	4	289 ± 15	4
184	297 ± 15	4	290 ± 10	8
192	259 ± 15	4	336 ± 8	12
194		0	286 ± 15	4
201	303 ± 8	12	303 ± 10	9
205	352 ± 7	15	330 ± 8	15
208	340 ± 8	12	324 ± 7	16
210	315 ± 10	8	317 ± 5	27

4) TEST OCCASION

There was a significant effect of test occasion ($F=5.98$; $D.F.=25,97$; $P<0.001$), but no trend towards a lower mean heart rate on subsequent test occasions. This would suggest that the time taken initially to accustom the birds to the experimental procedure was sufficient and that birds were not unduely distubed by the trolleys or their movement. The results presented below are

irrespective of whether or not the test occasion was a control or an experimental treatment. Since different random orders of treatments were used for each individual, it was not possible to investigate these separately. Nevertheless, variations between test occasions when there was a bird in the second trolley might be expected because the transmitter bird was always tested with an unfamiliar conspecific.

TEST OCCASION	HEART RATE (mean±SE)	N
1	313 ± 4.0	57
2	310 ± 5.8	38
3	312 ± 6.5	31
4	299 ± 8.8	16
5	317 ± 16.7	4
6	306 ± 16.7	4
7	325 ± 16.7	4

2:5 CONCLUSIONS

At first, it is necessary to say that there is no clear evidence from this experiment to demonstrate whether or not domestic fowl possess a personal space. There was a decrease in the amount of time spent feeding when the trolleys were brought together for the first time, but the heart rate of the birds was unaffected by trolley position.

The conclusion from the behavioural analysis, of the proportion of time spent feeding, is in line with that predicted if birds possess a personal space. The birds spent less time feeding when the trolleys were together, when there was a bird in the second trolley, than when the trolleys were together and the second trolley was empty.

The conclusion from the analysis of the heart rate data is not in line with that predicted if birds possess a personal space. There was no significant difference in the heart rate when the trolleys were together, when there was a bird in the second trolley, compared to when the trolleys were together and the second trolley was empty.

The proportion of time spent feeding at the start of each test period was approximately 0.95 in both the experimental and the control treatments. But when the trolleys were brought together for the first time, the decrease in the time spent feeding was significantly greater in the experimental treatment than in the control. This demonstrated that the subject bird responded to the presence of the bird in the second trolley in the experimental treatment. The decrease in time spent feeding in the control treatment may be due to the approach of the empty trolley or a consequence of the time since the food was presented. As time progresses the bird may become satiated and so more likely to look up from the feed trough.

Since there was a decrease in feeding time as the trolleys moved together, one might have expected an increase in feeding time as the trolleys moved apart again. That this did not occur in either treatment is probably due to any increase in feeding when the trolleys moved away from each other being cancelled out by the decrease in feeding resulting from satiation. Although it poses the question, if moving towards a trolley containing another bird resulted in a greater reduction in time spent feeding than moving towards an empty trolley, then moving away from a trolley containing another bird should have resulted in a greater increase in time spent feeding than moving away from an empty trolley. Since this was not the case, it may be that once another bird has been seen by the subject bird, the subject bird continues to respond to it (by spending less time feeding) even though the two birds have moved apart. This explanation would account for there being no further decrease in feeding time as the two birds approached for the second time.

There was no effect of trolley position on the heart rate of the birds. One reason for this could be that the experimental procedure itself was sufficiently stressful to mask any additional effects caused by the closeness of a conspecific. It has been shown (Duncan et al, 1986) that there is a ceiling in the heart rate of birds and that once this has been reached additional frightening stimuli do not cause a further increase in the heart rate of the

bird. There are several arguments against the view that the procedure iteself masked any response. Firstly, Duncan and Filshie (1980) have estimated heart rate using radiotelemetry to be between 280 and 320bt/min in undisturbed situations in the domestic fowl with a maximum of about 450 bt/min in a severely alarmed bird. The range in this experiment of 259 - 356bt/min is very similar to the normal range suggesting that the birds were accustomed to the experimental procedure. Secondly, an analysis of heart rate over successive test occasions of the same individual showed no trend towards lower heart rates on subsequent tests as would have been expected if birds were still becoming accustomed to the experimental situation.

The lack of a significant difference between the experimental and the control treatments implies that approaching a trolley containing a conspecific is no more stressful than approaching an empty trolley. This in turn implies one of the following; the transmitter bird did not recognize the other bird as a conspecific and only responded to the approach of the trolley irrespective of whether or not it contained another bird; the spacing mechanism did not apply because the birds were both inside cages ; approaching a conspecific was not sufficiently disturbing to cause an increase in heart rate.

It seems unlikely that a bird would not detect a conspecific inside the other trolley. In fact, we know this is not true because the behaviour of the bird was

affected by the presence of a conspecific in the second trolley. If it was the approach itself of the second trolley which was sufficient to stimulate a response in the test bird, then one would always expect the heart rate to be higher when the trolleys were together compared to when they were apart. This again seems unlikely as in some individuals, rather than the approach of the trolley causing an increase in heart rate, it produced a lowering of the heart rate. The cages were especially designed so that the birds' heads would be outside the cages, with no partition between them. The spacing mechanism, therefore should have operated under these circumstances. The final explanation, that approaching a conspecific is not sufficiently disturbing to cause an increase in heart rate, is the most feasible.

In the experiment by Jones et al (1981) which assessed fear in birds exposed to a looming human stimulus, cessation of feeding was the only behaviour which was found to correlate well with heart rate. At first this seems at variance with the results of this chapter. Looking up from a feed trough may be the initial response to an approaching object so the object can be identified. In the experiment by Jones et al (1981) the approaching object was a human being and hence frightening to the bird. Consequently there was an increase in heart rate. In my experiment, the approaching object was a conspecific and so possibly less disturbing. Consequently there was no

significant increase in heart rate. Although in effect, the level of disturbance would depend on the identity of the approaching individual. This point is discussed again later in the section with regard to the relative positions of the birds in the dominance hierarchy.

There was no consistent increase in heart rate when the trolleys were together compared to when they were apart. Some individuals showed a slight increase in heart rate when the trolleys were together whereas others showed a decrease. One must conclude, therefore, that if heart rate is an indicator of disturbance, that some individuals found moving away from a conspecific more disturbing than moving towards it. These variations represented how different individuals responded to the test situation, which in turn may imply that individual variation is one of the major factors in spacing behaviour.

If the interpretation from the heart rate analysis had been the same as that from the behavioural analysis, I would have investigated whether or not there was a particular distance between the two trolleys in the experimental treatment at which the birds responded to each other. Evidence of a so called critical interindividual distance would have supported the theory of personal space.

There was the possibility that this further investigation would have indicated a gradual change in the responses of

the bird, rather than a threshold. In this case, it would have cast doubt on the personal space theory since, to my mind, the theory of personal space is meaningless unless there is evidence of a critical interindividual distance. The previous post hoc explanations for the apparent lack of a critical interindividual distance have been that the distance varies according to the orientation of the birds and to their activities. In this experiment, both these variables were kept as consistent as possible and so should not be used as excuses.

The results of the heart rate analysis did not warrant any analysis of intermediate interindividual distances. A cursory look through the behavioural data had not shown any evidence of a consistent critical interindividual distance across individuals and so it was decided not to proceed with any further analysis. At best it would have emphasized the differences between birds.

In this experiment, the birds were not tested to establish which was the dominant and which the subordinate of each pair. Although the birds were unfamiliar to each other, it is possible that they might have responded differently depending on their eventual relationship to each other. For example, Candland et al. (1969) showed that although there was an increase in heart rate when strange cockerels were first exposed to each other, the extent of the increase was a good predicitor of the dominance outcome of

the meeting. Moreover, it has been demonstrated that a dominance relationship can be established through a wire partition (James and Foenander,1961). There is no reason, therefore, to suppose that a relationship between the two birds could not be established as the trolleys moved together, especially since the design of the trolleys ensured that there was a minimum of wire betweeen the birds when they faced each other. Variations in the real or potential dominance relationships between the birds in the trolley may account, in part, for the different responses in the present experiment.

From this experiment it appears that any effects due to trolley position either do not affect heart rate or are masked by the great variation between individuals. In the behavioual analysis, the only pattern which was consistent across birds was in the time spent feeding through the test period (Table 2.2). This treatment.position.movement interaction was not reflected in the heart rate of the birds.

In summary, although this experiment demonstrated that birds change their behaviour when in close proximity to another bird, there is no evidence that this closeness is disturbing to the bird. In fact, some birds appear to find it more disturbing to be separated from the bird in the other trolley. This is contrary to the personal space theory which states that birds try to avoid invading the

personal space of others or respond if their own personal space is invaded. Of all the times that birds were brought together in this experiment, on only one occasion did a bird aggressively attack the other. The level of aggressive behaviour, therefore, was much lower than would be predicted from the personal space theory, especially as most aggressive interactions occur around the feeder (and both birds were feeding at the time of the experiment) and birds were directly facing one another (where the personal space is supposed to be largest).

It is difficult to draw any clear conclusions from this experiment. That birds fed less when they were close together is not surprising since another bird (especially an unfamilar one) represents an important stimulus in the subject bird's environment. That there was no difference in heart rate when the trolleys were together compared to when they were apart would suggest that the closeness of the individual was not disturbing the subject bird. I therefore conclude that there is no evidence from this experiment that birds possess a personal space which they try to keep free of conspecifics.

CHAPTER 3

INTERINDIVIDUAL DISTANCES AND ORIENTATION IN LAYING HENS HOUSED IN GROUPS OF THREE IN TWO DIFFERENT SIZED ENCLOSURES

3:1 INTRODUCTION

The previous experiment cast doubt on the hypothesis that domestic fowl possess a personal space which they try to prevent other individuals from entering. However, it may be that the apparent lack of a critical interindividual distance between birds was a consequence of the fact that individuals had no choice but to approach each other when the trolleys were brought together, and their behaviour under these circumstances may be different from that which occurs in a free approach situation. To overcome this problem the birds in the present experiment were allowed to move freely around an enclosure and their locations recorded using overhead photography.

The obvious advantages of photography, to produce a permanent record of an observed spatial distribution which can be analysed later, have made it a useful tool for studying animals in their natural habitats (Miller and Stephen,1966; Gould and Hepner,1974; Major and Dill,1978). It has also been used successfully to study grazing and dispersion patterns in sheep and cattle over large ranges

(for a review see Arnold and Dudzinski,1978). At close quarters, overhead photography allows accurate, detailed studies of the spacing behaviour of animals.

In this experiment, the locations of each individual in the group were recorded as coordinates in the enclosure. The distances between pairs of individuals could then be calculated from their coordinates. It was assumed that if birds do have a personal space, there would be a minimum distance between pairs of individuals which represented the distance from the bird to the edge of its personal space. The photographs could also be used to investigate the orientation of birds in relation to each other. Since birds rely to a large extent on visual cues, orientation may be an important indicator of spacing behaviour.

There have been many studies of the effects of different densities on the general behaviour of birds (Al-Rawi and Craig, 1975 and Bessei,1985 for a review). But, there have been only three studies (McBride, James and Shoffner,1963; Doyen and Zayan,1984a&b; Nicol,1986) of how birds, housed at different densities, space themselves in relation to the other group members. Therefore, in addition to the aims outlined in the previous paragraph, groups of birds were kept in pens of two different areas. Group size and husbandry conditions were kept constant and only the space available to each bird varied in the two conditions. The experiment was divided into four sections :-

1) To investigate how the birds used the available area.

2) To determine the distances between individuals.

3) To determine whether or not the birds positioned themselves independently of each other in the pen.

4) To investigate the orientation of birds in relation to each other.

3:2 METHOD

A group of three female T-line (derived from Light Sussex x Rhode Island Red breeds), aged between 25 and 50 weeks, were selected at random from individual battery cages and placed together in a test pen. Two test pens were used in this experiment; a large pen, measuring 1.3 x 1.3m allowing 5633cm^2 per bird, and a small pen, measuring 0.65 x 0.65m allowing 1408cm^2 per bird. A time-lapse camera (Bolex H19 Reflex) was situated above the centre of the large pen. The small pen was filmed by placing it inside the large pen, under the camera. As a result, only one pen could be used at a time. The group was assigned to one of the pens at random and tested. Thereafter, successive groups of hens were formed in the same way and tested in either the large pen or the small pen. Ten groups were tested in total, five in the large pen and five in the small pen, the order of testing being random.

All birds were unfamilar to each other when they were

first placed in the test pen from individual cages. The birds were allowed nine days to become accustomed to the test pen. During this time the aggressive dominance hierarchy was determined for each group of three birds. This was an ordinal hierarchy based on who pecked whom (Rushen,1984) and in all cases the hierarchy was found to be linear (Appleby,1985). The aggressive dominance hierarchy was determined because in the previous experiment (Chapter 2) it was suggested that the response of an individual as it approached, or was approached, was influenced by the relative dominance relationship of the two birds. After the hierarchy had been determined, the birds were marked on the back, according to their rank, so they could be individually identified from above.

During this settling period the food and water troughs were removed each day, between 1400h and 1630h, and replaced in a different position within the pen. On days 10, 11, and 12, the birds were filmed between 1400h and 1600h while the food and water troughs were absent. One frame was taken every minute, on each of the three afternoons. In a provisional analysis, frames were only found to be independent from those preceeding when they were separated by at least 4 minutes. Consequently, from then on, only every fifth frame was analysed, resulting in 25 frames for each day, 75 for each replicate.

The film was developed and projected, via a mirror, onto

a digitiser pad (MOP-2, Reichert-Jung) placed below. The position of each bird's head and the centre of its back were then passed via a 'light pen' directly to a Prime 550 computer. The frames were analysed twice and the mean value taken as the final co-ordinates of the individuals. This procedure was also used to identify any obvious errors in transcribing bird locations from the photographs to the computer.

The following analyses were carried out:-

1) Distribution of bird locations within the pen

The locations of the highest ranking individuals (individuals numbered 1) in each replicate were plotted. The resultant scatter diagram of locations was then represented as a contour plot. To produce this map, areas with the same frequency of use were joined by contour lines in a similar way as contour lines on a map join areas of the same height above sea level. This process was repeated for individuals numbered 2 and 3 in each group.

2) Interindividual distances

The distances between individuals were calculated from the X and Y coordinates of each bird's back using Pythagoras' Theorem. In addition, since the position of each individual in the aggressive dominance hierarchy was known, interindividual distances could be determined for each rank pair combination i.e. between birds ranking 1

and 2, 1 and 3, and 2 and 3. This was repeated separately for birds in each group.

Measuring the distances between all individuals simultaneously was chosen rather than nearest neighbour distances even though there was the possibility for all three birds to be in a line and the interindividual distance between the end birds to include the centre bird. A provisional scanning of the frames showed that the birds were rarely found to be in a straight line. Normally their locations formed, in effect, the corners of a triangle and so interindividual distances for all combinations were used in the analysis.

In some experiments (McCort and Graves,1982; McBride et al,1963; Mankovich and Banks,1982/3) the location of the animal's head has been used to represent its location. The distances between the birds heads were also calculated in the present study, but were felt to be too variable, merely indicating where the bird was pecking rather than representing its actual location.

3) Comparison of observed and expected interindividual distances

The observed interindividual distances, from the previous analysis, were compared with those that would be expected if the three birds were positioning themselves independently of each other in the pen. These expected interindividual distances were calculated in two ways.

Firstly, coordinates for this distribution were generated so that there was an equal probability of a point occurring anywhere in the pen, and secondly so that the probability of a particular point occurring reflected the degree to which that location was used by the individuals.

The first comparison was used by Stricklin (1975) who showed that nearest neighbour distances in beef steers were significantly greater than expected from a random distribution. This method was also used by Burgess (1980) to investigate spacing behaviour in Rhesus Macaque troops (Macaca mulatta). He found that 1st - 7th nearest neighbour distances were significantly less than expected. But when he used the second comparison, which allowed for the fact that certain regions of the enclosure were used more frequently than others, he found that only distances to 1st and 2nd nearest neighbours were significantly less than expected. That is to say, the aggregation which seemed from the first comparison to extend from 3rd - 7th nearest neighbours could be explained by environmental preferences of the individuals. Consequently, the second comparison more accurately reflected whether or not the position of an individual was influenced by the locations of the other group members.

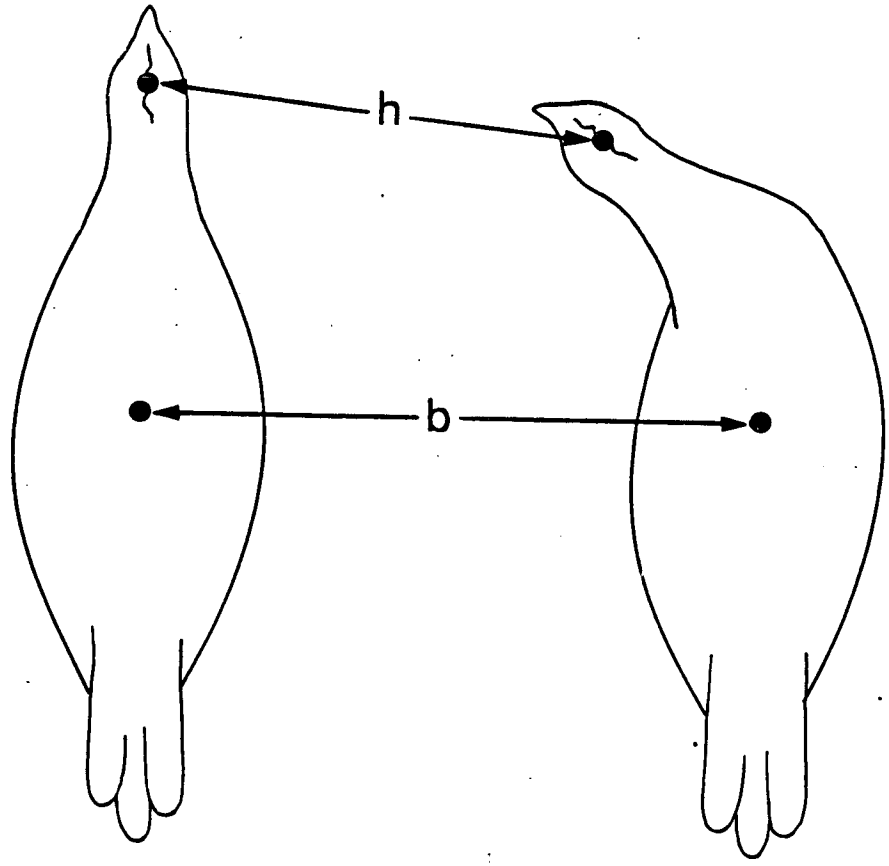
The methods used to generate the expected data for the two methods and the contraints applied to them before comparison with the observed data are discussed in section

3:3:3.

4) Orientation of birds in relation to each other

Previous experiments which have looked at orientation (McBride et al,1963; McCort and Graves,1982; Mankovich and Banks,1982/3) have determined the angle that one individual of a pair would have to turn through to directly face the other. Nicol (1986) measured the angle a bird would have to turn through to be parallel with another bird. Such analyses provide considerable information but angles are rather difficult to analyse and interpret. Since I was only interested in the relationship between orientation and interindividual distance a simpler approach was used here. The way in which the data were collected would have made it possible to analyse the present results as angles if necessary.

The coordinates of the birds' heads and backs were used to calculate the inter-head and inter-back distances for each pair of birds (Figure 3.1). The inter-back distance was then subtracted from the inter-head distance to provide a measure of the combined orientation of the two birds. A positive value meant the inter-head distance was greater than the inter-back distance ie. the birds were orientated away from each other. A negative value meant the inter-head distance was smaller than the inter-back distance ie. the birds were orientated towards each other. This value was then plotted against a measure of the distance between



KEY

h - Inter-head distance

b - Inter-back distance

Orientation = h-b

FIGURE 3.1 Orientation Of Pairs Of Birds

the two individuals. The process was repeated separately for individuals in the large and the small pen, and for the three possible rank combinations.

3:3 RESULTS

1) Distribution of bird locations within the pen

Within each pen size, the pattern of area use was found to be similar for all individuals numbered 1, similar for all individuals numbered 2, and for all individuals numbered 3. The data were therefore combined across replicates to produce three contour plots showing how the area was used by individuals of each rank. The three contour plots for the birds in the large pen and the three plots for the birds in the small pen are presented in Figure 3.2.

In the large pen, there were slight differences in area use according to the ranks of the individuals. The peak in the contour lines in the centre of the pen showed that the highest ranking birds tended to use this area frequently, whereas the lowest ranking birds used the pen more evenly. The second ranked birds showed a pattern of area use intermediate to that of the highest and lowest ranking individuals.

In contrast to the large pen, the contour plots of the small pen demonstrated very distinct differences in how the area was used by the individuals of each rank. In

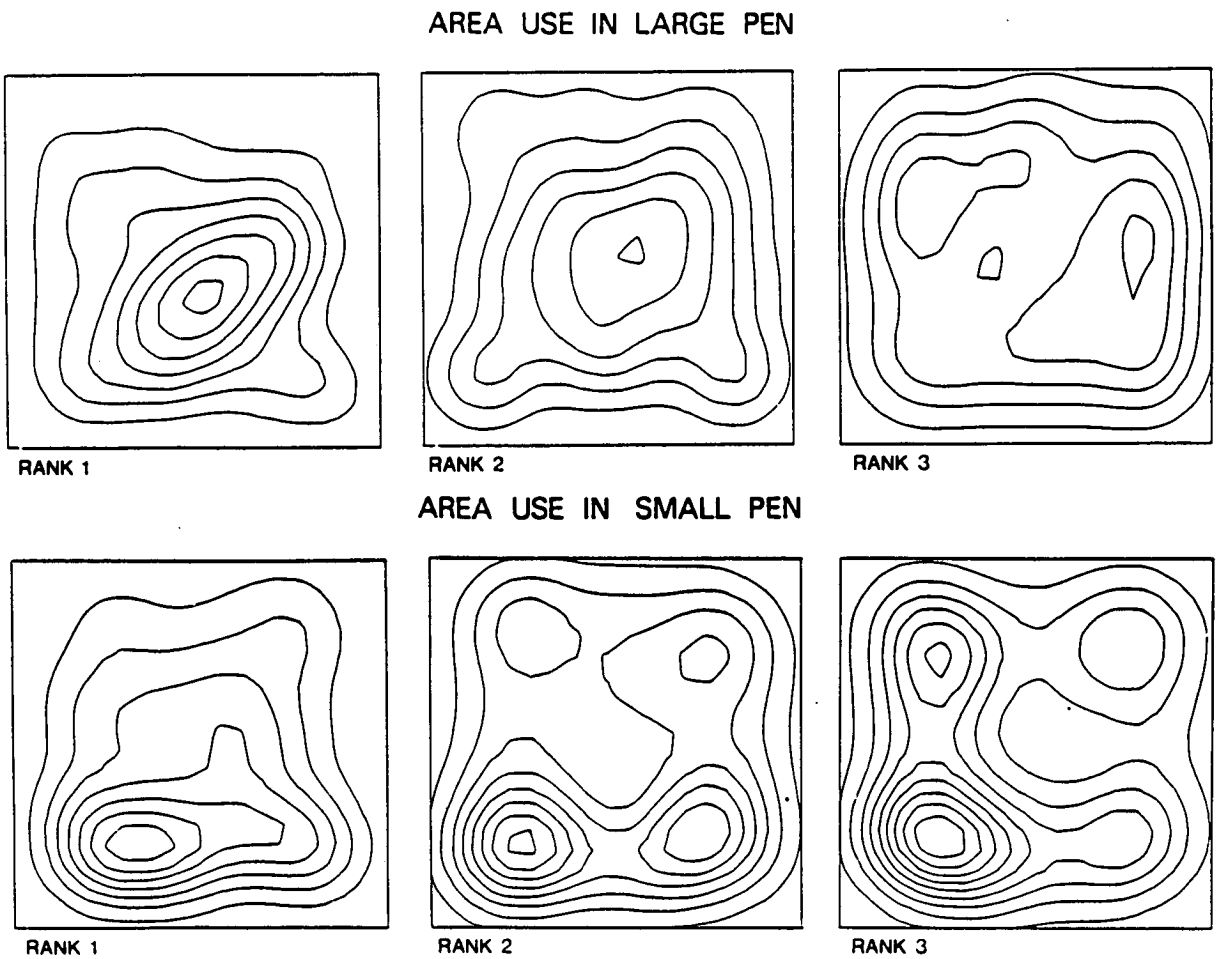


FIGURE 3.2 Contour Plots Demonstrating How The Area Was Used By Individuals Of Each Rank

The observed locations of birds in the pen were used to calculate a two dimensional kernel density estimate of the probability of a bird being at a particular position in the pen. Areas with the same density estimate were joined by contour lines in the same way as contour lines on a map join areas of the same height above sea level. A probability interval of 0.02 was used between contour

addition, all individuals in this pen size showed a preference for the front left-hand corner of the enclosure. This pattern cannot be explained by an association with the position of the food and water, as this was changed in a random fashion prior to filming and the troughs were removed during the observation period. This trend was probably due to some feature of the pen, such as light or temperature, as it was consistent in all replicates. However, since the small pen was placed in the large pen and no such preference was apparent in the large pen, even this explanation seems unlikely. Superimposed on this overall preference, nevertheless, there were variations in area use between the different ranked birds. The highest ranking individuals used predominantely the preferred area (front left-hand corner) of the small pen, whereas the 2nd and 3rd ranking individuals used all the corners of the enclosure. Birds were rarely recorded in the central region of the small pen.

2) Interindividual distances

When interindividual distances were plotted, the distribution was found to be close to normal in the small pen and slightly skewed in the large pen. Log-transforming the distribution produced a more normal distribution of interindividual distances in the large pen, but produced a skewed distribution in the small pen. Initially, therefore, statistical analyses were carried out on both the original and the transformed data but, since the

interpretations were the same in both cases, the results presented here are from the original, non-transformed data.

Using an Analysis of Variance, pen size, replicate, rank and the interactions of these variables were all found to have a significant effect on interindividual distances (Table 3.1).

TABLE 3.1 Analysis of Variance of Interindividual Distances

VARIABLE	D.F	F-VALUE
Pen	1	551.8 ***
Replicate	4	16.1 ***
Rank	2	5.6 **
Pen.Replicate	4	9.2 ***
Pen.Rank	2	8.3 ***
Rank.Replicate	8	4.8 ***
Remainder	2228	Mean Square = 0.0242
Total	2249	

However, because of the difficulties of interpreting results with many significant interactions, the analysis was repeated. In this second analysis the two pen sizes were analysed separately. Also, although there were significant differences between replicates, these were assumed to be random (as birds were selected at random to form groups) and so were not included in the second

analysis. This made it possible to investigate the effect of rank on interindividual distance. Differences between replicates are discussd in more detail later in this section.

There was no effect of rank on interindividual distance for the birds in the small pen (F=0.41, D.F.=2,1121, NS) . But, there were significant differences (F=8.68, D.F.=2,1110, P<0.001), in interindividual distances for the birds in the large pen according to the ranks of the individuals. These results are summarized in Table 3.2.

TABLE 3.2 Analysis of Variance of Interindividual Distances According to Rank

LARGE PEN

VARIABLE	D.F	F-VALUE
Rank	2	8.68 ***
Remainder	1110	Mean Square = 0.0389
Total	1112	

SMALL PEN

VARIABLE	D.F	F-VALUE
Rank	2	0.41
Remainder	1119	Mean Square = 0.0099
Total	1121	

The mean interindividual distances between the different rank pair combinations are presented in Table 3.3.

TABLE 3.3 Interindividual Distances Between Different Rank Pair Combinations In Both The Large Pen and The Small Pen

BETWEEN RANKS	LARGE PEN	N	SMALL PEN	N
1 AND 2	0.47 ± 0.04m	371	0.32 ± 0.01m	374
*				
1 AND 3	0.51 ± 0.04m	371 *	0.31 ± 0.01m	374
**				
2 AND 3	0.45 ± 0.02m	371	0.32 ± 0.02m	374

The greatest mean interindividual distance in the large pen (0.51 ± 0.04m) ocurred between birds 1 and 3 in the hierarchy. The smallest mean interindividual distance (0.45 ± 0.02m) ocurred between individuals ranking 2 and 3 in the hierarchy.

When each replicate was analysed separately, mean interindividual distances were not always in the same order as the overall pattern just described. In effect, once the ranks of the two birds and the replicate have been specified, a particular pair of individuals has been identified. Consequently, the significant interaction between replicate and rank pair combination (Table 3.1) implies that distances between individuals vary according to the two individuals concerned. Differences between individuals were also found to be important in the previous chapter (2:3). It was decided, therefore, to investigate the effect of rank again, but reclassifying

interindividual distances in three different ways.

a) Interindividual distances between birds next to each other in the hierarchy, that is, distances between birds ranking 1 and 2 and between birds ranking 2 and 3 were combined. These were then compared with the distances between birds which were not adjacent to each other in the hierarchy, that is, birds ranking 1 and 3.

b) Interindividual distances between pairs of birds, one of which was the highest ranking individual in the group, that is, distances between birds ranking 1 and 2, and 1 and 3 were combined. These were then compared with distances between birds ranking 2 and 3.

c) The final analysis was similar to the previous except that interindividual distances were separated as to whether or not the lowest ranking member of the group was involved. That is, interindividual distances between birds ranking 1 and 3, and 2 and 3 were combined and compared with distances between birds ranking 1 and 2.

In all three analyses (a,b and c) in the large pen there were still significant interactions using an Analysis of Variance between replicate and rank. That is to say, in analysis (a) the birds adjacent in rank to each other had neither consistently larger nor consistently smaller interindividual distances than those individual not adjacent in rank to each other. Likewise in analysis (c), distances between individuals where one individual of the

pair was the lowest ranking were neither consistently larger nor consistently smaller than interindividual distances between birds where neither individual was the lowest ranking. However, in analysis (b) for the large pen, the pattern was at least consistent for all replicates ie. interindividual distances between pairs of birds (one of which was the highest ranking) were always greater than interindividual distances between pairs of birds ranking 2 and 3 in the hierarchy. In the small pen, none of the analyses yielded a consistent pattern between replicates.

There appears to be some measure of agreement in interpretation between the overall analysis (irrespective of replicate) and the three separate analyses (a,b and c) when each replicate was analysed separately. That is, whilst interindividual distances differ according to the position of the individual in the hierarchy in the large pen, at least to the extent of distances from the highest ranking bird been greater, there is no indication of such a relation in the small pen. As a result of this corroboration and because birds were allocated at random to each replicate, it was decided to combine the results across replicates in further analyses investigating the effect of rank on interindividual distance.

In summary, the results of this section suggest that given sufficient space the dominance relationship between two

birds does influence the distance between them, with interindividual distances being greater when one bird of the pair is the highest ranking bird of the group.

3) Comparisons of observed and expected interindividual distances

The method used to determine interindividual distances was described in the previous section. When interindividual distances were calculated from the locations of birds in the same frame of film, they were called the observed interindividual distances. The expected interindividual distances were calculated in either of two ways. Consequently there were two comparisons between observed and expected interindividual distances.

FIRST COMPARISON - In the first comparison, X and Y values were generated as random numbers by computer and then the distances between these random coordinates calculated in the same way as distances between birds.

In order to ensure a realistic comparison between observed and expected interindividual distances, some constraints were applied to the computer generated coordinates. These were (a) no randomly generated point could be closer to the edge of the pen than points which were actually observed in the pen and (b) no two randomly generated points could be closer together than points which were actually observed in the pen. The constraints applied to

the data were different in the two pen sizes. The minimum observed distance from a bird to the pen boundary was 0.07m in the large pen and 0.04m in the small pen and the minimum observed distance between two birds was 0.1m in the large pen and 0.05m in the small pen. The observed and expected interindividual distances are presented in Table 3.4.

TABLE 3.4 Observed and Expected Interindividual Distances For Birds In The Large and The Small Pen

PEN SIZE	OBSERVED	N	EXPECTED	N
Large	0.47 ± 0.01m	1113	0.61 ± 0.01m	1113
Small	0.32 ± 0.01m	1122	0.31 ± 0.01m	1122

Using a Student t-Test, there was a significant difference between the observed and expected interindividual distances in the large pen ($t=9.90$; D.F.=2224; $P<0.001$). The difference between the observed and expected interindividual distances in the small pen was not significant ($t=0.70$; D.F.=2242; NS).

This analysis was repeated so that the mean interindividual distance for each rank pair combination was compared with the expected interindividual distance. The expected interindividual distances from the previous analysis (Table 3.4) were divided into groups of the same sample size as the observed data, that is, 371 in the large pen and 374 in the small pen. Eventhough this

division was random, there were small but insignificant differences between the expected interindividual distances within the same pen size.

TABLE 3.5 Observed And Expected Interindividual Distances For Different Rank Pair Combinations In Both The Large And The Small Pen

		OBSERVED	N		EXPECTED	N
LARGE PEN						
BETWEEN RANKS	1 & 2	0.47 ± 0.01	371	(1)	0.62 ± 0.01	371
	1 & 3	0.51 ± 0.01	371	(2)	0.60 ± 0.01	371
	2 & 3	0.45 ± 0.01	371	(3)	0.61 ± 0.01	371
SMALL PEN						
BETWEEN RANKS	1 & 2	0.32 ± 0.01	374		0.31 ± 0.01	374
	1 & 3	0.31 ± 0.01	374		0.32 ± 0.01	374
	2 & 3	0.32 ± 0.01	374		0.31 ± 0.01	374

Using Student t-Tests, there were significant differences in the large pen between the observed and expected interindividual distances :

(1) Ranks 1 and 2 in the large pen ($t=8.26$; D.F.=740; $P<0.001$)

(2) Ranks 1 and 3 in the large pen ($t=5.30$; D.F.=740; $P<0.001$)

(3) Ranks 2 and 3 in the large pen ($t=9.77$; D.F.=740; $P<0.001$)

In the large pen, all three mean observed distances were

less than expected. This showed that the birds in the large pen were clustering. However, no evidence of aggregation was found in the small pen, in which the observed interindividual distances did not differ significantly from those expected for any of the three rank pair combinations.

SECOND COMPARISON - In this comparison, the points were derived not from a totally random distribution (as in the first comparison) but from a distribution which took into consideration how the area was used by the individuals. By randomly recombining bird locations across different frames it was possible to produce an expected distribution of interindividual distances. Burgess (1979) suggested that such a randomly recombined set of data would preserve all the spacing relationships which are due to the animal's environmental preferences but not include spacing preferences which are a function of the position of surrounding group members.

Recombining bird coordinates in this way assumed that birds observed at different times did not influence each others positions. Hence this method would not be appropriate if the birds remained at the same location for long periods. It is valid in this experiment because the birds moved around the pen and, although there were preferences for particular areas, provisional analysis had demonstrated that the locations of the same individual in

successive frames were significantly different (3:2). Indeed, the reason for this analysis was to incorporate these slight preferences for particular areas of the pen into the random data.

Constraints were also applied to this generated data. As actual bird coordinates were used, none would be so close to the edge of the pen as to be physically impossible. In the previous comparison it was necessary to delete those generated points which were too close to the edge of the pen. Nevertheless, it was still necessary to delete points which were closer together than were actually observed between the birds. The minimum observed interindividual distances were 0.1m in the large pen and 0.05m in the small pen. These values were the same as those applied to the randomly generated data in the first comparison.

The large amount of data generated by calculating distances between bird cordinates taken from different frames made comparisons between observed and expected interindividual distances difficult. As a result, means were calculated of the expected interindividual distances, one mean for each rank pair combination for each replicate. This resulted in 15 mean interindividual distances for the expected distances in the large pen (5 for each rank pair combination) and the same number in the small pen.

The observed and expected interindividual distances for

this second comparison are shown in Table 3.6.

TABLE 3.6 Observed And Expected Interindividual Distances For Birds In The Large And The Small Pen

PEN SIZE	OBSERVED	N	EXPECTED	N
Large	0.47 ± 0.01m	15	0.51 ± 0.01m	15
Small	0.32 ± 0.01m	15	0.28 ± 0.01m	15

Using Student t-Tests there were significant differences between the observed and expected interindividual distances in the large pen ($t=2.86$; D.F.=28; $P<0.01$) and in the small pen ($t=2.86$; D.F=28; $P<0.01$).

The observed distances between birds in both pens differed significantly from expected. Birds in the large pen were again closer together than anticipated when the data, irrespective of rank were compared. This supported the results from the previous comparison indicating that the birds in the large pen were clustering. But, in addition, the results demonstrated that the birds in the small pen were in fact spacing out more than would be expected by chance. Consequently, this second comparison indicated that the locations of birds in both pen sizes were influenced by the locations of the other individuals in the group.

In the first comparison of observed and expected interindividual distances, the expected distances were

equivalent for all pairs of birds in the group since no consideration was given to the positions of the two individuals in the dominance hierarchy. However, it has already been demonstrated that individuals of each rank differed in how they used the available area, particularly in the small pen (Figure 3.2). In this second comparison, because the probability of a point ocurring in the computer generated data reflected the degree to which that location was actually used, the points could be specified based on the distribution of a bird of a particular rank. In this way, the expected distribution of interindividual distances could be generated for a particular rank pair combination. This expected distribution was then compared with the observed distribtion of interindividual distances for that rank combination (Table 3.7).

TABLE 3.7 Observed And Expected Interindividual Distances For Different Rank Pair Combinations In Both The Large And The Small Pen

		OBSERVED		EXPECTED	
LARGE PEN					
BETWEEN RANKS	1 & 2	0.47 ± 0.01m	15	0.49 ± 0.01m	15
	1 & 3	0.51 ± 0.01m	15	0.51 ± 0.01m	15
	2 & 3	0.45 ± 0.01m	15 (1)	0.53 ± 0.01m	15
SMALL PEN					
BETWEEN RANKS	1 & 2	0.32 ± 0.01m	15 (2)	0.28 ± 0.01m	15
	1 & 3	0.31 ± 0.01m	15	0.28 ± 0.01m	15
	2 & 3	0.32 ± 0.01m	15	0.31 ± 0.01m	15

Using Student t-Tests there were significant differences between observed and expected interindividual distances for:

(1) Ranks 2 and 3 in the large pen ($t=5.74$; D.F.=28; $P<0.01$)

(2) Ranks 1 and 2 in the small pen ($t=2.86$; D.F.=28; $P<0.01$)

In the small pen, although overall the expected interindividual distances were less than the observed, only distances between birds ranking 1 and 2 were significantly different from expected. In the large pen only two interindividual distances were greater than those observed, and only the distances between birds ranking 2 and 3 were significantly different from expected.

4) Orientation of birds in relation to each other

When the orientation of the birds was considered, there were no significant differences between replicates in either the large pen or the small pen. The data were therefore combined to produce orientation graphs for each rank pair combination in the large and small pens. As there were no significant differences in orientation according to the ranks of the individuals, the data were again combined, resulting in two graphs, demonstrating the orientation of individuals in each pen at different interindividual distances and these are shown in Figure 3.3.

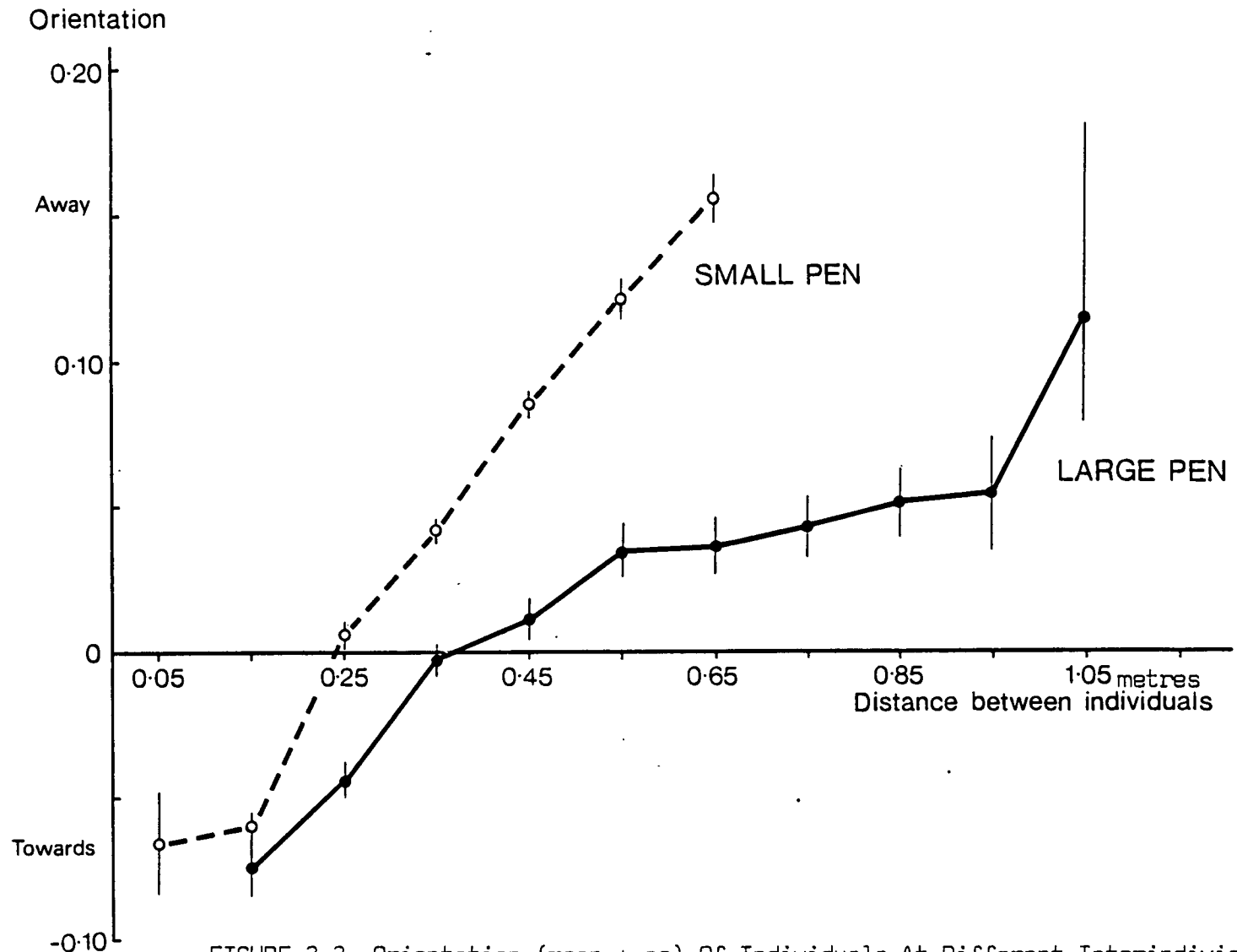


FIGURE 3.3 Orientation (mean ± se) Of Individuals At Different Interindividual Distances In Both The Large And The Small Pen

The shape of the graph was similar in both cases but there were obvious differences in orientation between birds in the large and birds in the small pen. In the large pen, on average, birds orientated away from each other at distances greater than 0.35m and only when the distance was less than this were the birds orientated towards each other. In the small pen, this change from being orientated away to being orientated towards, occurred at a distance of 0.25m.

3:4 CONCLUSIONS

It was apparent from the contour plots that the birds in the pen did not use the area available to them evenly. This was particularly obvious in the small pen where the front left-hand corner of the enclosure was used more frequently than the other regions. In the large pen, the first comparison of the observed interindividual distances with those expected from a totally random distribution, confirmed that this observed pattern of area use was unlikely to have occurred by chance. In the small pen, although there was no significant difference in interindividual distances from those expected, this may have been due to the fact that as the enclosure size decreases the probability that observed and expected interindividual distances will differ also decreases. In actual fact, it was obvious from the contour plots in the small pen that the birds were not using the area evenly.

For this reason, the more realistic second comparison was carried out, with the expected distibution incorporating a bias to allow for the increased tendency to use the front lefthand corner. In this second comparison, the expected interindividual distances in both pens were smaller than those expected from the first comparison. This reflected the fact that certain areas of the pen were used more than others and so there was a greater probability of two birds being close together. The significant overall differences between the observed and expected distances in the second comparison indicated that the birds were not moving independently of each other in either the large or the small pen.

The initial comparison of observed and expected interindividual distances could, at best, only demonstrate that the area was not being used randomly. It would not indicate whether the non-randomness was due to environmental features, which made certain areas of the pen preferrable to others, or whether it was due to social factors brought about by the birds themselves. The second comparison, however, incorporated the observed differences of how the area was used into the calculations of the expected interindividual distances. A significant difference in this comparison demonstrated that social factors, that is the positions of the other birds, were important in determining the locations of individuals in a group.

A non-significant difference in this comparison, nevertheless, would not have excluded the possibility of social influences. This could have occurred, for example, if the individuals were always located in the same area. This technique could not distinguish whether individuals remainined at the same location because each individual preferred that place (environmental influences), or whether the position of each individual was determined by the positions of the other individuals in the group (social influences) and so they remained in the same place.

Awarness of the positions of other individuals in the group was demonstrated very clearly by the orientation of the birds. The general pattern was similar in both pen sizes. The birds were orientated away from each other at large interindividual distances and only orientated towards each other at small interindividual distances.

These results are compatible with McBride's regression analysis of head orientation. He says ".... As a neighbour approaches, a bird tends to turn to face it. Neverthless, they tend to avoid each others frontal aspects in so far as this is compatible with the tendency already mentioned....." (McBride et al ,1963). However, one could question the validity of a regression analysis on this type of data. Neither of the two variables (head orientation or interindividual distance) could be varied

systematically and so holding one variable constant to investigate the effect of another may not be justified. Nevertheless, Mankovich and Banks (1982/3) demonstrated a similar orientation graph to the one presented in this experiment when they plotted absolute orientation angles against interindividual distance, and Stricklin (1975) and Nicol (1986) demonstrated that beef steers and laying hens, respectively, do not orientate at random with respect to conspecifics.

The most plausible explanation for the observed pattern of orientation would be that when the head is turned away the bird is using monocular vision when looking at its neighbour. At this time the eye is most sensitive to movement within the visual field. The orientation towards each other at small interindividual distances may reflect a change from monocular to binocular vision so that the distance between the birds may be judged accurately. This change from monocular to binocular vision is equally important to birds of all ranks and so one would not expect a difference in orientation according to the rank pair combination of the two birds.

Alternatively, it may be that orientation towards another individual is an aggressive, threatening gesture and that orientating away is a non-aggressive or submissive gesture. Consequently, birds would be more likely to be tolerated by each other if their heads were orientated

away. The orientation towards each other at close distances may have been a subtle threat preventing any further approach. If this was the case, one would anticipate that only one bird, probably the highest ranking of the two, should turn towards and that the other should turn away if the interaction was not to escalate into a more obvious aggressive encounter. In this analysis any such differences in the orientation of the two individuals could not be detected since a combined measure of the orientation was used.

In analyses which have measured the angle of orientation of each individual (Mankovich and Banks,1982/3 and McCort and Graves,1982) the results seem to suggest that position in the social hierarchy influences orientation. Mankovich and Banks, albeit only working with one group of birds, tentatively suggested that high ranking individuals orientated towards others more frequently than low ranking individuals. McCort and Graves demonstrated that, in pigs, the orientation of a reference animal was significantly affected by its own rank but they do not discuss whether or not its orientation was influenced by the rank of its nearest neighbour. The highest ranking animal had significantly less tendency to face away from its nearest neighbour than did low ranking animals.

In Figure 3.3 it was possible for the orientation value (ie. the difference between the inter-head and inter-back distances) to range between about 0.2 (2 x length of back

when the birds are tail to tail facing directly away from each other) and -0.2 (2 x head and neck length when the birds are head to head facing directly towards each other). Although these extremes only occurred occasionally, individuals orientated away from each other to a greater degree than they orientate towards each other. That is to say, the graphs extend further above the x axis than they do below the axis. This is probably because maximum distances between birds occurred when the individuals were at opposite sides of the pen. Since birds were frequently observed to peck at the wire netting surrounding the enclosure, it is likely that birds were orientating towards the edge of the pen at these large interindividual distances rather than orientating away from the other individual. This may account for the sudden increase in orientating away in the large pen size at interindividuals distances of between 1.0 and 1.1m. Stricklin (1975) observed that beef steers positioned themselves around the outer edges of the pens, but he does not specify the orientation of these animals.

Another, although unlikely interpretation, is that birds were orientated towards each other at small interindividual distances because they were both pecking at the same area or object. Whilst this was sometimes true it does not explain the significant orientation away at larger interindividual distances.

There is no evidence from this experiment that birds use a spacing mechanism, based on maintaining an area around themselves free of conspecifics. In this experiment, the results from the small pen would seem to suggest that there is some force, or combination of forces, acting to keep individuals apart, as the birds in the small pen were spaced out more than expected and used the corners of the enclosure. However, the results from the large pen seem to suggest that there is an opposite force or forces bringing the individuals together as the birds were not as far apart as was possible or even as would occur by chance. Consequently, one would expect the distance between two birds to reflect a balance between the forces of attraction and repulsion. Doyen and Zayan (1984a) have shown that pairs of birds in battery cages do not spread out as far as is possible in the cage, but they did not compare the observed interindividual distances with those expected by chance.

There were significant differences in the distances between individuals according to the ranks of the birds in the large pen but not in the small pen. It would seem unlikely that rank would be important in influencing interindividual distances in the large pen but unimportant in the small pen. More likely, this result suggests that there was insufficient space in the small pen, and the birds could not get far enough apart for the differences according to rank to be expressed. In other words, the

forces of repulsion were stronger than those of attraction in the small pen and so the birds were trying to get away from each other. In the large pen, the birds could get far enough apart for the forces of repulsion to be balanced by those of attraction. In these circumstances individual variation may be expressed suggesting that the relative strengths of the forces of attraction and repulsion are not fixed, but vary according to the individuals concerned.

CHAPTER 4

AN INVESTIGATION OF FACTORS INFLUENCING SPACING IN DOMESTIC FOWL IN A SEMI-NATURAL ENVIRONMENT

4:1 INTRODUCTION

It was suggested from the results of the previous experiment that the wide range of interindividual distances in groups of laying hens were a consequence of attractive and repulsive forces which acted to bring individuals together and keep them apart. Furthermore, the actual distance between two individuals was a balance between these two opposing forces.

In evolutionary terms, there may be a variety of different reasons for animals to group themselves eg. to reduce the risk of predation, to increase the probability of finding food, etc. (Huntingford,1984). I have used the term 'force of attraction' to mean the combination of factors which act to bring individuals together. Likewise, in evolutionary terms, individuals may keep apart for a variety of different reasons, eg. to decrease aggression between individuals, to prevent an individual searching for food over the same area as another conspecific, to minimize fear of the other individuals. I have used the term 'force of repulsion' to represent the combination of these factors which act to keep individuals away from each

other.

This experiment was designed to investigate the forces of attraction and repulsion between individuals by placing them in an enclosure which was sufficiently large so that physical constraints were unlikely to restrict the spacing behaviour of the individuals. Previously (Chapter 3), interindividual distances were found to vary significantly according to the positions of the individuals in the aggressive dominance hierarchy. Since the observed interindividual distance is the equilibrium point of attraction and repulsion between the birds, then the relative strengths of these two forces must also be influenced by the social rank of the individuals. Whilst this would explain, in part, the variation in mean interindividual distance between different pairs of birds, it cannot be used to explain the large variation in interindividual distances within the same pair, since the position of an individual in the social hierarchy rarely changes (Rushen,1982). Consequently, there must be other factors which change more frequently than position in the hierarchy and which also affect the relative strengths of the forces of attraction and repulsion.

Two experiments were carried out. The first experiment investigated social factors, other than position in the hierarchy, which may influence the distances between pairs of birds. The second experiment investigated whether or not changes in the newly identified social factor were

associated with changes in interindividual distance within pairs of birds.

Both experiments were carried out in a large outdoor enclosure measuring 110 X 80m. The area had been previously used as a market garden but was now grassed over. The garden was surrounded by a wall 4m high. There were no trees in the area and the only natural cover were bushes at the base of the wall. A roost consisting of a series of covered perches was constructed in one corner. A detailed map is shown in Figure 4.1.

Marks were placed at 2.5m intervals along two sides of the garden to help create an imaginary grid across the garden. The marks were used to help judge distances between individuals and also as reference points to define the locations of particular birds in the garden. All the birds were fitted with large numbered plastic wing-tags (Richey Tagg, Yorkshire) and could be easily identified using binoculars. To keep the conditions as uniform as possible, whole wheat was scattered three times a week over the area, so avoiding a concentration of bird movements around a food source.

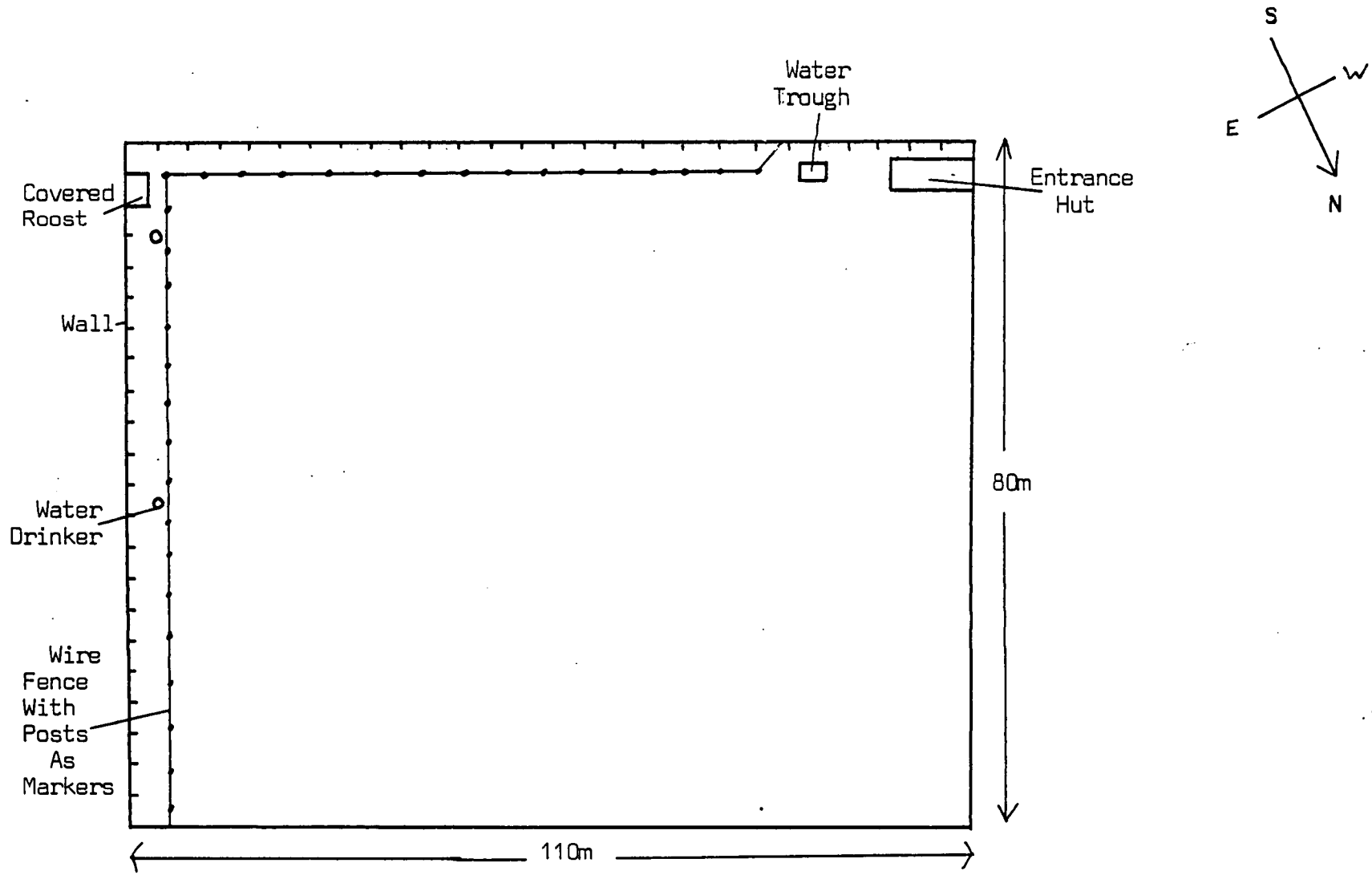


FIGURE 4.1 Plan Of Area Of Walled Garden (not to scale)

For observational purposes the fence posts were used as cues to divide the area up into imaginary grid squares. However, for the purposes of comparison between this figure and figures 4.2, 4.3 and 4.4, a simplifed grid system is presented.

EXPERIMENT 1

4:2 METHOD

In this experiment, 13 female and 2 male adult bantams and the same numbers of each sex of a medium hybrid laying strain (Isa Brown) were released into the walled garden. The bantams were of a mixed genetic background bred at the Poultry Research Centre (PRC) and were between 50 and 120 weeks old. The birds had been housed in mixed sex groups in pens prior to the start of the experiment. The medium hybrids were brought to the PRC as day old chicks and were aged between 28 and 30 weeks at the start of the experiment. They had been housed in individual battery cages from 18 weeks of age. The two groups were placed in two grassy outdoor enclosures each measuring 12.5 x 25.0m and with a hut for shelter, before being transferred to the walled garden. Both groups were kept in these outdoor enclosures for 3 months and during this time the diet of the birds was changed from mash to whole wheat.

Once the birds had been transferred to the walled garden they were allowed 2 months to settle before the observations started. Observations were consequently carried out in the months of September and October. The day was divided into three observation periods; 09.00-10.30hr, 11.00-12.30hr, and 14.00-15.30hr. For each set of observations, a random list of all the individuals was produced. A different random list was used on each

occasion. At the start of the observation period the first individual on the list was located within the garden and its activity, the distance to its nearest neighbour, and its neighbour's activity were recorded. Three minutes later, the second individual on the list, which could be of the same or a different strain, was located and the process repeated, and so on, for all individuals. At distances of less than 1m, estimates of nearest neighbour distance were to the nearest 10cm. At distances 1-10m, distances were estmated to the nearest 0.5m. Beyond 10m, distances were estimated to the nearest 2m using the marks along the sides of the garden.

Throughout the observation period the bantams and the hybrids remained as two distinct groups. This made it possible to compare features of the bantam flock with features of the hybrid flock. At 15min intervals the area occupied by each flock was estimated using the markers to determine the length and width of the flock. The area of the flock was calculated as length x width. At the same time, the main activity of the flock was also recorded. This was regarded as that activity being performed by the majority of individuals. In addition to this flock data, the most outlying individual from each flock was identified and the distance to its nearest neighbour was recorded.

The weather was consistently clear, but frosty, throughout

the twenty days of observations. This was fortunate, since casual observations had shown that heavy rain influenced the behaviour of the birds considerably; with many moving under the shelter of the covered perches during rain.

4:3 RESULTS

1) USE OF AREA

The location of each individual in the garden was specified as coordinates using the marks around the edge of the enclosure. When these were plotted, it was obvious that the birds were not using the area uniformly (Figure 4.2). However, as this plot included repeated observations (between 35 and 40) of all individuals, the observations for 5 birds of each strain, chosen at random, were plotted separately. The distribution of observations for these birds was found to be similar to the distribution for all birds. The distribution of observations for one typical bantam and one typical hybrid are presented in Figure 4.3.

The distribution of numbers and percentages of observations are presented in Figure 4.4. For simplification, the area has been divided into 9 grid boxes. As there were repeated observations of the same individuals, it was not possible to carry out a Chi square test on all the data. In fact, since the differences were so apparent, it was thought unnecessary to test the distribution of each individual separately. From Figure

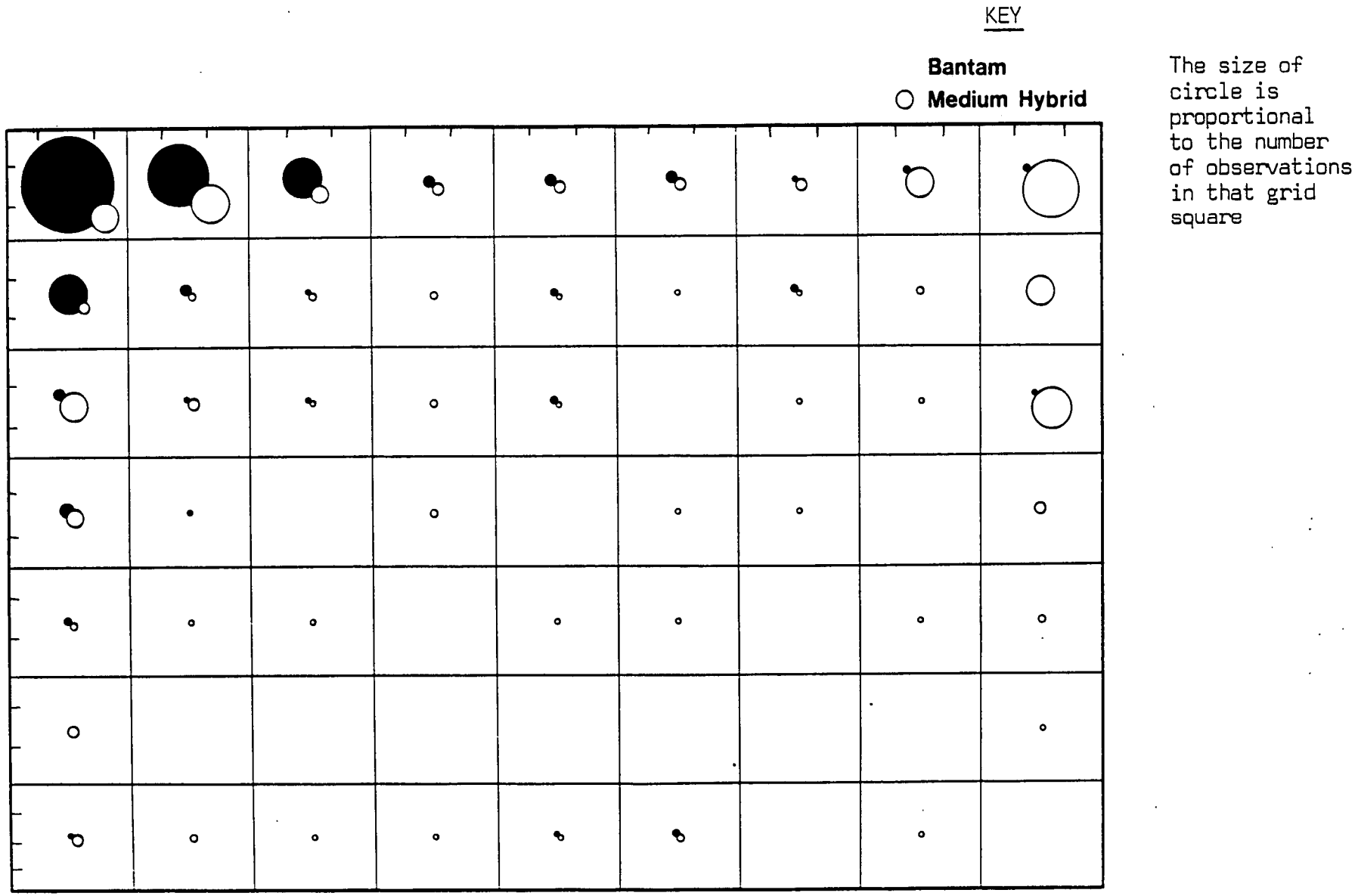


FIGURE 4.2 Distribution Of Bird Locations In The Walled Garden Over The Total Experimental Period For All Bantams And All Medium Hybrids

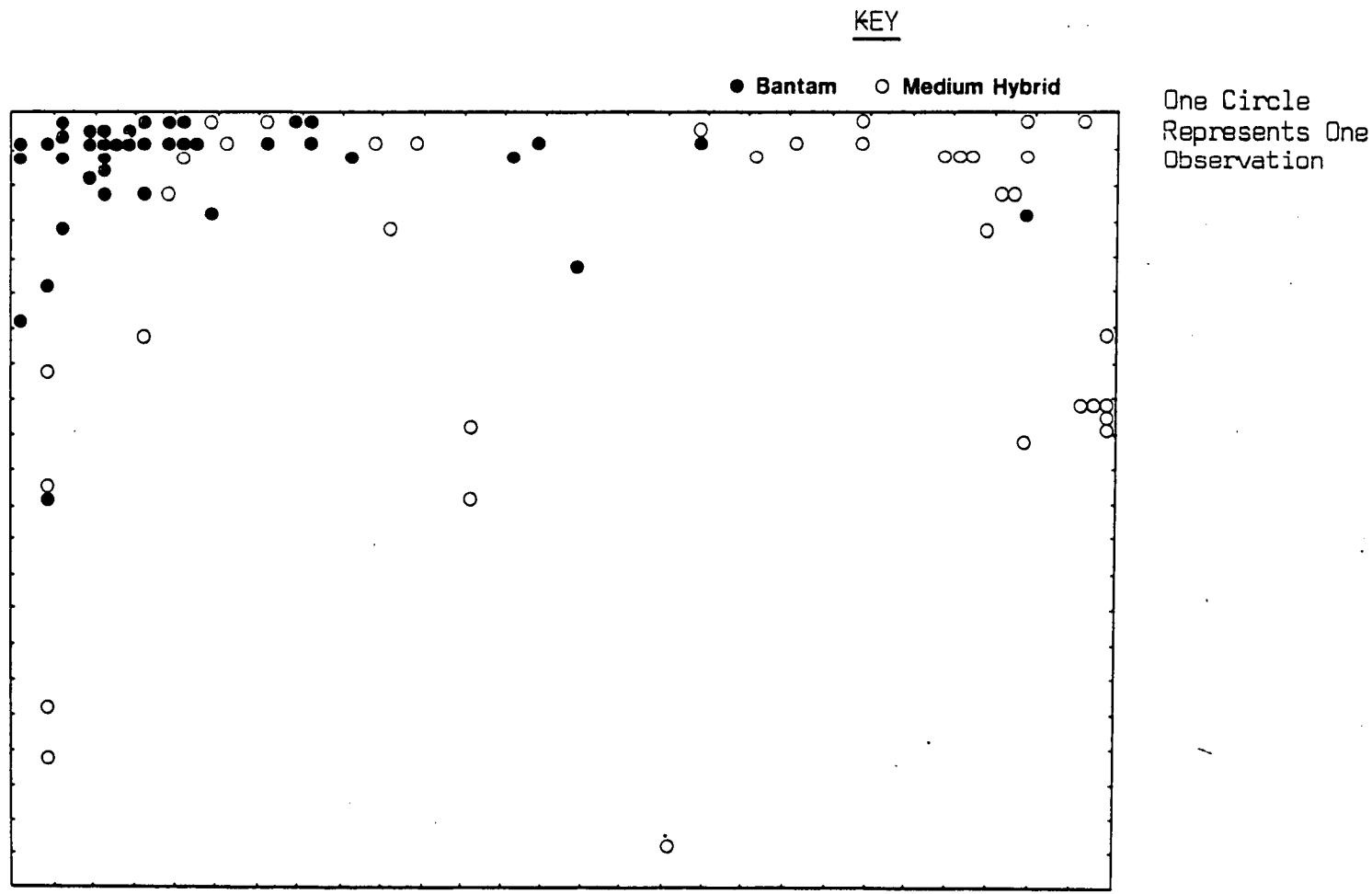


FIGURE 4.3 Distribution Of Bird Locations In The Walled Garden Over The Total Experimental Period For One Bantam (Wingband No.73) And One Medium Hybrid (Wingband No.22)

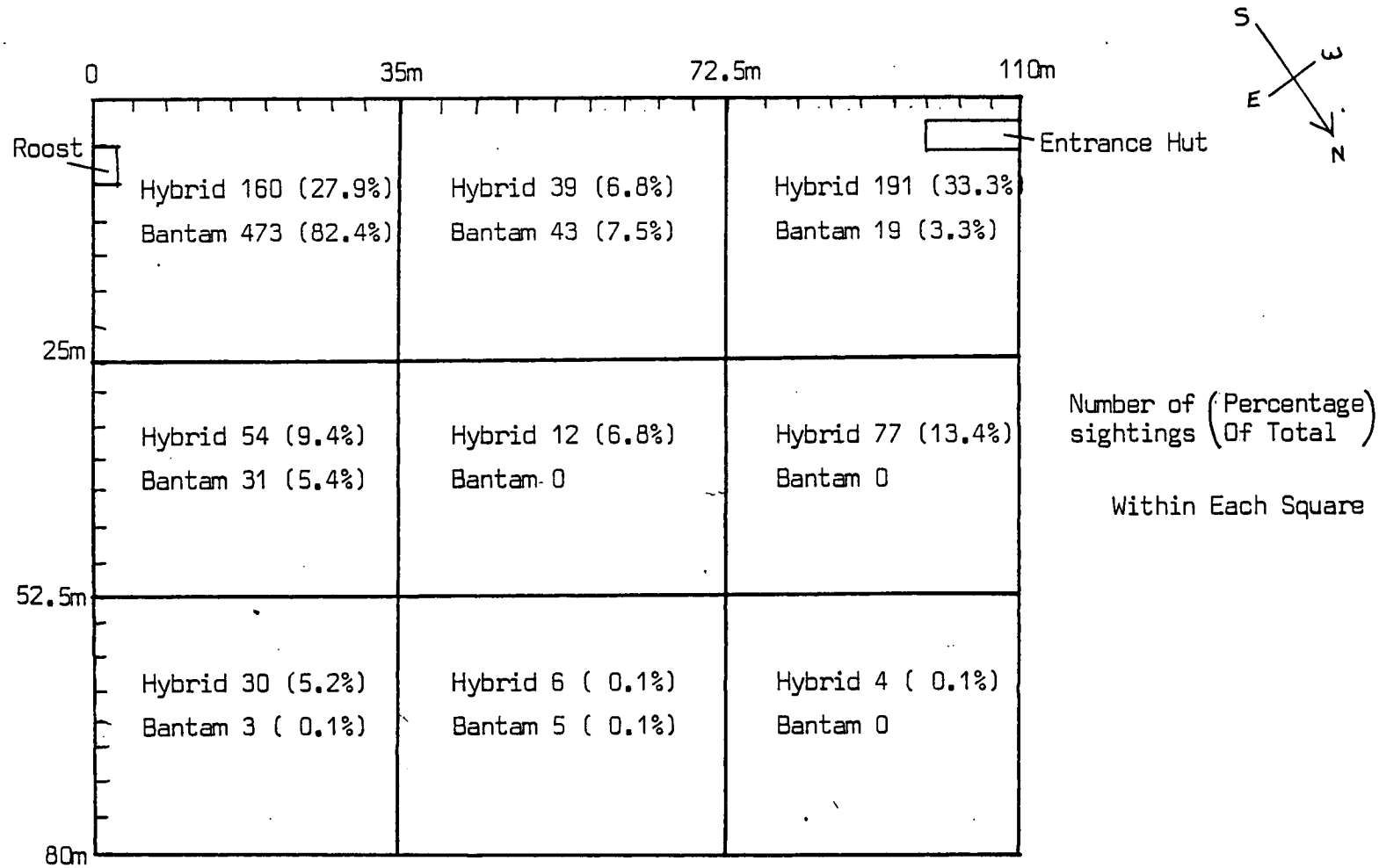


FIGURE 4.4 Distribution Of Locations In The Walled Garden Over The Total Experimental Period For All Bantams And All Hybrids

4.4 it is obvious that the bantams were mainly recorded in the corner of the enclosure nearest to the roost (82.4% of total observations). The hybrids used the area around the roost (27.9%), but they also used the corner near the entrance to the walled garden (33.3%).

In addition to favouring particular areas, it was noted that individuals of both strains used the edges of the enclosure more than the central region. The enclosure was therefore divided into a series of concentric areas. The outermost region was made up of all the grid squares at the edge of the enclosure, the next region of all grid squares one in from the edge, and so on, to the last region, which was composed of grid squares from the centre of the enclosure. The area of each concentric area, represented as a percentage of the total area of the garden, is given in Table 4.1. Again, because of the repeated observations, it was not possible to test the actual results with those expected. Although, as can be seen from Table 4.1, 69.5% of the observations in the bantams and 62.9% of the observations in the hybrids are within two grid squares of the wall (ie within 5m of the wall).

Columns represent the actual number of observations of bantams and medium hybrids, and these numbers expressed as a percentage of the total number of observations for each strain. To help comparison, the percentage area of the garden in each concentric area is also presented.

TABLE 4.1 Distribution Of Locations Of All Bantams And All Medium Hybrids In The Walled Garden Over The Experimental Period

Distance To Wall	BANTAMS No.Obs.	BANTAMS Percent.	MEDIUM HYBRIDS No.Obs.	MEDIUM HYBRIDS Percent.	AREA OF GARDEN Percent.
Within 2.5m	134	23.9	186	32.6	10.5
" 5.0m	256	45.6	173	30.3	9.9
" 7.5m	71	12.7	75	13.1	9.4
" 10.0m	35	6.2	32	5.6	8.8
" 12.5m	19	3.4	39	6.8	8.2
" 15.0m	12	2.1	3	0.5	7.7
" 17.5m	10	1.8	14	2.5	7.1
" 20.0m	5	0.9	8	1.4	6.5
" 22.5m	2	0.3	7	1.2	6.0
" 25.0m	2	0.3	7	1.2	5.4
" 27.5m	7	1.2	4	0.7	4.8
" 30.0m	2	0.3	4	0.7	4.3
" 32.5m	5	0.9	4	0.7	3.7
" 35.0m	0	0.0	3	0.5	3.1
" 37.5m	1	0.2	0	0.0	2.6
Central Region	0	0.0	12	2.1	2.0
Total	561		571		

2) FLOCK AREA

As stated previously, the main activities of the flocks were specified each time the flock area was calculated. The distribution of flock areas were slightly skewed so a log-transformation was used to normalise the data. A two-way Analysis of Variance of flock area was then carried out with activity (preening, ground pecking, walking or

standing) and flock (bantam or medium hybrid) as main effects. There was no significant interaction between flock and activity (F=1.29; D.F.=3,441; NS) although both flock and activity were found to have a significant effect on flock area. The Analysis of Variance was therefore repeated dropping out this interaction. The results of this analysis are presented in Table 4.2.

TABLE 4.2 Analysis Of Variance Of Flock Area

VARIABLE	DF	F-VALUE
Flock	1	309.12 ***
Activity	3	31.80 ***
Remainder	444	mean square = 0.285

The means and standard errors (original units) for the two flocks and for each activity are presented in Table 4.3.

TABLE 4.3 Flock Area

ACTIVITY	MEDIUM HYBRID	N	BANTAM	N
Preening	53 ± 19m^2	14	10 ± 2m^2	44
Ground Pecking	489 ± 48m^2	197	49 ± 5m^2	112
Standing	356 ± 184m^2	7	25 ± 3m^2	60
Walking	582 ± 355m^2	5	52 ± 18m^2	10
Total-Irrespective of activity	412 ± 37m^2	223	30 ± 3m^2	226

The medium hybrids occupied, on average, a much larger flock area (412 ± 37m^2, mean ± s.e.) than the bantams (30

$\pm$ 3m^2) when the flock areas, irrespective of activity were considered (F=309.1; D.F.=1,444; P<0.001). However, within each strain there were significant differences according to the main activity of the flock (F=31.8; D.F.=3,444; P<0.001). For example, the mean flock area was smallest when the major activity of the flock was preening and largest when the main activity was walking. This variation in flock area with activity (preening < standing < ground pecking < walking) was the same in both the hybrid and the bantam strains.

3) Nearest Neighbour Distances

The data on distances to nearest neighbour were log-transformed and then a two-way Analysis of Variance carried out with strain and activity as main effects. There was no significant interaction between activity and strain (F=1.28; D.F.=3,354; NS) although both activity and strain were found to have significant independent effects on nearest neighbour distance. The Analysis of Variance was therefore repeated dropping out this interaction. The results of this analysis are presented in Table 4.4.

Nearest neighbour distances, irrespective of activity, were significantly less in the bantams (0.24 $\pm$ 0.01m^2) than in the hybrids (0.40 $\pm$ 0.03m^2) (F=10.76; D.F.=1,587; P<0.01).

TABLE 4.4 Analysis Of Variance Of Nearest Neighbour Distances

VARIABLE	DF	F-VALUE
Flock	1	10.76 **
Activity	3	26.38 ***
Remainder	587	mean square = 0.2603

Apart from these flock differences, there were also significant differences in nearest neighbour distances within each strain according to activity (F=26.38; D.F.=3,587; P<0.001). Minimum nearest neighbour distances occurred when both birds were preening. The values are presented in Table 4.5 for pairs of individuals of the same strain e.g. a medium hybrid whose nearest neighbour was also a medium hybrid, and when both birds were performing the same activity e.g. both birds preening at the time of the observation.

TABLE 4.5 Nearest Neighbour Distances

ACTIVITY	MEDIUM HYBRID	N	BANTAM	N
Preening	$0.14 \pm 0.03m^2$	30	$0.11 \pm 0.01m^2$	64
Ground Pecking	$0.46 \pm 0.04m^2$	216	$0.32 \pm 0.02m^2$	157
Standing	$0.26 \pm 0.06m^2$	30	$0.25 \pm 0.03m^2$	68
Walking	$0.89 \pm 0.27m^2$	20	$0.28 \pm 0.10m^2$	7
Total-Irrespective of activity	$0.40 \pm 0.03m^2$	296	$0.24 \pm 0.01m^2$	296

4) DISTANCES OF OUTLYING INDIVIDUALS FROM THE FLOCK

As in the previous two analyses, distance to the outlying individual was log-transformed and then analysed using a two-way Analysis of Variance. There was no interaction between activity and flock (F=1.025; D.F.=3,441; NS). The Analysis of Variance was therefore repeated dropping out this interaction. The results of this analysis are presented in Table 4.6.

TABLE 4.6 Analysis Of Variance Of Distance To Outlying Individuals

VARIABLE	DF	F-VALUE
Flock	1	285.73 ***
Activity	3	5.29 ***
Remainder	444	mean square = 0.2116

There was a significant effect of activity (F=5.29; D.F.=3,444; P<0.01). There was also a significant difference between the two flocks (F=285.7; D.F.=1,444; P<0.001). Irrespective of activity, the mean distance of an outlying bantam from the flock (1.8 $\pm$ 0.01m^2) was significantly less (P<0.001) than an outlying medium hybrid (13.4$\pm$1.0m^2) (Table 4.7).

TABLE 4.7 Distances To Outlying Individuals From The Flock

ACTIVITY	MEDIUM HYBRID	N	BANTAM	N
Preening	11.0 ± 3.4m^2	14	1.1 ± 0.2m^2	44
Ground Pecking	13.7 ± 1.1m^2	197	2.2 ± 0.2m^2	112
Standing	11.0 ± 4.7m^2	7	1.6 ± 0.02m^2	60
Walking	11.9 ± 6.1m^2	5	3.2 ± 1.0m^2	10
Total-Irrespective of Activity	13.4 ± 1.0m^2	223	1.8 ± 0.01m^2	226

As can be seen from Table 4.7, there was a large variation around the mean distance within the hybrid strain. It was decided, therefore, to analyse the effect of activity on distance to the outlying individual separately for each strain using a one-way Analysis of Variance (Table 4.8).

TABLE 4.8 Analysis Of Variance Of Distances To Outlying Individuals

<u>HYBRID STRAIN</u>

VARIABLE	DF	F-VALUE
Activity	3	0.325
Remainder	220	mean square = 0.243

<u>BANTAM STRAIN</u>

VARIABLE	DF	F-VALUE
Activity	3	6.997 ***
Remainder	222	mean square = 0.182

As anticipated, although there was a significant effect of activity within the bantam strain ($F=7.00$; D.F.=3,222; $P<0.001$), there was no significant effect of activity within the hybrid strain ($F=0.33$; D.F.=3,220; NS). In the bantam strain, the largest mean distance of an individual from the flock occurred when the bird was either walking or ground pecking and was smallest when the bird was preening.

Throughout the experiment, this distance has been referred to as the distance of an outlying individual from the flock. However it is, in effect, another measure of the nearest neighbour distance. Although there were a few occasions when the outlying individual was closer to the other flock than to its own flock, in the majority of cases the nearest neighbour distance for the outlying individual was the distance to its usual flock. This distance could then be regarded as the largest nearest neighbour distance in the flock at that time. Unfortunately, no measure was made of the minimum nearest neighbour distance in the flock. But, it is still interesting that this maximum nearest neighbour distance was 7 times greater than the average nearest neighbour distance for the bantam strain, whereas in the hybrids, this distance was 33 times greater.

4:4 CONCLUSIONS

All birds roosted together and occasionally mixed within the enclosure, but they generally moved as two distinct flocks. This suggests that familiarity with previous flock members was an important factor influencing their distribution, as the birds were kept in separate groups for three months before being put into the walled garden. The effect of familiarity on spatial behaviour has been demonstrated in sheep by Winfield, Syme and Pearson (1981). There is also evidence that animals of the same strain will group together (Arnold and Maller,1985). In the present case, it is not possible to determine whether the birds formed two single-strain flocks because they had previously been housed as such or whether it was an attraction to individuals of the same strain. Whatever the reason, this pattern made it possible to investigate flock area as well as nearest neighbour distances for each strain of bird. There were no obvious subgroups in either flock of birds. Consequently, the differences in flock area between the two flocks reflects the fact that the nearest neighbour distances between bantams were, on average, much less than between the hybrids. This difference between the two flocks of different strains was not replicated, but was consistent with expectation on the grounds that bantams have been exposed to natural selection pressures including predation until more recently than the hybrids. They would therefore be expected to be more cohesive.

According to the idea of an equilibrium between attraction and repulsion proposed earlier, then either the factors keeping the birds together were stronger in the bantams an weaker in the hybrids, or the factors keeping

the birds apart were stronger in the hybrids and weaker in the bantams. When the ranges of nearest neighbour distances were examined, it was not at the lower end of the range that the two strains differed but at the upper limit of nearest neighbour distances. The minimum nearest neighbour distance was zero in both strains, but the maximum values were 5m in the bantams and 80m in the hybrids (Interquartile ranges Hybrids 0.2-1.0m, Bantams 0.1-0.5m). This suggests that it was the attraction towards other individuals which was stronger in the bantam strain, so preventing them drifting apart. This is supported by the fact that the distance of outlying individuals from the bantam flock was much smaller than the distance of outlying individuals from the hybrid flock.

The bantam-bantam distances may be shorter than hybrid-hybrid distances because of physical differences between the two strains. The hybrids were larger than the bantams and so could perhaps maintain contact at greater interindividual distances. However, this is unlikely to explain the seven-fold difference between the two strains in the distance individuals were observed away from the flock.

Alternatively, there may be behavioural differences between the two strains which influence the spacing. For example, one might expect antipredator behaviour to be more pronounced in the primitive bantam strain which has

probably been exposed to predation until more recently than the commercial strain. This factor would act to bring the birds closer together and so could explain why the bantams formed a more cohesive flock, with shorter nearest neighbour distances, than the hybrids. The relationship between the risk of predation and flock area has been reviewed by Myers (1984). For example, it has been shown in Sanderling (Calidris alba) flocks that interindividual distances decreased when a predator was present (Treisman,1975). In addition, more pronounced antipredator behaviour may explain, in part, why the bantam individuals stayed nearer to the roost (near the only cover) than the medium hybrids although both strains stayed near to the wall. Since this explanation was not tested it can only be speculative.

Differences in flock area according to the activity of the birds reflected the fact that nearest neighbour distances varied with activity. It was suggested that the difference in interindividual distances between the two strains of bird were a result of stronger forces of attraction in the bantams, rather than stronger forces of repulsion in the hybrids. It is more difficult to speculate why, within the same strain, the activity of the birds should influence the distance between them. Comparisons between species which live in groups suggest that the two main environmental influences on social behaviour are predation and food (Krebs and Davies,1981). It is likely that both

these environmental factors will affect the distances between individuals of the same species.

Individuals will be more vulnerable to predation when performing some activities than others. For example, birds eyes are closed for a large proportion of the time they are preening. It may follow, therefore, that an individual which is preening will position itself nearer to a conspecific than if it were perfoming an activity in which it was less vulnerable. Even if both individuals were preening, the risk of predation to each individual would be reduced due to increased vigilance and the dilution effect (Goss-Custard,1970). This means that a potential predator is more likely to be detected but, even if it is not, the chance of any specific individual being attacked is reduced. In this way, risk of predation may act to bring individuals together when performing particular activities.

Competition for resources, on the other hand, or the reduced probability of finding food in an area recently searched by a flockmate may act to keep individuals away from each other when foraging. However, environmental factors such as risk of predation and competition are unlikely to be the only factors affecting spacing behaviour, social factors and the internal state of the birds eg. hunger, thirst and fear, will also be important.

It was originally intended in this experiment to determine

the position of the individuals in the aggressive dominance hierarchy. But, because of the large number of individuals involved insufficient interactions were observed between particular pairs of birds to allow a hierarchy to be determined. At best, it would have been possible to divide each strain into high, middle and low ranking individuals. Consequently, only the effects of activity and the strain of bird on spacing behaviour were analysed in detail.

The present experiment and the one in the previous chapter (Chapter 3) together have demonstrated that the strain of a bird, its social rank and its activity are important influences on the distances between individuals.

EXPERIMENT 2

4:5 INTRODUCTION

It has been demonstrated that the distances between individuals are influenced by the strain of the birds (Chapter 4, Experiment 1), their relative positions in the social hierarchy (Chapter 3) and their activities (Chapter 4, Experiment 1). It has also been proposed that the distance between individuals is the distance at which there is an equilibrium between the forces of attraction and repulsion. Of these three influences, only activity changes from minute to minute. One would predict,

therefore, that if the activity of a bird changes then the equilibrium distance between the forces of attraction and repulsion should shift. Consequently, the birds should either move together or move apart to the new equilibrium distance. This equilibrium distance could be regarded as the "appropriate" distance between birds. This experiment, therefore, looked for a relationship between changes in activity and changes in interindividual distance. Such a relationship would support the idea that for particular circumstances there are "appropriate" distances between individuals which they try to achieve. When the circumstances change, the appropriate interindividual distance also changes and the birds move to a new interindividual distance. Since the appropriate distance is the distance at which the birds are neither too close nor too far away from each other, it would occur when the tendency to approach was balanced by the tendency to withdraw.

This hypothesis was investigated further by ascertaining whether or not activity transitions in one direction were accompanied by an increase in interindividual distance whereas activity transitions in the opposite direction were accompanied by a decrease in interindividual distance.

METHOD

This experiment was carried out in the summer following the previous experiment when a group of 20 adult females and 5 males of the medium hybrid strain were released into the walled garden. The birds had been housed as a single group in an indoor pen before been placed outside when they were 18 weeks of age. The birds were allowed two months to settle in the walled garden before observations were carried out in August. Food was scattered over the area as in the previous experiment.

The day was divided into three observation periods 9.00-10.00hr, 11.00-12.00hr and 14.00-15.00hr. For each observation period, the first individual from a random list of all the females was located within the field and its activity, the distance to its nearest neighbour, and its neighbour's activity were recorded. A different random list was used on each occasion. Only females whose nearest neighbour was also female were considered. The distance between the two birds and their activities were then noted every 10 seconds for 80 seconds. The second individual on the list was then located and the process repeated. Each individual was recorded between 22 and 25 times during the whole experiment

In this experiment, a distinction was made between birds that were stationary and pecking at the ground, which was called ground pecking, and those that that were moving and

pecking at the ground, which was called foraging. Mean nearest neighbour distances in this part of the experiment were calculated in order to allow comparison with the nearest neighbour distances for the medium hybrids in the previous section. However, since nearest neighbour distances for a particular pair of birds were recorded every 10 seconds, only the distance from the first 10 second observation was included in the analysis. Again, because of the slightly skewed distribution the data were log-transformed.

4:7 RESULTS

Nearest neighbour distances (original units) are shown in Table 4.9 and it can be seen that although the distances were much greater than in the first part of this experiment (Table 4.5), the same trends are present. In addition to nearest neighbour distances when both birds were performing the same activity, distances when birds were performing different activitites are also shown. Unfortunately, there were insufficient occasions when birds were preening to allow an analysis of distances during this activity.

TABLE 4.9 Nearest Neighbour Distances

ACTIVITY	DISTANCE	N
Ground pecking and Ground pecking	$0.35 \pm 0.40m^2$	64
Foraging and Foraging	$3.34 \pm 0.63m^2$	37
Standing and Standing	$0.61 \pm 0.40m^2$	22
Walking and Walking	$2.53 \pm 0.84m^2$	12
Ground pecking and Foraging	$2.25 \pm 0.59m^2$	19
Ground pecking and Standing	$1.42 \pm 0.33m^2$	25
Ground pecking and Walking	$1.65 \pm 0.47m^2$	16
Foraging and Standing	$2.22 \pm 0.56m^2$	21
Foraging and Walking	$1.35 \pm 0.55m^2$	8
Standing and Walking	$1.83 \pm 0.56m^2$	14
TOTAL	$1.23 \pm 0.16m^2$	238

There was a significant difference in nearest neighbour distance according to activity using an Analysis of Variance ($F=10.28$; $D.F.=9,236$; $P<0.001$). It can be seen that it was important to make the distinction between ground pecking which had the smallest nearest neighbour distance ($0.35 \pm 0.4m$) and foraging which had the largest ($3.34 \pm 0.6m$).

Activity transitions were said to have occurred when at least one individual of the pair changed activity in the 10sec interval between successive observations. The difference in interindividual distance between the preceding and succeeding observation was determined to investigate whether or not the birds had approached each other, withdrawn from each other or were still the same distance apart. For each time that a particular transition was observed, the total number of times the birds approached each other and the total number of times they withdrew from each other was determined. Only the first

transition from each 80sec observation was included in the analysis.

Each activity transition was paired with the change of activity in the opposite direction to form a 2x2 contingency table. For example, one activity transition would be where both birds were ground pecking (GPGP) and one bird stopped ground pecking and started foraging (GPFO). The reverse transition would be when one bird of a pair was ground pecking and the other foraging (GPFO) and the bird which was foraging changed activity to ground pecking (GPGP). These results are presented in Table 4.10.

Each 2x2 contingency table was tested separately using the Fisher Exact Test. Only transition tables 1,2 and 3 which involve ground pecking and foraging, ground pecking and standing, and ground pecking and walking were significant. For example, in the transition where both birds were ground pecking and one bird changed activity to foraging (GPGP-GPFO), the birds moved apart more often than they moved together (30 occasions apart, 10 occasions together). In the reverse transition, where one bird was ground pecking and the other bird foraging and the bird which was foraging changed its activity to ground pecking (GPFO-GPGP), the birds moved together more often then they moved apart (19 occasions together and 11 occasions apart).

TABLE 4.10 Numbers Of Approaches And Withdraws Associated With Activity Transitions

ACTIVITY TRANSITION	NUMBER OF APPROACHES	NUMBER OF WITHDRAWS
1) GPGP--GPFO	10	30
GPFO--GPGP	19	11
2) GPGP--GPST	11	20
GPST--GPGP	13	5
3) GPGP--GPWK	6	20
GPWK--GPGP	13	12
4) WKWK--WKST	1	4
WKST--WKWK	1	4
5) STST--STGP	5	5
STGP--STST	3	3
6) FOFO--FOGP	23	29
FOGP--FOFO	19	26
7) FOFO--FOWK	4	9
FOWK--FOFO	4	9
8) FOFO--FOST	10	15
FOST--FOFO	10	19
9) STST--STFO	1	5
STFO--STST	5	3
10) STST--STWK	6	2
STWK--STST	7	4
11) WKWK--WKFO	1	3
WKFO--WKWK	3	1
12) WKWK--WKGP	1	5
WKGP--WKWK	7	3

KEY
GP - Ground Pecking
WK - Walking
ST - Standing
FO - Foraging

One possible reason for the low number of significant contingency tables is the small number of observations for some activity transitions. To overcome this it was decided to test for an overall significant relationship between changes in activity and changes in interindividual distance using Cochran's method of combining contingency tables (Everitt,1977). This test includes all transition

tables in the analysis, but weights each transition table, giving more emphasis to those with a greater number of observations. It was, therefore, more representative of the overall situation than testing each table separately. A significant relationship ($T=2.87$; $D.F.=11$; $P<0.025$) was demonstrated between the movements of individuals, either towards or away from each other and changes in activity.

In Table 4.11 the number of approaches and withdraws, within a 10sec time period, when there was no activity transition is presented.

TABLE 4.11 Numbers Of Approaches And Withdraws Not Associated With Activity Transitions

ACTIVITY	NUMBER OF APPROACHES	NUMBER OF WITHDRAWS
STST--STST	1	7
GPGP--GPGP	40	51
WKWK--WKWK	3	5
FOFO--FOFO	46	78

As can be seen, there were always more withdraws than approaches. This is because individuals which were nearest neighbours were selected, so even without activity transitions, there was a greater chance of nearest neighbours moving apart than moving together. This effect would be superimposed on changes due to activity transitions. The effect seemed to be particularly pronounced when both birds were foraging and may explain

why in transition tables 6,7 and 8 (Table 4.10) the birds moved apart more often than they moved together irrespective of the direction of the activity transition.

It is possible, from the mean nearest neighbour distances, presented in Table 4.9, to predict how these distances should change when one or both birds change activity. For example, the mean nearest neighbour distance is 0.35m when both birds are ground pecking (GPGP), and 2.25m when one bird is ground pecking and the the other is foraging (GPFO). Therefore, if two birds are ground pecking and one bird changes its activity to foraging (GPGP-GPFO) one would predict an increase in the nearest neighbour distance ie. the birds should move away from each other. In the reverse situation, where one bird is foraging and the other is ground pecking, and the bird which is foraging changes its activity to ground pecking (GPFO-GPGP), one would predict a decrease in nearest neighbour distance i.e. the birds should move towards each other. In this example, one would expect birds to move 1.90m (2.25-0.35) closer together or further apart. The actual distance moved, however, would depend on when the activity transition occurred within the 10sec time interval between observations. If the transition occurred after 9sec, the birds would still be in the process of adjusting distances when the interindividual distance was recorded 1sec later. I think, therefore, it is unrealistic to predict the exact distance the birds would move apart or together. In

addition, any predictions must be treated cautiously as both the observed and the predicted changes in interindividual distance were derived from a single group of birds. Despite these reservations, when the actual number of approaches and withdrawals were compared, only 13 out of 22 transitions were in the predicted direction. The six transitions in the three significant contingency tables (1,2 and 3), however, were all in the predicted direction.

4:8 CONCLUSIONS

There was an overall trend for activity transitions in one direction to be associated with more withdraws than approaches, and for the reverse transitions to be associated with more approaches than withdraws. This was significant despite the fact that some activity transitions were only observed a small number of times. The paucity of observations for some transitions may also explain, in part, why only 13 out of 22 activity transitions were in the predicted direction. The transitions with few observation were generally the transitions which were not in the predicted direction. Nevertheless, the movements of the birds in all the activity transitions of the three significant contingency tables were in the predicted direction. In addition, the predictions were based on the difference between the mean

interindividual distances for each activity combination and it can be seen from Table 4.4 that the variance about the means was large, so adding noise to these predictions.

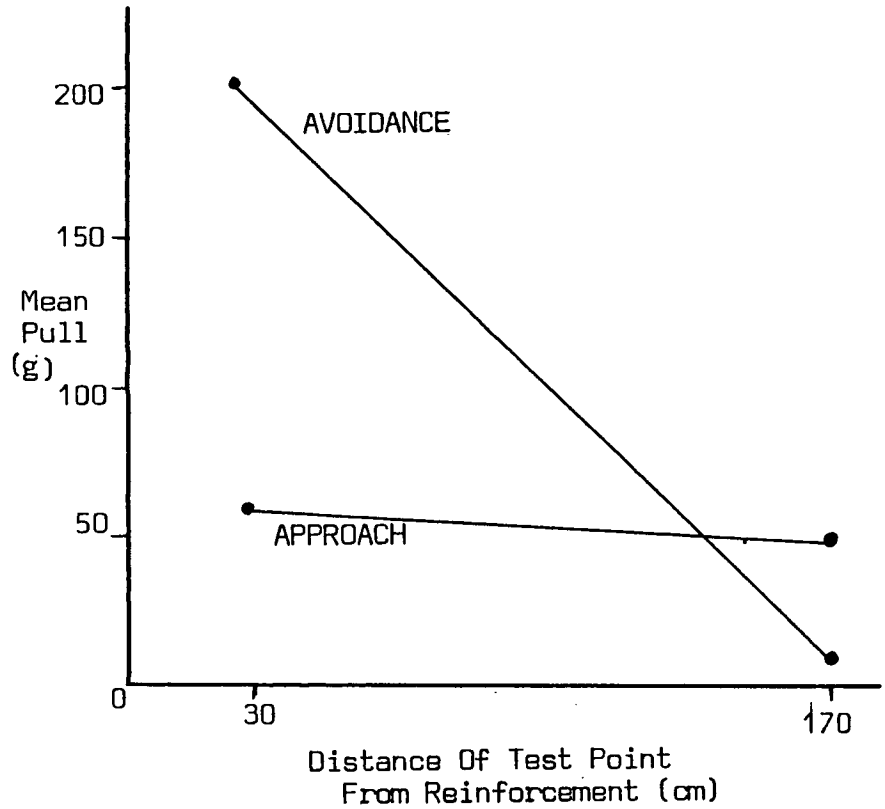
This experiment, therefore, supports the hypothesis that there is a change in the distance between birds when there is a change of activity. It also suggests that whether the individuals move together or move apart depends on the direction of the activity transition. It is concluded that spacing behaviour of domestic fowl can be described using the idea of forces of attraction and repulsion between individuals. These forces will vary according to the situation, but the actual distance between the individuals will correspond to the equilibrium point between these two forces, and that birds will move to the new equilibrium interindividual distance when it changes.

CHAPTER 5

AN INVESTIGATION TO DETERMINE WHICH INDIVIDUAL OF A PAIR IS RESPONSIBLE FOR THE DISTANCE BETWEEN THEM

5:1 INTRODUCTION

The idea that the distance between individuals is an equilibrium between the tendency to move together and the tendency to move apart, implies that the animals are in a conflict situation. Conflict behaviour has been reviewed (Yates,1962; Baerends,1975 and McFarland,1985) and will not be discussed here in detail. Nevertheless, the results of Brown (1948) are of direct relevance. He investigated the approach and avoidance of rats to two different stimuli. He placed a rat in a runway and then by attaching a harness to the animal, he could measure how hard the rat would pull, against a calibrated spring, to approach a food source which was attractive, or how hard it would pull to avoid an electric shock which was aversive to the animal. He measured the strength of the force of approach and avoidance (Figure 5.1) at two different distances from the stimulus. It can be seen that attraction was only slightly stronger when the animal was close to the food compared to when it was further away. Fear of the electric shock, however, produced a very different response. Avoidance was strong close to the stimulus, but fell off rapidly away from the source of reinforcement. As a



Brown (1948)

FIGURE 5.1 The Strength Of The Tendency Of A Rat To approach A Food Source Or Avoid An Electric Shock

result, the two lines crossed.

Brown used two different stimuli in his experiments, but it is possible for a stimulus to be both attractive and aversive at the same time (Lewin;1935). A child, for instance, might want to approach a dog to stroke it but be frightened of the animal at the same time. In domestic fowl, a conspecific may have these dual properties; a bird may be both attracted towards its nearest neighbour and fearful of it. Consequently, there is a conflict of tendencies, one to approach and one to move away. If as Brown suggests, these two tendencies have different slopes, then at small interindividual distances repulsion will be stronger than attraction and the birds will move apart. At large interindividual distances attraction will be stronger than repulsion and so the birds will move together. Where these gradients cross the two forces are balanced and the birds will neither move together nor move apart.

Brown (1948) also demonstrated that the actual positions of the lines representing the strength of attraction and avoidance shifted depending on the intensity of the stimulus. As one would anticipate, a stronger electric shock resulted in more avoidance so raising the avoidance line. But he also demonstrated that changes in the motivational state of the rat affected its response to the stimulus. If the rat was deprived of food, its attraction towards the food source increased and the approach line

was raised.

This experiment was designed to investigate the approach and withdrawal of a bird when the stimulus object was a familiar conspecific. Although changes in interindividual distances were recorded in the previous experiment (Chapter 4, Expt.2) it was not possible to say which individual of the pair was responsible for the change. In fact, when both birds are performing an activity which itself involves some movement, such as walking or foraging, it would be very difficult to identify which bird was responsible for the change in interindividual distance.

In the approach-avoidance conflict situation, where a conspecific bird is the stimulus, it may appear as a more attractive (or aversive) stimulus to a subject bird on different occasions for one of two reasons:
(a) due to the properties ie. motivation, of the subject bird (in the same way as hungry rats had a greater attraction to a food source than satiated rats), or
(b) due to its own changing properties as a stimulus (in the same way as a stronger electric shock increased aversion in the rats).

The same question applied to the second experiment in Chapter 4 would be whether adjustments in distance between individuals were brought about by the bird which changed its activity or whether they were brought about by the

bird which did not change activity. In the former situation, the bird would have changed the interindividual distance in response to its own activity, whereas in the latter situation, the change would have been in response to the other individual's activity.

As discussed previously (1:9), spacing cannot occur unless there are at least two individuals. The mere presence of a conspecific will, therefore, influence the behaviour of a subject bird which was previously on its own. This conspecific will have certain characteristics, ie. its body size, sex etc., which when combined with its geographical location, will influence how the subject bird positions itself relative to it. I have called these unintentional or non-goal directed signals, since they will be present even when there is no other individual there to receive them. However, there may also be signals directed towards the subject bird with the intention of influencing the subject's position. I have called these intentional or goal directed signals, since they will only be given in the presence of a conspecific.

This experiment was designed to separate these two types of signal by restricting the visual contact between the birds. Consequently, it was possible to investigate whether a subject bird regulates its own distance from a stationary stimulus bird (based on the latter's non-goal directed signals) or whether the stimulus bird

intentionally influences the position of the subject bird (by goal directed signals). The study of signals and communication is a complex area (Hinde,1972; Dawkins,1986). It was not the aim of the experiment to describe the signals or how much information was contained in the signals given by an individual. The only intention was to investigate whether there were goal directed signals which resulted in a change in the position of the other bird.

5:2 METHOD

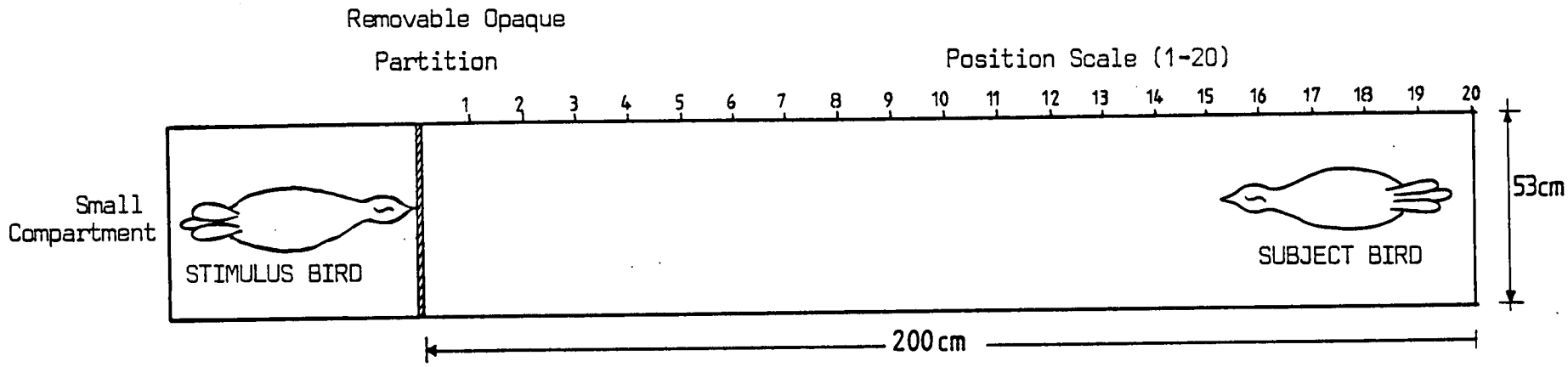
Eighteen pairs of mature medium hybrid (Isa Brown) laying hens were tested in a Murchison runway (Murchison, 1935 and Zayan,1985). Each pair of birds was taken from a group of three individuals housed in a conventional battery cage allowing 450cm^2 per bird. Consequently, each bird was familiar with the other pair member.

The birds were initially familiarized with the runway so that fear of the experimental apparatus would not inhibit movement in the runway during the test period. Each bird was therefore placed on its own in the runway for a period of one hour before it was due to be tested for the first time. Birds were not familiarized with the small compartment but were allowed a settling period of 5 minutes after being placed in the compartment before each test.

The runway (2.0m x 0.5m) was arranged as in Figure 5.2. The bird to act initially as the stimulus bird was selected at random from the pair and placed in the small compartment at the end of the runway. It was allowed 5min to settle before the start of each test.

It has been demonstrated that activity influences interindividual distances (Chapter 4). It was important, therefore, that the activity of the bird in the small compartment presented a constant stimulus to the bird in the runway. Wire partitions were placed in the small compartment so that the stimulus bird was confined, in that it was standing orientated towards the runway and hence the other bird, but not so restricted that it had an unnatural posture.

The other bird of the pair acted as the subject bird and was introduced into the opposite end of the runway to the small compartment through a door in the side, at the end of the 5min settling period for the stimulus bird. It was placed in the runway facing towards the stimulus bird. Its distance from the stimulus bird and its body orientation was recorded every 10s for 15min. The position of the bird was recorded from a scale of 1-20 on the side of the runway, where each division represented 10cm. The orientation of the individual was scored on a scale from 0-6 as indicated in Figure 5.3. Both birds were returned together to their home cage at the end of the trial.



Runway had one solid side and one wire side through which the birds could be observed. The floor was also wire.

FIGURE 5.2 Runway Apparatus

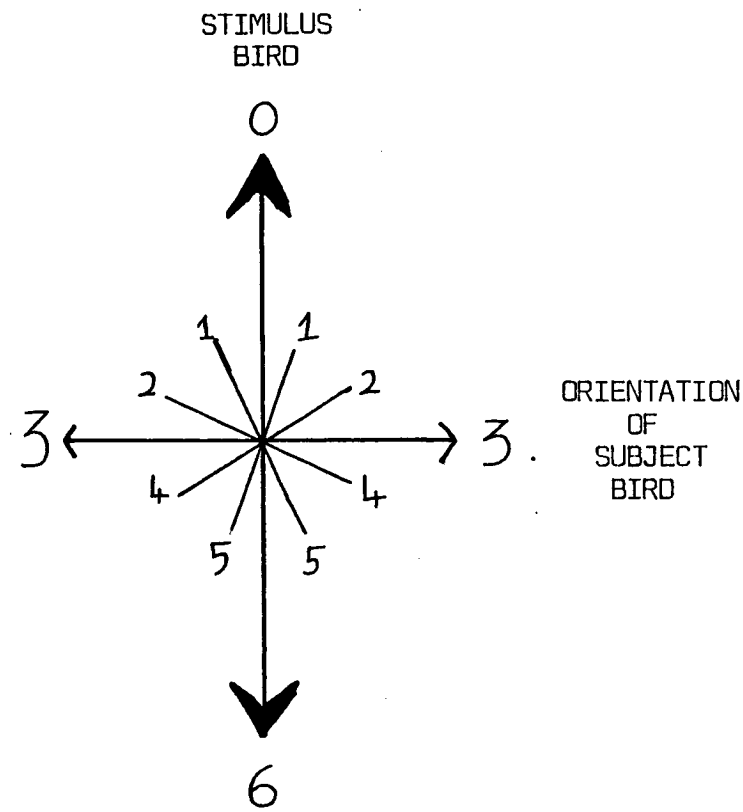


FIGURE 5.3 Scale Of Orientation (0-6) Of The Subject Bird Towards The Stimulus Bird

The opaque partition between the small compartment and the runway could be removed and replaced by either a one-way glass partition or a two-way Perspex partition. The birds were tested once with each of the three different partitions. The pair was then reversed and the subject bird was tested in the three different conditions with the previous subject bird now acting as the stimulus bird. Each pair of birds were, therefore, tested six times. Trials were arranged in a latin square design and each pair was tested only once a day at approximately the same time each day. At all other times the birds were in their home cages and kept under normal husbandry conditions.

The different partitions were used to evaluate the importance of visual signals in spacing. Vocal signals were not considered in this experiment. Although there were three different partitions, there were in fact only two treatments for each bird; a control treatment (where the bird could not see the other) and an experimental treatment (where the bird could see the other). These two conditions were not always the same for the subject bird as for the stimulus bird (Table 5.1).

TABLE 5.1

PARTITION	STIMULUS BIRD	SUBJECT BIRD
Opaque	Control	Control
One-way	Control	Experimental
Two-way	Experimental	Experimental

A two-way partition would permit both birds to see each other and hopefully simulate the normal situation. It would permit intentional goal directed signals from the stimulus bird to the subject bird (if there are any) as well as the non-goal directed information. The one-way partition allowed the bird in the runway to see the stimulus bird, but not the reverse. Consequently, the subject bird could receive information from the stimulus bird, but because the stimulus bird could not see the subject bird, the information would only be of the non-goal directed type. The opaque partition allowed no visual contact and so acted as the control situation, allowing only olfactory and auditory communication (Figure 5.4).

5:3 RESULTS

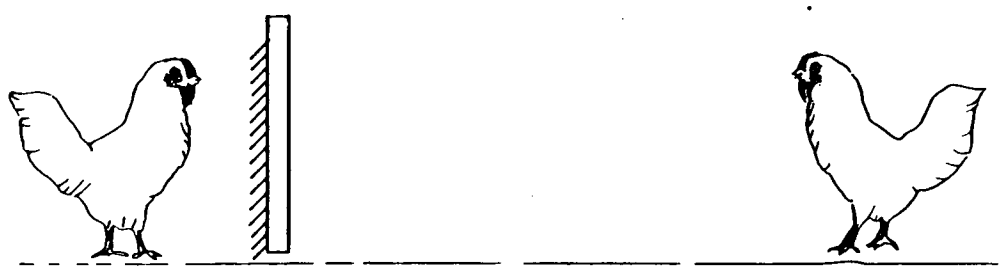
Although all birds were familiar with the apparatus before the start of the experiment, some birds never moved from their original position. It was decided to delete these test occasions from the analyses. A Chi Square was carried out on the number of occasions the subject bird did not move in each treatment. Observed and expected numbers of "non-movers" are presented in Table 5.2. The Chi square value was not significant indicating that these occasions were randomly distributed between the opaque, one-way and two-way partitions

a) OPAQUE PARTITION

Stimulus Bird
Cannot See Subject
Bird

Subject Bird
Cannot See Stimulus
Bird

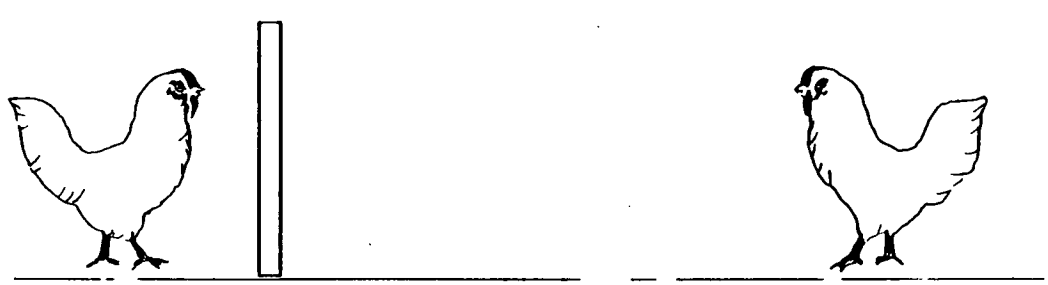
b) ONE WAY PARTITION



Stimulus Bird
Cannot See Subject
Bird

Subject Bird
Can See Stimulus
Bird

c) TWO WAY PARTITION



Stimulus Bird
Can See Subject
Bird

Subject Bird
Can See Stimulus
Bird

FIGURE 5.4 The Three Different Partitions

TABLE 5.2

	PARTITIONS		
	OPAQUE	ONE-WAY	TWO-WAY
Number of "non-movers"	10	8	6
Expected number	8	8	8

Chi-square =1.0; D.F.=2; NS

1) Nearest Distances

The nearest distance between the subject bird and the stimulus bird was the greatest distance the subject bird moved from its original position towards the stimulus bird. The control treatment (opaque partition), when the subject bird could not see the stimulus bird, was compared to the experimental treatment (one-way and two-way partitions combined), when the subject bird could the stimulus bird.

The distribution of nearest distances was not normal for either the control or the experimental treatment, probably because nearest distance represents the extreme of a larger distribution ie. all recorded interindividual distances. A non-parametric test was therefore used (Table 5.3).

TABLE 5.3 Nearest Distance The Subject Bird Approached The Stimulus Bird

TREATMENT	N	MEDIAN DISTANCE
Control (Opaque)	26	0.95m
Experimental (One-way and Two-way)	58	0.60m

Using A Kruskall-Wallis Test H=0.4; D.F.=1; NS

There was no significant difference in the nearest distance the subject bird moved from its original position in the control treatment ie. opaque partition, compared to the experimental treatment ie. one-way and two-way partitions. This was the initial comparison tested and, since the subject bird did not differ in the distance it approached when it could and could not see the stimulus bird, I did not proceed to test whether the nearest distance differed when the stimulus bird could and could not see the subject bird (one-way partition compared to two-way partition).

There were marked differences between subject birds in how long they remained near the stimulus bird. It was possible for a bird to approach to within 10cm of the stimulus bird, but to actually spend 90% of its time at the opposite end of the runway. In these situations the nearest distance was not a reflection of the time spent by the subject bird near the stimulus bird. Consequently, the mean of the nearest ten positions for each subject bird in

each treatment was calculated as a more realistic measure of the time spent near the stimulus bird.

As in the previous comparison of nearest distance, the initial analysis compared the control and experimental treatments for the subject bird. A kruskall-Wallis Test was used as the data were not normally distributed. The results of theis test are presented in Table 5.4.

TABLE 5.4 Nearest Distances Each Subject Bird Approached The Stimulus Bird

TREATMENT	N	MEDIAN DISTANCE
Control (opaque)	26	1.14m
Experimental (one-way and two-way)	58	0.76m

There was no significant difference between the control and the experimental treatments (Kruskal-Wallis H=2.05; D.F.=1; NS). Nevertheless, the trend was for birds to approach more closely in the experimental situation, when they could see the stimulus bird than in the control situation in both of these analyses (Table 5.3 and Table 5.4).

2) Mean Distance

The 10s records of the subject bird's position in the runway were used to give the mean distance for each test. As in the previous analyses, it was decided initially to

compare the mean distances when the subject bird could and could not see the stimulus bird (opaque partition compared with one-way and two-way partitions combined). Only if this comparison was significant would I proceed to compare distances when the stimulus bird could and could not see (and so respond) to the subject bird (one-way and two-way partitions compared)

An Analysis Of Variance was appropriate on the distribution of mean distances in the runway. The results of the full analysis are presented in Table 5.6 and the means for each treatment are presented in Table 5.7.

TABLE 5.6 Analysis Of Variance Of Mean Distance Of The Subject Bird From The Stimulus Bird

VARIABLE	D.F.	F-VALUE
Individual	31	2.95 **
Treatment	1	4.018 *
Residual	51	Mean Square = 10.58

When this first comparison was carried out there was a significant difference between the treatments ($F=4.02$; $D.F.=1,51$; $P<0.05$) with subject birds being closer on average when they could see the stimulus bird compared to when they could not.

TABLE 5.7 Mean Distance Of The Subject Bird From The Stimulus Bird

TREATMENT	N	MEAN ± SE
Control (Opaque)	26	1.29 ± 0.07m
Experimental (one-way or two-way)	58	1.13 ± 0.04m

The mean distance in the runway was smaller when the subject bird could see the stimulus bird (one-way and two-way partitions) than when there was an opaque partition between them. The difference is in the same direction as the trend in nearest distances. However, when the analysis was repeated, separating the response to the one-way and the two-way partitions, there was no significant difference between the two partitions (Table 5.8).

TABLE 5.8 Mean Distance Of Subject Bird From Stimulus Bird

TREATMENT	N	MEAN ± SE
One-way partition	28	1.15 ± 0.06m
Two-way partition	30	1.12 ± 0.06m

3) Orientation

When the mean orientations of the individuals in the runway were compared in the same manner, there was no difference between the control and the experimental treatments (Tables 5.9 and 5.10).

TABLE 5.9 Analysis of Variance Of Mean Orientation Of Subject Bird

VARIABLE	D.F.	F-VALUE
Individual	31	1.43
Treatment	1	0.59
Residual	51	Mean square = 1.37

TABLE 5.10 Mean Orientation Of Subject Bird

TREATMENT	N	Mean ± SE
Control (opaque)	26	1.79 ± 0.24
Experimental (one-way and two-way)	58	1.57 ± 0.16

Nevertheless, the mean orientation (1.6 ± 0.22), when all treatments were combined , was significantly different ($P<0.01$) from the expected orientation. Since orientation was measured on a scale from 0.0 to 6.0, with no distinction made between orientating to the left or right the expected orientation would be 3.0. The birds were therefore orientating towards the end of the runway that housed the stimulus bird, regardless of whether or not they could see it. This implies they were aware of the stimulus bird by olfactory and auditory cues.

The mean orientation of subject birds at the different positions in the runway were compared. This was repeated separately for the three different partitions. There was

no consistent relationship between position in the runway and orientation of the subject bird for any of the partitions. That is to say, the subject bird did not orientate more or less towards the stimulus bird when it was closer to it than when it was further away, or differ in its orientation when the partition was opaque, one-way or two-way. This is not in line with the orientation results in Chapter 3 where there was a definate relationship between orientation and distance between the two birds. This may be due to the greater distances between the birds in this experiment and the less detailed method used to record body orientation.

5:4 CONCLUSIONS

The difference in the mean distance of the subject bird in the control situation compared to the experimental, indicates that the subject bird adjusted its behaviour when it could see the stimulus bird at the end of the runway. The lack of a significant difference in the nearest position of the bird in the runway in the two conditions is more difficult to explain. It is known that spacing is non-random when birds can see each other, consequently, no difference between the experimental and the control conditions in all the measures would have indicated that this apparatus (with a partition between the two birds) inhibited normal spacing behaviour. This

was not the case as there were differences in the mean position of the test bird in the experimental and control conditions. It appears, therefore, that under these conditions the distance an individual chooses to position itself from another (on average) is a better representation of what happens in the natural situation than than the nearest or minimum distance between individuals. It is also consistent with other workers who have failed to find any way of measuring the so-called critical interindividual distance.

The fact that there was no difference in the mean position of the bird with the one-way partition compared to the two-way partition indicates that the spacing behaviour of the test bird was not affected by whether or not the stimulus bird could see it. The two obvious interpretations of this are either:

(a) the stimulus bird did not change its behaviour when it could see the subject bird compared to when it could not, or

(b) that any change in the behaviour of the stimulus bird did not influence the position of the subject bird in the runway.

The stimulus bird had the same characteristics (ie non goal directed signals such as body size, sex and location) in the two different treatments. One would expect, at least, some subtle change in the behaviour of the stimulus

bird when it could compared to when it could not see the subject bird, especially as there was a change in the behaviour of the subject bird between the control and the experimental treatments. However, even if the stimulus bird did show subtle changes in its behaviour, the change did not influence the position of the subject bird. It is unlikely that goal directed signals to influence spacing behaviour would have evolved if they were ignored. Therefore, one can conclude from this experiment, that birds control their own distances from conspecifics not that their positions are controlled by others.

These birds were familiar, consequently the subject bird could have based its distance from the stimulus bird on the basis of its previous experience of the that bird in the home cage. Spacing between unfamilar birds is more likely to involve one bird comtrolling the position of another by aggression. Nevertheless, this experiment suggests that once a stable relationship between birds is established, each bird positions itself with the respect to the other.

CHAPTER 6

GENERAL DISCUSSION

The topic of this thesis "Social Spacing in Domestic Fowl" could have been interpreted in many different ways and so have led to a variety of research projects. Starting with the knowledge that domestic fowl distribute themselves non-randomly in an area, I have tried throughout the course of this work to put forward, and then test, reasons as to how and why this might be. In Chapter 1, I summarised the various theories that have been proposed to account for observed spatial patterns, concentrating, because of the large amount of literature, on spacing between individuals of the same species and in the same social group.

The spatial patterns of social birds and fish are perhaps more obvious than those of most other animals, in that they show a clumped distribution when considered in the environment at large, but a regular pattern within each group. The regularity of spacing between group members can be very marked in some cases and it is probably this which has led, in the past, to an emphasis on spacing mechanisms based on the maintenance of so-called "critical" distances between individuals (Hediger,1941).

The most commonly quoted mechanism to account for the spatial patterns seen in flocking birds is that each

individual possesses a personal space around itself (McBride, 1971; Grubb, 1974; Crook, 1963). While this would agree with theories on spacing between humans beings (Hall, 1966; Sommer, 1969) all previous attempts, including the first experiment in this thesis, have been unsuccessful in determining the dimensions of the personal space in domestic fowl. It has been suggested that the dimensions of the personal space vary; for example, that it is larger in front of than behind the head and that it varies depending on the activity of the individual, and so on (McBride,1971). I would maintain, that if it is necessary to qualify personal space in such ways, then the term becomes almost meaningless having very little explanatory or predictive power.

If the only influence on spacing was the observance of minimum distances, then we should expect individuals at greater distances to be randomly distributed with repect to each other. Since this is clearly not the case in species which come together to form flocks, the term social distance has been coined to specify a so-called maximum distance between individuals. Between the minimum and the maximum distance is the living space (within which there are presumably no constraints). Difficulties arise when trying to measure the minimum or the maximum distance, and at best, it has only been possible to estimate a range of distances (Marler, 1956; Lill,1969).

Another criticism of the personal space theory is that it is based on the individual rather than the group. It confers the property of "personal space" to the individual whereas social spacing can only occur if there are two or more individuals present. At the very least then, the space between two animals must be a property of both individuals involved.

As a consequence of the above criticisms and the results of the trolley experiment (Chapter 2), I rejected the personal space hypothesis and concentrated on measuring freely occurring distances between pairs of individuals with a view to proposing an alternative hypothesis which could then be tested.

Consequently, in the next experiment (Chapter 3), I attempted to determine the appropriate distance by measuring the distances between birds as they moved freely in a pen. This was achieved by using overhead time-lapse photography. When the observed interindividual distances were compared, birds were found to be positioned further apart than expected in the small pen and closer together than expected in the large pen. This seemed to suggest that there were forces of repulsion keeping birds apart, but when there was sufficient space for the birds to spread out, forces of attraction became apparent. This led to the idea of a spacing hypothesis based on a balance of attraction and repulsion between individuals. This spacing hypothesis is not new and has been proposed previously by Schneirla (1959), Wiley and Hartnett (1980), Zajonc (1969) and Kummer (1969).

I have used the words force of attraction and force of repulsion throughout this thesis only for want of better terms. I have not specified whether there is a single force of attraction and another of repulsion or whether there are many forces acting together in a single direction. However, in order to simplify matters, single vectors are used to represent attraction and repulsion in the diagrams. In fact, it would probably prove very difficult to produce any accurate representation of the two forces, since they can never be measured separately. At best, it may be possible to measure the combined strength of the response (attraction + repulsion) of a bird to a conspecific, using an experimental design similar to that of Brown (1942,1948)).

Brown's experiment is described in detail in Chapter 5. In order to use his methodology to investigate attraction and repulsion between birds rather than towards food or an electric shock, it would be necessary to measure how hard a bird will work to approach or to avoid a conspecific at different distances from the stimulus bird. The interindividual distance at which it will neither work to approach nor work to withdraw from its position would represent the equilibrium point between attraction and repulsion and would be the appropriate interindividual distance. It is arguable, nevertheless, whether the appropriate interindividual distance under these artificial conditions would bear any relevance to normal

spacing behaviour and so this line of research was not pursued.

In addition to using straight lines to represent attraction and repulsion, I have also shown the range of interindividual distances to be distributed symmetrically around the equilibrium interindividual distance. This is partly because if attraction and repulsion are linear then the distribution of distances will be symmetrical. In the experiments which measured interindividual distances (Chapters 3 and 4), the distribution was either symmetrical or slightly skewed towards larger distances. This was particularly true in the walled garden and may have been due the the large size of the enclosure, although it may also indicate some curvature of the lines representing attraction and repulsion. Nevertheless, since the shape of the lines is largely conjecture at this stage it was decided to keep the diagrams as simple as possible.

A balance between attraction and repulsion has been proposed to explain spacing patterns in many different species. The hypothesis developed in this chapter, however, can only be applied at the moment to small groups of laying hens in a limited range of contexts. Spacing between parents and offspring or between males and females are not discussed.

6:2 ATTRACTION - REPULSION HYPOTHESIS

The hypothesis is based on the probability of individuals positioning themselves at certain interindividual distances. Since the two forces influencing interindividual distances are balanced at the equilibrium distance, individuals are most likely to be this distance apart (Figure 6.1). This does not exclude the possibility that individuals will be found closer together than the stated distance, but since repulsion will be stronger than attraction, these distances are less likely. Neither does it exclude the possibility that individuals will be found further apart than the stated distance. At these distances attraction between the individuals will be stronger than repulsion so again they will occur less frequently. The model of spacing that I am proposing is therefore a stochastic model.

By definition at least two individuals are required before social spacing can be studied. But for simplification, I have represented only one half of that relationship in Figure 6.1; that is to say, only the attraction and repulsion of one bird of the pair towards the other. Of course it is appreciated that this effect will work in both directions and the so-called stimulus bird will also be attracted and repelled by the subject bird. This point is discussed later.

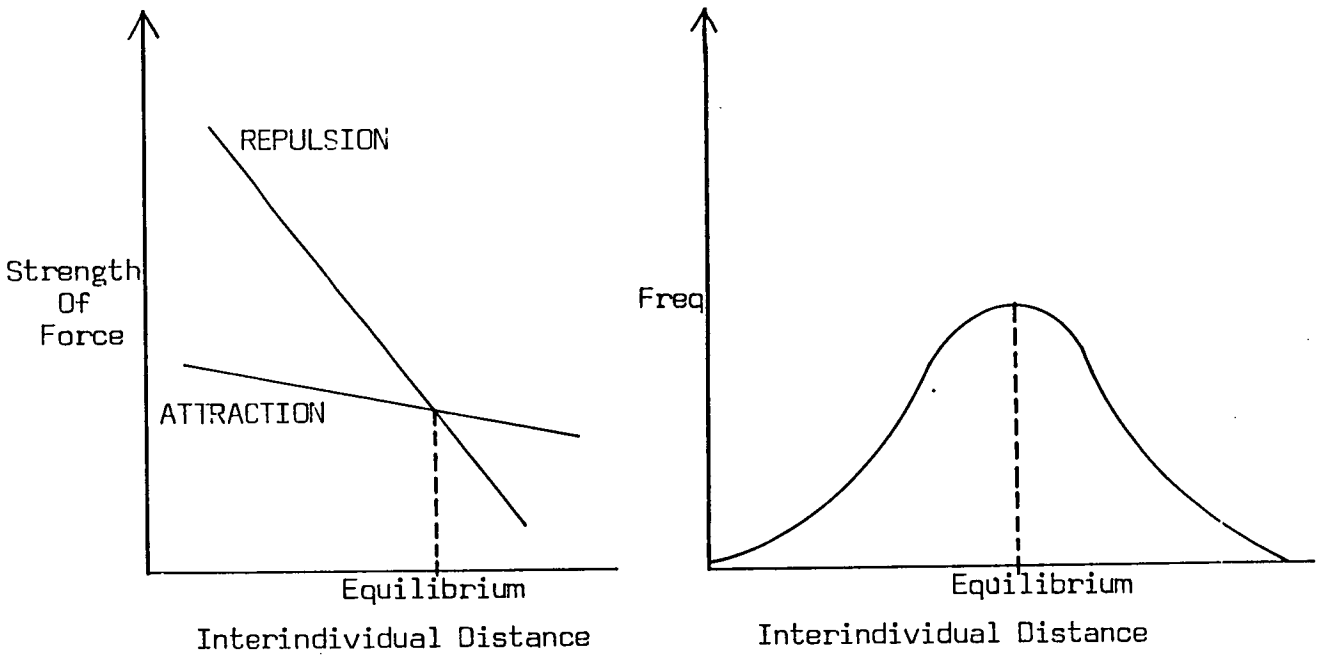


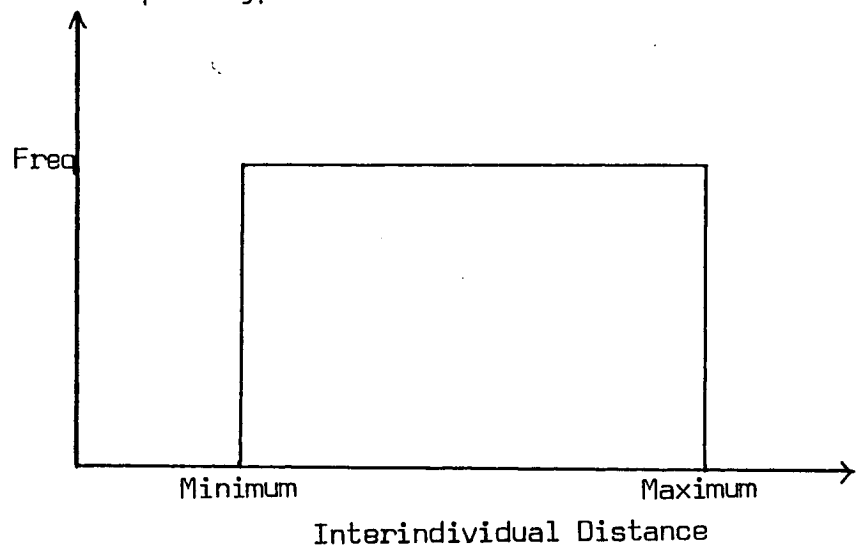
FIGURE 6.1 Distribution Of Equilibrium Interindividual Distances About The Mean

According to this model, repulsion will be so much stronger than attraction at small distances that the probability of observing individuals in very close proximity will be negligible. Likewise, the probability of observing very large interindividual distances will also be extremely small as attraction will be so much stronger than repulsion. This will result in areas around individuals which are not used by others and a distance beyond which individuals will not move away from the other group members. The difference between the personal space hypothesis and the attraction-repulsion hypothesis to explain the observed distribution is, in the former case, the so-called minimum and maximum interindividual distances determine the distribution (figure 6.2a) whereas, in the latter case, the interindividual distances will be distributed around the equilibrium distance (Figure 6.2b). The minimum and maximum interindividual distances according to the attraction-repulsion hypothesis represent the extremes of the distribution of interindividual distances. They do not determine the distribution.

6:3 VARIATATION IN ATTRACTION AND REPULSION TO ACCOUNT FOR THE VARIATION IN INTERINDIVIDUAL DISTANCE

As stated previously (6:1), it is not possible to specify the actual slopes of the lines representing attraction and repulsion. But, their slopes relative to each other will influence the distribution of particular interindividual

1) Expected Distribution Of Distances From The Personal Space Hypothesis



2) Expected Distribution Of Distances From The Attraction-Repulsion Hypothesis

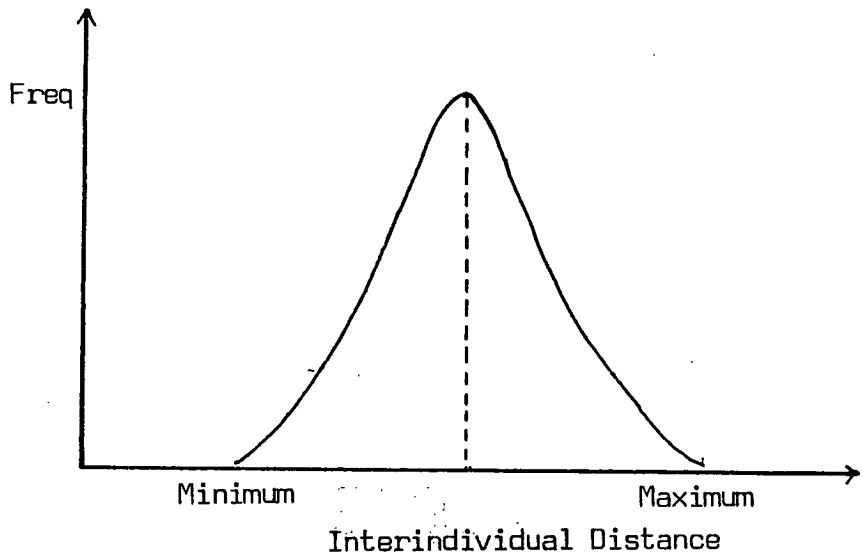


FIGURE 6.2 Expected Distributions Of Interindividual Distances According To The Personal Space And The Attraction-Repulsion Hypotheses

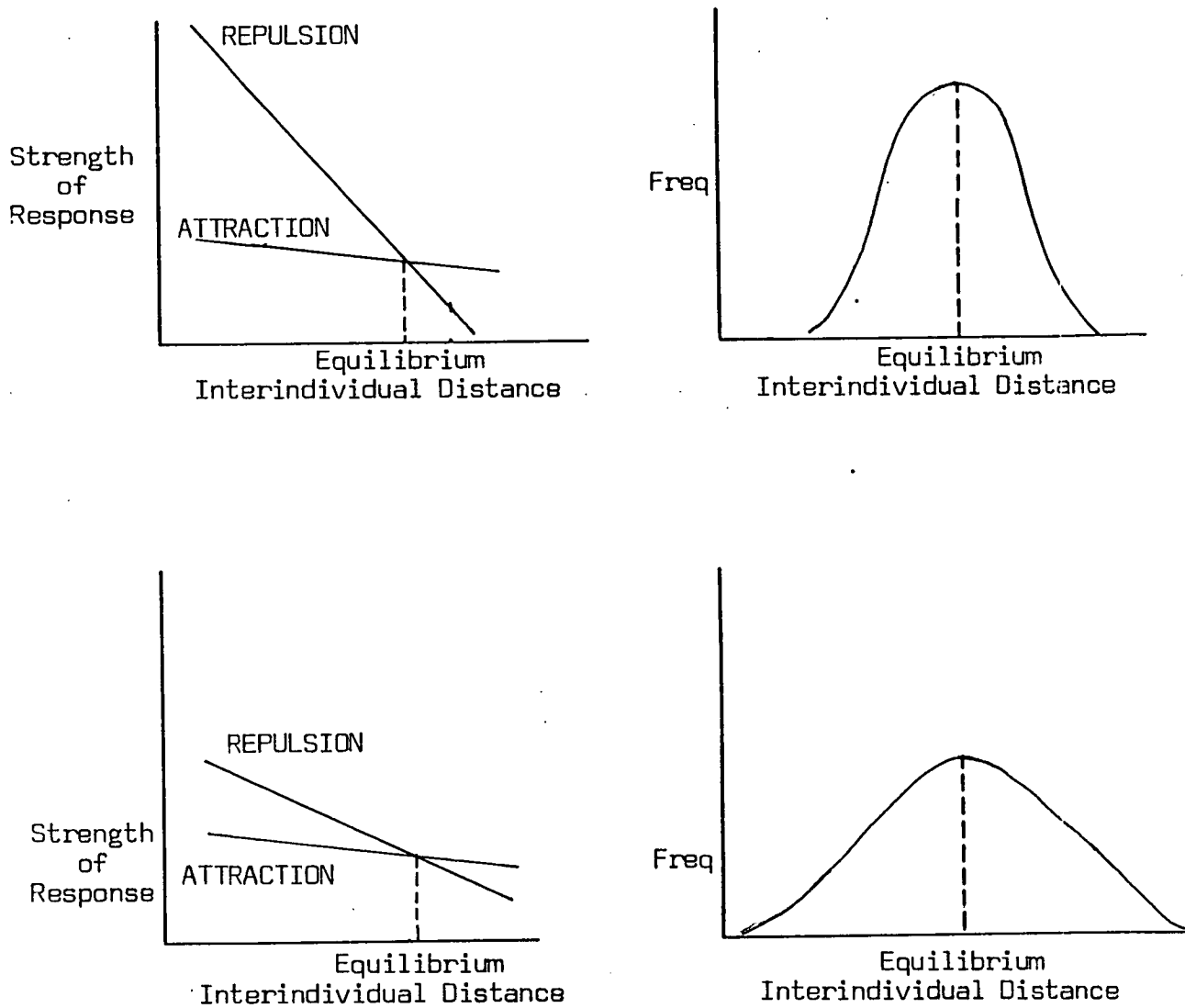


FIGURE 6.3 Variation About The Equilibrium Distance Related To The Slopes Of The Forces Of Attraction And Repulsion

distances (Figure 6.3). For simplification, this figure again only represents one half of the spacing relationship between the two birds. When the slopes are very different (i), then the range of interindividual distances around the equilibrium distance will be small. This is because even at distances only slightly away from the equilibrium, either repulsion will be much stronger than attraction, or attraction will be much stronger than repulsion. However, when the slopes are similar (ii), a wide range of interindividual distances are possible as the difference between the forces of attraction and repulsion will be small.

In the experiment using overhead photography (Chapter 3) and the first experiment in the walled garden (Chapter 4), it was possible to identify factors such as total space available (3:3:2), activity (4:3 and 4:7), orientation towards other birds (3:3:4) and position of the individual in the social hierarchy (3:3:2) which were important in influencing interindividual distance. Since the mean observed distance between individuals (equilibrium distance) was influenced by these factors then the relative strengths of the forces of attraction and repulsion must also have been affected. Possible reasons as to why individuals should be regarded as more attractive or aversive on some occasions than on others are discussed in the two chapters. The difference in the size of the variation about the mean for some activity

combinations compared to others is also indicative of differences in the relative slopes of the lines representing attraction and repulsion (4:7).

In these two experiments (chapter 3 and Chapter 4, Expt. 1), the appropriate distance between individuals was derived from a series of instantaneous, independent observations of interindividual distances. However, this does not represent the true situation as spacing is a dynamic process. A mechanism of spacing behaviour, based on maintaining a balance between the tendency to approach and the tendency to withdraw, is only credible if it is consistent with the observed movements of birds either towards or away from each other. The second experiment in the walled garden (Chapter 4, Expt.2) aimed to investigate these movements by recording interindividual distances, but using much shorter time intervals between instantaneous samples, so that the observations were dependent rather than independent of each other.

The results of the first experiment in the walled garden (4:3) suggested that the relative strengths of the forces of attraction, and hence the equilibrium point between them, varied according to the activities of the birds. The results of the second experiment in the walled garden (4:7) demonstrated a close association between changes in activity and changes in interindividual distance. This would be expected if birds adjusted their positions in an attempt to maintain appropriate interindividual distances.

The adjustment is necessary because what the birds' perceive as appropriate changes everytime there is a change in activity.

The association between activity transitions and changes in interindividual distances could have arisen from birds adjusting their spacing to suit their behaviour or birds adjusting their behaviour to suit their spacing. I would propose that given adequate space birds adjust their spacing to suit their behaviour. Although, of course, appropriate spacing behaviour will depend on other factors in addition to behaviour eg risk of predation and position in the social hierarchy. There will be some occasions when birds modify their behaviour to suit their spacing. Examples of this would be courtship behaviour by the male to reduce aggression in the female before he approaches to mate (Bastock,1967), or where a subordinate adopts a submissive posture in the presence of a higher ranking bird in order to remain where it is when it is approached (Syme and Syme, 1979). Nevertheless, I propose that in the majority of cases birds adjust their spacing to suit their behaviour.

A relationship was also demonstrated between orientation and interindividual distance (3:3:4). In this case, it seems more likely that distance influences orientation than that orientation influences distance. Consequently, a chain of effects may occur with, for example, the birds'

activity influencing spacing and spacing influencing orientation.

In order to discuss the results of the second walled garden experiment in the light of the proposed model, it will be assumed that the activity of the individuals determines the distance between them. Whether or not the birds approach or withdraw from each other for each activity transition, will depend on the probability of the original interindividual distance occurring under the new set of circumstances. Figure 6.3 represents two extremes of a continuum where there can be either (i) a narrow range or (ii) a wide range of interindividual distances around the equilibrium distance. Consequently, when there is a change in activity there will be a change from one distribution of interindividual distances to another. Taking the two extreme distributions (i and ii) for simplicity, there are three possibile combinations (Figure 6.4). These are:

(a) When there is a narrow range of interindividual distances (Figure 6.4a), the probability that the original interindividual distance will occur in the new range of interindividual distances is low. One would therefore predict an adjustment in the distance between the individuals.

(b) When there is a wide range of interindividual distances (Figure 6.4b), then the probabilty that the original interindividual distance will occur under the new

KEY

e_1 - Original equilibrium distance

e_2 - New equilibrium distance

- Probability of an original interindividual distance occurring under the new range of interindividual distances is equal to:

$$\frac{\text{The Area Of Overlap}}{\text{Area Of The Original Distribution}} \quad (1/1A)$$

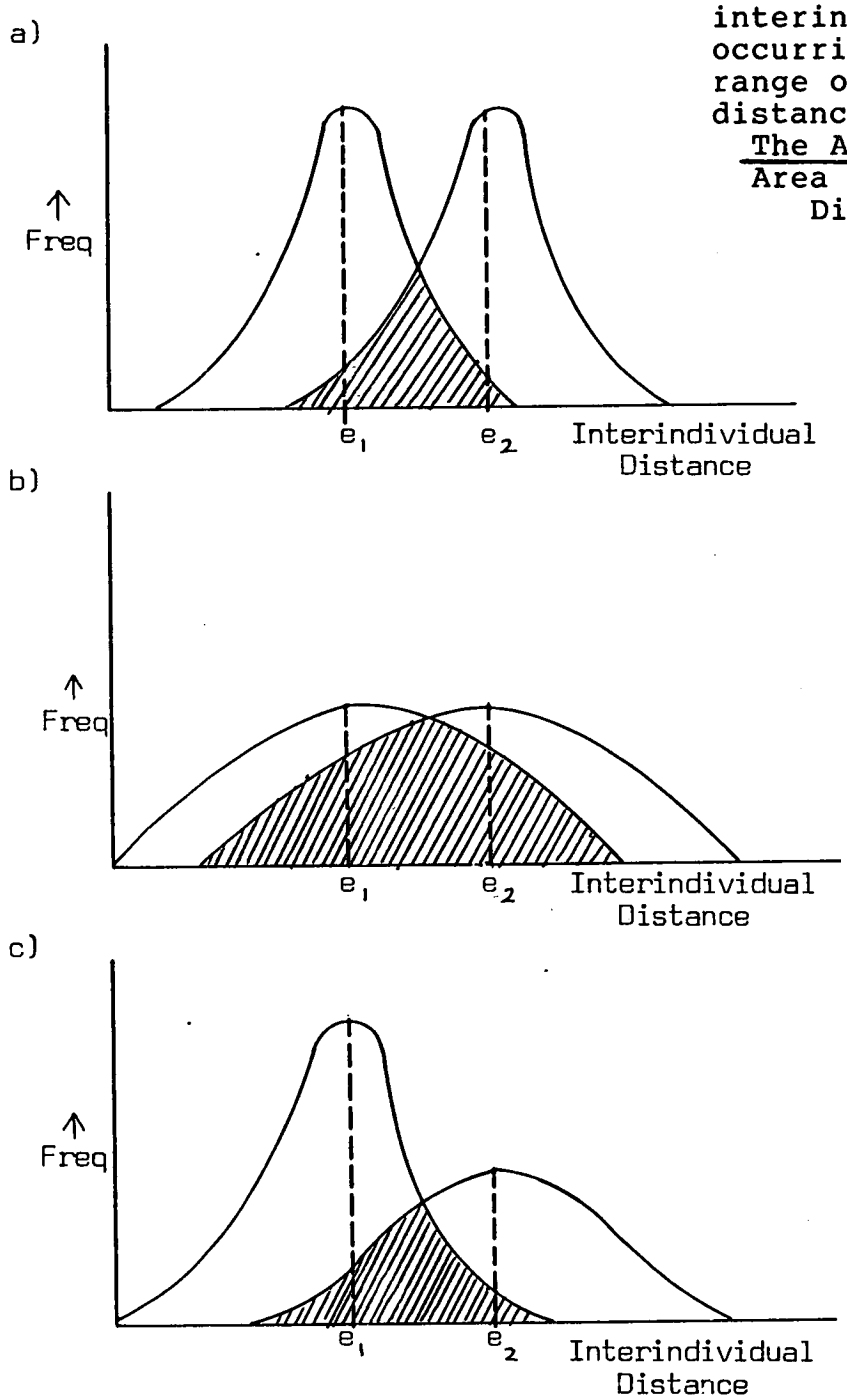


FIGURE 6.4 Probability Of A Change In Interindividual Distance Associated With A Change In Equilibrium Distance

range of distances is high. In this case there may not be a change in interindividual distance. In fact, when the new equilibrium distance is only slightly different from the original there is even a possibilty that the change in distance will be in the opposite direction to that predicted.

(c) The third situation (Figure 6.4c), when there is a difference in the range of interindividual distances around the mean in the two situations will occur most frequently. In this situation, the probability of an adjustment in interindividual distance is intermediate between the two examples listed above.

These predictions could be tested by determining the mean distance between a pair of birds and the variation about the mean for each activity combination. It would then be possible to calculate P_1 (the probability of the original interindividual distance occurring after an activity transition). Under these same experimental conditions, the birds could then be observed to see if the actual probability of a change in distance was the same as that predicted. In addition, as in example (b) (Figure 6.4b), the observed and expected probabilities of a change in interindividual distance which was in the opposite direction to that predicted could also be compared.

The only data of a suitable format to test this hypothesis was that from the walled garden (Chapter 4, Expt. 2). Since this experiment consisted of only one group of

birds, both the predicted and the observed data would have been derived from the same data set. Unfortunately, therefore, there was no opportunity to test this hypothesis further.

When an adjustment in interindividual distance is observed, there is a problem in deciding which individual is responsible for the adjustment. The runway experiment in Chapter 5 suggested, at least in these artificial conditions, that a bird is neither inhibited from approaching nor encouraged to approach by signals from a familiar conspecifc. This implies that in free moving groups, each individual is attempting to position itself in relation to others. It seems likely that the number of individuals to which it pays attention will be limited to those in its immediate vicinity, perhaps the first and second nearest neighbours or to a socially important bird. Whereas individuals may position themselves simultaneously, there is no evidence that they act mutually.

The simplest spacing situation is between a pair of birds. In this case, each bird will be attempting to position itself at what it perceives as an appropriate distance. If the perceived appropriate distances are similar for both individuals, a stable interindividual distance will result. However, if they are not similar, an unstable situation could arise with one individual continually approaching and the other continually withdrawing.

In Figure 6.4, the probability of an approach or withdrawal, for a particular activity transition, depends upon the range of interindividual distances around the equilibrium point for the original activity, and the range of interindividual distances around the equilibrium point for the new activity. The probability of the distance between two individuals being stable (or of it being unstable) can be represented diagramatically in a similar manner. Figure 6.5 demonstrates the range of appropriate distances for one individual and the range of appropriate distances for the second individual. This figure unlike previously, therefore, refers to both birds of a pair. The probability of a mutually appropriate interindividual distance will depend on the size of the overlap between the two distributions. In Figure 6.5a, the overlap between the two distributions is small, so there is only a low probability of a mutually appropriate interindividual distance. In Figure 6.5b, however, the overlap between the two distributions is large and so there is a high probability of a mutually appropriate interindividual distance. There may even be the possibility for an individual, unable to achieve the interindividual distance it 'perceives as appropriate' to change it activity and thereby its appropriate interindividual to one which is mutually appropriate. This emphasizes the circularity between whether spacing influences behaviour or behaviour influences spacing.

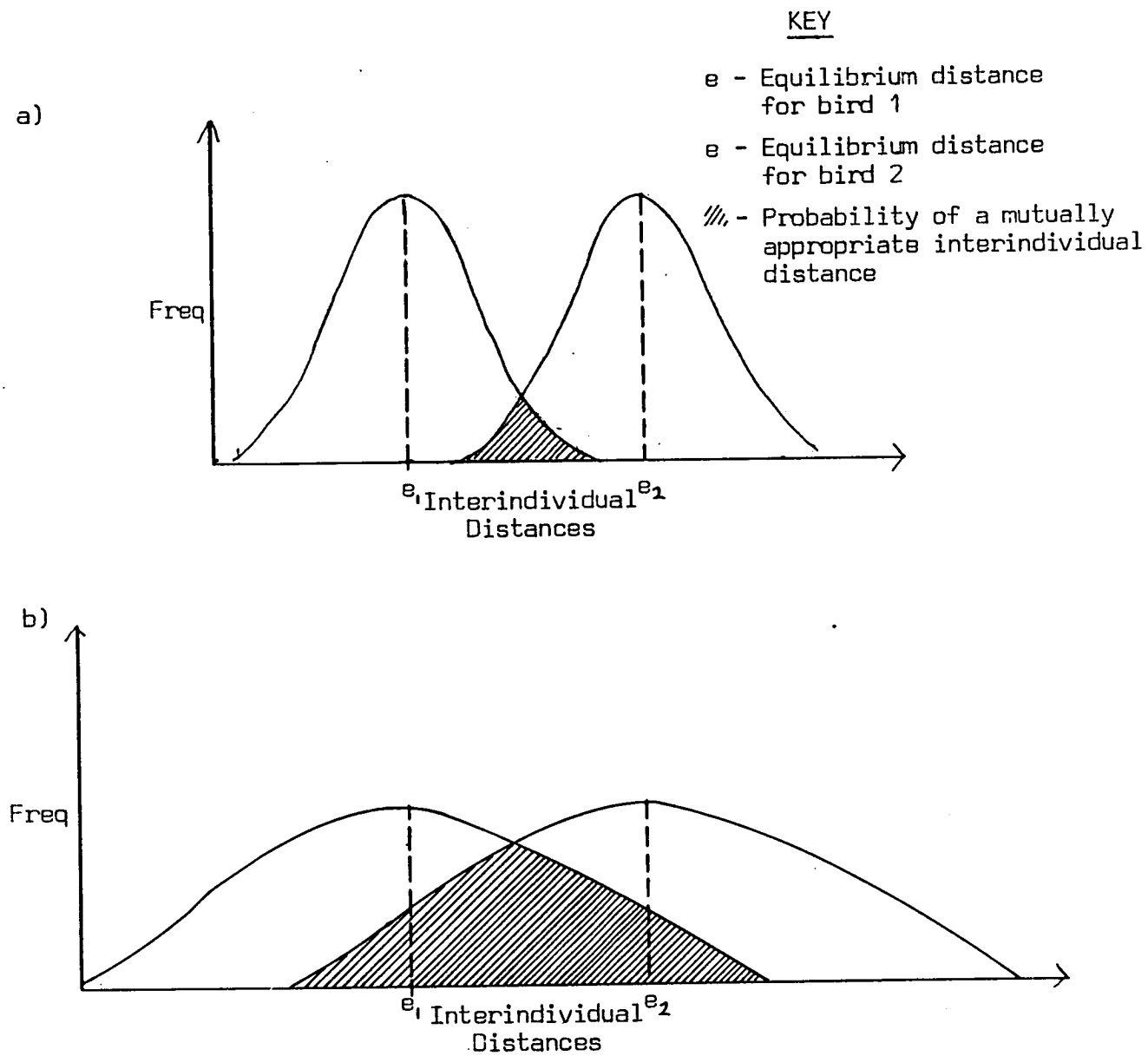


FIGURE 6.5 Probability Of A Mutually Appropriate Interindividual Distance Between The Two Birds

A possible way of predicting whether or not there will be a change in distance associated with an activity transition was demonstrated in Figure 6.4. It is more problematic to predict whether or not a mutually acceptable interindividual distance will occur. The difficulty arises in trying to measure the range of interindividual distances which are appropriate for one bird of a pair, independently from the range of interindividual distances which are appropriate for the other bird of the pair. Only when this has been achieved can the overlap be calculated. Nevertheless, variation between birds in what they perceive to be an appropriate interindividual distances for a given set of circumstances is likely to be the main variable affecting observed interindividual distances. Individual differences were found to be significant in all the experiments where individuals were included (as a variable) in the analyses.

6:4 ASSESSING SPATIAL REQUIREMENTS

In Chapter 1, I discussed ways of assessing the spatial requirements of domestic fowl. While this thesis investigated spacing behaviour per se rather than birds' requirements for space, the findings do have some relevance to this more applied question.

(a) If we can determine the appropriate or preferred distances between birds, we should be able to calculate the size of enclosure which would allow the birds to

achieve these distances. This method has been proposed by Innis, Balph and Balph (1985). They calculated the pen size that would allow all individuals to achieve their preferred distance from all other group members.

If the pen size was calculated so that individuals could only achieve their appropriate distances when they were maximally spaced, then no individual would be able to move from its position except by approaching another individual closer than the preferred distance. If, however, the pen size was calculated so that the random distance between individuals in the pen was equal to their preferred distance, then by chance nearest neighbours will be the preferred distance apart.

Nevertheless, it has been shown (Chapter 4) that the distances between birds vary according to their activity. Consequently, there is no single preferred interindividual distance, as suggested by Innis et al (1985), upon which to base the calculations of pen size. It may be possible to select the activity which "requires the most space" (ie. has the largest mean interindividual distance) and calculate how much space would be required for all individuals to perform this activity at the same time. This is fraught with the difficulties discussed earlier (6:3), for instance whether the activity determines the space required or the space available determines which activity will be performed. A question pertinent to this of whether " to adapt the environment to the bird or the

bird to the environment" was discussed by Faure (1980). Nevertheless, I have chosen to take the view that behaviour is most likely to influence spacing.

Calculations of pen size could be based on mean values of interindividual distance for a particular activity or, at some specified interindividual distance greater than the mean eg. the upper quartile or one standard deviation above the mean. These values would give a more generous space allowance than those based on the mean interindividual distance. However, even this method is circular, since the mean distance between individuals is also influenced by pen size (Chapter 3).

(b) The second method that could be used to assess spatial requirements is based on the experimental method in Chapter 3. In the small pen, the observed distances between individuals were (on average) greater than expected by chance. It could therefore be suggested that the small pen was not big enough as the birds were trying to get away from each other. In the large pen, the distances between individuals were (on average) smaller than expected by chance. It could therefore be suggested that the large pen was unnecessarily big, as it not only allowed the birds to get away from each other, it allowed their gregarious nature to be expressed and for them to appear to cluster together. In between these so-called extremes, there will be a pen size in which the birds neither try to get away from each other nor appear to be

clustering together. At this pen size the mean observed distance between individuals will be the same as that expected from a random distribution. This could perhaps be regarded as a compromise pen size between apparent overcrowding and inefficient use of pen space.

Figure 6.6 demonstrates the anticipated relationship between observed and expected interindividual distances in different sized pens. If the group size remains constant then the expected interindividual distances will increase in a linear fashion as pen size increases (D.Sales, per. comm.). In experiments which actually used a series of different sized battery cages, observed interindividual distances were found to increase with increasing area per bird only up to a certain level. Beyond this point no further increase in interindividual distance was observed (Doyen and Zayan,1984a). The results of the photography experiment (Chapter 3) are consistent with this anticipated relationship, since in the small pen observed interindividual distances were greater than expected and in the large pen observed interindividual distances were less than expected.

It is not possible, however, to extrapolate from my results to suggest a compromise pen size for commercial use because the conditions were different. Food and water were removed from the pens in the photography experiment so that the available area would be as uniform as possible. In this situation, it would be expected that the

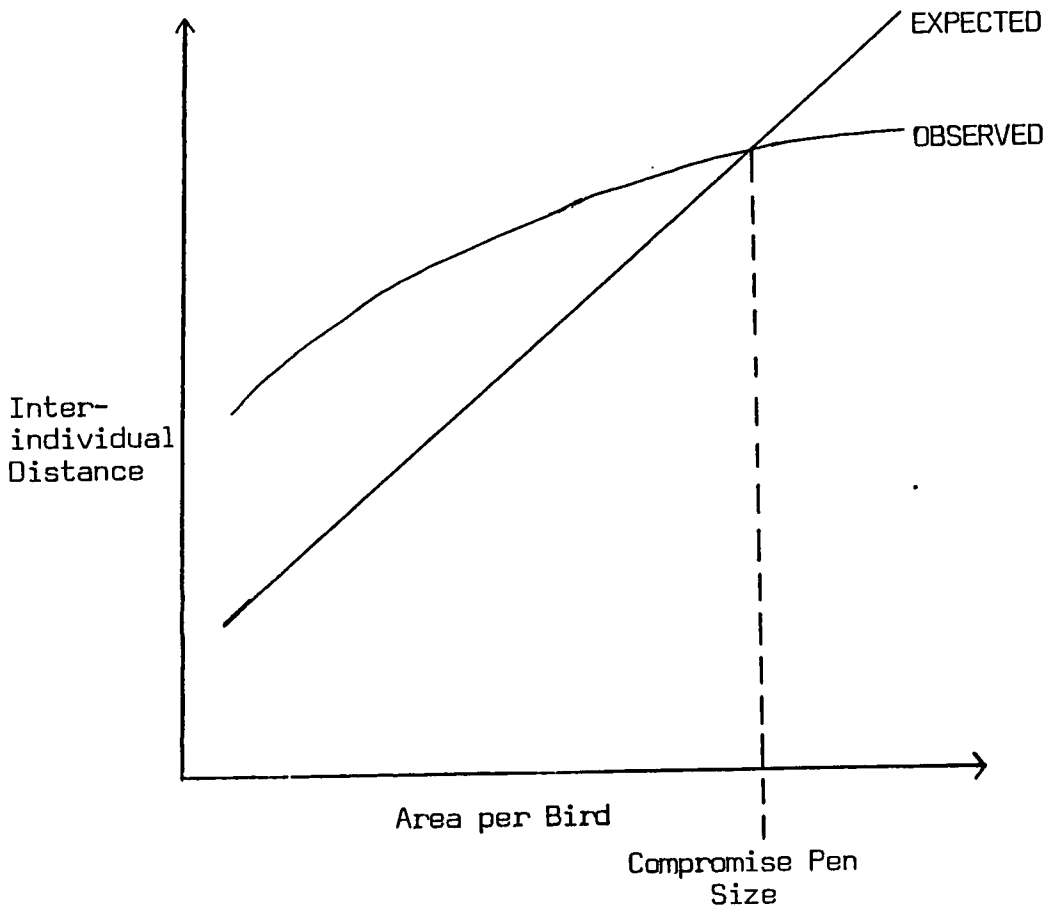


FIGURE 6.6 The Relationship Between Observed And Expected Interindividual Distances When All Factors Other Than Area Per Bird Remain Constant

birds were positioning themselves with respect to the other bird in the group and also to the sides of the pen. If the area contained various features such as food and water troughs, nest boxes and perches, then the distribution of these resources would also influence the spatial distribution of birds in the pen (Banks et al,1979).

The theoretical relationship between nearest neighbour distances in pens of different shapes (square, round and triangular) and of different group sizes (2,3,4 and 5 members) have been discussed by Stricklin, Graves and Wilson (1979). Pen shape was found to influence mean distances. When area was kept constant, the triangular pen resulted in the greatest mean distance between randomly generated points. Triangular battery cages may not be practical as the corners would be too acute for the birds to use. But if achieving appropriate distances between birds, rather than the area per se available to each bird, is important in spacing behaviour (as I am suggesting in this thesis), then modifications in enclosure shape may be more effective in providing adequate social space than changing pen area.

If either method (a) or (b) was used to estimate how much space should be allocated to a group of birds, the results would only hold true for the specific set of circumstances in which they were measured. In addition,

the pen would only be an adequate size for a proportion of the time. Large interindividual distance may only be observed occasionally, yet it may be very important for the birds to be able to achieve these distances in certain circumstances. In this sense, both the above methods are generalizations in that they are based on the frequency of interindividual distances not on the importance of the distance to the birds.

In intensive husbandry conditions, individuals may be unable to withdraw from each other but they are unlikely to be restricted from approaching each other. A study of social spacing in domestic fowl concerned with assessing spatial requirments would, therefore, necessitate an investigation of the motivation of indivduals to withdraw from each other and so achieve large interindividual distances, not on the tendency of birds to approach each other. The motivation of birds to withdraw from each other may be greater, for example, after an aggressive encounter or just before oviposition. As discussed throughout this thesis, the motivation (or tendency) for one individual to withdraw from another still has components of attraction as well as repulsion. It may be possible to overcome the problem of allowing for occasional large interindividual distances be appropriate environmental design eg. by providing refuges where the other bird can not be seen. This has been shown to reduce aggression in pigs (McClone and Curtis,1981).

However, there is no doubt that the application of one of the above methods would lead to more appropriate recommendations for the space allowances of poultry than the arbitary figures in force at present.

REFERENCES

Al-Rawi,B. and Craig,J.V., (1975). Agonistic behaviour of caged chickens related to group size and area per bird. Appl.Anim.Ethol.2:69-80.

Appleby,M.C., (1985). Hawks, doves...and chickens. New.Sci.105(1438):16-18

Arnold,G.W. and Dudzinski,M.L., (1978). Ethology of Free-Ranging Domestic Animals. Elsevier.

Arnold,G.W. and Maller,R.A., (1985). An analysis of factors influencing spatial distribution in flocks of grazing sheep. Appl.Anim.Behav.Sci.14(2)173-189.

Atkins,P., (1981). Behavioural determinants of the nocturnal spacing pattern of the yellow tang. Pac.Sci.35(3):263-264.

Baerends,G.P., (1975). An evaluation of the conflict hypothesis as an explanatory principle for the evolution of displays. In: Functions And Evolution In Behaviour. (Ed) G.P.Baerends, C.Beer and A.Manning. pp. 187-228.

Banks,E.M., Wood-Gush,D.G.M., Hughes,B.O. and Mankovich,N,J., (1979). Social rank and priority of access to resources in domestic fowl. Behav. Proc.,4:197-209.

Barnard,C.J., (1983). Animal Behaviour: Ecology and Evolution. pp. 240-266. Croom Helm, London.

Bastock,M.A., (1967). Courtship A Zoological Study. Heinemann Education Books Ltd. London.

Baxter,M.R., and Schwaller,C.E., (1983). Space requirements for sows in confinement.In: Farm Animal Housing and Welfare. (Ed. S.H.Baxter, M.R. Baxter and J.A.C.MacCormack). CEC Seminar. Martinus Njhoff..Dordretch/Boston/Lancaster.

Beiswenger,R.E., (1975). Structure and function in aggregations of tadpoles of the American toad (Bufo americanus). Herpetologica 31:222-233.

Berkoff.M., and Corcoran,J., (1975). A method for the analysis of activity and spatial relations in animal groups. Behav. Res. Method. Instrum. 7(6):569

Bessei,W., (1982). (Ed). Disturbed Behaviour In Farm Animals. Verlag Eugen Ulmer. Stuttgart.

Bessei,W., (1985). Effects of stocking density on production and social behaviour in laying hens. In: Social Space For Domestic Animals. pp. 71-85. CEC Seminar. Martinus Njhoff. Dordrecht/Boston/Lancaster.

Bischoff,N., (1975). A systems approach towards the functional connections of attachment and fear. Child Dev.46:801-817.

Bogner, Von.H., Peschke,W., Seda,V., Popp,k., (1979). Investigation about the area covered by the laying hen. Brel.Munch.Tierarzh.Wachenschr.,92(17):340-343.

Brambell,F.W.R., (1965). Report of the Technical Committee To Enquire Into The Welfare Of Animals Kept Under Intensive Husbandry systems. Command Paper 2836, H.M.S.O., London.

Breder,C.M., (1954). Equations descriptive of fish schools and other animal aggregations. Ecology 35(3):361-370.

Breder,F., Lum,A. and Wassersug,R., (1982). Body size and orientation in aggregates of toad tadpoles (Bufo woodhousei). Copeia (3):672-680.

Broom,D., (1981). Biology of Behaviour. Vail-Ballou Press.

Brown,J.L., (1964). The evolution of diversity in avian territorial systems. Wilson Bulletin,76(2):160-169.

Brown,J.S., (1942). The generalization of approach responses as a function of stimulus intensity and strength of motivation. J.Comp.Pychol.,33:209-226

Brown,J.S., (1948). Gradients of approach responses and their relation to level of motivation. J.Comp.Physiol.,41:450-465.

Brown,J.L. and Orians,G.H., (1970). Spacing in mobile animals. Ann.Rev.Ecol.Syst.,1;239-262.

Burgess,W.J., (1979). Measurement of spatial behaviour: methodology applied to rhesus monkeys, neon tetras, commumal and solitary spiders, cockroaches and knats in open fields. Behav. and Neural Biol.26:132-160.

Candland,D.K., Taylor,D.B., Dresdale,L., Leiphart,J.M. and Solow,S.P., (1969). Heart rate, aggression, and dominance in the domestic chicken. J.Comp.Physiol.Psychol.69(1):70-76.

Candland,D.K., Bryan,D.C., Nazar,B.L., Kope,K.J. and Sendor,M., (1970). Squirrel monkey heart rate during formation of status orders. J.Comp.Physiol.Psychol. 70(3):417-423.

Cherkovich,G.M. and Tatoyan,S.K., (1973). Heart rate (radiotelemetrical registration) in macaques and Baboons according to dominant-submissive rank in a group. Folia Prim.20:265-273.

Clark,P.J., and Evans,F.C., (1954). Distance to nearest neighbour as a measure of spatial relationships in populations. Ecol.,35:445-453.

Conder,J.P., (1949). Individual distance. Ibis 91:649-655.

Coss,R.G. and Burgess,W.T., (1981). Jewel fish retain juvenile schooling pattern after crowded development. Dev.Psychobiol.14(5):451-457.

Craig,J.V. and Bhagwat,A.L., (1974). Agonistic and mating

behaviour of adult chickens modified by social and physical environments. Appl.Anim.Ethol.1:57-65.

Crofton,H.D., (1958). Nematode parasite populations in sheep in lowland farms. VI. Sheep behaviour and nematode infections. Parasitology 48:251-260.

Crook,J.R., (1963). Thr basis of flock organization in birds. In: Currents Problems In Animal Behaviour. (Ed) W.H.Thorpe and O.L.Zangwill. pp. 125-149. Cambridge Univ Press.

Dantzer,R. and Mormede,P., (1981). Can physiological criteria be used to assess welfare in pigs? In: The Welfare of Pigs (Ed) W.Sybesma. pp.53-73. CEC Seminar. Martinus Njhoff. The Hague.

Dantzer,R. and Raab,A., (1985). On the interpretation and significance of behavioural and physiological indicators of stress related to social space in domestic animals. In: Social Space For Domestic Animals (Ed) R.Zayan. pp. 3-15. CEC Seminar. Martinus Nijhoff. Dordretcht/Boston/Lancaster.

Dawkins,M., (1980). Animal Suffering: The Science of Animal Welfare. Chapman and Hall. London.

Dawkins,M., (1981). Priorities in cage size and flooring preferences of domestic hens. Bri.Poult.Sci.22:255-263.

Dawkins.M., (1982). Elusive concept of preferred group size in domestic hens. Appl.Anim.Ethol.8:365-375.

Dawkin,M.S., (1985). Cage height preference and use in battery-kept hens. Br.Poult.Sci.24:177-182.

Dawkins,M.S., (1986). Unravelling Animal Behaviour. Longman.

Deag,J.M., (1980). Social Behaviour of Animals. Studies In Biology No.118. Edward Arnold, London.

Desor,J.A., (1972). Towards a psychological theory of crowding. J.Pers.Soc.Psychol.21(1):79-83.

Doyen,J. and Zayan,R., (1984a). Measures of space in pairs of hens in battery cages. Behav.Proc.9:157-170.

Doyen,J. and Zayan,R., (1984b). Observations on pushing and aggression in pairs of hens in battery cages. Behav.Proc.9:171-180.

Duncan,I.J.H., (1978). The interprtation of preference tests in animal behaviour. Appl.Anim.Ethol.4:197-200. (Letter to editor).

Duncan,I.J.H., (1981). Animal rights - Animal welfare: A scientist's assessment. Poult.Sci.60(3):489-499.

Duncan,I.J.H., (1982). Behavioural and physiological indices of stress. Paper presented at XXIV British Poultry Breeders' Round Table, Edinburgh.

Duncan,I.J.H. and Filshie,J.H., (1979). The use of radio telemetry devices to measure temperature and heart rate in domestic fowl. In: A Handbook on Biotelemetry and Radio Tracking. (Ed) C.J.Amlaner and D.W.MacDonald. pp. 570-588. Pergamon Press.

Duncan,I.J.H., Slee,G.S., Kettlewell,P., Berry,P. and Carlisle,A.J., (1986). Comparison of the stressfulness of harvesting broiler chickens by machine and by hand. Br.Poult.Sci.27:109-114.

Duncan,I.J.H., and Wood-Gush,D.G.M., (1971). Frustration and aggression in the domestic fowl. Anim.Behav.,19:500-504.

Economic European Community, (1986). The Welfare Of Laying Hens In Battery Cages. Great Britain European Community Directive 86/113/EEC.

Elmslie,L.J.,Jones,R.H., and Knight,D.W., (1966), A general theory describing the effects of varying flock size. 13th Wld's Poult. Cong., Kiev:490-495.

Everitt,B.S., (1977). The Analysis Of Contingency Tables. Chapman and Hall. London.

Faure,J.M., (1980). To adapt the environment to the bird or the bird to the environment. In: The Laying Hen And Its Environment. (Ed). R.Moss. pp. 19-42. CEC Seminar. Martinus Njhoff. Dordrecht/Boston/Lancaster.

Faure,J.M., (1985). Social space in small groups of laying hens. In: Social Space For Domestic Animals (Ed) R.Zayan. pp 99-110. CEC Seminar. Martinus Nijhoff. Dordretch/Boston/Lancaster.

Faure,J.M. and Jones,R.B., (1982). Effects of age, access and time of day on perching behaviour in the domestic fowl. Appl.Anim.Ethol.8:357-364.

Filshie,J.H., Duncan,I.J.H. and Clark,J.S.B., (1980). Radiotelemtry of avian electrocardiogram. Med.Biol.Eng.Comput.18:633-637.

Freeman,B.M., (1983), Floor space allowances for the caged domestic fowl. Vet. Rec.112:562-563.

Fuchs,S., (1980). Spacing patterns in a colony of guinea pigs: predictability from the environmental and social factors. Behav.Ecol.Sociobiol.6:265-276.

Gartlan,H.R., (1964). Dominance in East African Monkeys. Proc.E.A.Afr.Acad.Vol.2:75-79.

Goss-Custard,J.D., (1970). Feeding dispersion in some overwintering wading birds. In: Social Behaviour In Birds and Mammmals. (Ed) J.H.Crook. pp. 3-34.

Grubb,T.C., (1974). Individual distance in the herring gull. Auk 91(3):637-639.

Hall,E.T., (1966). The Hidden Dimension. Doubleday, Garden

City, New York.

Hall,R. (1972). Wild horses: Biology And Alternatives For Management. U.S.D.I. Bureau of Land Management, Billlings District, Unit Resource Analysis.

Hayward,J.L., Gillett,W.H. and Stout,J.F., (1976). Aggressive communication by Larus glaucescens Part V: orientation and sequences of behaviour. Behaviour 63(3-4):237-276.

Hazlett,B.A., (1975). Individual distance in the hermit crabs Clibanarius tricolor and Clibanarius antillensis. Behaviour.LII.,3-4:253-265.

Hedeen,S.E., (1982). Utilization of space by cative groups of lowland gorillas (Gorilla g. gorilla). Ohio J.Sci.82:27-30.

Hediger,H., (1941). Biologische Gesetzmassigkeiten im Verhalten von Wirbeltieren. Mitteilungen der Naturforschenden Gesellschaft Bern. pp. 37-45.

Hediger,H., (1950). Wildtiere in Gefangenschaft-ein Grundriss der Tiergartenbiologie. Benno Schwabe, Basle. (Reprinted as Wild Animals in Captivity: an outline of the biology of zoological gardens, translated by G.Sircom, Butterworth Scientific Publications, London.

Hediger,H., (1955). Studies of the psychology and

behaviour of captive animals. (Reprinted as The psychology and behaviour of captive animals in zoos and circuses), Dover, New York 1968.

Hill,A.T., and Binns,M.R., (1973). Effect of varying population density and size on laying performance. 4th Europ.Poult.Conf., London:605-609.

Hinde,R.A., (1952). The behaviour of the great tit (Parus major) and some other related species. Behaviour suppl.2.

Hinde,R.A., (1972). Non-verbal Communication. Cambridge University Press.

Hughes,B.O., (1975). The concept of optimum stocking density and its selection for egg production. In: Economic Factors Affecting Egg Production (Ed) B.M.Freeman and K.N.Boorman, British Poultry Science Ltd., Edinburgh. pp 271-298.

Hughes,B.O., (1977). Selection of group size by individual laying hens. Bri.Poult.Sci.,18:9-18.

Hughes,B.O., and Black,A.J., (1978). Agonistic behaviour in domestic fowls transferred between cages and pens. Appl.Anim.Ethol.,4:181-186.

Hughes,B.O. and Wood-Gush,D.G.M., (1977). Agonistic behaviour in domestic hens: the influence of housing method on group size. Anim.Behav.,25:1056-1062.

Hull,C.L. (1938). The goal-gradient hypothesis applied to some 'field-force' problems in the behaviour of young children. Psychol.Rev.45:271-299.

Huntingford,F.A., (1984). A Study Of Animal Behaviour. Chapman and Hall.

Innis,G.S., Balph,M.H. and Balph,D.F., (1985). On spatial requirements of captive social animals. Anim. Behav.33(2):680-682.

James,J.W. and Foenander,F., (1961). Social behaviour studies on domestic animals. 1. Hens in laying cages. Aust.J.Agric.Res.12:1239-1252.

Jones,R.B., Duncan,I.J.H. and Hughes,B.O., (1981). The assessment of fear in domestic hens exposed to a looming human stimulus. Behav.Proc.6:121-133.

Katz,L.C., Potel,M.J. and Wassersug,R.J., (1981). Structure and Mechanisms of schooling in tadpoles of the clawed frog (Xenopus laevis). Anim.Behav.29(1):20-34.

King,M.G., (1965). Peck frequency and minimal approach distance in domestic fowl. J.Gen.Pychol.106:35-38.

Krebs,J.R., and Davies,N.B., (1981). An Introduction To Behavioural Ecology. Blackwell Scientific Publications.

Kummer.H., (1969). Spacing mechanisms in social behaviour. In: Man And Beast: Comparative Social Behaviour. Smithsonian Institution Press, Washington. pp.221-233.

Lee,Y.P. and Craig,J.V., (1981). Agonistic and non agonsitic behaviours of pullets of dissimilar strains of White Leghorns when kept separately and intermingled. Poult.Sci.60:1759-1768.

Lewin,K., (1935). A Dynamic Theory of Personality. McGraw-Hill. New York.

Lill,A., (1969). Spatial organization in small flocks of domestic fowl. Behaviour 32(4):256-290.

Mankovich,N.J. and Banks,E.M., (1982/3). An analysis of social orientation and the use of space in a flock of domestic fowl. Appl.Anim.Ethol.9:177-193.

Ministry of Agriculture, Fisheries and Food, (1971). Codes of Recommendation for the Welfare of Livestock. Code No.3. Domestic Fowls. London, Her Majesty's Stationery Office.

Ministry of Agriculture, Food and Fisheries, (1987). Codes of Recommendations for the Welfare of Livestock: Domestic Fowls. London, Her Majesty's Stationary Office.

Marler,P., (1956). Behaviour of chaffinches (Fringilla

coelebs). Behaviour suppl.5.

Marler,P., (1956). Studies in chaffinches. 3. Proximity as a cause of aggression. Br.J.Anim.Behav.4:23-33.

Mashaly,M.M., Webb,M.L., Youtz,S.L., Roush,W.B. and Graves,H.B., (1984). Changes in serum corticosterone concentration of laying hens as a response to increased population density. Poult.Sci.63:2271-2274.

Mech,L.D., and Knick,S.T., (1978). Sleeping distance in wolf pairs in relation to the breeding season. Behav.Biol.23:521-525.

Meunier-Salaun,M.C., and Faure,J.M., (1984). On the feeding and social behaviour of the laying hen. Appl.Anim.Behav.Sci.13:129-141.

Miller,R.S. and Stephen,W.J.D., (1966). Spatial relationships in flocks of sandhill cranes (Grus canadensis). Ecology 47(2):323-327.

Mills,A.D., Duncan,I.J.H., Slee,G.S. and Clark,J.S.B., (1985). Heart rate and laying behaviour in two strains of domestic chicken. Physiol.Behav.35:145-147.

Murchison,C., (1935). Experimental measurement of a social hierarchy in gallus domesticus. 1. The direct identification and direct measurement of social reflex No.1 and social reflex No.2. J.Gen.Psychol.12:3-39.

Myers,J.P., (1984). Spacing behaviour of Nonbreeding

Shorebirds. In: Shorebirds: Migration and Foraging Behaviour. (Ed) J.Burger and B.L.Olla. pp. 271-321. Plenum Press.

MacArthur,R.A. and Geist,V., (1982). Physiological correlates of social behaviour in Bighorn sheep: a field study using electrocardiogram telemetry. J.Zool.London,196:401-415.

MacArthur,R.A., Geist,V. and Johnston,R.H., (1982). Cardiac and behavioural responses of mountain sheep to human disturbance. J.Wildl.Manage.46(2):351-358.

McBride,G., (1964). A general theory of social organization and behaviour. Univ. of Queensland papers. Faculty of vet sci.,1(2):75-110.

McBride,G., (1968). Social adaptations to crowding in animals and man. Proc. of symp. on impact of civilization on the biology of man.

McBride,G., (1971). Theories of animal spacing: the role of flight fight and social distance. In: The social use of space in animals and man. (Ed A.H.Esser.) New York, Plenum Press:53-68.

McBride,G., James,J.W. and Shoffner,R.N., (1963). Social forces determining spacing and head orientation in a flock of domestic fowl. Nature 197:1272-1273.

McBride,G., Parer,I.P., and Foenander,F., (1968). The

social behavior and organization of feral domestic fowl. Anim.Behav.Monog.2:125-181.

McCort,W.D, and Graves,H.B., (1982) Social dominance relationships and spacing behaviour of swine.Behav.Process.,7:169-178.

McFarland,D., (1985). Animal Behaviour: Psychology, Ethology and Evolution. pp. 399-405. Pitman, London.

McNeill Alexander,R., (1982). Optima For Animals. Arnold.

Nicol,C.J., (1986). A study of the behavioural needs of battery housed hens. Unpublished Ph.D.Thesis. Oxford.

Pielou,E.C., (1969). An Intoduction to Mathematical Ecology. Wiley-Interscience.

Polley,C.R., Craig,J.V., and Bagwat,A.L., (1974). Crowding and agonistic behaviour: a curvilinear relationship. Poult.Sci.53:1621-1623.

Rowell,T.E., (1974). The concept of social dominance. Behav.Biol.11:131-154.

Rushen,J., (1982). The peck orders of domestic chickens: how do they develop and why are they linear? Anim.Behav.30:1129-1137.

Rushen,J. (1984). Should cardinal dominance ranks be assigned? Anim.Behav.32(3):932-933. (Short communication).

Savory,C.J., (1974). Growth and behaviour of chicks fed on pellets or mash. Br.Poult.Sci.15:281-286.

Schneirla,T.C., (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. Nebraska symposium on motivation (Ed M.R.Jones).

Seligman,M.E.P., (1972). Learned helplessness. Dept.Psychiatry and Psychology, Univ. Pennsylvania. pp. 407-412.

Selye,H., (1951). The general adaptation syndrome. A.Rev.Med.2:327-342.

Semmlar.H.J., (1965). Radiotelemtry during cardiac exercise tests. In: Biomedical Telemetry. (Ed) C.A.Cacares. Academic Press.

Siegel,P.B., (1976). Social behaviour of the fowl. Poult.Sci.55:5-13.

Siegel,P.B. and Siegel,H.S., (1969). Endocrine responses of six stocks of chickens reared at different population densities. Pout.Sci.48(4):1426-1433.

Sommer,R., (1969). Personal Space - The Behavioural Basis Of Design. Prentice Hall.

Stokols,D., (1972). On the distinction between density and

crowding. Psychol.Rev.79(3):275-277.

Stricklin,W.R., (1975). Spatial and temporal dimensions of bovine behaviour and social organization. Unpublished Ph.D. Thesis. Pennsylvania State University.

Stricklin,W.R., Graves,H.B. and Wilson,L.L., (1979). Some theoretical and observed relationships of fixed and portable spacing behaviour of animals. Appl.Anim.Ethol.5:201-214.

Syme,G.J., (1983). Social dominance - a straw man revisted? : some comments on the paper by Beilharz and Zeeb. Appl.Anim.Ethol. 9:380-387.

Syme,G.J. and Syme,L.A., (1979). Social Structure in Farm Animals. Elsevier Scientific Publishing Company.

Tatoyan,S.K. and Cherkovich,G.M., (1972). Heart rate in monkeys (baboons and macaques) in different physiological states recorded by radiotelemetry. Folia primat.17:225-266

Thinus-Blanc,C. and Buhot-Averseng,M-C., (1985). A basic approach to space-behaviour relationships in mammals. In: Social Space For Domestic Animals. (E) R.Zayan. pp. 239-262. CEC Seminar. Martinus Njhoff. Dordrecht/Boston/Lancaster.

Thompson,H.E., (1956). Distribution of distance to Nth neighbour in a population of randomly distributed

individuals. Ecology 37;307-321.

Tind,E., (1985). Effect of group size on behaviour and production of egg layers at constant space per hen in deep and shallow cages. In: Social Space For Domestic Animals (Ed) R.Zayan. pp. 85-99. Martinus Njhoff. Dordrecht/Boston/Lancaster.

Triesman,M., (1975). Predation and the evolution of gregariousness. I. Models for concealment and evasion. Anim.Behav.23:779-800.

Walther,F.R., (1977). Sex and activity dependency of distances between Thomson's gazelles. Anim.Behav.25:713-719.

Warnier,A. and Zayan,R., (1985). Effects of confinement upon behavioural, hormonal responses and production indices in fattening pigs. In: Social Space For Domestic Animals (Ed) R.Zayan. pp. 128-151. CEC Seminar. Martinus Njhoff. Dordretch/Boston/Lancaster.

Waser,P.M., and Wiley,R.H., (1979). Mechanisms and evolution of spacing in animals. In: Handbook of Behavioural Neurobiology vol.3 Social Behaviour and communication. (Ed P.Marler and J.G.Vandenberg). pp. 159-224. Plenum Press.

Wells,R.G., (1973). Stocking density and colony size for caged layers. 4th.Europ.Poult.Conf., London. pp. 617-622.

Werner,C. and Latane,B., (1974). Interaction motivates attraction: rats are fond of fondling. J.Person.and Social Psychol.29(3):328-334.

Wiley,R.H. and Hartnett,S.A., (1980). Mechanisms of spacing in groups of Juncos: measurement of behavioural tendencies in social situations. Anim.Behav.28:1005-1016.

Wilson,E.O., (1975). Sociobiology: The New Synthesis. Belknap, Cambridge Massachusetts.

Winfield,C.G., Syme,G.J. and Pearson,A.J., (1981). Effect of familiarity with each other and breed on the spatial behaviour of sheep in open field. Appl.Anim.Ethol.7:67-75.

Yates,A.J., (1962). Frustration and Conflict. Methuen and Co. London.

Ylander,D.M., and Craig,J.V. (1980). Inhibition of agonistic acts between domestic hens by a dominant third party. Appl.Anim.Ethol.6:63-69.

Zajonc,R.B., (1969). Attraction, affiliation and attachment. In: Man And Beast: Comparative Social Behaviour. Smithsonian Institution Press, Washington. pp.143-179.

Zayan,R. (1985). Experiments on behavioural and cognitive

processes involved in social space of laying hens at the beginning and end of the laying period. In: Social Space For Domestic Animals. pp. 197-230. CEC Seminar. Martinus Njhoff. Dordretch/Boston/Lancaster.

Zayan,R. and Doyen,J., (1985). Spacing patterns of laying hens kept at different densities in battery cages. In: Social Space For Domestic Animals (Ed) R.Zayan. pp.37-71. CEC Seminar. Martinus Njhoff. Dordrecht/Boston/ Lancaster.

GLOSSARY

1) NEAREST NEIGHBOUR DISTANCE

The distance from the subject animal to the closest conspecific. Distances can also be given to the 2nd., 3rd., 4th. etc. nearest neighbours.

2) INTERINDIVIDUAL DISTANCE

The distance between any two individuals of the same species.

3) PERSONAL SPACE

The area around an individual which it tries to keep free of conspecifics. This area has also been called the personal space, personal sphere, personal field, intolerance space and individual area.

4) INDIVIDUAL DISTANCE

The distance at which another individual of the same species provokes aggression or avoidance in the focal animal (Hediger,1941). This distance has also been called personal distance. It is the distance from an individual to the edge of its personal space.

5) CRITICAL INTERINDIVIDUAL DISTANCE

In this thesis the term critical interindividual distance has been used instead of the term individual distance. It is the distance at which one individual approaching a subject animal provokes aggression or avoidance in the subject.

6) MINIMUM APPROACH DISTANCE

A term used by some authors to refer to the minimum distance one bird will approach another. It is not clear whether this is intended to be equivalent to the critical interindividual distance.

7) FLIGHT DISTANCE

The minimum distance an individual will allow a predator to approach before moving away (Hediger,1950).

8) SOCIAL DISTANCE

The maximum distance an individual group member will move away from its home group.

10) PHYSICAL SPACE

The volume of air displaced by an individual. It can be divided into:

a) STATIC SPACE - The volume of air displaced by a stationary individual.

b) DYNAMIC SPACE - The total volume of air displaced by a moving individual.

In practice, work on physical space requirements has concentrated on area, usually floor area, rather than volume.

11) SOCIAL SPACE

The total space required by a group of animals which allows each animal to position itself appropriately to the other group members.

10) SOCIAL SPACING

The mechanism by which individuals space themselves

11) SPACING BEHAVIOUR

The mechanism by which individuals space themselves in relation to conspecifics, predators or to their habitat. In the context of this thesis, spacing behaviour is used to refer only to spacing between conspecifics.

12) EQUILIBRIUM DISTANCE

A term used in this thesis to represent the distance at which there is a balance between the tendency to approach and to withdraw from a conspecific. This distance is the "preferred" or the "appropriate" interindividual distance.

APPENDIX

Radiotelemetry is a technique by which radio waves are used to transmit information. The advantage of radiotelemetry in biology is that physiological measurements can be made, with minimal disturbance, on unrestrained animals. As a result, it is an ideal technique to study environmental and social effects. Initially, radiotelemtry was used to monitor the alarm reaction in domestic fowl by recording changes in skin temperature, however, heart rate is now more commonly used. For a more detailed review see Duncan (1981). In Chapter 2, heart rate telemetry was used as an indicator of the internal state of a bird as it was moved towards an unfamiliar conspecific. Radiotransmitters were implanted in eight individuals, and the method used is described below.

Each bird was deprived of water for 24hr prior to surgery and was anaethetized with an intramuscular injection of 1.5ml/kg xylazine (Rompun, Bayer). An incision 40mm long was made in the skin 20mm to the right of the keel bone. The transmitter was then implanted subcutaneously, over the right pectoral muscle and the battery pack over the left, so the connecting lead between the two passed around the front of the breast bone and was held in place by a suture. The two electrodes were sutured, about 50mm apart, to the connective tissue covering the keel bone. The keel

bone is the best place to attach the electrodes as it is relatively inaccessible to the animal, is free from muscle noise and does not suffer from much skin movement. There are, therefore, no artifacts in the signal (Semlar,1965).

Radiotransmitters can be adjusted to emit signals at different carrier frequencies making it possible to record more than one signal at a time. For a more detailed description of the transmitter see Filshie, Duncan, and Clark (1980). Each heart beat is characterized by a burst of electrical activity (the QRS spike) on the electrocardiogram trace. This QRS spike can be used to trip a Schmitt Trigger and the lapsed time measured until the Schmitt Trigger is tripped again. Ten second averages can then be calculated and expressed as beats per minute. The usual heart rate is between 280 and 320 beats per minute, but it can go as high as 450 beats when the bird is disturbed (Duncan and Filshie, 1980).

Using heart rate telemetry it is possible to correlate physiological changes with obvious behavioural changes. Care must be taken, however, since the outward appearance of an animal can sometimes lead to a false impression of the animals internal state (Duncan and Filshie, 1980). In other words, changes in heart rate can help draw attention to more subtle behavioural changes which might otherwise be overlooked (MacArthur, Geist, and Johnston,1981).