Exploring the social behaviour of cattle: the effect of the presence of familiar and unfamiliar individuals

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Abstract

The social behaviour of cattle encompasses a large range of affiliative and agonistic behaviours. The collection of these behaviours contributes to the overall social structure, which influences how a group functions and survives. Dominance behaviour has been a large focus of the existing literature on cattle social behaviour, with less emphasis on the affiliative behaviours that contribute to group cohesion. Affiliative behaviours are displayed between familiar individuals with established social relationships, however, details on the process of familiarisation and the underlying social properties of a cattle relationship remain largely unexplored.

Over a series of experiments, this thesis explored the affiliative behaviours involved in relationship development between unfamiliar steers in different social contexts. The first experiment presented in Chapter 5 examined the trade off individual steers make between a food-reward and maintaining close proximity to a peer with which they were either familiar or unfamiliar. This experiment analysed the impact of familiarity on an individual steer's feeding motivation. It was found that the presence of an unfamiliar pen mate impacted on the test steer's decision to move away and consume food, while steers paired with familiar pen mates were more willing to consume food at greater distances. It was suggested that the presence of an unfamiliar steer as well as isolation from familiar group mates in an artificial environment elicited a stress response that modified the steer's behaviour.

Chapter 6 describes a pair-wise experiment quantifying the changes in temporal and spatial associations between pairs of steers during familiarisation, where inter-individual distance, behaviour, movement and encounter patterns of pairs of familiar and unfamiliar steers were compared over a 5 day period. It was shown that unfamiliarity affected behaviour, movement, close proximity encounters and inter-individual distance. Relationships had begun to develop between the unfamiliar steers within 3 days, yet consistent treatment differences revealed that relationships had not stabilised after 5 days. Based on the findings from the first two experiments, it was concluded that the presence of an unfamiliar peer created stress, which affected the steer's behavioural patterns in both artificial and natural physical environments.

A triad based experiment is detailed in Chapter 7, where an unfamiliar steer was introduced into a pair of familiar steers and the resultant changes in social encounters were monitored over a 5.5 day period. It was found that the introduction of the unfamiliar steer led to an increase in close proximity encounters between the familiar pair due to social disruption. To analyse the data in greater detail the same experiment was re-analysed in Chapter 8 using a new social network related method: the relational event model. The model was used to analyse the sequences of social encounters between the three steers and identify patterns of encounters indicative of relationship development. The model identified the importance of pair-wise relationships and described characteristics of an established social bond between two steers. It was shown that familiarisation with the unfamiliar steer was hindered by the familiar peers providing social support for each other which led to the exclusion of the third steer. The model also revealed how social processes unfold in sub-groups of steers and structural differences between dyads and triads of steers were identified. A second application of the model presented in Chapter 9 described the encounter characteristics of a socially stable group of steers, where both dyadic and triadic encounters were identified as important features of the steers' social system.

The research demonstrates that relational event modelling provides a novel predictive tool to identify and analyse the complex encounter structures of steers during periods of social disruption as well as social stability. It was also shown that proximity logging devices can be used to quantify the social relationships of cattle and differentiate between the encounter patterns of familiar and unfamiliar steers.

This thesis identified emergent properties of social relationships in steers and described the social properties of dyads and triads of steers. This work will enable future studies on cattle social systems to take into account the influence of dyadic and triadic pressures on social processes in order to interpret the higher order processes more clearly. Further work is required to investigate the importance of other sub-group sizes on the social dynamics of larger groups: such work would continue to develop an understanding of the underlying social principles of cattle social systems, which has the potential to provide benefits not only to scientists, but also producers and the welfare of domestic cattle.

Declaration

This is to certify that:

1. the thesis comprises only my original work towards the PhD except where indicated in the Preface,
2. due acknowledgement has been made in the text to all other material used,
3. the thesis is less than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.

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Kym Patricia PATISON

Preface

The research was conducted under the supervision of Dr Dave Swain, from CSIRO Livestock Industries in Rockhampton, and Professor Pip Pattison and Associate Professor Garry Robins, from the Department of Psychological Sciences at the University of Melbourne. Two original papers were published from this research in peer reviewed journals: these papers have been incorporated as Chapters 5 and 6. The ideas, development and writing up of the papers were the principal responsibility of the candidate.

The research presented in Chapter 5 resulted from collaboration with Dr. Greg Bishop-Hurley from CSIRO Livestock Industries in Rockhampton, where Dr. Bishop-Hurley was involved with discussions on the design of the experiment and proof reading. In Chapter 6, Dr Greg Bishop-Hurley was also involved in the experiment design and data processing and David Reid of Agri-Science Queensland from the Department of Employment, Economic Development and Innovation in Rockhampton was consulted for statistical advice.

List of publications:

Patison, K.P., Swain, D.L., Bishop-Hurley, G.J., Pattison, P., Robins, G., 2010. Social companionship versus food: the effect of the presence of familiar and unfamiliar conspecifics on the distance steers travel. *Applied Animal Behaviour Science*, *122* (1), 13-20.

Patison, K.P., Swain, D.L., Bishop-Hurley, G.J., Robins, G., Pattison, P., Reid, D.J., 2010. Changes in temporal and spatial associations between pairs of cattle during the process of familiarisation. *Applied Animal Behaviour Science*, *128* (1-4), 10-17.

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To my family and friends, thank you for your support and encouragement. All of your valuable qualities, especially your shared love of the land, have contributed to my passion for animals and agriculture. I would especially like to thank Mum, Dad and Netsy. Even though there are two states between us, your support and encouragement has been with me the whole time. Special thanks also go to Sue and Paul and Sam and Daniel for providing me with such wonderful hospitality during my time in Melbourne.

Finally, to my husband Troy. I could not have reached this point without you. You have provided me with never-ending love, support and encouragement, and for that I am eternally grateful. You are a constant source of positive energy and life with you is a wonderful, fun adventure. I dedicate this thesis to you.

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Chapter 1

Introduction

1.1. Background to the study

Domestic livestock are managed according to practices that maximise production efficiencies. This management has resulted in a change in the way animals are grouped, from wild populations where animals select their own group sizes based on social attraction (Keeling and Gonyou, 2001; Boe and Faerevik, 2003) to modern day farming practices where groups are based more on breed, age, gender or production level (Raussi et al., 2005) and less on individual compatibilities. These management decisions can impose sub-optimal conditions leading to conflict and stressful environments (Keeling and Gonyou, 2001). Of particular importance is the disruption caused by the introduction of new individuals into an existing group; this disruption can lead to compromised animal welfare and production. In dairy and beef cattle production systems, regrouping unfamiliar individuals is a common practice. The negative effects experienced by both the introduced cow and the resident herd can include an immediate increase in aggressive behaviour and social stress, as well as a decrease in production levels, such as weight loss and a decline in milk yield (Boe and Faerevik, 2003). Despite these effects mainly being short term (around 1-2 weeks), the impact on animal health and welfare is an important concern.

Conflict between newly introduced individuals arises from them competing for their place within the social order, with the winner gaining priority access to resources such as food, space and mating opportunities (Lindberg, 2001). Due to agonistic behaviour predominating initial social interactions between newly introduced cattle, dominance-like behaviour has been a focus of many studies investigating mixing in cattle. The time taken for a group to be considered socially stable is important both in terms of animal welfare and production levels. Stabilisation in cattle is said to occur when non-physical agonistic interactions predominate physical agonistic interactions, and the ratio of non-physical to physical agonistic interactions remains constant (Kondo and Hurnik, 1990). However, once hierarchies have stabilised, minimal agonistic behaviour is observed and most groups exist without any conflict (Bouissou et al., 2001). This suggests that agonistic behaviours are initially important during relationship establishment, but it is the more subtle affiliative behaviours, such as maintaining close proximity and allogrooming, that are important for maintaining social cohesion and preferential relationships (Reinhardt and Reinhardt, 1981; Bouissou et al., 2001).

A popular approach to investigate the integration of an unfamiliar animal into a new group has been to focus on individual behavioural responses and group averages, such as an individual's decrease in weight gain or milk production or an increase in the overall levels of agonistic behaviour, and to monitor these changes until behavioural measures and interactions have stabilised or returned to baseline levels (Kondo and Hurnik, 1990). Another approach is to consider the group as its own network, where the actions of each individual are interdependent on the individuals around it (Wasserman and Faust, 1994), and evaluate the introduction of the stranger in terms of the individual as well as the relationship changes that occur within the group. Social network analyses focus on the relationships between each individual within a group and explore the patterns and outcomes of these relationships (Wasserman and Faust, 1994). Pair-wise interactions are therefore an essential component of the network (Croft et al., 2008). Several studies have investigated various aspects of a cattle social systems, such as dominance hierarchies (e.g. Beilharz and Zeeb, 1982) and affiliative relationships (e.g. Reinhardt and Reinhardt, 1981), although there are limited studies that investigate cattle social structure using a whole social network approach. The wealth of information that could be gained via investigating the social relationships that exist within a cattle social network, such as identifying preferential relationships and disease transmission routes, has a large potential to influence livestock management practices in a manner that could maximise production levels whilst enhancing animal welfare.

1.2. Aim and scope

It is well known that the presence of an unfamiliar animal creates social disruption, but less is known about the processes that occur during relationship development between newly introduced individuals. Thus, the aim of this thesis is to explore the effect of the presence of an unfamiliar steer on the social behaviour of resident steers. The context of this study is restricted to analysing only small numbers of steers that form the fundamental level of social structure: the dyad and the triad. The benefit of studying these kinds of social units is to develop an understanding of how group sub-structures are developed and maintained. By gradually increasing the size of the group, the influence of the social context on the behavioural response towards an unfamiliar peer can be measured. However, previous research investigating fish social systems revealed that behaviour in an isolated dyad is different from a socially embedded dyad within a larger group (Chase et al., 2003), and thus questions the usefulness of researching isolated dyads and triads. But in human social systems there are certain social properties that are unique to dyads and triads that are not observed within groups larger than two or three (Simmel, 1950), which may also exist in cattle social systems. By first considering properties that are unique to dyads and triads, the effect of these properties between individuals can be explored, which can then be evaluated for their effect within larger groups. Additionally, any effects that are produced above dyadic and triadic effects can also be identified. Thus, studying social relationships between pairs and triads of animals will lead to a better understanding of how animal social systems function. The outcomes from this study therefore have the potential to advance theoretical knowledge, methodology and analysis of relationship development in cattle.

Chapter 2

The social behaviour of cattle – a review

2.1. Introduction

The aim of the thesis introduced in Chapter 1 is to investigate changes in behaviour caused by the introduction of an unfamiliar peer and to develop an understanding of how sub-structures in cattle are formed and maintained. To begin to address this aim it is important to understand the basic principles associated with animal behaviour, why individuals form groups and identify the interactions and relationships that contribute to social organisation. The aim of this chapter is to therefore provide an overview on the previous work that relates to the social behaviour of cattle. The chapter begins by introducing the evolutionary factors that favoured the development of social behaviour and the fundamental components of a social system are described. The remaining sections review previous studies that have investigated cattle social structure and the development of the social hierarchy. The affiliative behaviours that serve to keep groups together are discussed, as well as the important relationship between spatial behaviour and social relationships. The chapter concludes by reviewing existing research on the effects of mixing unfamiliar animals on production outcomes.

2.2. The evolution of animal social behaviour

The evolutionary history of a species provides an insight into the way the past has influenced the behaviours that are observed in the present (Stricklin, 2001). The evolution of behaviour occurs by the same mechanisms of natural selection as any other physical characteristic (Broom and Fraser, 2007). Wilson (1975) described the process of selection as a change in the frequency of a genotype, as shown by differences in phenotype, from one generation to the next, and natural selection as the process where one genotype increases at a greater rate than another. Genetic variation allows some individuals to survive better than others. Variability in genotypes can be driven by numerous factors, including the ability to survive parasite infestations, predatory attack or inhabit a new environment. Beneficial traits that are maintained by the population are said to be adaptive (Wilson, 1975). Wilson (1975) emphasised that natural selection is the most important aspect of evolution and is the driving force that shapes a species' characteristics.

Just as genetics are subject to evolutionary pressures so too are behavioural traits, and it is proposed that genetics and culture co-evolve (Laland, 2008). Culture is characterised by a complex of behaviour, traditions, knowledge and skills that is transmitted from one individual to another via social influences, such as social learning, social facilitation and imitation (Laland et al., 2010). For example, information on food location and identity can be gained by copying the behaviour of other foragers, such that the behaviour of a single individual can influence the behaviour of all individuals within a group (Dugatkin, 2004). Cultural influences therefore differ from environmental influences, which are caused by adaptation to the physical environment, and can be transmitted both within- and between-generations, allowing culture to evolve at much faster rates than genetics (Dugatkin, 2004). The co-evolution of genetics and culture is summarised by Laland (2008) who states that '*genetics are expressed through development and influence cultural learning, which is expressed though behaviour*'. Individual behaviour is influenced by genetics, culture and the environment and in turn modifies selection by acting back on genetics, with offspring inheriting both genetics and culture from their parents (Fig. 2.1). Cultural transmission is therefore a social process that leads to the behavioural adaptation of individuals to their environment and ultimately the diversification of individual behaviour.

The mechanisms underlying the expression of non-genetic factors on the brain and behaviour are driven by epigenetic factors. Epigenetics was initially described by Waddington (1942) as '*the mechanisms and developmental processes by which the genes of the genotype bring about phenotypic effects*' and thus describes changes in the way genes are expressed due to non-genetic factors, such as the environment, biochemical factors and cultural information (Rakyan and Beck, 2006). The transmission and expression of social behaviour, such as learning, memory and building affiliative relationships, is complex and diverse (Cushing and Kramer, 2005): the field of epigenetics investigates these changes at the molecular and neural level to explain the resultant behavioural modifications and changes to gene expression (Robinson et al., 2008). The process of social behaviour leading to epigenetic changes can occur from (a) social information influencing genetic expression in the brain which then influences individual behaviour, and (b) from individual variation in genetics which affects brain function and therefore behaviour (Fig. 2.2) (Robinson et al., 2008). Inheritance of behaviour via epigenetic factors explains the mechanisms involved when offspring develop survival behaviours from their parents without actually experiencing the original challenging conditions (Harper, 2005). The process of cultural transmission and epigenetic inheritance therefore leads to the development of non-genetically coded social behaviours that influence the survival of a population.

Characteristics that improve the survival of an individual and its relatives will be more predominant in future generations (Broom and Fraser, 2007). Survival is quantified in terms of *fitness*, or reproductive success, of an individual (Dugatkin, 2004). Hamilton (1964) introduced the concept of ‘inclusive fitness’, which is the combination of individual fitness and the effect of the individual on the fitness of relatives and neighbours. Hamilton (1964) predicted that fitness gained from cooperative and altruistic behaviour was proportional to the level of relatedness of the recipient, with greater levels of fitness gained by assisting closely related individuals, such as siblings or cousins, than unrelated individuals. Hamilton (1964) presented a model that described the evolution of social behaviour and predicted that the selection of a trait would be based upon the consequence of its inclusive fitness. Four behavioural categories were identified: cooperative, spiteful, altruistic and selfish. Traits that improve inclusive fitness would be selected for, such as cooperation, while detrimental traits would be selected against, such as spiteful behaviour. The selection of behaviour that benefits one individual more than the other, such as altruistic or selfish behaviour, depends on the balance between individual risks and returns to inclusive fitness (Fig. 2.3).

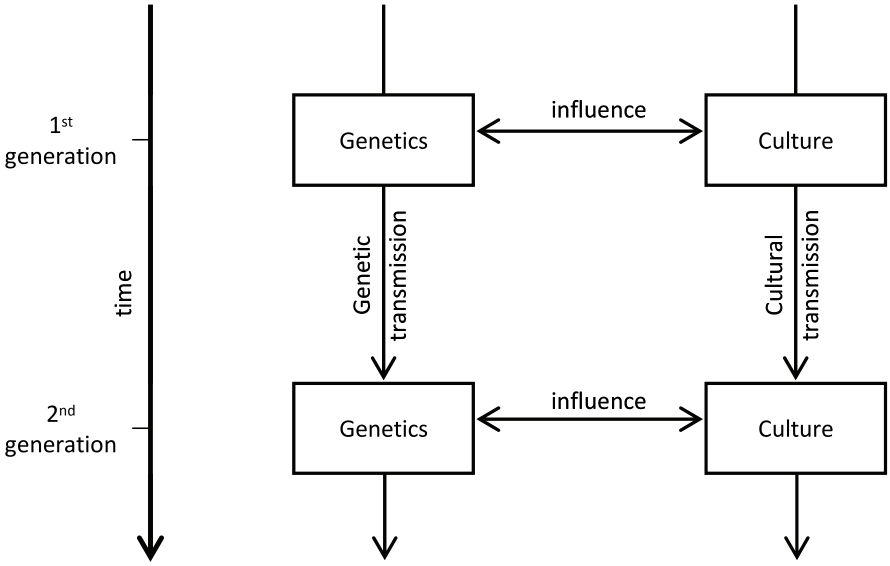


Figure 2.1. The co-evolution of genetics and culture. Genes and culture interact. Genetics are expressed through development and influence an individual's behaviour and what cultural information is learnt. Socially transmitted cultural information is expressed through individual behaviour and influences genetic selection. Offspring inherit both genetics and culture from their parents (modified from Laland, 2008).

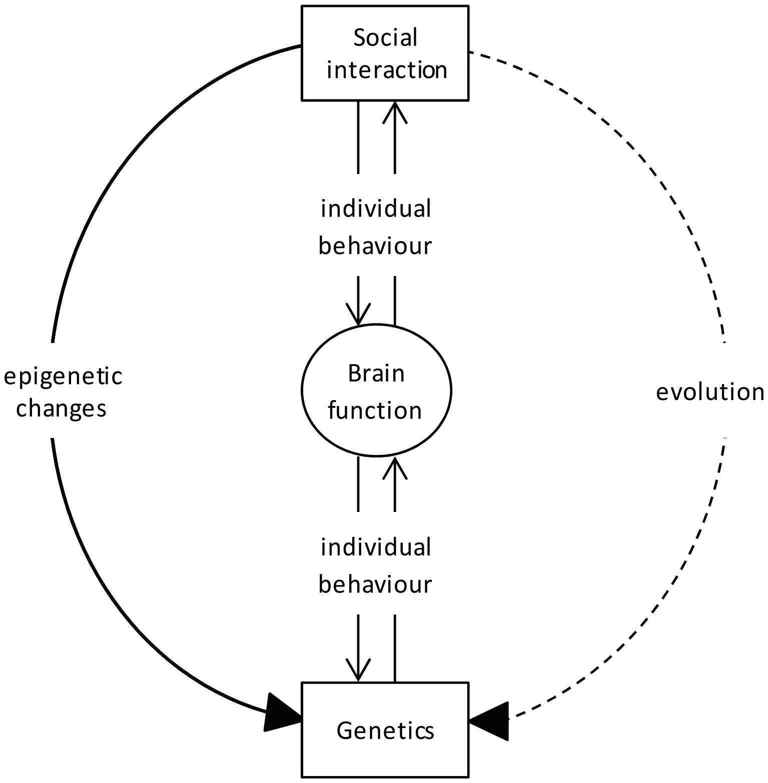


Figure 2.2. The inter-relationship between social behaviour, genetics and the brain. From social behaviour to genetics, social interaction influences genetic expression in the brain directly through individual behaviour, indirectly through epigenetic modification in the genome and via evolutionary time through the process of natural selection. From genetics to social interaction, genetic expression influences individual behaviour through brain function. Both the environment and genetics influence how social information is received and expressed (modified from Robinson et al., 2008).

Recipient

		Benefit	Detriment
Individual	Benefit	Cooperative behaviour *selected*	Selfish Behaviour *unknown selection*
	Detriment	Altruistic Behaviour *unknown selection*	Spiteful Behaviour *not selected*

Figure 2.3. The selection of a trait is predicted from the consequence of the trait on the fitness of an individual and the recipient (modified from Hamilton, 1964).

Altruistic behaviour is behaviour that is detrimental to individual fitness but increases an individual's inclusive fitness and its selection will depend on the coefficient of relationship with the recipient. Selfish behaviour is behaviour that improves individual fitness at the expense of others, and Hamilton (1964) stated that this behaviour will not evolve if the fitness losses of relatives are too great. Hamilton (1964) used the example of an alarm call by a bird to signal a predator to demonstrate his point: the bird exposes itself to the predator by signalling an alarm call to other birds but the resultant reduction of risk to another bird closer to the predator must be greater than the apparent risk to the caller. The potential gains from such an action would be maximised if the other bird was related, as the altruistic act increases the chance of genes shared with the recipient surviving into the next generation (Stricklin and Mench, 1987).

Hamilton (1964) provided strong evidence that individuals will act cooperatively and altruistically towards related individuals, specifically kin. However cooperative and altruistic behaviour also exists between non-kin individuals. Broom and Fraser (2007) suggested that social behaviour between non-kin individuals may have evolved when kin groups gathered in response to an abundant resource, such as food and shelter, and discovered the fitness benefits that could be gained by forming associations. Additionally, it is suggested that domestic livestock will behave towards group members, particularly those that they have been raised with, as if they were related and will thus give greater value to group member's fitness than unknown individuals (Stricklin, 2001). Altruistic behaviour between group members that is reciprocated at some stage in the future will be selected for, while cheating or exploiting altruistic behaviour by not reciprocating would be selected against (Wilson, 1975). The evolution of social behaviour therefore has favoured group living by increasing the fitness gains received by all members and explains the selection and adaptation of social behaviour.

2.3. The importance of social behaviour for survival

The benefits of abandoning solitary life to join a group is quantified by the gain in inclusive fitness (Wilson, 1975). Conditions in a group will be optimal when the benefits of living in a group outweigh the associated costs (Lindberg, 2001). In wild populations, individuals will leave a group due to illness, dispersal of offspring following weaning or to search for resources such as mating opportunities and food (Newberry and Swanson, 2001). However, domestication has removed the ability of individuals to choose their own group size and composition, which is controlled by farm management practices aimed at maximising production efficiencies. Nevertheless, an animal's behaviour is strongly driven by its evolutionary past and they will therefore continue to act in a way that maximise their fitness, even if the benefits obtained are only short term (Stricklin and Mench, 1987); behaviours have not been lost or gained through domestication, only modified (Stricklin, 2001). The advantages and disadvantages of group life are outlined below, with many features derived from an animal's evolutionary past when escaping from predators and finding food were essential for survival.

In grazing herbivores, the main benefits of forming groups are associated with anti-predation (Leuthold, 1977). Large groups have a greater chance of detecting predators as well as diluting the chances of being attacked, thus the chance of individual survival is increased (Dehn, 1990; Molvar and Bowyer, 1994). Through cooperative behaviour, groups of individuals have the potential to form defensive mechanisms against predators (Griffith, 1988). Groups are more efficient than individuals at detecting resources, such as food and shelter; through cooperation and learning, valuable foraging locations can be discovered and exploited by the whole group (Krause and Ruxton, 2002). Additionally, reproduction is only possible by forming associations. Offspring survival, and therefore gene flow, is increased by cooperative parenting behaviour, such as crèche formation (Sato et al., 1987). The major cost of association is resource competition. Most feeding bouts are synchronised between group members (Rook and Penning, 1991), thus forage and space is being competed for, resulting in a faster depletion of the food source (Shrader et al., 2007). This competition can result in aggressive behaviour and spreading out during grazing, which can compromise the protective cover created by the group (Rind and Phillips, 1999; Harris et al., 2007). Increased group numbers also increase the chance of being detected and attacked by predators as groups are less conspicuous than individuals (Lindström, 1989). Additionally, disease transmission within groups can be accelerated by close proximity contacts, increasing the risk of epidemics (Loehle, 1995).

The balance between the costs and benefits of group life will influence not only group size and dynamics, but also the types of social interactions that occur among group members (Stricklin and Mench, 1987). Social interactions can be divided into agonistic or affiliative (non-agonistic) behaviours (Bouissou et al., 2001). Agonistic behaviours include all forms of competitive behaviour, from physical aggression such as butting, pushing and fighting, to non-physical aggression such as threatening and avoiding (Kondo and Hurnik, 1990). Affiliative behaviours include all forms of cooperative behaviour, such as allogrooming, providing protection and social support, remaining within close proximity, resting in contact and synchronising behavioural activities (Newberry and Swanson, 2001). Competitive behaviours serve to maintain order while cooperative behaviours serve to maintain group cohesion (Stricklin and Mench, 1987).

Just as group living behaviours are inherited from wild ancestors so too are social behaviours that facilitate social interaction and social organisation. The existence of large groups has driven the development of complex social behaviours that are essential for individual and group survival (Dumont and Boissy, 1999; Mendl and Held, 2001). Examples of these complex behaviours include: social foraging, where individuals learn about food preferences and avoidances through others (Mirza and Provenza, 1994) and also share information on the location and quality of forage availability (Fortin and Fortin, 2009); group defence strategies where individuals band together to ward off or even attack predators (Berger, 1979; Griffith, 1988); crèche formation, where groups of young calves rest together guarded by one or two mothers while the rest of the group spread out to graze (Rankine and Donaldson, 1968; Sato et al., 1987); and allogrooming, which offers both social bonding and hygiene benefits (Sato et al., 1991). Individuals learn these behaviours through several mechanisms, including genetic influences, maternal interactions and individual experience (Provenza, 1995). Learning from others allows individuals to adjust to changing environmental conditions through their behaviour at a faster rate than natural selection or individual trial and error would allow (Galef and Laland, 2005). The information learnt from a mother occurs during a time when learning social skills are of primary importance to develop basic survival skills, such as what foods to consume once weaned and how to avoid predators (Galef and Laland, 2005). Maintaining such valuable information within the one population, for example in free-ranging herbivores where extended family units exist and matriarchies are allowed to develop, serves great advantages to group survival, cultural inheritance and inclusive fitness as the benefits are passed directly onto related kin (Hamilton, 1964).

2.4. Social organisation

Social organisation is the collection of social interactions and spatial relationships between all group members, which has been shaped by numerous environmental and social evolutionary pressures (Crook, 1970; Leuthold, 1977). The social organisation of a species provides a structural framework that influences how resources are distributed among members, cooperative relationships are formed and maintained, and survival behaviours are implemented (Croft et al., 2008). Social organisation is used interchangeably with social structure, social system or society (Whitehead, 2008). The ability of individuals to interact and organise themselves socially is what distinguishes a ‘group’ from an ‘aggregation’ of individuals (Wilson, 1975), where an aggregation is merely the co-location of any number of animals due to some environmental factor, such as an attractive feeding location, rather than a result of social attraction (Leuthold, 1977). The structure of a human social group is built from dyadic interactions between pairs of individuals and the patterning of these interactions into relationships (Hinde, 1976). Pair-wise interactions are therefore an essential component of a social group (Croft et al., 2008). The social complexity of a group rapidly increases with increasing group size, for example, when evaluating dominance hierarchies the outcome of interaction between each pair of individuals is measured against all others pairs. With five animals in a group there are 10 possible relationships to observe and compare, while there are 45 possible dyadic relationships in a group of 10 animals. In Australia, the average dairy herd size is estimated to be around 220 cows (DairyAustralia, 2010) equating to 24,090 possible dyadic relationships that form the social structure of an average Australian dairy herd.

In humans, there is an implicit understanding of what constitutes a relationship, which is described by Hinde (1976) as a series of interactions between two individuals that are influenced by the pattern of prior interactions and also the expectation of future interaction.

A definition of an animal relationship is based more on observations of behavioural patterns over time, where preferential relationships between cattle are formed and maintained through displays of affiliative behaviour by one or both individuals, such as allogrooming, providing protection and maintaining close proximity (Newberry and Swanson, 2001). Relationships provide a link between individual behaviour and group level processes as relationships are *embedded* within groups and define the characteristics of a group, while groups themselves are more than just aggregates of individuals and have emergent properties such as hierarchies and cohesiveness that influence the types of interactions and relationships that are likely to exist between individuals (Rubin et al., 1998).

The social structure of cattle arising from interactions between dyads and triads is largely unknown. Zayan (1990) suggested that to investigate social relationships in animals, systematic experimental work should focus on interactions between pairs and small groups, as their social stability is greater than larger group sizes. There has been a large amount of work done in human social sciences specifically relating to the importance of dyads and triads in terms of relationship development and social structure, and these principles might be relevant to studies in domestic livestock. The majority of the social principles reviewed below relate to human research, and where there are references to animal societies, most of these models have been based on human social systems.

2.4.1. Fundamental components of group structure: dyadic relationships

Interactions between two individuals, or a dyad, provide the fundamental component of a social system. In humans, a relationship between two individuals has unique social properties that are not observed with larger numbers of individuals (Simmel, 1950). At the simplest level, two individuals may have no relationship, known as a null relationship, or a dyadic relationship, which can be either mutual and reciprocated or one directional (asymmetric) (Fig. 2.4). Both forms of dyadic relationships have important structural properties when considered within a group (Wasserman and Faust, 1994).

When a pair is isolated from a group, the dyadic relationship has characteristic features that distinguish it from other group sizes and lead to greater cohesion. Simmel (1950) stated that a characteristic feature of a human dyad is the mutual dependence of the two individuals involved; for the dyad to exist it needs both individuals to survive thus strengthening the cohesion between the pair. Additionally, the strength of the relationship can only grow from

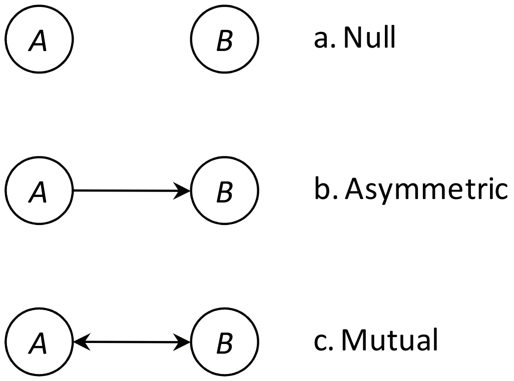


Figure 2.4. The three possible directed dyadic relationships between actors A and B.

the input of the two individuals. This relationship can be quantified based on the participation or the number of roles occupied by each individual, and equally, a decline in activity can indicate the weakening of the relationship (McCall, 1988). Furthermore, for a relationship to survive each individual has a responsibility to act in the best interest of the relationship, which in turn is rewarded by a sense of membership and cooperation between the pair (McCall, 1988). Studying dyadic interaction has several major advantages: the direct behavioural response of one individual in relation to the other can be measured (Lewis, 1984; Rubin et al., 1998); collecting, analysing and interpreting data on a pair of isolated individuals is easier and associated with less error than when observing larger groups (Feinman and Lewis, 1984); and the emergent social properties arising from dyadic interaction that influence how the social system evolves into a functional unit can be assessed (Lewis, 1984; Zayan, 1990).

The outcome of paired dyadic interactions, however, has been deemed insufficient to explain group and hierarchy structure. In a series of experiments, Chase et al. (2003) investigated the establishment of dominance relationships between pairs of cichlid fish either isolated from the group or 'socially embedded' within groups of three or four fish. The authors tested for differences between the two social contexts over a series of two experiments, specifically quantifying the stability of relationships over time and also if the same dominance relationships were formed after a period of separation. The first experiment involved determining the dominance relationships between pairs of fish or pairs of fish within groups of three or four fish, where a fish was considered dominant when it performed eight aggressive acts towards another fish in a row without any retaliation. The fish were assessed for dominance behaviour at 4 and 24 hours post-introduction. During the pair tests two fish were introduced in a single tank while in the group tests a third fish was introduced to the pair once their dominance relationship was established followed by a fourth fish for some groups. In total, 36 pairs, 19 triads and 23 tetrads were observed. The authors found that the relationships formed within an isolated pair were relatively stable compared with relationships within groups of three or four; no relationship reversals were observed between isolated pairs of fish 24 hours later, while 35% of fish in groups of four continued to direct aggressive behaviour towards the dominant fish and some relationship reversals were recorded. Pairs in groups of three showed no differences in relationship stability when compared with groups of four fish. Chase et al. (2003) concluded that the presence of other individuals influenced the nature of the dominance relationship. The second experiment was similar to the first experiment, where dominance relationships between pairs or groups of three or four fish were sequentially determined. After 2 hours of observations the fish were removed and kept isolated for 2 weeks, which was considered long enough for the fish to forget the identify of others. The pairs and groups were reassembled in the same pairings and groups as before and dominance relationships recorded. The authors found that isolated pairs replicated their relationships 93% of the time, whereas relationship reversals occurred in 24% of the group's trials. The authors summarised that the presence of other individuals lowered the probability that the same relationship will form in the future. The overall findings identified that dominance behaviour within a pair is different from socially embedded behaviour and therefore does not represent dominance relationships that are formed within a group context. It was concluded that dominance relationships should be considered contextual to groups, rather than independent pairs.

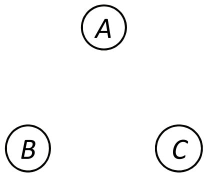
Most human social interaction occurs as a part of a larger group (Lansford and Parker, 1999), where an individual's behaviour is influenced by the social context, including not only the number of individuals in the group but also their social characteristics and their interactions and relationships with other group members. To study the influence of others on behaviour and relationships, Lewis (1984) suggested to introduce a third individual to a dyad and observe the behavioural responses. This step-wise approach provides basic information on the social properties of a triad. However, Lewis (1984) also acknowledged that the artificial nature of dyadic and triadic investigations limits the implications for group processes.

2.4.2. Fundamental components of group structure: triadic relationships

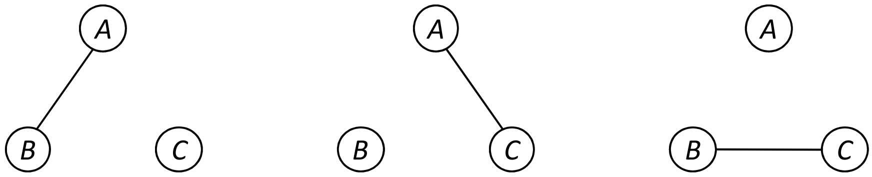
The relationship between three individuals is more complex than a relationship observed between a dyad. With three individuals, there is the potential for 64 different triadic configurations to occur when the direction of the relationship between each individual is known (Wasserman and Faust, 1994). However when only mutual ties are considered (i.e. non-directional), there are eight possible relationships (Fig. 2.5). Knowing how relationships are structured is essential for understanding the theoretical implications of such relationships (Wasserman and Faust, 1994).

Simmel (1950) was among the first to describe the social differences that exist between human dyads and triads, particularly the type of interactions that occur among individuals and the roles they fulfil within the group. These fundamental differences are important for understanding triadic interactions in group level processes. Simmel (1950) stated that the role of a third individual was both beneficial and detrimental to the cohesion of the group. In human groups, the third individual provides an objective perspective to resolve conflict which leads to group unity. In contrast, the triad is the smallest group size where there can be both a majority and a minority, such that the third individual can use their position within the triad for personal gain, for example, by creating conflict between the other two individuals to gain a dominant position, or conversely, two individuals can join forces to gain power over the third (Feinman and Lewis, 1984).

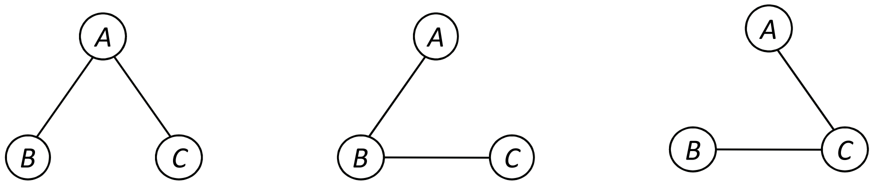
The triad is the smallest group size that can form a subset of a complete social system (Zayan and Dantzer, 1990), thus there are certain social processes that exist within triads that are not possible in individuals or pairs (Faust, 2007). Additionally Chase (1980) outlined that a minimum of three individuals are required to form a hierarchy. A study by Chase (1982) investigated the behavioural processes leading to hierarchy formation in chickens. Chase (1982) observed the dominance interactions of 24 two-year-old hens in groups of three using a sequential introduction method. The three chickens were placed into a 1 m cage and observed continuously for 4 hours recording all aggressive behaviour. A hen was considered dominant when she delivered three uncontested aggressive acts within a 30 minute period. The order of dominance establishment was quantified by designating the first hen to become dominant as *A*, the initial subordinate *B*, and the bystander *C*. Transitive and intransitive hierarchies are possible in triads, where transitivity indicates linear hierarchy structures, for example, A dominates *B, B* dominates *C*, and *C* is dominated by *A*, while a non-linear hierarchy indicates that at least one of the three dominance relationships will be intransitive, for example, *A* dominates *B*, *B* dominates *C*, and *C* dominates *A* (Fig. 2.6). Chase (1982) discovered that most hierarchies were transitive, thus winning follows winning and, if winning is not followed by winning, losing frequently follows losing. To test the occurrence of the same sequence in larger groups, Chase (1982) performed a second experiment using groups of four hens. Even though there was only one additional hen the possible relationship combinations were much more complex as four triadic configurations were possible as opposed to only one in a group of three. Twenty-one hens from the first experiment were used in the study and 14 groups of four hens were tested. The hens were observed in a cage and the same dominance classifications were used as before. To establish the sequence of dominance establishment, the groups were broken down into the four possible component triads and the sequences of dominance establishment were determined for the first two relationships in each triad. Chase (1982) found a strong tendency towards linear hierarchies, which was driven by the effect of the bystander dominating the initial subordinate. To determine the effect of the bystander on the resultant dominance relationships, Chase (1982) compared the results of real triads, where all four hens were present at the one time, with 'constructed' triads that were theoretically determined based on the dominance results of pairs of hens that only met as pairs within different tetrads. Chase (1982) found that transitive hierarchies were formed in all of the real triads but only in 86% of constructed triads, suggesting that the structure of dominance relationships are influenced by the presence of the bystander. Thus, the bystander was able to gain knowledge on the dominance ability of the pair during the initial encounter and used this to their advantage in future encounters. Chase (1982) argued that the dynamic patterns of hierarchy establishment observed between the hens were more than a result of differences in individual characteristics, as the patterns leading to linear hierarchies were much more frequent than sequences that led to non-linear hierarchies. Additionally the dominance ability of individual hens was not consistent across all social contexts. Chase (1982) concluded that interactions between one pair have important implications for interaction between other pairs and are responsible for the relationship structure within groups. Chase's (1982) work identified the importance of the third individual and its effect on the outcome of dominance relationships among a triad, which was not changed by the presence of a fourth individual. This finding is consistent with Simmel's (1950) theory that the addition of a third individual has a greater effect on group behaviour than when four or more individuals are present. Triadic characteristics therefore have important group properties that go beyond dominance hierarchy structures and dyadic relationships.



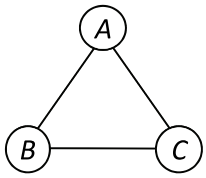
a. Null



b. Single relationship triads



c. Two relationship triads



d. Triangle

Figure 2.5. The eight possible non-directed triad configurations between actors, A, B and C.

Transitive

Intransitive

Figure 2.6. The relationship configuration between triads in transitive and intransitive triangular formations.

Hierarchies in cattle have been reportedly based on both dominance hierarchies (e.g. Beilharz and Zeeb, 1982) and affiliative relationships (e.g. Reinhardt and Reinhardt, 1981). Chase's (1982) model of hierarchy establishment was specifically based on agonistic interactions leading to dominance relationships, but it is not known if the development of affiliative relationships follows the same model. Additionally, analysing the outcomes of dyadic and triadic interactions leading to relationship development and the implications of these relationships on group structure has not previously been investigated in cattle.

2.5. Cattle social systems

Cattle are a social species that benefit from social interaction with others. They form affiliative relationships with group members and maintain cohesive group structures (Hart, 1985). The social structure of cattle is described as permanent groups with the existence of social hierarchies (Bouissou, 1980). A basic description of cattle social organisation includes the physical structure, such as the size and attributes of the group members including their age, sex and relatedness; the social components, such as the dominance hierarchy and communication; and group cohesion, described by the individual relationships responsible for keeping the group together (Broom and Fraser, 2007). The physical structure is group specific, however properties relating to social components and cohesion are more generic to animal systems. The basic principles of the dominance hierarchy and affiliative forces maintaining the group and communication mechanisms are described in the next three sections.

2.6. The dominance hierarchy

Social dominance has been a major focus of social behavioural research (Syme and Syme, 1979; Arnold, 1985). The function of a dominance hierarchy is to minimise agonistic behaviour within the group thereby maintaining group cohesion and reducing social stress (Mendl and Held, 2001). Stricklin and Mench (1987) describe a dominance relationship as '*a learned, predictable relationship between a pair of animals, where one of the pair is consistently deferred to by the other*'. A dominance hierarchy is therefore composed of a combination of all the dominance-submissive relationships within a group (Syme and Syme, 1979), while a dominance rank describes the relative position of each individual within the hierarchy (Stricklin and Mench, 1987). The dominance rank of an individual is group specific, such that the dominance rank in one group does not predict dominance rank in another group (Lindberg, 2001).

2.6.1. Establishing dominance

There are a number of factors that can contribute to an individual's ability to become dominant, but the predominant characteristics are age, weight and the presence of horns. A study by Bouissou (1972) investigated the effect of horns and live weight on the dominance rank of Friesian heifers. The study involved 20 heifers that were reared together since birth to control for factors such as rearing conditions and social experience. The animals were assigned to one of four groups based on age and horn status: heavy with horns (group A), heavy with no horns (group B), light with horns (group C) and light with no horns (group D). The animals in the 'heavy' groups were three months older and thus greater live weight than animals in 'light' groups while the animals in the 'no horns' groups were dehorned at 4 months of age. The experiment began when the youngest heifer was 18-months-old and the groups were formed with one animal from each of the four treatment groups (A, B, C and D). The heifers were introduced in an unfamiliar location and observed continuously for 3 hours, and then for 1 hour each day over the next 6 days. Dominance relationships within each group were determined by recording the direction of aggressive (butts and threats) and submissive (withdrawal) behaviour between the four heifers and also by a feed competition test, where two heifers had to compete for access to food in which only one could gain access to. Each heifer was then assigned a rank according to their dominance status, with one being the most dominant and four being the most submissive. In total, the dominance relationships of 25 groups were determined, as well as the dominance status of each individual against all individuals from other groups. Bouissou (1972) found that the presence of horns was highly correlated with attaining dominance. Animals from the heavy with horns group ranked higher than animals in all other groups, while animals in the light with horns group ranked higher than the heavy with no horns group, and animals in the light with no horns group ranked the lowest. These results were replicated when pair-wise ranks were analysed: horned and heavier heifers gained dominance in 97.5% of cases, while horned and lighter heifers were dominant over de-horned but heaver heifers in 75% of cases. When heifers were of similar weight, the presence of horns was positively related to dominance, and when both heifers were either horned or de-horned, the heavier animal was the more dominant. Bouissou (1972) concluded that when individuals are introduced for the first time and they have similar social experiences, the presence of horns is a major determination of dominance over and above the influence of live weight.

A further set of studies by Bouissou (1974b; a) investigated the nature of initial interactions between newly introduced heifers and the rate that dominance was established. Twenty groups of four, 18-month-old heifers were formed with animals that had previously not met before; the heifers had experience with meeting strangers on one prior occasion. The groups were observed for 6 days following group formation and all social behaviours, such as agonistic interactions and exploratory behaviour such as sniffing, were recorded as was the time and nature of the first encounter between each pair of heifers. The first study analysed the nature and frequency of encounters between the newly introduced heifers while the second study investigated the time taken for dominance relationships to establish. In the first study, Bouissou (1974b) found that 73% of initial encounters between two heifers that met for the first time were agonistic in nature, although only 37% of these interactions resulted in a fight, with most dominance relationships determined without any physical contact. The physical interactions reported by Bouissou were short in duration (less than 30 seconds) and were not observed after the first day. Bouissou (1974b) concluded that social structure is established rapidly and that physical contests are not essential for establishing a dominance relationship, which might be based more on evaluation of physical characteristics and previous mixing experience of the individuals. In the second study (Bouissou, 1974a), dominance relationships were considered established when the direction of agonistic behaviour from one animal to another resulted in undisputed submission of the second animal. Bouissou (1974a) found that almost half of all dominance relationships were established within the first 5 minutes, with all relationships determined after 2 hours. The established relationships remained relatively stable, with very few relationship reversals; it was the relationships that were established without any physical contact that were less prone to change. Bouissou (1974a) argued that the rapid establishment of relationships were not influenced by the small number of individuals in each group. Similar results were obtained by Bouissou (1974a) in a previous unpublished study when 16 unfamiliar animals were introduced and the relationships between all 16 animals were established within an hour and remained stable for at least a year. Bouissou (1974a) concluded that social experience is important for establishing dominance relationships quickly and without any physical contact. The results of Bouissou’s (1974b; a) studies show that individuals use prior knowledge to avoid potentially damaging behaviours and only engage in physical contests when there is a chance of success. The infrequent display of agonistic behaviour and the long term stability of relationships contribute to a cohesive social structure, and makes it difficult to identify the direction of dominance relationships between group members (Bouissou et al., 2001).

2.6.2. Benefits of dominance

Domestic livestock are managed according to two general types of management systems: intensive and extensive systems. Intensive production systems involve large numbers of animals within small areas of space, requiring high inputs of resources and labour and are common to dairy, poultry and swine production (Stricklin and Mench, 1987). In comparison, extensive farming systems utilise larger areas of space with relatively low inputs of resources and labour and is the predominant form of management for beef and sheep production (Stricklin and Mench, 1987). The intensification of animal production has meant that animals experience increased competition for resources, such as food and space (Bouissou, 1980).

2.6.2.1. Intensive production systems

A study by Manson and Appleby (1990) investigated the effect of dominance on spacing behaviour between cows at a feed trough. The dominance relationships of a milking herd of 50 British Friesian-Holstein cows and heifers were determined based on the display of dominance-submissive behaviour, and the herd was divided into three categories of high, medium and low ranking cows. The authors observed the social and spacing behaviour of the herd at the food trough. The trough was separated into 44 feeding positions, where only one cow had access to a feeding position at the one time. The feeding positions were 0.65 m apart and used to indicate spatial proximity between individuals, where a distance of one equalled one feed position apart (directly next to each other), two equalled two feeding positions apart, and so on. Over a 15 day period, observations were recorded throughout the middle of the day at 10 minute intervals several hours after food had been dispensed. The study identified that dominance rank was a major determinant of spacing between cows: cows of similar rank fed closer together than cows of different ranks, with the greatest difference seen between low and high ranking pairs (4.4 feeding positions apart). Manson and Appleby (1990) concluded that spacing was non-random and cows spaced themselves with respect to rank, with dominant individuals experiencing greater spatial separation from lower ranked individuals.

The relationship between dominance rank and access to food and lying space was investigated by Friend and Polan (1974). The authors used time lapse photography to record feeding and lying behaviour of 21 Holstein dairy cows over a 2 month period. The cows were housed in an observation lot and had access to 20 free stalls (individual stalls for resting) and a 10.4 m feed trough that could accommodate 66% of the herd at the one time. Each individual was assigned a dominance rank from one to 21 based on the outcome of physical interactions between individuals, with 21 being the most dominant individual. The authors determined that dominance rank influenced both time spent at the feeder and also the lying location of the cows. Dominant cows spent more time at the feed trough immediately after fresh fodder had been dispensed. The results suggested that subordinate cows spent more time at the feeder than middle ranked cows, although this was well after food had been dispensed and food supply was limited. There was a strong tendency for individuals to prefer certain stalls over others; the dominant cows occupied the stalls closest to the entrance and subordinate cows avoided using stalls that dominant cows used regularly. Friend and Polan (1974) concluded that the cows displayed territorial behaviour by repeatedly using the same stalls and the dominance rank of individuals determined their resting location.

2.6.2.2. Extensive production systems

The studies described by Mason and Appleby (1990) and Friend and Polan (1974) demonstrate the potential benefits gained from being dominant in an intensive housing system. Competition for space is expected to be lower under extensive pastoral systems as individuals generally have more access to space, although there are still advantages associated with being dominant. Stricklin (1983) investigated the effect of dominance and spatial relationships among a mixed group of Hereford and Angus cattle. Two groups of 20 cattle were observed in 10 ha plots. The proportion of wins and losses of physical encounters during group formation and also during field observations were used to assign a dominance rank to each individual. Thirty spatial observations were recorded by estimating the number of body lengths between individuals within each plot and calculating the mean distance to all cows and the distance from the group centre. The authors found that higher ranking cows were more frequently found in the centre of the group, which was thought to provide the greatest protection from predators. This finding is consistent with that of Beilharz and Mylrea (1963), who studied the relationship between spatial position and dominance of 27 mixed breed dairy heifers under three different movement orders: movement from yards, free movement when grazing and forced movement along a fence line. Dominance rank was assigned on the proportion of encounter wins and losses over a 2 week period, and the heifers were further classified as high, medium or low ranking animals. The authors found that the three different movement orders resulted in different spatial positions of the three dominance categories. In general, animals of higher dominance rank were found more often in the middle of the herd and were not observed as leaders of any movement. Middle ranked animals were more likely to lead during free movement, while lower ranked animals tended to be at the front during forced movement, being bunted by the higher ranked animals. Thus, there appears to be a relationship between dominance and movement, with higher ranked animals maintaining central positions and protection from predators and insects.

2.6.2.3. Mating opportunities

Rupp et al. (1977) explored the effect of social rank on the number of heifers mounted by four bulls within a group of up to 100 Hereford heifers. The animals were kept in a 450 ha paddock with a bull to female ratio of one bull to 25 heifers. Each bull was fitted with a chin-ball marking harness and a specific colour was assigned to each bull. The marking system was designed to leave a mark on the rear of each heifer that was mounted by a bull. Observations were collected at 12 hour intervals over a 21 day period, where the marks on each heifer were noted as well as any dominance behaviour between the bulls to determine their dominance rank. The authors found that the highest ranking bull recorded the overall greatest number of marks. When heifers had been mounted by more than one bull, the dominant bull was recorded more often than other bulls. It was concluded that dominance in bulls was related to the number of heifers mounted, and resulted in the potential for the dominant animal’s genetics to succeed into the next generation.

A series of experiments performed by Blockey (1979) investigated the effect of dominance on the behaviour and performance of bulls. Earlier, Bouissou (1972) determined that dominance in heifers was highly related to the presence of horns followed by body weight. To investigate if the same relationship between weight and dominance was observed in bulls, Blockey (1979) compared the dominance status of two groups of bulls with age, seniority and body weight. Seniority, or time in the same group, was included in the experiment as bulls are often kept in mixed-age groups. The first group consisted of 50 Hereford bulls, which ranged in age from 2.5 to 9 years and the time spent in the same group ranged from 8 to 49 months. There were 26 bulls in group two, whose ages ranged from 2 to 5.5 years and time in the same group varied between 2.5 and 50 months. Dominance was determined by forcing the bulls to compete for space within a 20 m by 20 m yard until 35% to 53% of all possible pair combinations had been observed. Bulls were ranked in order of the proportion of bulls they dominated in relation to the number of bulls they contested. Blockey (1979) found that all three factors were important for determining dominance, although seniority was found to have the most significant effect on dominance rank. This effect was demonstrated by the high proportion of losses encountered by bulls that were recently introduced into the groups. A second experiment by Blockey (1979) investigated the effect of age and dominance on bull performance. Four groups of bulls were tested for mounting ability. Groups one and two comprised 17 and 11 2-year-old bulls, respectively, while groups three and four comprised eight and 12 mixed-age bulls, respectively, whose ages varied between 2.5 to 5 years. The dominance rank of each bull in each group was determined using the same method described in the previous experiment. The bulls were added to groups of 14 to 31 heifers and maintained on 0.7 ha plots. Visual observations were used to record all mounting behaviour. Blockey (1979) found that dominance orders were significantly more stable in the mixed-age groups than the younger bulls, which tended to have more complex hierarchies and frequent rank reversals during repeat encounters. Additionally, there was no correlation between dominance rank and the number of mounts recorded within the 2-year-old bulls. However, the results of the mixed-age groups agreed with those of Rupp et al. (1977), where the most dominant bulls were not only the most sexually active but they also inhibited the mounting activity of lower ranked bulls. The most dominant bulls in each group were the oldest, thus confirming the results from the previous experiment. Blockey (1979) concluded that stability of the dominance hierarchy influences bull performance at pasture and that seniority appears to be more important than age in determining dominance rank in bulls.

2.6.3. The effect of dominance on production

Although the studies mentioned above have shown a link between dominance and access to valuable resources such as space, food and mating opportunities, there is no conclusive evidence to prove that dominance results in greater production levels. Beilharz et al. (1966) investigated the effect of dominance on production traits, including milk production, of 76 Holstein dairy cows. The cows were managed as six separate groups according to lactation stage and pregnancy status. The cow's social behaviour was recorded over 3 days and a dominance rank was assigned to each individual by calculating the proportion of wins each cow had over all other cows. Milk production data was collected during the week that behavioural observations were recorded, as well as the 2 weeks prior and 2 weeks after. The total milk production over the 5 week period was compared with the dominance rank of each cow. The authors found no significant correlation between milk production and dominance. As expected, production levels were highly correlated with stage of lactation and pregnancy status while dominance rank was correlated with weight. In support of this finding, Dickson et al. (1967) also found no relationship between milk production and dominance in a herd of 24 Holstein dairy cows. The cows were kept as two groups of 12 and represented a range in age, weight and lactation stage. The behaviour of each cow was recorded by observations for 8 hours a day over a 5 day period, which was repeated one month later, with the winner and loser of each agonistic encounter used to calculate the dominance rank of each individual in relation to all others. There was no relationship found between dominance rank and milk production, while the only significant correlation identified was between dominance and weight. Dickson et al. (1967) concluded that the rank order of cows within the herd remained stable over the month and dominance rank is more related to age and weight than to production level.

A further study on dominance and production was explored by Phillips and Rind (2002). The authors first performed a similar study to those mentioned previously and found no relationship between dominance and production in a group of 80 British Friesian dairy cows. The authors hypothesised that removing the dominant animals from a herd would lead to greater forage intake and thus an increase in production by subordinate animals. To investigate this hypothesis, 72 of the cows used in their first experiment were divided in half based on their previous dominance rank, either dominant or subordinate. The animals were then allocated into one of four treatment groups: animals of same rank offered hay supplement; animals of same rank offered no hay supplement; animals of both ranks kept together and offered hay supplement; animals of both ranks kept together with no hay supplement. Four observation periods with a sample interval of 10 minutes over a 24 hour period were recorded of the animals in their groups, noting the grazing and social behaviour of each cow. Additional observations of 3 minute intervals were recorded when the cows were consuming hay. Production data was collected on two milking occasions per week over a 4 week period. The authors found that when separated by rank, dominant cows produced more milk than the group of subordinate cows when they were offered additional fodder. There were no differences in the amount of forage consumed between the two groups, although the dominant animals chewed at a faster rate. Additionally, when separated the two groups spent longer lying than when the two ranks were mixed together. The hypothesis that the subordinates would perform better when isolated from the dominant individuals was rejected, as there were no production or intake gains observed by any of the subordinate cows. The authors suggested that the presence of the subordinate cows created tension in the higher ranked animals, and competition between the ranks resulted in faster biting and chewing rates in the dominant animals. The difference in chewing rate identified by Phillips and Rind (2002) suggested that dominant cattle modify their behaviour to gain an advantage over other group members. Although Phillips and Rind (2002) discovered some interesting results, the applications of the study are limited as it would not be possible to maintain a group solely composed of dominant individuals; over time the group dynamics would change and a new social order would be established. Thus, individuals that were of high dominance rank in the previous group may become a lower ranked animal within the new group structure.

Further evidence to suggest dominance has minimal effect on production level was provided by McPhee et al. (1964), who studied the effect of feeding behaviour on growth in groups of beef steers. Seven groups of six animals were fed from troughs in yards, and their dominance rank determined every 2 weeks over an 8 month period. In addition to dominance behaviour, feeding behaviour was also recorded including the time at the feeder and the amount of undisturbed feeding time. The steers were weighed every 2 weeks and the behavioural records and weight measurements were compared with dominance rank. The experiment was run concurrently with a drought feeding experiment, which saw the steers provided with either *ad libitum* low quality hay or restricted rations of low quality hay. Consequently all steers lost weight during the trial, and the average weight loss by high and low ranking steers was the same. Although there were feeding differences between high and low ranking steers, high ranking steers spent more time feeding and had longer undisturbed feed intervals. On average, low ranking steers were disturbed from feeding every 10 minutes, compared with 14 minutes for high ranking steers. McPhee et al. (1964) concluded that even though the higher ranking animals had greater access to food, this was not reflected in growth differences between the ranks. The study highlights that even under conditions of feed restriction low ranking animals are able to consume similar proportions of forage as higher ranking animals, possible due to faster consumption rates. Additionally, competition for access to the feed trough was minimised in McPhee et al.'s (1964) study, with 0.60 m of space provided for each animal, so although the lower ranked animals were disturbed more often, there was still space available to resume eating. Competition is minimised in a domestic situation as the supply of resources such as food and space are regulated (Price, 2008), thus the effect of dominance on behaviour and production is reduced under these conditions.

Higher levels of agonistic interactions have been reported in larger groups of cattle, as found by Rind and Phillips (1999), who investigated the effect of group size on behaviour. The study involved 48 British Friesian dairy cows that were allocated into four groups of four cows, two groups of eight cows and one group of 16 cows. Over a 53 day period, the groups were observed in 1.5 ha plots for their general, social and feeding behaviour as well as their inter-individual distances every 10 minutes for one hour each day. The amount of agonistic behaviour observed between groups was greatest for the cows in the largest sized group; each cow exchanged an average of 7.3 agonistic interactions in the large group compared with only 2.7 interactions for cows in the smallest group size. The authors suggested that the cows in the large group required more frequent interaction to confirm each other's social status, thus the increased agonistic interactions were a result of cows preventing others from entering their personal space. There may have also been greater competition among the cows for grazing space, thus resulting in more displays of agonistic behaviour. It was concluded that the size of the group affects individual behaviour but there was no evidence to suggest that group size influences production, possibly as there were adequate resources available. Although the study by Rind and Phillips (1999) presents some interesting results, the lack of replication of the large group size and few replicates for the medium sized groups limits the interpretation of these findings for groups other than those used within this study. Nevertheless, the results do suggest that dominance affects group behaviour and further studies on group size and behaviour are important.

2.6.4. Dominance hierarchy structure

A simple linear hierarchy appears to exist when group sizes are small (less than 10 members), where the top ranking animal *A* dominates all group members, and the second ranking animal *B* dominates all other animals except *A*, and so on until the bottom ranking animal dominates no one (Chase, 1974; 1980) (a in Fig. 2.7). However, hierarchies are more complex in larger groups of cows and triangular formations may arise (b in Fig. 2.7). This involves three animals within a larger group, where animal *B* might dominate *C*, and *C* dominates *D* but *D* might dominate *B* (Hart, 1985), thus one animal is not dominant over the other two. Equal dominance status can also occur when two individuals dominate over all others below in rank, but there are no clear distinctions of dominance between the pair (c in Fig. 2.7).

Beilharz and Zeeb (1982) studied the dominance hierarchies of three dairy herds. The herds ranged in size from 43 to 53 animals, and were composed of mixed breed cattle of a variety of ages and lactation stages. Approximately 20 hours of observations of dominance behaviour within each herd were recorded, and a dominance rank assigned to each individual. Not all pair wise relationships were observed within each herd, thus dominance ranks were calculated as a proportion of the number of relationships observed; over 20 relationships were identified for each individual. Of the three herds, there was not one single animal that was dominant over all others, with a high correlation between seniority and dominance rank among the top ranking cows. The authors discovered a relatively linear hierarchy in one herd between all the heifers within the group that had been raised together since birth, however their interactions with older cows in the herd varied and contributed to the non-linear group order. There were several cases where dominance results appeared 'odd' animals identified illness, late pregnancy and the presence of horns as the reason for many of these cases. In one herd, horns were positively correlated with dominance, while negatively correlated in another herd. Beilharz and Zeeb (1982) concluded that dominance is predominately a learning process that varies according to individual factors, and they expect the rank order of each herd to vary according to the individuals involved.

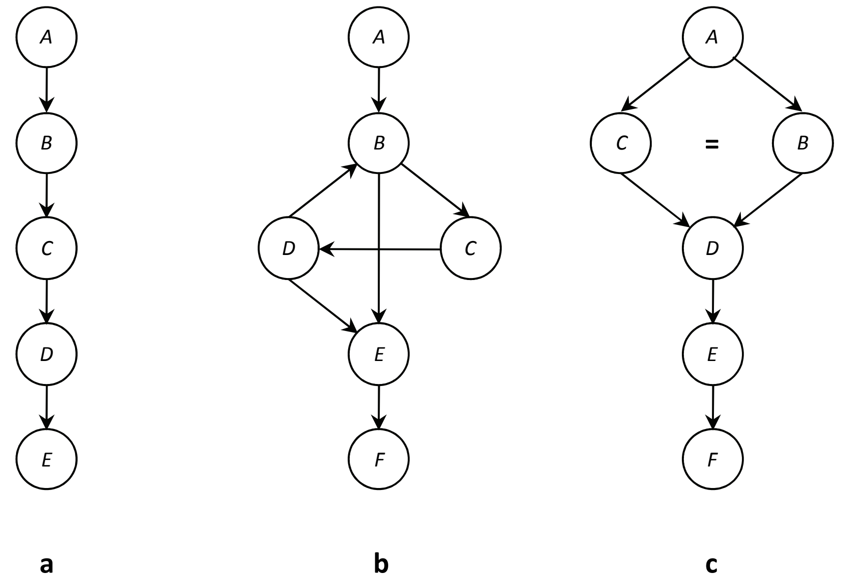


Figure 2.7. Different types of hierarchies. The animals are represented by circles and the direction of the dominance relationship indicated by arrows. (a) Strictly linear hierarchy; (b) linear hierarchy with a triangular relationship; (c) linear hierarchy with two individuals of equal dominance status (modified from Hart, 1985).

In a similar study, Collis (1976) also observed a complex hierarchy in a herd of 49 British Friesian dairy cows. The group were raised together as calves and had been in the milking group for almost 3 years. Over a 2 month period, the cows were observed for 2-3 hours a day between 2 and 3 days per week and all agonistic behaviour was used to determine the dominance rank of each individual. Although the author was able to assign a single rank to each cow in a linear order, there were many examples where lower ranking cows dominated cows of greater dominance rank providing evidence of more complex structures, such as triangular formations, within the hierarchy. Collis (1976) suggested that the similarity in age between herd members minimised the effect of weight and experience on the rank of each cow, resulting in many animals with similar dominance ranks. In contrast to the study by Beilharz and Zeeb (1982), the hierarchy studied by Collis (1976) identified one top ranking cow that was dominant over all other cows. However, the overall findings of Collis' (1976) study corresponds with the observation by Beilharz and Zeeb (1982) that each herd has its own unique hierarchy dependent on individual characteristics, thus making it difficult to assess generic traits that will consistently predict the dominance rank of individuals from one hierarchy to the next.

2.7. Affiliative behaviour

The literature reviewed in the previous section highlights the extensive research on dominance related behaviour in cattle. Investigating the establishment and function of dominance in cattle was the focus of many of the early studies on cattle social behaviour (e.g. Schein and Fohrman, 1955; Dickson et al., 1967; Rowell, 1974), which were followed by investigations into the effects of dominance under different management systems (e.g. Stricklin, 1983; Manson and Appleby, 1990). Correspondingly, the function of dominance behaviour is well understood (Lindberg, 2001). More recent studies have tended to focus on other aspects of social behaviour both in conjunction with and separate from dominance behaviour. From the reviewed literature it is clear that establishment of a dominance hierarchy serves to maintain social order whilst minimising agonistic behaviour and governing access to limited resources. However, in domestic environments where the supply of resources is regulated there are no clear production advantages gained by being dominant and it is generally accepted that dominance status varies according to the individuals involved. However, due to the large focus on dominance behaviour, other areas of social behaviour remain largely unexplored (Arnold, 1985; Lindberg, 2001). This is surprising given that the basic structure of a natural cattle herd is matriarchal with preferential relationships between non-kin individuals (Reinhardt and Reinhardt, 1981). These relationships are formed and maintained through affiliative behaviours, such as social grooming and social grazing, and displays of aggression and dominance are rare. Thus it is the affiliative behaviours and preferential relationships that form the cohesive structure of the herd. The following section evaluates aspects of affiliative behaviours that influence group cohesion, including the effect of familiarity, the characteristics of preferential relationships, and the principles of spacing behaviour that reflect an individual's sociability.

2.7.1. Familiarity

Familiarity influences the strength of attraction between individuals, thus promoting stability within the social structure (Syme and Syme, 1979; Ruddell et al., 2007). Familiarity is said to occur from recognition and social history between the individuals involved, including knowing who occupies what position in the social structure (Hinde, 1976). The added benefits of familiarity is the increased level of social support conspecifics provide, with familiar group members maintaining closer proximity to each other than to unfamiliar conspecifics (e.g. Murphey, 1990; Takeda et al., 2000). A study by Murphey (1990) investigated the effect of breed and familiarity on group behaviour by comparing groups of cattle raised in same-breed groups with those raised in mixed-breed groups. The study involved two separate observations of free-ranging herds of yearling heifers and mature cows. The herds were of three different breeds that varied in colour and shape: the Brahman's used were all red in colour, the Charolais were white and the Brangus cattle were black. The first observation period consisted of three groups of same-breed cattle that had been raised with members of their own breed in isolation from other breeds. The groups were made up of 57 reds, 18 whites and six blacks and were mixed for the purposes of the study. Observations of nearest neighbours were recorded, noting the identity and breed of the nearest neighbour of each focal animal. The author found that nearest neighbours tended to be of the same breed and the groups separated themselves by breed. The groups were herded to a different property for the second observation period where they were introduced to two groups of same-breed cattle and one group of mixed-breed cattle. The same-breed groups were made up of 42 whites and 62 blacks, while there were 38 heifers in the mixed-breed group including red, white and black heifers. Murphey (1990) found that the mixed-breed group tended to maintain a sub group within the larger herd and performed rubbing and grooming with their original herd mates. As with the cattle from the first property, cows that had been raised together continued to associate together.

Murphey (1990) concluded that cattle tend to associate with their most familiar herd mates regardless of genetic or phenotypic similarity.

The effect of familiarity is also said to influence grazing behaviour. Scott et al. (1995) conducted a series of four experiments to examine the effect of food and social preference on the spatial location of sheep. The first experiment investigated the effect of food preference on spatial location. Twelve lambs that had been raised together since birth were separated into two groups and introduced to two different food sources, either sorghum or wheat, and were conditioned to form a preference toward one food source over 14 days. The groups were then exposed to the other food source treated with a mild toxin to develop and aversion to the novel food. The lambs were tested for their spatial and feeding behaviour in three different sub group configurations based on their food preferences: the first group consisted of three lambs conditioned to prefer wheat and three lambs conditioned to prefer sorghum; the second group was composed of one lamb conditioned to wheat and three lambs conditioned to sorghum; the third group included three lambs that preferred sorghum and one lamb that preferred wheat. The groups were located in a 0.25 ha pasture plot with the grains located at opposite ends of the plot. Equal amounts of wheat and sorghum were supplied for group one, while only a quarter of wheat was supplied for the second group and a quarter of sorghum for group three. A final test observed foraging behaviour of the original two groups when both grains were offered at opposite ends. All sub groups of lambs were exposed to the plot for 30 minutes a day over 3 days and the spatial location (which half of the pasture) and feeding activity (consuming wheat or sorghum) of each lamb was recorded once every minute. The results showed that lambs foraged on their preferred grains irrespective of the location of group members; even when only one lamb had a preference for either grain, the lamb spent the first 10 minutes consuming its preferred grain away from the other three lambs before re-joining the group. In the second experiment, a separate group of lambs that had not been exposed to the toxin were reared separately in three treatment groups from 1 month of age. Each group comprised six lambs that were conditioned to prefer either wheat or sorghum over a 4 month period: the lambs in group one were conditioned to prefer sorghum, group two were conditioned to prefer wheat and three lambs in group three were conditioned to prefer sorghum and the other three conditioned to prefer wheat. The lambs were located in a 1.0 ha experimental plot for 30 minutes per day over 6 days to observe their location and feeding behaviour: during the first 4 days the lambs had access to sorghum and wheat located 100 m apart at opposite ends of the plot. On the last 2 days of testing the authors also recorded the lamb’s behaviour when no food was present to investigate if the lambs foraging behaviour was affected by the presence of supplementary food. In support of Experiment 1, the results showed that feeding location was influenced by food preference when accompanied by peers that preferred the same food, however, the results varied when for the mixed-preference groups. In some groups, lambs that preferred sorghum grazed nearby companions consuming wheat and then those that preferred wheat grazed nearby while companions consumed sorghum, while in other groups some lambs ate their preferred grain irrespective of the presence of social partners. The results suggest that when peers have different food preferences the decision to consume a preferred food source or maintain proximity to peers is influenced by the individual’s level of sociability and feeding motivation. When there was no supplementary food, lambs showed no preference for either area during the first 10 minutes, thus confirming that the location of food is an important determinant of foraging location. To investigate if food aversion influenced pasture use, the lambs in each group were given the alternate food containing a mild dose of a toxin before being tested in the experimental plot using the same procedure as Experiment 2. The lamb’s behaviour did not change from the previous experiment and showed no sign of increased affinity in the area with their preferred grain. Experiment 4 investigated the role of familiarity on lamb foraging location. Three lambs from the wheat group and three lambs from the sorghum group in Experiments 2 and 3 were combined to form a group of unfamiliar lambs with mixed food preferences as well as an aversion to the alternate food source. The lambs were tested for location and feeding activity as per the previous two experiments. During the first 10 minutes of the test the lambs foraged on their preferred grains before forming a single group and grazing the plot without any bias. Scott et al. (1995) concluded that feeding preference is a primary determinant of foraging location when lambs are reared separately and prefer different foods. To further test the effect of unfamiliarity and rearing conditions, it would have been interesting to record the grazing location of sub groups formed from two groups of mixed preference lambs (i.e. three lambs conditioned to wheat and three lambs conditioned to sorghum from one group and three lambs conditioned to wheat and three lambs conditioned to sorghum from a second group) to see if unfamiliarity affected grazing location and the extent to which lambs ate their preferred grain in the presence of unfamiliar lambs with the same feeding preference. The study by Scott et al. (1995) provides evidence that sub group formation and pasture use by herbivores is influenced by both feeding preference and social relationships.

A study by Boissy and LeNeindre (1997) investigated the physiological effect of isolating a heifer and reuniting her with either a familiar or unfamiliar peer. Twelve Friesian and 12 Aubrac 15-month-old heifers were kept as four groups of six according to breed with contact restricted between groups. The experimental set up consisted of a bail crush to restrict one animal at a time, which faced a triangular test arena that was large enough to hold all 6 heifers. A remote control gate led to a corridor that connected the test arena to the crush entrance. The use of a crush and remote control gate limited the amount of physical handling of the heifers. The heifer groups were gradually introduced to the experimental set up and testing procedure over a period of 12 days. Once the heifers were familiar with the set up, three habituation tests were performed followed by two test sessions. During the habituation tests, a test animal was restrained in the crush while the five other group mates were in the test area. After 8 minutes, a person entered the test area and moved around the edge of the area generating movement within the pen mates before leaving. This was repeated 8 minutes later and the test session ended after 25 minutes. During the test sessions the same habituation procedure was repeated except when the person left the arena the first time the pen mates were removed as well. Eight minutes later the person returned with either the five familiar pen mates or five unfamiliar heifers of the other breed. The familiar or unfamiliar peers were left in the test arena until the test animal had been restrained for 25 minutes. A single observer recorded all behavioural responses, including contact with peers, vocalisations and struggling behaviour of the test animal. Additionally, cardiac activity was recorded by a heart rate monitor at 15 second intervals during each test session and cortisol levels were measured from blood samples taken immediately upon entering the crush and again at the conclusion of the test session. Elevated levels of cortisol have been linked to stress and anxiety behaviour in cattle (Bristow and Holmes, 2007). The results of the habituation sessions showed an increase in overall activity, heart rate and cortisol levels when the test heifer was restrained. However, these levels decreased over the three habituation sessions. A marked difference was observed between breeds with Aubrac heifers recording higher levels of behavioural activity, heart rate and cortisol than Friesian heifers. During the test sessions, heifers showed a strong behavioural reaction to being isolated: isolated heifers struggled for 40% of the isolation period and their behavioural activity increased tenfold with a large increase in vocalisations. Additionally, heart rate and cortisol levels were significantly increased during this period. When peers were returned all three factors decreased although the decline in heart rate was more pronounced in the presence of familiar pen mates than unfamiliar peers. The authors summarised that social isolation is a very strong psychological stress in cattle and the extent of this effect is influenced by breed, and it was observed that Aubrac heifers were more reactive than Friesian heifers. The sight of heifers of either familiarity was enough to reduce the distress of being isolated, although the presence of familiar peers was more effective at reducing cardiac activity than unfamiliar peers and therefore suggests that familiar peers have a calming effect.

A similar test was conducted by Faerevik et al. (2006) to investigate the effect of social isolation and the presence of familiar and unfamiliar peers on the behaviour of calves. The study involved 20 Holstein Friesian mixed-sex calves that were divided into five groups of four. At the time of grouping the calves averaged 21-days-old. One group was kept out of sight of the other groups to form the unfamiliar group while three calves from each of the other four groups were selected as test animals, leaving one calf per group as a familiar stimulus. When the calves reached 6 weeks of age, the 12 test calves were subject to two different experimental tests. The first test was a social preference test, where the test calf could choose between a familiar or unfamiliar calf located at the end of a Y-maze. The Y-maze consisted of a start box where the test calf was held prior to the test that was connected to a 3 m narrow corridor. At the end of the corridor was the entrance to the two 'arms' of the Y-maze, which were also 3 m in length, where the stimulus calves were tethered. Video recording devices were used to capture the behaviour of the test calves during each session and were analysed for the time taken to enter the maze and initiate contact with either stimulus calf, the proportion of time spent in each arm of the maze and the number of social contacts with familiar and unfamiliar stimulus calves. The calves were observed for 20 minutes in the maze before being returned to their pens. The second test was a separation test where the test calves were placed in a 1.8 m x 1.8 m pen that was unfamiliar to them and observed under three different test conditions: with a familiar calf; with an unfamiliar calf; and with no other calves present. Each condition was repeated three times for each test calf. The calf's general activity, including the number of steps taken and number of vocalisations were recorded by direct observations and a heart rate monitor collected cardiac activity for the duration of the 20 minute test. The results of the Y-maze tests showed that calves spent the majority of time within close proximity to familiar stimulus calves, although there was no difference in the amount of physical contact with either familiar or unfamiliar calves. The results of the separation test showed that calves vocalised more when isolated or with an unfamiliar calf than when in the presence of a familiar calf, where no vocalisations were recorded. The test calves interacted more with familiar stimulus calves the first time they were subject to the separation test, however this effect decreased over the three repetitions. There was no difference in the amount of activity expressed by the test calf when in the presence of either familiar or unfamiliar stimulus calves, however there was a significant decrease in activity when isolated. The test calves heart rate was higher when in the presence of familiar calves than when separated with unfamiliar calves or isolated. This finding was unexpected but explained by the positive correlation between heart rate and increased activity during these tests. The results from the two tests suggested that calves prefer the company of familiar over unfamiliar peers and it is likely that the familiar calf provided a calming effect in the novel environment. In agreement with the results of Boissy and LeNeindre (1997), separation from peers caused the greatest amount of distress which led to increased vocalisation, more immobility and less exploration of the test pen. The finding that the calves did not vocalise in the presence of a familiar calf reinforces the suggestion that familiar calves provide a calming influence.

The results of studies by Boissy and LeNeindre (1997) and Faerevik et al. (2006) provide evidence that familiar peers provide a calming effect and suggest that cattle will preferentially select a familiar peer over an unfamiliar peer. This has also been found in other animal species, such as chickens (Marin et al., 2001), sheep (Boissy and Dumont, 2002) and pigs (McLeman et al., 2005). However, these experiments rely on conditioning tasks or stressful environments that may influence the behavioural response of the test animals. The effect of the presence of a familiar animal has not been thoroughly tested in cattle and is an area of research that requires further investigation.

2.7.2. Preferential relationships

A preferential relationship, or a social bond between two individuals, is '*a mutual relationship that is relatively long lasting and survives temporary separation*' (Keeling and Gonyou, 2001). Reinhardt and Reinhardt (1981) observed a cattle herd under a semi-natural environment for 5 years and found evidence of long lasting relationships between particular herd members. The semi-natural environment involved mustering the herd into yards at night but allowing the herd to graze freely during the day, with no other human interference such as milking, castration or grouping. At the beginning of the study the herd consisted of 30 cows, 3 calves and one bull. After 4 years, 74 offspring were born into the herd increasing the herd size to 108. At this time 17 bull offspring were sold and a large portion of the herd was moved on to another property, leaving the bull, 11 of the original cows and their 35 offspring for the remaining 11 months of observations. Observations were recorded intermittently over the 5 year period. The authors recorded the identity of animals that consistently grazed together and groomed together and defined a relationship as two individuals that were observed grooming or grazing together for three or more consecutive years. Relationships were assessed for the effects of relatedness between adults and calves. The authors found evidence of 36 preferential relationships between the adults: 20 relationships were observed for grooming and 16 for grazing, with 6 cohesive relationships identified where individuals were both preferred grazing and grooming partners. Within these associations, some cows were more popular than others. A single cow 'Alma' was identified as the most popular grazing partner and was also observed as the leader of all grazing movement, which may explain why others chose to remain within close proximity to her. In the grooming relationships, one cow 'Daisy' received more grooming than any other cow, although she showed no particular attributes to explain her popularity. Additionally, the direction of the associations varied according to activity: 60% of grazing associations were mutual while only 5% of grooming associations were reciprocated. Analysis of the calf associations found that sibling associations were the strongest and related calves grazed together more than unrelated calves. Although, there were still friendships observed between non-related calves in 67% of calves, which were predominately based on similarities in age and not influenced by sex. In contrast, there were no grooming association formed between calves. The associations between non-related heifer calves tended to decline when the heifers gave birth for the first time as their attention was focused on their own offspring, and it is not known if these relationships were restored once the offspring matured. In contrast, the bull-bull calf relationships remained strong. Associations between cows and their related calves were stronger than any other association for both grazing and grooming and the authors rarely observed a cow grooming a calf other than her own. Reinhardt and Reinhardt (1981) found that the cow-calf bond still remained strong even after weaning and the birth of second and third offspring and the cow retained more contact with her own offspring than non-related calves. There were no differences observed between mother-heifer and mother-bull relationships over the 4 year period. In wild populations it is expected that the males calves would be driven away from the herd when they reach sexual maturity, however the herd's management meant that the males were forced to remain in the herd thus suggesting that if no other external factors interfere with mother-bull relationships the close association may continue. In total, 83% of individuals formed associations with each other, although there were clearly popular individuals, such as Alma, who received the most grazing preferences and was also observed as the leader of all grazing movement. Reinhardt and Reinhardt (1981) summarised that the basis of relationships between cattle are founded on matriarchal families formed by attachments between siblings and cow-calf bonds, and kin relations are interconnected by friendships between non-related partners. These relationships are extremely stable and form a complex social structure of associations based on personal inter-individual attractions.

2.7.3. Allogrooming

Allogrooming has been identified as a key indicator of preferential relationships (Boissy et al., 2007). In a study by Sato et al. (1991), the authors investigated the function of allogrooming in calves. The authors observed two separate groups of mixed-sex Holstein yearlings, aged between 12 and 15 months of age, with 13 animals in group one and 14 animals in group two. The time that the group had been together varied: some calves had been together longer than 4 months, some between 3 and 4 months and others between 1 and 2 months. The dominance rank of all animals was determined during a preliminary observation period, as well as during observations recorded during the experimental period. Two calves per group were chosen as focal animals based on preliminary observations as the most frequent performers of allogrooming from group one and the most frequent receivers of allogrooming from group two. The calves were housed in a barn and fed silage twice a day, and the barn was cleaned every 5 days. To explore the effect of environmental conditions on grooming behaviour, the afternoon feed was removed and the barn was not cleaned on a regular basis for part of the experiment. Social and grooming behaviours involving the focal animals were recorded via video camera for 13 days, noting if the grooming behaviour was initiated by the receiver, referred to as solicitation, or if the grooming commenced without solicitation. On average, the focal animals performed allogrooming nearly 5 times per hour, with an average grooming bout lasting 43 seconds. The frequency of grooming increased when the barn was dirty, which provided evidence to confirm that grooming is performed for cleaning purposes. There was also more grooming when the calves had not been fed in the afternoon, which Sato et al. (1991) suggested was a displacement activity to relieve the tension created by not being fed. There was more unsolicited grooming than there was solicited grooming, however the solicited grooming tended to last for longer duration and confirms that grooming is desired by the receiver. Sato et al. (1991) also suggested that allogrooming has a tension relieving effect as some animals were observed to half close their eyes while receiving grooming, which was also reported by Brownlee (1950) when describing aspects of behavioural patterns observed in domestic cattle. Sato et al. (1991) found a positive relationship between allogrooming and familiarity, with more grooming occurring between calves that had been together the longest. There was no association between dominance rank and the performer or receiver of grooming, confirming that grooming behaviour is not dependent on social rank. Sato et al. (1991) concluded that the act of allogrooming not only has hygiene benefits, such as cleaning and parasite removal, but also has emotional properties that can reduce stress and reinforce social bonds between group members. A further study by Sato and Tarumizu (1993) investigated heart rate changes caused by the act of allogrooming. The authors fitted heart rate monitors to five steers and compared their heart rates before, during and after allogrooming when mixed with five other steers. Heart rate data was analysed only when the animals were standing and only when grooming bouts exceeded 24 seconds in duration. The heart rate data was collected for 2 minutes after grooming had ended. In total, 27 observations of grooming were analysed. The results showed a statistically significant decrease in heart rate during grooming, with the average heart rate reduced by 4 beats per minute when compared with pre-grooming rates. The heart rate returned to a level comparable with pre-grooming rates once grooming had finished. Sato and Tarumizu (1993) suggested that allogrooming has a calming effect in cattle and this may help to ease tension in a stressful situation.

The relationship between allogrooming and social preference was also explored by Val-Laillet et al. (2009). The study involved 48 Holstein cows that were grouped into six groups of eight and allowed 15 days to stabilise relationships before the experiment began. The cows were fed twice a day immediately following milking. After 21 days of continuous observations using video recording equipment, space at the feeder was reduced from 0.60 m per cow to 0.30 m per cow to investigate the effect of competition and dominance on allogrooming. The video footage was analysed for agonistic and affiliative behaviour, nearest neighbour identities and dominance rank. On average, cows performed 5-6 grooming bouts per day, which is much less than the 5 times per hour reported by Sato et al. (1991); however Sato et al.’s (1991) study involved much younger animals that were also confined in a smaller space, which may have influenced the rate of grooming. The effect of reducing feeding space resulted in less time spent at the feeder but there were no significant reductions in the number of allogrooming bouts, only the length of grooming was reduced. Val-Laillet et al. (2009) suggested that if allogrooming served to reduce tension, then allogrooming should have increased when competition was greater during feed space restriction. However there was no evidence of increased allogrooming with increased competition and the authors suggested that further studies should investigate the role of allogrooming during periods of tension, such as regrouping individuals. In agreement with Sato et al. (1991), Val-Laillet et al. (2009) found no relationship between dominance rank and time spent grooming, however there was a positive correlation between preferential relationships and grooming partners: cows identified as nearest neighbours during feeding were observed grooming each other more often. Val-Laillet et al. (2009) argued that the cows shared a mutual attraction rather than similar feeding habits, as the cows were also observed allogrooming away from the feeder and were consistently seen together over the experimental period, even when space available at the feeder was reduced and competition was increased. The findings correspond with those of Reinhardt and Reinhardt (1981) who observed preferential grooming associations between individuals regardless of their physical and social characteristics. It was concluded that allogrooming has a cohesive role in maintaining preferential relationships. The existence of preferential relationships is described as the 'fundamental element' of cattle social structure (Reinhardt and Reinhardt, 1981), thus knowledge on factors that contribute to these relationships can provide information on the basis of group social cohesion as well as a measurement of positive welfare.

2.7.4. Spatial behaviour and individual distance

The spatial relationships between individuals within a group are a characterising feature of the group's social structure. Each individual has specific spatial properties that contribute to the function and cohesion of the social system. McBride (1971) described the area that an individual will maintain free from others as a 'personal field', and will avoid entering the personal fields of others. The distance maintained between two individuals is referred to as the 'individual distance' (Hediger, 1963) or 'inter-individual distance', and the distance that an individual will allow another to approach before responding, either with aggression or avoidance (Price, 2008). The inter-individual distance between two animals results from a balance between the tendency to approach and withdraw from each other (Keeling, 1995), thus inter-individual distance provides an indication of the social attraction and relationship status between the pair. McBride (1971) described 'living space' as the space that an individual will move in, somewhere between the personal spheres of group members and the 'social distance', defined by Hediger (1963) as the maximum distance individuals will move away from the group (Fig. 2.8). The social distance is therefore an important cohesive

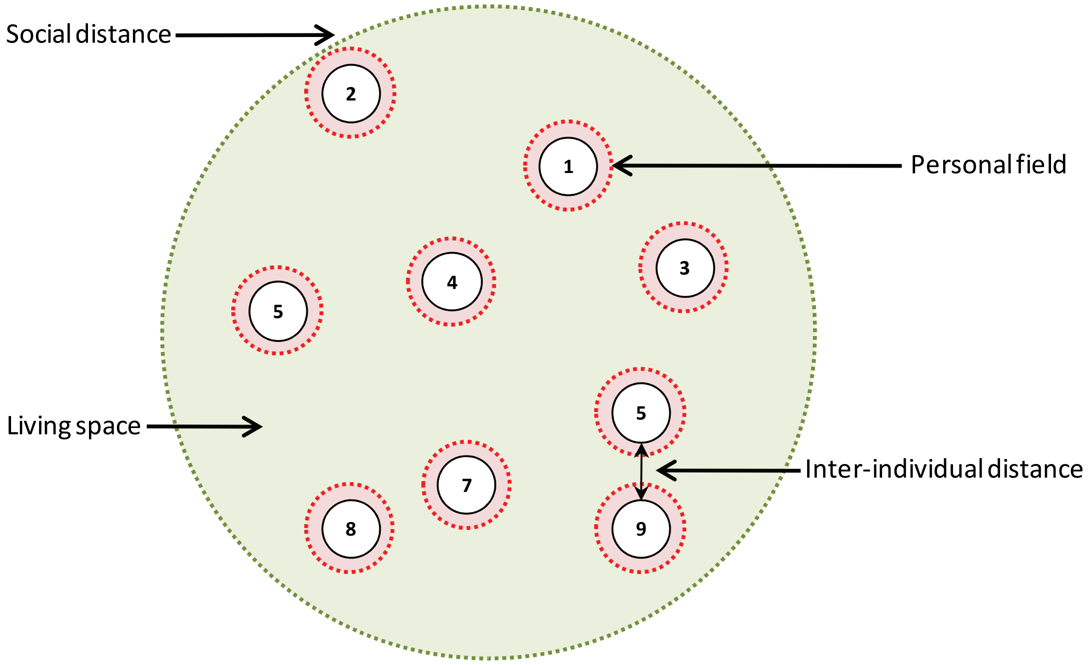


Figure 2.8. Diagrammatic example of spacing principles. The circles represent animals. The red shaded area represents an individual's 'personal field'. The green dotted line represents the 'social distance' or the maximum distance that an individual is willing to move away from the group, thus social distance is an individual measure that is defined by the centre of the group. The green shaded area represents the 'living space', or the space that individuals will move in, defined by the social distance and the personal fields of others.

factor keeping group members together. Maintaining close proximity to group members also strengthens social cohesion by facilitating communication and information transfer within the group, such as foraging opportunities and predator detection (Warburton and Lazarus, 1991).

Murphey and Duarte (1990) investigated the effect of familiarity on spatial associations by introducing three unfamiliar groups of cattle together into a large paddock (between 120 to 480 ha). The groups consisted of 94 cows of the Caracú breed, 118 cows of the Nellore breed and 142 cows of the Gyr breed. The groups had been together for over a month prior to the introduction and had not been in contact with animals from the other groups. Observations of nearest neighbours were recorded four times after the groups were introduced. The authors found a strong tendency for same-group members to be nearest neighbours. The authors went on to investigate the effect of breed on nearest neighbour occurrences by observing groups of mixed-breed individuals that had been raised together when introduced to same-breed cows that had been raised together. Murphey and Duarte (1990) found that familiarity was the strongest predictor of nearest neighbour frequencies:

cows that were familiar with each other were more frequently found within close proximity to group members than non-group members. This feature of a social group has been observed regardless of the amount of space available (Price, 2008).

There are many factors that affect the spatial distribution of a group. At a functional level, spatial positioning is influenced by anti-predation strategies and resource distribution, whilst at a local level, the dominance hierarchy and behavioural activity influences the distance between individuals (Keeling, 1995). The dominance relationship between individuals will affect their spatial distribution, with animals further apart in rank tending to maintain the greatest distances (e.g. Manson and Appleby, 1990). Activities associated with greater predation risk, such as resting, will draw individuals together, while competitive activities, such as grazing, will keep individuals apart (Keeling, 1995). The average distance individual cattle keep between themselves and other group members when resting is 2-3 m, compared with 4-10m when grazing (Broom and Fraser, 2007). Additionally, the size of the social group and thus the number of individuals available to provide protection influences the distance individuals maintain between themselves and others. In the study by Rind and Phillips (1999) (section 2.6.3) that investigated the effect of group size on behaviour, the authors found that spacing between individuals in groups of four was smaller than inter-individual distances in groups of 16 (6.5 m and 13.8 m, respectively). Rind and Phillips (1999) suggested that the smaller distances were a result of greater cohesion between the individuals in response to greater predation fear. Thus, maintaining close spatial proximity reinforces a sense of safety and protection provided by group members.

2.7.5. Sociability

The distance between animals can provide not only an indication of the relationship strength between each pair within the group, but also the individual's level of sociability. Sociability is the '*tendency to be close to others*' (Sibbald et al., 1998), and can therefore be predicted based on consistent spatial patterns between group members. Sibbald et al. (1998) developed a sociability index that was later refined by Sibbald and Hooper (2004), which was used to rank individuals based on their sociability by calculating the proportion of time that each individual was recorded as the nearest neighbour of any other animal in the group. Sibbald and Hooper (2004) describe this method using Scottish Blackface sheep as an example. Four groups of 11 animals were observed in a grazing environment over a 3 week period, noting the identity of each animal's nearest neighbour at every 5 minute scan. To calculate the sociability index, the number of observations that each animal was recorded as a nearest neighbour of all other animals was summarised in a matrix, with focal sheep listed across rows and neighbours listed in columns. The values for each cell were divided by the total number of observations recorded, and the column totals were divided by 100 to give a sociability index for each animal. The sociability index values ranged from 0 to 1.0, with larger numbers indicating more sociable animals. To investigate the application of the sociability index, Sibbald and Hooper (2004) explored the relationship between sociability and the distance individuals would move away from their group to feed. From each of the four groups, two sheep with high sociability indices and two sheep with low sociability indices were selected to take part in a food motivation test. The sheep were introduced to three different grazing environments: a control treatment where a test animal was placed in a bare 65 m plot separated from group mates by a wire fence; a near treatment, where the test sheep had to travel 15 m from the penned group mates to reach preferred forage; and a far treatment, where the test animal had to travel 35 m to reach the desired forage. Prior to testing, the group were confined for 1 hour without food. Observations began 2 minutes after the test sheep was released, and the behaviour of the test animal (e.g. grazing, standing, lying) and its distance from the penned sheep was recorded every 30 seconds over a 75 minute period. At 15 minute intervals, the bite rate of the test animal was also recorded. The authors found that overall the highly sociable sheep remained closer to the penned sheep on all treatments than the less sociable sheep, while less sociable sheep tended to spend more time grazing with faster bite rates than highly sociable sheep. Sibbald and Hooper (2004) found that there were significant differences between sociability types in the distances they travelled to graze and suggested that the distance between group mates and food in the near treatment provided an environment similar to a grazing situation, thus identifying endogenous sociability tendencies. However on the far treatment, 35m is greater than nearest neighbour distances normally observed between Scottish Blackface sheep and the distance may have been too far to create a trade-off for any of the sheep, and there were no clear differences between sociability types at this distance. Sibbald and Hooper (2004) suggested that moving away from the social group may have elicited a fear response of being socially isolated, and may account for the faster bite rate to reduce the time away from the group. It is also suggested that the lower bite rate by the more sociable sheep may indicate greater vigilance and anxiety at being separated from their peers, whereas the less sociable sheep appeared less fearful when at greater distances from the group. Sibbald and Hooper (2004) concluded that sociability affected the choice between foraging and staying close to peers when the food source was close, however when the foraging source was a greater distance away other factors, such as fear, influenced the decision to remain with peers or to move away.

The relationship between sociability and the trade-off between feeding and social companionship was further investigated by Sibbald et al. (2006). The authors designed a test to measure an individual's motivation to remain close to a pen of group mates by recording the distance that the individual would move away for a highly palatable food. The experiment involved 40 Scottish Blackface sheep that were kept in four groups of 10 animals, and their sociability index was calculated using the same method mentioned above. The animals were exposed to two different test conditions: a control test, where no food was offered, followed by three pellet tests, in which pellets were offered in bowls at 5 m increments down the centre of a 65 m test arena. During each test, a single sheep was released into the arena and the animal's behaviour was recorded every 30 seconds over a 30 minute period, while all bowl visits and walking and vigilance behaviour were recorded as they occurred. Sibbald et al. (2006) found that highly sociable sheep showed greater levels of vigilance, took longer to explore all of the food bowls during the first pellet test and remained in closer proximity to the penned group than less sociable sheep. Sibbald et al. (2006) suggested that the highly sociable sheep were more anxious about moving away from the group and this limited their motivation to obtain a desired food some distance away.

The work by Sibbald et al. (2006) on sociability in sheep explored the fundamental relationship between spatial proximity and sociability, and demonstrated how individual sociability effects behaviour and foraging decisions. Future investigations should consider extending the application of these principles to cattle systems, where knowledge on individual social tendencies and spatial behaviour would provide a valuable tool when assessing social behaviour and relationship status.

2.8. Communication and individual recognition

Communication between individuals occurs when a signal expressed by one individual is received and responded to by another (Wilson, 1975). The function of communication is to share information, such as details on an individual's internal state, such as fear, hunger or excitement, their environment, such as the appearance of a predator, or to recruit others to the same location, such as an attractive food source (Millman and Duncan, 2001). Other functions of communication also include identifying and locating others, giving orders and reinforcing social status (Hart, 1985). Therefore, communication is essential for establishing and maintaining social organisation within a group (Leuthold, 1977; Murphey and Duarte, 1990; Lindberg, 2001). Communication between animals occurs via four signals, including visual signals, such as posture and movement, auditory signals, such as vocalisations, olfactory signals, such as scents, and tactile signals, such as touch or physical contact with others. The sensory modalities of cattle are summarised as a panoramic field of vision with limited depth perception, acute hearing capable of detecting high frequency noises, and sensitivity to touch and odours (Grandin, 1980).

Similar to communication, recognition is essential for social interaction (Arnold, 1985). Recognition relies on memory and recollection of previous social encounters and behavioural observations of others (Broom and Fraser, 2007). Recognition also uses visual, auditory, olfactory and tactile sensory cues. The behaviour of cattle provides evidence that individuals are capable of individual recognition, in particular is the ability to establish and maintain a dominance hierarchy: avoiding dominant animals suggests subordinate individuals remember the outcome of past encounters. Additionally, evidence of individual recognition is supported by other behaviours: fighting between unfamiliar animals suggest that individuals discriminate between familiar and unfamiliar; and preferences for grooming and grazing partners suggests individuals recognise specific herd mates from other group members (Millman and Duncan, 2001). Bouissou (1980) stated that the number of individuals that cattle are able to recognise had not been established and 30 years later it is still not readily known. Studies in sheep have shown that they are capable of recognising images of 50 different sheep faces and can retain this information for over 2 years (Kendrick et al., 2001). Broom and Fraser (2007) reported that cattle are able to recognise between 50 and 70 different individuals, although they provided no evidence to support this claim. It is suggested that there is a maximum number of individuals that cattle are able to recognise and individual recognition will diminish with increasing group size, as knowledge on all individual social positions becomes increasingly difficult to maintain (Price, 2008). The processes of recognition and communication overlap (Hart, 1985), thus the function of each sensory cue is discussed in terms of both recognition and communication.

2.8.1. Visual signals

The visual display of an animal's posture and movements are primarily related to transmitting information on social status, such as submission or repulsion (Arnold, 1985), while vigilance behaviour can be used to transmit information on the presence of a fear inducing stimulus. A study by Welp et al. (2004) investigated the visual displays of cattle in response to fear, in particular vigilance behaviour, which was classified as an alert response when a cows head was in a raised position. The authors conducted two separate experiments. In the first experiment, 40 Holstein dairy cows were exposed to two different fear-eliciting stimuli, including a dog and an unfamiliar person, and a control where no stimuli were present. The cows were tested on 12 separate occasions with each of the three test factors over a 5 week period. The cow's behavioural response was recorded by direct observation. The second experiment used 24 Holstein cows from the first experiment and exposed them to people that had treated them gently, people that had treated them adversely or people that were unfamiliar to the cows. Observations were recorded via video recording equipment. The authors found that the presence of a dog resulted in the greatest amount of vigilance behaviour, while there was no difference between vigilance in response to an unfamiliar person or the control with no stimulus present. Additionally, there was a habituation effect towards the fearful stimuli as was shown by a decrease in vigilance from 84% in the first session to 43% at the end of the experiment. Welp et al. (2004) suggested that the novelty of the dog induced greater fear as compared with people, which were encountered on a daily basis. The cattle in experiment two showed the greatest amount of vigilance towards the aversive handler than either the positive handler or an unfamiliar person, while there was no difference between vigilance displayed in the presence of a person who had treated them gently or an unfamiliar person. In contrast to the first experiment, the cows showed no sign of habitation; although, the level of vigilance recorded was comparable to the final levels recorded in experiment one. Welp et al. (2004) summarised that the results prove that cattle are able to recognise the difference between handlers and that cows alter their vigilance response according to the threat posed by the stimulus, rather than unfamiliarity. It was concluded that fear induces vigilance behaviour in cattle.

The tail position of an animal can also transmit information to others. Cattle will elevate their tail during various activities, such as running, fighting, greeting or suckling, and equally cattle will depress their tail when cold, chased or frightened (Kiley-Worthington, 1976). However, it is unclear whether tail posture is a relevant signal for others or simply an expression of an individual's internal state (Leuthold, 1977). It is suggested by Kiley-Worthington (1976) that tail movements are displayed as a component of overall body posture, rather than a standalone communication signal.

It is thought that visual cues are the most important for recognition (Schloeth, 1961). Cattle have been shown to discriminate between individuals using physical features such as body weight and horn size (Bouissou, 1972). A study by Hagen and Broom (2003) investigated the ability of heifers to discriminate between familiar peers using live animals as stimuli. Ten mixed-breed heifers that had been reared together were used in the study. A Y-maze was used to measure the choice of each test animal with a given stimulus. The Y-maze consisted of a holding pen located 10 m away from the start of the maze arms. Four heifers were trained as stimulus heifers that were tethered at the end of each arm while six heifers were designated as test animals. The four stimulus heifers were allocated into pairs. In pair A, one heifer was a cross-bred while the other was pure-bred and in pair B, both heifers were pure-bred. Each test animal was subject to two discrimination tests. In the first round, test animals were allocated one animal from either pair A or B as a positive stimulus while in round two, the alternate pair was used and a different stimulus heifer allocated to the test heifer. The heifers were first introduced to the maze set up during a learning phase, where each heifer was led into the maze by a human experimenter and allowed to make a choice between each stimulus heifer. A food reward was offered by the experimenter if the correct choice was made. The food was dispensed in a bucket behind the correct stimulus heifer while the bucket behind the incorrect heifer remained empty. If an incorrect choice was made the test heifer was confined in the maze arm for 30 seconds before being allowed to access food in the other arm. A learning criterion of 16 trials without any incorrect choices or 20 trials with one incorrect choice was set. Once the learning criterion was met, the heifers advanced to the discrimination tests. During the testing phase, the maze was altered so that the holding pen was connected to the start of the Y-maze, there was no food present in the buckets and the experimenter was not present to lead the heifers into the maze. When a correct choice was made (i.e. the test animal selected a heifer that had previously been associated with a food reward), the experimenter gave the heifer a food reward but no food was offered if the choice was incorrect. Each test heifer was subject to between five and eight discrimination sessions in round one. The same learning criterion was set prior to the second round of discrimination tests where the stimulus pairs were swapped and a new correct stimulus was assigned. Three heifers failed to reach this criteria thus only three heifers were tested a second time. Additionally, two heifers that reached learning criterion quickly were subject to a retention test where they were tested with stimulus heifers from round one. Video recordings were used to capture the behavioural responses of each heifer during the tests and analysed for the proportion of correct outcomes as well as behavioural activity. The results showed that overall the test heifers learnt to discriminate between pair

A (cross-bred and pure-bred) quicker than individuals in pair B (both pure-bred). The two individuals that perfected the discrimination tasks were also found to choose correctly during all eight retention trials, proving that the heifers retained the information they had learnt for at least 12 days. Hagen and Broom (2003) concluded that the heifers used individual attributes to identify familiar peers, which was easier when additional cues such as breed differences were present.

A further study on individual discrimination using visual cues was undertaken by Coulon et al. (2007). In this study, photographic images were presented to 10 Holstein heifers and the heifers had to make correct choices based on a prior learning task. Before tests began, the heifers were subject to a learning phase where each heifer was required to choose between a photograph of a cow of the same Holstein breed and a sheep. The experimental set up involved a test pen where the heifers were initially held and presented with two images 2.5 m away. Once the heifer had viewed both images an experimenter opened the gate and the heifer could walk towards one of the two images. For each pair of photographs, the image of the cow was consistently associated with a food reward that was accessed by pushing a panel that the image was attached to. If an incorrect choice was made the panel was blocked making the food inaccessible. Heifers were required to meet learning criteria of four correct choices out of two consecutive five-trial sessions before they could proceed to the experiment. In the first experiment, the heifers were required to discriminate between 10 faces of different cattle breeds, including the same image used in the learning phase, and 10 faces of other domestic species, including the sheep presented in the learning phase and images of horses, a goat and a dog, thus 18 new images were presented. Food rewards were offered for choosing the cow image. When the heifers had successfully completed the first experiment, a second experiment was undertaken where the food reward was offered for selecting faces of other domestic species over images of cow faces. The same learning procedure as experiment one was undertaken prior to experiment two, where the heifers had to discriminate between an image of a cow and an image of a sheep, except this time a food reward was offered for choosing the sheep. The same set of 20 images from experiment one was used in test phase of experiment two. Coulon et al. (2007) found that nine out of the ten cattle in experiment one were able to discriminate cattle faces from faces of other animal species within 4 sessions, ranging from 2 sessions for the fastest and 9 sessions for the slowest. Experiment two proved to be more challenging than experiment one, taking an average of 8 sessions to reach the learning criterion, ranging from 4 to 13 sessions. Coulon et al. (2007) concluded that the heifers were able to discriminate individuals using visual cues alone as opposed to live stimuli in the study by Hagen and Broom (2003).

The studies by Hagen and Broom (2003) and Coulon et al. (2007) on cattle recognition were based on learning tasks and experimental settings. These studies show that cattle are efficient task learners and can memorise images, and the results provide evidence that cattle use visual cues to recognise others. Murphey (1990) investigated the sensory cues that calves use to identify their mothers in a natural environment, and identified specific characteristics that assist individual recognition. Forty six cow-calf pairs of the Gyr breed were chosen for the study based on the cow's coat colour, either red or white. The cows were tethered to a feed trough with approximately 4 m between cows and the calves were released into the same yard one or two at a time. Two observers were present to record the behaviour of one focal calf at a time, noting the identity of the cow it approached, the colour of the cow's coat as well as the response of the cow, either rejection or a successful nursing bout. If a calf approached a cow other than its mother an error was recorded. The procedure was repeated six times and each calf was recorded twice. The initial response of a calf was to approach a cow based on visual discrimination and then attempt to smell or lick her. Errors were made 68% of the time, which was much higher than the authors had anticipated. When errors were made, calves tended to approach cows that were the same colour as their mothers rather than mothers that matched their own coat colour. Additionally, younger calves tended to make more errors than older calves. Murphey (1990) suggested that recognition is an adaptive learning process in calves, which may account for the high proportion of errors. The calves had access to food prior to rejoining their mothers and may not have desired milk. Murphey (1990) concluded that calves initially use visual cues to discriminate between individuals.

2.8.2. Auditory signals

Cattle vocalisations provide information on the physiological state of the animal, as well as its motivations and intentions (Watts and Stookey, 2000). Vocalisation can also be used to communicate distress in response to pain, fear and frustration (Millman and Duncan, 2001). An example of this was in the studies by Boissy and LeNeindre (1997) and Faerevik et al. (2006) where heifers and calves vocalised significantly more when isolated and distressed. Vocalisations are not always situation specific and are also expressed in response to excitement and interest in a stimulus (Kiley, 1972), for example when anticipating a desired event such as food or milking (Bouissou et al., 2001). Additionally, individual cattle have characteristic calls that can be used to distinguish one individual from another (Kiley, 1972). A study by Hall et al. (1988) investigated individual differences in vocalisations of bulls in a herd of free-ranging Chillingham cattle. The herd varied in size between 46 and 57, but included at least 11 mature bulls and 3 calves less than 6 months of age. The authors used a tape recorder to capture the vocalisations of any animal that vocalised over a 2 day period and the sounds were analysed using various frequency plots. The recorded vocalisations were compared with over 500 hours of visual observations, which defined the nature of each call as either maintenance, self expression, social or other. The authors found that each bull had its own characteristic vocalisation and bulls were able to alter their calls depending on a change in social context, such as to express its dominance status. The dominance status of each bull had previously been documented and the authors could interpret differences between calls in relation to their dominance status, with dominant bulls producing more calls of a higher frequency than subordinate bulls. The difference in call frequency may be related to an animal's size, which has been found to be positively correlated with dominance (e.g. Bouissou, 1972). Hall et al. (1988) found an effect of season on the vocalisations made by bulls, with more calls made during spring and summer, while cows vocalised more during winter. Additionally, the authors identified differences in sound between mature bulls and calf bulls and could thus distinguish the age of a bull from its vocalisation. It was concluded that individual cattle have specific calling characteristics that can be used to identify their age, sex and dominance status.

A study by Barfield et al. (1994) investigated the ability of calves to identify their mothers using only auditory cues. The study followed on from Hall's (1988) study, which only recorded a few vocalisations from cows and calves and it was not determined if cows and calves calls were also individually distinctive as bulls. The authors recorded the vocalisations of 9 Hereford cows when separated from their 2-week-old calves. When the calves were 3, 4 and 5 weeks old, each calf was tested for their response to recordings of their own mother and a non-related cow. The calves were placed in a 7 x 4 m test arena with two speakers placed diagonally opposite each other. A recording from the calf's mother was played through one speaker while the non-related cows call was played through the other, with the position of the mother's call alternated between speakers to control for side preferences. During the test, calls from the calf's mother and the non-related cow were played in an alternate sequence with a 1 minute silent interval between each call until a total of three calls from each cow were played. The calf's behaviour and the amount of time spent within

2 m of each speaker were recorded by visual observations. The authors found that calves consistently spent more time within close proximity to the speaker that amplified their mothers call than the speaker playing the non-related cow's call, irrespective of the calf's age. Only two calves vocalised in response to hearing their mothers call and the authors summarised that cows are more likely to vocalise when separated from their young than calves due to the calf's vulnerability to predators. Thus, the lack of vocalising by calves is most likely an anti-predatory response. Barfield et al. (1994) concluded that calves are able to recognise their mothers by auditory cues alone and distinctive vocalisations are important for mother-offspring relationships.

2.8.3. Olfactory and tactile signals

There is less literature published on the function and process of olfaction cues for recognition and communication in cattle than visual and auditory cues, and even less on the role of tactile cues. Animals can communicate specific information via scents using three modes: (i) scents originating from the body that transmit information on an individual's identity, physiological status or other characteristics; (ii) scents contained within urine and faeces; and (iii) scents produced by glands used to mark specific features of the environment, such as a territory (Leuthold, 1977). The main functions of chemical signals are to convey information on reproductive status, facilitate bonding particularly between a mother and offspring, identify territories and as a response to stressful situations (Arnold, 1985). A study by Boissy et al. (1998) investigated the behavioural reactivity of heifers to the presence of urine from stressed peers. Four groups of five 12-month-old Aubrac heifers were exposed to two different test conditions. In the first test, heifers were individually placed in a 6 x 4 m test pen and given access to a bucket of food elevated 0.80 m off the ground. Inside the bucket was a panel of fine wire mesh located 0.15 m from the bottom of the bucket where urine from stressed or non stressed heifers was dispensed and 1 kg of food was placed onto the mesh to hide the urine from view. Stressed urine was collected from heifers other than the test animals that had been tethered continuously for 12 hours to evoke a stress response while non-stressed urine was collected from the same heifers after they had been tethered continuously for 30 days. Behavioural measurements and plasma cortisol levels indicated that the heifers habituated to tethering and were no longer stressed after 30 days. Visual observations were used to record the behaviour of the test heifers including feeding, sniffing, vocalising and overall activity. Two groups of heifers were tested with urine from stressed heifers and two groups were tested with non-stressed urine. The authors found that test animals exposed to urine from stressed animals took longer to feed and spent less time eating than heifers exposed to urine from non-stressed animals, otherwise the behaviour between the two treatments was the same. In the second test, a novel object (an 0.80 m tall traffic cone) that had been sprayed with urine from stressed or non-stressed animals was positioned in the test pen where the food bucket was located in the previous test. Immediately prior to entering the test pen the test heifers were exposed to the same type of urine it was going to be tested with. Two of the four groups from test one were exposed to opposite treatments in test two, such that one group tested with stressed urine in the previous test was tested with non-stressed urine and similarly one group exposed to non-stressed urine in test one was tested with stressed urine in test two. The results showed that heifers tested with urine from stressed animals took longer to enter the test pen, avoided the area surrounding the novel object and spent more time immobile than heifers exposed to urine from non-stressed animals. Boissy et al. (1998) concluded that heifers can perceive the state of stress in peers via olfactory cues present in urine and actively avoid the source of the odour.

The function of touch as a communication signal is not as well defined as visual, auditory and olfactory signals (Leuthold, 1977). Nevertheless, it is still a relevant form of communication between individuals, particularly in mating behaviour, mother-offspring relationships, establishing dominance rank and maintaining preferential relationships through affiliative behaviours such as allogrooming (Bouissou et al., 2001).

2.9. Changing group composition

Introducing new individuals into a group or regrouping existing group members is a common practice on commercial farms, where groups are based on similar attributes such as age, sex or production requirements. The presence of an unfamiliar animal is considered a threat to an individual’s social status as well as competition for resources (Price, 2008). This disruption creates social stress as the new social structure is established and can adversely affect animal welfare and reduce production. Social stress is defined as ‘*abnormal or extreme physiological or behaviour adjustments and animal has to make in order to cope with its social environment*’ (Syme and Syme, 1979). Social stress is an interdependent factor, such that stress experienced by one animal will influence the stress levels of other group members (Zayan and Dantzer, 1990). The social stress experienced by a group will persist until social stabilisation is reached, thus the time taken for a social group to be considered stable is important both in terms of animal welfare and production.

As well as experiencing social stress, newly introduced animals are faced with various environmental factors that can also create stress. The new individuals may be faced with an unfamiliar environment, separation from familiar group members, a change in group size and human handling (Zayan and Dantzer, 1990; Newberry and Swanson, 2001). It is therefore uncertain what key factors are responsible for the behavioural changes associated with mixing (Newberry and Swanson, 2001).

2.9.1. The effect of mixing unfamiliar animals on production

In cattle, behavioural changes resulting from the social stress of mixing unfamiliar animals can result in high levels of agonistic behaviour immediately following introduction. A study investigating agonistic behaviour in bulls and steers following regrouping was conducted by Tennessen et al. (1985). Thirty-two bulls and 32 steers were formed into eight groups of eight animals, with bulls and steers housed separately. When the animals were 9, 12 and 15 months old, they were regrouped so that each animal was grouped with six strangers and one familiar pen mate. The groups were observed for 9 hours per day for 10 days. There were immediate increases in agonistic behaviour, with bulls showing the greatest amount of aggression. The greatest increase in agonistic behaviour was seen during the second regrouping when animals were 12 months of age, although the average fight length was less. Additionally, the decline in agonistic interactions was more rapid at 12 and 15 months of age, suggesting that the animals had gained experienced from their first regrouping encounter. After 10 days, there were very few observations of agonistic behaviour by both bulls and steers at all three ages. Tennessen et al. (1985) concluded that the steers were behaviourally less mature than the bulls, which led to their lowered aggression rates and the differences between bulls and steers increased with age.

The occurrence of agonistic behaviour is not restricted to males, with female cattle showing similar agonistic responses to newly introduced individuals. Kondo and Hurnik (1990) investigated social stabilisation in dairy cows following regrouping in three groups of dairy cattle. Thirty-two Holstein dairy cows were formed into two groups of 16 for a period of 8 weeks (groups A and B), before eight cows were randomly selected from each group to form a third group of 16 cows (group C). Behavioural observations lasting 2 hours were carried out immediately following each introduction, then every 48 hours up until 18 days post-mixing. For all three groups, the greatest number of agonistic encounters were observed during the 2 hours immediately following regrouping, and reached between three and five times the amount of agonistic encounters observed 8 weeks later. The level of agonistic interactions tended to decline thereafter. The authors separated physical from non-physical interactions, and found that immediately following mixing the ratio of physical from non-physical interactions was around 80% physical to 20% non-physical interactions for both groups A and B. After 4 days the ratio changed and the non-physical interactions accounted for over 60% of all interactions for groups A and B; the authors determined the groups to be socially stable at this ratio. However, the cows in group C changed their behaviour relatively faster than groups A and B, and the proportion of non-physical interactions exceeded physical interactions between 2 and 4 days post-mixing. The findings highlight that immediate increases in agonistic behaviour are short-lived and affected by the previous mixing experience of the individuals. Kondo and Hurnik (1990) concluded that the ratio of 40% physical interactions to 60% non-physical interactions was a useful measure to determine social stabilisation in newly introduced cattle.

The study by Kondo and Hurnik (1990) showed the importance of stabilisation in agonistic behaviours as a measure of social stabilisation, however, social stress caused by the presence of an unfamiliar individual does not always result in agonistic behaviour, and can be expressed by changes in physiological and psychological behaviours (Zayan and Dantzer, 1990). Several studies have investigated the behavioural changes resulting from the social stress of mixing unfamiliar animals. A study by Gupta et al. (2008) investigated the effect of repeatedly regrouping and relocating 72 Holstein-Friesian steers. The steers were housed in 12 groups of six steers and assigned to either control or regrouped treatments. Those in the regrouped treatment experienced six regrouping and relocation events, where each individual was introduced to a completely new set of group mates in a new pen and allowed to stabilise for 14 days before being regrouped and relocated again. The control steers remained in the same pen with the same pen mates for the duration of the experiment. The steers behaviour and body contact were observed for 1 week following each regrouping and relocation via video recording equipment. Gupta et al. (2008) found that the regrouped and relocated steers spent less time lying and more time standing than the control steers for the first day following the first relocation and regrouping, and suggested this was in response to the higher level of competition for lying space and also a defensive response to avoid being threatened while lying down. The difference in lying and standing disappeared following the first regrouping and relocation, which the authors suggested was a partial adaptation to the social stress experienced by the steers. The steers used in Gupta et al.'s (2008) study were not completely unfamiliar, as they had previously been housed within sight of each other, and this may have influence the rate of stabilisation within groups. Nevertheless, the results clearly show that regrouping had an effect on the lying and standing behaviour of the steers.

A study by von Keyserlingk et al. (2008) also investigated the behavioural effects of regrouping dairy cows, specifically examining feeding behaviour, social behaviour and milk production. Eighty cows were divided into four groups of 11 and three groups of 12. Four cows from each of the three groups of 12 were selected as focal animals. The focal cows were observed in their original groups for 3 days before being introduced into one of the four groups of 11 and observed for a further 4 days, thus the stocking rate for the introduced cow remained constant. Observations were continuously recorded via video equipment and analysed at 1 minute intervals, while data loggers attached to the focal cow's hind leg were used to record the total number of lying bouts and duration of lying. The authors compared behaviours pre- and post-mixing, and found no change in the total amount of time spent feeding, however after regrouping less time was spent at the feeder immediately following food dispersal, suggesting competition between the focal cow and the new group members. Competition was also reflected in the increased number of times the focal cow was displaced from the feeder in her new group as compared with her home group; this effect gradually decreased and had disappeared after 3 days post-mixing. In comparison with the study by Gupta et al. (2008), von Keyserlingk et al. (2008) also reported a decrease in lying behaviour immediately following regrouping, although this effect was only evident on the day of introduction. The authors attributed the lower lying rate to the focal cows avoiding displacing other cows from the lying area. Allogrooming was also affected by the introduction, with focal cows receiving and performing less allogrooming over the first 3 days post mixing before returning to baseline levels. von Keyserlingk et al. (2008) also found a decrease in average milk production by 3.7 kg on the day of introduction, which returned to baseline levels the following day. The results of von Keyserlingk et al.'s (2008) study determined that the disruption caused by introducing a single animal into a small stable group affected the introduced cows feeding behaviour, social behaviour and milk production, with allogrooming behaviour taking the longest to stabilise.

In addition to the behavioural disruptions reported, others have found mixing cattle to effect short term feed intakes leading reduced weight gain and milk production. In a study by Nakanishi et al. (1991), the authors investigated the behavioural and physiological response of eight horned Japanese Black cattle to the introduction of a single cow. The cattle were housed in a 225 m^2 experimental dry-lot (approximately 15 m x 16.5 m) and fed supplementary forage twice per day. The group was observed for all social behaviours for 2 days prior to the introduction and 5 days post-introduction, with 8 hours of observations recorded each day. The physical characteristics of each individual (e.g. body weight) were recorded pre-introduction and 11 days post-introduction. The authors observed an immediate 4-fold increase in agonistic interactions following introduction. The majority of these interactions were non-physical, which tended to decline over the next 7 days. Nakanishi et al. (1991) suggested that the increase in agonistic behaviour reflected investigation of the new cow with the resident cows to establish her social rank. The behaviour could also represent displacement behaviour or frustration as a result of being removed from her previous group. Similar allogrooming patterns were found by Nakanishi et al. (1991) as reported by von Keyserlingk et al. (2008), which tended to decline over the first 4 days post-mixing before gradually returning to near baseline levels after 7 days once agonistic interactions had declined. Nakanishi et al. (1991) suggested that allogrooming, being an affiliative behaviour, counter balances the negativity of agonistic interactions. The introduced cow showed a 13 kg weight loss over the 11 days post-mixing, while half of the group also lost weight (between 2 and 8 kg). The feeding behaviour of the cattle was not reported nor was the amount of feeding space available per animal, thus it is unknown if there was a large reduction in time spent feeding or competition at the feeder to explain the weight loss experienced by the cattle, however the authors attribute the weight loss to the social stress of introducing a new animal into an established cattle herd. Although the results reported by Nakanishi et al. (1991) are noteworthy, greater replication and detail of the study would provide a better understanding of the relationship between weight loss and the introduction of new individuals into a stable group.

A study by Hasegawa et al. (1997) explored the effect of regrouping dairy cows on production. Two groups of lactating Holstein heifers housed in a group of 28 (group A) and a group of 23 (group B) were used in the trial. Fourteen heifers from group A and 12 heifers from group B were selected for exchange between the two groups. All agonistic interactions between group members were recorded 5 days pre-mixing and 5 days post-mixing and used to determine the dominance rank of each individual. Social behaviour observations of the exchanged heifers were recorded at 5 minute intervals over a 24 hour period on one day pre-mixing and days 2, 9 and 15 post-mixing. Of the 26 heifers that were moved, only six of these retained their level of dominance, or gained dominance rank, after regrouping. Overall, the exchanged heifers showed a significant reduction in weekly milk yield during the second week post-mixing. The authors discovered a relationship between change in dominance rank and milk production: animals experiencing the greatest decrease in social status had the greatest reduction in weekly milk production. Heifers with the greatest loss in dominance status produced 3.5% less milk in the first week and 5.7% less milk in the second week following mixing. The decrease in milk production may be related to the decrease in time spent feeding, standing and lying. These behaviours returned to baseline after 15 days post-mixing, however average milk production was still below pre-mixing levels after 15 days. The results of Hasegawa et al.'s (1997) study reflect those of von Keyserlingk et al. (2008) in terms of the behavioural and production changes associated with regrouping dairy cows, however von Keyserlingk et al. (2008) only observed production losses on the day of introduction with behavioural stabilisation occurring within 3 days post-mixing. The longer term production and behavioural changes reported by Hasegawa et al. (1997) may be related to the extensive disruption created by exchanging half, or more than half, of the group at the one time. When new groups are formed, the resultant social order is based upon a collection of pair-wise interactions between all group members, thus with larger numbers of individuals stabilisation is expected to take longer (Tennessen et al., 1985). This is reflected in the results of Hasegawa et al.'s (1997) study when compared with the studies by von Keyserlingk et al. (2008) and Nakanishi et al. (1991), which explored the effect of introducing a single animal into an established herd, resulting in short term disruptions to behaviour and production. The welfare and production implications of mixing unfamiliar individuals suggests the need for a greater understanding of the processes involved in familiarisation in order to create welfare orientated management practices.

2.9.2. Social stabilisation following mixing unfamiliar animals

Familiarisation has previously been documented in cattle by recording the level of agonistic interactions between individuals and defining stabilisation as the time it takes for non-physical interactions to predominate physical interaction and the ratio of non-physical to physical agonistic interactions remains constant (e.g. Kondo and Hurnik, 1990). There are varied results in the literature, ranging from 3 to 15 days. Of the shortest stabilisation time, Grant and Albright (2001) summarised that the negative impacts of regrouping dairy cows lasts approximately 3 days, which is consistent with von Keyserlingk et al.'s (2008) results investigating the disruption experienced by the introduced cows. However the single group study by Nakanishi et al. (1991) reported behavioural stabilisation after 7 days, while the results from Gupta et al.'s (2008) study on regrouping and relocation concluded that the regrouped steers developed social bonds within 14 days and the time taken to establish social bonds decreased with increasing regrouping and relocation experience. The study by Hasegawa et al. (1997) reported behavioural stabilisation 15 days post-mixing, although milk production was still below pre-mixing levels at this time, suggesting that the new social groups had not stabilised and provides evidence that stabilisation may take longer when larger numbers of individuals are introduced simultaneously. The majority of these studies ceased recording behavioural observations after 14 days, however a study by Sato et al. (1990) monitored the behaviour and interactions of five heifers introduced into a group of 18 cows over a 3 month period and found that up to 45 days was required before the new heifers were completely integrated into the herd. The results of this study suggest that longer term subtle changes are occurring as the unfamiliar is incorporated into the group and may indicate that individuals continue to experience social stress during this time. The rate of stabilisation will depend on various animal factors, such as the breed, age, gender and previous mixing experience of the individual, as well as various environmental factors, such as the availability of food and water, the space available for each animal and the number of animals in the group (Kondo and Hurnik, 1990). The varied reports of the extent and duration of behavioural and production disruption in the literature is therefore a reflection of the numerous endogenous and exogenous factors that affect the integration of new individuals into an established herd.

2.9.3. Re-grouping strategies

There have only been a few studies investigating the effect of alternative introduction strategies on stabilisation time and social disruption. Knerim (1999) introduced single and groups of three heifers into an established dairy herd. Knerim (1999) found that group-heifers formed their own subgroup and interacted less with resident herd members than singly introduced heifers. There were no differences in the amount of agonistic interactions or time spent lying and feeding between group sizes, implying that the social stress experienced by group and single heifers was the same. A similar study by Menke et al. (2000) introduced both single and groups of three heifers into an established dairy herd but in contrast to Knerim (1999) observed more agonistic interaction between group heifers and the resident herd than heifers introduced on their own. The contradictory results of these studies make it difficult to conclude any benefits from introducing cattle either singly or in small groups. More recently, Neisen et al. (2009) found that introducing pairs of familiar heifers into an established dairy cow herd was more favourable than introducing a single heifer. The authors introduced single and paired-heifers into six dairy farms, ranging in size from 44 to 66 animals per herd. Visual observations of social behaviour were recorded as well as positional data via a local position-measurement system, which recorded the two-dimensional position of each animal wearing a transponder. The transponders emitted a signal that was detected by antennas fixed to the barn walls. The positional data as well as the time of the record was relayed from the antennas to a central computing unit once every minute. The cows were housed in a loose-barn system consisting of three functional areas: feeding, lying and exercise areas. Some farms also allowed access to pasture during the day and although pastoral areas were not covered by the automatic tracking system, each animal was observed in the barn between 57-94% of the time. The resident herds were monitored for 1 week prior to the introduction of the heifers. A single heifer was introduced into three herds while a pair of familiar heifers was introduced into the other three herds. Four weeks later, when the introduced heifers were considered integrated into the herd a single heifer was introduced into herds that previously had a pair of heifers introduced while a pair of heifers was introduced into herds that received a single heifer previously. Visual observations were recorded during the first 3 days following introduction as well as continuous recording of positional data for 4 weeks following introductions. The authors found that the resident herd directed less agonistic behaviour towards the pair than the single heifer. The singly introduced heifers were found to be more synchronous with the resident herd and maintained closer distances to the herd than the heifers introduced as a pair, which tended to maintain closer distances to each other. Neisen et al. (2009) concluded that familiarity provided the introduced pair with a sense of security and support, and the welfare of the pairs was less at risk than the singly introduced heifer. The outcome of Neisen et al.'s (2009) study compared with those of Knerim (1999) and Menke et al.'s (2000) may be explained by the greater social stability experienced by a pair when compared with larger groups, particularly triads, which are more vulnerable to dissolution.

Based on a suggestion by Lamb (1976) that introducing unfamiliar animals at night when animals are socially less active should alleviate some of the social stress associated with mixing, Nakanishi et al. (1993a) investigated the effect of a night introduction. The study involved observing the behaviour of two groups of seven Japanese Black cows before and after the introduction of a single cow into each group. Behavioural observations were recorded for 3 days prior and 7 days post-introduction of the unfamiliar cow, for 8-9 hours each day. The unfamiliar cows were introduced after dark, between 20:00 h and 21:00 h. Observations were recorded immediately following the introduction, although due to the darkness the behaviours could not be described in detail. Nevertheless, the authors were able to observe some agonistic interactions during the first 12 minutes, which were mainly initiated by the resident cows. The frequency of agonistic behaviour tended to decline 2 days post-introduction and had stabilised after 7 days. Nakanishi et al. (1993a) also noted a decrease in lying behaviour and an increase in standing behaviour, which took 5 days to return to pre-introduction levels. The introduced cows were observed to spend less time eating and more time moving than the resident group members. Although Nakanishi et al. (1993a) state that there were no real advantages to introducing cattle at night as the time taken for agonistic interactions and behavioural changes to stabilise was comparable with other day-time introductions (e.g. Tennessen et al., 1985; Nakanishi et al., 1991), including a day time introduction would have enabled a comprehensive evaluation of the effect of day when introducing unfamiliar cattle. There is a lack of research investigating alternate strategies for reducing stress when introducing new individuals into an established herd. There is a need to thoroughly investigate the usefulness of different strategies that could lead to practices that create less social stress and disruption to normal behaviour and production.

2.10. Conclusions

The review demonstrates that cattle exist within complex social structures. Social behaviour research in cattle has largely focused on dominance behaviour and the function of these behaviours is well understood. Less is known about affiliative behaviours, although there is a consensus that they are largely responsible for the cohesive nature of familiar groupings. The review also identified several studies investigating the behavioural effect caused by introducing new individuals into an established herd and the results of these studies show that the presence of an unfamiliar individual creates social disruption. The aims of these studies were primarily production based, however the conclusions drawn could not recommend suitable practices to reduce the negative effect of incorporating new individuals into established groups, with the current advice stating to avoid mixing individuals altogether (Boe and Faerevik, 2003). In applying such a commercial focus on the study outcomes, the investigations failed to provide information on underlying social properties and detailed descriptions of behavioural factors involved in the process of familiarisation between individuals. Further work is needed in the area of affiliative behaviours and their role during relationship development. Such investigations require a multi level approach to cattle social systems that consider the fundamental processes that occur between individuals and the impact of these processes for group level outcomes. Experience from human social studies reveals that dyads and triads have important structural properties (e.g. Simmel, 1950) and it was suggested by Chase (1980) and Lewis (1984) to focus on these fundamental units to develop a greater understanding of social structure. The focus of the current study is to therefore explore the social behaviour of dyads and triads of steers during relationship development. Steers were chosen as the model for studying cattle social behaviour as they are not subject to hormonal behavioural changes caused by oestrous or pregnancy.

2.10.1. Aims

To explore the social properties of dyadic relationships and the effect of the presence of familiar and unfamiliar steers, a series of experiment were conducted to:

1. develop an understanding of the trade-off individual steers make between food and social companionship in the presence of familiar and unfamiliar peers. The hypothesis that steers paired with unfamiliar peers would travel further to receive a food reward than those paired with familiar peers was tested;
2. explore the behavioural response of steers to the presence of an unfamiliar steer by identifying the behavioural differences between pairs of familiar steers and pairs of unfamiliar steers. It was hypothesised that the behavioural differences observed between familiar and unfamiliar pairs of steers over time could be used to identify some of the features of the familiarisation;
3. investigate the change in temporal and spatial associations between pairs of unfamiliar steers during the process of familiarisation. The hypothesis that evidence of familiarisation between the unfamiliar steers would occur within 5 days was tested.

Following on from exploring dyadic relationships, the second part of the thesis investigates the social properties of a triad and explores the effect of the presence of an unfamiliar steer on the social relationship between a pair of familiar peers. The secondary aims of the thesis are to:

4. explore the behavioural response of a pair of familiar steers to the presence of an unfamiliar steer by evaluating the close proximity encounters of the familiar pair before and after the introduction of the unfamiliar steer. It was hypothesised that the introduction of the unfamiliar steer would lead to an increase in close proximity encounters between the familiar pair;
5. investigate the process of relationship development between a pair of familiar steers and an unfamiliar steer by exploring the regular patterns of close proximity encounters

between the triad. The hypothesis was that the difference in close proximity encounters between familiarity types would decrease as the unfamiliar steer was integrated into the triad.

Chapter 3

Measurement considerations

3.1. Introduction

The social behaviour of cattle was described in Chapter 2, as well as studies that have investigated the functional aspects of this behaviour. As outlined in the previous chapter, the term ‘social behaviour’ refers to a suite of different behaviours, from dominance to allogrooming to spatial proximity. Various measures are required to capture both the obvious and subtle behaviours that signify an individual’s social tendencies and characterise a social relationship, from general routine behaviours such as walking, grazing and resting, to identifying certain forms of interaction, such as physical or non-physical encounters. Collecting information on an animal’s social behaviour may include recording the number of individuals present and their identity, identifying the sender and the receiver of social behaviour, noting the sequence of behaviour by its frequency and duration, recording the spatial position of individuals relative to the overall group as well as proximity to neighbours, and noting the temporal patterning of these behaviours (Altmann, 1974). To obtain this information generally requires several measurement techniques (Broom and Fraser, 2007). Previously, there has been a strong reliance on observational methods to acquire qualitative and quantitative data on social behaviour in animals, although the use of technology to record animal behaviour is increasing (D'Eon and Delparte, 2005). The aim of this chapter is to provide a review of methods available to collect data on animal social behaviour. The principles of recording animal social behaviour are described in section 3.2, followed by a review of some of the automatic methods available to record animal behaviour: the review focuses on technological devices that have been developed to record an animal’s absolute or relative spatial location. The basic principles of each method are discussed as well as their main advantages and disadvantages and the chapter concludes with a justification of the research methods chosen for use in the thesis.

3.2. Recording animal social behaviour

3.2.1. Approaches to the study of animal behaviour

The study of animal behaviour stems from the fields of ethology and psychology. Ethology is characterised as the '*biological study of behaviour'* (Tinbergen, 1963), and can be studied using conceptual, theoretical or empirical approaches (Dugatkin, 2004). Empirical ethological studies are principally focused on asking questions about the cause of behaviour, how it has evolved and has developed, and what its function is (Tinbergen, 1963). Ethology has traditionally taken an observational approach to the study of animal behaviour by recording the naturally occurring behaviour of animals in their natural habitat, without any manipulation or an attempt to control factors within their environment (Manning and Dawkins, 1998). Psychology, the study of the mind and behaviour, has traditionally focused on asking questions about the causation of behaviour and factors involved in learning, and has tended to rely on laboratory based studies and experimentation (Martin and Bateson, 1993). Experimentation involves manipulating the environment in some way, allowing researchers to investigate the cause of a specific behaviour by observing the outcome when some condition is purposely varied (Martin and Bateson, 1993; Manning and Dawkins, 1998). Both ethology and psychology have evolved to incorporate aspects of the other discipline, and other fields of studies have evolved from their foundations, including ecology, sociobiology and behavioural biology (Martin and Bateson, 1993).

The nature of an agricultural system in which domestic livestock are managed is much more controlled and manipulated than a natural system, thus agricultural based research has taken more of an experimental research approach. For example, digestion trials are used to determine the amount of nutrients an animal absorbs from a particular food source (Mitchell, 1942). In these trials, animals are individually housed in metabolism crates and the amount of food ingested is compared with the waste produced to determine the digestibility of the food source (Vallentine, 1956). Such controlled experimental approaches rely on breaking down a system into its principal components to test hypotheses about the mechanisms underlying the cause and effect, thus this type of research generally relies on the individual being removed from its natural context. An experimental approach towards studying animal behaviour is somewhat different due to a range of behavioural interdependences, for example, studying social behaviour relies on the presence of a 'social' context, thus it is difficult to control every aspect of an animal's environment whilst varying a single condition (Dawkins, 2007). Nevertheless, simple and detailed behavioural studies are still possible when a range of observational techniques and approaches are used to minimise disruption, and an animal's natural behaviour can be recorded (Dawkins, 2007). This thesis applies a reductionist approach to the study of cattle social behaviour to explore the effects of familiarity on dyads and triads of steers: both replicated experiments and analytical models will be used. It is anticipated that the findings will enable future work on larger groups to account for the influence of dyadic and triadic pressures on higher order social processes.

3.2.2. Research design

The research approach (either observational, experimental or a combination of both) provides the foundation of the overall research design. Another fundamental component of the research design is the data collection method, which can be either cross-sectional or longitudinal. A cross-sectional study measures individuals or groups at one point in time whereas longitudinal studies take repeated measurements on the same individuals or groups at several points in time (Zeger and Liang, 1992). Cross-sectional studies provide descriptive information on associations between groups or individuals at that point in time, although their use is limited in defining cause-and-effect relationships (Paffenbarger, 1988). Longitudinal studies on the other hand can be used to investigate causation, as well as long term effects, change, and similarities and differences between and within subjects over time (Cohen et al., 2007). In comparison to cross-sectional studies, longitudinal studies have increased statistical power as there are twice as many observations on the same number of individuals (Zeger and Liang, 1992). Additionally, longitudinal studies can be analysed both cross-sectionally at each point in time, as well as longitudinally through time (Thomson and Holland, 2003). The main challenges of a longitudinal study include the labour intensive data collection process, analysing large and complex data sets, as well as keeping the same subjects throughout the duration of the study (Thomson and Holland, 2003): missing data becomes an issue if one or more subjects drop out before the end of the study (Hedeker and Gibbons, 2006). Longitudinal studies are seemingly more challenging and complex than cross-sectional studies, but the nature of the data set means that individual, pair and group social properties can be investigated.

3.2.3. Recording representative samples of behaviour

Behaviour refers to a complex of movements and events produced in response to internal and external stimulus (Martin and Bateson, 1993) which can be observed at multiple levels from groups to individuals to specific body parts (Dawkins, 2007). Additionally, an animal's behaviour is influenced by other individuals around it, those it interacts with and the interactions of others, as well as features of the environment (Dawkins, 2007). Thus it would be extremely difficult to record everything about an animal and its behaviour at once. Recording animal social behaviour involves selecting the most appropriate methods to provide the greatest representation of total behaviour (Dawkins, 2007). A general methodological approach to record animal social behaviour involves selecting the most appropriate: (i) type of behaviour; (ii) level of observation; (iii) sampling method; (iv) type of record; and (v) amount of behaviour to record (Fig 3.1) (Dawkins, 2007). The selection of *what* social behaviour to record will depend on the research question. As mentioned above, social behaviour encompasses a wide range of behaviours and taking representative samples of such behaviour relies on collecting detailed information on various factors, including individual and group attributes, the identity of the senders and receivers of social behaviour, spatial relationships and the temporal patterning of behaviour (Altmann, 1974). The level of observation refers to unit being described, from the behaviour of a whole group to individual behaviour, right down to the behaviour of individual body parts, for example, the leg movement of a cow while walking. The behavioural level chosen will depend on the research question and the behaviour of interest.

3.2.4. Sampling methods

Sampling methods are used to provide a representative sample of the total behaviour and the most appropriate method to use will depend on the focus of the experiment. The sampling methods available include scan sampling, focal sampling, *ad libitum* sampling and behavioural sampling (Fig. 3.1). The principles of each sampling method including their main advantages and disadvantages are outlined below.

Scan sampling involves 'scanning' the group and recording a snapshot of each individual's behaviour at that time, and repeating the observation some time later (Dawkins, 2007). The method is best suited to general and social behaviours that can be easily described and recorded quickly (Altmann, 1974). Scan sampling provides a good description of a group's overall behaviour and behavioural synchrony (Altmann, 1974). However, observers are usually restricted to recording only simple categories of behaviour as the method becomes complicated with an increasing number of behavioural categories to record at each scan (Dawkins, 2007). Additionally, the method only provides a measure of the frequency and duration of behaviour relative to the total number of scans taken (Martin and Bateson, 1993).

Focal animal sampling involves identifying a 'focal' animal (or a dyad or some other unit) from within a larger group and recording all instances of a specified behaviour of that same individual over the selected sample period (Martin and Bateson, 1993). The method provides a good representation of general behaviour but because the method ignores behaviour initiated by individuals other than the focal animal, the method is generally not suited to record information on general social behaviour and behavioural synchrony among groups (Altmann, 1974). Additionally, the choice of focal animal can create a bias if the most active or noticeable animal is selected, and problems arise when the focal animal moves out of sight (Martin and Bateson, 1993; Dawkins, 2007).

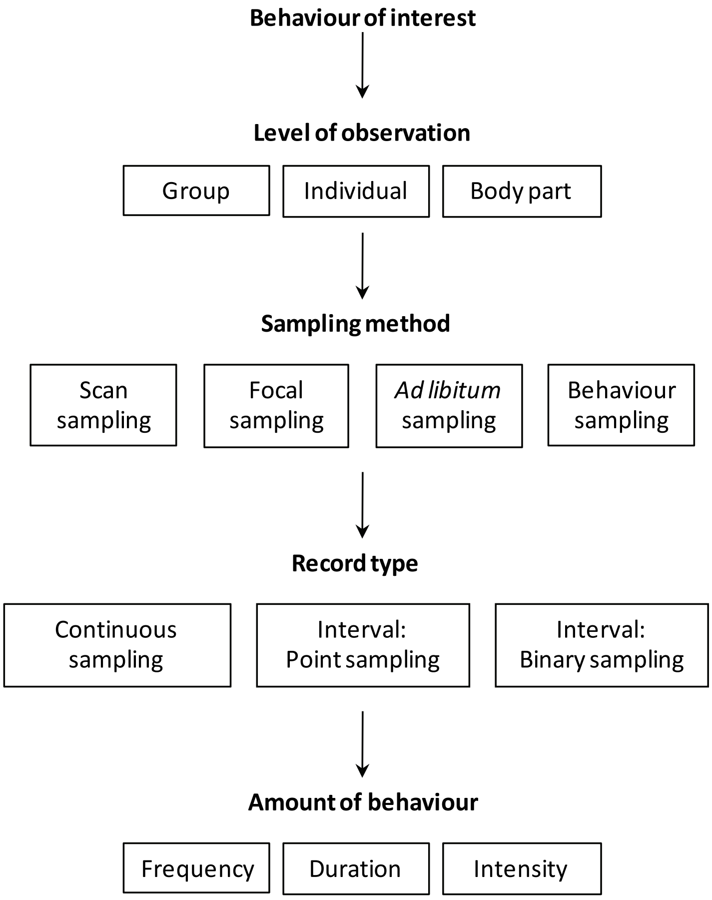


Figure 3.1. The process of selecting the most appropriate sampling and recording methods to collect representative samples of social behaviour (modified from Martin and Bateson, 1993).

Ad libitum sampling and behavioural sampling are much less structured than scan and focal animal sampling. *Ad libitum* sampling involves observing a group of animals and recording every behaviour that is observed, noting the time of occurrence and identity of the animal. Behavioural sampling is similar to *ad libitum* sampling but only a specific type of behaviour is recorded, for example, grooming events (Altmann, 1974). Both methods are useful to describe rare behavioural events or record the behaviour of species that are not easily observable (Dawkins, 2007). However, the methods are unlikely to provide an indication of the animal's overall behaviour because records are not taken at regular intervals, less conspicuous animals are likely to be recorded more often than others thus biasing the sample of the species observed and observations may be limited to certain times of the day when the animals are more active (Dawkins, 2007). Each of the four sampling methods has its own strengths and weaknesses in terms of observing general animal behaviour. In terms of recording the social behaviour of groups of cattle, scan sampling appears to be the most suitable method to record the frequency and duration of behavioural events between individuals.

3.2.5. Record type

In addition to the sampling method the type of record used to collect the sample of behaviour is also an important consideration, which can be either continuous or interval (Fig. 3.1). Continuous sampling involves recording all events of a certain behaviour during a specified time frame, and noting the time that each behaviour starts and stops, while interval sampling involves sampling behaviour at specified sample intervals (Martin and Bateson, 1993). Continuous sampling provides precise information about the frequency and duration of behaviour, although records are difficult to collect when the behaviour of the animal is frequently changing (Dawkins, 2007). Often the number of behavioural categories is reduced to accommodate the ability of the observer to record the specified behaviour (Martin and Bateson, 1993). Depending on the behaviour of interest, sequences of behaviour are not always required, thus interval sampling methods provide an adequate representation of the occurrence of a behaviour (Dawkins, 2007).

Interval sampling can take two forms: point sampling or binary sampling. Point sampling involves dividing an observation period into sample intervals and only recording the behaviour at the end of each sample interval or the 'sample point', while binary sampling, or one-zero sampling, involves recording '1' if the behaviour occurred or '0' if the behaviour did not occur during the previous sample interval (Martin and Bateson, 1993). Behaviours recorded with binary sampling are expressed as a proportion of the total observation time, which introduces several sources of error primarily because the method does not directly record the duration of an event and tends to overestimate duration and underestimate frequency (Martin and Bateson, 1993). Point sampling, however, allows a broader range of behaviours to be recorded that cannot be achieved using continuous time sampling, and when short sample intervals are used the proportion of time spent performing a behaviour can be directly estimated (Martin and Bateson, 1993). Additionally, the lower demand on the observer makes the method reliable (Martin and Bateson, 1993). The disadvantage with point sampling is that rare behavioural events are often missed, and the observer may unknowingly be biased towards behaviours that have occurred prior to the sample point, resulting in the predominant behaviours being overestimated (Martin and Bateson, 1993). Using both continuous and interval sampling methods together can be useful when recording social behaviour, as general behaviours such as grazing and walking can be recorded at intervals while specific behaviours such as fighting or allogrooming can be recorded as they occur (Broom and Fraser, 2007).

3.2.6. The amount of behaviour to sample

The amount of behaviour observed can be quantified by the duration, frequency or intensity of the behaviour (Fig. 3.1). Duration refers to the amount of time the behaviour is exhibited, the frequency quantifies the number of times the behaviour is exhibited while the intensity measures of the magnitude of the behaviour (Dawkins, 2007). The frequency and duration of behaviour provide different yet complimentary measures: together frequency and duration can be used to indicate the nature and quality of behaviour. For example, the number of times two animals groom each other and the duration of their grooming bouts can be used to define the quality of their social relationship (Martin and Bateson, 1993).

3.2.7. Measuring spatial aspects of behaviour

The above sampling methods relate to recording behavioural events and quantifying how much and when certain behaviour occurs. A separate behavioural classification used to describe social behaviour is *where* behaviour occurs, which quantifies where individuals are with respect to other individuals or features of their environment and indicates an individual's selection preferences (Dawkins, 2007). In social behaviour studies, quantifying inter-individual distances between group members provides valuable information on an individual's preference for others. However distance can be difficult to estimate accurately when the observer is some distance away and the two reference points (e.g. animals, objects) appear smaller than they actually are, thus making it difficult to estimate the actual distance between them (Dawkins, 2007). A common method to overcome this problem is to use relative distance reference points, such as fixed spatial references. Fixed spatial references may include permanent fixings of known distance, such as the spacing between individual food bins in a food trough as used by Manson and Appleby (1990) to investigate the effect of dominance on spacing behaviour between cows at a feed trough, or the distance between equally spaced fence posts as used by Hirata (2003) to estimate the distance between cows and calves. The animals themselves can also be used as a reference, such as the number of body lengths between individuals as used by Stricklin (1983) to estimate the distance spread of a group of beef cattle. Additionally, recording the identity of an individual's nearest neighbour, rather than the distance between neighbours, provides an estimate of the amount of time that one individual is found within close proximity to any other animal in the group, as used by Sibbald et al. (2005) to quantity individual sociability in sheep.

3.3. Observations

The majority of studies reviewed in Chapter 2 used visual observations to record behavioural data. Visual observations can potentially provide the most thorough description of an animal's behaviour. Observations can be recorded directly at the time the event occurs via human or computer assisted recording, or video recording equipment can be used to collect video footage at the time that can be analysed afterwards. However there are some major problems associated with the approach. For example, full records are difficult to collect as most observations are based on identifying specific behavioural events or discontinuous sampling periods, thus a large portion of an animal's total behaviour is being missed (Prange et al., 2006). The majority of problems are associated with the observer, specifically observer bias, fatigue, interference and variation within and between observers (Martin and Bateson, 1993; Turner et al., 2000). Equally, observations are difficult to conduct continuously and at night, and it is difficult to record all of the events occurring at once, thus making it difficult to track large groups of animals.

Video footage can overcome some of the problems associated with visual observations, such as recording rapid changes in behaviour or when many behaviours are occurring at the one time (Broom and Fraser, 2007), while the footage can also be slowed down to provide a greater depth of analysis (Martin and Bateson, 1993). The use of a video recorder removes the need for an observer thus avoiding observer interference and allows continuous recording (Broom and Fraser, 2007). However, video footage is only a visual record of behaviour which therefore needs to be sampled and analysed. Analysing video footage can be extremely time consuming and can take much longer than if the behaviour was recorded in person. Additionally, the area in view is restricted and the quality of the image can lead to a loss of visual depth, which can then lead to the loss of key details (Martin and Bateson, 1993).

Recording visual observations of animal behaviour is not a straight forward procedure, and as reported, there are various aspects to consider that will affect the accuracy of the data collected. Many errors are due to the observer, thus there is a demand for methods that remove the reliance on human operation and move towards more automated systems.

3.4. Radio telemetry systems

Technological devices provide researchers with a means to collect behavioural data in greater quantities and often greater detail than can be obtained with visual observations, thus overcoming some of the difficulties faced with observational methods. Most technological devices designed to record animal behaviour are non-invasive, continuously record data and perhaps most importantly, remove the need for observers to be present thus minimising human error as well as observer interference. The behaviour of the animal can therefore be recorded in its more natural state. Furthermore, large numbers of animals can be recorded at once over a wide array of locations and recording continues during conditions that would normally interfere with manual and video observation recording, such as darkness and inclement weather. Radio-telemetry, also known as radio-tracking, provides the basis of a variety of technological devices used to remotely monitor an animal's spatial location, and they can also be used to indicate an animal's physiology, movement and resource selection (Millspaugh and Marzluff, 2001). The system relies on a radio-emitting device fitted to the animal in the form of a collar or a tag that can be detected by a radio receiver (Rodgers, 2001). The frequency and pulse rate of the radio signal is used to determine an individual's identity and spatial position relative to the transmitter (Rodgers, 2001). Along with the radio transmitter, the device also comprises a power supply and an antenna, and some devices have the potential to include sensors that can detect the physiological status of the animal, such as body temperature and heart rate (Rodgers, 2001). The radio-emitting device was initially designed to emit a continuous radio signal but was later refined to transmit signals at specified intervals to conserve battery life (Kenward, 2000). There are several techniques that can be used to receive the emitted signal. The simplest technique relies on manually tracking the signal with a hand-held antenna and a portable receiver (Mech, 1983). Manually tracking can only occur in areas that are accessible on foot thus a large area of land can be covered, although the method is time consuming, inefficient at locating sparsely distributed animals and animals are likely to be disturbed by the researchers presence (Mech, 1983). An alternative radio-tracking technique is a fixed antenna positional system, where antennas are fixed in certain positions within the animal's home range and their location acquired by triangulation of at least two spatial estimates (White and Garrott, 1990). Stationary tracking systems are efficient at detecting movement within small areas, although the area of coverage is limited and less suited to species that cover large areas of the landscape (Mech, 1983). Further technology developments during the 1990's saw the inclusion of automated microcontrollers in the radio transceiver system that allowed the detected radio signals to be logged and stored in an on-board memory (Rodgers, 2001). On-board data storage not only increased the type of telemetry devices available but also allowed a greater amount of data to be collected on a wider range of animal species (Rodgers, 2001). Tracking animals on foot has been widely used in wildlife studies for free-ranging species that are highly mobile and move long distances (Rodgers, 2001). However unlike free-ranging species, domestic livestock are generally constrained by fences and radio telemetry studies have favoured the use of fixed antennas and automatic recording devices that require less labour.

The advantages of using radio-telemetry to study animal behaviour are numerous. Radio-telemetry allows researchers to precisely identify individual animals and collect detailed spatial information on the animals daily movement patterns as well as track the migratory and dispersal patterns of free-ranging species (Mech, 1983). When combined with additional production parameters positional data can indicate an individual's preference for a particular location, for example, a preferred grazing location (White and Garrott, 1990), while the distance that an animal travels within a specified time period can be used to determine habitat use and energy requirements (Pépin et al., 2004). Additionally, an individual's physiological status can be inferred from their spatial position relative to the group, as animals are known to isolate themselves when sick (Newberry and Swanson, 2001) and prior to giving birth (Broster et al., 2010). The use of automatic recording has removed the need for operators to be present and efficient power supplies allow continuous recording.

However, the behavioural data obtained using radio-telemetry methods cannot substitute information obtain from visual recording, with most devices designed to identify only specific types of behaviour, such as movement or spatial position. Telemetry methods can collect large volumes of data, however this can be a disadvantage when it comes to sampling, analysing and storing the data. Additionally, remote monitoring requires devices to be attached to the study animal and it is possible that the device may modify the animal's natural behaviour. For example, tagging has been shown to reduce breeding success rate and survivorship of geese fitted with back-mounted harness transmitters when compared with geese fitted only with a coloured leg band (Ward and Flint, 1995). A study by Swenson et al. (1999) found that radio-transmitting ear tags had a detrimental effect on the survival of newborn moose calves. The authors were unable to ascertain why calves with radio-transmitting ear tags had lower survival rates than calves marked with plain ear tags, but they posit that the presence of the transmitter altered the calves' behaviour which disrupted the mother-calf relationship in some way. However, neck collars designed for use on large adult mammals, such as cattle and deer, rarely affect the behaviour of the collared animal (Withey et al., 2001).

Location estimates using radio-telemetry are known to have spatial inaccuracies. Environmental variables are known to create positional errors, such as vegetation type and cover, electromagnetic fields, animal movement, the height of the animal and its distance to the ground, and the distance between the radio-tagged animal and the receiver (Mech, 1983; Withey et al., 2001). Location precision is a measure of consistency and location accuracy is a measure of how close a location estimate is to the actual location (Withey et al., 2001). Preliminary static tests from different locations within the study area are used to estimate precision and accuracy of the devices (Harris et al., 1990). However, it is important to note that the level of inaccuracy may be insignificant depending on the behaviour being studied. For example, cattle are known to graze within 4-10 m of each other (Broom and Fraser, 2007), thus a social encounter could occur anywhere in the range of 0-10 m. A radio-telemetry device with a known inaccuracy of, say, up to 2 m is relatively inconsequential given that the error is smaller than the range of a designated social encounter and also smaller than the average body length of a mature cow (the average body length from nose to tail of a mature Holstein cow is reported to be around 2.6 m (Anderson, 2003)), while spatial errors larger than 10 m would pose considerable problems when recording cattle social behaviour.

The quantity and quality of data that can be automatically recorded by radio-telemetry devices has the potential to gain a greater understanding of animal behaviour that has not been achieved in the past. The following sections provide an overview of some of the devices that have been used to remotely record the absolute or relative spatial positions of domestic livestock, including proximity logging devices, fixed antenna positional systems and global positioning system devices.

3.4.1. Proximity logging devices

The social behaviour of an individual with other individuals can be observed by measuring the frequency and duration of close proximity encounters. A proximity logging device that uses ultra high frequency (UHF) radio waves to transmit and receive signals between units was developed by Sirtrack Ltd. (Havelock North, New Zealand) to detect contact between individuals within a specified distance. The devices were designed to overcome some of the problems associated with manually radio-tracking animals, namely wildlife species that are difficult to observe continuously. The devices were first described by Ji et al. (1999) to record the social interactions of possums. When activated the devices emit a unique identification code via radio signal every 1.5 s, which can be detected by other devices that are located within their detection range. In between emitting signals, the device listens for other broadcasting signals. The devices are mounted on a collar fitted around the neck of the animal and a detection range is set according to the size of the species and the information required. When two collared individuals come within detection range a contact is recorded and the loggers store the identification of the contacted logger as well as the date, time and duration of the contact into a temporary memory. A ‘contact’ is defined as two collared individuals within close proximity, regardless of their behaviour. Once a pre-defined separation period has elapsed, the data is then stored into the on-board memory. The separation period is the time that the loggers must remain separated before the contact is defined as ended and allows for short interruptions in the radio signal if the same two loggers remain within the detection range. The data can be used to quantify the frequency and duration of the time that two individuals spend within the detection range.

Prange et al. (2006) performed a series of tests on the devices in both the laboratory and field using a detection distance of 1 to 1.5 m to represent contacts that could transmit disease between racoons, and separation periods of 15, 40 and 60 s. The laboratory tests involved comparing the duration recorded by the devices against known durations by moving one collar toward a stationary collar within detection range for 10 s, 30 s, 60 s, and 300 s. The ability of the loggers to record long durations was tested by leaving three pairs of collars within detection range for 14 hours. Additionally, the effect of multiple loggers in contact at the one time was analysed by gradually adding up to five collars into the detection range of a single collar and analysing the output. The results of the laboratory tests showed that the devices performed well in the short duration tests and recorded contacts only deviated within 3 s of the actual durations, which may also be caused by the observer's ability to remove the logger at the precise time. When the collars were tested over a longer duration, all collars recorded multiple contacts rather than one single contact, with those set at shorter separation times recording more multiple contacts than those with longer separation times. The authors attributed this discrepancy to the loggers transferring the logged contact into permanent memory, which occurred more frequently when shorter separation times were used. However the overall difference in contact time recorded was less than 30 s. When multiple collars were tested, collars set to a separation time of 15 s recorded multiple contacts when more than two loggers were in contact. By the time all five loggers were in contact all loggers recorded multiple contacts, but the overall time discrepancy was small (less than 30 s). However, loggers set to 40 or 60 second separation times all recorded a single continuous contact. The field tests involved fitting the devices to 42 racoons via a capture and release technique with a detection distance of 1 to 1.5 m. Over a 12 month period, 35 collared racoons were recaptured and data downloaded from the devices 59 times. Additionally, post-field experiments were conducted on six pairs of collared racoons to determine similarities in contact information between pairs over a 2 week period. Sixty percent of the collars recaptured worked faultlessly. The remaining collars did not record complete data sets and 12 collars were unable to be fixed in the field. The authors found that the majority of problems occurred early in the deployment and performance stabilised after 3 months. When pairs of racoons were compared, the authors found that some collars of a pair recorded slightly more contacts than the other. The authors determined that this discrepancy was caused by contacts occurring near the edge of the detection range resulting in additional 1 s contacts. However, when these contacts were removed differences between pairs were no longer significant, thus the authors suggested removing 1 s contacts to eliminate less reliable data. Overall, the authors concluded that proximity logging devices provide a novel approach to assess close proximity contacts between individuals.

Proximity loggers were first applied to a commercial cattle herd by Swain and Bishop-Hurley (2007) to investigate maternal affiliations between beef cows and their calves. A herd of 100 Belmont Red cattle that were due to calve over a 3 month period were checked on a daily basis and any new calves were fitted with an ear tag for identification and their date of birth and mothers identification was recorded. Each week, cows that had calved in the previous week were brought into the yards and both the cows and calves were fitted with proximity loggers (Fig. 3.2) before being relocated to a 7 ha paddock as a single group for 7 days. The loggers were set to a detection range of 7 m. The authors set a minimum requirement of five cow-calf pairs per week and no more than 10 cow-calf pairs, thus if more than 10 cows calved during the week the 10 most recently born calves were selected. Over 7 weeks 52 cow-calf pairs were monitored, although some collars failed to perform both transmitting and receiving functions resulting in 34 cow-calf pairs with reciprocal data and 18 collars with only transmitting or receiving functions. However, the 34 fully functioning collars showed a high correlation between contacts being received and transmitted, thus the authors justified using data from the 18 collars operating with only one function. Swain and Bishop-Hurley (2007) suggested that the data could be used to explore the relationship between maternal investment and calf growth rates. The study demonstrated that the devices are capable of identifying maternal linkages, which are not always recorded in extensive in beef production systems due to a high labour investment, but knowledge on maternal linkages and mating events provides important information on breeding success and genetic traceability (Prayaga et al., 2008). Proximity loggers have also been used to quantify maternal behaviour in sheep, where the contact behaviour of ewes with single lambs and ewes with twin lambs was recorded when exposed to different types of shelter (Broster et al., 2010). The loggers were used to confirm maternal lineages, as contact between non-related ewes and lambs were less than 1% of that recorded between related ewe-lamb pairs: this data provides detailed information that could not previously be obtained through visual observations alone.

Figure 3.2. Proximity logger fitted to a cow and her calf (photo supplied by Dave Swain).

Proximity logging devices provide continuous automated data collection for all close proximity encounters between collared individuals. The devices contain their own power source, store large amounts of data and operate in natural field-based settings. The above studies show that the devices are suited for recording contact information on domesticated livestock. There were some instances where collars failed to record reciprocal contacts, although overall reciprocal correlations have shown to be significant (Bohm et al., 2009). A limitation of the devices is a lack of spatial reference, as only the relative position of one individual in relation to another is recorded. Additionally, the nature of the contact is not known, for example there is no distinction between agonistic or affiliative interactions. However inference from the contact duration and frequency could be used to assign contact quality, with longer durations tending to indicate more affiliative associations as agonistic behaviour is relatively short lived (Bouissou, 1974b). The use of proximity loggers in social behavioural research has the potential to provide greater insight into animal behaviour.

3.4.2. Fixed antenna positional systems

A local positioning system designed to track the position of dairy cows within a barn was evaluated by Gygax et al. (2007). The base system involved six antennas located in fixed positions, capable of detecting movement within a 500 m^2 area. To determine the position of an animal, a transponder programmed to receive and send signals was mounted on a collar fitted around an animal's neck. A central antenna designated as a master base station sent out a specifically coded radio signal, which was identified by the transponder and responded by transmitting its own unique signal to all of the other antennas. The time that the signal was received by each antenna was recorded and relayed to a central computer, where the position of the transponder was calculated from the difference in time taken for the signal to reach each antenna. The transponders could be set to emit a radio signal continuously or at pre-defined time intervals. The transponders were powered by on-board batteries and could last 24 hours with continuous sampling, while battery power was conserved with interval sampling, with operation time extended by 7 days using a 10 s sample interval. The authors set up the positional system in a loose-housed dairy barn and performed preliminary tests using static transponders. Twelve antennas were set up in the barn to ensure adequate signal coverage. Transponders were placed in fixed locations in the barn and also moved in circular motions to simulate moving. Gygax et al. (2007) found that on average the system accurately recorded the position of the transponders within 0.50 m of the actual position. Some locations showed greater variability, which the authors suggested may have been caused by the metal materials in the barn interfering with the signal or the position of the antennas did not allow adequate coverage, however the deviation was less than 1 m. The circular motions were also well captured by the positional system, with the largest deviation extending only 0.40 m greater than the actual position. Gygax et al. (2007) concluded that the devices provided accurate location measurements as the errors were smaller than the animal's body length. The authors also validated the data recorded by transponders worn by cattle with that recorded by visual observations over a 9 hour period. A herd of 14 dairy cows were fitted with transponders set to emit a signal once every second. Visual observations continuously recorded all displacement activity at the feed trough and the nearest neighbour of each animal (within 2 m) was recorded by point sampling at 10 minute intervals in the three different functional areas of the barn: feed trough; lying cubicles; and activity area. To compare the transponder data with nearest neighbour observations a program was developed to process the data in the same way as the observations and proximity matrices were constructed for each method, which detailed the number of times each pair were observed within 2 m. Gygax et al. (2007) found that transponders accurately quantified the time spent by each animal within the three functional areas, although displacement behaviour was not well recorded, possibly because the behaviours were short in duration and the cows did not move very far away once displaced (less than 2 m). Thus it was concluded that the devices were not yet suitable to measure agonistic behaviour between animals. The nearest neighbour observations were found to be positively correlated with the transponder system and the authors concluded that the devices could be used to measure social relationships between animals.

A similar system was used by Neisen et al. (2009) to record the spatial position of dairy cows when either a single heifer or a pair of familiar heifers were introduced into an established dairy herd (Chapter 2, Section 2.9.3). The transponder system has been shown to provide reliable spatial information of cows within fixed structures, and with further processing and analysis, the spatial relationships between individuals can also be inferred. However, the devices rely on infrastructure to transmit and receive radio signals, they have a short battery life and the behavioural data collected is limited as only a spatial position of the animal is recorded, thus further processing is required to infer an animal's behaviour.

3.4.3. Global positioning systems

Global positioning system (GPS) devices have been used to track the movements of many animal species, including cattle (Harris et al., 2007) and sheep (Rutter et al., 1997), and to explore animal interactions with the environment (Handcock et al., 2009). Global positioning systems work by obtaining position fixes from earth-orbiting satellites that continuously transmit radio signals. Once the GPS device secures contact with at least three satellites the radio signals are relayed to the device and converted into a location estimate. The devices are set to acquire satellite signals at pre-determined intervals. Each location attempt can result in three different outcomes: a 2-Dimensional location (2D); a 3-Dimensional location (3D); or failure to establish contact with the required 3 satellites. A 2D location is calculated from the triangulation of three satellites, while a 3D location is calculated from four satellites with the fourth satellited providing an altitude measure. The accuracy of the location estimate is subject to various errors, which include interference from dense vegetation and tree cover (Moen et al., 1996) and estimates acquired prior to May 2000 were subject to errors intentionally caused by the military (Dussault et al., 2001). In general, these errors are expected to be within 10 m of the actual position (Swain et al., 2011). Some of the error can be minimised by differentially correcting the GPS location with the coordinates of a known position nearby, which can increase the accuracy of the location estimate to within approximately 3 and 7 m (Swain et al., 2008a; Swain et al., 2011). The GPS system and its application for monitoring the movement behaviour of moose was evaluated by Moen et al. (1996). The authors tested the devices in fixed positions and also fitted a GPS device to a free ranging moose. The static tests involved positioning the GPS device in a fixed location for 6 days and repeating this process under varying levels of canopy cover using a 30 minute fix interval. The authors found that the GPS device was able to secure a location estimate 95% of the time in open areas and areas of thin canopy cover, while under closed canopies GPS locations were achieved in 60% of attempts to obtain satellite signals. Additionally, Moen et al. (1996) found that on average the 3D fixes were more accurate than the 2D fixes, however the 3D fixes occurred at a lower frequencies than 2D fixes. The animal test involved fitting a single moose with a GPS device mounted on a collar and the location of the moose was tracked within a 2.5 km^2 paddock for 15 days. The authors were able to identify specific areas that the moose was choosing to occupy and found that the movement of the moose did not affect fix success. From the 3D fixes and collar orientation the authors could identify whether the moose was lying or standing. Moen et al. (1996) outlined that GPS devices are more expensive than standard radio-tracking devices which may limit the amount of animals that can be monitored at the one time. Moen et al. (1996) additionally suggested that a compromise needs to be made between acquiring data with a potentially large error and eliminating the data point altogether. Overall, the authors concluded that GPS devices have the potential to collect valuable information on patterns of animal movement and habitat selection.

A study by Swain et al. (2008b) investigated the effect of fix rate on the accuracy of GPS data and the implications of these errors on animal resource use. A high GPS fix rate of four times per second (4 Hz) was used to collect positional data and movement speed of six cows over a 4 day period. Histograms of each cows speed were created and combined to derive a probability density function. A gamma probability density function most closely matched the actual histograms and was used to derive prediction errors for varying patch sizes. The authors found that higher fix rates were able to more accurately predict smaller patch sizes, for example, a fix rate of 1 hour was able to predict a 1 ha patch with 30% accuracy, while a fix interval of at least 10 s was required to accurately predict a 100 m^2 patch with 99% accuracy. Furthermore, to accurately predict a patch size of 1 m^2 required a GPS fix every 2 s. The investigation emphasised the importance of using frequent fix intervals to increase spatial precision and the potential errors that could result from using low fix rates, especially when trying to create animal movement models and predict resource use. Using high fix rates comes at a cost of high power consumption, although the results demonstrate that longer operation times gained from using lower fix rates come at the expense of location accuracy.

Ganskopp (2001) used GPS technology to assess the effect of water and salt provision on the distribution of cattle in an extensive landscape. Three pastures ranging in size from 825 and 859 ha were used in the study to explore the effect of three treatments performed at weekly intervals. The treatments involved salt and water in a common location, water moved to a distant location with salt remaining in the original location, and salt moved to a distant location while water was returned to the original location. Of the 40 cow-calf pairs that grazed the pastures, two cows were selected to wear GPS collars set to acquire positional data at 20 minute intervals. The GPS devices were also fitted with motion sensors to quantity horizontal and vertical movements of the animal’s head, which were compared with 12 hours of visual observations over the 3 week period. Only data from the GPS collar with the greatest performance was used in the analysis. Geographic information system (GIS) software was used to overlay the GPS data on a map of the paddock. Ganskopp (2001) found that when salt and water shared a common location, the cows remained within 250 m of the resources. When water was moved away, the cattle were found within 250 m of the water the majority of the time, while when water was moved back to its original location and salt moved away, cattle were located within 250 m of water 354 times compared with 38 times within 250 m of salt. Overall, cattle chose to remain within 1.16 km from water, regardless of treatment. Additionally, when the resources were separated the position of water or salt did not affect the time spent grazing or resting, with cattle visiting water on a daily basis and salt every 1-2 days. Ganskopp (2001) concluded that the GPS devices provided quantitative information on resource use by cattle, although the activity of the animals could not be adequately modelled from the animal’s location and motion sensors when compared with visual observations. Ganskopp (2001) suggested that using a shorter fix interval would provide greater detail on animal movement, which could then be used to develop behaviour activity models. The study by Ganskopp (2001) highlights the advantage of using GPS in extensive landscapes to determine animal location and resource use, which would be otherwise unattainable with manual observations or other tracking means. The study also highlights the applicability of GPS technology to investigate factors other than spatial positioning, such as resource use, when shorter fix intervals are used to increase spatial precision and accuracy.

In an attempt to infer animal behaviour from GPS data, a study by Ungar et al. (2005) used GPS devices fitted with motion sensors to investigate the accuracy of GPS data to predict animal activity. The motion sensors detected forward-backward movements (left-right) and also vertical-horizontal (fore-aft) movements. The number of times the sensors were activated within a pre-defined time interval was recorded and compared with behavioural observations and the distance between spatial locations. The measurements were used to develop regression equations that could be used to predict animal activity from the GPS data. Two data sets collected from separate locations with different environmental conditions were analysed. The first data set was collected in the United States of America. Two cows from each of three groups of 40 Hereford X Angus cow/calf pairs were fitted with GPS collars, set to obtain positional data every 20 minutes and record animal activity data every 3 minutes. Continuous visual observations were also recorded of the collared cow's activities for up to 13 hours per cow. The second data set was collected in Israel over a period of 2 years. During the first year, two collars were fitted to cows in two different herds while four collars were deployed in the second year. The collars were set with a GPS fix interval of 5 minutes and an activity sampling period of 4 minutes. Continuous visual observations of the collared cows were used to record the transition of one activity to another. The use of distance alone to predict animal activity did not correlate well with the behavioural observations, however when combined with the motion sensor data the predictive ability improved, particularly due to the left-right sensor counts: low counts correlated with resting activity while high counts were associated with travelling and grazing. Greater accuracy was achieved by using a shorter fix interval in the Israel data (5 minutes) compared with the US data (20 minutes), as frequent changes in activity were more likely to be detected. Models from each data set were created to delineate between the four activity states: grazing, travelling, standing and lying. Lying and standing resulted in similar motion sensor responses making it difficult to separate the activities in the predictive model, thus the two activities were grouped into a single 'resting' category which saw an improvement in the level of misclassification between observed and predicted activities from 22% (lying and standing separate) to 12% (lying and standing combined). Grazing was much more accurately predicted than other activities, although some activities were misclassified as grazing, particularly resting. It was suggested that using the speed of movement could help improve the classification of some activities, but because grazing and travelling can occur simultaneously, including the speed of movement was unlikely to improve the ability of the model to distinguish between grazing and travelling. Ungar et al. (2005) were surprised that the distance measurements could not be used to clearly distinguish between resting and grazing, which they attributed to the accuracy of the GPS devices. Resting activity was not always associated with zero movement as animals may move their heads while resting, for example to groom, which was therefore detected by the motion sensors. Stationary tests of the collars used in the US study found that the errors in distance ranged from 1.7 m to 5.8

m, thus GPS error may have over emphasised movement while resting and distances similar to grazing were recorded. Ungar et al. (2005) concluded that distance alone could not be used to infer animal activity as calculating the distance between GPS fixes using straight lines underestimated the animals actual travel path, however the combination of the motion sensors with accurate spatial positions to develop activity models provided the best method currently available to infer animal activity from GPS data.

The models created by Ungar et al. (2005) provided evidence for the opportunity to predict behavioural states from positional and movement data, although the accuracy of the models to discriminate between certain behavioural states requires further refinement and only general locomotive behaviours were considered. The results of Swain et al.'s (2008b) study clarify the suggestion by Ungar et al. (2005) that GPS error was a factor in their model predicting animal activity from GPS data: even a fix rate of 5 minutes as used in the Israel data may have resulted in patch errors of more than 100 m^2. These errors make it difficult to create a generic model for animal activity and confirm that to accurately determine social associations from GPS data at such a fine scale as can been achieved with visual observations requires the use of high fix rates.

A study by Guo et al. (2009) used high fix rate GPS data to develop and evaluate a model to predict cattle behaviour and movement. Six cows were fitted with GPS collars set to record a position every 10 s and an inbuilt accelerometer was used to collect directional speeds and angular speeds. The first 2 days of data recording were used to develop the model, while the following 2 days were used to evaluate the model. As cattle tend to spend longer periods of time in some areas than others, areas of high and low use were identified and used as the basis of the model. Areas that were occupied for longer than 1 hour at a time were classified as 'stay regions' and included features such as shade and watering points, while the areas in between were designated 'travel regions'. The behaviour of the cattle varied between the two regions, thus two different models were developed: one to predict the behavioural state within each region and one to predict the trajectory of movement. The combination of angular and directional speeds was used to distinguish between three behavioural states: grazing, resting or moving. For example, a high angular speed with a low directional speed was used to represent grazing behaviour while a low angular speed with a high directional speed was used to represent moving behaviour. A Hidden Markov model was used to predict the transition probabilities between the three behavioural states. For example, if a cow's current state was foraging the model predicted that the probability of resting in the next state was 0.0085, while the probability that the cow would continue grazing was 0.9953. A long term prediction model was used to generate parameters for a range of different movement trajectories between stay regions. The two models were combined to produce a final model to simulate the cow's movement. The model was able to accurately replicate both the fine scale behavioural patterns and also the large scale movement patterns. Guo et al. (2009) concluded that the model identified non-homogenous grazing patterns and this information could be used to improve management practices to increase forage utilisation.

Guo et al.'s (2009) study presented a very specific model that demonstrated the potential of using a combination of behavioural and movement models to simulate animal activity from actual data. The use of high fix rate GPS in Guo et al.'s (2009) study overcame some of the accuracy problems faced in Ungar et al.'s (2005) study, as the animals actual travel path and location estimate were obtained with greater precision. Additionally Guo et al. (2009) also used fewer behavioural categories, avoiding the problem of misclassifying behaviours with similar motion sensor responses as initially faced in Ungar et al.'s (2005) study. Yet both studies only considered general locomotive and resting behaviours.

The use of GPS technology to study animal movement and behaviour has increased considerably in recent years and there have been many studies investigating the development and refinement of GPS devices. Due to the high cost of the devices, many studies rely on tracking only a few individuals at a time, however social behavioural studies rely on collecting information on all of the social interactions between individuals within the group, thus presenting a challenge for the use of GPS devices in these types of studies. The cost of the devices, the errors associated with location estimates and the high demand on battery power are the technology's greatest limitations. Further developments are required to improve GPS accuracy and refine the technology into more readily accessible forms at lower costs. While the technology provides a means to collect spatial information, acquiring behavioural information from the data currently relies on additional data collection and analysis methods and limits the use of this technology for studying detailed animal social behaviour.

3.5. Selection of recording methods

Based on the review of data collection methods described above, visual observations can potentially provide the greatest description of an animal's behaviour, although there are several challenges associated with the method that are mainly created through human error and bias. The use of technology to record animal behaviour is gradually being more widely adopted. Each device has been developed to target specific behaviours, with no single technology deemed satisfactory to collect information on an animal's entire spectrum of behaviours and technological devices still need to be used in combination with observations to gain a complete overview of animal behaviour. Although, the amount of data collected by the devices is still greater than what could be achieved using visual observations. One technology that has been proven as a standalone device for collecting social interaction data and can therefore be used to infer social relationships are proximity logging devices. The use of proximity loggers in domesticated livestock studies has not been widespread, although the results of studies using proximity loggers to quantify maternal contact between cattle and sheep demonstrate the potential of the devices to be used in social behavioural based studies. Although GPS units have the potential to collect greater levels of spatial information than other devices, the technology has not been proven to collect information on social behaviour and still requires further development and testing.

Based on the research aims and experimental plan set out in Chapter 2, observations and proximity logging devices have been chosen as the preferred methods to collect social behaviour data in this thesis. Visual observations are a 'tried and trusted' method and even though there are various errors associated with the method, the errors are known and attempts to reduce observer bias can be made. Nonetheless, observations potentially provide the greatest description of an animal's behaviour and remain a benchmark for other technologies. In the current studies, observations have been chosen to provide a detailed description of cattle behaviour using a scan sampling method with short sample intervals. The behaviours of interest are related to an animal's general and social behaviour, movement patterns and inter-individual distances, thus scan sampling allows time for the observer to record the specified measurements, minimising errors associated with trying to record too much information at once. When required, behaviours of interests will be recorded by continuous sampling. Proximity logging devices have been selected to record the frequency and duration of close proximity encounters between individuals. The two methods will be used independently and also in combination: using both methods together provides complimentary information on an animal’s social behaviour and ensures that adequate behavioural detail is recorded. Additionally, using proximity logging devices as a standalone data collection method allows the application of this novel method to be further explored and provides further evidence of the value of using proximity loggers in social behaviour studies.

3.6. Statistical approaches

Analysing animal social behaviour data involves describing the interactions and relationships between individuals within a group, which has not received much attention in the past (Whitehead, 2008). Social network analysis is one method that considers interaction between members as a function of the group, rather than an isolated component (Krause et al., 2007). By focusing on the relationships between individuals, the patterns and outcomes of these relationships can be explored: it is the regular patterns in relationships that form the *structure* of the group (Wasserman and Faust, 1994). The method originated in the 1930’s to understand social patterns and processes of human relationships, and has recently been adopted by behavioural biologist to study relationship and interaction patterns among animal species (James et al., 2009).

In social network terminology, individuals are referred to as ‘actors’, where an actor can represent any form of social entity, from an individual to a collective group to an organisation (Wasserman and Faust, 1994). The relationships between actors are known as ‘ties’, where a tie defines any form of linkage between two actors, from a friendship to a business transaction (Wasserman and Faust, 1994). Thus, dyads or pair-wise relationships form the basic unit of analysis, and the accumulation of all pair-wise relationships within a group describes the overall network structure (Croft et al., 2008). Describing the structural properties of ties in relation to social theory is a key feature of social network analysis that distinguishes the method from other statistical approaches, such as regression and analysis of variance, which are unable to quantify social and behavioural concepts from relational data (Wasserman and Faust, 1994).

Various measures can be calculated from social network data, from descriptive properties to more advanced statistical tests, which include the development of statistical models to characterise and compare network structures (Croft et al., 2008). The general aim of a using a statistical model is to derive parameter estimates from data which are then evaluated for how well the parameters describe the data (Robins et al., 2007). In a social network context, statistical models are used to identify, describe and evaluate social processes within a network (Wasserman and Faust, 1994). For example, statistical models allow researchers to identify if specific network properties occur more or less frequently than expected by chance, while different hypotheses relating these properties to social processes can be tested and the potential outcomes from such processes can be evaluated (Robins et al., 2007). A new social network related model known as the relational event model will be used in the thesis to describe and analyse the encounter structures between triads and groups of steers.

The relational event framework proposed by Butts (2008) is a modelling framework for analysing sequences of social interaction to determine regularities in patterns of interaction between actors. A 'relational event' is described as social action between actors. Each potential relational event is considered to be independent of all other events, but conditional on the collection of interactions that have occurred in the past. In other words, the model estimates the probability of possible future events based on the history of prior events between actors. The model was applied by Butts (2008) to study radio communication during the early stages of the Wold Trade Centre disaster. A similar model was applied by Brandes et al. (2009) to study political conflict. The theoretical background to the model is described below.

3.6.1. The relational event model overview

In its most general form, the model is based upon a form of statistical analysis termed event history analysis. Event history analysis statistically describes the process of change by analysing sequences of social processes over time that were correlated with the change (Blossfeld and Rohwer, 1995). Thus, event history models are used to describe if and when an event occurs, and when applied to social relational data, can be used to describe the process of social influence and social selection (De Nooy, 2011). Social influence occurs when an individual's attribute, such as behaviour, attitude and beliefs, is influenced by the attributes of other network partners, while social selection occurs when social relationships are formed or modified on the basis of individual characteristics, where individuals *select* or are selected for their individual attributes (Robins et al., 2001). A social relationship characterised by repeated close proximity encounters between familiar and unfamiliar steers could be described as social selection. Applications of event history modelling to describe social selection data are rare (De Nooy, 2011). The current model uses a simplified ordinal form of event history analysis to investigate the formation of ties, or close proximity encounters, between two familiar steers with an unfamiliar steer.

Event history models posit survival and hazard functions to describe the occurrence of a potential event given the past history of events. The random variable, T, represents the waiting time until the occurrence of an event. The cumulative distribution function of T is described by the function:

$$F(t) = P(T \leq t)$$

which is the probability that an event has occurred prior to time t. The density function of $F(t)$ is $f(t) = dF(t)/dt$, which describes the probability that an event will occur at time t. The survival function is complementary to the cumulative distribution function and describes the probability that an event will occur beyond a certain point in time, t. The survival function takes the form:

$$S(t) = 1 - F(t) = P(T \geq t)$$

The survival function assumes that the probability of survival at time zero, t_0, is one and declines towards zero, given that all events have an end point (Cameron and Trivedi, 2005).

Another important component of event history analysis is the hazard function, which describes the instantaneous probability that an event occurs at time t, given that it has not occurred in the past. The hazard function is a transition rate, which describes the propensity to change from one state to another at time t. The hazard rate is defined as:

$$h(t) = \lim_{\Delta t \to 0} \frac{P(t \leq T \leq t + \Delta t | T \geq t)}{\Delta t} = \frac{f(t)}{S(t)}$$

The relationship between the hazard and survival functions shows that the hazard rate is conditionally dependent on events that have occurred up until, but not including, t, hence the '*past conditions the present, and what happens in the present shapes the future*' (Blossfeld and Rohwer, 1995, p.31). The realisation of all hazard functions in the data set provides a complete description of the whole process, which is equivalent to the distribution of T, and is used to describe how a process evolves over time (Blossfeld and Rohwer, 1995).

The relational event model builds on event history analysis by incorporating relational effects that have been used in cross-sectional models for interaction or relational data and hence have become familiar in models for network structure (e.g. Snijders et al., 2006). Relational events, however, are modelled sequentially, and the model specifies the probability of a potential relational event at time, *t*, that takes the form of an interaction between social actor, *i*, and social actor, *j*. The sequence of observed events between actors before time *t* is termed the sequence of prior events and is comprised of discrete events of the form $a_m = (i,j)$, where a_m is an encounter between actor *i* and actor *j* at the *m*th moment in time. The sequence of events up to and including the actual event at time *t* is written as:

$$A_t = \{a_m : m \leq t\}$$

where *m* is the time at which the event *a* occurs. The potential relational event at time *t* that involves an interaction between *i* and *j* is also denoted Y_{ijt} which has the value 1 if actor *i* encounters actor *j* at time *t* and has the value 0, otherwise. Both of these notations are used here.

In a relational event model, it is assumed that each potential relational event has a constant hazard of occurrence given a particular history of prior events and the duration between events is conditionally exponentially distributed, thus for a relational event occurring at time *t* following an earlier event at time $t'<t$, the hazard function takes the form of $h(t) = \lambda$ and the survival function becomes $S(t) = exp(-\lambda\ (t-t'))$. The probability of an event occurring at time *t* is equal to the hazard of the event at *t* (i.e. the probability of an event *a* occurring at time *t* given it has not occurred in the past) multiplied by the survival functions for all possible events that could have occurred in the time interval from *t′* to *t* (i.e. the joint likelihood that none of the possible events occurred in the interval between *t′* and *t*) (Butts, 2008). The model therefore considers the probability of events that did occur as well as the probability of events that could have occurred at time *t* but did not (Butts, 2008).

3.6.2. Ordinal relational event models

An ordinal form of the model is used to specify the probability of the next relational event but, as explained in Chapter 8 (section 8.2), predictors of the next event may be based on continuous time recordings of prior events. Butts (2008) showed that, in the case where only the order of events is taken into account, the probability that a particular event *a* will be the next in the sequence is the occurrence rate for *a* divided by the sum of rates for events that might occur including *a* itself, and hence the probability of the event *a* is:

$$p(a) = {}^{\lambda_a}\!\Big/\left(\sum\nolimits_{a'} \lambda_{a'}\right)$$

where λ_a is a rate parameter associated with event *a* and the events *a′* run over all possible events that may occur next in the sequence. The parameter λ_a is assumed to depend on the prior history of relational events and exogenous covariates such as characteristics of the actors, and can be parameterized in the form:

$$\lambda_a = \exp\left(\sum\nolimits_h \theta_h s_h\right)$$

where the statistics s_h depend on the prior history of relational events and exogenous covariates (see Chapter 8, Section 8.2) and θ_h are corresponding parameters. The parameters can be used to explain how prior events are related to future events: a large positive (negative) value of θ_h indicates that an event *a* is more (less) likely if the statistic s_h summarising relevant prior events is high.

Since the model takes the form of a conditional logistic regression model (e.g. Agresti, 2002), it may be fitted using the SPSS COXREG procedure, specifying each event as a stratum within the model. In fact, in the applications of the model presented here, a separate model is fitted for each of a number of possible types of event observed in the sequence. In other words, as well as conditioning on the type of event, the ordinal relational event model is used to characterise how the past history of events explains which animals are involved in events of that type.

A general overview of the relational event model has been provided here, however a detailed statistical description of the relational event model is provided by Butts (2008). Further detail on the application of the model to the social encounters of triads and groups of steers is presented in Chapter 8 and Chapter 9, respectively.

Chapter 4

General methods

4.1. Introduction

The research aims outlined in Chapter 2 were proposed to investigate animal social behaviour under different social contexts by varying familiarity and group size. As a result, a series of experiments involving different social contexts were designed. Given the sequential progression of the experiments, a longitudinal research design was chosen to provide a record of each individual's social tendencies across a variety of social contexts and to also obtain information on the social changes caused by the experiments. Additionally, measuring the same individuals repeatedly minimised behavioural variation due to differences in social history, as each individual's age, breed and management were the same. The current chapter outlines the general methods that were used throughout the thesis, including the animals and their management, as well as the specific details of the data recording methods.

4.2. Animals and management

The experiments were conducted at Belmont Research Station (150° 13′E, 23° 8′S), 26 km north of Rockhampton, Australia. The experimental period commenced in May 2008 and was completed by October, 2009. The procedures used within the experiments were approved by the CSIRO Rockhampton Animal Ethics Committee (Approval numbers: RH243-07, RH252-08 and RH258-09).

4.2.1. Resident steers

At the beginning of the study, two groups of steers were purchased to serve as 'resident' steers. The resident steers were used in each of the experiments and the behaviour of each steer was repeatedly measured over the series of experiments. Forming the resident steers into groups of familiar steers ensured that the within- and between-group familiarity levels were known and managed according to experimental requirements. Additionally, using the same steers reduced the requirement for new steers to be trained to wear collars and become accustomed to the observers and animal handlers.

The two resident groups of steers were purchased from the local sale yards in February, 2008. Each group consisted of 14, 18-month-old Brahman (*Bos indicus*) steers with a mean live weight (± standard error) of 317 ± 6.0 kg. Included in the 14 steers per group were two 'spare' steers to serve as replacement animals in case any steer needed to be removed from the experiment. Information on the steers management and rearing procedures prior to purchase was not available, however within groups the steers had the same brand and between groups the steers had different brands. It is therefore assumed that the steers within each group came from the same property and experienced the same management practices, while it is also assumed that the two groups came from different properties and had no prior encounters with the other group. Once on the research property, the two groups were restricted from any visual contact and kept separate at all times to maintain unfamiliarity between the groups. A buffer zone of at least 100 m separated the two groups when at pasture while there was at least 20 m separation between the groups when held in yards. The steers were maintained on unrestricted Rhodes grass (*Chloris gayana*) dominant pastures and were provided with supplementary fodder when required.

After arriving on the property, the groups were given 10 weeks stabilisation before any experiments were conducted. Social stabilisation in cattle is said to occur 30 to 45 days following the introduction of unfamiliar animals (Sato et al., 1990), thus within groups animals were considered to be socially stable at the beginning of the first experiment. Within the last 2 weeks of stabilisation, steers were trained to wear proximity logging collars. When the first experiment began the two spare steers per group were removed.

4.2.2. Unfamiliar steers

In January, 2009, a third group of 'unfamiliar' steers were purchased specifically for the third experiment (Chapter 7) to serve as animals that were completely unfamiliar with the two groups of resident steers. The steers were sourced directly from a property at Lotus Creek, approximately 225 km north of Rockhampton. The group of unfamiliar steers consisted of 52 Brahman (*Bos indicus*) steers with a mean weight (± standard error) of 484 ± 3.3 kg. The steers were selected based on a similar age and weight to that of the resident steers, and also for their quiet temperament. The unfamiliar steers were purchased 4 weeks prior to the start of the experiment and were trained to wear collars during this time. Similar restrictions on distance between the unfamiliar steers and the resident steers were put in place to maintain unfamiliarity between steers. Additionally, enough steers were purchased to ensure that each unfamiliar steer was only introduced once to the resident steers before being removed from the experiment.

4.3. Data collection

4.3.1. Visual observations

Visual observations were used to record occurrences of certain social behaviours in experiments one and two (Chapters 5 and 6). Observations were carried out between 08:00 h and 16:00 h to capitalise on the periods when the animals were most likely to be active. In general, cattle at pasture have peak feeding and moving activities in the morning and afternoon, with a small rise in grazing around midnight (O'Connell et al., 1989). Observations were recorded using a scan sampling method with point sampling, where at regular time intervals the entire group was ‘scanned’ and the behaviour of each individual at that instant was recorded. Additionally, behaviours of interest were recorded by continuous sampling when required. Each observation period was divided into short sample intervals (ranging from 30 s to 2 minutes). A limited number of behavioural classifications were used to aid in quick reporting. These categories included fundamental cattle behaviours, such as grazing, walking, standing and lying, and also included experiment specific measures. Rarely observed behaviours were reported individually but classified as ‘other’ in analyses.

Several procedures were followed to minimise potential sources of error associated with visual observations. Firstly, the same two observers performed the recordings throughout to minimise both within- and between-observer bias and to ensure consistent measures were obtained. Secondly, to aid identification numbers were painted on both sides of each steer’s rump and used as a reference during observations. Thirdly, pre-determined distances between fence posts were used as guides to estimate distances, either the individuals distance from a certain point (experiment one; Chapter 5) or inter-individual distances (experiment two; Chapter 6). During experiment two, an average body length of 2.5 m was also used to estimate inter-individual distances at close ranges. Lastly, to reduce the presence of the observers on the steers, observation towers approximately 3 m tall were used where possible. This elevation attempted to remove the observer out of the direct sight of the steers. During experiment one, an observation tower was positioned directly in the middle and adjacent to the test arena (see Appendix A), while at pasture in experiment two, one tower was positioned strategically among four sub plots to maximise the viewing area. When observation towers could not be used, observers positioned themselves out of sight as much as possible and avoided sudden movements.

4.3.2. Proximity logging devices

The proximity loggers used were manufactured by Sirtrack Ltd. (Havelock North, New Zealand) and are the same as those described in Chapter 3, Section 3.4.1. Throughout the studies, the detection range was set to 4 m and the separation time was set to 30 s. Based on cattle spacing principles and mean inter-individual distances of between 4 and 10 m when grazing (Chapter 2, Section 2.7.4.), it was anticipated that a detection distance of 4 m was a small enough to identify close proximity encounters that represented meaningful contact between two individuals, such as allogrooming, exploratory behaviour and agonistic behaviour, yet large enough to accommodate the spatial fields of all steers. Figure 4.1 shows the 4 m detection in relation to the size of the animals used. The accuracy of the range cannot be determined due to the reflection, refraction and absorption of radio waves by naturally occurring compounds in the environment (Mullen et al., 2004). The loggers used were capable of storing up to 32,768 records and each recorded contact detailed the record number, identification of the encountered logger, the encounter date and start time and the encounter length.

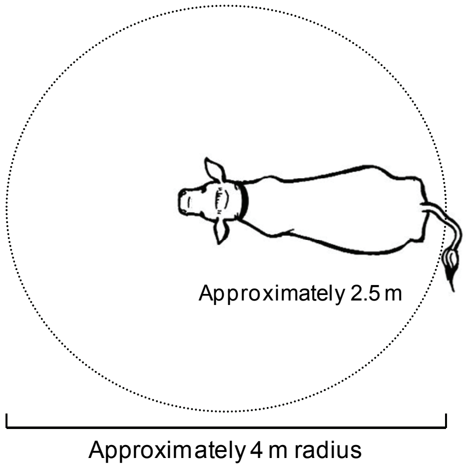


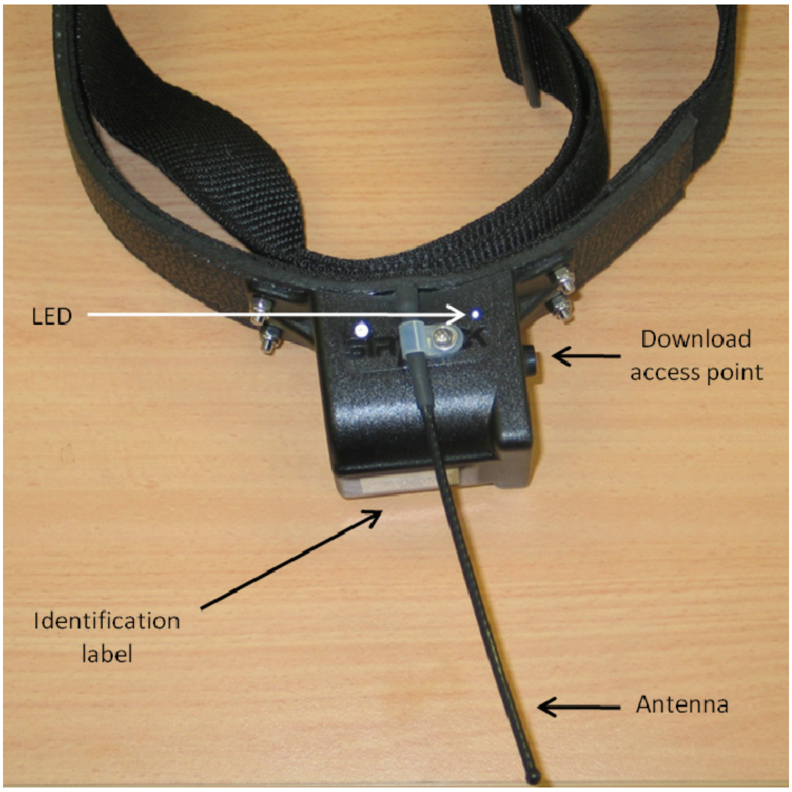
Figure 4.1. Proximity logger read range on an 18-month-old Brahman steer.

The proximity logging unit was mounted onto a synthetic collar with a strap adjustor and a quick release side squeeze buckle for fastening. The body of the proximity logging unit contained an external aerial, individual logger details and a red LED light (Fig. 4.2a). The loggers were initiated by moving a magnet over the area of the LED where a magnet switch is located and the LED flashed once to indicate that the unit had been turned on. The logger was turned off by similarly moving a magnet over the switch and the LED responded by flashing several times. When turned on and in contact with another logger, the light would intermittently flash until the contact was broken and the LED emitted one long pulse to signal that the data had been stored in memory.

Two people were required to fit the devices to steers. The steers would be quietly moved from the yards into the race and each steer in turn would enter the holding crush, where movement was minimised. The collar, weighing approximately 0.5 kg, was passed around the steer’s neck and the quick release buckle fastened (Fig. 4.2b). The collar was then assessed for size, ensuring that the palm of a hand could be easily moved around between the collar and the animal’s neck. This fit ensured the collar was not too tight to cause rubbing nor too loose to come off when the steers head was in a downwards position, as when grazing. Any excess collar strapping was folded up and tied to the collar using electrical tape. The animals were then released from the crush and monitored for a minimum of 30 minutes to ensure there were no complications associated with the collars or excessive head shaking by the steers. To remove the collars, the steers were returned to the holding crush while the buckle was undone and the collar gently removed from the steer’s neck.

Introducing the steers to the collars prior to any experimentation was essential to familiarise the steers with the collars, to make sure no steers had any adverse reactions to wearing the collars and to ensure the data collected by the loggers was not a result of the steers adjusting to wearing collars for the first time. The first stage of collar training involved fitting each steer with a collar while in the holding crush leaving the collar on for several minutes before removing the collar and releasing the steer from the crush. The second phase involved leaving the collars on the steers and returning them to their paddock for a period of several days before removing the collars again.

(a)



(b)

Figure 4.2. (a) External components of a proximity logger designed for use on cattle (photo supplied by Chris O'Neill) and (b) steer fitted with a proximity logger.

Once removed, a USB interface was connected to the logger from a computer to download the data. The data was then saved in an excel spreadsheet for processing. The first 5 hours of data collected after fitting collars were discarded to account for the time taken to handle the steers and return them to their designated plot, as was the 5 hours prior to removing collars. Theoretically, each contact recorded by a proximity logger should be reciprocated by the contacted proximity logger, however this is not always achieved due to reflection, refraction and absorption of radio waves (Prange et al., 2006; Swain and Bishop-Hurley, 2007; Bohm et al., 2009). Additionally, Prange et al. (2006) reported that some proximity loggers record multiple shorter contacts rather than one single contact. To overcome this, contacts from both loggers were assessed according to the beginning and end time with any overlap removed. A contact was defined as beginning when either logger recorded a contact and ending when either logger failed to maintain contact, given that there was continuous recording by either logger within the start and end time (Hamede et al., 2009). Thus, a single file of contacts was created per pair. One-second contacts can erroneously occur when near the edge of the detection range (Prange et al., 2006) and were removed from the data prior to analysis, thus the minimum contact length between two steers was 2 s. Details of the statistical analyses used are reported in the specific chapters.

Chapter 5

The effect of familiarity on the trade-off individual steers make between food and social companionship

5.1. Introduction

Close spatial proximity is a prominent feature of affiliative social behaviour (e.g. Murphey, 1990; Sibbald et al., 1998). The tendency to remain within a group's living space provides an indication of group cohesion, while inter-individual distances provide an indication of the social attraction and relationship status between two individuals. Therefore, spatial proximity can be used to indicate the level of social attraction between two individuals. Social attraction is not shared equally between group members, as individuals at opposite ends of the hierarchy maintain greater inter-individual distances (e.g. Manson and Appleby, 1990) and preferential relationships exist between some individuals rather than others (e.g. Reinhardt and Reinhardt, 1981; Val-Laillet et al., 2009). The aim of the current experiment was to develop an understanding of the differences in social attraction between familiar and unfamiliar steers.

A motivational conflict exists between the priority for behaviours that maintain social bonds with other group members and the priority for foraging behaviour that entices individuals away from the group to maximise their feeding opportunities. The conflict between social and feeding behaviour is dependent on interactions between multiple factors, such as the distance to a feeding site (Dumont and Boissy, 2000), the size of the social group and the level of familiarity among peers (Boissy and Dumont, 2002). Differences in sociability can also influence an individual’s behaviour in a motivational conflict. A social trade-off test developed by Sibbald et al. (2006) used food bowls placed at incremental distances to entice individual sheep away from a group of familiar peers. Sibbald et al. (2006) determined that highly sociable sheep were less inclined to move away from the group when faced with the conflict of social versus food motivation. It is not known how motivated a steer is to remain within proximity to a peer when faced with a desired food source, and whether this response is influenced by the familiarity of the peer.

The current experiment was developed to compare the willingness of individual steers to remain within close proximity to either familiar or unfamiliar steers when faced with a food reward using a similar trade-off test to that described by Sibbald et al. (2006). Preference tests, such as those designed by Sibbald et al. (2006), have been used in animal welfare research to quantify the biological and social requirements of an animal, and can be used to quantify an individual’s preference for different foods, temperature or social companionship (Broom and Fraser, 2007). It was suggested by Sibbald et al. (2006) that the distance individuals are willing to travel for food represents a trade-off point between food and social companionship. It was hypothesised that steers paired with unfamiliar peers would travel further to receive a food reward than those paired with familiar peers because the steers would have lower levels of social attraction towards the unfamiliar steer.

5.2. Methods

5.2.1. Animals and management

The experiment was conducted in May 2008. The two groups of 12 steers and their management procedures were the same as those described in Chapter 4. Briefly, the two groups of steers were located a minimum of 100 m when at pasture and at least 20 m when held in yards. At the time of the experiment the steers mean weight (± standard error) was 352 ± 7.3 kg and 389 ± 8.6 kg for groups 1 and 2, respectively. When not being tested the steers were maintained on unrestricted Rhodes grass (*Chloris gayana*) dominant pastures. On the day of testing, animals were sorted into required or non-required and those not involved in tests were returned to their paddock. Animals being tested were given access to hay and water up until a minimum of 1 hour prior to testing. The procedures used within the current experiment were approved by the CSIRO Rockhampton Animal Ethics Committee (Approval number RH243-07).

5.2.2. Experiment design

The test arena consisted of a 140 m × 30 m grass area with adjoining portable fencing creating a holding pen for the penned steer (2.3 m × 6.9 m) and a release yard for the observed steer to be held in before testing (4.6 m × 6.9 m; Fig. 5.1). Images of the test arena can be seen in Appendix A. The portable fence frames were made of 32 mm galvanised steel with six rails approximately 0.26 m apart, allowing minimal visual obstruction between the penned and observed steers. An observation tower approximately 3 m tall was positioned half way along the test arena. Portable electric fence posts (1.05 m tall; Multiwire Polymer Treadin, Gallagher Animal Management Systems, Melbourne, Victoria, Australia) were labelled with corresponding distances and placed every 10 m on both sides of the test arena to assist with estimating the steer's position. The original groups were located approximately 70 m away and could not be seen from the test arena.

5.2.3. Familiarisation with experimental arena

Familiarisation events were carried out prior to each of two designs; one without-food and one with-food[1]. Each group of 12 was held in the adjoining holding yards and then released into the arena via the entry gate. The access allowed the steers to familiarise themselves with the features of the test arena as a group. After 30 minutes, the group was herded back through the exit gate. The same procedure was conducted with both groups of 12 in the presence of food rewards. Forty-eight plastic food bowls, 0.20 m in height and 0.44 m in diameter placed within a car tyre for stabilisation, were randomly placed throughout the arena. Each bowl was filled with 250 g pelleted grain (Rumevite beef weaner pellets, Ridley AgriProducts, Melbourne, Victoria, Australia), which the steers had been familiarised with over a 6-week period prior to the beginning of the experiment. This process was repeated once per group prior to the without-food tests and three times per group over a 2-week period prior to the with-food tests.

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[1] The with-food and without-food treatments relate to presence or absence of supplementary food. The test arena was established on mown pasture thus there was always a source of food available to the steers under both the with- and without-food test conditions.

5.2.4. Tests

Two tests were designed: a without-food test and a with-food test, with a familiarisation period before each test phase. There were no food bowls present in the without-food tests. During the with-food tests, 13 food bowls were placed at 10 m increments in the centre of the test arena, directly in front of the penned steer (Fig. 5.1). Before the beginning of each test, approximately 250 g of the food source was dispensed into each food bowl. The food allocation was based on the manufacturers guidelines, with the daily ration divided evenly between the 13 food bowls. For each test design, 24 familiar pairings and 24 unfamiliar pairings were tested. Six tests were completed each day with testing spread over a 4-week period. The without-food tests were conducted first, with the familiar tests completed before the unfamiliar tests. The same order was repeated for the with-food tests, with all pairings randomised. The order of testing was structured to avoid holding animals in the yard for longer than necessary and to also lower the chances of the two groups encountering each other via sight or smell before the unfamiliar tests.

To control for variables other than familiarity, the steers were not deprived of food prior to testing to ensure each individual had an equal level of hunger/satiation. The groups were maintained under normal grazing conditions prior to and in between testing. Food was therefore not a variable in the test and the intake per individual was not measured. It is possible, however, that individual differences in motivation for food may have affected their performance in the test.

5.2.5. Experimental procedure and behavioural measurements

Each test involved two steers, an observed steer and a penned steer, or social attractant. Each steer performed both roles as an observed steer and as a social attractant in both the without-food and with-food experiments and familiar and unfamiliar treatments, thus each steer participated in eight tests.

The test procedure involved securing the penned steer in the holding pen and the observed steer in an adjacent release yard (Fig. 5.1). The entry gate into the test arena was manually opened and the observed steer was allowed to enter the test arena in its own time. The test began when the steer's entire body was in the test arena, with each test lasting 30 minutes.

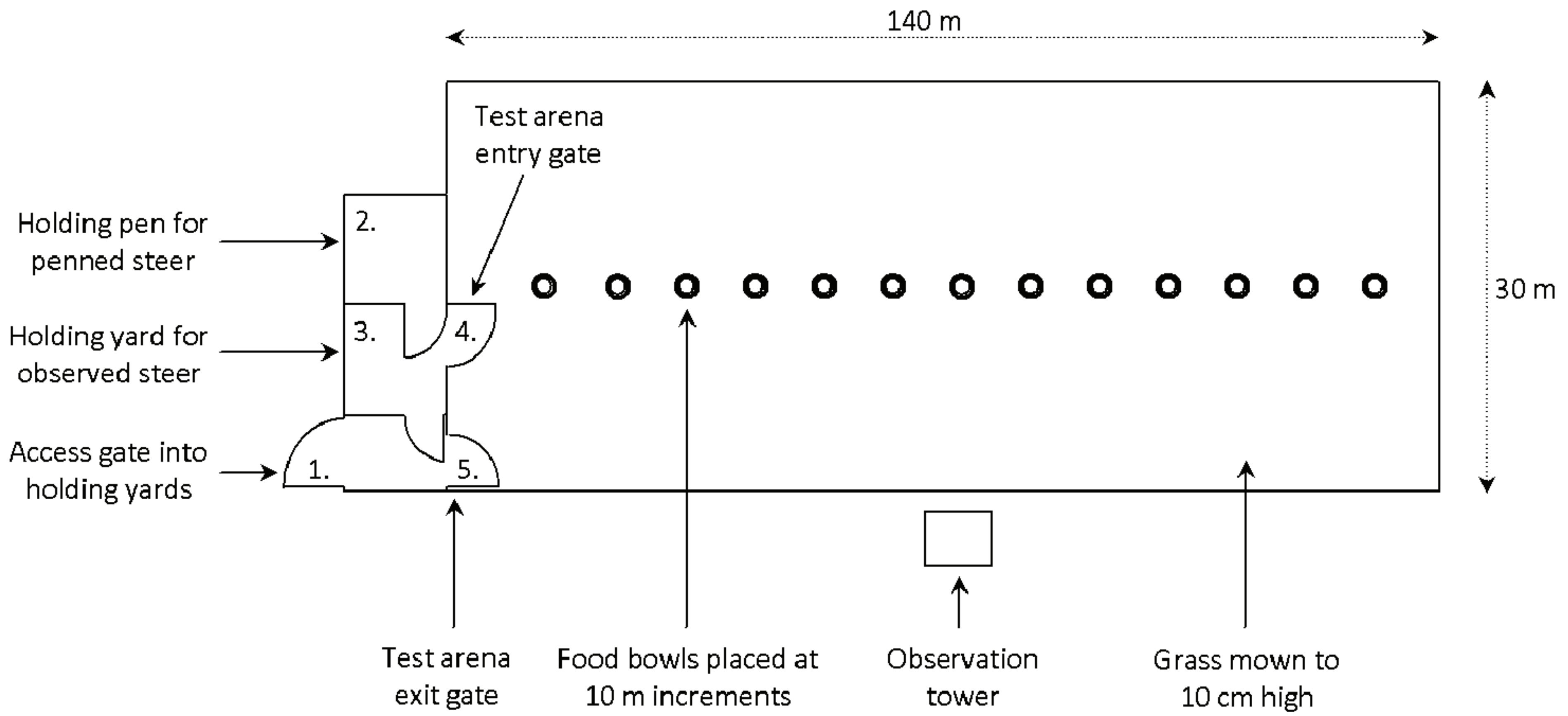


Figure 5.1. Test arena layout. Numbers indicate the sequence of test events: (1) Steers enter the holding yards. (2) The penned steer is secured in the holding pen. (3) The observed steer is secured in the holding yard. (4) The observed steer enters the test arena through the entry gate. (5) At the completion of the test, the observed steer leaves the arena via the exit gate.

Observations were recorded by a single observer every 30 s, noting the distance (within 5 m) of the observed steer from the penned steer. At each sample point, the behaviour of the observed steer was recorded (standing, walking, grazing, lying, ruminating, grooming and bowl visiting during the with-food tests). In between sampling points, all bowl visiting events were also recorded, with the distance of every bowl visit noted. After 30 minutes, the observed steer exited the test arena by a separate exit gate and both the observed steer and penned steer were returned to their original groups.

During the unfamiliar tests, the two steers only encountered each other immediately prior to entering the penned area. At the end of the test each individual was returned back to their original groups. If a steer was tested in an unfamiliar pairing, that steer would be given a one-day re-stabilisation period with members of its original group before being used in another test.

5.2.6. Data processing and statistical analysis

Individual animal data were analysed over the two different test types (without-food versus with-food) and two different treatment types (familiar versus unfamiliar). The effect of test type (within tests) and treatment type (between tests) was analysed independently of each other.

The distance the steer moved from the penned steer was calculated as the mean of 60 distance observations recorded every 30 s over 30 minutes. Distance observations were also averaged over 5-minute periods. The mean number of bowl visits was taken as the mean of all bowl visits per treatment. The mean distance when bowl visiting was calculated as the mean of all distances recorded. The rate of bowl visiting was calculated as the mean number of bowl visits per 5-minute interval. Behavioural events, including bowl visits, were expressed as a percentage of observations.

Statistical analyses were carried out using Genstat 10th edition (Payne et al., 2007). A two-way between groups analysis of variance (ANOVA) was used to determine any differences in means between test (without-food vs. with-food) and treatment (familiar vs. unfamiliar), while a one-way ANOVA was used to analyse differences in means within tests, using treatment as a factor in the model. Differences were considered significant at $P < 0.05$. Preliminary inspection of the distributions of distance, bowl visiting and time spent performing each behaviour and comparison of variances across treatments suggested that the assumptions for the ANOVA of normality and homogeneity of variance were plausible. Results for distances, behaviours and bowl visiting are expressed as mean ± standard error.

5.3. Results

5.3.1. Differences between familiar and unfamiliar without-food and with-food tests

Mean distance was affected by the presence of food (test main effect: $F_{1,95} = 6.53$, $P = 0.012$, $\eta^2 = 0.07$), but not by familiarity (familiarity main effect: $F_{1,95} = 0.13$, $P = 0.717$, $\eta^2 = 0.00$) or any interaction between the test types (without-food and with-food) and familiarity (interaction: $F_{1,95} = 0.85$, $P = 0.359$, $\eta^2 = 0.01$). The greatest difference between tests was seen between steers in the familiar with-food tests that travelled an average of 8.7 m further from the penned steer than the without-food test (ANOVA; familiar without-food = 5.1 ± 0.98 m, familiar with-food = 13.8 ± 2.88 m; $F_{1,46} = 8.26$, $P = 0.006$, $\eta^2 = 0.15$; Table 5.1). ANOVA performed at each 5-minute time interval revealed that the difference between the without-food and with-food tests for familiar test steers was significant during the first 15 minutes of the test (time = 5 minutes, $F_{1,46} = 32.67$, $P < 0.001$, $\eta^2 = 0.42$; time = 10 minutes, $F_{1,46} = 16.68$, $P < 0.001$, $\eta^2 = 0.27$; time = 15 minutes, $F_{1,46} = 4.70$, $P = 0.035$, $\eta^2 = 0.09$), while only the first 5 minutes proved to be different for the unfamiliar test steers (time = 5 minutes, $F_{1,46} = 17.6$, $P < 0.001$, $\eta^2 = 0.28$; Fig. 5.2).

The introduction of the food bowls caused a decrease in the amount of time spent standing for both familiarity types as steers actively explored the food bowls (test main effect: $F_{1,95} = 3.79$, $P = 0.054$, $\eta^2 = 0.13$; familiarity main effect: $F_{1,95} = 13.7$, $P < 0.001$, $\eta^2 = 0.03$), however there was no interaction between test and familiarity (interaction: $F_{1,95} = 0.08$, $P = 0.775$, $\eta^2 = 0.00$). The consumption of supplementary food also caused a notable decrease in ruminating behaviour between the without-food and with-food tests for both familiarity types (test main effect; $F_{1,95} = 6.34$, $P = 0.014$, $\eta^2 = 0.06$). However, the proportion of time spent ruminating was not affected by familiarity (treatment main effect; $F_{1,95} = 0.76$, $P = 0.385$, $\eta^2 = 0.01$) nor was there any interaction effect between test and familiarity (interaction: $F_{1,95} = 0.32$, $P = 0.573$, $\eta^2 = 0.00$).

5.3.2. Differences within tests

Differences in distance between familiarity types were not large enough to reach statistical significance during either the without-food or with-food tests. Less than 20% of tests resulted in the entire length of the test arena being reached (Table 5.1). One steer reached the end in both treatment types in the without-food tests and a different steer reached the end in both treatment types in the with-food tests.

During the without-food tests, the mean distance of the observed steer from the penned steer was non-significant between familiar and unfamiliar tests, with a difference of only 1.4 m (Table 5.1). Over the duration of the test the mean distance of the steer from the penned steer gradually increased for both treatment types, before declining after 25 minutes, as shown in Figure 5.2.

During the with-food tests, the difference in mean distance between the test steer and the penned animal was non-significant between treatments, with steers in the familiar treatment averaging 3.2m further from the penned animal than steers in the unfamiliar tests (Table 5.1). From Figure 5.2 it is seen that the familiar steers reached their maximum mean distance from the penned steer after 15 minutes before their mean distance gradually decreased, whereas the unfamiliar steer's greatest mean distance occurred during the first 5 minutes and declined over the remainder of the test.

Bowl visiting events were greater for familiar steers than unfamiliar steers (familiar = 12.0 ± 1.24 bowl visits, unfamiliar 7.5 ± 1.22 bowl visits, $F_{1,46} = 6.46$, $P = 0.014$, $\eta^2 = 0.12$; Table 5.1). Higher bowl visit rates were seen in the familiar steers at 10 minutes (familiar = 2.5 ± 0.40, unfamiliar, = 1.2 ± 0.47, $F_{1,46} = 4.07$, $P = 0.05$, $\eta^2 = 0.08$) and 25 minutes (familiar = 1.6 ± 0.36, unfamiliar, = 0.3 ± 0.11, $F_{1,46} = 13.36$, $P < 0.001$, $\eta^2 = 0.23$) into the observation period (Fig. 5.3). The rate of bowl visiting declined over time for both familiar and unfamiliar pairs, with the exception of a spike at 25 minutes for familiar steers. The time spent bowl visiting was greater for familiar steers by almost 10% (familiar: 22.6 ± 3.27, unfamiliar 12.6 ± 3.13, $F_{1,46} = 4.81$, $P = 0.033$, $\eta^2 = 0.09$; Table 5.1). Other behaviours, however, were not different between treatments.

Table 5.1. Maximum and mean distances of the observed steer from the penned steer, mean number of bowl visits and percentage of time spent performing four behavioural states for the without-food and with-food test for familiar and unfamiliar treatment types (±SEM.). Stars represent statistical significance at $P < 0.05$. Differences within tests relate to significant differences found between familiar and unfamiliar treatments per test (familiar versus unfamiliar); differences between tests relate to significant differences found within each test per treatment (without-food versus with-food).

	Within tests					Between tests	
	Without-food		With-food				
	Familiar	Unfamiliar	Familiar	Unfamiliar		Familiar	Unfamiliar
Maximum distance of test animal from penned animal (m)	31.0 (8.21)	32.5 (9.31)	54.8 (7.32)	45.2 (7.55)		*	
No. test animals to reach maximum distance (130^+ m)	2	3	2	2			
Mean distance of test animal from penned animal (m)	5.1 (0.98)	6.5 (2.25)	13.8 (2.88)	10.6 (3.31)		*	
Mean no. of bowl visits			12.0 (1.24)	7.5 (1.22)	*		
Behavioural states:							
% of time standing	72.9 (2.92)	79.1 (2.90)	57.9 (3.98)	66.3 (4.90)		*	*
% of time walking	14.2 (2.26)	14.3 (1.75)	14.9 (1.52)	13.1 (1.47)			
% of time grazing	4.5 (1.82)	1.8 (1.04)	2.7 (1.22)	5.7 (3.15)			
% of time ruminating	7.0 (3.36)	4.1 (2.17)	0.8 (0.63)	0.1 (0.14)		*	*
% of time bowl visiting			22.6 (3.27)	12.6 (3.13)	*		

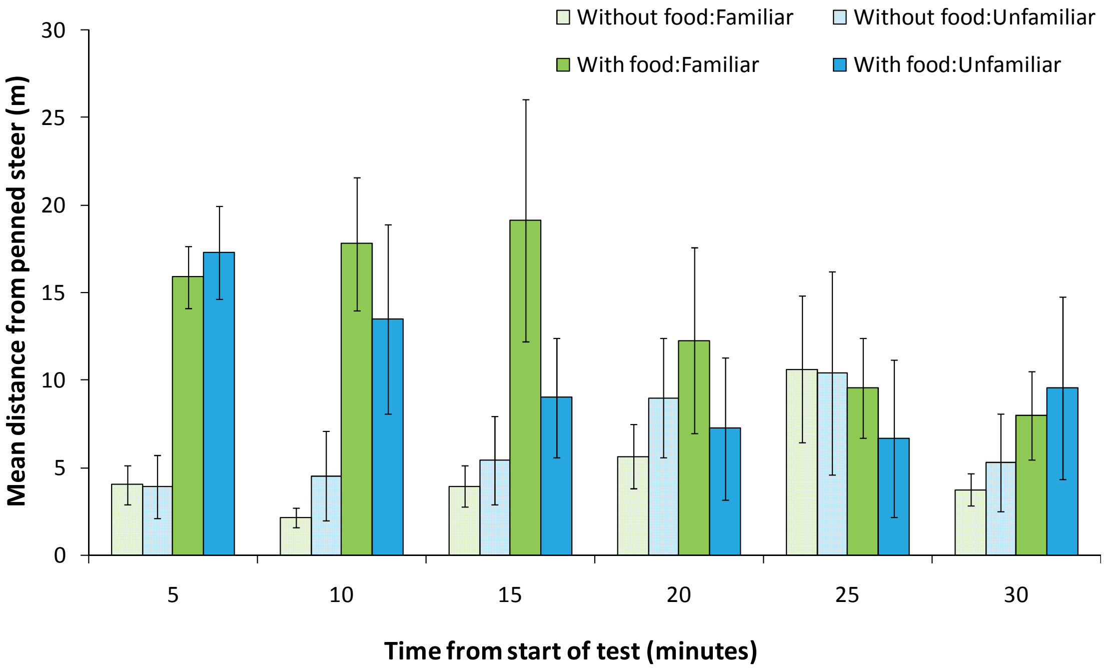


Figure 5.2. The effect of time on the mean distance of the observed steer from the penned steer during the without-food and with-food tests. Error bars represent the standard error of the mean.

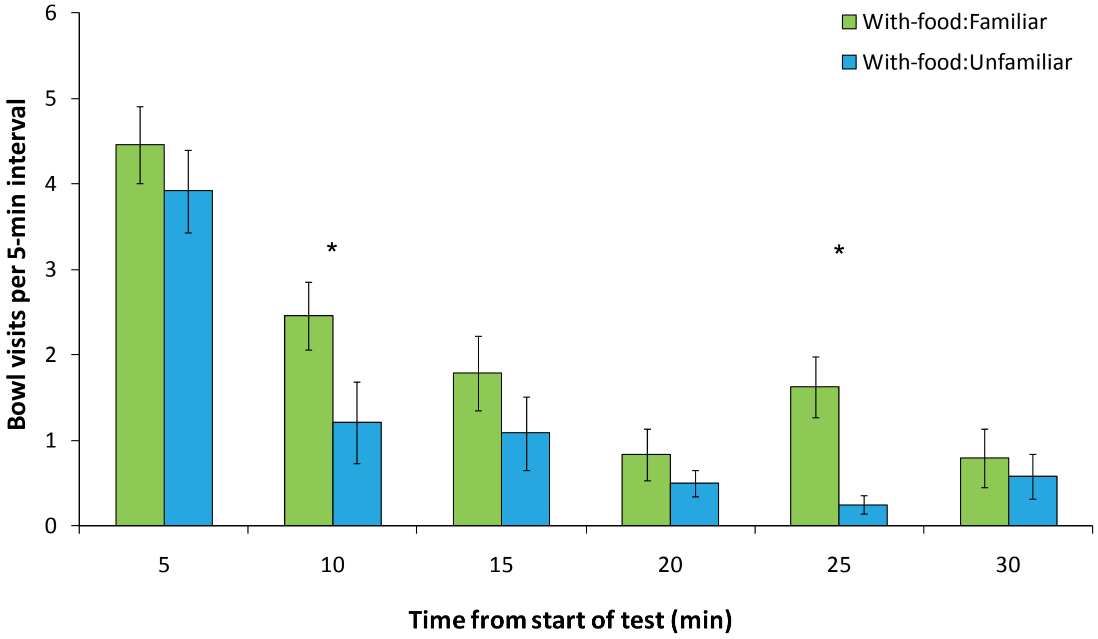


Figure 5.3. The mean rate of bowl visiting of steers paired with familiar and unfamiliar steers during the with-food test. Error bars represent the standard error of the mean. Stars represent statistical significance at $P < 0.05$.

5.4. Discussion

The aim of the experiment was to compare the social attractiveness of a familiar peer over an unfamiliar peer by creating a trade-off between social companionship and a preference for food, similar in design to that described by Sibbald et al. (2006). The results showed that without a feeding motivation steers remained in close proximity to either familiar or unfamiliar peers. The mean inter-individual distance between cattle when grazing is reported to be within 4 and 10 m (Broom and Fraser, 2007), thus mean distances less than 10 m between the observed steer and the penned steer were considered to be close. When faced with a trade-off between feeding and social preferences, steers were willing to move further to consume supplementary food in the presence of a familiar pen mate than an unfamiliar peer. Therefore, although a significant impact of familiarity was identified on the bowl visiting behaviour between the two treatment types, the effect was in the opposite direction to that hypothesised.

Sibbald et al. (2006) showed that sheep travelled an average 21.8 m away from the group the first time they were exposed to a similar food rewards test and visited an average of 42.5 bowls, with all sheep reaching the end of the 65 m test arena during this test. Thus, it was expected that the overall mean distance travelled by steers and the number of bowl visits would be greater than what was observed. It was also anticipated that most individuals would be prepared to travel the entire length of the test arena to gain a food reward, however, only seven individuals travelled to the end. The maximum distance travelled by each individual is a measure of their willingness to move away from a social companion to feed, indicating the trade-off point between food and social support. Similarly, the difference in distance travelled between the without-food and with-food test demonstrates the importance of food as a motivator. When food was present, steers in the familiar tests showed a significant increase in the distance travelled away from the penned animal when compared with the without-food tests, confirming that the presence of a familiar peer provided social support that allowed individuals to express their own feeding choices. Steers in the unfamiliar tests, however, showed no increase in distance between the without-food and with-food tests, indicating that the decision to move away for food was complicated by unfamiliarity and a lack of social support.

Other similar experiments that include a trade-off between an individual’s preference for social contact over feeding found that the familiarity of a grazing companion and the size of the companion group positively influenced the grazing choice of the animal (Boissy and Dumont, 2002). Scott et al. (1995) found familiarity to have a positive effect on grazing preference; lambs conditioned to prefer wheat when in the presence of familiar lambs conditioned to prefer sorghum elected to graze on their preferred grain some distance away. Additionally, Boissy and Dumont (2002) reported that animals in the presence of unfamiliar companions had shorter mean distances to the penned animals, vocalised more and had greater nearest neighbour distances, which was attributed to the loss of social support previously provided by familiar companions. Similarly, Sibbald and Hooper (2004) reported that sheep were more willing to graze a preferred feeding site that was close (15 m) than far away (35 m) from penned conspecifics due to the apparent fear of social isolation. The combination of lost social support and fear of social isolation as suggested by Boissy and Dumont (2002) and Sibbald and Hooper (2004) could similarly be used to interpret the shorter distances and fewer bowl visits by the steers during the unfamiliar with-food tests.

Cattle are gregarious animals and rely on group members for protection and support; removing this support can result in behavioural and physiological changes associated with stress (Boissy and LeNeindre, 1997). Socially isolated cattle in unfamiliar environments exhibit increased heart rates, increased plasma cortisol levels, increased elimination frequency and increased vocalisations (Rushen et al., 1999a). Unfortunately the test design did not allow for these stress indicators to be measured in the resident steers, although their behaviour during the unfamiliar tests showed signs of discomfort, such as a lower rate of bowl visiting behaviour, a tendency to spend a greater amount of time standing and a desire to maintain close proximity to the penned steer, more so than what was observed in the familiar tests. These behaviours may indicate fear in response to social isolation or the presence of an unfamiliar conspecific, with fear a known stressor in cattle (Grandin, 1997). According to Hamilton (1971), individuals should approach their nearest neighbour to decrease fear and risk of predation. If the test steers were experiencing fear of social isolation, maintaining close proximity to its nearest neighbour, which in this case was an unfamiliar steer, might indicate a form of stress alleviation.

Other motivational factors might have also influenced the change in behaviour caused by the presence of the unfamiliar penned steer during the with-food tests. For example, a motivational conflict may have existed between exploring the test arena versus investigating the unfamiliar steer. While the steers were given a familiarisation phase as a group in the test area with numerous food bowls present, the steers had not experienced the arena or access to the food bowls by themselves. Individuals differ in their levels of inquisitiveness and motivation to explore novel situations, which is necessary for learning and familiarisation with a new environment (Price, 2008). Additionally, younger cattle aged between one and two responded more to novelty (Murphey et al., 1981), thus the steers tested in this experiment could be considered highly inquisitive. Although it was only evident within the familiar with-food tests that steers showed greater levels of exploration of the food bowls. This suggests that during the unfamiliar with-food tests the presence of the unfamiliar steer created a distraction from the novelty of the environment and the observed steers were more interested to investigate the unfamiliar penned steer than the food bowls. This concurs with results obtained by Souza et al. (2006) who proposed that piglets gave higher priority to investigating unfamiliar conspecifics over exploration of a new environment.

One possible explanation for the test steers behavioural response towards the unfamiliar penned steer may have been the perception of the unfamiliar individual as a competition threat. Individuals within a group may compete for food, space and social status; the presence of an unfamiliar animal is considered a threat to all of these resources and may result in agonistic behaviour (Price, 2008). Even though the pair was restricted from physical interaction, steers were unrestricted from distinguishing each other via visual, auditory and olfactory cues. Remaining within close proximity may indicate the observed steer was evaluating the unfamiliar steer's characteristics, for example, predictors of dominance ability such as weight, sex and age. Furthermore, a grazing situation provides a highly competitive environment (Phillips and Rind, 2001), with high quality feed inducing dominance behaviours (Barroso et al., 2000). Therefore, the observed steers may have maintained close proximity to monitor the actions of the unfamiliar steer and its location to the highly desired food source.

Modification of the test design is required to formally test the proposed theories relating to social stress, curiosity and competition, and as such, no conclusive remarks can be made about the behavioural changes observed between the familiar and unfamiliar with-food tests. In future, it would be advantageous to measure behavioural indicators of stress, such as defecation/urination (e.g. Kilgour, 1975), head movements (e.g. Kondo and Hurnik, 1988) or heart rate (e.g. Rushen et al., 1999b). Similarly, additional information on the observed animal's location via grid co-ordinates would provide greater spatial accuracy and could be used to indicate if individuals were favouring specific areas of the arena, such as the exit gate, which may influence the response of the observed animal (e.g. Kilgour, 1975). Furthermore, the inclusion of an additional penned animal on the opposite side of the arena could be used to evaluate the observed animal's preference for one individual over another, for example a familiar versus an unfamiliar conspecific.

5.5. Conclusions

It was concluded that familiar peers provide social support that allows individuals to express their own feeding choices, thus the hypothesis that steers would be less attracted to an unfamiliar penned steer and travel further to receive a food reward was rejected. It was anticipated that the lower attraction would be a result of the lack of opportunity for unfamiliar steers to develop social bonds. The results showed that the opposite was true and steers in the presence of unfamiliar pen mates consumed less food than steers paired with familiar pen mates, while steers with familiar pen mates travelled further when food was present. Furthermore, the presence of an unfamiliar introduced additional factors that influenced the decision of the observed steer to move away from the unfamiliar conspecific to feed, although the reasons for this are varied and inconclusive but may relate to loss of social support previously provided by familiar peers, the priority to investigate the social environment over the physical environment or the competition threat posed by unfamiliar steers to valuable resources.

Chapter 6

The social behaviour of steers paired with either a familiar or unfamiliar peer

6.1. Introduction

Chapter 5 investigated the behaviour of steers when faced with a conflict situation between feeding and social companionship that was either familiar or unfamiliar. The behaviour of the steers was modified by the presence of the unfamiliar peer. Familiar peers provided social support that allowed individuals to express their own feeding choices while the observed steers were less willing to travel further away for food in the presence of the unfamiliar peer, possibly due to social stress, competition or curiosity. The test environment restricted any physical contact between the steers and the potential to develop a relationship, thus only individual behavioural responses towards the presence of the steer was measured. Familiarisation occurs via a process of repeated encounters and recollection of the outcomes of these encounters (Hinde, 1976), thus social interaction is fundamental for relationship development, including establishing dominance and maintaining social bonds through behaviours such as allogrooming. The current experiment examined the effect of familiarity on pair-wise behaviour in a natural environment and used several behavioural measures to identify and evaluate some of the spatial and temporal factors involved in the process of familiarisation, including inter-individual distance, the detailed movement response of one individual in relation to another and the frequency and duration of close proximity encounters.

Familiarisation has previously been documented in cattle by recording the level of agonistic interactions between individuals and defining stabilisation as the time it takes for non-physical interactions to predominate physical interaction (e.g. Kondo and Hurnik, 1990). A study by Bouissou (1974a) found that dominance relationships between newly mixed cattle were established relatively quickly; almost half of all dominance relationships were established within 5 minutes and all relationships determined after 2 hours. Changes in other social behaviours, such as locomotion and standing and lying time (Nakanishi et al., 1993b; Hasegawa et al., 1997; Grant and Albright, 2001) can take between 3 to 15 days to return to baseline levels. This suggests that agonistic behaviours are initially important during relationship establishment, but other social processes, such as learning and recognition, continue to occur after the direction of dominance relationships are established and are important factors during relationship development (Lindberg, 2001).

The aim of the current experiment was to compare the change in social interaction over time between familiar and unfamiliar pairs of steers in order to investigate the process of familiarisation. It was hypothesised that evidence of familiarisation would be seen within 5 days. By studying pairs in isolation, the aim was to investigate the types of pair-wise interactions involved in relationship development, whilst minimising both social interference and observational errors associated with large groups. It was anticipated that isolating unfamiliar pairs of steers would accelerate the process of familiarisation due to the lack of interference from other group members. Additionally, cattle are naturally herding animals and rely on group members for protection and support; being socially isolated is a stressful situation (Boissy and LeNeindre, 1997), thus there is mutual benefit for the unfamiliar steers to quickly form a relationship and provide social support for each other.

6.2. Methods

6.2.1. Animals and plots

The experiment was conducted in July 2008. At the time of the experiment the two groups of steers mean weight (± standard error) was 352 ± 7.3 kg and 389 ± 8.6 kg for groups 1 and 2, respectively. The steers gained some experience with being paired with unfamiliar steers in the previous experiment, although the unfamiliar animals paired in the current experiment had not previously been paired with each other. Pairs were monitored for 5 days in 3 ha plots with a minimum 20 m buffer zone between each plot. The steers had previous experience with the yards, plots and paddocks. The procedures used in this experiment were approved by the CSIRO Rockhampton Animal Ethics Committee (Approval number RH243-07).

6.2.2. Experimental procedure

The pair was treated as the experimental unit with two treatment levels: familiar and unfamiliar. In total 15 pairs of familiar animals and 15 pairs of unfamiliar animals were monitored over 5 deployments. Each deployment lasted 5 days with 3 familiar and 3 unfamiliar pairs monitored per deployment. The total duration of the experiment was 5 weeks.. On the day of introduction (day 1: between 14:00 h and 15:00 h), each steer was fitted with a proximity logger weighing approximately 0.5 kg. Steers were paired off and moved to their designated plot, approximately 1 km from the cattle handling yards. The unfamiliar pairings were randomised; the only pre-requisite was that the two individuals had not previously been paired together. At the end of the 5 days, the steers were returned to the yards and the collars removed. Over the 5-week period, some steers were re-used. The re-use occurred so that a steer was always paired with another steer that had the same level of experience with the test conditions. At the outset, all steers had previous experience with being paired with other steers in the yard. To test whether experience with the test conditions affected behaviour, the distance results of novice and experienced pairs were compared by day, where ‘novice’ refers to pairs of steers that were new to the study. Re-used steers were given a 1 week social re-stabilisation period with original group members between monitoring weeks.

6.2.3. Proximity logger data statistical analysis

The contact data over the first 5 days were summarised on a daily basis as the total number of contacts per hour and the average length per contact. The number of contacts per hour and the average length per contact were analysed for treatment and day effects, blocked by week, using a repeated-measures analysis of variance (ANOVA) (Rowell and Walters, 1976). The repeated-measures ANOVA estimates the Greenhouse-Geisser epsilon to account for the degree of temporal auto-correlation, with the significance levels of the F-tests adjusted accordingly. Differences were considered significant at $P < 0.05$. Approximate least significant differences at the 5% level were used to assess pair-wise differences between treatment means for the same day. Distributional assumptions were assessed by visual inspection of residual and normal probability plots resulting in the proximity logger data being square-root transformed prior to analysis with back transformed values presented in the text.

6.2.4. Behavioural observations

Visual observations were used to estimate inter-individual distances per pair, to describe the behavioural state of each individual within a pair and to detail the movement of one individual in relation to another. Observations commenced the day following introduction (day 2) and were performed by the same two observers each day from days 2 to 5. Observations were carried out between 08:00 h and 16:00 h, with each pair observed for two periods per day. An observation period lasted 30 minutes, with a scan every 2 minutes to record an estimate of the distance (shoulder to shoulder) between animals in the pair, the general behaviour of each steer (grazing, lying, standing, walking or other, where 'other' included behaviours that were rarely recorded, such as drinking, self-grooming, allogrooming and head rubbing) and the direction of movement between the two steers relative to each other (Table 6.1). To assist estimating inter-individual distances, posts of the sub plots set 20 m apart were used as distance guides, while for closer ranges an average body length of 2.5 m was used. Wet weather conditions during weeks one and two restricted observations on one day for each of these weeks, thus pairs monitored during weeks one and two were observed for six observation periods rather than eight.

Table 6.1. Movement vectors and their designated codes to describe the movement of one individual in response to another.

			Movement vector code
MV 1	●	●	No movement
MV 2	●→	←●	Animals move towards each other
MV 3	←●	●→	Animals move away from each other
MV 4	●	●→	One animal moves away from the stationary other
MV 5	●→	●	One animal moves towards the stationary other
MV 6	●→	●→	Following movement
MV 7	▲	▲	Animals moving together side by side

6.2.5. Observational data processing and statistical analysis

The visual distance estimates for each pair were averaged per observation period per day. The movement vectors were recorded on a per pair basis and expressed as a proportion of the 16 observations per observation period per day. The behavioural measurements were recorded for each individual steer for each of the 16 observations per observation period, thus 32 behaviour observations were recorded per pair per observation period. These were summed for each behavioural state and expressed relative to the 32 observations recorded per observation. All observational measurements were analysed for the effects of familiarity and day with a repeated measures analysis using restricted maximum likelihood (REML) to model the variance-covariance matrix; an antedependence model of order 1 adequately modelled the variance structure. A one-way ANOVA was used to analyse daily differences in distance estimates between novice and experienced pairs and also between experienced familiar and unfamiliar pairs on days 2 and 5. Results for distance estimates are expressed as mean ± standard deviation. The movement vectors were also analysed for the effect of distance by examining the distance distributions per movement vector and reporting the mean distance ± standard deviation. Residual and normal probability plots were visually assessed for distributional assumptions resulting in all movement vectors and behavioural data being arcsine-transformed prior to analysis with back transformed values presented in the text. Differences were considered significant at $P < 0.05$ and statistical trends are reported at $P < 0.10$. Approximate least significant differences at the 5% level were used to assess pair-wise differences between treatment means for the same day.

All statistical analyses were conducted using Genstat 12th edition (Payne et al., 2009).

6.3. Results

6.3.1. Proximity logger data

There was no interaction ($F_{4,112} = 1.50$, $P = 0.219$, $\eta^2 = 0.02$) between level of familiarity and day for the number of contacts recorded between pairs per hour (Fig. 6.1). However, overall there was a significant ($F_{1,24} = 12.24$, $P = 0.002$, $\eta^2 = 0.11$) effect of familiarity on the number of contacts per hour; familiar pairs had more contacts per hour than unfamiliar pairs, regardless of time (back transformed means: 3.8 and 2.3 contacts/h, respectively).

There was no interaction ($F_{4,112} = 0.54$, $P = 0.659$, $\eta^2 = 0.01$) between familiarity and day for the average contact length between pairs, nor any effect of familiarity ($F_{1,24} = 0.51$, $P = 0.484$, $\eta^2 = 0.01$), with an overall average contact length of 57.1 s.

6.3.2. Observational data

A significant ($w = 17.14$, df = 3, $P = 0.002$) interaction effect between treatment and day on the visually assessed distance maintained between pairs was observed; the difference between treatments decreased with time. The difference existed on days 2 and 3 but had disappeared by day 4 (Fig. 6.2).

There was a significant ($P < 0.05$) interaction between treatment and day in the proportion of time spent moving towards each other (movement vector code 2; Table 6.2). Unfamiliar pairs spent more time moving towards each other on days 3 and 5 compared with familiar pairs. Overall, unfamiliar pairs spent a greater ($P < 0.01$) percent of time moving apart from each other (movement vector code 3) than familiar pairs. Familiar pairs tended to spend a greater ($P < 0.10$) percent of time motionless than unfamiliar pairs, regardless of time (movement vector code 1). The percent of time spent performing other types of movement (movement vector codes 4-7) did not differ ($P > 0.05$) between familiarity treatments.

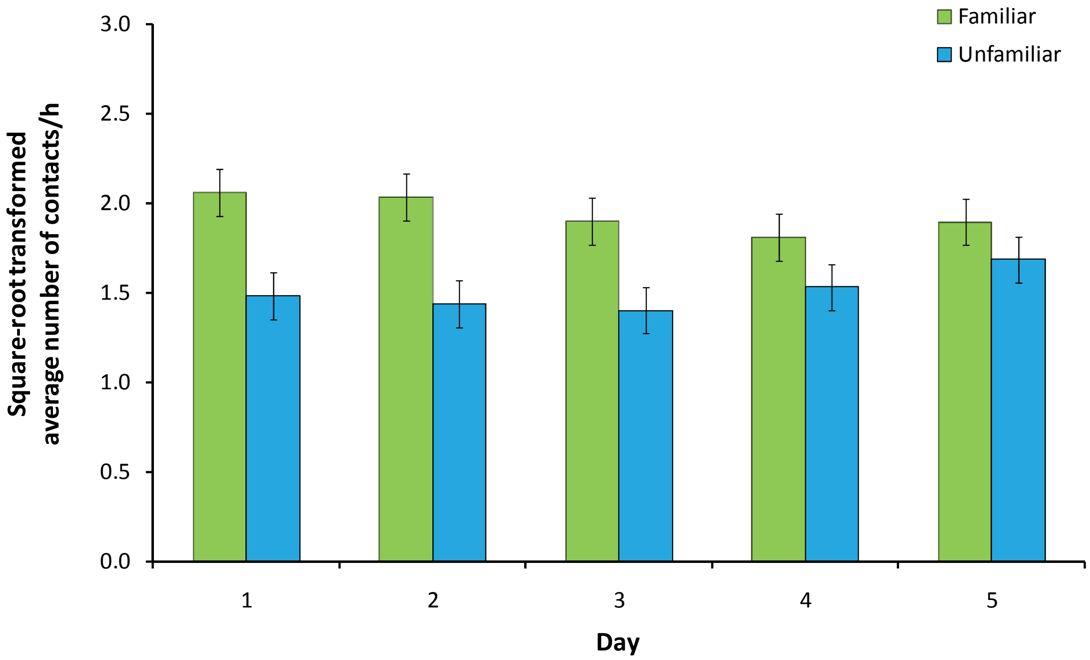


Figure 6.1. The average number of close proximity encounters per hour (±SE) between familiar and unfamiliar pairs per day. Data are square-root transformed interaction means.

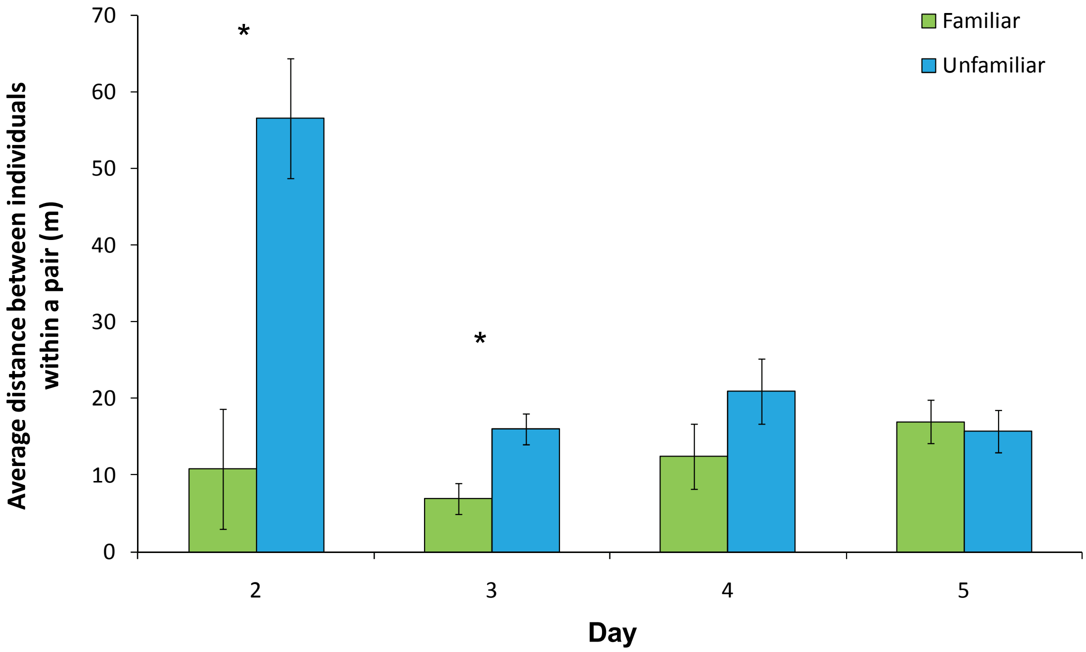


Figure 6.2. The average proximity (±SE) between familiar and unfamiliar pairs per day as recorded by visual observations. Asterisks indicate statistical significance at P = 0.05 between familiarity treatments.

Table 6.2. The percent of time steers were observed moving in the directions classified by movement vectors 1-3 per treatment per day. Values shown are arcsine transformed means with back transformed values shown in parentheses. Significant (P < 0.05) effects between familiarity treatments per day are indicated with an asterisk.

	MV 1				MV 2				MV 3			
	●		●		●→		←●		←●		●→	
Day	Familiar		Unfamiliar		Familiar		Unfamiliar		Familiar		Unfamiliar	
2	0.48	(20.9)	0.44	(18.4)	0.10	(1.0)	0.05	(0.2)	0.12	(1.4)	0.26	(6.5)
3	0.51	(23.8)	0.30	(8.8)	0.08	(0.6)	0.18	(3.3) *	0.08	(0.7)	0.22	(4.9)
4	0.55	(27.3)	0.44	(18.3)	0.12	(1.4)	0.17	(2.7)	0.16	(2.5)	0.23	(5.3)
5	0.37	(13.0)	0.28	(7.4)	0.11	(1.1)	0.21	(4.5) *	0.15	(2.4)	0.21	(4.2)
s.e.d. (interaction)	0.14				0.05				0.06			
Mean	0.48	(21.0)	0.37	(12.8)	0.10	(1.0)	0.15	(2.3)	0.13	(1.7)	0.23	(5.2)
s.e.d. (mean)	0.06				0.02				0.03			
Significance of effect (*P* value)												
Treatment	0.068				0.009				0.005			
Day	0.087				0.059				0.777			
Treatment x Day	0.931				0.039				0.669			

When movement vectors were examined according to distance, the spread in distance between treatments was greater for some movement vectors than others (Table 6.3). Of the three movement vectors that were reported to show differences between treatments irrespective of distance (Table 6.2), only movement vector 1 showed an effect of familiarity on distance (Fig. 6.3); when there was no movement between pairs, familiar pairs were observed more often in closer proximity (< 20 m) than unfamiliar pairs. Movement vectors 2 and 3 showed similar distance deviations for familiar and unfamiliar pairs.

There was no interaction (P > 0.05) between familiarity and day for the percent of time spent performing each behaviour (grazing, lying, standing, walking or other behaviour). However, overall unfamiliar pairs spent a greater (P < 0.01) percent of time grazing than familiar pairs, and familiar pairs showed a tendency to spend a greater (P < 0.10) percent of time lying and standing than unfamiliar pairs (Table 6.4).

Table 6.3. The average distance observed between familiar and unfamiliar pairs for each movement vector (mean ± standard deviation).

Movement	Familiar	Unfamiliar
MV 1	7.1 (12.68)	35.6 (47.37)
MV 2	9.2 (11.01)	12.3 (15.28)
MV 3	25.8 (25.55)	26.6 (21.39)
MV 4	16.8 (20.03)	26.4 (31.65)
MV 5	10.7 (15.29)	27.0 (36.66)
MV 6	12.7 (15.17)	15.4 (16.78)
MV 7	9.1 (10.82)	15.8 (19.95)

Table 6.4. The main effect of familiarity on the percent of time spent performing each behaviour type. Values shown are arcsine transformed means with back transformed values shown in parentheses.

	Familiar	Unfamiliar	s.e.d.	*P* value
Behavioural state:				
Grazing	0.85 (56.0)	1.09 (78.3)	0.08	0.003
Lying	0.25 (6.2)	0.16 (2.5)	0.06	0.080
Standing	0.41 (15.7)	0.28 (7.8)	0.06	0.085
Walking	0.08 (0.6)	0.05 (0.3)	0.02	0.142
Other	0.10 (1.1)	0.09 (0.9)	0.02	0.538

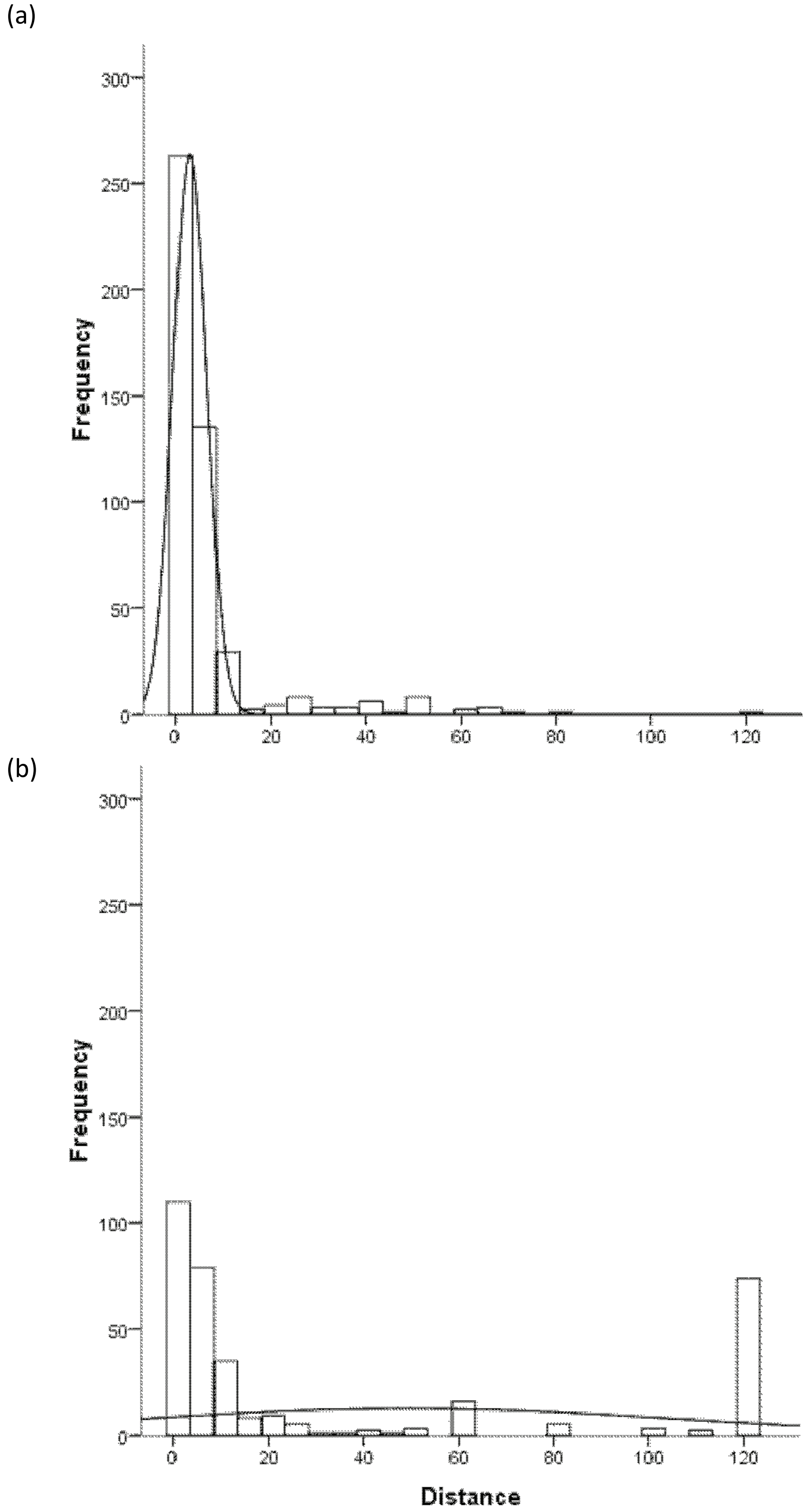


Figure 6.3. The distance distributions for movement vector 1 for (a) familiar pairs and (b) unfamiliar pairs.

6.3.3. Steer re-use

On the first day of observations (day 2), there was a difference (ANOVA: $F_{1,16} = 4.51$, $P = 0.050$, $\eta^2 = 0.22$) between novice pairs and experienced pairs; experienced pairs had closer inter-individual distances in the unfamiliar treatment than pairs that were new to the test condition (novice = 105.0 ± 15.00 m, experienced = 32.9 ± 22.59 m). Nevertheless, there was still a difference ($F_{1,10} = 4.88$, $P = 0.052$, $\eta^2 = 0.33$) between familiar and unfamiliar experienced pairs (familiar = 10.8 ± 9.67 m, unfamiliar = 32.9 ± 22.59 m). There was no difference ($F_{1,25} = 0.34$, $P = 0.563$, $\eta^2 = 0.01$) in distance between novice and experienced pairs on day 5, nor was there any effect of familiarity ($F_{1,16} = 0.10$, $P = 0.757$, $\eta^2 = 0.01$).

6.4. Discussion

The aim of the study was to investigate the spatial and temporal differences between familiar and unfamiliar pairs and use these differences to characterise features of the familiarisation process between pairs of unfamiliar steers. The results show that unfamiliar pairs interact differently from familiar pairs but, as unfamiliar pairs build social bonds, these differences become less clear indicating that a familiarisation process was occurring between the pair. In the current experiment, the unfamiliar pairs initially maintained greater distances apart than familiar pairs, but after 3 days their distances were similar to familiar pairs (Fig. 6.2). Additionally, the unfamiliar pairs gradually increased their movement directly towards each other (Table 6.2, movement vector 2), which exceeded the same movement observed by familiar pairs after 2 days. These gradual changes provide evidence that the unfamiliar pairs were engaging in behaviours that facilitated the process of familiarisation. However, overall familiar pairs had more close proximity encounters and showed a tendency to spend a greater percentage of time lying and standing than unfamiliar pairs; these differences were constant over the 5 day period indicating that complete familiarisation had not occurred within 5 days.

The change in inter-individual distances and movement vectors over the first 3 days suggests the steers in an unfamiliar pair were initially avoiding each other. Avoidance behaviour was also reflected in the unfamiliar pairs general and social behaviour; unfamiliar pairs spent more time grazing than familiar pairs and tended to spend less time lying and standing than familiar pairs. The lower percent of time spent inactive by individuals within an unfamiliar pair may reflect a lack of social support and trust within the pair. Without the social support of familiar group members, individuals may feel vulnerable to predation and spend more time in motion as they do not feel safe to rest (Meddis, 1975). Wild dogs and wild pigs are prominent in the local areas thus it is possible that the steers had experienced predators in the past, especially as calves as they are more vulnerable. Domestic livestock have inherited survival behaviours from their wild ancestors with no behaviours lost or gained through domestication (Stricklin and Mench, 1987; Stricklin, 2001), thus the steers may still display anti-predator behaviour even without the presence of a strong predation threat due to their evolutionary history. Additional explanations to account for the unfamiliar steers displaying greater movement could relate to the feeling of being isolated from their social group inducing a fear response: movement could therefore be a way of searching for familiar group members. Although, if the steers were experiencing stress from fear then it would be expected that other stress-like behaviours would be observed, such as lower intakes as reported in Chapter 5, however, the pairs of unfamiliar steers grazed more and moved more than the familiar pairs, thus there is no evidence to suggest that fear was a strong behavioural driver. Nonetheless, the results indicate that behaviour is disrupted by the presence of an unfamiliar individual.

The gradual decrease in inter-individual distance and increase in movement towards each other suggest that the unfamiliar pairs were adjusting to each other's presence and indicates a learning phase of familiarisation. Familiarisation involves a social conditioning process (Kondo and Hurnik, 1990), whereby individuals develop a social history based on both agonistic and affiliative interactions. During this process, individuals learn to recognise the other as familiar; this recognition process is important in establishing social order and building relationships (Lindberg, 2001). The stabilisation of distance after 3 days suggests that the process of familiarisation between pairs begins early and correlates with similar findings of Grant and Albright (2001), who report the effects of mixing dairy cows stabilise after 3 days. Other studies have shown that familiarisation can be a lengthy process; from 14 days (Gupta et al., 2008) up to 45 days for complete integration of an unfamiliar cow into an established herd (Sato et al., 1990). To provide evidence of complete familiarisation, the unfamiliar pairs would be expected to progress towards the same patterns observed within a familiar pair. The overall differences in close proximity encounters and certain behaviours between familiar and unfamiliar pairs highlights that the current experiment was not long enough to show complete familiarisation and prevents comparison with other studies that report stabilisation occurring after this time frame; these types of behaviours could be considered characteristics of a well established relationship, which develop via social encounters over a period longer than 5 days.

The spread in distance between familiar and unfamiliar pairs when motionless reflect the main results that the familiar pairs maintained closer distances. Although there were significant treatment differences in movements towards and away from each other (movement vector codes 2 and 3), the distributions were similar. This result suggests that unfamiliarity effects are not always spatial and instead tend to be more related to frequency. The average distance observed when moving together was within 15 m; cattle generally graze within 4 and 10m of each other (Broom and Fraser, 2007), thus it is likely that the pair were in visual contact with each other and suggests that their behaviour was more co-ordinated than random. Other movement vectors were more related to proximity than frequency. Further work is required on cattle visual acuity to interpret the meaning of certain movements at different distances and to determine what extent the activity is co-ordinated between two animals or simply random movement.

Based on the results of previous mixing studies, it was surprising that no agonistic behaviour was observed between any of the steers. Nakanishi et al. (1991) reported an immediate four-fold increase in agonistic behaviour between a group of nine cattle, which took 7 days to stabilise. Several reasons are possible to explain the lack of agonistic behaviour recorded in this study, including the absence of observations immediately following introduction when the majority of agonistic behaviour takes place (Bouissou, 1974b). Additionally, the pair-wise nature of the experiment may have reduced competition for social status and thus lowered the requirement for physical interaction. Also, the steers had previous re-grouping experience, which has been found to lower aggression in steers when re-grouped multiple times (Gupta et al., 2008). The current results suggest that introducing pairs of unfamiliar steers could be less disruptive than introducing larger groups of individuals. Further work is required to investigate the potential welfare benefits of introducing pairs of steers prior to incorporation into a larger unfamiliar group.

There was an effect of experience on steers being re-used in the study on day 2, although no evidence to suggest that re-use of steers affects the interpretation of the results of the study. The fact that there was a difference between novice and experienced pairs suggests that behaviour depends both on familiarity with the conditions and familiarity with the other steer. This supports the underlying interpretation of the results.

6.5. Conclusions

Four independent social measures were used to quantify interaction differences between treatments, with each measure resulting in different rates of stabilisation: distance stabilised after 3 days, movement patterns varied across days but there were more movements toward each other after 2 days, and there were overall differences in the number of close proximity encounters and an overall tendency for the time spent performing certain behaviours to differ. The hypothesis that evidence of familiarisation between the unfamiliar steers would occur within the 5 day period was confirmed, however evidence of complete familiarisation was not shown. The results indicate that familiarisation involves various social processes that occur as individuals recognise and learn each other's behavioural tendencies and build relationships. It is therefore suggested that single behavioural measures are insufficient to describe the entire familiarisation process. The decrease in proximity between unfamiliar pairs over time suggests familiarisation between pairs begins early (after 3 days). However, overall familiar pairs had more close proximity encounters per hour than unfamiliar pairs and showed a tendency to spend more time lying and standing than unfamiliar pairs. Consistent interaction within close proximity and behavioural stabilisation may be features of a well-developed relationship and appear to require a greater level of familiarity than can be achieved within 5 days.

Chapter 7

Introducing an unfamiliar steer into a pair of familiar steers and the effect on social interaction

7.1. Introduction

Chapter 6 investigated the temporal and spatial associations of pairs of unfamiliar steers during relationship development by comparing their social behaviour with pairs of familiar steers. Familiarity affects spatial proximity, behaviour and movement in steers and it was suggested that familiarisation involves various social processes. Spatial proximity and movement patterns were identified as the first social factors that changed in response to the developing relationship between the two steers. However, there were still behavioural and encounter differences between familiarity types, suggesting that these social factors had not stabilised within the 5 day period. Social properties of dyads are inherently different from triads and larger groups (Simmel, 1950) and pair-wise interactions have been deemed insufficient to explain hierarchy structure in fish (Chase et al., 2003), which is better explained by evaluating outcomes from triadic encounters (Chase, 1980). To study the effect of a third individual on the behaviour of a pair, the aim of the current study was to investigate the response of a pair of familiar steers to the introduction of an unfamiliar steer by evaluating close proximity encounters of the familiar pair before and after the introduction of the unfamiliar steer. To evaluate the social factors involved in relationship development and therefore the evolution of social structure, the current experiment also investigated the duration and frequency of close proximity encounters of the unfamiliar steer with the two familiar steers during relationship development.

Maintaining close proximity is a characterising feature of a familiar relationship that facilitates communication and information transfer and strengthens social cohesion (Warburton and Lazarus, 1991; Newberry and Swanson, 2001). In contrast to visually obvious behaviours, such as physical contests and allogrooming, the frequency and duration of the time spent in close proximity is not something that can be readily measured using intermittent recording methods. In the previous chapter, proximity loggers allowed these more subtle behavioural patterns to be identified and clear differences were observed between familiar and unfamiliar pairs of steers with more encounters recorded between pairs of familiar steers. In the current study, proximity loggers were used to record behavioural data on pairs and triads of steers.

It was hypothesised that the introduction of an unfamiliar steer would disturb the established social interaction patterns of familiar pairs, leading to an increase in close proximity encounters as the familiar pair reinforced their social bond in the presence of the unfamiliar steer. Based on the results of the previous chapter, it was also hypothesised that familiar steers would have more frequent and longer duration close proximity encounters than those recorded with the unfamiliar steer, but as the unfamiliar steer engaged in bond forming behaviour, the difference in contact between familiar and unfamiliar steers would gradually decrease.

7.2. Methods

7.2.1. Animals and plots

The experiment was conducted between February and March, 2009. At the time of the experiment, the two groups of resident steers were 2.5-years-old and had a mean weight (± standard error) of 546 ± 7.4 kg. The two groups of resident steers continued to be managed as separate groups although as some steers had been paired with members from the other resident group, the two groups were no longer considered unfamiliar. Thus, a third group of steers were purchased to form a group of steers that were completely unfamiliar with the resident steers. The unfamiliar steers were purchased one month prior to the start of the experiment and were trained to wear collars during this time. The group of unfamiliar steers comprised 42 Brahman (*Bos indicus*) steers with a mean weight (± standard error) of 484 ± 3.3 kg. Pairs and triads were monitored in 1.5 ha plots with a minimum 5 m buffer zone between each plot. The familiar steers had previous experience with the yards, plots and paddocks. The procedures used within this trial were approved by the CSIRO Rockhampton Animal Ethics Committee (Approval number RH252-08).

7.2.2. Experimental procedure

The experiment comprised three deployments, with each deployment lasting 8 days. In total, 36 triads were monitored over a 6-week period. Triads were formed using a step-wise approach: familiar pairs were first monitored together to record baseline social interaction measures before the unfamiliar steer was introduced. The familiar pairs were formed using steers from their own resident group with all pairings balanced for live weight. On the first day pre-introduction (between 09:30 h and 13:00 h, depending on deployment), the resident steers were each fitted with a proximity logging collar in a holding crush and systematically paired whilst in the cattle handling yards before being walked to their respective plots, approximately 1 km from the yards. The familiar pairs were monitored for 2.5 days. On the day of introduction (between 14:00 h and 15:30 h), 12 unfamiliar steers were randomly selected from the unfamiliar group and fitted with proximity logging collars before being walked to the sub-plots containing the pairs and introduced at approximately the same time between pairs. The triads were then monitored for a further 5.5 days before being returned to the yards and the collars removed. Once an unfamiliar steer had been used it was removed from the experiment to ensure that each familiar pair was only grouped with steers that were completely unfamiliar. The resident steers were given a 7 day stabilisation time with original group members before the beginning of the next deployment.

Based on the results presented in Chapter 6, it would have been desirable to extend the monitoring period longer than 5.5 days. The 6 week experiment design, however, was condensed as much as practically possible to ensure that differences between deployments were kept to a minimum, for example weather, pasture species and pasture availability, and that each triad represented a replicated experimental unit. Additionally, the change in distance between familiar pairs after 3 days as reported in Chapter 6 suggested that some notable differences were possible within this time frame. Thus it was decided to continue using 5.5 day monitoring periods.

From the two previous experiments, all resident steers had experience with being paired with both familiar and unfamiliar individuals, thus there were considered to be no individual-level effects due to familiarity or unfamiliarity with the experimental conditions. Additionally, the same pair of resident steers was never used more than once to form a triad. Each triad in the experiment was considered to be independent from each other.

7.2.3. Data processing and statistical analysis

The first contact recorded between the unfamiliar steer with either of the familiar steers was taken as the time of introduction and all data recorded by the unfamiliar steer's proximity logger prior to this was removed. A single file of contacts was created for each pair within the triad and all unfamiliar contacts were classified into the one category, regardless of which familiar animal was involved in the contact. All unfamiliar contacts were then expressed as an average of the two unfamiliar pairs within the triad.

The contact data were summarised on a daily basis as the total number of contacts per hour and the average length per contact. The change within familiar pairs due to the introduction of the unfamiliar steer was compared using a one-way analysis of variance, with pre- and post-introduction used as the treatment factor blocked by pair within deployment. To investigate the differences in contact between familiar and unfamiliar steers, the number of contacts per hour and the average length per contact were analysed for treatment and day effects, using a repeated measures analysis of variance (Rowell and Walters, 1976), with day as the within-subjects effects and familiarity as the treatment factor blocked by triad within deployment. The repeated measures analysis of variance estimates the Greenhouse-Geisser epsilon to account for the degree of temporal auto-correlation, with the significance levels of the F-test adjusted for this. Differences were considered significant at the 5% probability level. To meet the distributional assumptions of the statistical analyses, residual and normal probability plots were inspected for normality. The large proportion of short duration contacts and infrequent contacts per hour produced positively skewed distributions (Fig. 7.1a). A square root transformation provided the closest fit to normality (Fig. 7.1b), and was applied to all proximity logger data prior to analysis. All statistical results presented in the text are back transformed values. Statistical analyses were carried out using Genstat 12th edition (Payne et al., 2009) and graphical representations of the data were created using PASW Statistics 18.0 (SPSS Inc).

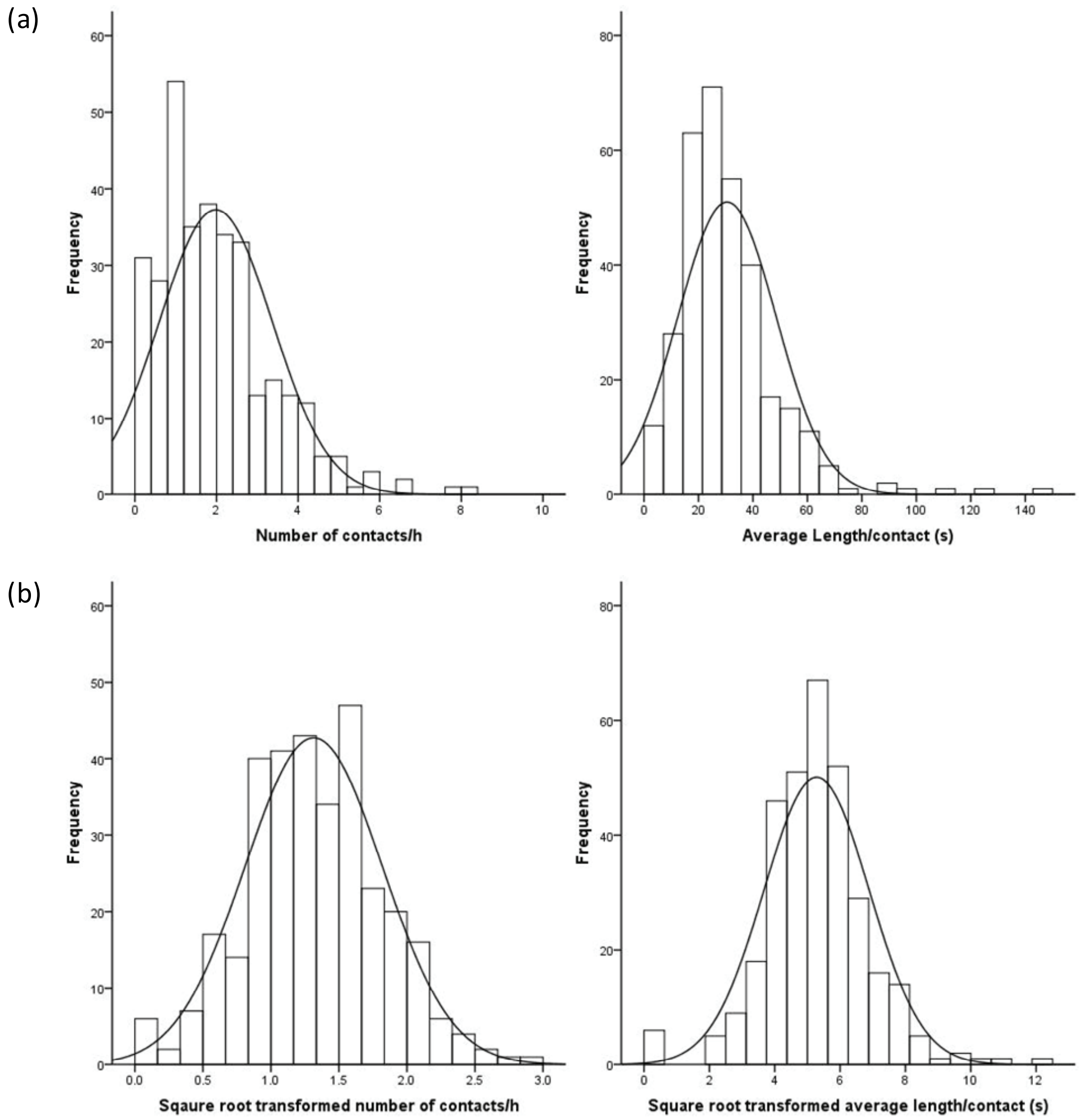


Figure 7.1. The distributions of the number of contacts per hour and the average length per contact (a) in raw form and (b)after a square root transformation.

7.3. Results

7.3.1. Changes within familiar steers

The introduction of the unfamiliar steer caused a significant ($F_{1,35} = 19.21$, $P < 0.001$, $\eta^2 = 0.04$) increase in the number of contacts per hour between familiar pairs from 1.51 to 1.93 contacts/h (Fig. 7.2). However, the introduction of the unfamiliar steer had no effect ($F_{1,35} = 2.78$, $P = 0.105$, $\eta^2 = 0.01$) on the length of contact between familiar pairs, with an overall average contact length of 29.9 s.

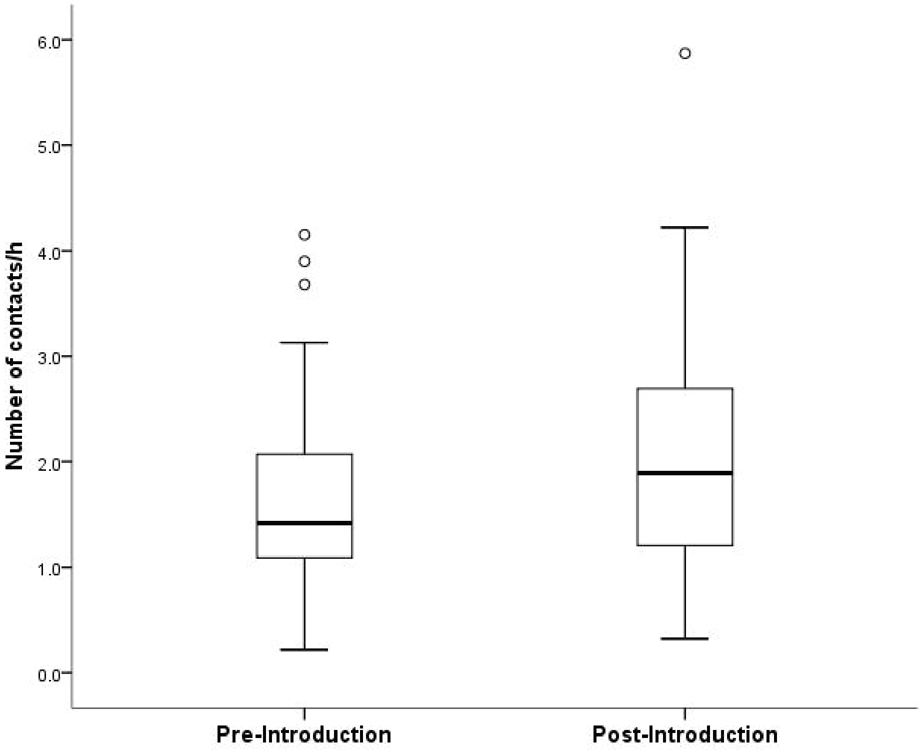


Figure 7.2. A box plot of the number of contacts per hour between familiar pairs pre- and post-introduction. Data presented are back transformed vales.

7.3.2. Changes within unfamiliar triads

There was no interaction ($F_{1,431}$ = 2.23, *P* = 0.087, η^2 = 0.01) between familiarity and day on the number of contacts per hour within triads (Fig. 7.3). There was a significant ($F_{1,431}$ = 37.71, *P* < 0.001, η^2 = 0.27) effect of familiarity on the number of contacts between individuals within the triads; familiar pairs had more contacts with themselves than with the unfamiliar steer (1.86 and 0.54 contacts/h, respectively). There was also a significant ($F_{1,431}$ = 8.08, *P* < 0.001, η^2 = 0.02) effect of day on the number of contacts per hour, regardless of familiarity (Table 7.1); the number of contacts per hour differed between days, with the greatest number of contacts recorded on the day of introduction.

There was no interaction ($F_{1,431}$ = 0.43, *P* = 0.736, η^2 = 0.001) between familiarity and day on the average length of contact within triads (Fig. 7.3). The significant ($F_{1,431}$ = 60.4, *P* < 0.001, η^2 = 0.33) effect of familiarity on the average length per contact identified familiar pairs having longer durations per contact than contacts with the unfamiliar steer (29.0 s and 9.7 s, respectively). There was no influence ($F_{1,431}$ = 1.36, *P* = 0.257, η^2 = 0.005) of day on the length of contacts between individuals, regardless of familiarity.

Table 7.1. The number of contacts per hour between all individuals within a triad per day post-introduction, regardless of familiarity. Values shown are square root transformed data with back transformed means shown in parentheses. Means not followed by a common letter are significantly different (P = 0.05).

Day post-introduction	Number of contacts/hour		
1	1.17	(1.37)	a
2	1.04	(1.09)	b
3	1.03	(1.06)	b
4	1.12	(1.24)	c
5	1.05	(1.10)	b
6	0.88	(0.78)	d
s.e.d.	0.05		

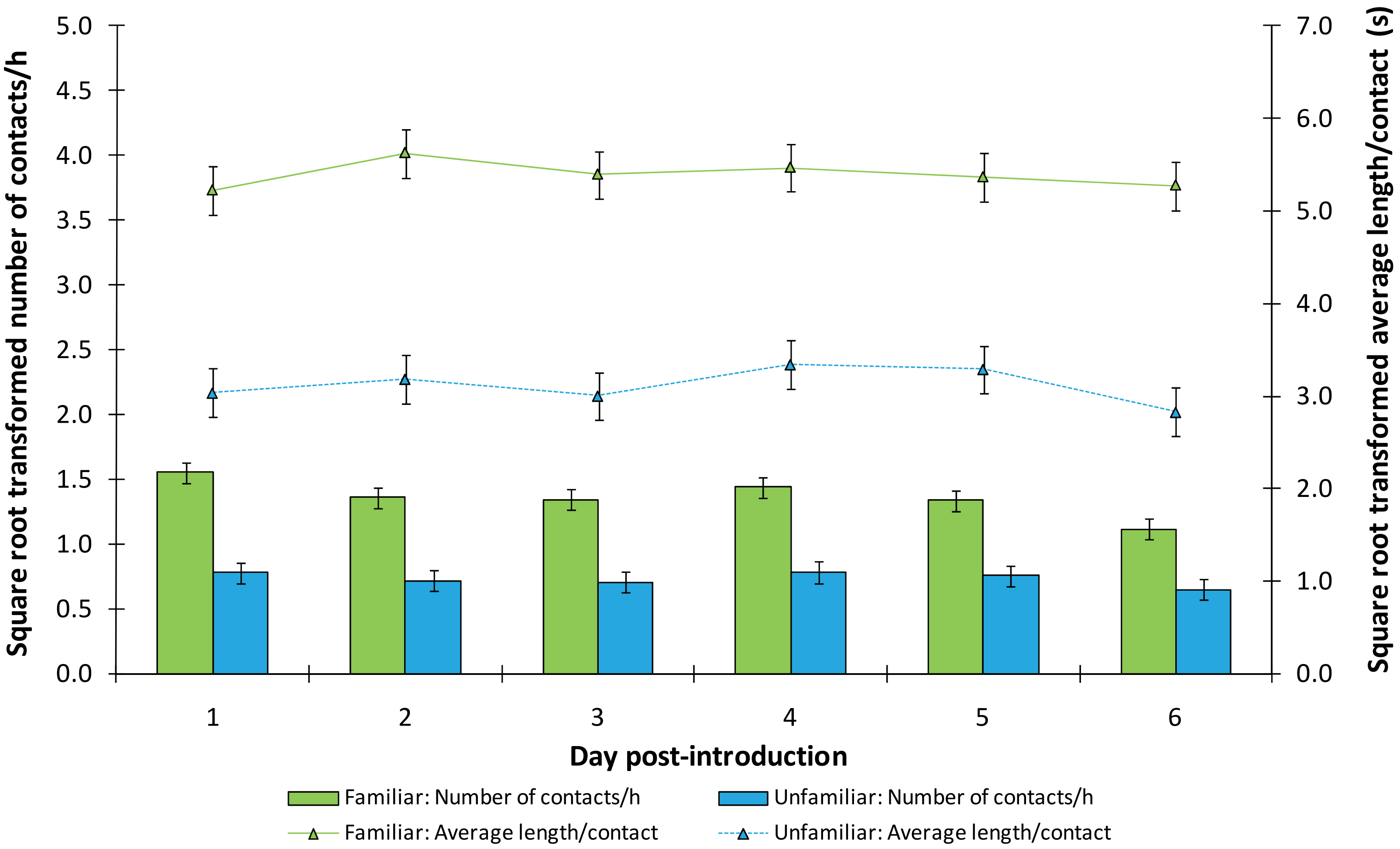


Figure 7.3. The number of contacts per hour (±SED) and the average length per contact (±SED) for contact between familiar and unfamiliar individuals within a triad per day post-introduction. Data are square root transformed interaction means.

7.4. Discussion

It was hypothesised that familiar pairs would increase their encounters with each other when an unfamiliar steer was introduced. Familiar steers did increase the number of encounters per hour, but there was no change in the average length of each encounter. This result indicates that the introduction of the unfamiliar steer caused a disruption to the normal encounter behaviour of the isolated familiar pair, resulting in the familiar pair having more close proximity encounters. There are a number of reasons why the familiar pair may have increased their close proximity encounters when the third unfamiliar individual was introduced, including fear, competition for resources and reinforcing social bonds.

Fear created by the presence of the unfamiliar steer may have led to the increased contact frequency between familiar pairs to seek out each other for support. Familiar peers have been shown to provide social support, particularly in stressful situations (Boissy and LeNeindre, 1997), whilst it has also been stated that the presence of an unfamiliar peer creates fear behaviour (Archer, 1976). This fear may impact on functional decisions. For example, in Chapter 5 it was suggested that the fear created by the presence of an unfamiliar peer restricted the test steers from foraging a desired food source some distance away. Thus, the resultant increase in contact frequency may represent social reinforcement between the familiar pair to buffer the fear caused by the presence of the unfamiliar individual.

The change in encounter behaviour between familiar pairs may relate to the competition threat posed by the unfamiliar steer. Cattle will physically compete for resources when their supply is restricted, such as food and space (Bouissou et al., 2001). An unfamiliar individual is a potential threat to all valuable resources (Price, 2008), thus the intrusion of the unfamiliar steer into the space occupied by the familiar pair might have been perceived as an attempt to compete for resources. In the current study, access to food and space were not limited, although it is possible that the familiar individuals could have attempted to defend their access to desired spaces such as resting locations. The number of social positions, however, was limiting as there were only three positions available, thus it is possible that the familiar steers were competing to retain their social status and prevent the unfamiliar steer from elevating up the small hierarchy. This competition for resources might have resulted in more cooperative behaviour between the familiar pair to defend their space and social status, thus increasing their contact behaviour.

Reinforcing social bonds between the familiar pair may also be responsible for the increased number of encounters between familiar pairs. Cattle recognise others as familiar based upon a history of social interaction where they learn the physical and behavioural characteristics of other group members (Lindberg, 2001). A study in fish by Brown (2002) showed that the process of social reinforcement continues once a relationship is established, which allows individuals to learn others behavioural tendencies under different situations. The same process has also been identified in humans by Hinde and Stevenson-Hinde (1976) who describe a stable relationship as something that changes continuously to meet the demands of the social and physical environment and individuals are required to adapt to each other's behavioural responses to maintain stability. Thus to maintain stability, the familiar pair may have increased their contact frequency to reinforce their familiarity and to learn any changes that may have occurred to each other during interactions with the unfamiliar.

When considering the process of relationship development, it was hypothesised that familiar pairs would maintain greater encounters with themselves than with the unfamiliar pair due to their existing relationship, but this difference was expected to decrease as the triad developed a stable and familiar social relationship. The hypothesis was partially supported by the finding that familiar steers had more encounters per hour and longer duration per encounter as compared with unfamiliar steers. Nevertheless, in this study the non-significant result for the interaction between day and close proximity encounters (frequency and duration) does not support the hypothesis that the newly introduced animal was eventually accepted as a familiar group member. However, it should be noted this study only monitored social behavioural interactions over 5.5 days. Although the current results were unable to describe all of the features of familiarisation, it is possible to speculate the conditions that may enhance or inhibit the process. Internal social factors, such as individual differences in sociability, may accelerate or hinder the integration of an unfamiliar Highly sociable individuals spend more time within close proximity to others (Sibbald et al., 2006) and may therefore act as a catalyst to initiate relationship development with an unfamiliar. Environmental factors that force individuals to congregate or cooperate, such as areas of high predation risk, may facilitate familiarisation while evolutionary pressures that require individuals to transmit cultural information for improved survival, such as which pasture species to eat or how to access water, may also accelerate familiarisation in less domesticated species. Future studies should consider monitoring newly introduced animals for much longer time periods to understand the way animals form and maintain relationships.

In Chapter 6, familiar pairs of steers had more encounters per hour than unfamiliar pairs (3.8 and 2.3 contacts/h, respectively) however there was no difference in the length of the close proximity encounters (average contact length 57.1 s). In the current experiment the difference in the number of encounters per hour between familiar pairs was expected, although the extent of the durational differences between familiar and unfamiliar steers was not; the length of contact between familiar steers was three times greater than encounters between unfamiliar steers. Additionally, encounter frequency and duration were much lower within triads than pairs. Given there is more opportunity for an encounter to occur with increased numbers, it was anticipated that there would be more overall encounters within a triad than a pair. Earlier work on social structure in human groups found that interaction in pairs is fundamentally different to that observed in larger groups, both in terms of social processes (Simmel, 1950) and hierarchy structure (Chase, 1980). Simmel (1950) further stated that increasing group size from two to three involved more significant social changes than increasing group size to four or more, outlining the importance of the triad for group structure. The difference in encounter frequency and duration between pairs and triads supports the above claims that behaviour in a pair of steers is fundamentally different to that observed within groups of three.

Relationship development involves learning and individual recognition (Lindberg, 2001). The greatest number of encounters per hour was seen on the day of introduction, indicative of individuals coming within close proximity to learn the physical characteristics of each other. After the initial encounter, contact frequency and duration between familiar and unfamiliar steers was relatively stable; encounters with the unfamiliar steer remained at a level around half that of contacts recorded between familiar steers (Fig. 7.3). The results of the current study support Bouissou’s (1974a) finding that relationship direction is established early and remains stable after this time. Bouissou (1974a) reported that newly introduced cattle establish relationships relatively quickly, with half of all relationships determined within the first 5 minutes and no longer than 2 hours after the first encounter. Bouissou (1974a) also stated that relationships remained stable after the initial encounter with very few changes in relationship direction, indicating that learning individual characteristics can occur relatively quickly. The current study extends the work of Bouissou by considering behavioural indicators of relationship development other than dominance. The results also suggest that the development of a stable familiar relationship requires longer than 5.5 days. Stability in a relationship requires time and experience under different social and physical environments to learn behavioural preferences under a range of different situations (Brown, 2002), thus the current experiment was not long enough for this level of familiarisation to occur.

7.5. Conclusions

It was concluded that social disruption caused by introducing an unfamiliar into an established pair of steers led to an increased frequency in close proximity encounters between the familiar steers, thus accepting the hypothesis that familiar steers would have more close proximity encounters with themselves than with the unfamiliar steer. There were also durational differences recorded between familiarity types, with familiar steers having longer duration encounters than encounters with the unfamiliar steer. Furthermore, differences in encounter behaviour between familiar and unfamiliar steers led to the conclusion that complete integration of the unfamiliar steer into the pair did not occur within 5.5 days. The structural differences that exist when increasing group number from two to three may create social complexities that result in longer integration times when introducing new individuals into a group. The social support provided by a familiar peer has the potential to make an unfamiliar social situation less stressful.

Chapter 8

Relationship development in steers: an application of the relational event model

8.1. Introduction

Chapter 7 investigated the introduction of an unfamiliar steer into a pair of familiar steers. Daily measures of close proximity encounters recorded by proximity logging devices were used to identify changes in encounter patterns during the first 5.5 days post-introduction. The results indicated that the greatest amount of interaction occurred on the day of introduction and after 5.5 days there were still discernible differences, on average, between unfamiliar and familiar steers. The analysis used in the previous chapter only considered pair-wise encounters. This was not an issue in Chapter 6 because only two individuals were monitored at the one time, however when a third animal was introduced in Chapter 7 there was no analytical method in place to model the interactions among all three individuals simultaneously. Thus different statistical approaches were investigated to identify a suitable method for characterising interactions among groups of three or more animals.

The relational event framework proposed by Butts (2008) (described in Chapter 3, section 3.6) was chosen to analyse the sequences of encounters between the three steers. This model was highly suitable because it considers each interaction as a discrete event within a time series and allows every contact recorded by a proximity logger to be analysed with respect to its temporal patterning; this is specifically important when considering relationship development between unfamiliar individuals, as each interaction is likely to alter the context for future contact and the evolving quality of the relationship. The additional advantage of the model is that it is highly flexible, allowing specific types of events to be modelled in a way that is appropriate to the observational context, and can accommodate interactions involving more than two individuals at the one time.

The aim of the current chapter is to develop a relational event model that can be used to analyse regular patterns of interaction between a pair of familiar steers with an unfamiliar steer during the process of relationship development. The aim of the model is to predict whether and when a relational event occurs between pairs within the triad based on the history of prior events. The chapter describes the methods that were used to develop the model, beginning with the steps taken to process the data into a suitable format prior to input, the specification of the model parameters and an explanation of the possible model parameters. The actual model estimates are then presented, followed by an interpretation of the results in terms of the possible social roles that the familiar and unfamiliar steers have in forming certain encounter structures and the likely meaning of these structures for relationship development.

8.2. Model development

8.2.1. Data input

The model was used to analyse the proximity logger data that was collected in Chapter 7. Briefly, the data set contained 36 triads of steers, where an unfamiliar steer was introduced to a pair of familiar steers and monitored for 5.5 days. All close proximity encounters (within 4 m) were recorded by proximity logging devices. The data set contained sequences of discrete relational events between pairs within each triad and each encounter had a specific start and end time. Prior to analysing the data, the temporal interaction sequence was transformed into a suitable format using the processing outlined below.

In addition to the data processing outlined in Chapter 7, the proximity logger data per triad was further processed by assigning each animal in each triad a unique animal identification code, from 1 to 3, to represent the identity and familiarity status of each animal: animals 1 and 2 represented the familiar animals and the unfamiliar animal was coded as animal 3. Relational events were also coded to identify the pairs of animals involved in a close proximity encounter, with a familiar pairing between animals 1 and 2 coded as a relational event of type ‘1’ and the unfamiliar pairings between animals 1 and 3 and animals 2 and 3 coded as types ‘2’ and ‘3’, respectively.

The data from the original data set was restricted to include only close proximity encounters recorded after the unfamiliar steer was introduced, with this latter point in time considered as time zero in the model. The time of each encounter was defined as the number of seconds that had elapsed since the point of introduction. The original data was further restricted by removing all data recorded after day 5. This ensured that only full daily records were analysed and was also specified because the number of events recorded on day 6 was not substantial enough to include in the model.

The model was fitted on a daily basis to a pooled data set across all 36 triads, although all statistics used in the model were computed on a triad by triad basis. To test the validity of pooling the triad data across all 36 triads, the data was visually assessed by comparing a simplified model created with all 36 triads against separate models for each triad. To create the simplified model, the number of parameters from the actual model was reduced and fitted to the pooled data set as well as each of the 36 triads separately. Frequency distributions of the parameter estimates obtained by fitting the simplified model to each of the 36 triads were created and the placement of the parameter estimate from the pooled data set within the distribution was used to compare the two data sets. The results of the data validation tests can be seen in Appendix B. Overall, the parameter estimates of the aggregated data set fell within 95% of the distribution of the individual triad parameter estimates, confirming that pooling the triad data was justified.

8.2.2. Model components

The model was developed specifically for onset interaction events. An onset event was characterised as one in which a close proximity encounter was initiated between any pair within the triad, thus the pair was the basic unit of analysis (Fig. 8.1). The model was developed to predict the likelihood of future onset events based on the history of prior onset events. Onsets were of particular interest because they relate specifically to the formation of an encounter between two or more individuals and can potentially be used to characterise the nature of a social relationship. For example, a consistent pattern of onset events between the same pair may represent affiliative behaviours such as mutual grooming or grazing within close proximity, which could therefore be used to indicate a preferential relationship. Separate from onset events were offset events, which occurred when an existing encounter between any of the three steers was ended by one or more steers moving out of the 4m detection range. Offsets therefore relate to the dissolution of an existing encounter, and were important to understand the processes that occur when encounters break apart. Hence, the nature of onset and offset events were different.

While it is possible that onset and offset events could potentially be considered in the same model, the model developed here accounted specifically for the formation of ties between steers and the model framework was not suitable to predict the probability of future offset events. Offset events, however, were still considered as a function of the onset event sequence, as every onset event has an associated offset event and the occurrence of offset events were important to determine the type of onset event that occurs. Different onset event types were possible depending on the number of animals involved in the event and their configuration (see section 8.2.3 below), thus the model used the sequence of onset and offset events to identify the involvement of animals in prior events, which was then used to determine the onset event type.

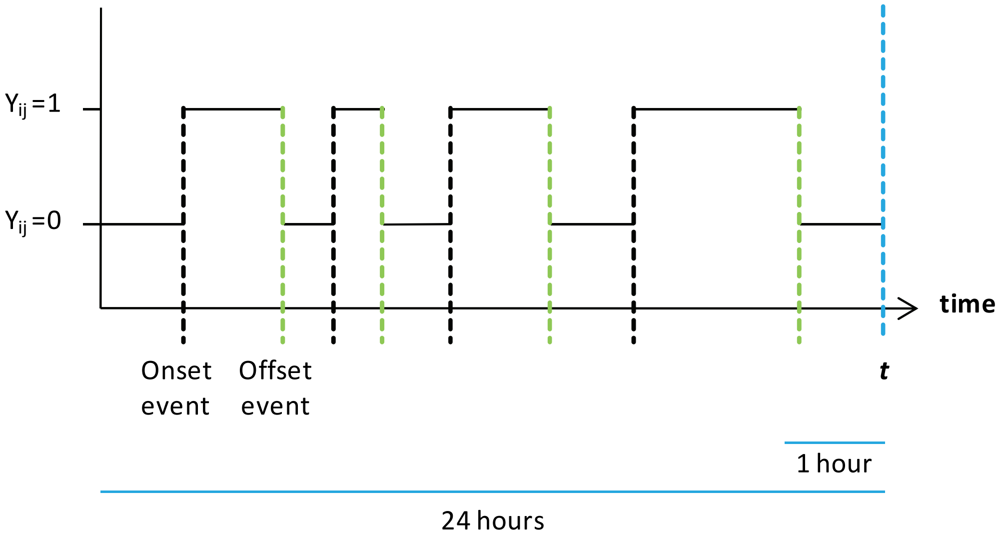
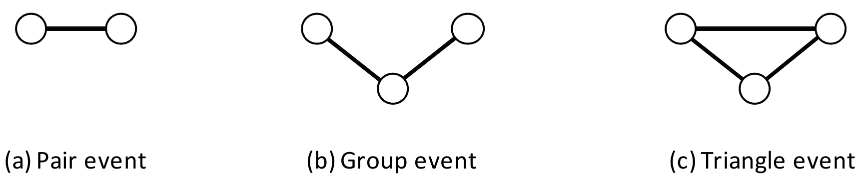


Figure 8.1. An example of an onset event sequence between two steers, *i* and *j*, showing the occurrence of an onset event and an offset event between the two steers. The model developed predicts the probability of an onset event based on the history of onset events occurring within the past hour or the past day, as well as animal familiarity.

8.2.3. Creating the sequence of prior events

A custom-developed java application was used to transform the actual event stream in the proximity logger data set into a set of actual and potential onsets and the statistics based on prior relational events for each triad of steers (see section 8.2.5 for an example). The java program calculated statistics for each event or potential event in terms of (i) the familiarity of the animals involved, (ii) the type of the event that occurred, and (iii) statistics based on the frequency of relevant prior events. The type of encounter was classified as either: (i) an event involving an interaction of an isolated dyad (a pair event); (ii) an event involving simultaneous contact of one animal with the other two (a group event); or (iii) an event involving pair-wise contact among all three animals at once (a triangle event) (Fig. 8.2).



(a) Pair event (b) Group event (c) Triangle event

Figure 8.2. The three event types that could potentially occur between the three steers. The solid lines represent a tie between two steers.

A pair event involved a change in state from no existing contact to the creation of a single contact tie between two steers, while a group event was conditional on the contemporaneous existence of a pair event. A triangle event was formed when a tie was created between the two animals that were not connected in the prior group event, thus all three individuals were in contact at the one time. A triangle event was conditional on the contemporaneous existence of a group event.

While it is possible that a change in state could occur from an isolated animal to simultaneous contact with two others, the probability of such a change was extremely small and there was only one event of this type identified in the current data set. In this instance, the model counted the two pair onset events that occurred at the same time, and therefore have no duration, as well as the onset of the group event. Thus events that occur at the same time are treated the same as any other onset event, irrespective of their duration.

It is important to note that the potential events under consideration with each actual event varied according to the current configuration of animals. For example, if two animals were already in contact, they cannot be associated with the next onset event. Likewise, if the current event was a group event, the next onset event cannot be either a pair event or a group event, but must instead be a triangle event. Indeed, in this latter case, the only onset event that could occur was a triangle event and if an actual onset event occurred there were no potential onset events that were not actual events. As a result, the onset of triangle events could not be handled within this conditional framework as the probability that the event occurs, given that it is an onset event, was 1.

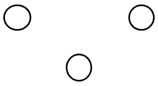
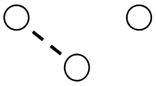
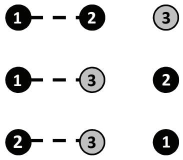
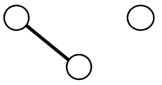
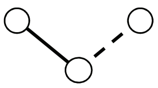
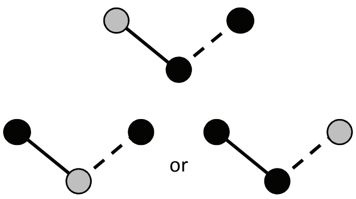
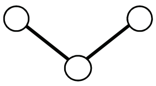
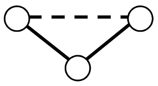
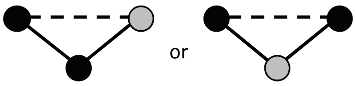
For potential onset events, the statistics included: (i) an indicator variable signifying whether the unfamiliar animal was involved in the potential event (coded as 1 if an unfamiliar animal was involved, 0 otherwise); (ii) the frequency within specified periods of prior pair events involving the steers linked by the potential event; and (iii) the frequency within specified periods of prior group events involving a contact between the steers linked in the potential event. Specified periods of 1 hour and 24 hours were used to capture potential short and longer term regularities in contact patterns. These statistics were chosen as they allow quantification of any tendencies involving differential contact on the basis of animal familiarity, differential contact as a function of past contact in pair events, and differential contact as a function of past contact in group events. The distinction between prior pair events and prior group events was a potentially important one, since pair events indicate isolated dyadic interaction and local activity, whereas group events relate directly to interaction involving all three individuals and the potential for group forming behaviours to occur.

The possible configurations that could occur for an onset event are shown in Table 8.1. For pair events, three events could potentially occur, a familiar pair between animals 1 and 2, an unfamiliar pair between animals 1 and 3 and an unfamiliar pair between animals 2 and 3. For a group event, there were only two possible events that could occur, a group event where the prior pair involved the unfamiliar or an event where the unfamiliar animal was involved with the creation of a tie with either familiar steer to form a group. Although there were two possible structural configurations in the latter case (either the unfamiliar animal was already involved in a pair event or the unfamiliar animal was the animal joining the existing pair), the model considered which animals were involved in the creation of the tie, thus the two formations were considered to be equivalent.

8.2.4. Time

As indicated above, onset events were modelled as a function of prior onset events. Such events could have occurred at any moment in the time interval from the introduction of the unfamiliar animal (t = 0) to the present time t. In order to reflect potential distinctions among prior events in terms of longer cumulative or shorter, more fleeting effects, separate statistics were computed to capture short and longer term regularities in interaction patterns; the short term interval was based on the immediate past hour, while the longer term past was based on daily patterns within each day post-introduction. Both time frames have potentially important implications for social processes and allow both regularities in short term interaction patterns and regularities over a longer period to be discerned. The latter may be potentially representative of long term contact preferences (e.g. the preference of a pair of animals for social interaction).

Table 8.1. The three onset event types that could occur between the three steers, their prior configuration state and the predicted configuration possibilities.

Pre-existing state	Pre-existing configuration	Predicted event	Predicted configuration	Possible configurations
Isolated animal		Pair event		
Pair		Group event		
Group		Triangle event		

Key:

● = familiar animal

◍ = unfamiliar animal

○ = animal of either familiarity

——— = existing tie

- - - - - - - = predicted tie

8.2.5. Event sequence summary

A sample of onset event data as summarised by the java application is shown in Table 8.2. The sample data shows encounters between steers in triad 8 and the frequency of events that occurred in the past day. The column *event type* specified if an event had occurred or not, and the type of even that occurred: '0' indicates an offset event while onset events were indicated by the values '1', '2' and '3', indicating pair, group and triangle events, respectively. The animals involved in the onset or offset event are indicated in the *onset pair* and *offset pair* column. In the sample shown, pair 1 (familiar animals 1 and 2) came within close proximity in the first listed event ('419' in column *Event ID*), and were together for 25 s before breaking apart in the next event ('420' in column *Event ID*).

The column *pair count (past 24 h)* shows a tally of onset events between pairs 1, 2 and 3. In this instance, the familiar pair (pair 1) had encountered each other 15 times without being in proximity to the unfamiliar steer. The *group count (past 24 h)* column specified the number of times an existing pair had led to the creation of a tie to form a group event. For example, a change in state from a pair to a group event occurred at *event ID* '424'. Here, animals 2 and 3 (pair 3) were already in close proximity and animal 1 created a tie with animal 3 to form a group event, thus in the next row (*event ID* '425') the group count for pair 3 increased by one. As a pair event between animals 1 and 3 occurred to complete the group event, the pair count for pair 2 also increased by one in the *pair count (past 24 h)* column.

The *triangle count (past 24 h)* column tallied the number of times a triangle event had occurred. An example of this is shown in *event ID* '429'. The two onset events prior to the triangle event was a pair event between animals 1 and 3 (pair 2, *event ID* '427'), followed by a group event when a tie was created between animals 2 and 3 (pair 3, *event ID* '428'). The creation of a tie between animals 1 and 2 (pair 1) completed the triangle. A graphical example of this event sequence is shown in Fig. 8.3. Here, the tallies for the pair, group and triangle counts incremented by one in the row following the occurrence of the event. Note that the group count for pair 2 increased by one at the same time that the triangle count increased, as a second group event between animals 3 and 2 occurred when a tie was created between animals 1 and 3 to complete the triangle.

Table 8.2. A sample of onset data taken from triad 8 following transformation using a custom developed java application.

Event ID	Triad ID	Time	Event Type	Onset Pair	Offset Pair	Pair count (past 24 h)			Group count (past 24 h)			Triangle count (past 24 h)
						Pair 1	Pair 2	Pair 3	Pair 1	Pair 2	Pair 3	
419	8	180590	1	1	0	15	6	5	2	1	0	0
420	8	180615	0	0	1	16	6	5	2	1	0	0
421	8	180666	1	2	0	16	6	5	2	1	0	0
422	8	180678	0	0	2	16	7	5	2	1	0	0
423	8	180730	1	3	0	16	7	5	2	1	0	0
424	8	180732	2	2	0	16	7	6	2	1	0	0
425	8	180733	0	0	3	16	8	6	2	1	1	0
426	8	180734	0	0	2	16	8	6	2	1	1	0
427	8	180818	1	2	0	16	8	6	2	1	1	0
428	8	180825	2	3	0	16	9	6	2	1	1	0
429	8	180827	3	1	0	16	9	7	2	1	2	0
430	8	180829	0	0	1	17	9	7	3	2	2	1
431	8	180847	0	0	3	17	9	7	3	2	2	1
432	8	180882	0	0	2	17	9	7	3	2	2	1
433	8	181008	1	2	0	17	9	7	3	2	2	1
434	8	181009	2	3	0	17	10	7	3	2	2	1
435	8	181048	3	1	0	17	10	8	3	2	3	1
436	8	181060	0	0	3	18	10	8	4	3	3	2
437	8	181078	0	0	2	18	10	8	4	3	3	2
438	8	181102	0	0	1	18	10	8	4	3	3	2
439	8	181145	1	2	0	18	10	8	4	3	3	2
440	8	181150	0	0	2	18	11	8	4	3	3	2

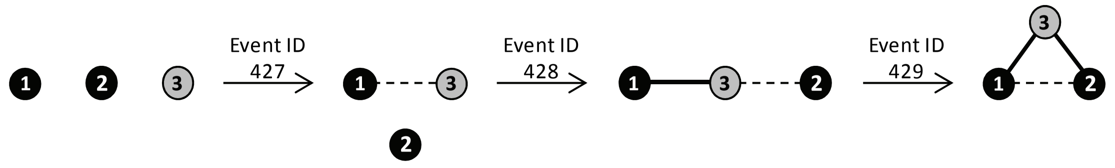


Figure 8.3. The sequence of onset events between the steers in triad 8 leading to a triangle event at event ID 429. A dashed line represents a tie that was formed in the current event, while a solid line represents a tie that continued to exist from the previous event.

8.3. Model parameters

The potential and actual onset events were analysed using the COXREG procedure within SPSS. The model was for the probability of the next event as a function of weighted statistics associated with the potential next events; the weights are the parameters of the conditional logistic regression model introduced earlier. A parameter was estimated for each statistic, or effect, in the model, and each model involved five effects: (i) unfamiliarity; (ii) prior pair events (past hour); (iii) prior pair events (past 24 hours); (iv) prior group events (past hour); (v) prior group events (past 24 hours). Two separate models were fitted on each day to predict pair events and group events. A basic overview of the modelling process is shown in Fig 8.4.

The onset event parameters (unfamiliarity, prior pair events and prior group events) are described in detail below and summarised in Table 8.3. The effects are discussed in terms of what a positive or negative parameter estimate would represent for the configuration of ties between pairs within the triad.

8.3.1. Unfamiliarity effects

To account for the difference in familiarity among the triad, an animal specific parameter relating directly to the unfamiliar animal was included in the model. There was an assumed homogeneity between the two familiar animals. The parameter estimate related to the propensity of the current event to involve the unfamiliar, where the current event was either a pair event or a group event. The unfamiliarity effect, unlike pair and group effects, was not related to the involvement of the unfamiliar animal in pair or group events in the past hour or past 24 hours, but was a measure of the number of past events involving the unfamiliar animal and was therefore a prediction of the involvement of the unfamiliar animal in future encounters within the triad. When a pair event was being predicted, the parameter estimate related to the propensity for a future pair event to involve the unfamiliar. A positive and significant result indicated a high probability that the unfamiliar animal was involved in a future pair event whereas a negative effect suggested the future pair events were less likely to involve the unfamiliar.

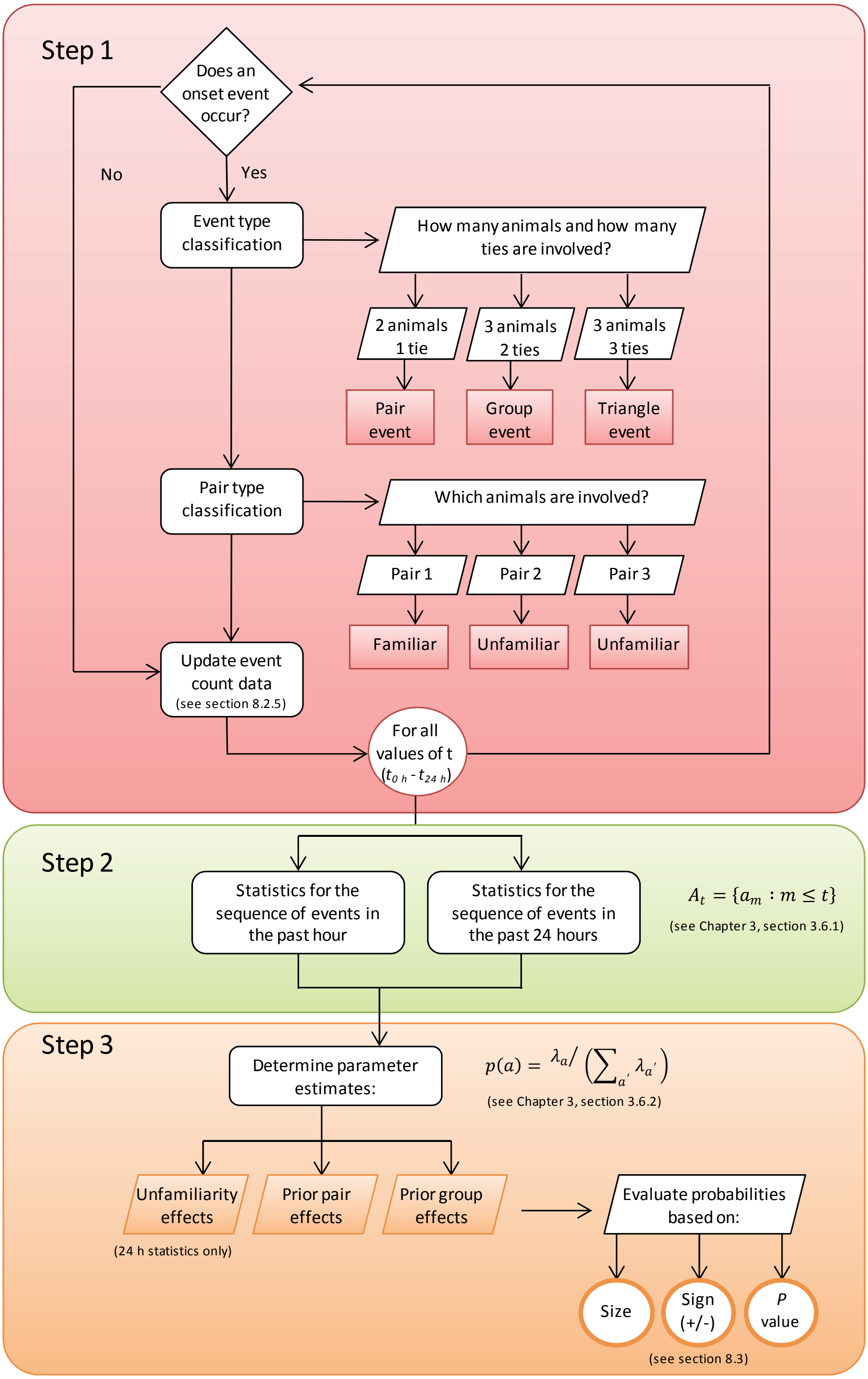
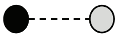
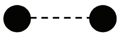
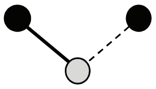
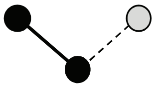
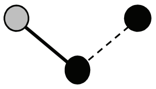
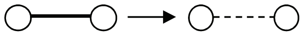
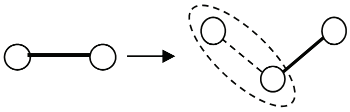
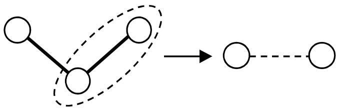
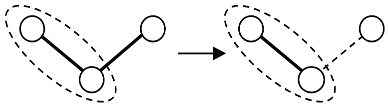


Figure 8.4. Basic outline of the relational event modelling process when applied to encounter data recorded among three steers per day. Step 1: creating the sequence of events per day; Step 2: calculating the statistics of events that did occur and events that could have occurred but did not; Step 3: using COXREG analysis in SPSS with strata defined by events to determine the probability of a future event based on the sequence of events in the past.

Table 8.3. The interpretations for both positive and negative significant parameters when the effect of unfamiliarity and the frequency of prior past events are used to predict the onset of future pair and group events.

Predictor	Event being predicted	Description	Positive	Negative
Frequency of prior events involving the unfamiliar animal	Pair event	The propensity for a current pair event to involve the unfamiliar	High probability that the current pair event will involve the unfamiliar animal 	Low probability that the current pair event will involve the unfamiliar animal 
	Group event	The propensity for the unfamiliar animal to be involved in the creation of a new tie leading to a group event	The current group event is created by a tie involving the unfamiliar animal  or 	The unfamiliar animal is not involved in forming the current group event 
Frequency of prior pair events	Pair event	The propensity for prior pair events to predict future pair events	Being in a pair in the past leads to more pair events in the future (persistence) 	Being in a pair in the past leads to less pair events in the future (avoidance)
	Group event	The propensity for prior pair events to predict a future group event	Pairs seen together in the past are more likely to form a tie to create a group event 	Pairs seen together in the past are less likely to join a group and remain as a pair
Frequency of prior group events	Pair event	Participation in past group events predicts participation in future pair events	Being in a group in the past leads to more pair events in the future 	Being in a group in the past leads to less pair events in the future
	Group event	Participation as a pair in past group events predicts participation in future group events	Pairs seen together in past group events are more likely to remain together in future group events, thus the existing pair creates the beginning of the group 	Pairs seen together in past group events are less likely to be seen together in future group events

Key:

● = familiar animal

◉ = unfamiliar animal

○ = animal of either familiarity

—— = existing tie

- - - - - - = predicted tie

When a group event was being predicted, the unfamiliarity effect referred to the propensity for the unfamiliar animal to be involved in the creation of a new tie leading to a group event. A positive parameter estimate indicated that the creation of a new tie leading to a group event involved the unfamiliar animal; either the unfamiliar animal was already a part of the existing pair leading to the group event or the unfamiliar joined the existing pair event between the two familiar animals. A negative unfamiliarity effect indicated that the unfamiliar animal was not involved in the tie that created the group event, and therefore was already connected in a pair with either of the familiar animals. A negative unfamiliarity effect here indicated a tendency for a familiar to prefer the other familiar individual in a group event.

8.3.2. Prior pair effects

To measure the propensity for an event to occur based on the characteristics of prior paired encounters, a pair specific parameter was included in the model. The history of prior pair events was used to predict the likelihood of future pair events and future group events. Prior pair events leading to future pair events were measures of 'persistence' between actors, thus a positive parameter indicated a tendency for prior encounters to predict future events and 'persistence' for future configurations to remain the same (Butts, 2008). Conversely, a negative pair parameter indicated avoidance, thus the more a pair had encountered each other in the past the less likely the same pair would encounter each other in the future.

In terms of pair events leading to future group events, the estimate related to the configuration of pairs within the group. A positive and significant parameter indicated sociability between the same pair; pairs seen together in the past were more likely to form a tie to complete a group event. On the other hand, a negative and significant parameter predicted that the same pair were less likely to create a tie to form a group event, thus the resultant group was based upon each steer being connected to a different steer to that of the past. This change in partner configuration is known as partner swapping. An example of partner swapping arising from prior pair events is shown in Fig. 8.5a, where the prior pair combination of steers *i* and *j* is used to illustrate the potential configurations that could occur during a partner swapping event. Here prior events involving *i* and *j* predict that in a group event arising from an existing contact between *i* and *k*, steer *j* will prefer proximity to *k*, rather than *i*. Thus the tie that was shared between animals *i* and *j* in the past is less likely

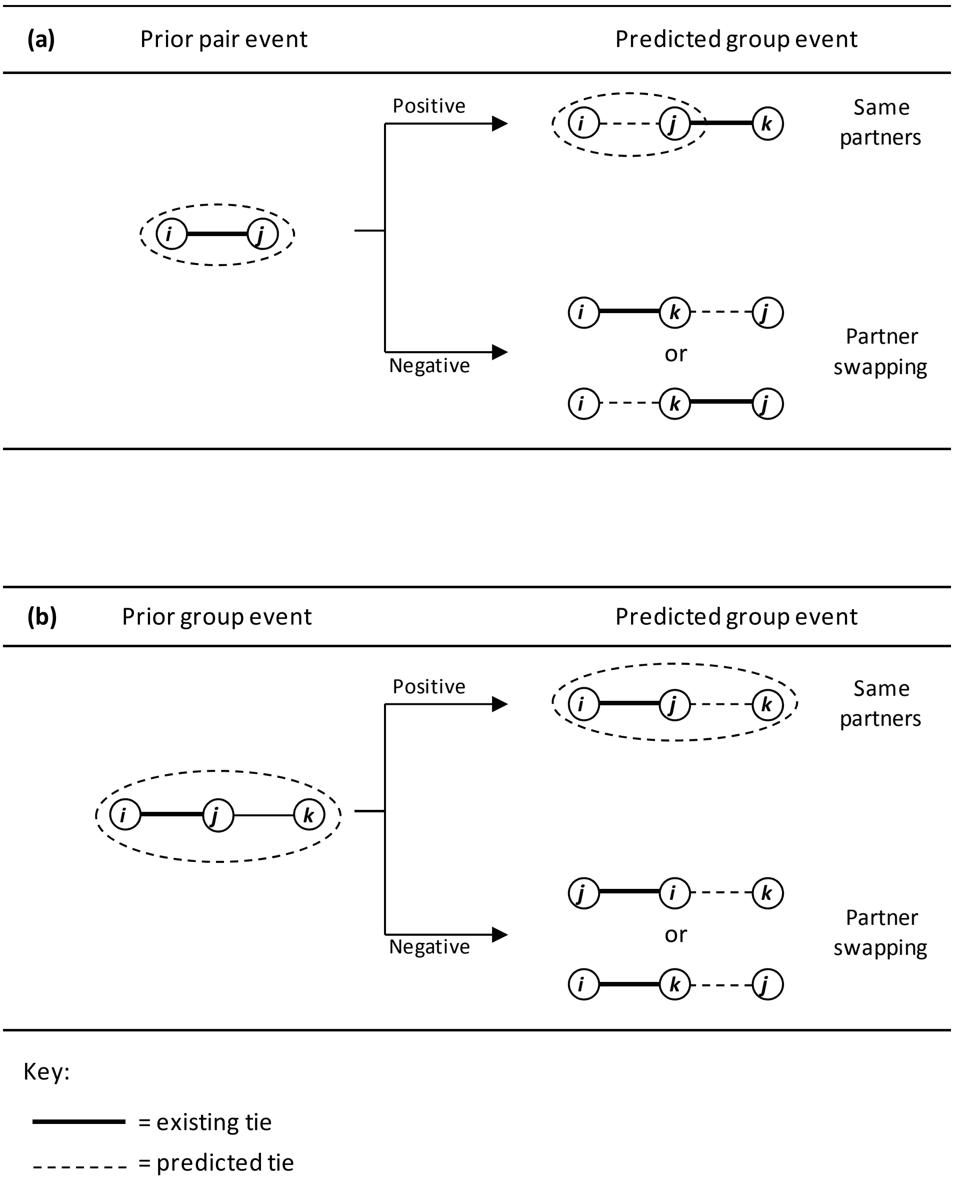


Figure 8.5. A description of positive and negative significant parameter effects when the onset of a group event was predicted from the sequence of (a) prior pair events, and (b) prior group events.

to be repeated in the future. This type of behaviour reflects '*information seeking behaviour*', where individuals make multiple contacts and gather information on each one (Butts, 2008).

8.3.3. Prior group effects

The group effect parameter evaluated the tendency for prior group events to lead to future pair and group encounters. The triadic nature of the encounter meant that one central steer, *i*, was in simultaneous contact with the two other steers, *j* and *k*, but *j* and *k* were not connected to each other. When predicting future pair events using the history of group events, the parameter estimate referred to the tendency for participation in prior group events to lead to more pair events in the future. A positive estimate indicated that ties shared between pairs in past group events were likely to lead to pair-wise interaction in the future. On the other hand, a negative parameter suggested that ties shared between pairs in past group events were less likely to lead to future pair events and may signify avoidance.

When predicting future group events from prior group events, the parameter estimate referred to the probability that interaction as a pair in past group events predicted further participation of the same pair in a group event in the future. A positive estimate signified that there was an increased probability that the configuration of ties between pairs in future group events was the same as that of the past, while a negative parameter indicated that the pair configuration of future group events was different to that of the past, and signified partner swapping (Fig. 8.5b). Thus, the steer that was the central animal in past group events was no longer the central animal in future group events.

8.4. Results

8.4.1. Descriptive statistics

A summary of the events identified by the relational event model is shown in Table 8.4, quantifying the total number of pair events, group events and triangle events. Generally, the number of pair and group events was consistent across days. The lower number of events on day 1 was due to the day of introduction comprising only half a day. Overall, there were consistently more pair events than group events. The occurrence of triangle events was rare and constituted only a fraction of the total number of events.

Table 8.4. A summary of the number of events per type identified by the relational event model for onset events.

Day	Pair events	Group events	Triangle events	Total
1	1296	170	50	1517
2	2757	298	70	3126
3	2835	285	34	3155
4	3030	455	83	3569
5	2816	309	72	3198

8.4.2. Model outputs

The following section analyses the results from each of the two models for onset events. The outputs from each model are complex, and it is difficult to interpret all of the patterns that were observed, thus it is the main findings with clear conclusions that are discussed.

8.4.2.1. Predicting future pair events

Overall, there was a negative effect of the unfamiliar animal (Table 8.5). The negative unfamiliarity effect indicated that a future relational event between two animals was less likely to involve the unfamiliar animal. Likewise, being familiar with another animal was associated with an increased probability of a future interaction. The strength of this effect varied across days; but in general, the effect was greatest on the day of introduction.

There was a strong and positive effect of prior pair events leading to future pair events (Table 8.5). This effect was consistently strong across all days for both the short and long term, except for a recency effect on day 1. Thus, the more two animals have had encounters in the past the more likely they are to have encounters in the future. This effect suggests that repeated encounters involving two animals reflect a *relationship* between them: the encounters signify both a pattern of past encounters and the expectation of future ones. Overall, prior contact between a pair leads to future contact.

There was an enhanced probability of an encounter between two animals if the same animals had encountered each other in the past day as a part of a group event (Table 8.5). This effect was variable over the 5 days, but was generally most notable on the day of introduction, when both the short and daily trends were positive. Together with the prior pair results, these effects suggests that the pattern of future contact between two animals is affected positively by the same two animals being within close proximity in the past, either as an isolated pair or as a function of a more complex encounter involving a third animal.

Table 8.5. Parameter estimates and standard errors predicting future pair events. Asterisks represent significance at *P < 0.05 and **P < 0.10.

Predicting future pair events			Day														
			1			2			3			4			5		
Parameter			B	SE		B	SE		B	SE		B	SE		B	SE	
Frequency of prior events																	
	Unfamiliarity effect		-0.49	0.09	**	-0.35	0.05	**	-0.43	0.05	**	-0.09	0.05		-0.52	0.05	**
	Prior pair events:	past hour	-0.50	0.33		2.67	0.35	**	2.25	0.34	**	2.32	0.33	**	2.89	0.35	**
		past day	2.59	0.24	**	1.96	0.12	**	2.15	0.13	**	2.35	0.12	**	1.88	0.11	**
	Prior group events:	past hour	0.43	0.20	*	0.14	0.16		0.78	0.15	**	0.24	0.14		0.59	0.18	**
		past day	0.62	0.21	**	0.31	0.13	*	0.11	0.12		0.03	0.12		0.44	0.13	**

8.4.2.2. Predicting future group events

In the models predicting future group events, there was a positive and consistent effect of the unfamiliar animal over the 5 day period (Table 8.6). This result indicates that future group events are created by a tie involving the unfamiliar: either the pre-existing pair creating the foundation of the group event involved the unfamiliar or the unfamiliar approached a familiar animal while it was within close proximity to the other familiar animal.

The frequency of pair events leading to future group events in the past day had a strong and positive effect on the day of introduction (Table 8.6). In other words, the more two animals interacted on the day of introduction, the more likely were group events involving proximity between those two animals on that day. This effect was variable over the remaining 4 days, suggesting that there was a high level of interaction on day 1, which settled out from day 2 onwards.

The propensity for group events in the past to lead to future group events was variable (Table 8.6). On the day of introduction, the short term effects were positive yet the daily effects were negative. The positive short term effects indicate that the group event was created by the addition of the third animal to the same pair of animals that were tied together in past group events, which suggests short term group building behaviour. While the negative daily effect suggests that the pair configuration of future group events was different to that of the past, or partner swapping (Fig. 8.5b), and represents information seeking behaviour where all three steers were actively engaging to learn each other's characteristics and features, particularly with the unfamiliar steer. Taken together, the results for day one suggest instability within the triad resulting from the disruption caused by the introduction of the unfamiliar steer.

From day 2 onwards, the pattern of prior group events leading to future group events was also variable between short term and daily patterns. The daily effect was consistently strong and positive. Indeed, being within close proximity in the past means it is more likely that the same pairs will be in close proximity in the future: this effect suggests stability. The change from a negative effect on day 1 to a positive effect on consecutive days suggests the same pairs were remaining together in future group events, which could suggest relationship building between the unfamiliar steer with one of the two steers. The hourly effects,

Table 8.6. Parameter estimates and standard errors predicting future group events. Asterisks represent significance at *P < 0.05 and **P < 0.10.

Predicting future group events		**Day**														
		1			**2**			**3**			**4**			**5**		
Parameter		B	SE		B	SE		B	SE		B	SE		B	SE	
Frequency of prior events																
Unfamiliarity effect		0.98	0.26	**	0.29	0.17		0.88	0.20	**	0.36	0.14	*	0.44	0.17	*
Prior pair events:	past hour	-2.07	1.30		-1.60	1.26		-0.69	1.53		0.29	1.20		0.76	1.55	
	past day	2.35	1.06	*	1.30	0.51	*	1.80	0.78	*	0.39	0.47		1.40	0.54	**
Prior group events:	past hour	1.19	0.56	*	-0.08	0.37		-1.00	0.40	*	0.84	0.38	*	0.61	0.38	
	past day	-1.57	0.75	*	1.20	0.42	**	2.27	0.55	**	1.49	0.45	**	1.08	0.47	*

however, were not consistently repeated and alternated between negative and positive effects on days 3 and 4, respectively. These variable patterns are difficult to explain, but may indicate a continuing instability in the triad as the unfamiliar tried to be incorporated into the familiar pair, perhaps unsuccessfully.

8.5. Discussion

The aim of the chapter was to apply a relational event model to the data that was analysed in Chapter 7. The current results demonstrate that the previous analysis in Chapter 7 was not adequate to describe the social encounters between all three steers; the encounter patterns between the three steers were more complex than previously reported. The results from the relational event model concur with the previous analysis that the day of introduction proved to be the most disruptive to social stability, however the effects included in the model provided a greater description not only of the interactions involving the unfamiliar steer but also of the encounter structures and relationships that existed within the triad.

The results show that overall familiarity was an important determinant of social interaction between steers. Familiar steers were more likely to form a tie with each other than they were with an unfamiliar steer, and there was an enhanced tendency for group events to be created by the unfamiliar joining an existing pair between the familiar steers. This behaviour indicates a stable relationship between the familiar pair and suggests the unfamiliar steer was being excluded. This result is similar to that obtained by Neisen et al. (2009), who found that pairs of familiar heifers introduced into an established dairy herd tended to remain within close proximity to each other and received half as many agonistic advances from the resident herd when compared with a heifer introduced on her own. The familiar pair had each other to rely on for social support; the presence of a familiar peer is known to provide social support in cattle, especially in stressful situations (Boissy and LeNeindre, 1997). Conversely, the single unfamiliar steer was more vulnerable due to a loss of social support, and may have led to the unfamiliar steer attempting to join the pair of familiar steers. In Neisen et al.’s (2009) study, the heifer introduced on her own into the dairy herd remained in close proximity to the resident cows and showed more synchronous behaviours regardless of the higher level of agonistic advances received, and thus could be seen as trying to be incorporated into the established herd.

The results from the current study indicate that initially the familiar pair was cautious about interacting with the unfamiliar steer and protected their social bond by excluding the unfamiliar individual. It is suggested that social stress results from presence of unfamiliar individuals (Zayan and Dantzer, 1990), while other studies have shown that the presence of an unfamiliar peer is less effective at reducing stress in stressful situations when compared with a familiar peer (Boissy and LeNeindre, 1997; Faerevik et al., 2006; Meyer et al., 2010), thus it is possible that the familiar steers may have experienced social stress caused by the presence of the unfamiliar steer. Further indicators of stress such as blood cortisol levels or heart rate are required to confirm this speculation. The presence of the unfamiliar steer may also have created a threat to resources, in particular social status, thus the behavioural changes recorded between the familiar pair could represent a defensive or territorial strategy to prevent the unfamiliar steer from attaining a higher social status and displacing either of the familiar steers. It is assumed that the unfamiliar individual will eventually become familiar within the triad and the unfamiliarity effect (difference in social encounters between familiar and unfamiliar individuals) would no longer exist. It is concluded that longer than 5 days is required for an unfamiliar steer to become integrated with two previously familiar steers.

A prominent feature of the model outputs was the importance of pair-wise interaction on future events; pairs that were together in the past were likely to remain together in the future. The regular encounter patterns between the same pair of steers not only indicates a preferential relationship between the pair, but also enforces the positive association between spatial proximity and social proximity; individuals with well developed social bonds were more likely to approach each other at closer distances more often. Pair-wise relationships and associated social bonding have been identified in cattle, where individuals have specific grazing and grooming partners (Reinhardt and Reinhardt, 1981); these relationships facilitate cooperation and communication (Lindberg, 2001), as well as providing hygiene benefits through mutual grooming (Sato et al., 1991; Sato and Tarumizu, 1993). The behavioural patterns of individuals within a pair-wise relationship provide a strong foundation for understanding the structure of the group. The expectation that pair encounters in the past will lead to future encounters strengthens group cohesion and promotes group forming behaviours.

The results from the relational event modelling identified patterns of regularity in both the short term and longer term social encounters: dyadic effects were strongly repeated in both the short and long term, enforcing the inherent importance of pair-wise interaction for social structure, while group effects tended to be repeated only in daily patterns, suggesting overall stability on a daily basis with short lived periods of activity. The change in patterns that occurred between days 1 and 2 not only highlighted the disruption caused by the introduction of the unfamiliar steer, but also relate to flexibility within the social system. In a domestic livestock system, cattle are managed according to production efficiencies, which may include short and long term location changes, as well as fluctuations in group composition. The social system is therefore required to exhibit some aspects of flexibility to accommodate these changes followed by periods of stability: the encounter patterns observed could reflect this pattern of adaptation. The stabilising of encounter patterns after day 1 suggests that the direction of dominance relationships were established early. Dominance relationships between cattle are said to occur relatively quickly, (within the first hour) and remain relatively constant after this time (Bouissou, 1974a). However, stabilisation of social processes and interaction patterns require a longer time frame (up to 45 days) (Sato et al., 1990), which may explain why some short term effects in the model vary in significance over the 5 days during this period of adjustment. These interpretations highlight the importance of the time component in the model for describing both the endogenous pair properties and the emergent group patterns that occurred as a result of the change in social composition.

8.6. Conclusions

The relational event model identified how the social system of a pair of steers was impacted by the introduction of an unfamiliar steer. Regularities in encounter patterns were explored to reveal the importance of familiarity, paired encounters and group encounters on relationship development with the unfamiliar steer. It was discovered that the familiarity was an important driver of the initiation of social interaction. Additionally, the strong persistence of dyadic encounters suggested the familiar pair provided a strong structural foundation of the group, while variability in group encounters reflected initial investigation of the unfamiliar steer followed by a stable pattern of short lived activity. This investigation illustrates the potential application of a relational event model for analysing animal social systems by providing an insight into the encounter structures of steers and how they respond and adapt to change.

Chapter 9

Social encounters of familiar steers in larger groups

9.1. Introduction

The relational event model developed in Chapter 8 considered the structural configuration of pair-wise encounters between an unfamiliar steer with a pair of familiar steers. The model identified whether the unfamiliar steer was involved in an encounter and distinguished between encounters involving isolated pairs, group events (where one steer was in simultaneous contact with the other two), and triangle events involving all three steers in close proximity at the same time. It was found that familiarity was a strong driver of social interaction and the familiar pair actively excluded the unfamiliar steer. It was also found that pair-wise encounters were important in forming the basis of a social group and strengthening social relationships. The findings from Chapter 8 relate specifically the evolution of cattle social structure and understanding how relationships form and develop.

Pair-wise relationships are described as the fundamental component of a social system (e.g. Simmel, 1950; Hinde, 1976), and the study by Reinhardt and Reinhardt (1981) demonstrates that pairs of cattle form preferential relationships. However, Chase et al. (2003) suggested that pair-wise encounters are insufficient to explain hierarchy structure, which is better explained by the outcome of triadic interactions. Chase (1982) demonstrated that the presence of a third 'bystander' individual was important for the replication of relationships while the presence of a fourth individual did not affect the outcome of dominance relationships. This finding was consistent with Simmel's (1950) theory that an increase from two to three individuals has a greater effect on social processes than the addition of a fourth individual. Thus, triadic effects are expected to have a large influence on social properties, more so than encounters involving dyads or quads of individuals.

The aim of the current chapter is investigate the patterns of encounters between familiar steers in larger groups by modelling the pair-wise interactions across an entire herd of 14 steers using localised event structures that involve two, three and four individuals. The social dynamics identified in the larger groups can then be compared with the processes previously identified in triads of steers to determine whether higher order processes affected the encounter behaviour of triads of steers. The relational event model described in the previous chapter will be applied to proximity logger data collected on the two groups of resident steers prior to any experimentation. In this chapter, events involving simultaneous contact between four steers will be modelled in addition to the pair, group and triangle events identified in Chapter 8: the importance of each of these events for social structure will be investigated. It is hypothesised that both paired and triadic encounters will be a strong feature of the encounter patterns observed in a larger group.

9.2. Methods

9.2.1. Animals and management

The monitoring period was conducted in April, 2008, 8 weeks after the steers had been purchased from the sale yards. At the time of the study, the two groups of steers were 18-months-old and had a mean weight (± standard error) of 350 ± 6.6 kg and 389 ± 8.7 kg for groups 1 and 2, respectively. Each group consisted of 14 steers as the two spare steers per group had not yet been removed. The groups had been on the research property for 8 weeks prior to the experiment and had been managed as separate herds during this time. Based on other literature stating that stabilisation following mixing of cattle occurs between 7 and 45 days (e.g. Sato et al., 1990; Nakanishi et al., 1991; Gupta et al., 2008), the two groups were considered to be socially stable at the time of the experiment. During the study the groups were monitored in separate 7 ha paddocks for 7 days. A minimum 100 m separated the two paddocks. The steers were fitted with proximity logging collars at 09:00 h on the first day of the deployment, and were removed 8 days later. The data collected on day 8 was removed, as it did not represent a full day.

9.3. The relational event model for groups

The model takes the same form as that described in Chapter 8 and was designed to predict whether and when a potential onset event will occur, based on the encounter patterns recorded in the past. For each of the event types (see section 9.3.1 below), the model analysed the involvement of specific pairs in an encounter, thus the pair was the basic unit of analysis. It was necessary to distinguish between the different pairs within the group, thus each animal in the group was identified and the involvement of each possible pair was evaluated. For each group of 14, there were 91 possible pair configurations. The involvement of a specific pair in each event type was quantified as the proportion of time that the dyad had been a part of each event configuration out of the total the number of times the configuration existed.

The time frames used to analyse the past encounters were based on events that had occurred in the past hour, the past 24 hours and also the pattern of encounters over the entire 7 day period. It was expected that the daily patterns would be relatively consistent as the groups were considered to be socially stable, thus the daily time frames per group were analysed using data pooled across all days, although the statistics used in the model were calculated on a day by day basis.

9.3.1. Model components

The java program introduced in Chapter 8 was modified to incorporate the additional animals and effects. The program was used to transform the proximity logger data into a set of actual and potential onsets and the statistics based on prior relational events for each pair of steers within each group. The java program calculated statistics for each event or potential event in terms of (i) the identity of the animals involved; (ii) the type of the event that occurred; and (iii) statistics based on the frequency of relevant prior events.

An animal specific parameter was included to identify the participation of individual animals in each of the events. This effect replaced the unfamiliarity effect included in the previous model. Because all of the steers were familiar, this effect was included to investigate individual differences within the group.

The event types were modified to account for the larger social context. The type of events that were considered in the current groups model include pair events, string events (formerly group events), triangle events and popularity events, a new event type to identify individual popularity (Fig 9.1).

A pair event was the same as identified in the previous chapter. Pair events were created when two individuals who were not previously involved in an encounter came within close proximity of each other, thus the pre-existing state for a pair event was two isolated individuals.

A string event was previously designated a group event in Chapter 8, and occurred when a third individual joined an existing pair event. Due to the larger group size, it was possible that encounters could involve more than three individuals, thus the classification of a ‘group event’ did not capture the full potential of this encounter configuration. Based on the possible configurations for an event involving simultaneous contact of one animal with two others, it was possible that the animals could have been aligned in a ‘string’ formation, hence the name. This event could represent animals aligned together in a horizontal line (Fig. 9.2a) or leader-follower movement (Fig. 9.2b): the distinction between the two configurations has important implications for the social roles that individuals fulfil within the group and their influence over others. However, the data collected by the proximity loggers is only a *relative* spatial position, not an *absolute* spatial position, thus the exact location of individuals within an encounter cannot be specified. The use of GPS devices with high spatial accuracy would be required to record such measures.

A triangle event was the same as described in Chapter 8. Triangle events occurred when three individuals encountered each other at the same time. The close proximity nature of the event signifies a form of sub-grouping within the larger group context.

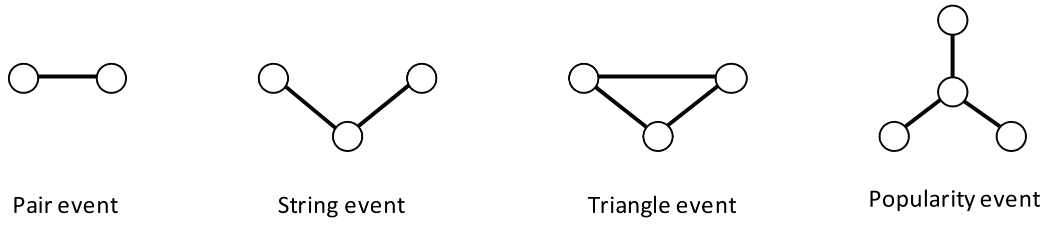


Figure 9.1. The four event types that were used to model the encounter patterns of groups of steers.

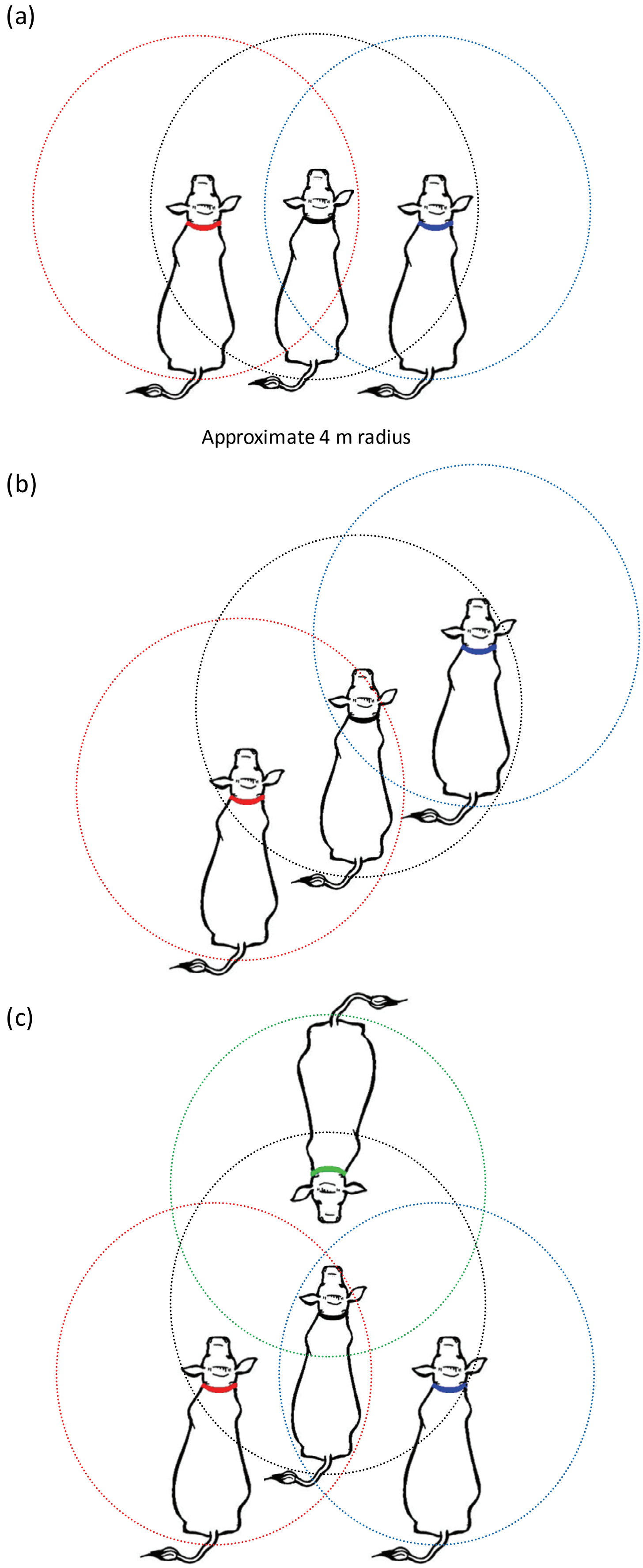


Figure 9.2. An example of the possible animal configurations in a string event (a), (b) and a popularity event (c), showing the approximate 4 m detection range of a proximity logger.

A popularity event represented one individual, *i*, in simultaneous contact with three others, *j,k* and *l,* at the one time, yet *j*, *k* and *l* were not in contact with each other (Fig. 9.2c). This effect represents ‘popularity’, as one individual was central to three others. A popularity event was built on the contemporaneous existence of a string event. The configuration for a popularity event is also known as a star configuration.

9.4. Results

9.4.1. Descriptive statistics

A summary of the raw proximity logger data per group is shown in Fig. 9.3. The number of encounters per pair per hour was relatively consistent across days. There were more encounters between pairs in group 2 on day 1, which could be explained as a prolonged response to returning to their paddock after being handled in the yards. This effect stabilised over the remaining 6 days. The average encounter length of pairs in group 2 was marginally lower than those of group 1.

A network diagram visualising the associations between animals within each group is shown in Fig. 9.4. The total length of encounters was used to indicate the strength of association between each pair, thus pairs that spent more time within close proximity were regarded as having stronger associations and the strength of the association is visually represented by the colour of the tie joining the two steers. Here, only steers that spent more than a total of 5 hours within close proximity are shown. A red line indicates that a pair spent between 5 and 7.5 hours within close proximity of each other, green represents between 10 and 12.5 hours and the strongest association is shown by a blue line between two steers, indicating that they spent in excess of 12.5 hours in close proximity over the 7 days. The size of the node representing each animal is an indication of the number of encounters recorded with all other steers. Thus a larger node indicates a highly active animal, while the smallest size represents the animal with the least number of close proximity encounters.

The diagrams reveal differences between group 1 and group 2. While both groups displayed a tendency for one animal to be involved in encounters more than others; stronger associations were displayed by group 1: five pairs displayed associations greater than 12.5 hours spent within close proximity. Only one individual in group 1, animal 71, did not

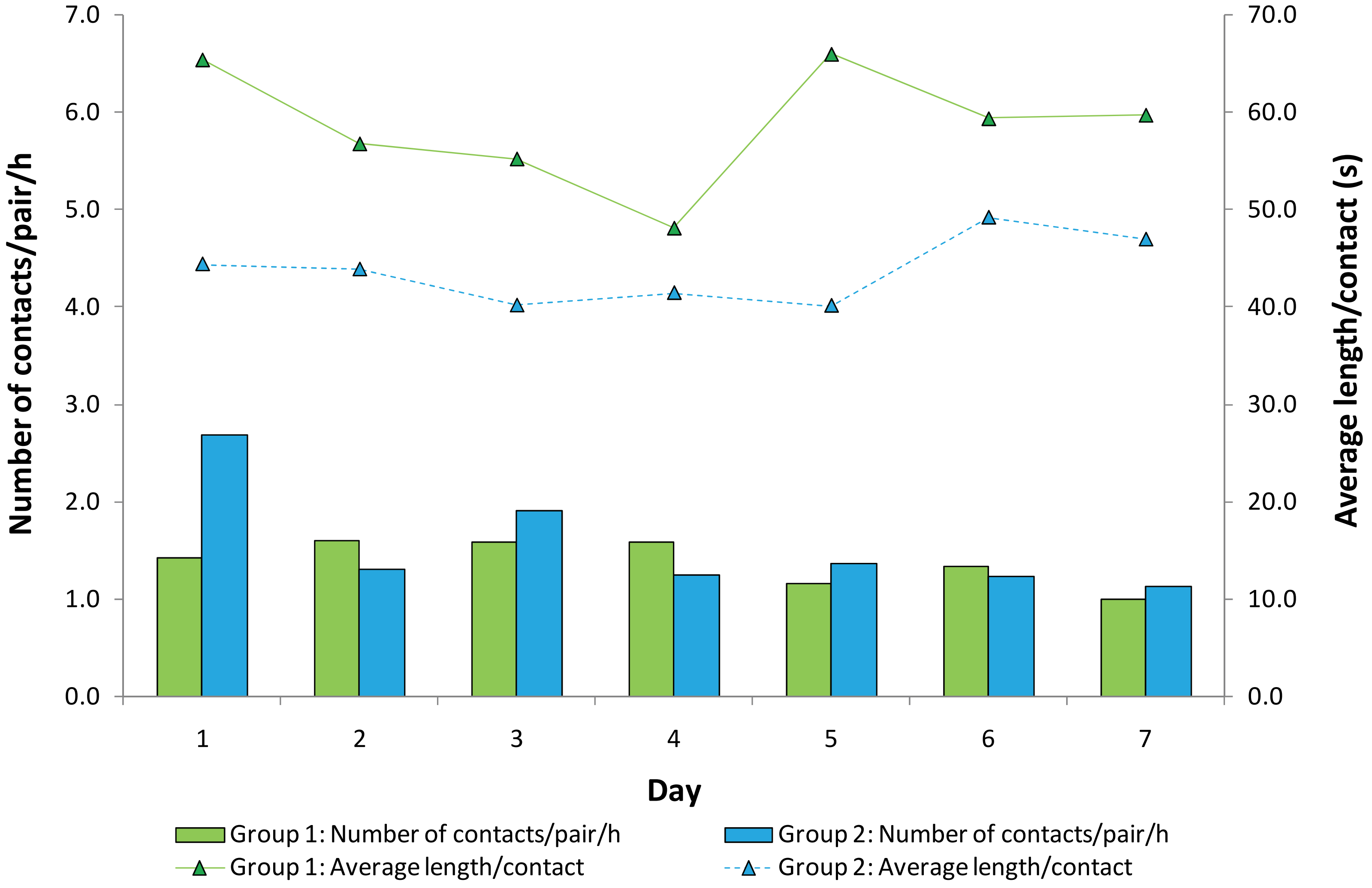


Figure 9.3. The number of contacts per hour and the average length per contact for contact between pairs within group 1 and group 2 per day.

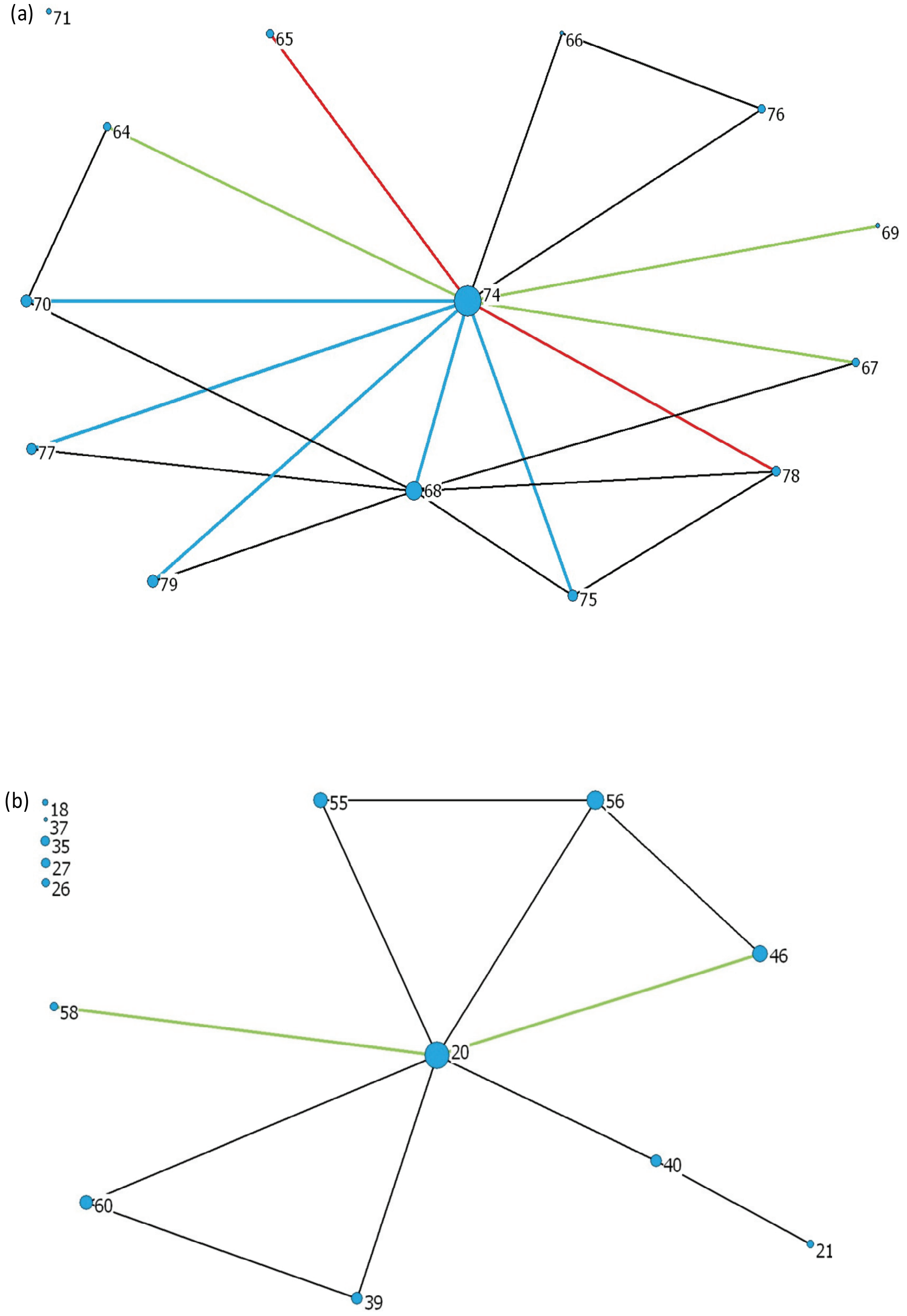


Figure 9.4. Network diagrams representing pair-wise interaction between steers in (a) group 1 and (b) group 2. The lines represent the strength of association between steers based on the total amount of time spent within close proximity over the week. Only associations longer than 5 hours in total duration are shown. The colour of the line represents the strength of association: black = between 5 and 7.5 h in close proximity; red = between 7.5 and 10 h; green = between 10 and 12.5 h; blue = greater than 12.5 h. The size of the node represents the total number of times an individual encountered all other steers, and is a measure of activity and/or popularity.

associate with other individuals for more than 5 hours over the week. In contrast, there were five animals in group 2 who were isolated from the diagram with less than 5 hours spent within close proximity of any other individual. Additionally, there were only two associations in group 2 that were longer than 10 hours and no pairs spent more than 12.5 hours in close proximity. These results suggest that cohesion was stronger in group 1 as individuals interacted more than those in group 2.

A summary of the events identified by the relational event model is shown in Fig 9.5. Overall, there were a larger proportion of pair events than any other event type. There were marginally more string events than popularity events while triangle events were recorded the least.

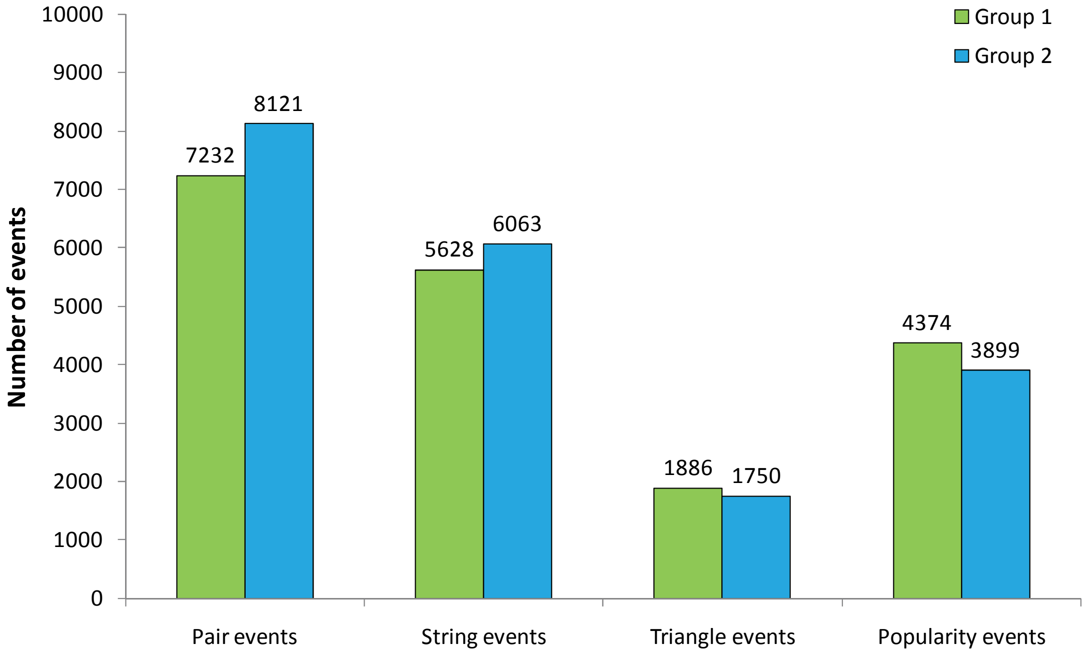


Figure 9.5. The number of events per type identified by the relational event mode for onset events within groups 1 and 2

9.4.2. Model outputs

To assist in interpretation, the model outputs are presented in a series of tables comparing models for each of the four event types in each of the two groups: in other words, eight models were fitted in all and the two groups were modelled separately. Each of the tables to follow summarises the effects of a specific set of predictors across the eight models

9.4.2.1. Animal effects

The results for the animal effects showed variability among individuals for both group 1 and group 2 (Table 9.1). Most animals had a significant effect for at least one event type. The majority of the animal effects were negative, with only two animals having a consistently positive effect in group 1 and four animals in group 2. This result showed that there were some individuals that were more likely to be involved in an encounter than others, suggesting that these individuals were highly sociable. Equally, some individuals showed strongly negative results (animal 66 group 1 and animal 37 in group 2), suggesting that these individuals were overall less sociable. The size of the effect increased as the number of animals involved in an encounter increased, thus it may be that these individuals tended to avoid group-like encounters.

9.4.2.2. Predicting future events from the pattern of prior pair events

Dyadic encounters were a strong feature of the encounter patterns recorded in group 1: paired encounters in the past generally resulted in the same pairs seen together in the future (Table 9.2). Time was an important factor for the recurrence of encounters involving more than two animals: triangle events were more likely repeated over the week, while string events were repeated on a daily scale. There was an enhanced recency effect on all four event types: the occurrence of all pair events in the immediate past was a strong predictor of future encounters.

The patterns of paired encounters in the past leading to future encounters in group 2 also showed evidence of cohesion, but not as strong as group 1 (Table 9.2). Group 2 tended to repeat pair-wise encounters less frequently than group 1. Trends of paired encounters leading to future encounters were repeated in the immediate and daily past but did were not repeated over the course of the week. String events were likely to be repeated on a daily basis, and similar to group 1, recently occurring pair events were a strong predictor of all four event types in the future.

Table 9.1. Parameter estimates and standard errors predicting future pair, string, triangle and popularity events based on participation of individual animals. Asterisks represent significance at *P < 0.05 and **P < 0.10.

Animal effects		Future event being predicted											
		Pair event			String event			Triangle event			Popularity event		
		B	SE		B	SE		B	SE		B	SE	
Group 1:													
	a64	-0.06	0.05		-0.17	0.06	**	-0.14	0.09		-0.31	0.07	**
	a65	-0.07	0.05		-0.21	0.06	**	-0.07	0.09		-0.44	0.07	**
	a66	-0.37	0.05	**	-0.74	0.07	**	-0.80	0.12	**	-1.18	0.09	**
	a67	-0.15	0.05	**	-0.23	0.06	**	-0.18	0.10		-0.40	0.07	**
	a68	0.09	0.05	*	0.29	0.05	**	0.31	0.09	**	0.38	0.07	**
	a69	-0.48	0.06	**	-0.54	0.06	**	-0.50	0.11	**	-0.78	0.08	**
	a70	0.02	0.05		-0.01	0.05		0.11	0.09		-0.15	0.06	*
	a71	-0.13	0.05	*	-0.60	0.06	**	-0.68	0.12	**	-1.05	0.09	**
	a74	0.06	0.08		0.73	0.08	**	-0.16	0.19		1.64	0.11	**
	a75	-0.02	0.05		-0.08	0.05		0.09	0.09		-0.31	0.07	**
	a76	-0.05	0.05		-0.37	0.06	**	-0.31	0.10	**	-0.67	0.07	**
	a77	-0.05	0.05		0.03	0.05		0.16	0.09		-0.06	0.06	
	a78	-0.08	0.05		-0.22	0.05	**	-0.17	0.09		-0.34	0.07	**
Group 2:													
	a18	-0.17	0.05	**	-0.49	0.06	**	-0.76	0.11	**	-0.39	0.07	**
	a20	0.04	0.06		0.42	0.07	**	0.10	0.14		0.91	0.09	**
	a21	-0.11	0.05	*	-0.31	0.06	**	-0.52	0.10	**	-0.54	0.08	**
	a26	-0.19	0.05	**	-0.14	0.05	**	-0.40	0.10	**	-0.10	0.07	
	a27	-0.08	0.05		-0.17	0.05	**	-0.31	0.10	**	-0.05	0.07	
	a35	0.05	0.04		-0.20	0.05	**	-0.51	0.10	**	-0.64	0.08	**
	a37	-0.24	0.05	**	-0.57	0.06	**	-1.03	0.13	**	-0.96	0.09	**
	a39	-0.03	0.04		-0.03	0.05		-0.08	0.09		-0.08	0.07	
	a40	0.06	0.04		-0.09	0.05		-0.12	0.09		-0.14	0.07	*
	a46	0.07	0.04		0.11	0.05	*	-0.17	0.09		0.13	0.06	*
	a55	0.04	0.04		0.16	0.05	**	0.16	0.08		0.10	0.06	
	a56	0.01	0.05		0.21	0.06	**	-0.05	0.11		0.66	0.07	**
	a58	-0.13	0.05	**	-0.25	0.06	**	-0.30	0.10	**	-0.21	0.07	**

Table 9.2. Parameter estimates and standard errors predicting future events from the history of pair events. Asterisks represent significance at *P < 0.05 and **P < 0.10.

Prior pair events		**Future event being predicted**											
		Pair event			**String event**			**Triangle event**			**Popularity event**		
		B	SE		B	SE		B	SE		B	SE	
Group 1:	past week	0.30	0.05	**	0.09	0.06		0.33	0.10	**	0.10	0.07	
	past day	0.16	0.04	**	0.14	0.05	**	-0.16	0.09		0.00	0.06	
	past hour	0.34	0.01	**	0.22	0.01	**	0.21	0.02	**	0.17	0.02	**
Group 2:	past week	0.05	0.03		0.12	0.04	**	0.02	0.08		0.13	0.06	*
	past day	0.09	0.03	**	-0.06	0.04		0.02	0.07		-0.05	0.05	
	past hour	0.24	0.00	**	0.15	0.01	**	0.11	0.03	**	0.12	0.03	**

9.4.2.3. Predicting future events from the pattern of prior string events

There was a negative effect of string events in the past week leading to future pair events for both groups, indicating that pairs tended to stick together and were less likely to form a string with one other (Table 9.3). Negative estimates were also obtained when string events in the past were used to predict future triangle events for group 1 and future string events for group 2. This result indicates that future string events were likely to be a different configuration to that of the past, and suggests interaction between different animals within the group.

Table 9.3. Parameter estimates and standard errors predicting future events from the history of string events. Asterisks represent significance at *P < 0.05 and **P < 0.10.

Prior string events		**Future event being predicted**											
		Pair event			**String event**			**Triangle event**			**Popularity event**		
		B	SE		B	SE		B	SE		B	SE	
Group 1:	past week	-0.56	0.13	**	-0.02	0.14		-0.71	0.27	**	-0.12	0.18	
	past day	-0.04	0.12		-0.24	0.13		0.55	0.24	*	0.13	0.14	
	past hour	-0.03	0.01	**	0.17	0.01	**	0.12	0.04	**	0.14	0.03	**
Group 2:	past week	-0.37	0.10	**	-0.23	0.10	*	0.24	0.19		-0.14	0.15	
	past day	0.28	0.09	**	0.18	0.10		-0.26	0.19		-0.07	0.13	
	past hour	0.00	0.01		0.16	0.01	**	0.24	0.04	**	0.17	0.05	**

The trend for prior string events to lead to future events became positive when patterns in the more recent past were analysed. This effect was seen in group 1 when triangle events were predicted and was also shown in group 2 when pair events were predicted. String events in the past hour were also positive predictors of future string, triangle and popularity events. Thus, animals associating in the recent past as a string were more likely to associate together in the future when more than two individuals were involved. This effect suggests group building behaviour and may indicate a number of individuals performing the same activity during certain times of the day, such as periods of grazing or resting.

9.4.2.4. Predicting future events from the pattern of prior triangle events

When the pattern of triangle events in the past were used as a predictor for future events, only triangle events in the recent past were found to be significant for both groups (Table 9.4). This effect was consistently positive across all event types, except for the absence of triangle events leading to popularity events for group 2. Thus, when three animals were all within close proximity there was a tendency for the same animals to remain together in future events. This effect suggests consistency in short term interaction, such as remaining together during grazing bouts or rest periods.

Table 9.4. Parameter estimates and standard errors predicting future events from the history of triangle events. Asterisks represent significance at *P < 0.05 and **P < 0.10.

Prior triangle events		**Future event being predicted**											
		Pair event			**String event**			**Triangle event**			**Popularity event**		
		B	SE		B	SE		B	SE		B	SE	
Group 1:	past week	0.08	0.05		-0.04	0.06		0.02	0.11		-0.13	0.07	
	past day	0.03	0.05		0.03	0.05		-0.01	0.10		-0.03	0.05	
	past hour	0.02	0.01	**	0.03	0.01	**	0.29	0.02	**	0.03	0.01	*
Group 2:	past week	0.09	0.06		-0.03	0.06		-0.21	0.11		-0.02	0.09	
	past day	-0.06	0.05		0.03	0.06		0.15	0.11		0.10	0.07	
	past hour	0.05	0.01	**	0.03	0.01	**	0.18	0.02	**	0.03	0.03	

9.4.2.5. Predicting future events from the pattern of prior popularity events

The popularity parameter referred to the probability of a future popularity event to be of the same configuration as was seen in the past, and thus the identity of the central animal was the same. The results were varied across groups and also across time frames (Table 9.5). The weekly patterns in group 1 showed a greater effect of prior popularity events leading to future events: the same animals in a popularity event were likely to associate together in future pair and triangle events. Popularity events were also repeated daily, although in the opposite direction to the overall patterns. The negative daily popularity effect suggests that the same animal was not central to forming the same star configuration that was seen in the past. The change from a positive effect in the overall patterns to a negative effect in the daily patterns may reflect differences in leadership for different activities during the day. For example, one animal may have been responsible for initiating grazing behaviour while another was more influential when initiating periods of rest. There was a positive tendency for popularity events in the recent past to lead to the same animals involved in future string and popularity events. This result suggests stability in group-like encounters in the short term. The results also indicate that certain animals were central to forming groups and may provide evidence of recruitment, as animals that are together in previous event types are likely to join other pairs to form the star configuration.

Table 9.5. Parameter estimates and standard errors predicting future events from the history of popularity events. Asterisks represent significance at *P < 0.05 and **P < 0.10.

Prior popularity events		**Future event being predicted**											
		Pair event			**String event**			**Triangle event**			**Popularity event**		
		B	SE		B	SE		B	SE		B	SE	
Group 1:	past week	0.52	0.10	**	-0.14	0.10		0.55	0.21	**	0.03	0.13	
	past day	-0.33	0.09	**	0.13	0.10		-0.53	0.19	**	-0.18	0.10	
	past hour	-0.02	0.01	*	0.02	0.01	*	-0.03	0.03		0.14	0.02	**
Group 2:	past week	0.18	0.05	**	0.10	0.06		-0.05	0.12		-0.11	0.09	
	past day	-0.15	0.05	**	-0.08	0.05		0.12	0.10		0.12	0.07	
	past hour	-0.01	0.01		0.01	0.01		-0.01	0.02		0.16	0.02	**

Similar to group 1, the probability of popularity events leading to future pair events was repeated in group 2: over the week the same pairs tended to remain together in future pair events. Also similar to group 1, the daily effect of popularity events leading to different pair configurations in future dyadic events was negative, reflecting differences in leadership during the course of a day. There was a positive recency effect of popularity events leading to the same popularity event in the future. This result suggests that group 2 displayed similar stable short term encounter patterns between more than 3 individuals as was seen in group 1.

9.5. Discussion

The aim of the chapter was to investigate the patterns of encounters that occurred between groups of steers that were socially stable. Encounters involving pairs, three individuals in contact together or one animal in simultaneous contact with two others as well as encounters involving four individuals were evaluated. It was hypothesised that dyadic and triadic events would comprise a large component of the interactions, and although string events occurred more predominantly than triangle or popularity events, the results showed that string events were not as influential on future events as pair events. Thus, the effect of encounters involving three individuals was not as important as expected.

The effect of pair-wise interaction was a prominent feature of the model outputs for both groups: pair-wise interactions in the past positively influenced the occurrence of events in the future, thus the same pairs that were together in the past were likely to be seen together in the future. This result suggests that specific pairs were interacting regularly and indicates the existence of preferential relationships within the group. Pair-wise relationships between cattle have been described by Reinhardt and Reinhardt (1981), where grooming and grazing associations were formed between certain animals and the majority of group members had one or more preferred grazing or grooming associates. Reinhardt and Reinhardt (1981) also reported that grazing associates would locate themselves away from the group during grazing activities. The current results may reflect grazing and grooming associations between specific individuals, as there was a strong tendency for pairs to remain together.

There was a tendency for the same triadic encounter structures being repeated in the short term, although the type of triadic configuration differed between groups: where group 1 showed a greater tendency for triangle events, string events were a stronger feature of the encounters in group 2. Both event types relate to group-forming behaviour, however the nature of triangle events indicate more localised grouping and may suggest greater cohesion in group 1: this effect was also visually seen in the network diagrams, where group 1 had stronger associations than group 2. The greater tendency for triangle events to occur in group 1 may also suggest the possibility of sub-group formation. Ramseyer et al. (2009) found that sub-groups in cattle were based on preferential relationships, where a sub-group involved between two and five individuals. In the same study, individuals with preferential relationships were also found in close proximity during movement. Thus it is possible that three steers could have formed alliances and maintained proximity during short-lived activities, such as grazing or resting. It is important to note that these effects are present even after the individual propensities for sociability have been taken into account. Thus, the propensity for triadic encounters to form is not just a reflection of some individuals being more socially active than others but represents an organising dynamic in the herd. Further investigation is required to quantify the existence of preferential relationships between two or more steers and the potential for sub-groups to form.

The animal effect showed that some individuals were more social than others and demonstrates that associations within the group were more ordered than random. Individual differences in sheep sociability have previously been reported (e.g. Sibbald and Hooper, 2004; Sibbald et al., 2006), where it was found that highly social sheep were less likely to move away from a group to forage and instead preferred to remain in proximity to others. Thus, it is possible that highly sociable steers maintained a higher level of social contact with others to receive necessary social support and reassurance from group members. Further profiling is needed to confirm the social role that these more sociable individual fulfil within the group, but their contact structure suggests that these individuals are essential for group cohesion and may serve to transmit information within the group.

The negative animal effects suggest that some steers were less likely to be involved in an interaction: this effect grew in size with the number of individuals involved in the predicted encounter. This effect may be interpreted in several ways: the negative effects may reflect the propensity for some individuals to only associate with certain others, while the results may also reflect an inherent feature of a cattle social system to avoid large sub-groupings. In support of the latter interpretation, the results also showed that popularity and triangle events occurred less frequently than pair or string events and tended to be localised in the short term. Thus, overall there was a tendency for encounters not to involve more than three individuals. The number of individuals that can participate in an encounter is limited for practical reasons, as there are only a certain number of individuals that can be located within a 4 m radius. Also, it is expected that individuals will avoid grouping together frequently to avoid competition for forage while grazing and space during rest, as it would compromise their individual fitness (e.g. Rind and Phillips, 1999; Harris et al., 2007). Cattle have specific spacing principles that reflect not only properties of individual relationships but also group-specific properties. For example, individuals maintain certain distances with others depending on their relationship status (Keeling, 1995), while individuals also have a maximum distance that they will move away from the group (Hediger, 1963): these spatial properties contribute to group functioning and cohesion. Thus, the negative animal effects and lower proportion of group-like encounters in the longer term may be related to social factors that maintain a balance between the forces keeping the group together and breaking the group apart.

The temporal patterning of encounters revealed that weekly trends were in general repeated more so than daily trends, and hourly trends were repeated the most. Thus there were regular patterns of short-lived activity as well as longer term behavioural trends. The majority of significant effects in the short term were positive, thus there were short-lived periods of stability that may reflect times when all group members were engaged in the same behaviour, such as grazing or resting. Additionally, it was indicated that there were certain individuals who were more popular than others in both groups, although this effect was more evident in group 1. Reinhardt and Reinhardt (1981) found that the most popular cow in the herd was also the predominant leader of movement. Other studies, however, have found more than one individual to be responsible for group movement (e.g. Beilharz and Mylrea, 1963). In a study on the determinants of group movement, Ramseyer et al. (2009) reported that amongst a group of 15 heifers, most grazing bouts were initiated by one of three individuals. Thus, in the current study there may have been more than one specific individual per group that was responsible for initiating grazing and movement activities. Ramseyer et al. (2009) also found that leaders tended to be socially independent and displayed less cohesive social properties. In this sense, steers with highly negative animal effects may be more responsible for group movement than highly sociable steers with positive animal effects. Further investigation is required to correlate the results of the individual animal parameters with social roles, such as leadership.

The lack of daily patterns was surprising, as cattle on pasture are reported to display diurnal activity patterns, with grazing and moving activities generally performed in the early morning and late afternoon (O'Connell et al., 1989). Although, Lewis (1977) reports that the number of grazing bouts can vary between two and ten bouts per day. Additionally, daily activity can also vary depending on the ambient temperature (Lewis, 1977) and also on the season (e.g. Howery et al., 1998), thus the encounter patterns recorded within the groups may reflect variation in behavioural activity according to the physical environment.

The overall weekly results revealed that pair events were likely to be repeated, thus reinforcing the strong dyadic effect and existence of preferential relationships. There was an overall tendency for triangle events in group 1 and string events in group 2 to be of a different configuration to that of the past: these effects are opposite to that recorded in the short term. This effect shows that there is general interaction among all group members when encounters involved more than two animals. This behavioural pattern may be observed when the group collectively changes activity, for example, when the group ceases resting together to spread out and graze.

Overall there were some differences between the two groups, in particular were the differences in triadic configurations and individual animal effects. As the relational event model is a novel approach to investigate animal's social systems, the extent to which the two groups represent cattle systems in general is unknown and further work is required to develop the methodology for wider application and also apply the model on a substantial range of animal groups. It is therefore difficult to generalise the reasons behind the differences between the two groups, however, it is possible to speculate that differences in genetics, such as breed, as well as management factors, such as re-grouping experience, may contribute to differences in social organisation.

9.6. Conclusions

The relational event model identified specific endogenous properties of a stable cattle social system. It was shown that pair-wise encounters are important for group cohesion and suggestive of preferential relationships within the group. Although triadic encounters were not as influential as predicted, the pattern of the same triadic encounters being repeated in the short term demonstrates stability: group 1 had a greater tendency to repeat triangle events while string events were a greater feature for group 2. Both encounter patterns indicate cohesion. There was large variation in individual animal activity, which may relate to sociability levels and social roles. The model identified both short-term and longer term behavioural patterns that represent typical animal movement where individuals group together for certain periods and spread out during others. This investigation demonstrates that the relational event model can be used to identify inherent features of cattle groups based on patterns of close proximity encounters.

Chapter 10

General discussion

The overall aim of the thesis was to investigate the effect of the presence of an unfamiliar steer on the social behaviour of resident steers. In contrast to previous mixing studies that have focused on agonistic behaviours within commercial sized groups (e.g. Hasegawa et al., 1997; von Keyserlingk et al., 2008), the focus of the current studies targeted the affiliative behaviours responsible for group cohesion. The underlying social properties involved in relationship development in steers were investigated using dyads and triads of steers as the fundamental components of social structure. It was anticipated that the social properties of dyads and triads could be used to describe social processes that occur within larger groups. Overall, the findings show that behavioural responses towards an unfamiliar are various and depend on the social context. The findings from each of the experimental chapters are now discussed.

The general differences between the behavioural response of a steers towards a familiar and an unfamiliar peer showed that there are various benefits of being familiar. Different levels of social support were identified based on the social and physical environment. During the trade-off test, steers paired with familiar pen mates were more willing to consume food at greater distances than steers paired with unfamiliar pen mates. In the pairs monitoring study, familiar pairs had more close proximity encounters, moved towards each other more and tended to spend more time lying and standing than unfamiliar pairs. These behaviours could be considered characteristics of a well established relationship. It is concluded that the presence of a familiar peer provides social support that allows individuals to express their own feeding and resting choices. When an unfamiliar steer was introduced into a pair of familiar steers, it was found that the existing relationship between the familiar pair strengthened due to the presence of the unfamiliar steer and there was little evidence to suggest relationships were developing in the triad. The modelling approach used in Chapter 8 allowed a greater investigation of simultaneous encounter patterns between the three steers, where it was shown that the strong and consistent unfamiliarity and dyadic effects explained why the unfamiliar steer was not integrated into the triad within 5 days. It is suggested that the familiar pair resisted the unfamiliar steer's attempts to develop a relationship. The results demonstrate that established dyadic relationships translate into predicable and regular encounter patterns, which promotes relationship stability and group forming behaviours. It is therefore concluded that the social support provided by a familiar peer allows individuals to cope with unstable social environments. These findings build on existing knowledge that the presence of a familiar peer provides a calming effect in stressful situations (e.g. Boissy and LeNeindre, 1997; Faerevik et al., 2006).

The behavioural differences between familiar and unfamiliar pairs were used to assess the effect of the presence of an unfamiliar steer under different environmental settings. The pair-wise experiments evaluated the individual responses of steers when paired with either familiar or unfamiliar peers. The trade-off test showed that the actual trade-off made by the steers when paired with an unfamiliar pen mate went beyond a desire for food or social companionship but was instead related to social insecurity. The pairs monitoring experiment showed that initially the unfamiliar pairs avoided each other. The reasons for the behavioural differences between familiar and unfamiliar treatments were varied, however, it was suggested that the presence of an unfamiliar steer as well as isolation from familiar group mates elicited a stress response that modified the steer's behaviour. Various environmental factors can contribute to the social stress associated with introducing new individuals, such as the loss of social support from familiar group members, a change in group size as well as the possibility of experiencing an unfamiliar environment (Zayan and Dantzer, 1990; Newberry and Swanson, 2001). It is possible to quantify the contribution of unfamiliarity on the social stress experienced when mixing unfamiliar animals by comparing the behavioural responses towards both familiar and unfamiliar peers under identical circumstances (Zayan, 1990). The studies described in Chapter 5 and 6 showed that differences were recorded between the familiar and unfamiliar treatments, although the sudden isolation from familiar group members may have contributed to the social stress experienced by both familiar and unfamiliar treatments. However, when triadic based outcomes were quantified in Chapter 7 it was shown that the presence of an unfamiliar elicits a behavioural response, even when familiar peers are present. It is therefore concluded that the presence of an unfamiliar steer creates social stress, which was demonstrated by a reluctance of steers to travel away from the unfamiliar animal to consume food, avoidance behaviour and an increase in contact frequency between familiar peers. Further work is suggested in the following areas:

- Investigation of the encounter patterns of three familiar steers. The current triad experiment only investigated one familiarity combination: two familiar pairs with one unfamiliar steer. The behaviour and encounter patterns of familiar triads could be compared with the current results to determine if steers in such a small group size were experiencing social stress caused by isolation from a larger group.
- Measure the physiological response towards an unfamiliar steer in combination with proximity logging devices. The data from the proximity loggers gives no indication of the nature of the encounter quality, however there is an established link between blood cortisol levels, heart rate and stress (e.g. Sato and Tarumizu, 1993; Bristow and Holmes, 2007). Future studies should consider correlating encounter characteristics (frequency, duration) with physiological responses to determine if certain encounters lead to increased stress responses, such as the presence of an unfamiliar or an agonistic interaction. This approach also has the potential to differentiate between affiliative and agonistic interactions.

When the steer's behavioural response toward an unfamiliar peer was monitored in a paddock-based environment allowing the steers to interact and develop relationships, it was found that that the process of familiarisation was complex and various social processes were involved as relationships developed. Initially the unfamiliar pairs avoided each other but changes in inter-individual distance and movement indicated that familiarisation was occurring between the pair. The results prove that factors other than dominance are involved in the familiarisation process and affiliative behaviours, such as close proximity encounters, spatial proximity and movement patterns, are important in the establishment and maintenance of social relationships between steers. The use of movement vectors provided a novel observational tool to record individual movement patterns and differences between familiar and unfamiliar social encounters were identified. It was demonstrated that the repeated pattern of movement both towards and away from each other was an important component of familiarisation between steers: this behaviour facilitates learning, recognition and communication, each of which are fundamental components of a relationship. However, due to a lack of knowledge on the distance perception and depth perception of cattle vision (e.g. Arnold et al., 2007), it was not possible to identify the point at which the steers were behaving either dependently or independently of each other. It is assumed that the behavioural synchrony of two steers is influenced by the distance between them, but not enough is known about the spatial acuity of cattle to draw definitive conclusions between proximity and movement. Further work is warranted in this area.

It was anticipated that familiarisation would be accelerated in small groups as there would be fewer relationships to establish and less interference from other group members. However, it was not expected that there would be such contrasting differences in the encounter patterns between pairs and triads. The results showed evidence of familiarisation between pairs within 5 days, yet marked differences in both the frequency and duration of encounters between familiar and unfamiliar steers in the triads provide little evidence to demonstrate familiarisation within the triad. It is therefore suggested that structural differences exist between dyads and triads of steers and as a result social stabilisation will take longer between triads than pairs of steers. In human social systems, the addition of a third individual can be detrimental to group unity if two individuals join forces to gain power over the third (Feinman and Lewis, 1984). Thus, it is suggested that the familiar pair formed a majority which led to the exclusion of the unfamiliar steer.

The relational event model provided a novel approach to investigate the encounter patterns of pairs and triads of steers when an unfamiliar steer was introduced, and to also identify the structural properties of a stable social system. It was shown that paired encounters were indeed a strong feature of the social system, with evidence of preferential relationships as well as sociability and possibly popularity. There was a tendency for individuals to form triadic encounters with the same individuals when engaging in short term activities, such as grazing or resting, while the overall weekly patterns indicated that there was interaction among group members with different partners, which may indicate grouping and breaking apart at certain times, such as a change in activity from resting to grazing. The model identified both short-term and longer-term behavioural patterns that represent typical animal activity. It was concluded that the relational event model can be used to identify inherent features of cattle groups based on patterns of close proximity encounters.

The encounter patterns observed within a stable system can be used as a comparative tool to identify periods of instability and quantify the extent of the disruption: knowing normal animal behaviour is a prerequisite for recognising abnormal behaviour (Broom and Fraser, 2007). The main encounter differences between triads and groups of steers were seen on the day of introduction. After day 1 the triads showed a stabilising trend similar to that observed in the groups encounter structures, although only the encounter patterns between the familiar pair were stabilising and longer time was needed for the integration of the unfamiliar steer. This result demonstrates that the familiar pair recovered quickly from the social disruption caused by the unfamiliar steers introduction and suggests that cattle relationships are flexible, which allows them to respond and adapt to change. Further applications of this work could include:

- Introducing unfamiliar animals into group sizes of four, five and six animals to investigate if there are differences in the rate of integration of an unfamiliar. Knowledge on the social properties of small group sizes has the potential to advance knowledge on bovine social structure as well as improve management practices.
- Using the encounter patterns of a stable social system to measure the impact of other sources of social disruption. For example, a change in location such as cattle handling facilities or introduction to a new paddock, the presence of a predator such as a wild dog, or the illness or removal of a group member. The relational event model can also be applied to other contact animal species to investigate the social properties of a system or process.
- Developing the current relational event model to include both onset and offset events in the one framework. The current model only considered the initiation of encounters between steers, and while familiarity was shown as a predominant driver of social interaction, the breakdown of social structures was not investigated. Currently it is not known what factors lead to animals spreading out during periods of stability or social disruption.

Proximity logging devices have not been extensively used to monitor the social interactions of domestic livestock, or more specifically, to quantify individual social relationships. The encounter differences recorded between familiar and unfamiliar steers suggests there is a relationship between familiarity and close proximity encounters. More compellingly, the relational event model identified that individuals with well developed social bonds were more likely to approach each other at closer distances: the pattern of encounters in the past were repeated between the same individuals in the future, signifying a relationship between the pair. It is proposed that regularity in close proximity encounters are an underlying behavioural component of an established social relationship, which may be used as a comparative tool to indicate familiarisation between cattle and other social animals. In the current studies, unfamiliarity was used as a contrast to compare the behavioural characteristics of a familiar and unfamiliar social relationship. It was shown that proximity logging devices captured the social differences between familiarity types, and thus it is concluded that proximity loggers are capable of quantifying social relationships in cattle.

The behavioural responses of the same individuals were repeatedly measured over a series of discrete experiments, thus it is possible with suitably developed analytic techniques that individual animals could be analysed for their social tendencies or influence within the group. Quantifying individual 'personalities' was not a specific aim of the thesis but is something that could be undertaken in the future with this type of longitudinal data. Longitudinal studies are important to explore tendencies across populations and larger groups, which go beyond analyses that use averages to understand general trends. The development of analytical methods to quantitatively assess individual animal involvement with respect to the whole group was introduced in Chapters 8 and 9. Further development of analytical techniques to analyse real time interaction data and individual responses in the context of longitudinal data is a topic for future investigation.

In conclusion, this thesis investigated the effect of the presence of an unfamiliar steer on the social behaviour of resident steers. Behaviours that were affected by the presence of an unfamiliar peer were identified and the spatial and temporal changes that occurred during the initial stages of familiarisation between steers were described. The behavioural patterns that occurred during relationship development were discussed in relation to the evolution of social structure. The main conclusions drawn from the research are:

1. The presence of a familiar peer provides social support. This support allows individuals to express their own feeding and resting choices and provides reassurance in an unstable social environment.
2. The presence of an unfamiliar peer elicits social stress. The social stress created by the presence of an unfamiliar steer affected spatial proximity, behaviour, close proximity encounter patterns and movement.
3. Familiarisation between pairs was indicated by a decrease in spatial proximity and movement towards and away from each other.
4. Structural differences exist between dyads and triads of steers: the addition of a third party complicates and extends the process of relationship development.
5. Pairs of familiar steers will form a majority to exclude an unfamiliar steer.
6. Socially stable cattle groups display regular dyadic and triadic encounter structures in both the short-term and longer-term behavioural patterns.
7. Relational event modelling provides a novel predictive tool to identify and analyse the complex encounter structures of steers during periods of social disruption as well as social stability.

8. Proximity logging devices can be used to quantify social relationships in cattle and differentiate between the encounter patterns of familiar and unfamiliar steers.

Appendix A

Images from trade-off test experiment

Holding yard for penned steer

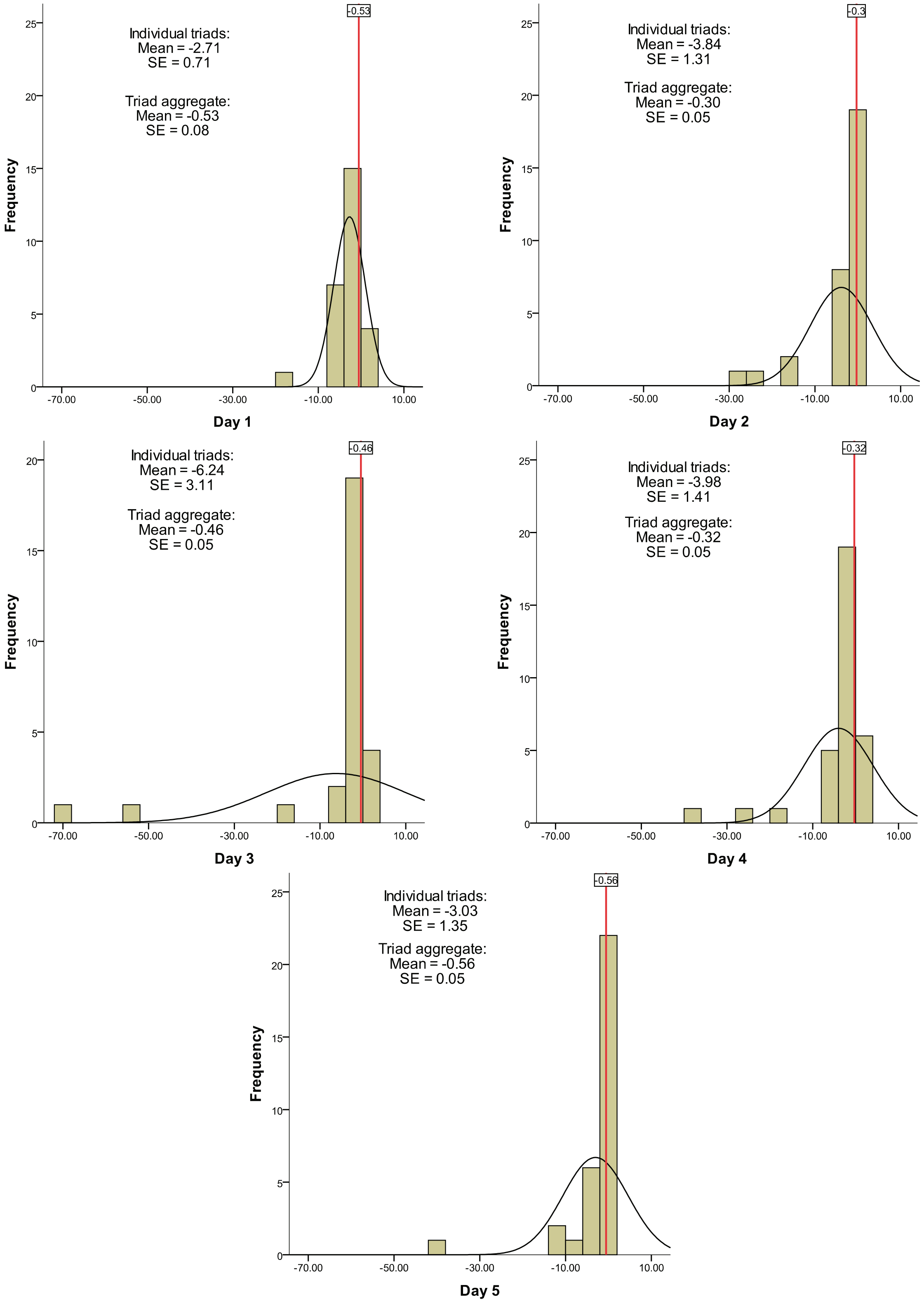
Test steer release yard

Test steer consuming food

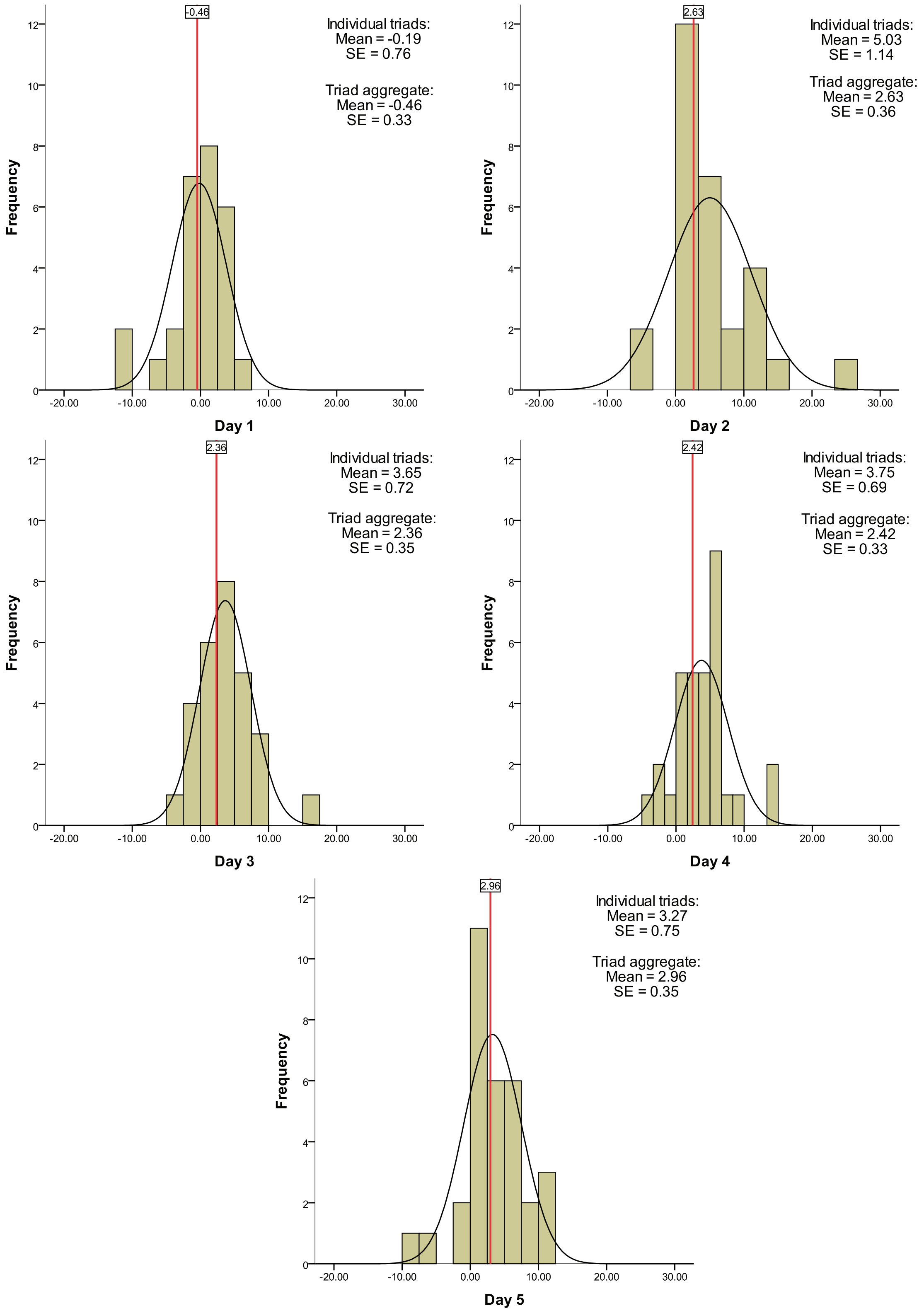
Appendix B

Validating assumptions

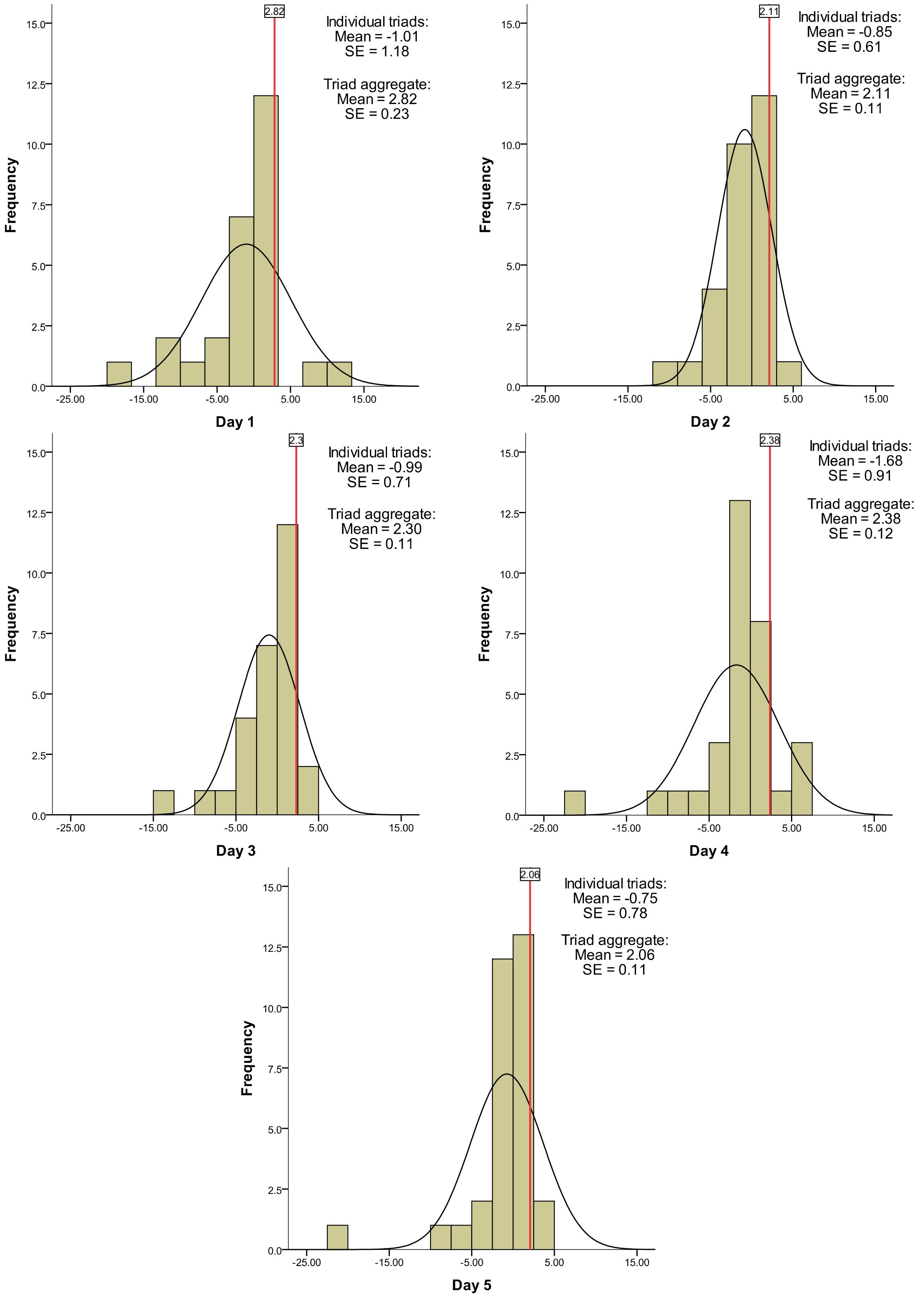
The frequency distributions of the parameter estimates obtained when a simplified version of the model was fitted to each triad separately are shown below. The model was fitted on a daily basis to obtain the parameter estimates for the effect of unfamiliarity and prior pair events in the past hour and past 24 hours. The same model was also fitted to the pooled data set. The placement of the parameter estimate from the pooled data set within the individual triad distribution was used to assess the validity of pooling the triad data in Chapter 8.



The distribution of the parameter estimate predicting the involvement of the unfamiliar animal in the current event for each of the 36 triads, with the placement of the parameter estimate of the aggregated data set shown as a red line.



The distribution of the parameter estimate predicting future pair events from pair events in the past hour for each of the 36 triads, with the placement of the parameter estimate of the aggregated data set shown as a red line.



The distribution of the parameter estimate predicting future pair events from pair events in the past 24 hours for each of the 36 triads, with the placement of the parameter estimate of the aggregated data set shown as a red line.

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