QUANTIFYING INTERACTIONS IN A HIGH-DENSITY BADGER (*MELES MELES*) POPULATION

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ABSTRACT

The frequency of interactions between animals, the duration of any interaction, where and when they occur, play a vital role in many aspects of a species' behavioural ecology. Interactions are important in social group formation and maintenance, in mating, in dispersal, in foraging and are fundamental to understanding infectious disease transmission. This study aims to quantify interactions between badgers in a high-density population at Woodchester Park in the south west of England.

The Eurasian badger (*Meles meles*) has been implicated as the main wildlife reservoir for Bovine tuberculosis (TB), therefore, understanding patterns of interactions between badgers will aid our understanding of how the disease is maintained, and spreads, within the badger population.

This study uses radio tracking to investigate the extent to which individual badgers utilise shared resources, both spatially and temporally. Analysis of patterns of space use reveals that badgers occupy distinct territories with little overlap of shared areas between social groups.

The application of novel proximity loggers to record direct interactions between badgers shows that badgers within social groups spend a large amount of time with each other. Badgers from different social groups do interact occasionally; most inter-group contacts are between badgers from neighbouring social groups. Inter-group contacts between non-neighbouring groups are rare.

Inter-group contact rates were highest in spring between males and females. This may be due to extra-group mating activities and may potentially reduce inbreeding in badger populations.

The study has demonstrated the usefulness of proximity loggers for studying interactions between free-living animals. The data recorded by the proximity loggers over long periods of time provide a unique insight into behavioural patterns of nocturnal free-living animals such as the badger. The proximity loggers have potential applications to aid our understanding of key processes in behavioural ecology.

CONTENTS

ABSTRACT 2

LIST OF TABLES 9

LIST OF FIGURES 11

ACKNOWLEDGEMENTS 13

AUTHORS DECLARATION 15

Chapter 1 Introduction 17

1.1 Interactions between animals 17

1.1.1 The role of interactions between group living animals and social group formation 17

1.1.2 The role of interactions between animals with respect to mating 18

1.1.3 The role of interactions between animals in dispersal mechanisms 18

1.1.4 The role of interactions between animals with respect to foraging 18

1.1.5 The role of interactions between animals in the spread of disease 19

1.2 Existing approaches to studying direct interactions in animals 19

1.2.1 The use of proximity loggers to study direct interactions between animals 21

1.3 Importance of understanding interactions in badgers 21

1.3.1 Badger ecology 22

1.3.2 Bovine tuberculosis 23

1.3.2.1 The role of badgers in the transmission of TB 24

1.3.2.2 The role of interactions between badgers in the transmission of TB 25

1.4 Thesis aims 26

1.5 The Woodchester Park badger population 26

1.6 Thesis structure 27

Chapter 2 General Methods 28

2.1 Introduction 28

2.2 Chapter aims 28
2.3 Study site 28
2.4 Methods 30
2.4.1 Territory delineation 30
2.4.2 Badger trapping 30
2.4.3 Badger sampling 31
2.4.4 Social group allocation 38
2.4.5 Proximity logger collar information 40
2.4.5.1 Proximity logger data recovery 41
2.4.5.2 Collar fitting 42
2.4.5.3 Radio tracking 42
Chapter 3 Investigation into sources of error that affect accurate recording of animal locations by radio tracking 45
3.1 Introduction 45
3.1.1 Radio tracking 45
3.1.1.1 Radio tracking in the study of badgers 45
3.1.1.2 Existing radio tracking methods 46
3.1.1.3 Accuracy of radio tracking 47
3.1.2 Sources of error 48
3.1.2.1 Error arising from using a VHF radio tracking system 48
3.1.2.2 Error arising from using a GPS system 50
3.1.3 Reporting of error 51
3.1.3.1 Measurement of error 52
3.2 Chapter aims 53
3.3 Methods 54
3.3.1 GPS precision 54
3.3.1.1 Study design and analysis 54
3.3.2 Radio tracking accuracy 55
3.3.2.1 Study design and analysis 55
3.3.3 Travel distance and home range size error 57
3.4 Results 58
3.4.1 GPS precision 58
3.4.2 Radio tracking accuracy 59
3.4.2.1 Bearing error 59

3.4.2.2 Distance Error 60
3.4.2.3 Linear Error 61
3.4.3 Travel distance and home range size error 65
3.5 Discussion 67
3.5.1 GPS precision 67
3.5.2 Radio tracking accuracy 68
3.5.2.1 Bearing error 68
3.5.2.2 Distance error 68
3.5.2.3 Linear error 69
3.5.2.4 Travel distance and home range size error 71
3.5.3 Implications 72
Chapter 4 Home range analysis and space use behaviour of badgers determined from radio tracking data 73
4.1 Introduction 73
4.1.1 What is a home range? 73
4.1.2 Home range estimators 74
4.1.2.1 Accounting for telemetry error in home range estimates 76
4.1.3 Core areas 77
4.1.4 Static Interactions 78
4.1.5 Dynamic Interactions 78
4.2 Chapter aims 80
4.3 Methods 81
4.3.1 Data collection 81
4.3.2 Incorporating error associated with radio tracking 81
4.3.3 Home Range Analysis 82
4.3.4 Core area analysis 83
4.3.5 Static interaction analysis 83
4.3.6 Dynamic interaction analysis 84
4.4 Results 85
4.4.1 Home range sizes 85
4.4.2 Core area sizes 92
4.4.3 Static Interaction 98
4.4.4 Dynamic Interaction 99
4.5 Discussion 103

4.5.1 Summary 107
Chapter 5 Consistency and reliability of proximity loggers under laboratory and field conditions 108
5.1 Introduction 108
5.1.1 Importance of understanding contacts in animals 108
5.1.2 Existing methods for quantifying contacts 108
5.1.3 The advantage of using proximity loggers to study contacts between animals 110
5.1.3.1 The advantage of using proximity loggers specifically to study contacts between badgers 110
5.1.3.2 Previous studies using proximity loggers to study contacts between animals 111
5.2 Chapter aims 112
5.3 Methods 113
5.3.1 Investigating the accuracy of the collars in a controlled environment 113
5.3.2 Field study methods 114
5.3.2.1 Validating the consistency and accuracy of collars returned from the field 114
5.4 Results 116
5.4.1 Investigating the accuracy of the collars in a controlled environment 116
5.4.2 Validating the consistency and accuracy of the collars returned from the field 119
5.4.2.1 Downloading data and functioning of the collars 119
5.4.2.2 Corrupt contacts 120
5.4.2.3 Collar battery life and clock time keeping 120
5.4.2.4 Removal of one-second contacts 121
5.4.2.5 Combining broken contacts 121
5.4.2.6 Removal of reciprocal contacts 122
5.5 Discussion 127
5.5.1 Summary 129
Chapter 6 Quantifying contacts between badgers in a high-density badger population 130

6.1 Introduction 130
6.1.1 What constitutes a contact? 130
6.1.2 Importance of understanding contacts in animals 130
6.1.3 Importance of understanding contacts in badgers 131
6.1.4 Models of disease in badgers 131
6.1.4.1 TB models 132
6.1.4.2 Rabies models 134
6.1.4.3 Summary regarding models of diseases in badgers with reference to contact rates 134
6.1.5 Movements of badgers 134
6.1.5.1 Movement of badgers with respect to TB 136
6.2 Chapter aims 137
6.3 Methods 138
6.3.1 Frequency of contacts 138
6.3.2 Contact rate and contact duration 138
6.3.2.1 Statistical analysis 139
6.3.3 Badger 37R as a case study 139
6.3.4 Time of day contacts occurred 140
6.3.5 Locations of contacts 140
6.3.6 Contact probabilities 140
6.4 Results 141
6.4.1 Overview of data collected 141
6.4.2 Intra-group contacts 144
6.4.2.1 Frequency of contacts 144
6.4.2.2 Contact rate and contact duration 145
6.4.3 Inter-group contacts 149
6.4.3.1 Frequency of contacts 149
6.4.3.2 Potential for contacts 150
6.4.3.3 Contact rates and contact duration 151
6.4.4 Badger 37R case study 156
6.4.5 Time of day that contacts occur 164
6.4.6 Locations of contacts 166
6.4.7 Contact probabilities 170
6.5 Discussion 172

6.5.1 Summary 178
Chapter 7 Discussion 179
7.1 Summary of thesis aims and results 179
7.2 Summary of methods used to study interactions in this thesis ... 182
7.3 Implications 184
7.4 Further applications 185
References 187

LIST OF TABLES

Table 2.1. Trapping history details for all badgers fitted with proximity logger collars at Woodchester Park. 37

Table 2.2. Minimum number of animals present in each social group used in this study at Woodchester Park.. 39

Table 2.3. Summary data showing details of badgers used in this study. 44

Table 3.1. Values of Linear Error (in meters) at different estimated distances for experienced and inexperienced people based on the GLS model predictions. 65

Table 3.2. Mean total distance travelled and mean 100% MCP area for each group 65

Table 4.1. Number of location fixes collected for different badgers between Autumn 2004 and Summer 2005. 86

Table 4.2. Home range size estimated by both MCP and 95% kernel estimates for each badger that had an asymptotic home range for that season 87

Table 4.3. Summary mean home range sizes (±SEM) estimated by both 100% MCP and 95% kernel methods for different badger categories 87

Table 4.4. Core area estimates for badger home ranges that had reached an asymptote for that season 93

Table 4.5. Summary mean core range sizes (±SEM) estimated using the 70% kernel for different badger categories 93

Table 4.6. The potential for, and realised numbers of overlaps between badger dyads, and the proportion of overlap estimated using both 95% and 70% core kernel home range estimates. 98

Table 4.7. Mean proportion overlaps between different badger dyads estimated using both the 95% kernel and 70% core kernel home range estimate.. 99

Table 4.8. Mean intra-group separation distances between different badger dyad categories 101

Table 4.9. Mean inter-group separation distances between different badger dyad categories. 101

Table 4.10. Cumulative proportion of frequencies of separation distances within specified distances for badgers belonging to the same social group. 102

Table 4.11. Cumulative proportion of frequencies of separation distances within specified distances for badgers from neighbouring social groups..... 102
Table 5.1. Example data downloaded from each collar..... 115
Table 5.2. Mean initiation and termination distances for new and old versions of proximity collars at different UHF settings 117
Table 5.3. Agreement between reciprocal pairs of collars for the original data and the adjusted data (one-second contacts removed and contacts from the same badger occurring less than 21 seconds apart combined) 125
Table 5.4. Summary of data collected at each download event and how the different processes applied to the data affects the overall number and duration of contacts..... 126
Table 6.1. Overview of which badgers were fitted with proximity loggers and how long for..... 143
Table 6.2. Mean daily contact rates and contact durations for pairs of badgers contacting each other belonging to the same social group 147
Table 6.3. Linear mixed-effects model for differences in the intra-group daily contact rate and intra-group daily contact duration 148
Table 6.4. Numbers of pairs of badgers that made contact between social groups, and the total number of pairs that had the potential to make contact between social groups 150
Table 6.5. Mean daily contact rates and contact durations for pairs of badgers belonging to neighbouring social groups..... 154
Table 6.6. Linear mixed-effects model for differences in inter-group daily contact rate and inter-group daily contact duration 155
Table 6.7. Daily contact probabilities found from this study compared to those reported by Smith and Wilkinson (2002; "S&W"), and those found in Dalby forest (Newton-Cross (2003); "Dalby") 171

LIST OF FIGURES

Figure 2.1. Bait marking results from Spring 2005 32

Figure 2.2. Social group boundaries, with social groups used in this study highlighted 33

Figure 3.1. Diagrammatic representation of the calculation of Linear Error. 57

Figure 3.2. (A - left). 95% confidence ellipse for site 1: open habitat. (B - right). 95% confidence ellipse for site 2: wooded habitat 58

Figure 3.3. Mean displacement distances for site 1 (open habitat) (red) and site 2 (wooded habitat) (blue) over time. 59

Figure 3.4. Frequency histogram of bearing errors 60

Figure 3.5. Box and whisker plot of distance error 61

Figure 3.6. Frequency histogram of Linear Error 62

Figure 3.7. Box and whisker plot of Linear Error 63

Figure 3.8. Values of Linear Error (in meters) at different estimated distances for experienced and inexperienced people based on the GLS model predictions. 64

Figure 3.9. An example of a route obtained from one person during one two-hour session..... 66

Figure 3.10. An example of a 100% MCP obtained from one person during one two-hour session based on the route shown in Figure 3.9 66

Figure 4.1. Diagrammatic representation of 100% MCP and 95% kernel estimates for all badgers whose home range had reached an asymptote for Autumn 88

Figure 4.2. Diagrammatic representation of 100% MCP and 95% kernel estimates for all badgers whose home range had reached an asymptote for Winter.. 89

Figure 4.3. Diagrammatic representation of 100% MCP and 95% kernel estimates for all badgers whose home range had reached an asymptote for Spring..... 90

Figure 4.4. Diagrammatic representation of 100% MCP and 95% kernel estimates for all badgers whose home range had reached an asymptote for Summer..... 91

Figure 4.5. Diagrammatic representation of 70% kernel core area estimates for all badgers whose home range had reached an asymptote for Autumn..... 94
Figure 4.6. Diagrammatic representation of 70% kernel core area estimates for all badgers whose home range had reached an asymptote for Winter..... 95
Figure 4.7. Diagrammatic representation of 70% kernel core area estimates for all badgers whose home range had reached an asymptote for Spring 96
Figure 4.8. Diagrammatic representation of 70% kernel core area estimates for all badgers whose home range had reached an asymptote for Summer 97
Figure 5.1. Example data obtained from the termination experiment with version 1 of the proximity collars (set to UHF31). 118
Figure 5.2. Example data obtained from the termination experiment with version 2 of the proximity collars (set to UHF45). 118
Figure 6.1. Correlation between average daily contact rate and average daily contact duration between badger pairs belonging to the same social group. 146
Figure 6.2. Correlation between average daily contact rate and average daily contact duration between badger pairs belonging to neighbouring social groups..... 151
Figure 6.3. Contact pattern time-line for badger 37R over the period she wore a proximity collar..... 159
Figure 6.4. Annotated contact pattern time-line for badger 37R.....160
Figure 6.5. Monthly time of day (on a 24-hour scale) badger 37R contacts other badgers 161
Figure 6.6. Average proportions of contacts showing the time of day during which contacts occurred..... 165
Figure 6.7. Locations of contacts recorded between three badgers belonging to the Beech social group (13G, 18G and J87), and two badgers belonging to the Septic Tank social group (19G and U51) on five nights in Autumn 2004. 168
Figure 6.8. Locations of contacts recorded between two badgers (32R and H43) belonging to the Wych Elm social group on one night in winter. 169

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AUTHORS DECLARATION

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Emily Louisa Goodman

DEDICATION

To my parents and to Ally

Chapter 1 Introduction

1.1 Interactions between animals

Interactions between animals play a vital role in many species' behavioural ecology. Interactions are important in the spatial and social structure of the population, in mating, dispersal, foraging and social group behaviour. Interactions also provide opportunities for the transmission of other organisms that live in association with a population, such as infectious agents. The contact patterns of a population are therefore important not only for the integrity of the social structure of that population itself, but also for the population dynamics of any associated infectious diseases.

1.1.1 The role of interactions between group living animals and social group formation

It is thought that group living evolves under certain conditions, namely when the benefits to individuals in terms of lifetime reproductive success outweigh the costs of living in a group, or, if this is not the case, the costs outweigh the benefits but there are ecological constraints on dispersal from the natal territory (Gittleman 1989). Once group living has evolved, it is thought selective pressures will encourage greater sociality through associated benefits such as alloparental behaviour (Baker et al. 1998), boundary surveillance, territory defence of food resources from neighbouring groups (Gittleman 1989), maintenance of the breeding environment and increased reproductive access to group members (Wrangam 1986), predator avoidance, and inheritance of the territory (Kruuk and Macdonald 1985, Lindstrom 1989). This requires interactions between animals within the group, either directly or indirectly, and the maintenance of a territorial system requires interactions between members of the same and different groups. Interactions between members of the same social group are predominantly positive and reinforce social cohesion. They may also enable rapid and effective transfer of information between animals such as the location of food, and animals may therefore modify their movement patterns in order to bring about intra-group encounters (White and Harris 1994). Interactions between members of different social groups are mainly negative. Conflicts with neighbours may be costly (Parker 1974), and avoidance of inter-group encounters are expected (White and Harris 1994).

1.1.2 The role of interactions between animals with respect to mating

Populations may employ different mating systems, and the description of pair bonding and the competition for such bonds help to understand the particular mating system (Clutton-Brock 1989), the spacing of one or both sexes in a population may be a response to the distribution of the other sex, in order to maximise interactions that can lead to mating opportunities (Minta 1993, Gehrt and Fritzell 1999). Mating provides opportunities for the horizontal transmission of genes and in order for most species to successfully mate, they have to interact.

1.1.3 The role of interactions between animals in dispersal mechanisms

The mechanisms influencing dispersal behaviour in animals is unclear, but two hypothesis for dispersal point to social contacts being of primary importance. The social subordination hypothesis (Christian 1970), suggests a direct causative link between increasing aggression from dominant animals and the dispersal of subdominants. The social cohesion hypothesis (Beckoff 1977), however, proposes that the level of affiliative behaviour received by an animal very early in life determines its subsequent dispersal behaviour. For example, Harris and White (1992), showed that fox cubs that received more grooming early in life from their littermates were less likely to disperse the following autumn. Both of these hypothesis require some degree of interaction between animals.

1.1.4 The role of interactions between animals with respect to foraging

Interactions between animals may allow the transfer of information between individuals such as the location of food resources (White and Harris 1994, Klaassen et al. 2006), or the locations of over-exploited food patches potentially to be avoided (Beauchamp 2005). Interactions may aid cooperative foraging (Blundell et al. 2002), enabling food resources to be exploited that individuals would not be able to otherwise exploit without some form of interaction and cooperation. Conversely, interactions between animals may be aggressive in nature (Totton et al. 2002), deterring other animals from accessing a food resource (Grenier et al. 1999), and ensuring exclusivity to certain individuals.

1.1.5 The role of interactions between animals in the spread of disease

For directly transmitted wildlife diseases, the rate at which new infections occur in a population, or the rate at which an existing infection spreads through the population, is a product of the contact rate; the proportion of these contacts that are with susceptible individuals and the proportion of these contacts that result in infection (McCallum et al. 2001). The number of contacts between individuals is, therefore, the rate determining step in the spread of directly transmitted diseases (White and Harris 1995b). Despite interactions between animals being fundamental to infectious disease transmission (McCallum et al. 2001, Lloyd-Smith et al. 2005), relatively little is known about them, primarily because they are difficult to study.

1.2 Existing approaches to studying direct interactions in animals

The simplest method of observing interactions between animals is by direct observation of individuals. Direct observations are possible for species that are easy to observe, e.g. species that are large (Schneeberger and Jansen 2006) or that occupy open habitats (Schaller 1972), or species that habituate quickly to observers (Rood 1989). Where it is not possible to observe species in the wild, animals in captivity can be observed (Macdonald 1996, Day et al. 2000). However, captive animals often show abnormal behaviour which is not necessarily representative of wild behaviour (Lambrechts et al. 1999). Short-term direct observations may be possible for some species, for example, where a species may aggregate at a feeding site, be it natural (Cote 2000) or artificial (Totton et al. 2002). However, these results may be biased as they only provide a snapshot of activity, and if, for example, a highly concentrated feeding site is supplied, unusual behaviours may be exhibited.

Radio-telemetry has been used to investigate contacts between individuals, either to take observers to the locations of species where they can then be observed directly (Baker and Harris 2000), or by simultaneously radio tracking several individuals and recording their locations with respect to each other (White and Harris 1994, White et al. 1995). Radio tracking has a certain level of error associated with position estimates of individuals (Kauhala and Tiilikainen 2002, Moser and Garton 2007), and is very labour intensive. It is also usually only carried out for short periods of time and thus provides only a snapshot of the species' behaviour.

Passive integrated transponder (PIT) tags have been used in automatic acquisition systems to monitor individuals' proximity to certain structures or certain areas (Prentice et al. 1990, Rogers et al. 2002, Sutherland and Singleton 2003). However, they require high-powered readers for close range and so cannot be attached to small or medium-sized animals to investigate individual to individual contacts (Gibbons and Andrews 2004). Micro data-loggers have been used in biomedical and physiological telemetry applications, e.g. body temperature loggers (Woakes 1992) and depth recorders for sea mammals (Bodkin et al. 2007). However, they are not able to detect contacts between individuals or again, are too large for attachment to smaller species.

The MateID system is the forerunner to proximity loggers; one collar contains a VHF transmitter whilst another collar contains a low-power wideband VHF receiving device and data-logger (Ji et al. 1999, Douglas et al. 2006). Collars are attached to individuals; usually a subset of the population or one gender wears one type of collar whilst another subset or gender wears the other type. Contacts can be estimated between the two groups wearing the collars, but not within the groups.

With the recent advances in technology, the use of global positioning system (GPS) collars is becoming more common. Collars fitted to individuals can be programmed to either record their location onto the collar, or relay the information to a satellite that can then be transmitted to a computer or mobile phone. Collars can be programmed to transmit locations at certain time intervals or to keep trying to transmit a fix until it has been successful. However, under certain conditions many fix attempts are unsuccessful, e.g. up to <50% of fix attempts (Johnson et al. 2002, D'Eon 2003); factors such as vegetation cover and topography can introduce bias as they influence the success of the fix being obtained (Moen et al. 1996, Frair et al. 2004, Visscher 2006). When comparing locations between individuals in order to compare contacts, there is still a certain level of error associated with the location recorded and it is unlikely that locations are synchronous between individuals. GPS collars have been used successfully to investigate contacts in deer (Schauber et al. 2007), but their large cost, relatively large size and weight and the fact they are not suitable for all species, e.g. species that live in unsuitable habitat or topographical conditions, means that their use is limited.

Genetic techniques have been used to determine relatedness between animals, brought about through successful mating and the production of offspring (Evans et al. 1989, Domingo-Roura et al. 2003). However, DNA techniques can only determine when an

interaction has occurred that has resulted in a successful mating (Carpenter et al. 2005); unsuccessful matings and non-sexual contacts cannot be detected.

Finally, where contact rates have been used as a parameter in disease models, they have been estimated by experts in the field as best guesses (Smith and Wilkinson 2002), or derived from other model parameters (White and Harris 1995b).

1.2.1 The use of proximity loggers to study direct interactions between animals

A novel data-logging device has been developed by Sirtrack Ltd. (Havelock, New Zealand) that enables interactions to be studied between individuals fitted with the device. The logger records when other loggers are in close proximity to it, and the date, time, identity and duration of the other device in proximity is logged. Data are stored on the device, so the logger needs to be retrieved to obtain the data. Data-loggers, (henceforth referred to as proximity loggers) can be fitted to a wide range of species and enable accurate and reliable quantification of interactions. Data is collected remotely and continuously as and when contacts occur, without the need for constant human monitoring. This means the individual is relatively undisturbed and is more likely to behave in a natural way.

1.3 Importance of understanding interactions in badgers

The Eurasian badger shows a complex social system, from living solitarily to living socially in groups. The badger is a generally well-studied species, but their contact behaviour is still largely unknown. Badgers are nocturnal and secretive, so studying direct interactions between badgers is difficult. Studying interactions between badgers is particularly important, because in the UK, badgers are thought to be the main wildlife host for bovine tuberculosis (Krebs 1997). Studying interactions in badgers enables the development of novel techniques, and the knowledge gained from badger contact behaviour can be applied to other wildlife species.

This thesis is concerned mainly with direct interactions between badgers rather than indirect interactions. Less is known about direct interactions because of the difficulty in studying them as described above. In contrast, indirect interactions, where badgers can be separated spatially or temporally but transmit information to other badgers through the use

of scent marks, are relatively well studied. Indirect interactions are generally more visible and longer lasting than direct interactions; for example, badgers regularly deposit scent marks and excretory products at specific and predictable latrine sites (Neal and Cheeseman 1996).

1.3.1 Badger ecology

The Eurasian badger is a member of the Mustelidae (weasel) family, which belongs to the Carnivora order. Eurasian badgers (*Meles meles*) occupy a wide geographic range; they are widespread throughout the UK and also occur all over temperate Eurasia (Griffiths and Thomas 1993). Badgers are highly adaptable to a variety of habitats, from woodland, moorland, sea cliffs and mountainous country in Britain, to coastal lakes and sand dunes in other parts of Eurasia (Neal and Cheeseman 1996). Badgers can be found at a range of altitudes, from sea level to 3000 meters (Neal and Cheeseman 1996), although in Britain, most badgers are found at altitudes between 100 and 200 meters (Griffiths 1993).

Badger populations are thought to be either stable or increasing throughout much of Europe at present (Griffiths and Thomas 1993), although populations have come under many kinds of pressure over the last 100 years or so including from hunting, road traffic deaths and death from the rabies virus (Neal and Cheeseman 1996). The badger is a protected species in much of Europe, and in the UK is afforded protection by the Badgers Act in 1973, and the Protection of Badgers Act 1992.

Badgers show a variety of social structures, from the classical mustelid model of intra-sexual territoriality and inter-sexual overlap to very large, mixed-sex, mixed-age, distinct groups (Johnson et al. 2000). In Britain, badgers are generally group living with numbers in each social group ranging between 2 and 27 individuals (Rogers et al. 1997). Each social group actively defends a territory (Kruuk 1978) from members of other social groups, either directly by fighting and/or indirectly via scent marking at latrines located around the sett and at territory boundaries (Roper et al. 1993). Although badgers live in groups, they forage solitarily. Badgers are opportunistic feeders (Roper 1994) and will eat a variety of food types depending on their habitat and food available. The main dietary constituent in the British Isles is earthworms (*Lumbricus terrestris*), comprising up to 90% of their diet (Kruuk and Parish 1982), other prey items include insects, mammals, birds, amphibians, reptiles, cereals and fruit.

Within each social group badgers share one communal main sett (Cheeseman et al. 1987), the maintenance of one main sett is thought to help to reinforce social cohesion between group members, as interactions such as play, grooming, scent marking and allo-marking occur near to the main sett (Neal and Cheeseman 1996, Buesching et al. 2003. Buesching and Macdonald 2004). Badgers can, however, also occupy other setts away from the main sett, including annexe, subsidiary and outlier setts (see review by Thornton (1988) for definitions of sett types). This use of annexe and subsidiary setts may function to reduce the energetic costs of travelling to foraging areas in populations which occupy large territories (Kowalczyk et al. 2004), to avoid agnostic interactions with other members of their social group (Roper 1992), to reduce the accumulation of ectoparasites (Roper et al. 2001), or to serve as refuges for breeding females (Rogers et al. 2003). Outliers are often dug as temporary shelters (Rogers et al. 2003).

Interactions between badgers from neighbouring social groups as well as movements and dispersal between groups is though to be rare (Cheeseman et al. 1988a, Rogers et al. 1998) as movements between social groups may be risky for individual badgers because of the increased likelihood of aggressive encounters from other territory holders (Kruuk 1978). However, studies have shown that movements and dispersal can occur at low levels (Cheeseman et al. 1988a, Christian 1994, Woodroffe et al. 1995). Furthermore, recent genetic studies have shown extra-group matings to occur more frequently than previously thought, implying that interactions between male and female badgers from different social groups must occur (Carpenter et al. 2005).

1.3.2 Bovine tuberculosis

Mycobacterium bovis, the bacterium that causes bovine tuberculosis (TB), is infectious in both free-ranging and captive wildlife, and produces progressive disease in most domestic animals, especially those of economic importance (Amanfu 2006), it can also infect humans. TB occurs in many countries including Great Britain, Republic of Ireland, Northern Ireland, Italy, Spain, Africa and New Zealand.

In the UK, TB is one of the most complex animal health problems that the farming industry faces (Reynolds 2006); TB is particularly associated with cattle and the significant economic and animal welfare consequences of TB in cattle for the farming industry is of concern (Ministry of Agriculture 1971-1999). The cost of TB control is estimated to be in

the region of between £90,000 and £2.3 million, and is expected to increase (Cox et al. 1999).

1.3.2.1 The role of badgers in the transmission of TB

A TB infected badger was first found dead on a farm in Gloucestershire in 1971 where resident cattle were also infected (Muirhead and Gallagher 1974) and since then it is believed that badgers are the primary wildlife reservoir for the disease (Dunnet et al. 1986). Transmission from badgers to cows may be via direct contact, or indirectly via cattle encountering badger excreta. Direct contact between badgers and cattle in a field situation is unlikely because badgers have been shown to avoid cattle when they can (Benham and Broom 1989). Indirect contact of cattle with badger excreta can occur when cattle are at pasture or housed inside. Cattle investigating and/or ingesting the excreta of infectious badgers is believed to be the major route of transmission of TB from badgers to cattle (Hutchings and Harris 1997). Cattle are most likely to graze pasture away from badger latrines that may be infected by badger urine or faeces, however badger faeces excreted at latrines or at other linear features will be grazed once grass sward length in the rest of the field is reduced, and cattle with a low rank in the herd are more likely to graze these areas (Hutchings and Harris 1997). Badgers can also exploit farm resources and contaminate areas or resources that may then subsequently be used by cattle. Badgers have been shown to use cowsheds, feed sheds, barns, haystacks, slurry pits, cattle troughs and farmyards (Garnett et al. 2003). Badgers in the advanced stages of infection have been shown to behave abnormally in ways that could increase the likelihood of infection being transmitted to cattle or other badgers (Cheeseman and Mallinson 1981).

The prevalence of TB in badger populations has been found to be as high as 34.5% (Cheeseman et al. 1981), but is usually around 4% (Krebs 1997), and the prevalence has consistently been found to be greatest in Southwest England, with very few cases recorded in Scotland and the North and East of England (Cheeseman et al. 1989); this correlates well with the locations of herd breakdowns in cattle (Woodroffe et al. 2005b).

Because TB in cattle is of such economic concern, control measures have focussed on controlling TB in badgers. Various strategies for controlling cattle TB have involved lethal control of badgers in the vicinity of TB-affected cattle herds. However, to date these operations have been unsuccessful in reducing the incidence of TB in cattle or badgers

(Woodroffe et al. 2006b). One hypothesis to explain this is that culling causes social perturbation in badger populations. Culling alters their spatial organisation and their population density, and may result in increased immigration of badgers in to culled areas, disruption of territoriality, increased ranging and increased interactions between social groups, therefore increasing the rate of contacts between cattle and infected badgers, and between infected badgers and uninfected badgers (Woodroffe et al. 2006a, Carter et al. 2007). Understanding patterns of interactions between badgers will aid our understanding of the spread of disease, and improve model predictions of the disease (Smith and Cheeseman 2002), and aid in the efficiency of future control operations, such as culling (Smith et al. 2007), or vaccination (Delahay et al. 2003).

1.3.2.2 The role of interactions between badgers in the transmission of TB

Three routes of infection of TB between badgers have been suggested; vertical transmission between females and cubs, horizontal transmission via bite wounding, and indirect transmission from the inhalation of TB laden aerosols (Krebs 1997). All three routes require some degree of direct or indirect interaction between individuals.

Infection is highly localised in badger groups, with some social groups having no infection despit neighbouring territories having groups that are infected (Cheeseman et al. 1988b). This is reinforced by the fact that setts provide ideal conditions for protracted and repeated contact between infectious and susceptible group members, especially when sharing sleeping chambers (Neal and Cheeseman 1996). In addition, since badgers are social animals they frequently nuzzle and examine each other (Neal and Cheeseman 1996). Environmental conditions, (the relative humidity and ambient temperature) within setts also favour the survival of the bacteria (Moore and Roper 2003). These factors have led to the suggestion that transmission is much more likely to occur between members of the same social group, and that only limited transmission occurs between groups (Delahay et al. 2000b). However, movements between groups may enhance transmission by increasing the frequency of contacts between previously segregated individuals (Vicente et al. 2007). Movements may also increase the likelihood of aggressive encounters, including bite wounding (Delahay et al. 2006b), and may contribute to the development of the disease through the physiological stress of moving, resulting in reduced immunocompetence and increased susceptibility to infection (Clifton-Hadley et al. 1993).

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Badgers are also susceptible to other diseases such as rabies (Smith and Wilkinson 2002), Canine Distemper Disease (Hammer et al. 2004), mustelid herpes virus (King et al. 2004), and paratuberculosis (Beard et al. 2001), although very little research has focused on these compared to TB. However, badgers have been found to be infected with rabies on the Continent, and although there is currently no endemic rabies in the UK, if rabies was to enter the UK, badgers may be involved (Smith and Wilkinson 2002). Therefore, understanding the dynamics of the disease and how it may spread is important, and understanding interactions between badgers has direct implications for this.

1.4 Thesis aims

The underlying objective of this thesis was to obtain quantifiable data on direct interactions between badgers in a high-density population. Badgers are a relatively well-studied species, but little is known about their contact behaviour and patterns of interactions. The importance of contacts in spread of disease is often cited, yet few studies have attempted to quantify contacts directly, meaning there is a large gap of knowledge in this area. Recent developments in telemetric technology mean that it is now possible for the first time to obtain data on the contact behaviour of free-living wild animals directly and remotely using proximity data logger collars. This thesis describes attempts to apply these devices, and other methods, to quantify interactions between badgers.

1.5 The Woodchester Park badger population

This study uses badgers at Woodchester Park as the study population. The Woodchester Park badger population has been extensively studied since the 1970s and as a result is one of the longest running and most detailed ecological studies of a mammal population in Britain (Rogers et al. 1999). Research started initially to investigate the badgers potential role in the transmission of bovine TB to cattle, but since then population dynamics, reproductive biology, behaviour, social organisation, and study techniques have been investigated. The population density has been found to one of the highest recorded in the UK, with up to 25.3 adults per km^2 being recorded in 1993 (Rogers et al. 1997). At this density it is thought that the population reached maximum carrying capacity, and since then

the population density has declined slightly (Vicente et al. 2007). However, the density of badgers is still much higher than in other areas of the UK (Clements et al. 1988).

Much is already known about this badger population, which has benefited this thesis greatly by providing extra information about this particular population's ecology and behaviour that would not have been able to be collected during the time period of the PhD.

1.6 Thesis structure

Chapter 2 describes the Woodchester Park study site where fieldwork took place. The general methods used in subsequent chapters are described.

Chapter 3 investigates the accuracy of using radio tracking to record animal locations. Factors influencing accuracy are identified and the main sources of error are quantified.

Chapter 4 describes the social and spatial organisation of badgers within the study area determined by radio tracking. Home range sizes and core areas are identified. Areas of home range overlap are found to enable the degree to which these areas are shared between different groups to be quantified. Individual movement patterns are used to investigate dynamic interactions between badgers from the same and different social groups, to further evaluate the relative importance of social contacts in both intra-group cohesion and inter-group territoriality.

Chapter 5 investigates the consistency and accuracy of contact data collected using proximity loggers. Collars are tested in a controlled environment and under field conditions. The suitability of using proximity loggers to record contacts between badgers is discussed.

Chapter 6 describes the results from proximity loggers used to quantify contacts between badgers within the Woodchester Park study area. Contact rates and contact durations are found between badgers from the same and ffrom different social groups. The locations of where contacts take place and when, and between which badgers is found.

Chapter 7 provides a summary discussion of the main findings of the work. The methodologies used are discussed, and the findings of this study are related to current and future approaches to quantifying contacts between animals.

Chapter 2 General Methods

2.1 Introduction

Many different techniques exist to study wildlife in the field. Techniques range from well established and accepted methods to modern and controversial, from simple and easy methods to complicated, lengthy or high-tech methods. With so many available options, choosing the best methods to meet the objectives of the study requires considerable investigation and deliberation. The techniques described in this chapter have been chosen because they are believed to represent the most accurate, safe, least intrusive to the animal, cost-effective or time-effective methods in order to conduct research. With the exception of the use of proximity loggers, the techniques of bait marking, badger trapping and sampling and radio tracking have been used for many years and are well established for studying both badgers and other wildlife (Wilson and Delahay 2001). Where adaptations or improvements have been made to the methods these are described in the text. The proximity loggers are a novel technology; they have been tested on brushtail possums (*Trichosurus vulpecula)*(Ji et al. 2005), raccoons (*Procyon lotor)*(Prange et al. 2006), and cattle (Swain and Bishop-Hurley 2007), but never before on badgers. All procedures described here were carried out under the appropriate Home Office licence.

2.2 Chapter aims

This chapter aims to describe the main methods used throughout chapters three, four and five. As the techniques described here are applicable to the different chapters, describing them all together saves repetition and allows the reader a broader understanding of how they relate to each other and to refer back to them easily.

2.3 Study site

Woodchester Park (National Grid Reference SW81,01) lies in a Cotswold limestone escarpment in the South-West of England in Gloucestershire (Cheeseman and Mallinson 1981). Central to Woodchester Park, running from west to east is a steep-sided heavily-wooded valley surrounded by an escarpment of mainly farmland (Delahay et al. 2006a). The terrain is mainly hilly, between 47m and 210m above sea level (Rogers et al. 1998).

The valley consists primarily of blocks of deciduous, coniferous and mixed woodland, but also contains permanent pasture, areas of open water, scrub and a few buildings. The escarpment surrounding the valley consists mainly of agricultural grassland, interspersed with patches of arable farmland, scrub and woodland (Delahay et al. 2006b). Grazing on the pasture is primarily by beef and dairy cattle with some sheep (Rogers et al. 1998). Most of Woodchester Park is owned by the National Trust and is open to the public for recreation. Aside from a caretaker to look after a Victorian mansion in the park, there is no permanent human habitation in the park, although on the escarpment surrounding the valley there are several farmsteads.

The Woodchester Park badger population has been studied extensively since 1976 by the Central Science Laboratory (CSL) as part of long-term research, and a considerable amount of knowledge has been gained about the badger population (Delahay et al. 2000a). Badger density at Woodchester Park is amongst the highest recorded in the UK (Rogers et al. 1997). This is due to an exposed band of soft Cotteswold sandstone in the lower regions of the valley slopes allowing setts to be easily dug, combined with a mild, wet climate and plentiful food supply in pasture areas (Rogers et al. 1997). There are approximately 25 social groups covering a core area of approximately 7km^2 (Vicente et al. 2007), and badger density is the highest known, having been recorded at over 20 adult badgers/km^2 (Neal and Cheeseman 1991, Rogers et al. 1997).

2.4 Methods

2.4.1 Territory delineation

The configuration of badger social groups in Woodchester Park is determined by bait marking, carried out yearly by CSL staff. A bait of peanuts and golden syrup containing small, brightly coloured plastic pellets was fed for 10 days at the main sett of each social group. Each group was fed different colour or shaped pellets to other groups. Subsequent surveying of the area identified the pellets passed out in faeces at latrines, and latrines could be attributed to different social groups based on the colour or shape of pellets found. Boundaries between social groups could be identified by the presence of two or more different coloured setts of pellets (Delahay et al. 2000a). For this study, the results from bait marking in Spring 2005 are used. The location of latrines and boundaries with coloured pellets in them (bait-mark returns) were entered into a mapping programme (ArcView version 3.2, ESRI, Redlands, California, USA) and plotted on a map of the area (Figure 2.1). The 100% Minimum Convex Polygon (MCP) method was used to join the outermost fixes, with some adjustment to take into account outlying bait-marking returns and known territorial boundaries from badger runs and habitat features such as open water (Delahay et al. 2000b). Based on the social group delineation determined by bait marking a subset of contiguous social groups were selected for this study (Figure 2.2). Most social groups are distinct and mutually exclusive, however, the Larch social group has two main setts (Larch and Box), and Taxus and Top should be treated as one 'supergroup' called Yew, although bait marking and trapping takes place at both locations, and badgers have been labelled according to these locations. Taxus and Top were once separate social groups but over recent years have merged to form one large group, and it is believed that Taxus is the main sett and Top is a subsidiary sett (P. Spyvee, *personal communication)* (Figure 2.2).

2.4.2 Badger trapping

Each social group was routinely trapped four times a year by CSL staff. Trapping took place in spring, summer, autumn and winter but excluded the months of March and April to avoid separating mothers from young cubs (Tuyttens et al. 1999a). Badgers were caught in steel mesh box traps placed next to active setts or on badger runs in the vicinity of

the sett. Setts were identified as being active by signs of recent digging or fresh footprints. latrines being used and unobstructed sett entrances. Traps were pre-baited with peanuts for 4-8 days and then set for two consecutive nights. More traps were set than the expected number of badgers present to maximise trapping success (saturation trapping) (Tuyttens et al. 1999a). Traps were visited at dawn if they had been set the night before, and trapped badgers were transferred to holding cages and transported to a sampling facility for examination. Badgers caught during the first night of trapping were sampled during the day and kept overnight in a heated darkroom to be released the following morning at the point of capture, whilst badgers caught during the second night of trapping were sampled during the day then released the same afternoon at the point of capture (Garnett 2002). This was done to minimise social group disturbance and prevent badgers from being re-trapped.

2.4.3 Badger sampling

Badgers were anaesthetized with a mixture of Ketamine hydrochloride (Vetalar™ V, Pharmacia and Upjohn, Crawley, UK), medetomidine hydrochloride (Domitor®, Pfizer, Sandwich, UK) and butorphanol tartrate (Torbugesic®, Fort Dodge Animal Health Ltd, Southampton, UK) after (de Leeuw et al. 2004). At first capture badgers were marked with a unique identifying tattoo in the inguinal region (Cheeseman and Harris 1982). At each capture event a variety of biometric data was taken. This included sex, weight, age (if year of birth was known), body length, body condition, reproductive status and condition and TB status (Table 2.1). TB status was diagnosed by ELISA (Goodger et al. 1994), and by bacterial culture of faeces, urine, pharyngeal sputum and pus swabbed from open bite-wounds. Badgers were categorised into the following disease states based on the sampling results: negative (no positive results), exposed (1 positive result from ELISA but none from culture), excretor (none or some positive ELISA results, 1 positive culture result), and super-excretor (none or some positive ELISA results, two or more positive culture results) (Delahay et al. 2000b). For the purpose of this study badgers were subsequently categorised into two TB states; negative (negative or exposed), or positive (excretor or super-excretor), due to the uncertainty of ELISA tests (ELISA has a sensitivity of approximately 41% (Forrester et al. 2005)). Table 2.1 summarises the data obtained for each badger used in this study each time it was trapped, as well as the number of times and locations at which it has been trapped previously.

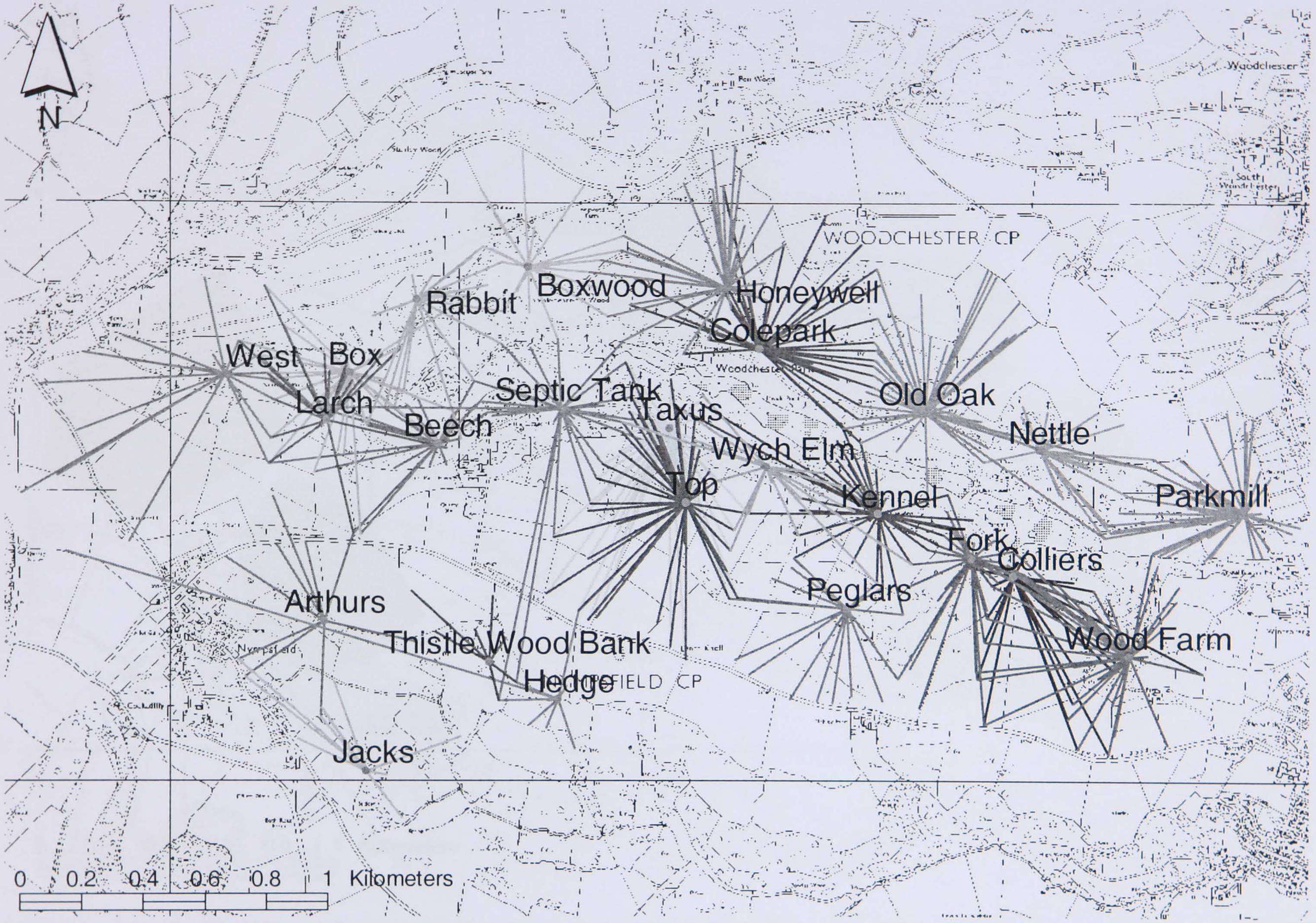


Figure 2.1. Bait marking results from Spring 2005. Main setts are labelled, and the different coloured lines represent bait returns from latrines attributed to the different setts/social groups.

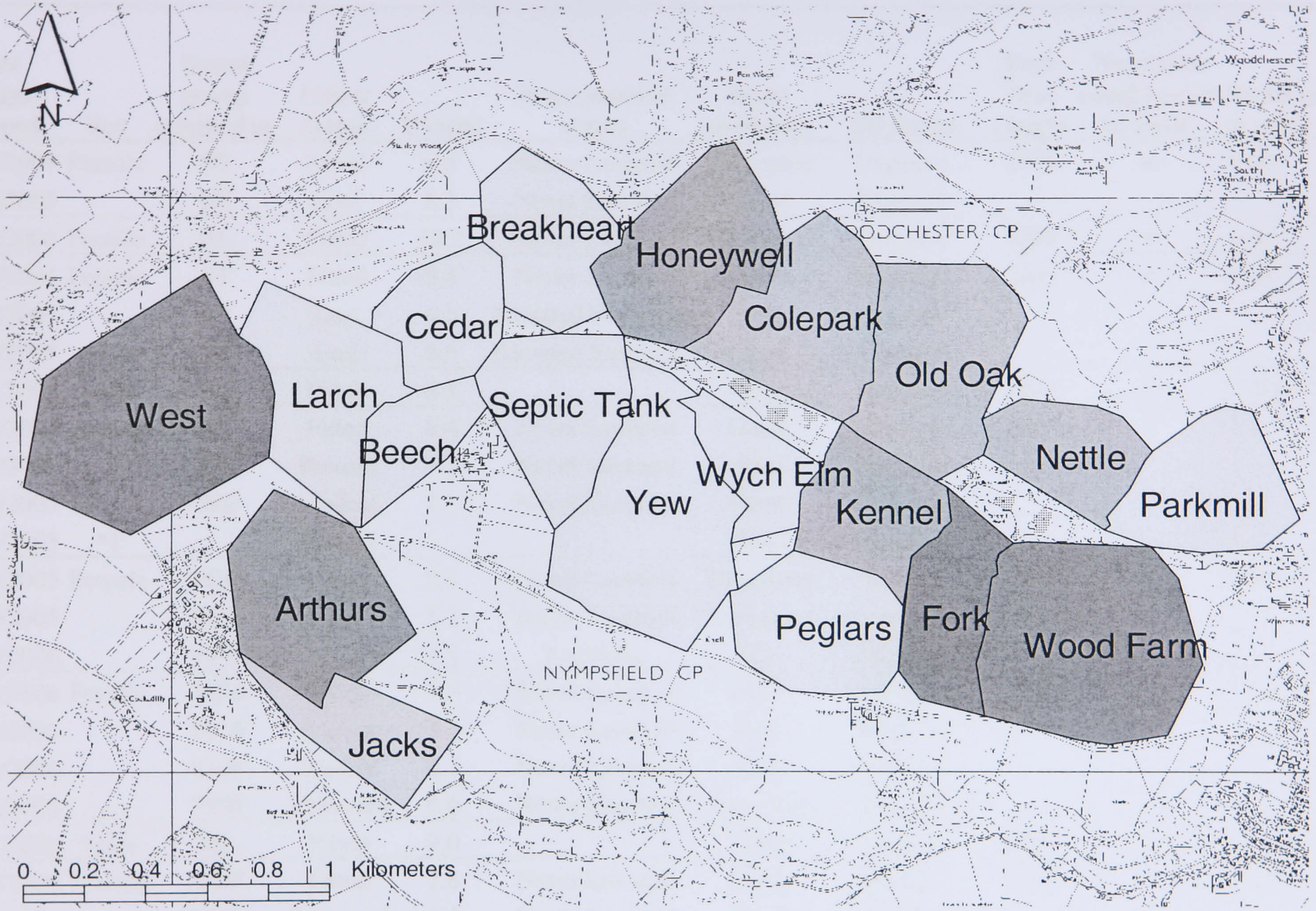


Figure 2.2. Social group boundaries, with social groups used in this study highlighted in bright yellow (Breakheart, Cedar, Larch, Beech, Septic Tank, Yew, Wych Elm and Peglars). From the social groups used in this study, Larch is unusual in that it has two main setts, and the Yew social group is unusual in that it comprises Taxus and Top, which were two separate social groups that have merged over recent years to form one large 'supergroup' called Yew. All other social groups are distinct and mutually exclusive.

ID	Date badger trapped	Sex	Social group trapped at	Collar status	Weight	Reproductive status	Body condition	TB status	Year first caught	No. times caught prior to study	Social groups caught at prior to study
13G	22/09/2004	Female	BE	Fitted	9.5	Never Lactated	Very good	Exposed	2003	4	4xBE
13G	02/08/2005		BE	Lost	8.3	Never Lactated	Good	Exposed			
18G	09/11/2004	Female	BE	Fitted	12.2	Never Lactated	Very good	Exposed	2003	4	4xBe
19G	22/09/2004	Female	ST	Fitted	9.4	Never Lactated	Good	Exposed	2003	4	4xST
19G	02/08/2005		ST	Lost	6.6	Lactated Sometime	Poor	Exposed			
19G	27/09/2005		ST	Lost	8.5	Lactated Sometime	Good	Exposed			
32R	18/01/2005	Male	WE	Fitted	8.5		Good	Excretor	2004	3	3xWE
37R	18/01/2005	Female	ST	Fitted	8.4	Never Lactated	Good	Negative	2004	3	3xST
37R	07/06/2005		WE	Present	7.3	Never Lactated	Fair	Negative			
37R	02/08/2005		WE	Present	7.1	Never Lactated	Good	Negative			
37R	26/10/2005	*1		Present			Good	Negative			
38R	18/01/2005	Female	PEG	Fitted	9.7	Never Lactated	Very good	Negative	2004	3	3xPEG
38R	02/08/2005		PEG	Lost	8.2	Never Lactated	Very good	Negative			
38R	16/05/2006		PEG		7.5	Lactating	Fair	Negative			
39W	10/01/2006	Female	YEW	Fitted	7.3	Never Lactated	Good	Exposed	2005	3	2xTOP, 1xYEW
39W	16/05/2006		YEW	Present	7.2	Never Lactated	Fair	Exposed			
39W	01/08/2006		YEW	Present	6.3	Never Lactated	Fair	Exposed			
39W	07/11/2006		YEW	Removed	9.6	Never Lactated	Very good	Exposed			
43W	10/01/2006	Male	BE	Fitted	9.0		Good	Exposed	2005	3	1xBE
44R	19/01/2005	Female	TOP	Fitted	7.8	Never Lactated	Good	Negative	2004	2	1xTOP, 1xYEW
44R	02/08/2005		YEW	Removed	6.5	Never Lactated	Good	Negative			
44R	27/09/2005		YEW		7.8	Never Lactated	Good	Exposed			

Table 2.1. Trapping history details for all badgers fitted with proximity loggers at Woodchester Park, table continues....

ID	Date badger trapped	Sex	Social group trapped at	Collar status	Weight	Reproductive status	Body condition	TB status	Year first caught	No. times caught prior to study	Social groups caught at prior to study
47R	01/02/2005	Female	BH	Fitted	9.2	Never Lactated	Good	Negative	2004	3	3xBH
47R	22/06/2005		BH	Lost	8.2	Never Lactated	Good	Negative			
47R	16/08/2005		BH	Lost	7.7	Never Lactated	Good	Negative			
50W	10/01/2006	Male	ST	Fitted	7.5		Good	Exposed	2005	2	2xST
50W	02/08/2006		ST	Present	7.9		Good	Exposed			
52W	16/05/2006	Male	WE	Fitted	8.7		Very good	Exposed	2005	4	1xTOP, 3xYEW
52W	01/08/2006		WE	Present	8.6		Very good	Exposed			
52W	07/11/2006		WE	Removed	11.4		Very good	Exposed			
53W	16/05/2006	Male	WE	Fitted	8.0		Good	Exposed	2005	4	2xTOP, 2xYEW
53W	01/08/2006		WE		7.8		Good	Exposed			
54G	17/05/2006	Male	WE	Fitted	8.6		Good	Excretor	2003	5	2xTOP, 3xYEW
54G	01/08/2006		WE	Present	8.6		Good	Excretor			
54R	01/02/2005	Male	CE	Fitted	8.1		Good	Negative	2004	3	3xCE
54R	21/06/2005		CE	Present	7.1		Poor	Negative			
55G	07/06/2005	Male	WE	Fitted	8.8		Good	Negative	2003	5	4xKEN, 1xOO
55G	27/09/2005		WE	Removed	9.8		Very good	Negative			
55G	16/08/2006		HW		9.2		Good	Negative			
67R	02/02/2005	Female	BH	Fitted	8.0	Never Lactated	Good	Negative	2004	1	1xBH
68R	02/02/2005	Female	CE	Fitted	7.8	Never Lactated	Fair	Negative	2004	1	1xCE
68R	22/06/2005		CE	Present	7.4	Never Lactated	Fair	Negative			
68R	16/08/2005		CE	Lost	6.6	Never Lactated	Good	Negative			
76R	18/01/2005	Female	TOP	Fitted	8.9	Never Lactated	Good	Exposed	2004	1	1xOO

Table 2.1. continued.

ID	Date badger trapped	Sex	Social group trapped at	Collar status	Weight	Reproductive status	Body condition	TB status	Year first caught	No. times caught prior to study	Social groups caught at prior to study
D19	07/06/2005	Male	BE	Fitted	9.4		Good	Excretor	1997	21	4xBE, 13xST, 4xYEW
D19	20/07/2005		LA	Removed	8.1		Fair	Excretor			
D59	27/09/2005	Female	BE	Fitted	8.4	Lactated Sometime	Good	Negative	1997	15	14xBE, 1xST
H43	10/11/2004	Female	WE	Fitted	10.4	Lactated Sometime	Good	Super-excretor	1995	33	3xCP, 1xKE, 29xWE
H43	07/06/2005		WE	Present	6.9	Lactated Sometime	Fair	Super-excretor			
H43	02/08/2005		KE	Present	6.6	Lactated Sometime	Fair	Super-excretor			
H43	18/10/2005	*2		Present			Poor	Super-excretor			
H69	10/11/2004	Female	PEG	Fitted	10.5	Lactated Sometime	Good	Negative	1995	18	3xPEG, 11xPO, 4xWE
H69	02/08/2005		PEG	Present	6.6	Lactated Sometime	Fair	Negative			
H69	28/09/2005		PEG	Removed	8.5	Lactated Sometime	Good	Negative			
H69	16/05/2006		PEG		6.6	Lactacted this year	Good	Negative			
H69	01/08/2006		PEG		5.5	Lactated Sometime	Fair	Negative			
J15	22/09/2004	Female	BE	Fitted	9.8	Lactated Sometime	Good	Exposed	1998	13	13xLA
J15	19/10/2004		LA	Lost	11.0	Lactated Sometime	Very good	Exposed			
J15	08/06/2005		BE	Fitted	7.7	Lactated this year	Fair	Exposed			
J15	19/07/2005		LA	Lost		Lactated Sometime	Fair	Exposed			
J15	04/10/2005	*2					Good	Excretor			
J87	22/09/2004	Female	BE	Fitted	11.1	Lactated Sometime	Very good	Negative	1998	11	11xBE
J87	28/09/2005		BE	Lost	8.3	Lactated Sometime	Good	Negative			
U51	22/09/2004	Male	ST	Fitted	10.9		Good	Negative	2001	7	6xST, 1xYEW
U57	16/05/2006	Female	YEW	Fitted	7.0	Lactating	Fair	Negative	2001	9	8xTOP, 1xYEW
U57	01/08/2006		YEW	Present	6.9	Lactated Sometime	Fair	Negative			
U57	07/11/2006		YEW	Lost	9.4	Lactated Sometime	Good	Negative			

Table 2.1. continued.

ID	Date badger trapped	Sex	Social group trapped at	Collar status	Weight	Reproductive status	Body condition	TB status	Year first caught	No. times caught prior to study	Social groups caught at prior to study
U68	07/06/2005	Female	YEW	Fitted	6.2	Lactated Sometime	Fair	Negative	2001	10	10xTOP
U68	11/11/2005		TOP	Removed	11.0	Lactated Sometime	Very good	Negative			
U68	16/05/2006		YEW		6.9	Lactated this year	Fair	Negative			
U68	01/08/2006		TOP		6.3	Lactated Sometime	Fair	Negative			
U69	16/05/2006	Female	ST	Fitted	7.0	Lactated this year	Fair	Exposed	2001	4	4xTOP
U69	01/08/2006		TOP	Lost	6.8	Lactated Sometime	Fair	Exposed			

*1. Post mortem carried out on this date; badger run over on road.

*2. Post mortem carried out on this date; badger died and was retrieved from study site.

Table 2.1. Trapping history details for all badgers fitted with proximity logger collars at Woodchester Park. Trapping events that took place during the study period are shown in detail, along with a summary of the number of past trapping events and where the badger was trapped. In all cases badgers were caught as cubs hence their age can be calculated from the year they were first trapped. Social group abbreviations are;

BE	Beech
BH	Breakheart
CE	Cedar
CP	Cole Park
HW	Honeywell
KE	Kennel
LA	Larch
OO	Old Oak
PEG	Peglars
PO	Pontins
ST	Septic Tank
TOP	Top
WE	Wych Elm
YEW	Yew

2.4.4 Social group allocation

Badgers were allocated to a particular social group in each year from 2004 to 2006 based on the number of times and the location at which they were trapped. Badgers were allocated to the social group in which they were most frequently trapped in that year, but if they were trapped in more than one social group an equal number of times, then the location of trapping events in adjacent years was taken into consideration. If this still did not resolve the issue then they were allocated to social group in which they were first trapped (Vicente et al. 2007).

Trapping success is high for this population of badgers due to the intensity of trapping effort and knowledge of the site gained from many years of research (Rogers et al. 1997, Wilson and Delahay 2001). Approximately 92% of badgers have been caught at some point in their lives (Hounsome et al. 2005) and on average a badger will be trapped twice a year (Vicente et al. 2007). For example, between 1987 and 1997 the population size calculated from the numbers of badgers trapped was within 10% of the population size based on the minimum number alive estimate (calculated retrospectively using data from subsequent years (G. Wilson, unpublished data and Wilson and Delahay). Very few unmarked badgers found dead within the study site also suggests the trap catch in any given year is likely to be a good approximation of the true population size (Wilson et al. 2003). Due to the high trapping success rate (Rogers et al. 1997), the estimates of numbers of individuals in each social group can be used as a good estimation of true badger numbers within each social group (Table 2.2).

		Numbers per group/Year		
Social group		**2004**	**2005**	**2006**
Beech	Total	7	7	3
	AF	5 (3)	4 (4)	1 (1)
	AM	2	1 (1)	1 (1)
	CF	0	0	1
	CM	0	2	0
Breakheart	Total	7	11	6
	AF	2	6 (2)	3
	AM	0	1	3
	CF	4	2	0
	CM	1	2	0
Cedar	Total	7	6	5
	AF	3	3 (1)	3
	AM	1	1 (1)	2
	CF	2	2	0
	CM	1	0	0
Larch	Total	20	12	14
	AF	9 (1)	8 (1)	7
	AM	4	2	0
	CF	4	1	4
	CM	3	1	3
Peglars	Total	9	8	7
	AF	4 (1)	4 (2)	4
	AM	4	0	0
	CF	1	2	1
	CM	0	2	2
Septic Tank	Total	6	8	5
	AF	2 (1)	2 (1)	3 (1)
	AM	2 (1)	2 (1)	2 (1)
	CF	1	1	0
	CM	1	3	0
Top	Total	9	14	5
	AF	3	4 (1)	4
	AM	3	2	0
	CF	2	5	0
	CM	1	3	1
Wych Elm	Total	5	4	5
	AF	2 (1)	2 (2)	1
	AM	2	2 (2)	4 (3)
	CF	0	0	0
	CM	1	0	0
Yew	Total	3	8	6
	AF	1	3 (2)	3 (2)
	AM	0	2	1
	CF	1	1	1
	CM	1	2	1

Table 2.2. Minimum number of animals present in each social group used in this study at Woodchester Park. Numbers are determined from trapping records with slight adjustments where a badger fitted with a collar is known to be in that social group but not trapped. Numbers in brackets are numbers of badgers in each age/sex class fitted with a proximity logger collar at some point during that year. AF = adult female, AM = adult male, CF = female cub, CM = male cub. In this table the adult age class includes yearlings.

2.4.5 Proximity logger collar information

Proximity logger collars made by Sirtrack Ltd, Havelock North, New Zealand were used in this study. Each unit consists of a battery, ultra-high frequency (UHF) transmitter unit, and very-high frequency (VHF) transmitter unit encased in epoxy resin, attached to a leather collar, with an aerial encased in plastic wrapped around the leather. The epoxy resin potting provided a high degree of waterproofing and attaches the unit to the leather collar. A small metal screw that can be screwed flush with the epoxy protected the computer interface in the unit. Leather was chosen as the collar material because it is strong yet soft and pliable and quickly moulds to the shape of a badger's neck thus minimising discomfort to the badger and hopefully discouraging it from attempting to remove the collar (Cheeseman and Mallinson 1979). A hole was punched in the leather at the neck diameter of the badger being fitted and a brass buckle fastened through the hole to join the two ends of the leather together. The whole unit weighs approximately 150 grams, which although slightly heavier than a conventional VHF (radio tracking) unit, is still less than two percent of an average badger's weight; well within the five percent guideline for radio tracking studies to minimise the burden on the animal and have no influence on their behaviour (Cochran 1980).

Herein, the term collar is used to refer to the whole unit, rather than the actual leather collar.

The proximity logger collars differ from conventional VHF collars used for radio tracking in that each collar can communicate with one or more other collars over a short-range radio data link. A transmitter unit broadcasts a unique ID code every 1.5 seconds over an UHF channel, and when not transmitting listens for other collars with different ID codes on the UHF channel. A UHF frequency of 916.5 MHz was chosen; this is a narrow frequency band reserved for industrial and medical telemetry and is licence free. The maximum range for any device operating in this band will be several hundred meters because it is limited by low power output, resulting in a low probability of false records being received by the collar. In addition, at this frequency there are very small transceiver modules available and the transmit-receive aerial can be very small in size; much smaller than that required for a VHF aerial (Prange et al. 2006).

When two or more units are within a specified range of each other and their ID code(s) are detected, the unit queries an onboard real-time clock and time of initial contact

is recorded and a timer starts counting. If the ID code is received again before a specified time the timer continues, if it is not the contact ends and the data is stored in a non-volatile memory. The memory can hold up to 8120 non-volatile data blocks (for the first version of the collars; the upgraded second version can hold many more); in each block the record number, ID code, date, time and duration of contact is recorded. Each unit also contains a VHF transmitter that acts as a radio-transmitter transmitting at a specified frequency within the 173kHz frequency band (the frequency reserved for wildlife research).

The UHF transmitter power can be changed to alter the range at which other units are detected, as can the separation time; the time specified by the user that designates a definite break in contact between individuals (SirtrackLtd. 2006a). The date and time can also be altered by the user as can the ID code and the VHF pulse rate. Each unit contains a small red light-emitting diode (LED) that flashes when contacts are recorded. However, this can be turned off, as was the case in this study to avoid disturbance to badgers. Battery life of these collars is approximately one year, but actual battery life may be a function of the frequency of logged contacts (Prange et al. 2006). This battery life is shorter than for VHF collars using a similar battery size due to the increased power consumption from using UHF and from on-board circuitry. The battery is encased in the unit and cannot be changed by the user but needs to be sent back to the manufacturer for battery replacement and refurbishment. In this study eight collars were refurbished resulting in two different versions of the collar being used. The refurbished collars contained upgraded software and hardware; the upgraded software meant the user interface was easier to use and the upgraded hardware meant a greater UHF range was available and the real-time clock was improved (T. Jordan, Sirtrack Ltd., *personal communication*).

2.4.5.1 Proximity logger data recovery

Contact data are stored on the collar until they are downloaded. If all the memory spaces are full no more data is recorded but the collar still transmits a signal so other collars may record contacts with it. The data are downloaded via an interface unit and cable connected to a computer and the collar, and accessed on the computer using software developed by Sirtrack. Data can then be erased from the memory in the collar and the collar used again – the collar does not need to be removed each time data are downloaded, but the badger needs to be immobilised in order to attach the collar to the interface unit and computer for approximately five minutes (depending on how full the memory is). Data

were downloaded each time a collared badger was caught during a trapping event, or if the collar had dropped off and was recovered from the field.

2.4.5.2 Collar fitting

Collars were fitted to badgers caught at the selected social groups (see social group allocation above). Collars were fitted to anaesthetised adult or yearling badgers with no health problems that would impair their ability to wear a collar such as open bite wounds or enlarged lymph glands. The neck fur was trimmed with clippers down to approximately one and a half centimeters long to minimise initial discomfort to the badger. The collar was fitted so that it was a snug fit around the badgers' neck: approximately three fingers could fit between the collar and the neck. Achieving a correct fit was essential; if it was too tight it would cause discomfort to the badger, especially when it put on weight for the winter months and if too loose, it would come off easily, either through other badgers removing it or the collar becoming snagged on an obstacle (P. Spyvee, *personal communication*).

Initially, 20 available collars were fitted to badgers based on the order in which they were trapped. Some collars were subsequently recovered, either from the field if they had dropped off, or removed at subsequent trapping sessions. Eight of these collars were refurbished and fitted to other badgers and one collar was re-fitted without being refurbished, resulting in 29 different badgers from the nine social groups wearing a collar during the study period (Table 2.3).

2.4.5.3 Radio tracking

Badgers were not radio tracked until at least three days after capture to allow them to acclimatise to wearing a collar and recover from capture. Individual badgers were radio tracked on foot using a 3-element Yagi antenna (Biotrack, UK) and a M-57 Mariner receiver (Marine Radar, UK) or a Telonics TR-4 receiver (Telonics Inc. USA). Badgers were radio tracked continuously for six hours from dusk (or slightly earlier in summer) and location fixes were recorded every five minutes (with a short break after three hours for refreshments for the tracker). The locations of individual badgers were determined by homing-in on the signal, and recording the radio tracker's own position using a GPS unit, the compass bearing to the signal and the estimated distance the badger was from the radio tracker (based on the strength of the signal). This method is discussed further in chapter 3.

section 3.1.1.2. Details were recorded onto a pocket dictaphone for later transcription. Care was taken to avoid disturbing and altering badgers' behaviour; walking on badger paths and approaching setts was avoided, and a distance of approximately 50 meters was maintained between the badger and the tracker during radio tracking. For each location fix, a badger's estimated position could be calculated as an Ordnance Survey grid reference to the nearest meter using the following formula (equation 2.1):

$$Easting = d \times Sin(\theta \times \frac{\pi}{180}) + GPSeasting$$

$$Northing = d \times Cos(\theta \times \frac{\pi}{180}) + GPSnorthing$$

Where :

d = estimated distance from tracker to badger (meters) (eqn. 2.1)

θ = estimated bearing from tracker to badger (degrees)

GPSeasting = tracker current easting position as given by GPS unit

GPSnorthing = tracker current northing position as given by GPS unit

To enable comparison between radio tracking and data logger data, any data collected when in British Summer Time (BST), were converted to Greenwich Mean Time (GMT). Any times referred to in this thesis refer to the 24-hour clock and are in GMT.

Badger ID	Sex	Social group allocated to	Badger radio-tracked?	VHF frequency (MHz)	Proximity data retrieved?	Number of download events
13G	Female	Beech	Yes	173.34	Yes	1
18G	Female	Beech	Yes	173.37	Yes	1
19G	Female	Septic Tank	Yes	173.36	No	0
32R	Male	Wych Elm	Yes	173.35	No	0
37R	Female	Wych Elm	Yes	173.3	Yes	3
38R	Female	Peglars	Yes	173.39	Yes	1
39W	Female	Yew	No	173.25	Yes	3 *2
43W	Male	Beech	No	173.34	Yes	1
44R	Female	Top	Yes	173.25	Yes	1
47R	Female	Breakheart	Yes	173.31	Yes	1
50W	Male	Septic Tank	No	173.38	Yes	2
52W	Male	Wych Elm	No	173.33	Yes	1
53W	Male	Wych Elm	No	173.41	Yes	1
54G	Male	Wych Elm	No	173.3	Yes	2
54R	Male	Cedar	Yes	173.24	Yes	2
55G	Male	Wych Elm	Yes	173.28	Yes	1 *2
67R	Female	Breakheart	No	173.4	No	0
68R	Female	Cedar	Yes	173.27	Yes	2
76R	Female	Top	Yes	173.42	No	0
D19	Male	Beech	Yes	173.38	Yes	1
D59	Female	Beech	No	173.24	Yes	1
H43	Female	Wych Elm	Yes	173.41	Yes	3
H69	Female	Peglars	No	173.33	Yes	2 *2
J15	Female	Larch	No	173.29	Yes	1
J15 *1	Female	Larch	No	173.31	No	0 *2
J87	Male	Beech	Yes	173.26	No	0
U51	Male	Septic Tank	Yes	173.32	Yes	1
U57	Female	Yew	No	173.28	Yes	1
U68	Female	Yew	No	173.23	Yes	1
U69	Female	Septic Tank	No	173.29	No	0

*1. This badger had previously been fitted with a collar which it had lost so was fitted with another at a later date, although the later collar failed.
*2. The collar failed during part or all of the study; either to record contacts or to both transmit and record contacts.

Table 2.3. Summary data showing details of badgers used in this study. Social group allocated to is for the year(s) in which radio tracking and proximity data were collected only, based on the trapping data for those years. As mentioned earlier, although Yew and Top badgers are sampled separately they should be considered as belonging to the group. Number of download events refers to the number of separate times proximity data were downloaded from the badgers' collar.

Chapter 3 Investigation into sources of error that affect accurate recording of animal locations by radio tracking

3.1 Introduction

Radio tracking is a commonly used technique in animal ecology studies, yet too often little consideration is given to the accuracy of locations found by radio tracking and locations are considered error free when in fact this may not be the case. This chapter provides an overview of the different approaches taken in radio tracking, before considering some of the sources of error that may affect the accuracy when undertaking a radio tracking study. An in-depth field study allows the conditions under which badgers are radio tracked (as in chapter 4) to be replicated, and therefore sources of error specific to this, and similar, studies to be quantified.

3.1.1 Radio tracking

Following the introduction of the technique of radio telemetry in the early 1960's (Cochran and Lord 1963), radio tracking has revolutionized the field of wildlife research (Mech and Barber 2002) and provided answers to many biological questions (Macdonald and Almaner 1981). Radio tracking is the study of the movement behaviour of individual animals and therefore lends itself to comparing differences between individuals (Harris et al. 1990); it provides a tool to investigate many aspects of wildlife ecology including migration and dispersal patterns, space use and home range size, resource use and selection, population abundance and density, survival and fecundity (Garton et al. 2001).

3.1.1.1 Radio tracking in the study of badgers

Radio tracking has been used successfully in many different studies of badgers. Studies have involved fitting radio-collars to one or more badgers from the same or different social group(s). Studies have used radio tracking to investigate patterns of dispersal (Cheeseman et al. 1988a, Christian 1994, Roper et al. 2003b), territory size and shape (Blackwell and Macdonald 2000), space use and activity (Rodriguez et al. 1996), the effect of weather conditions on

activity and movement patterns (Cresswell and Harris 1988), spatial organisation and group living (Revilla and Palomares 2002), sett use (Roper et al. 2001), and disease (Cheeseman and Mallinson 1979), in many different habitat types and population densities. Tuyttens et al. (2002) investigated the effect of fitting badgers with radio collars and found that after an initial acclimatization period there was no effect on body condition, body weight and testes size in any age class between badgers wearing collars and those not. There is also no difference in the probability of a badger subsequently being caught in a cage trap if they are wearing a radio collar and have been radio tracked compared to un-collared badgers (Tuyttens et al. 1999b). Brown (1993) found no difference in the emergence time and the time spent away from the sett between badgers that had been captured and fitted with a collar compared to badgers that had not been handled recently. These few studies support the assumption that radio collared animals are representative of the entire study population and that tagging does not affect the health, condition or behaviour of the animal, although it is not possible to conclude that no difference exists between tagged and untagged animals (White and Garrott 1990).

3.1.1.2 Existing radio tracking methods

Several methods exist to locate and radio track animals; the animal can be located at varying time intervals from very infrequent to continuously, and the animal can be located using different forms of transport for the locator, including on foot, from a vehicle, from a fixed non-movable base station, from an aircraft or by satellite.

Once a signal from an animal has been picked up, it needs to be located more precisely. This may be done by 'homing-in' on the animal (Mech 1983) or by triangulation (White and Garrott 1990). Homing-in on the signal involves using a directional antenna to follow the transmitter signal's increasing strength until the animal can be observed or its location can be inferred. This can be accomplished by circling a small area and assuming the animal is in this area, sandwiching the animal between the receiving point and a physical barrier, or searching a narrow belt and assuming the animal is within this habitat (White and Garrott 1990). Triangulation involves obtaining three or more directional

bearings recorded at known locations remote from the animal and calculating the animal's position based on the intersection of the bearings (Saltz and Alkon 1985). Triangulation is the method most commonly used in radio tracking studies where animals are located infrequently, they range over large areas, or the habitat makes close access to the individual being studied hard. Homing-in on the animal was used in the present study because it enables detailed behavioural and habitat data to be collected simultaneously. However, when using the homing-in method, care must be taken to avoid disturbance to the animal and it may be difficult to detect long-distance sudden movements (Kenward 2001).

Continuous radio tracking is where locations are obtained for the individual at short intervals, over a set period of time. Discontinuous radio tracking is where locations are obtained for the individual at discrete or random time intervals throughout the study period (Harris et al. 1990). Discontinuous radio tracking has the advantage that data on many individuals can be collected concurrently rather than focusing on one individual, however, continuous radio tracking has the advantage of providing a better approximation of the animal's travel route than discontinuous radio tracking and was used in this study. It is also useful for showing the intensity of home-range use by the individual, dispersal by individuals, movement and activity patterns and interactions, and effects of parameters such as weather on the individual being studied (Harris et al. 1990). However, it is only successful when the chance of losing the study animal due to sudden movements is small, and there is suitable terrain (Harris et al. 1990).

3.1.1.3 Accuracy of radio tracking

Animal locations obtained remotely by radio tracking are best estimates of the animal's location, rather than accurate locations (Springer 1979), and the probabilistic nature of these estimates defines the precision with which we can measure space use and resource selection (Nams 1989). Radio telemetry locations therefore should not be treated as error-free, as this may falsely conclude that there are differences in animal movements, resource selection, home-range size and area (Springer 1979), or survival (Garton et al. 2001) when in fact there are none. Many studies pay little regard to the error associated with

locations determined by radio tracking and report them as absolute locations, when in fact the level of error associated with these locations may vary depending on a multitude of different factors; many of which will be investigated further in this chapter.

3.1.2 Sources of error

The factors contributing to error arising from radio tracking have been well documented e.g. (Lee et al. 1985, Powell 2000, Withey et al. 2001, Mech and Barber 2002), and consist of two main classes of error: bias and sampling error. Bias, or system-related error is a result of equipment peculiarities and is constant irrespective of sample size. Sampling error is caused by imprecision in the receiving system, the observer and landscape features, (Springer 1979) and varies with sample size. The sources have been split into two sections: (1) errors arising from using a VHF radio tracking system, including mapping error, electromagnetic interference, vegetation cover, topography and signal bounce, animal movement and distance effects and observer effects, and (2) errors arising from using a GPS including geometric dilution of precision, atmospheric effects, multipath effects, empheris and clock errors and receiver errors. A brief summary of these errors is given below.

3.1.2.1 Error arising from using a VHF radio tracking system

Mapping error is the error arising from placing an animal or individual on a map and may arise when using maps at different scales or resolutions. It tends to be a greater problem when radio tracking in habitats that lack obvious features (Mech 1983). The use of a GPS unit and computerized mapping software has largely reduced the effect of mapping error and so will be considered as negligible in this study.

Electromagnetic interference may disrupt signal transmission and reception or introduce bias to the signal direction. For example, taking bearings close to high voltage power lines has been found to significantly increase error compared to taking bearings from further away (Parker et al. 1996). The effects of mobile phone transmissions or other electronic systems on the reception of a

signal from radio tracking have not been tested. During the course of this study it was noted that holding a mobile phone close to the receiver disrupted the signal. However, the advantage of using a hand-held and mobile antennae and receiver meant that it was easy to move position or change the plane of the antennae to avoid disruption.

Vegetation cover has been shown to affect signal transmission and reception where large trees (Cottam 1988) or thick foliage (Chu et al. 1988) may decrease signal strength and dense vegetation may cause signal bounce (Samuel and Kenow 1992). However, other studies have found no difference in accuracy between open and wooded habitats (Hupp and Ratti 1983, Cottam 1988). Signal bounce occurs when there is no direct clear path between the transmitter and the receiver and results in the signal from the transmitter being bounced off reflective surfaces and appearing to come from a direction that is not the true direction (Garrott et al. 1986). Topographic features such as hills or valleys may block a direct signal path and reflective surfaces such as wet snow, canyon walls (Beaty and Tomkiewicz 1990), dense vegetation (Samuel and Kenow 1992) or proximity of antennae elements to tree limbs (Hupp and Ratti 1983) may cause signal bounce.

If the animal is moving when a fix is taken it may be difficult to pinpoint the location; it can take a couple of minutes to find the strongest direction of the signal and line up the compass to record a fix, during which time the animal may have moved. Many studies investigating accuracy have used fixed locations rather than moving targets, and therefore, potentially under-report the effect of error (Kauhala and Tiilikainen 2002). In a simulation study using triangulation, animal movement increased the error ten-fold compared to stationary animals (Schmutz and White 1990). It is likely that animal movement may be more of a problem when using the triangulation method to find an animal's position and taking successive rather than simultaneous bearings compared to using the homing-in method. Location error may also increase with increased distance between the receiving equipment and the transmitter (Theuerkauf and Jedrzejewski 2002), and therefore the distance to the transmitter should be minimized (Springer 1979). Again, this will be more of a problem when using triangulation and using fixed locations to record a fix from, compared to using

the homing-in method as this can attempt to minimize distance when locating the animal.

Observer error can contribute significant error to location estimates (Hoskinson 1976, Withey et al. 2001). For example different observers may have different levels of expertise in using the radio tracking system, or put different levels of effort into locating the animal. Observers may also perform differently if they know they are being tested (Mills and Knowlton 1989). The animal under study may be affected by the observer, causing the animal to exhibit unusual behaviours (Prosser et al. 2004), to move away or to spend longer periods in certain habitats (Lariviere and Messier 1998).

3.1.2.2 Error arising from using a GPS system

The global positioning system (GPS) is a satellite-based navigation system comprising 24 satellites that circle the earth twice a day on a precise orbit. The satellites transmit signal information to earth, which is picked up by GPS receivers. By determining the position of and distance to, three or more satellites the GPS receiver can compute its position using trilateration. A 3D position can be determined comprising latitude, longitude and altitude. However, there are numerous sources of measurement error that influence GPS performance and affect the accuracy of this 3D position. These sources have been well documented (e.g. (Parkinson 1996b, Misra and Enge 2001)), so only a brief summary is given below.

Geometric dilution of precision, or GDOP, is the geometric effect of the spatial relationship of the satellites relative to the user. Generally, the more satellites that can be observed the more accurate the position. The spread of the satellites, e.g. whether they are spread around the horizon or high in the sky will affect the precision of recording either the vertical or horizontal position (Ganskopp and Johnson 2007).

The speed of GPS signals as they pass through the Earth's atmosphere can be affected by inconsistencies in the ionosphere and troposphere. Dispersion and refraction cause time delays in passing through the ionosphere and usually contribute the greatest to the overall error but can be corrected for relatively easily because changes occur relatively slowly. Ionospheric delay is usually less

during the night (Parkinson 1996b). Variations in the temperature, pressure and humidity in the troposphere cause variations in the speed of light of radio waves but because changes in these can occur relatively quickly, precise measurement and compensation is difficult.

Multipath effects can occur where the radio signal reflects off surrounding terrain including buildings, canyon walls, metal structures, hard ground etc. causing it to arrive at the GPS receiver from more than one path and causing inaccuracies. Averaging the signal over time, e.g. from different satellite configurations, can help to reduce the effects of multipath (Harre 2001).

Satellite empheris errors are errors in the prediction of a satellite position due to orbit perturbations. A lack of synchronisation between receiver and satellite clocks or random time drifts in the satellites' atomic clocks will introduce errors to the recorded position. Selective availability (SA) introduced intentional random errors in the transmitted clock to purposely degrade the satellite signal to create position errors. The US Government turned off SA in 2000 but it could in theory be turned on again (Lawler 2000).

Receiver errors include noise associated with the ability of the GPS unit to measure a finite time difference and interference to the GPS receiver such as from electromagnetic radiation. Electromagnetic radiation such as solar flares, geomagnetic storms or the metal embedded in some car windscreens to prevent icing can desensitise the receiver and degrade the signal (Harre 2001).

3.1.3 Reporting of error

Many studies use radio tracking to obtain data, yet few studies attempt to study, quantify and report the accuracy and any bias of the data obtained (Saltz 1994). Saltz (1994) conducted a review of papers published in the Journal of Wildlife Management that used the triangulation method of radio tracking, and found that during 1986-92, 29% of papers did not mention error, 48% provided incomplete information and only 29% provided acceptable information. This was subsequently extended by (Withey et al. 2001) for the years 1993 to 1999. Using the same criteria they found figures of 23%, 23% and 53% respectively for no mention of error, incomplete information and acceptable information provided. Therefore, although the reporting of errors has improved somewhat

the situation could still be improved upon. No such review of the accuracy of recording locations using the homing-in method exists, and only a few studies using this method reported any assessment of error being carried out ((Newton-Cross 2003, Palphramand et al. 2007).

3.1.3.1 Measurement of error

Methods for measuring error usually involve a beacon test, whereby the position of the beacon is known and radio tracking is used to estimate its position. Error polygons (Heezen and Tester 1967) can be constructed from the error arcs formed by the intervals around estimated bearings to define a four-sided polygon; the area of this polygon can be used as a measure of precision and the telemetry system can be assessed as to whether it is precise enough to meet the objectives of the study (Hupp and Ratti 1983, Nams 1989). Similarly, instead of a polygon, an ellipse can be estimated (usually 95% confidence) from the error arcs from estimated bearings using Lenth's 1981 (Lenth 1981) maximum likelihood estimator (MLE). The linear distance between actual and estimated locations of beacons can also be used to estimate location error (Zimmerman and Powell 1995), which can also be termed linear error (Withey et al. 2001). The first two methods of error measurement (error polygons and ellipses) were developed for use with triangulation and are not suitable when using the homing-in method of radio tracking. Linear error, however, uses a direct measure of error and can be applied to any method used to estimate animal locations (Zimmerman and Powell 1995). Furthermore, the first two methods are a better method of precision rather than accuracy (precision being a measure of consistency of the tracking system under investigation and accuracy a measure of how close the estimated location is to the actual location (Withey et al. 2001)), whereas linear error is a better measure of accuracy.

3.2 Chapter aims

This study aims to investigate some of the sources of error that may contribute to the accuracy or precision of recording radio tracking locations. Whilst many studies make use of radio tracking as a technique few explicitly take into account the error involved in a satisfactory way; this study attempts to resolve this. The precision of the GPS will be measured separately from the radio tracking study to allow the two components to be isolated. The errors associated with radio tracking, and the factors that affect the accuracy will be quantified. The results obtained from this study have implications for interpreting animal movements based on the homing-in method of radio tracking, and are of particular importance in the home range analysis and space use behaviour of badgers discussed in chapter 4.

3.3 Methods

The study involved three separate investigations. The first aimed to investigate the precision of using a GPS when radio tracking, the second aimed to investigate the accuracy of a VHF radio tracking system to locate an animal and the third to investigate the effect of using potentially inaccurate locations found from radio tracking to predict distance moved and home range size. In summary:

- Experiment 1: Investigated GPS precision; GPS readings were obtained from the same location over time from two different sites (one open and one wooded) to give a measure of overall precision and precision over time.

- Experiment 2: Investigated radio tracking accuracy; A variety of parameters that may affect the accuracy of radio tracking were investigated; bearing error, distance error and linear error were calculated. Parameters that significantly affect linear error were used to formulate a generalized least squares model to predict linear error.

- Experiment 3: Investigated the total distance travelled for the 'badger' every 30 seconds, every 5 minutes and every 5 minutes as estimated by the radio tracker. These distances travelled were compared, and home range sizes (found using the minimum convex polygon estimator), were computed and compared for the 'badger' every 30 seconds, every 5 minutes and every 5 minutes as estimated by the radio tracker.

3.3.1 GPS precision

This experiment intended to isolate any error that may arise from using a GPS unit to record a location. The precision of the unit was determined overall and the effect of time to record a position investigated.

3.3.1.1 Study design and analysis

The study took place in Dalby Forest, North Yorkshire (Ordnance Survey co-ordinates 492000-490500 of approximate centre of study area), in habitats similar to those found in Woodchester Park where radio tracking of badgers took place. A Garmin® GPS 12 Personal Navigator® (Garmin Europe, Romsey, UK) unit was placed in an exact location and the position shown on the unit recorded every 30 seconds for 10 minutes. This

was repeated five times at the same exact location at different times of day and different days. Two sites were used, one in open habitat and one in wooded habitat.

Data were recorded as Ordnance Survey eastings and northings and downloaded onto a computer. The eastings and northings were tested for normality and 95% error ellipses plotted about the mean location. These were based on the standard deviations of the eastings and northings using a specific multiple of 2.449 to represent the 95% integration contour (Harre 2001). The displacement distance (the distance each location was from the mean) was calculated using trigonometry and plotted against time for both locations. Analysis was performed using the 'R' statistical and programming environment (R Development Core Team 2006).

3.3.2 Radio tracking accuracy

This experiment aimed to investigate the effect of some of the potential sources of error mentioned above on the accuracy of recording animals' locations using radio tracking.

3.3.2.1 Study design and analysis

The study took place in Dalby forest, North Yorkshire in habitats similar to those found in Woodchester Park where radio tracking of badgers took place. The study took place during daylight hours, when badgers are most likely to be inactive in order to avoid disturbance to them. Volunteers with an interest in radio tracking, including those involved with radio tracking badgers at Woodchester Park, were paired. One person attached a radio-collar to their lower leg as low as possible to reflect the height a collar is worn on a badger. The person wearing the radio-collar, known as the 'badger', started from a known position (usually a known badger sett) and moved around the study site at a walking pace, recording their position using a handheld Global Positioning System (GPS) unit every 30 seconds. The other person radio tracked the 'badger' using the methods described in chapter 2 (section 2.4.5.3). In addition to the usual data collected during radio tracking the following information was also recorded: the vegetation cover the radio tracker was in (classed as open, light cover or dense cover), the topography of the area (classed as flat, gently sloping or steeply sloping), whether the radio tracker could see the 'badger' being radio tracked or not and the weather conditions during the course of the radio tracking session (classed as good, fair or bad). Each session lasted two hours and was repeated

twice, no routes taken by the 'badger' being the same. Volunteers were later asked about any previous experience of radio tracking and how confident they felt radio tracking.

The co-ordinates of the estimated position of the 'badger' were calculated based on the GPS position of the radio tracker, the estimated bearing and distance to the 'badger'. The co-ordinates of the actual position of the 'badger' were known from their GPS; the difference between the two positions could be calculated to give the linear error (Figure 3.1). In addition to the linear error, the distance error (the difference in the estimated distance to the 'badger' compared to the actual distance) and the bearing error (the difference in the estimated bearing to the 'badger' and the actual bearing) were also calculated.

To investigate the effect of the parameters mentioned above (vegetation cover, topography, whether the badger was visible to the observer, weather conditions and observer effects) on linear error a generalized least squares (GLS) (Pinheiro and Bates 2001) statistical mixed modelling approach was used with the 'NLME' package (Pinheiro et al. 2006) in 'R' (R Development Core Team 2006).

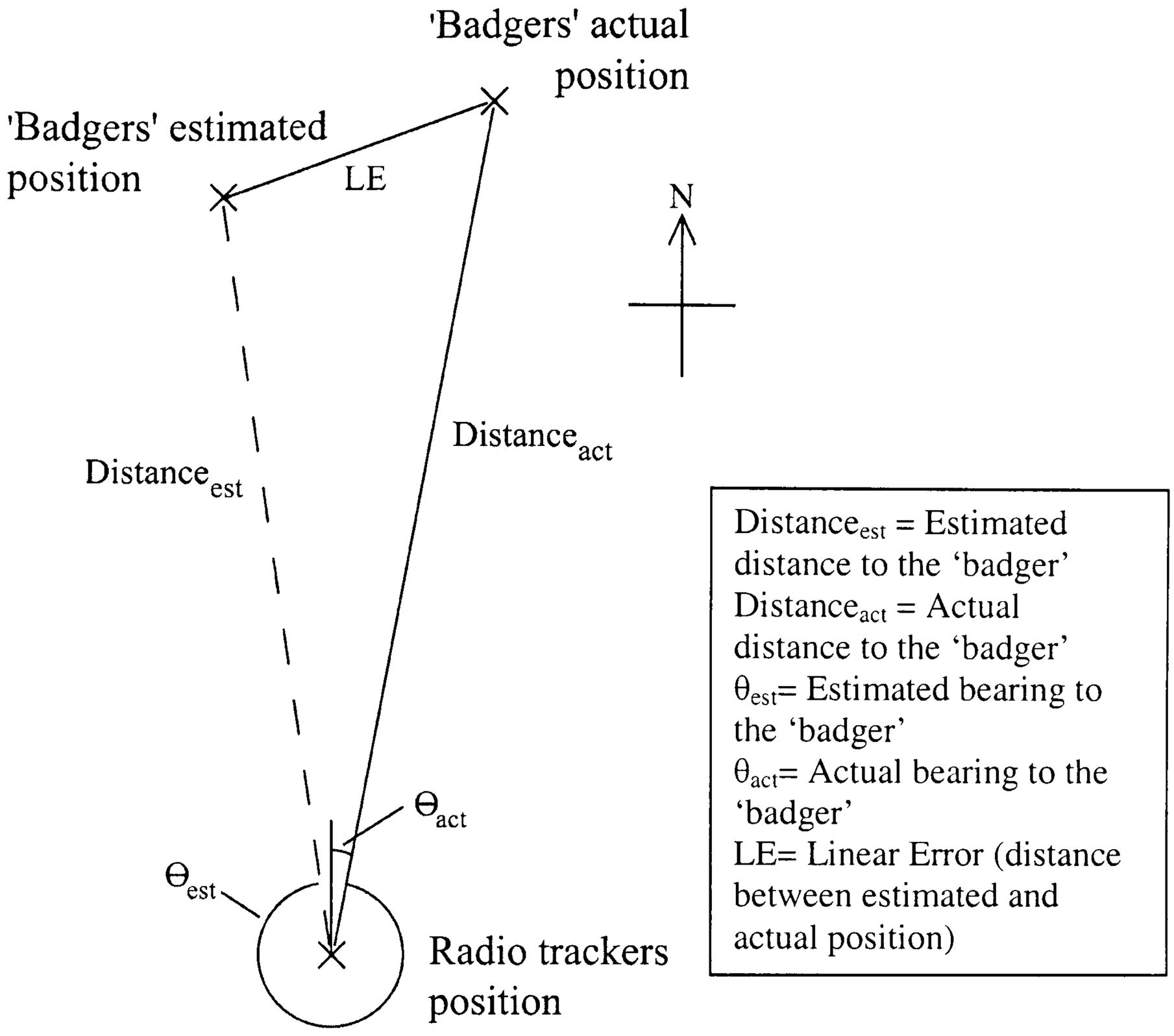


Figure 3.1. Diagrammatic representation of the calculation of Linear Error.

3.3.3 Travel distance and home range size error

The total distance travelled by the 'badger' was calculated from successive GPS locations that were recorded every 30 seconds by the 'badger' ('Badger'$_{act}$30), to represent the true route travelled by the 'badger'. These were compared to the total distance travelled recorded by GPS locations by the 'badger' every 5 minutes ('Badger'$_{act}$5) and the total distance travelled estimated by radio tracking every 5 minutes ('Badger'$_{est}$5). 100% Minimum Convex Polygon (MCP) home ranges were also calculated for each of the three data sets and the areas compared (see chapter 4 for further details of MCP's). Analysis was performed using the 'R' statistical and programming environment (R Development Core Team 2006).

3.4 Results

3.4.1 GPS precision

Eastings and Northings were tested separately for normality and found to be normally distributed ($GPS_{Easting}$ site 1: Z = 1.27, N = 105, $p = 0.08$, $GPS_{Northing}$ site 1: Z = 1.3, N = 105, $p = 0.07$, $GPS_{Easting}$ site 2: Z = 1.17, N = 105, $p = 0.13$, $GPS_{Northing}$ site 2: Z = 1.26, N = 105, $p = 0.08$) therefore ellipses could be plotted for both sites as ellipses assume a bivariate normal distribution. The areas of the 95% confidence ellipses were 68.85m² for site one (open habitat) and 181.40m² for site two (wooded habitat). The lengths of the major and minor axes were found to be 2.12m and 1.72m for site one and 3.69m and 2.61m for site two (Figure 3.2 A and B). The manufacturers of the GPS state the unit is accurate to 15m RMS (the square root of the average of the square errors) (Garmin 1999). The equivalent values found here are 2.73m and 4.52m for site one and two respectively, implying the unit is more accurate than stated.

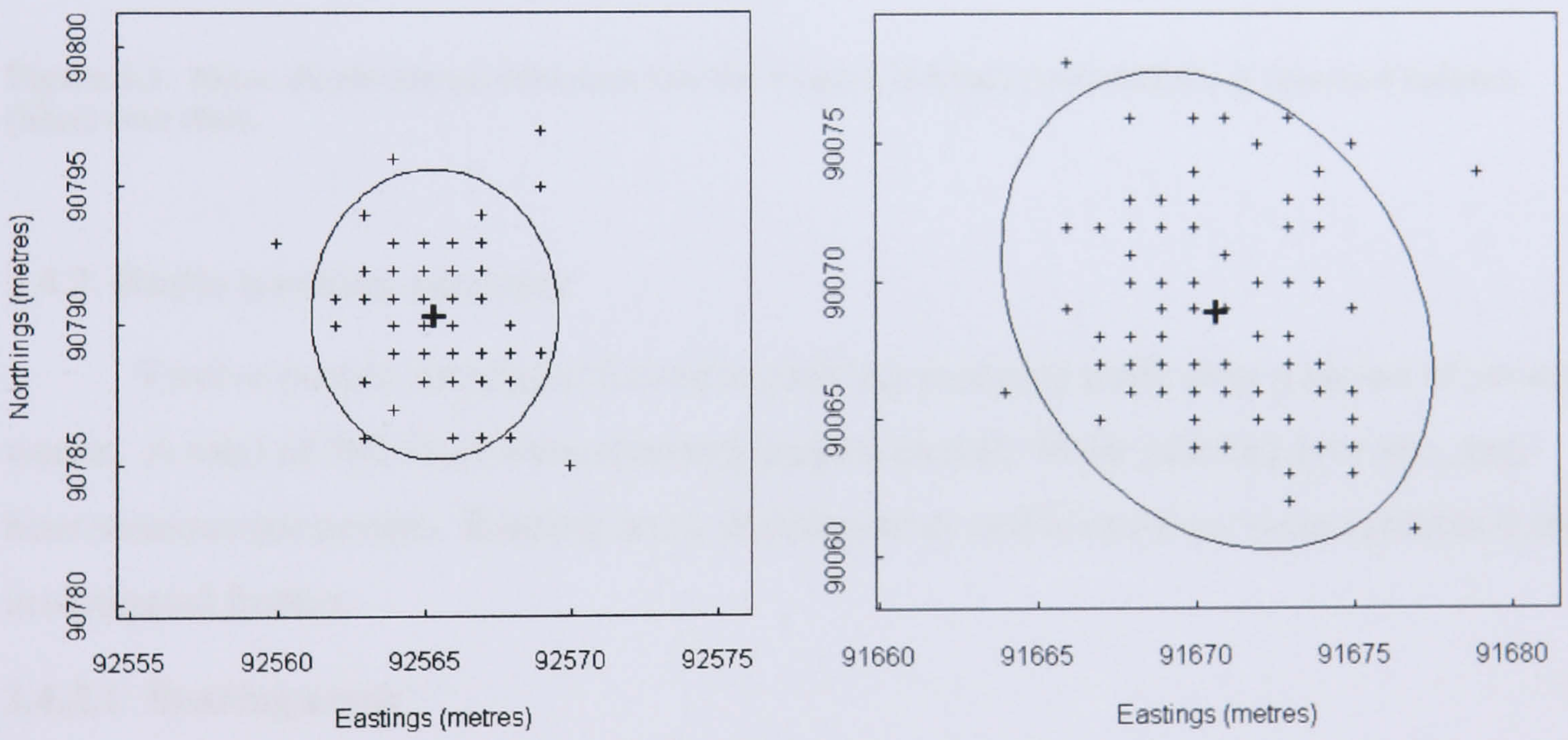


Figure 3.2. (A - left). 95% confidence ellipse for site 1: open habitat. The mean location (and the centre of the ellipse) is marked by the bold cross. (B - right). 95% confidence ellipse for site 2: wooded habitat. The mean location (and the centre of the ellipse) is marked by the bold cross.

Plots of mean displacement distance (the difference in the distance between the recorded location and the mean location) for each site reveal that when the GPS unit is first switched on the displacement distance is large. This distance decreases with time as the co-

ordinates converge on the average location. Both sites show a similar pattern, but site two has larger displacement distances (Figure 3.3).

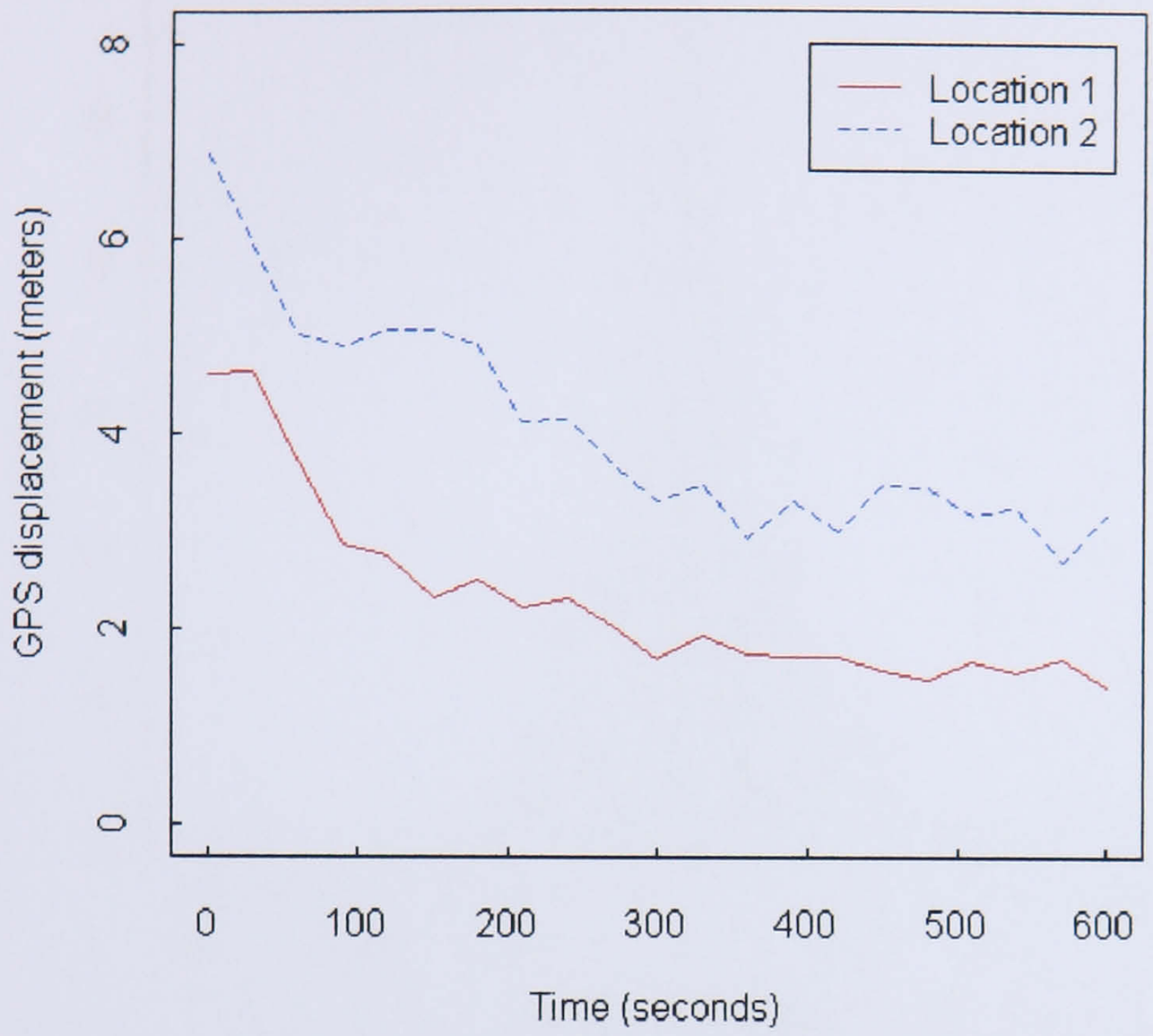


Figure 3.3. Mean displacement distances for site 1 (open habitat) (red) and site 2 (wooded habitat) (blue) over time.

3.4.2 Radio tracking accuracy

Twelve people completed the radio tracking accuracy study over a period of several weeks. A total of 565 fixes were obtained (approximately 48 per person) over two, two-hour sessions per person. Bearing error, distance error and linear error were calculated and investigated further.

3.4.2.1 Bearing error

A large consistent deviation away from zero in the bearing error data would indicate bias in the data. The bearing error ranged from -149.75° to 154.11° and showed a lepotkurtotic distribution with a mean of 3.24° ± 30.66° (two standard deviations) (Figure 3.4). A sign rank test on the bearing error data compared to zero was significant ($Z = -2.1$, $p = 0.03$, $N = 565$), indicating that overall the bearing error was not different from zero and therefore no adjustment to the data was needed. Bearing error was not correlated with estimated distance, distance error or linear error ($R_s = -0.03$, $p = 0.52$, $R_s = -0.04$, $p = 0.32$, $R_s = 0.08$, $p = 0.54$).

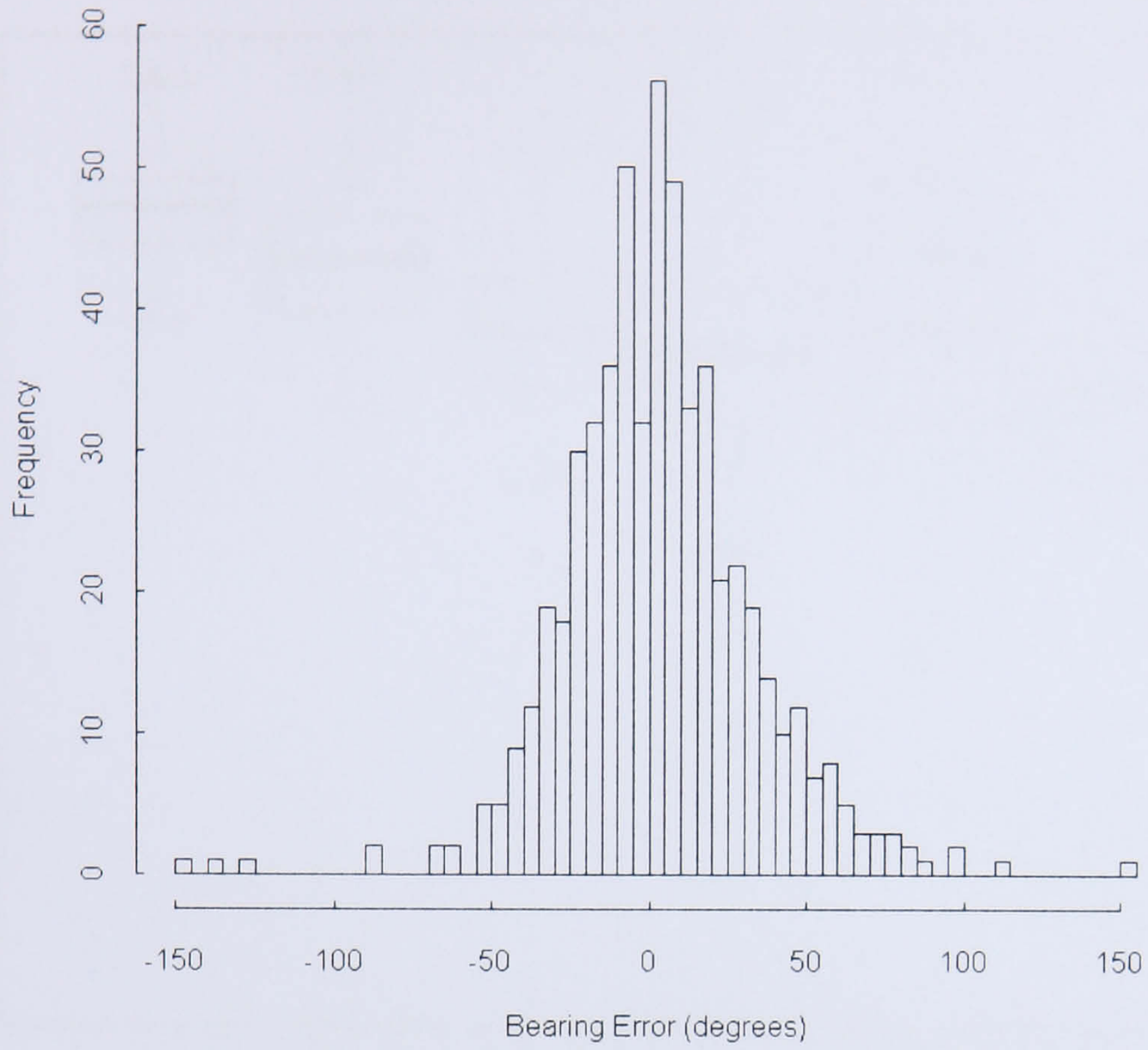


Figure 3.4. Frequency histogram of bearing errors; each bar represents 10° intervals.

3.4.2.2 Distance Error

The mean error in estimating the distance to the 'badger's' position compared to the actual distance to its position was –20.50 meters. The error ranged from –267.09 meters to 60.38 meters, indicating that distances are consistently underestimated and to a greater scale than overestimated, i.e. the distance is estimated to be 50 meters when it is actually 100 meters. However, a box and whisker plot of distance error and the actual distance shows that distances are overestimated at smaller distances and underestimated at distances greater than 50 meters. The greater the actual distance from the tracker to the 'badger', the greater the error in estimating distances (Figure 3.5).

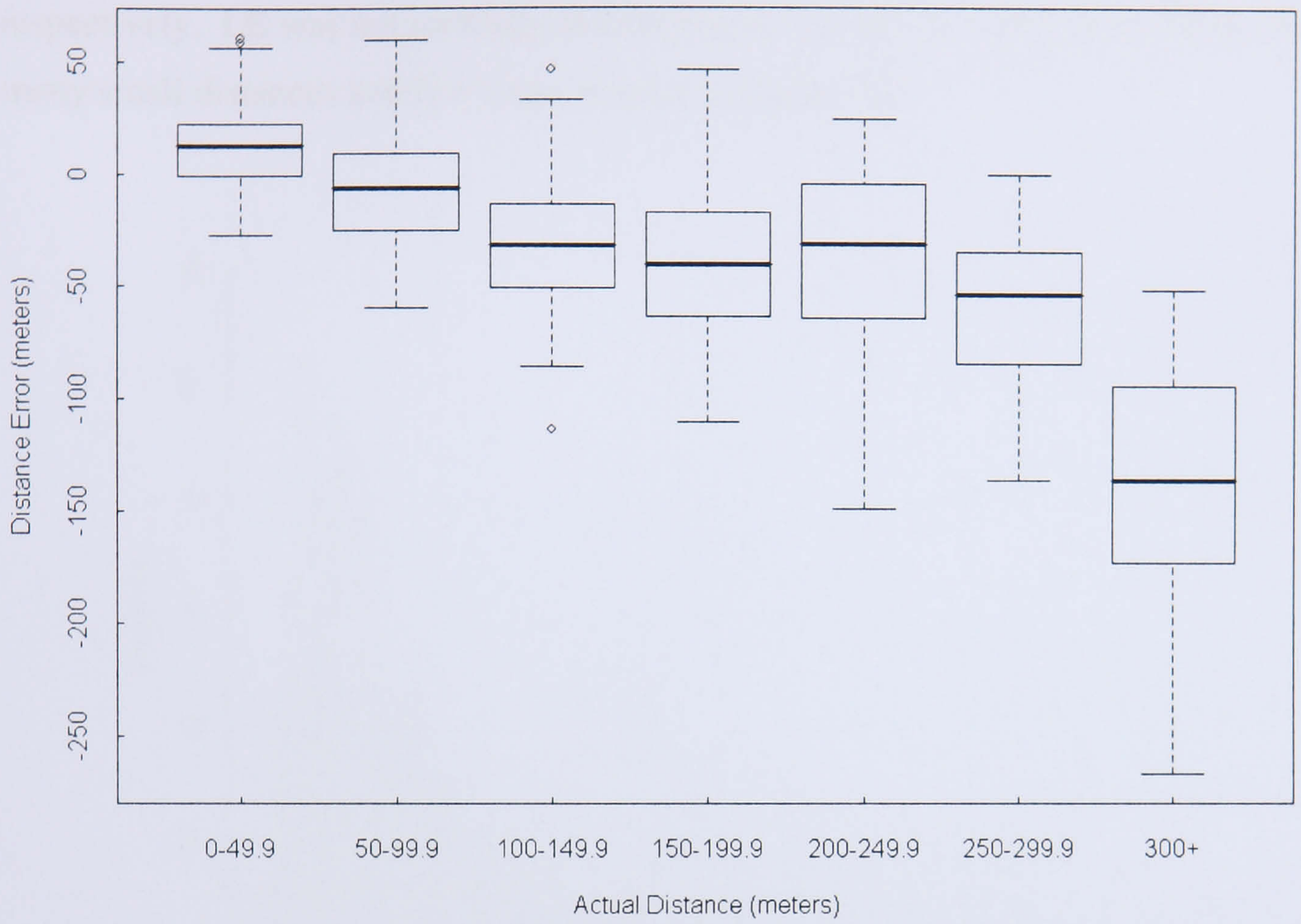


Figure 3.5. Box and whisker plot of distance error (actual distance minus estimated distance) and actual distance (separated into 50 metre intervals). The median value is represented by the thick bar, the interquartile range as the box and the full range as the whiskers, with outliers represented by circles.

Further investigation of the estimated distance revealed the maximum distance given was 250 meters even when the actual distance was upwards of 500 meters. Although the distribution of the estimated distance could be continuous it appeared to have several discrete steps, especially at larger estimated distances, e.g. distances were estimated mainly in 50-metre intervals. However, the estimated and actual distances were positively correlated (Spearman's rank correlation, $r_s = 0.808$, N = 565, $p < 0.001$).

3.4.2.3 Linear Error

The linear error (LE) (the distance between the estimated 'badgers' position and the actual 'badgers' position) incorporates both the bearing error and the distance error (to find the estimated position) and therefore is a better measure of accuracy than either bearing or distance error alone.

The mean LE was 54.93 meters, (SD = 49.12, range = 1.03-296.11m, N = 565). The 50% (median) and 95% confidence intervals were 40.89 and 151.20 meters respectively. LE was not normally distributed ($Z = 4.143$, $N = 565$, $p < 0.001$); there were many small distances and few large distances (Figure 3.6).

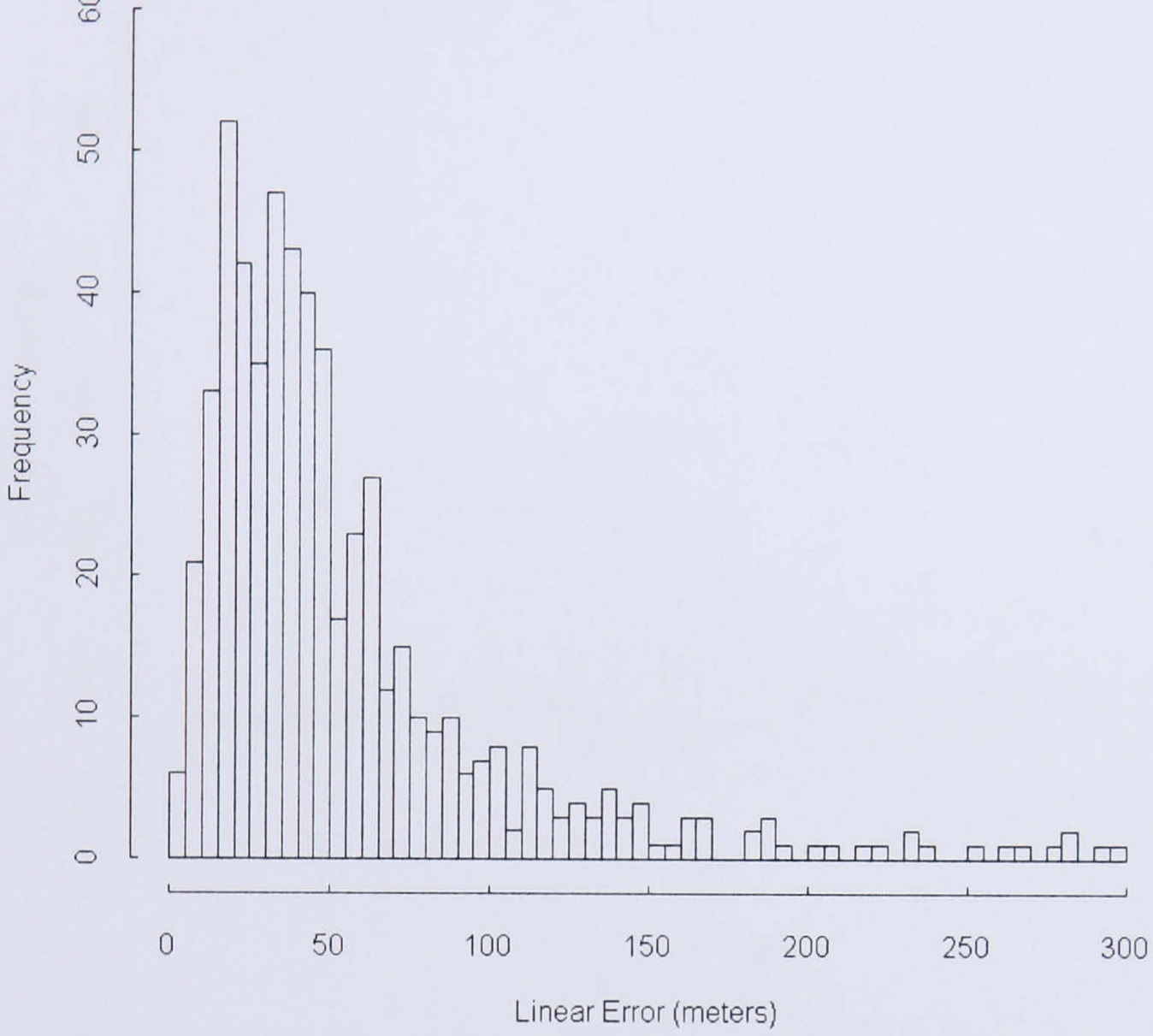


Figure 3.6. Frequency histogram of Linear Error (the distance between the 'badgers' estimated position and its actual position). Each bar represents a five-metre interval.

The estimated distance and actual distance to the 'badger' were positively correlated with LE ($R_s = 0.48$, $N = 565$, $p < 0.001$ and $R_s = 0.62$, $N = 565$, $p < 0.001$ respectively). As vegetation cover increased, LE also increased ($R_s = 0.72$, $N = 565$, $p = 0.04$) and when the 'badger' was visible to the radio tracker LE was significantly smaller ($Z = -5.14$, $N = 565$, $p < 0.001$). Topography and weather condition had no obvious significant linear effect on LE. LE varied between persons, the mean error varying from 36.74m to 89.21 m for the 'best' and 'worst' person respectively ($F_{11, 553} = 5.61$, $p < 0.001$) (Figure 3.7). For the purpose of the GLS model, people were subsequently divided into two categories: inexperienced or experienced at radio tracking. The allocation of people to either category was based on the approximate number of nights each person had been radio tracking for (less than 30 days or greater than 30 days respectively) and how confident they felt at radio

tracking. With the exception of one inexperienced person who was clearly very good at radio tracking and who was therefore moved into the experienced category, this information agreed with the mean LE for each person and there were five people in the inexperienced category and seven in the experienced category.

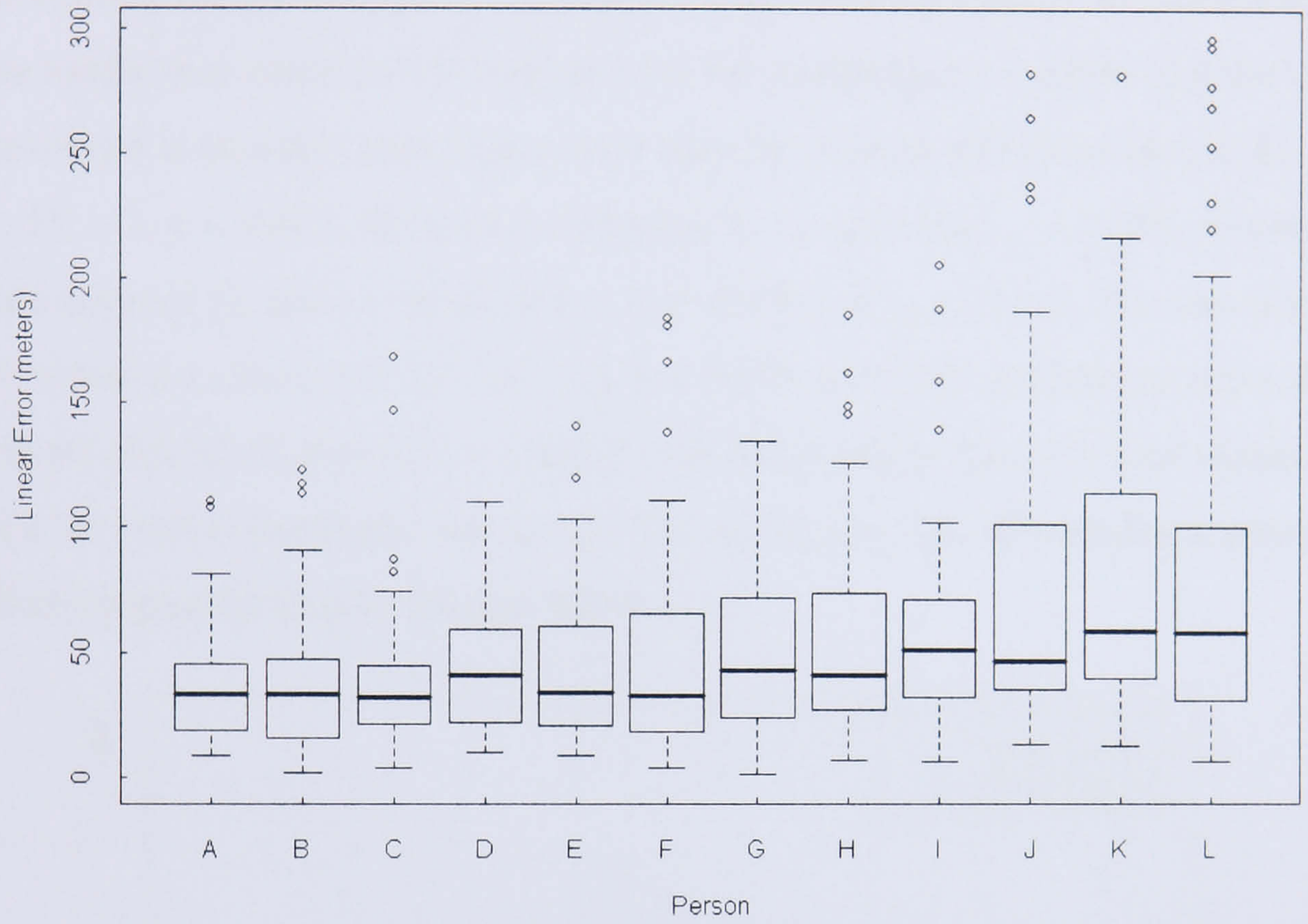


Figure 3.7. Box and whisker plot of Linear Error (distance between estimated 'badgers' position and actual 'badgers' position). The median value is represented by the thick bar, the interquartile range as the box and the full range as the whiskers, with outliers represented by circles. Each person has been ranked according to his or her mean Linear Error value.

A linear regression model was fitted to verify underlying statistical assumptions were not violated, heterogeneity of variances and non-normality were identified so a GLS model was used in preference to transforming the data. Experience (coded as experienced or inexperienced), vegetation type (coded as open, light cover or dense cover), topography (coded as flat, gentle slope or steep slope), weather conditions (coded as good, fair or bad), whether the badger was visible (coded as yes or no), and estimated distance to the 'badger' were used to model linear error. One variance covariate term was allowed and backwards stepwise selection using maximum likelihood (ML) was carried out manually to remove insignificant terms. The final model was presented using restricted maximum likelihood (REML; (West et al. 2007)).

The minimal adequate model was a linear regression with a GLS extension incorporating one two-way interaction term and two single terms (adjusted R-squared = 0.38). The two single terms were expected distance and experience code. The two-way interaction was experience code × estimated distance. The variance-covariate term was estimated distance. Using a likelihood ratio test and the drop in the adjusted R-squared value as a proxy for the variables importance in the model (Dyson et al. 2007), the full adequate model was compared to models with the independent variable and the interaction it was involved in omitted; experience code had the greatest influence on LE (L-ratio = 184.41, d.f. = 3, $p < 0.001$, decrease in adjusted R-squared (R^2_{dec}) = 0.30), followed by estimated distance (L-ratio = 50.42, d.f. = 3, $p < 0.001$, R^2_{dec} = 0.10). The two-way interaction had a L-ratio of 27.55, d.f. = 4, $p < 0.001$ and 95% confidence intervals (coefficient) of 0.32 (0.20-0.43), $p < 0.001$. LE increased as the estimated distance increased for both experienced and inexperienced people, but increased at a greater rate for inexperienced people (Figure 3.8 and Table 3.1).

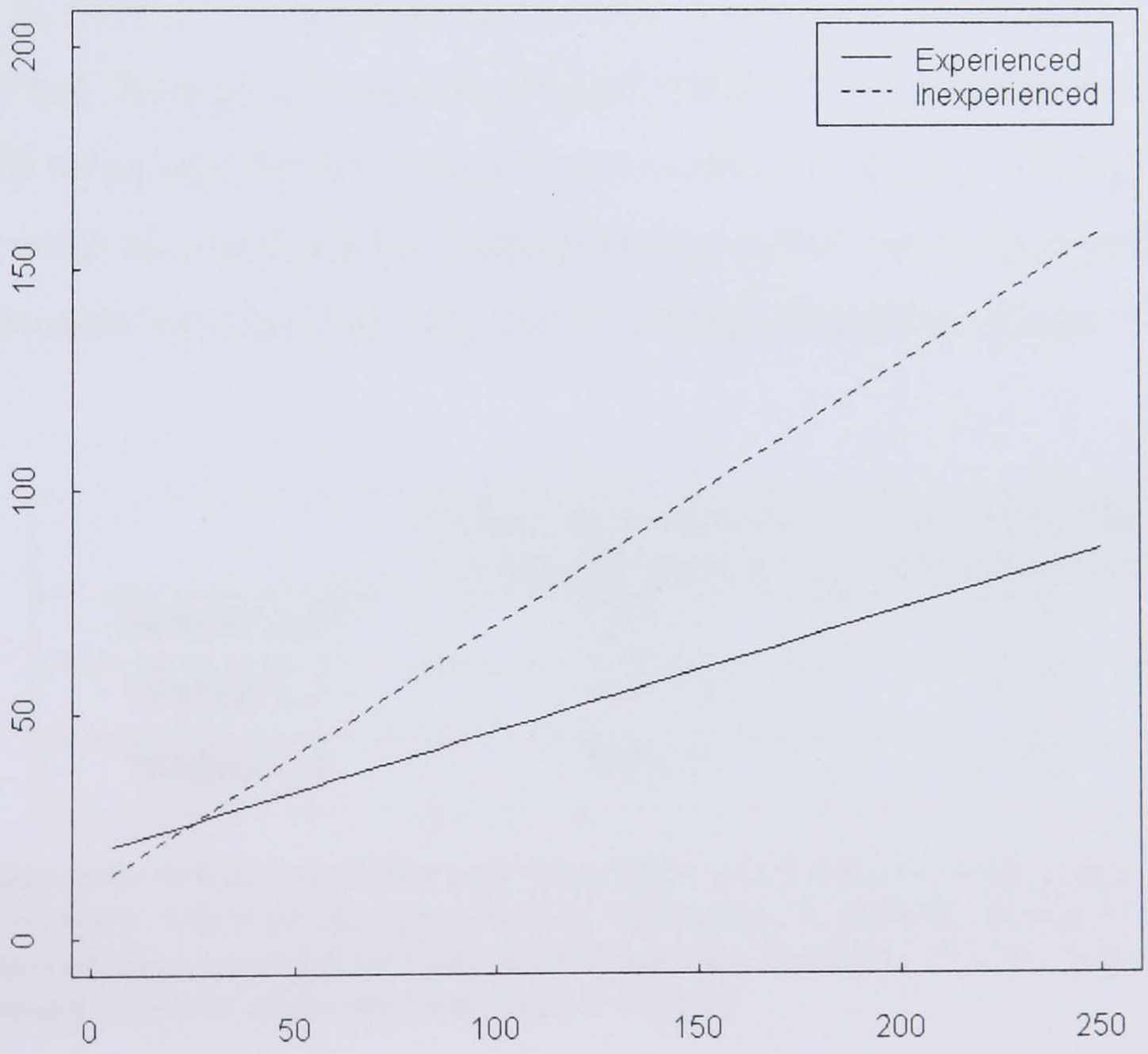


Figure 3.8. Values of Linear Error (in meters) at different estimated distances for experienced and inexperienced people based on the GLS model predictions.

Estimated distance (meters)	Inexperienced	Experienced
0	11.23	19.06
15	20.04	23.14
25	25.91	25.86
50	40.59	32.66
75	55.26	39.46
100	69.94	46.26
150	99.30	59.86
200	128.66	73.46
250	158.01	87.06
300	187.37	100.65
350	216.73	114.25
400	246.09	127.85
500	304.80	155.05

Table 3.1. Values of Linear Error (in meters) at different estimated distances for experienced and inexperienced people based on the GLS model predictions.

3.4.3 Travel distance and home range size error

The differences in total distance travelled between the three groups ('Badger'$_{act}$30, 'Badger'$_{act}$5 and 'Badger'$_{est}$5) were significant (ANOVA: $F_{2, 69} = 7.44$, $p = 0.001$), with 'Badger'$_{act}$30 being significantly longer than the other two groups. Taking locations at five-minute intervals shortened the total distance travelled, but estimating the locations every five minutes increased the route, due to incorporating error (Figure 3.9 and Table 3.2).

	Mean total distance travelled (meters)	Mean 100% MCP size (hectares)
'Badger'$_{act}$30	2526.24	13.28
'Badger'$_{act}$5	1895.08	10.25
'Badger'$_{est}$5	2094.03	10.02

Table 3.2. Mean total distance travelled and mean 100% MCP area for each group; 'Badger'$_{act}$30 refers to the 'badgers' actual position recorded by GPS every 30 seconds, 'Badger'$_{act}$5 refers to the 'badgers' actual position recorded by GPS every 5 minutes, 'Badger'$_{est}$5 refers to the 'badgers' estimated position found by radio tracking every 5 minutes.

There was no difference in the 100% MCP size between the three groups (ANOVA: $F_{2, 69} = 2.11$, $p = 0.129$), indicating that recording locations at different time intervals did not significantly affect home range size, although MCP size was largest when recording the 'badgers' actual position every 30 seconds (Figure 3.10 and Table 3.2).

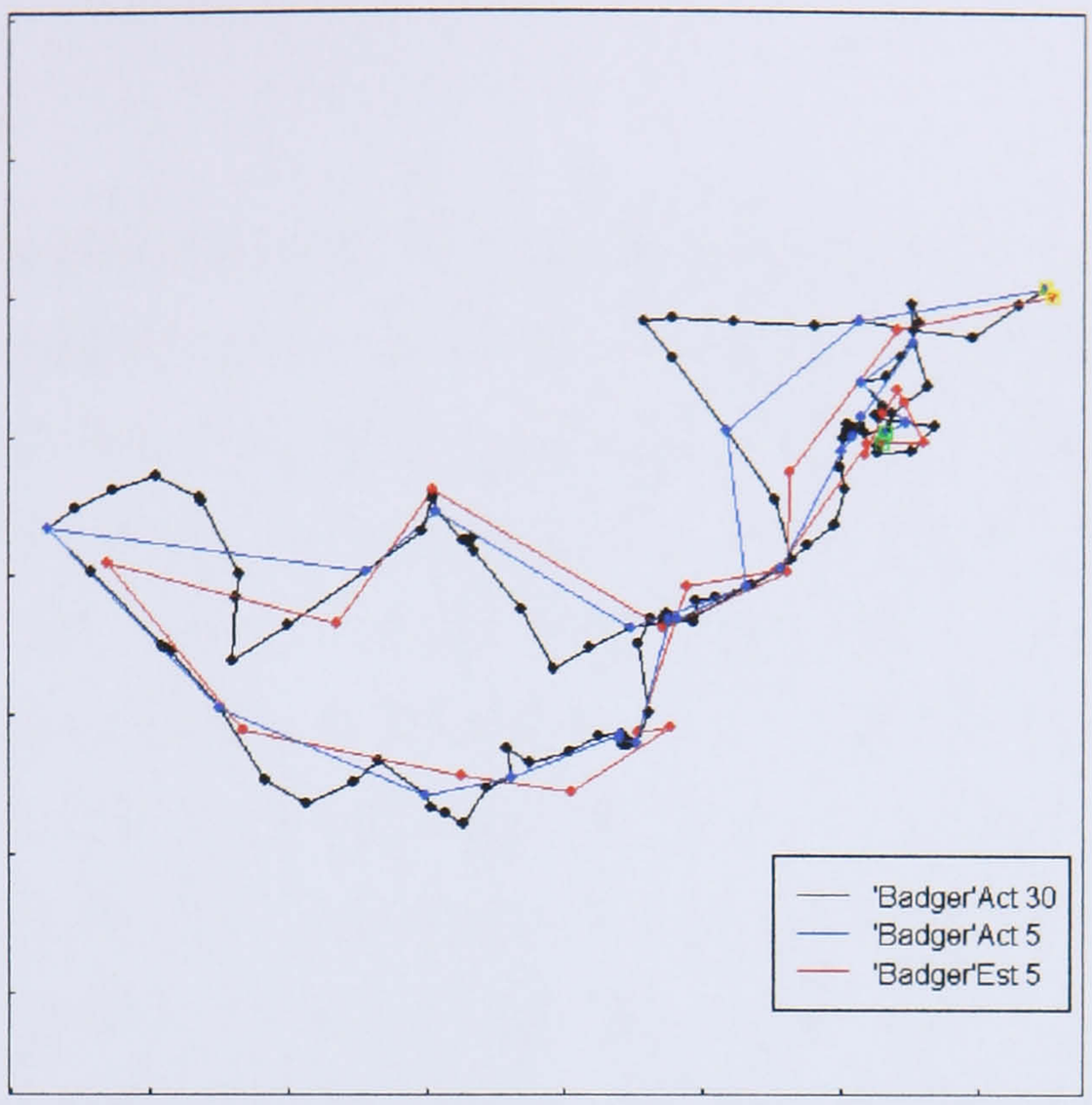


Figure 3.9. An example of a route obtained from one person during one two-hour session. 'Badger'Act 30 refers to the 'badger's' actual position as recorded by GPS every 30 seconds, 'Badger'Act 5 refers to the 'badger's' actual positions as recorded by GPS every 5 minutes, 'Badger'Est 5 refers to the 'badger's' estimated position found by radio tracking every 5 minutes. The green point refers to the initial location and yellow to the final location, axis ticks mark 100-metre intervals. In this example total distances travelled are 2682.57m ('Badger'Act 30), 1901.18m ('Badger'Act 5) and 1824.15m ('Badger'Est 5).

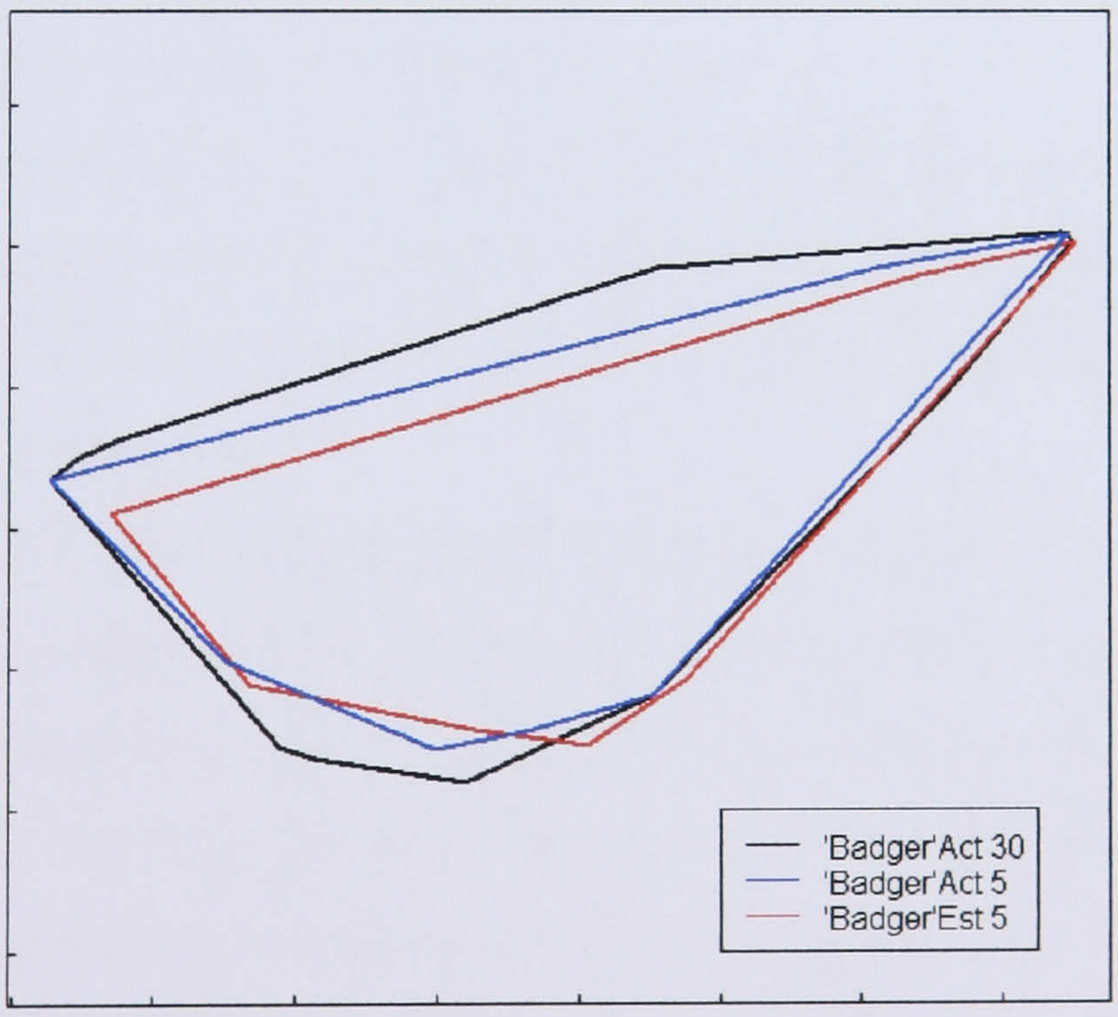


Figure 3.10. An example of a 100% MCP obtained from one person during one two-hour session based on the route shown in Figure 3.9. 'Badger'Act 30 refers to the 'badger's' actual position recorded by GPS every 30 seconds, 'Badger'Act 5 refers to the 'badger's' actual positions recorded by GPS every 5 minutes, 'Badger'Est 5 refers to the 'badger's' estimated position found by radio tracking every 5 minutes. Axis ticks mark 100-metre intervals. In this example 100% MCP areas are 14.84ha ('Badger'Act 30), 12.10ha ('Badger'Act 5) and 10.78ha ('Badger'Est 5).

3.5 Discussion

3.5.1 GPS precision

The error in the precision of the GPS was found to be small in comparison to the errors obtained from radio tracking. The GPS was found to be more precise in open areas where there is a clearer view of the sky compared to areas with overhead vegetation cover. In open areas the GPS was also more precise more quickly, due to the GPS being able to find satellites more easily, which is consistent with other studies, e.g. (Cargnelutti et al. 2007). The main limitation with this experiment is that all precision and displacement values are based on the mean GPS position. This may have an inherent error or bias that would not be detected during this experiment. The only way to overcome this problem would be to have the location surveyed which is expensive and time consuming and beyond the remit of this experiment, therefore, the mean location was considered the next best alternative.

For the current radio tracking regime, fixes are recorded every five minutes, by which time the GPS unit is relatively precise (mean displacement error at five minutes is 1.88 m and 3.68 m on open and vegetated areas respectively). During radio tracking the observer will be moving around (unless the animal is stationary) to record the location of the animal, and the GPS unit will be constantly updating its position. In this experiment the GPS unit was switched on at the start of the ten-minute period so would have to register satellites from an unknown starting position, unlike during radio tracking where it is updating its position. This will mean the unit is more precise during radio tracking than the experimental values found here.

The fact that the GPS is less precise in areas with overhead vegetation cover is most likely due to signal multipath effects; the signal is reflecting off the vegetation and terrain. The unit will automatically average the signal over time to help reduce these effects (Harre 2001), but when radio tracking the observer may also move to different areas with less overhead cover if they are aware there is not a very strong GPS signal. When radio tracking, the observer has a map with them as well as a GPS unit, and the map has grid references marked which correspond to the GPS position, so if the GPS unit shows a position that may be suspect it can be checked on the map.

It has also been shown that a better GPS signal can be obtained during the night due to ionospheric effects (Parkinson 1996a). This experiment was conducted mostly during

the day and early evening whereas radio tracking is conducted from dusk onwards, thereby further increasing the precision of the signal.

In conclusion, whilst there is some slight imprecision and error associated with using a GPS, it is negligible compared to the potential error obtained when radio tracking. The values found during this experiment are also inflated compared to the values when actually radio tracking further increasing the precision of the GPS position, meaning the error can effectively be ignored when used as part of a radio tracking system.

3.5.2 Radio tracking accuracy

This study was very comprehensive compared to other similar studies with a total of 565 location fixes obtained from 12 different people (c.f. (Zimmerman and Powell 1995, Marzluff et al. 1997, Kauhala and Tiilikainen 2002)). This type of study is generally thought of as being time consuming, expensive and site specific, so not carried out often enough (Withey et al. 2001). However, it aids in understanding the factors affecting telemetry accuracy in specific study areas and is relevant to any study involving radio tracking.

3.5.2.1 Bearing error

The mean bearing error was +3.24°, which was not considered to be significantly different from zero to need to be accounted or adjusted for in this study. The slightly positive value is probably due to observer inaccuracy in recording the compass reading and rounding error, as values are usually rounded up. A consistent bias in the bearing error would indicate a particular location is favoured, as a result of a problem with the compass or if the compass is held near to something magnetic. Observers were aware that the compass reading may be affected if held close to the yagi antennae or GPS unit when radio tracking, so were able to alleviate the problem.

3.5.2.2 Distance error

Analysis of the distance error revealed that distances are usually underestimated, especially as the distance increases. Distances were also estimated in steps of up to 50 meters at larger distances. This is because judging the distance is based on the strength of

the radio signal, and it is often hard to discriminate between strengths, especially at larger distances when the signal is weak. It takes considerable practice to be able to estimate the distance, but feedback from this study is likely to help improve the accuracy of distance estimation if observers know they are likely to underestimate the distance. The maximum distance estimated was 250 meters; this was probably because it was thought this was the approximate maximum range of the radio tracking equipment under certain circumstances, though this study has shown it to be much larger.

Under field conditions, if the observer loses the signal to the badger or it becomes too weak to accurately detect the direction of the signal, the observer would record the badger's position as temporarily unknown for the particular 5-minute fix and spend the time trying to find and get closer to the signal. In this study, because the observers knew they were being assessed on their ability, they were more likely to record any location rather than no location; therefore under field conditions such inaccurate fixes are less likely to occur.

3.5.2.3 Linear error

The factors that were best able to predict LE in this study were the experience level of the observer and the estimated distance to the 'badger'. Other factors investigated - vegetation type, weather conditions, slope type and whether the 'badger' was visible - were not used in the final model. All these variables were initially considered because they can be recorded at the time of radio tracking. The actual distance may be a better predictor of LE than the estimated distance but this is not known at the time of tracking. Classifying the experience level of the observer into two categories (inexperienced and experienced) may be over-simplistic, but it makes for a simpler and easier to apply final model. The effect of both observer experience and distance to the transmitter on radio tracking accuracy are consistent with other studies (Hoskinson 1976, Springer 1979, Withey et al. 2001, Theuerkauf and Jedrzejewski 2002).

Whether the 'badger' was visible or not to the observer was intended to be a proxy for whether the badger could be heard when radio tracking in field conditions. Because of their secretive nature, badgers are seldom seen but can often be heard snuffling about in the undergrowth (Neal and Cheeseman 1996), alerting the observer to their position, and decreasing the error in recording their position. In practice, the human 'badger' in this

experiment could be seen at long distances away in open flat areas (fields) and could get quite close without being seen in forested areas if they were quiet and there were elevated levels of background noise compared to night time, therefore this was not as good a proxy as originally intended and could be one reason why it was not used in the final GLS predictive model.

Observers may be putting more effort into detecting the radio signal in denser vegetation areas or areas where the signal is weaker or directionality harder to detect, and therefore compensating for the potentially more inaccurate signal and may be the reason these variables were not significant in the model. In the study area there were also no extremes of habitat, e.g. no canyons or mountains, no snow or high voltage power lines which may cause signal bounce (Beaty and Tomkiewicz 1990, Parker et al. 1996) or affect the accuracy.

In this study all the people completing the radio tracking knew they were under observation, potentially biasing the results (Mills and Knowlton 1989); this was not possible to avoid because if the study was carried out at night during radio tracking of real badgers the person being the study 'badger' would need a torch to see where they were going, allowing the observer to see them easily and to see what was happening (as well as disturbing active badgers).

The mean LE of 54.93 ± 2.07m (SE), range 1.03-296.11 meters, found in this study is larger than that found by Palphramand (2005) in the same habitat (33.16 ± 4.01m (SE), range 7.23-65.79m). However, Palphramand (2005) based this result on just 15 locations, of which only seven were moving, and this was the result from just one (experienced) person. It is also larger than that found by Newton-Cross (2003), in the same habitat of 29.94 ± 3.34m (SE), but this was based on just 21 locations and they were all stationary, suggesting further that moving beacons have larger errors associated with them (Schmutz and White 1990). The LE found in this study is smaller than many other studies on badgers, e.g. Kowalczyk et al., (2003) had a location error ranging from 100-150 meters, and Revilla and Palomares (2002), found a location error of less than 245 meters 95% of the time (range 50-2700 meters). Many studies of badgers using radio tracking do not report at all on the accuracy (e.g. (Kruuk and Parish 1982, Rodriguez et al. 1996, Broseth et al. 1997)), giving no indication of the reliability of the results. Kauhala and Tiilikainen (2002) imitated hare movements and found a mean LE of 281 meters (range 20-1123 meters), and also found that distance and different observers effected LE, they also found a difference in LE

between seasons, something that was not investigated here. Zimmerman and Powell (1995) found a mean LE of 279 meters (range 10-440 meters, 95% less than 766 meters), when investigating the accuracy of locating black bears (*Ursus americanus*) in America. This was with stationary beacons so may under-estimate the accuracy compared to moving beacons (Schmutz and White 1990), and observers did not know they were being tested (Mills and Knowlton 1989).

LE in this case refers to a study using the homing-in method of radio tracking, and estimating the distance to the transmitter has been found to affect LE, whereas the bearing error does not. In the majority of radio tracking studies, the animal is located by triangulation and the distance does not need to be estimated as the animal's position is estimated by the intersection of the bearings. This eliminates one source of error but introduces others, so care must be taken in applying these results to other studies using different methods. Neither method is better for locating an animal; each has their advantages under different circumstances and depends on the objectives of the study.

3.5.2.4 Travel distance and home range size error

The route considered to be the true route travelled by the 'badger' was significantly longer than the 'badger's' route sampled at 5-minute intervals and the estimated route at 5-minute intervals. The estimated route was longer than the 5-minute 'badger's' route which is due to errors in locating the badger, but the increase in the error does not make up the whole distance of the true route. If the distance travelled is the main focus of the study it may be possible to apply a correction factor to the estimated route to account for this difference (Rouys et al. 2001, Kauhala and Tiilikainen 2002).

There was no significant difference in the size of 100% MCP's estimated from the different sampling intervals, indicating that sampling interval and location error is accounted for to a certain extent within the MCP. Only 100% MCPs have been used in this study; other home range estimators may give different results and should be investigated further.

3.5.3 Implications

This study has shown not only that LE varies at different location estimates, but also that it varies with different people and distances. Many studies do not report on the accuracy of the radio tracking positions (Saltz 1994), but as it can vary and potentially affect the results to a large degree it should be given a higher priority. Too many studies use radio locations as a true position of the animal when they are only an estimate (White and Garrott 1990), and there is some error associated to them.

Once LE has been quantified it can be used in several ways. Firstly, it will alert observers to areas in the study area and circumstances under which LE may be greater, allowing the observer to compensate for a potentially greater error, and either put more effort into obtaining an accurate position estimate, or move to a different area where the accuracy may be increased. Secondly, it may allow a threshold to be set for data inclusion; (Saltz and Alkon 1985) data which are found to have too great an error associated with them can then be excluded or used with caution. Thirdly, when using radio locations for estimating home range sizes, habitat use or distances travelled, LE can be incorporated into the results; the tracking resolution can be increased or the size of the habitat patch the animal is estimated to be in can be increased or a correction factor applied; the LE value can be used to provide a radius for a circle about the location within which the animal is likely to be found.

With advances in technology and the increased use of GPS collars, radio tracking may well become a less favoured technique. However, many studies have used radio tracking in the past, and many will continue to use it in the near future, so investigation of the error associated with this technique and incorporation of these errors into the analysis is important to assess the reliability of any conclusions.

Chapter 4 Home range analysis and space use behaviour of badgers determined from radio tracking data

4.1 Introduction

Understanding how individuals of different sex, age and disease status use the space and resources within the area in which they live allows us as external observers to understand the interactions that occur between these animals. Within this chapter the use of different statistical approaches to understanding the space use of individual animals are discussed and how these data can also be interpreted so that the interactions between individual animals can be understood with relevance to their sex, age and disease status. Specifically, the spatial organisation of badgers from different social groups in a high density population (Woodchester Park) is investigated.

The preferred method of data collection for this project has been radio tracking of badgers and hence the statistical methods discussed are biased towards the most appropriate methods for this data collection technique, the accuracy of the radio tracking methods used in this study has been discussed in chapter 3 and is relevant here. The collars fitted to badgers in this study also act as proximity loggers, but in this chapter only the radio tracking data are considered; the proximity data are considered in chapters 5 and 6.

4.1.1 What is a home range?

Burt (1943) first defined a home range as "the area traversed by an individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range." This definition however, does not specify a temporal component; seasonal factors and status of an individual can influence home range dynamics and should be fundamental to its definition (Morris 1990), therefore a home range should be redefined as "the extent of area with a defined probability of occurrence of an animal, during a specified time period" (Kernohan et al. 2001).

For many behavioural and ecological studies, being able to quantify an animal's home range size, shape and pattern of utilisation is important. For example, studies investigating population density, foraging behaviour, resource availability and habitat

selection, spacing and movement of individuals and interactions between individuals all require knowledge of home range size, shape or utilisation (Harris et al. 1990).

Several methods exist to determine home range. These include visual observation of tagged individuals (Metcalfe 1986), spotlighting of marked individuals at night (Mills and Gorman 1987), trapping and recapture data (Dice and Clark 1953), bait marking methods (Delahay et al. 2000a), fluorescent dye methods (Mullican 1988) or radio-telemetry methods. Radio tracking as described in chapters 2 and 3 is the technique utilised here to determine home ranges because of its ability to compare differences between individuals (Harris et al. 1990). However, whilst using radio tracking the method of data collection, the method of analysis and the software used can give widely varying results (Lawson and Rodgers 1997), and care should be exercised in the interpretation of the findings.

4.1.2 Home range estimators

Home range estimators fall into three groups; polygon methods, grid cell methods and probabilistic methods.

Polygon methods were the first to be developed and the Minimum Convex Polygon (MCP) (Mohr 1974) is the oldest home range estimator and one of the most commonly used. A MCP connects the outermost location points of an animal's movements to form a shape with external angles greater than 180 degrees (Southwood 1996). The 100% MCP includes all the locations but a convex polygon can be plotted around a lesser proportion of the locations to give a core area. Other polygon methods include concave polygons, restricted polygons or cluster analysis. These methods connect locations but with the possibility of concave lines between points or restricting certain areas to not be included in the polygon.

Harris et al. (1990), suggest MCPs should always be quoted in studies (along with another method) to allow comparison between studies. As such they are widely used as a home range estimator. However, MCPs are highly sensitive to sample size (Seaman et al. 1999), spatial resolution (Hansteen et al. 1997) and sampling duration (Swihart and Slade 1985a). Therefore if MCPs are to be used for comparison between studies the sample sizes should be matched, along with matched sampling durations and similar treatment of outliers. The major disadvantages of using MCPs to define home ranges is that peripheral

location fixes have a strong influence on range size and they include areas never visited by the individual and provide no information on intensity of range use. Other methods attempt to overcome these problems.

The second group of home range estimators are grid cell methods. Siniff and Tester (1965), developed the method that uses a set grid overlaid on a series of location points. The set of occupied grids allows for simple three-dimensional contouring of ranges for graphical representation but does not calculate home range as effectively as other techniques (Harris et al. 1990). This technique is not widely used as better techniques have replaced it.

The final group of home range estimators are probabilistic methods. These use interpolation and extrapolation based on the distribution of the data and describe the relative frequency distribution for the location data over a specific time period: the utilization distribution (Van Winkle 1975). The main advantage of probabilistic methods therefore is that the home range boundary is calculated based on the complete distribution of an animal's location points, rather than just the outermost set of points (Kernohan et al. 2001). Probabilistic methods fall into two groups; parametric methods and non-parametric methods. Parametric methods assume that an individual's pattern of space use conforms to a particular probability distribution. These methods include circular (Hayne 1949) and elliptical (Jenrich and Turner 1969, Dunn and Gipson 1977) approaches; the boundary used to define home range size and more restricted circles or ellipses is used to represent the internal range structure. Both these techniques assume a bi-variate normal distribution of the location data around only one centrally placed peak of activity, and that the location fixes are independent. These assumptions are generally violated with radio tracking data (Powell 2000).

Non-parametric methods do not require a known probability distribution, but instead characterise a variety of utilization distributions. Methods include Fourier series (Anderson 1982), harmonic mean distribution (Dixon and Chapman 1980), and kernel estimators (Worton 1989). Kernel estimators have become the most widely used of these methods; they can fit multi-modal and irregular shaped distributions, they are robust to variable sample sizes and they are not so sensitive to the problems of auto-correlation compared to parametric methods (Seaman et al. 1998).

Kernel methods estimate the density of a distribution at any point. By adding the proximity of observations to each evaluation point, a density estimate is obtained, on which

contours are modelled (Seaman et al. 1998). A smoothing factor (bandwidth), *h*, is used to describe the search radius about the evaluation point. A fixed kernel uses a single smoothing factor (*h*) for evaluation of the entire dataset, whereas an adaptive kernel evaluates a new smoothing factor for areas of the dataset with different densities. Kernel methods are sensitive to the smoothing factor chosen, and minor changes in the smoothing factor can have a relatively large effect on range size (Harris et al. 1990). Two statistical methods exist to choose an appropriate smoothing factor; reference smoothing and least-squares cross validation (LSCV). The reference smoothing parameter is the standard deviation of x and y coordinates divided by the sixth root of the number of locations, and LSCV estimates various bandwidths to find one that minimises the difference between the unknown true density function and the kernel density estimate (Seaman and Powell 1996).

One main drawback of probabilistic and non-probabilistic methods is that they assume independence of successive location data (Dunn and Gipson 1977), i.e. that the location of an individual at time *t* is independent on the location at time *t-1* (Swihart and Slade 1985a). The assumption is that auto-correlated data yield less information than independent data and underestimate home range size (Swihart and Slade 1985b). Methods of avoiding auto-correlated data are to use a time interval between successive locations that is large enough to assume data is independent, or to sub-sample the data. These methods, however, may exclude biologically meaningful data (Reynolds and Laundre 1990), and sampling locations adequately throughout the duration of the study is more important than determining a statistically significant time interval (McNay et al. 1994).

4.1.2.1 Accounting for telemetry error in home range estimates

As chapter three described, there is a certain level of error associated with radio tracking to record animal locations; radio tracking provides a best estimate rather than an accurate location (Springer 1979). This error may affect the home range estimate; the size and shape of the home range boundary may be affected, as may the pattern of space use within it. Several methods have been proposed to account for, or overcome the error, the simplest of which is to apply a boundary strip to polygon edges and areas. The boundary strip is half the width of the resolution of the data (Kenward et al. 2003), the resolution being the accuracy of the radio tracking. This method effectively applies a buffer to the home range estimate boundary; however, it can only be used with polygon home range

estimators. Moser and Garton (2007) investigated the effect of telemetry error when calculating home range estimates using the fixed kernel density estimator. They found telemetry error was unlikely to have a significant effect on fixed kernel density estimates for most wildlife telemetry studies provided there was an adequate sample size. Due to the smoothing function of kernels, they may be inherently more robust to telemetry error than other home range estimators (Marzluff et al. 2001). Moser and Garton (2007) proposed using an error ratio (ER) as way to evaluate the effect telemetry error may have before a study is undertaken; the ER can be calculated before the study starts to see if the study design is appropriate to the hypothesis being tested. They defined the error ratio as (equation 4.1):

$$ER = \frac{CEP_{0.50}}{A} \qquad \text{(Eqn. 4.1)}$$

Where $CEP_{0.50}$ is the Circular Error Probable (Moen et al. 1997), which is a circle with a radius based on the median location error, and A is the approximate area of the home range of the animal under investigation. Moser and Garton (2007) calculated the error ratio for many published wildlife studies and subsequently suggest categorising the error ratio into the following intervals: 0 (no error in the study), 0.001 – 0.009 (most wildlife telemetry studies), 0.010 – 0.049 (some telemetry studies with a relatively inaccurate telemetry system), and 0.050 – 0.200 (extreme cases with unacceptable telemetry error).

4.1.3 Core areas

A core area is an area that is used more extensively than expected, resulting in statistically clumped locations within the home range (Powell 2000). Core areas provide a clearer interpretation of changing patterns of range use within a home range and allow better insight into intra-specific and inter-specific patterns of area use than the total home range area (Harris et al. 1990). Total home ranges may overlap, whereas core areas may be mutually exclusive. Core areas may indicate higher concentrations of important resources, and may be more important to aid understanding of an individual's life requisites than peripheral areas (Powell 2000). Core areas can be determined by plotting percentage area home range against probability of use. In theory, random space use results in a straight-line

plot, even space use results in a convex curve, and clumped space use results in a concave curve (Powell 2000). The core can be identified as the point where the gradient of the slope changes on a concave curve (the point of inflection) (Harris et al. 1990).

4.1.4 Static Interactions

Estimation of home and core ranges allows the size, shape and pattern of utilisation to be quantified for individual badgers. Furthermore, the degree of space use overlap between individuals is also of interest. As well as affecting the spatial organisation of individuals and groups of badgers, the degree to which home ranges overlap and the level of interaction that take place within the shared area may play a role in territoriality, competition, sexual segregation, mother-offspring interactions, site fidelity and disease spread (Millspaugh et al. 2004). Where home ranges overlap there is potential for badgers to come into contact or interact with each other; this is termed static interaction. Static interaction analysis calculates a measure of association between two individuals during a specified time period. Rasmussen (1980) suggests three criteria are desirable in a static interaction analysis; (1) the similarity in the location of high-use areas should be assessed, (2) it should not be affected by sample size, and (3) differences in the size of the spatial frame should not affect it. Several methods have been developed to assess static interaction but the simplest and most intuitive techniques are to superimpose two-dimensional home range maps and compute the percent area overlap between the ranges (Mizutani and Jewell 1998), or the proportion overlap of the two combined home ranges (Millspaugh et al. 2004). Static interaction analysis does not, however, consider whether animals were in close proximity at any particular point in time within the overlapping area (Kernohan et al. 2001), and assumes animals are moving independently of each other. It also does not consider differential levels of use within the home range boundary (Kernohan et al. 2001).

4.1.5 Dynamic Interactions

Whilst static interaction analysis provides information on the potential for interactions to occur between individuals in a shared area, it does not take into account the temporal aspect of any interactions; that is, an area may overlap between two individuals but they may actively avoid each other when using the overlapping area and not interact at

all (Kenward 2001). Dynamic interaction analysis considers the temporal nature by using simultaneous locations to assess temporal aspects of interaction (Minta 1992).

Analysis of dynamic interactions falls into three broad groups. The first compares the distance of simultaneous observations taken from pairs of individuals (or dyads) (Kenward et al. 1993). The second group compares the association between two animals over a specified time period based on how often they are observed together to compute a coefficient of association (Cole 1949). The third group compares the use of a shared area at the same time to compute present or absent use frequencies to be compared against expected frequencies (Minta 1992).

The first method is generally the most robust of all the methods because no assumption is made that pairs of observations (or dyads) are statistically independent (Kenward 2001). Doncaster (1990) compared separation distances from simultaneously radio tracked individuals against baseline data made from artificially paired separation distances from the same data. White and Harris (1994) extended this to use separation distances from simulated movement data as a comparison. The main limitation with the second group of methods is that it relies on animals being easily and readily observable; for nocturnal or cryptic species this is not the case. The main problem with the third group of methods is that a binomial frequency is used to summarise the data, this assumes the data are independent and that a shared area is actually present. It also can only be used to look at interactions between two animals even if more animals are present (Minta 1992). Dunn (1979) developed a multivariate Orstein-Uhlenbeck model where the movement data of two animals follow Markovian patterns. This model however, assumes that animal movement distributions are bivariate normal. Macdonald et al. (1980), developed a similar model but one that assumed a bivariate normal (elliptical) distribution of locations. However the assumption that animals' locations conform to these distributions is often unrealistic (White and Garrott 1990, Minta 1992). Few studies have attempted to quantify interactions between species based on radio tracking data due to the time consuming nature of data collection (Minta 1993), however, it can provide insight into how animals move with respect to each other and how likely animals are to interact as a result of their movements.

4.2 Chapter aims

The aims of this chapter are to investigate the spatial organisation of badgers from different social groups at Woodchester Park using data collected by radio tracking. Radio tracking allows detailed information on individual badgers to be collected at a large spatial resolution. Seasonal variations in home and core area ranges can be compared between badgers belonging to different social groups, and between different sexes, ages and TB status of badgers. In addition, the potential for interaction to occur between badgers (static interaction) can be investigated, and taking into account the temporal nature of radio tracking data actual interactions between badgers or how badgers move with respect to one another (dynamic interactions) can also be investigated. Results from bait marking show that generally social groups have distinct boundaries with little overlap between groups (see chapter two for further details). The radio tracking data should reflect this pattern, although individual differences in space use and behaviour can be determined in greater detail.

4.3 Methods

4.3.1 Data collection

The trapping and fitting of collars to badgers took place as described in chapter two (sections 2.4.2 and 2.4.5.2 respectively). The radio tracking methods were also followed as described in chapter two (section 2.4.6) resulting in an x and y co-ordinate to the nearest metre for each location fix for each badger when it was radio tracked.

Radio tracking took place between Autumn 2004 and Summer 2005. Radio tracking data were divided into seasons to reflect changing patterns of badger behaviour throughout the year. These were: Autumn (September to November), to cover the slightly less than spring, peak of territoriality and mating activity; Winter (December to February), to cover the gestation period and the birth and rearing of cubs; Spring (March to May), to cover the main peak in territoriality and mating activity and cub emergence; and Summer (June to August), to cover the independence of cubs.

4.3.2 Incorporating error associated with radio tracking

The error ratio was estimated prior to data collection and found to be 0.035 (equation 4.1). This was based on a median error of radio tracking of 40.89 meters (found from the radio tracking accuracy investigation as described in chapter three, (refer to section 3.4.2.3 for results), and an approximate individual badger home range size of 15 hectares (Cheeseman and Mallinson 1979). Thus this method lies within the second lowest accuracy band (0.010 – 0.049) as defined by Moser and Garton (2007).

To further increase the accuracy of the results radio tracking data were screened before analysis; any location fixes where the badger was estimated to be more than 200 meters away from the tracker were removed from the dataset. Removing data in this way could potentially bias the data by excluding locations where it is not possible to get within 200 meters. However, with a thorough knowledge of the study site, there are no known areas where it was not possible to get within 200 m during the study period. In practice there were very few fixes that were removed due to this criteria. Furthermore, knowing that experienced radio trackers were generally more accurate, experienced people were asked to help collect data in preference to inexperienced people. If an inexperienced person was involved in collecting data, an experienced person was usually allocated a badger to

radio track from the same social group as the inexperienced person to offer advice if needed.

4.3.3 Home Range Analysis

Only fixes where the badger was recorded as being active were used for home range and core area analysis; this was to prevent any bias towards the core area (Harris et al. 1990). Home ranges were first tested to see if they were asymptotic to ensure that the sampling duration covers the full range of behaviour exhibited by the animal. Home range asymptotes were identified for each badger for each season by examining plots of home range size at increased sample sizes. Locations were added consecutively as the radio tracking data was collected continuously (Harris et al. 1990). Asymptotes were determined visually and any home range not reaching an asymptote was excluded from further analysis.

Both 100% MCPs and 95% kernel density methods were used to determine the boundaries of individual home ranges. 100% MCPs were included in this analysis so that this study can be compared to others of similar sample size and temporal duration (Harris et al, 1990). Fixed kernels were used rather than adaptive kernels as these are generally considered a more accurate and less biased estimator especially in the outer contours of the home range (Worton 1995, Seaman and Powell 1996, Seaman et al. 1999) and a smoothing parameter (h), was found using reference h with a multiplier of 1.6. Reference h was used in preference to h found using LSCV because LSCV has been shown to work less effectively with small sample sizes and where data has a large resolution relative to sample size (Seaman et al. 1999), and tends to have a high failure rate where data are clustered and auto-correlated (Hemson et al. 2005).

Home ranges and core ranges were determined using Ranges6 v1.2 (Kenward et al. 2003), and displayed using ArcView GIS 3.3 (Environmental Systems Research Institute Inc.) on a seasonal basis. Individual badgers were classified according to the social group they belonged to (based on the trapping data; see chapter two for further details), sex (male or female), age (yearling or adult), and TB status (positive or negative). Social group allocation, age and TB status may change throughout the period of the study as badgers may be classified as belonging to one social group in 2004 and another in 2005 and yearlings become adults on the 1st of January. Statistics were performed using R (R Core Development Team 2006) and Brodgar (Highland Statistics, Newburgh, UK). The effects

of season, sex, age and TB status on home ranges and core areas were investigated using linear mixed-effects models fitted by residual maximum likelihood (REML). Data were log transformed prior to analysis. Season, sex, age and TB status were treated as nominal fixed variables, individual badgers were treated as random effects and badger × season was the repeated effect.

4.3.4 Core area analysis

For asymptotic home ranges the isopleth value delineating the core area was found for each badger for each season using the MCP home range estimator. The overall mean point of inflection (70%) was then applied to all the data to allow comparability, and the core areas were plotted using kernel methods using the same parameters as for 95% kernels.

4.3.5 Static interaction analysis

The potential for interaction between badgers was determined by calculating the home range overlap as a proportion of the total combined home range size for each badger dyad. The term dyad is used to refer to two badgers instead of the term pair, as the word pair implies some sort of association between badgers when in fact there may be none. Static interactions were calculated for dyads of badgers with asymptotic home ranges on a seasonal basis using 95% kernel and 70% kernel core areas by the following method (equation 4.2):

$$Overlap = \frac{A_{1,2}}{(A_1 + A_2) - A_{1,2}} \quad \text{(Millspaugh et al. 2004)} \qquad \text{(Eqn. 4.2)}$$

Where A_1 and A_2 are the home range areas of animal 1 and 2 respectively, and $A_{1,2}$ is the area of overlap between the home ranges of animals 1 and 2. Non-parametric analyses were used to investigate the effect of season, sex, age or TB status on proportion overlaps due to small sample sizes.

4.3.6 Dynamic interaction analysis

Simultaneous separation distances were calculated for all inter- and intra-group badger dyads on each night that radio tracking took place for each five minute fix based on the estimated co-ordinates of each badger determined by radio tracking. Separation distances were calculated for all intra- and inter-group badger dyads irrespective of whether the badgers in question had asymptotic home ranges or not; non-neighboring badger dyads were not used in the analysis. The separation distances were then placed into categories of ≤41 meters, 42-82 meters, 83-123 meters, 124-200 meters, 201-300 meters, 301-500 meters and 500 meters plus. These categories were chosen based on the telemetry error found in chapter 3: 40.89 meters being the median error. Separation distances of less than 41 meters denotes two badgers being highly likely to be within close proximity of each other and a contact occurring, whereas separation distances less than 82 meters takes into account the median error that may occur for both badgers and for them still to be in close proximity with each other. Separation distances larger than 82 meters do not indicate any contact occurring. The proportion of separation distances occurring within these specified distances were calculated to enable comparisons due to the different number of fixes and dyads obtained for each season. Separation distances were square root transformed prior to analysis, then linear mixed-effects models fitted by REML used to investigate the effect of season, sex, age and activity status on intra- and inter- group separation distances.

4.4 Results

Fifteen badgers were radio tracked at some point during 2004-2005. A total of 7124 location fixes was collected, of which 3130 were active over 24 nights (six per season). After disregarding data from badgers whose home ranges were not asymptotic, home range estimates were produced for 10 different badgers for at least one season from four different social groups (Table 4.1).

4.4.1 Home range sizes

Table 4.2 and Figure 4.1 to Figure 4.4 show the 100% MCP and 95% kernel home range estimates per season for badgers with asymptotic home ranges. 100% MCP size estimates were significantly different compared to kernel estimates (Wilcoxon signed ranks test, $Z = -3.95$, d.f. = 21, $p < 0.001$), with MCPs generally being larger. Overall mean home range size was 14.57 ± 1.53ha (100% MCP estimate) or 10.62 ± 1.06ha (95% kernel estimate). Mean home ranges were smallest in winter, followed by autumn then spring, with summer being the largest. Other visible patterns in the data were; overall males had slightly larger home range sizes than females, adults had larger home ranges in Autumn, Spring and Summer, and yearlings in Winter. Badgers with a negative TB status had larger ranges in Spring and Summer, whereas the TB positive badger had a larger range in Autumn and Winter (Table 4.3). However, none of these results were significant ($F_{season} = 1$, d.f. = 3,8, $p = 0.48$; $F_{sex} = 0$, d.f. = 1,6, $p = 0.52$; $F_{age} = 0$, d.f. = 1,6, $p = ,0.98$; $F_{TBstatus} = 4$, d.f. = 1,6, $p = 0.10$ for 100% MCPs; 95% kernels also produced non-significant results). No interaction effects were investigated due to small sample sizes.

Badger 37R changed social groups during the period of the radio tracking study from the Septic Tank social group to the Wych Elm social group. This is shown by both the results from the social group allocation which places her in Septic Tank for 2004 and Wych Elm for 2005 and from the radio tracking data for the home and core areas for winter and summer (Figure 4.2 and Figure 4.4 for home range areas and Figure 4.6 and Figure 4.8 for core areas). Unfortunately insufficient radio tracking data were collected for this badger during spring to be able to estimate her home range as this may have been the transitory period, however the winter and summer data do show two clearly different patterns of range use.

Badger ID	Sex	Social group	Autumn			Winter			Spring			Summer			Totals per badger		
			Total	Inactive	Active	Total	Inactive	Active	Total	Inactive	Active	Total	Inactive	Active	Total	Inactive	Active
13G	F	Beech	165 (3)	132	33	413 (6)	342	71	191 (5)	115	76				769	589	180
18G	F	Beech	310 (5)	213	97	391 (6)	338	53	240 (6)	140	100	239 (5)	74	165	1180	765	415
19G	F	Septic Tank	208 (4)	148	60	92 (2)	72	20							300	220	80
32R	M	Wych Elm	25 (1)	9	16										25	9	16
37R	F	ST/WE*1				189 (3)	101	88	62 (1)	20	42	170 (5)	57	113	421	178	243
44R	F	Top				58 (1)	56	2							58	56	2
47R	F	Breakheart							160 (3)	154	6				160	154	6
54R	M	Cedar							331 (6)	152	179	98 (3)	59	39	429	211	218
55G	M	Wych Elm										260 (5)	48	212	260	48	212
68R	F	Cedar							275 (6)	116	159	156 (4)	76	80	431	192	239
76R	F	Top				53 (1)	35	18							53	35	18
D19	M	Beech										186 (3)	94	92	186	94	92
H43	F	Wych Elm	348 (6)	177	171	306 (6)	201	105	307 (5)	20	287	278 (5)	38	240	1239	436	803
J87	M	Beech	247 (4)	168	79	393 (6)	357	36	252 (5)	102	150	209 (5)	84	125	1101	711	390
U51	M	Septic Tank	265 (6)	160	105	155 (4)	67	88	112 (2)	89	23				532	316	216
Totals per season			1568	1007	561	2050	1569	481	1930	908	1022	1596	530	1066			

Table 4.1. Number of location fixes collected for different badgers between Autumn 2004 and Summer 2005. Underlined badgers represent those that had reached an asymptotic home range for that season; numbers in brackets after total number of fixes for each badger are the number of different nights that badger was tracked over.

*1 This badger was assigned to the Septic Tank social group for 2004 according to the social group allocation rules (see chapter 2 for further details), and the Wych Elm social group for 2005

Badger ID	Autumn 100% MCP	Autumn 95% Kernel	Winter 100% MCP	Winter 95% Kernel	Spring 100% MCP	Spring 95% Kernel	Summer 100% MCP	Summer 95% Kernel
13G			4.72	2.54	13.28	11.04		
18G	8.42	5.03			7.13	6.35	14.73	12.47
19G	9.62	8.12						
37R			10.79	5.29			17.28	11.93
54R					18.01	10.79		
55G							16.98	11.23
68R					27.52	14.89	11.01	10.68
H43	33.06	20.82	15.84	12.97	11.44	6.07	11.37	10.59
J87	6.59	5.66			18.23	12.76	25.01	21.40
U51	11.79	8.12	13.22	14.29				

Table 4.2. Home range size estimated by both MCP and 95% kernel estimates for each badger that had an asymptotic home range for that season, all values are in hectares.

		Autumn	Winter	Spring	Summer	Overall
Males	N	2	1	2	2	7
	100% MCP	9.19 ±2.6	13.22	18.12 ±0.11	20.99 ±4.01	15.69 ±2.21
	95% kernel	6.89 ±1.23	14.29	11.78 ±0.99	16.32 ±5.09	12.04 ±1.90
Females	N	3	3	4	4	14
	100% MCP	17.03 ±8.02	10.45 ±3.21	14.84 ±4.42	13.60 ±1.49	14.02 ±2.07
	95% kernel	11.32 ±4.83	6.93 ±3.12	9.59 ±2.10	11.42 ±0.47	9.91 ±1.28
Adults	N	3	2	2	2	9
	100% MCP	17.15 ±8.10	14.53 ±1.31	14.84 ±3.40	18.19 ±6.82	16.28 ±2.72
	95% kernel	11.53 ±4.70	13.63 ±0.66	9.42 ±3.35	16.00 ±5.41	12.52 ±1.91
Yearlings	N	2	2	4	4	12
	100% MCP	9.02 ±0.6	7.76 ±2.04	16.49 ±4.30	15.00 ±1.45	13.29 ±1.78
	95% kernel	6.58 ±1.55	3.92 ±1.38	10.77 ±1.75	11.58 ±0.39	9.20 ±1.06
TB –ve	N	4	3	5	5	17
	100% MCP	9.11 ±1.09	9.58 ±2.53	16.83 ±3.35	17.00 ±2.29	13.78 ±1.51
	95% kernel	6.73 ±0.81	7.37 ±3.55	11.17 ±1.41	13.54 ±1.99	10.15 ±1.11
TB +ve	N	1	1	1	1	4
	100% MCP	33.06	15.84	11.44	11.37	17.93 ± 5.15
	95% kernel	20.82	12.97	6.07	10.59	12.61 ± 3.09
Overall	N	5	4	6	6	
	100% MCP	13.90 ±4.86	11.14 ± 2.38	15.94 ±2.88	16.06 ±2.10	14.57 ±1.54
	95% kernel	9.55 ±2.89	8.78 ±2.87	10.32 ±1.43	13.05 ±1.69	10.62 ±1.06

Table 4.3. Summary mean home range sizes (±SEM) estimated by both 100% MCP and 95% kernel methods for different badger categories (found from badgers with asymptotic home ranges only), values are in hectares.

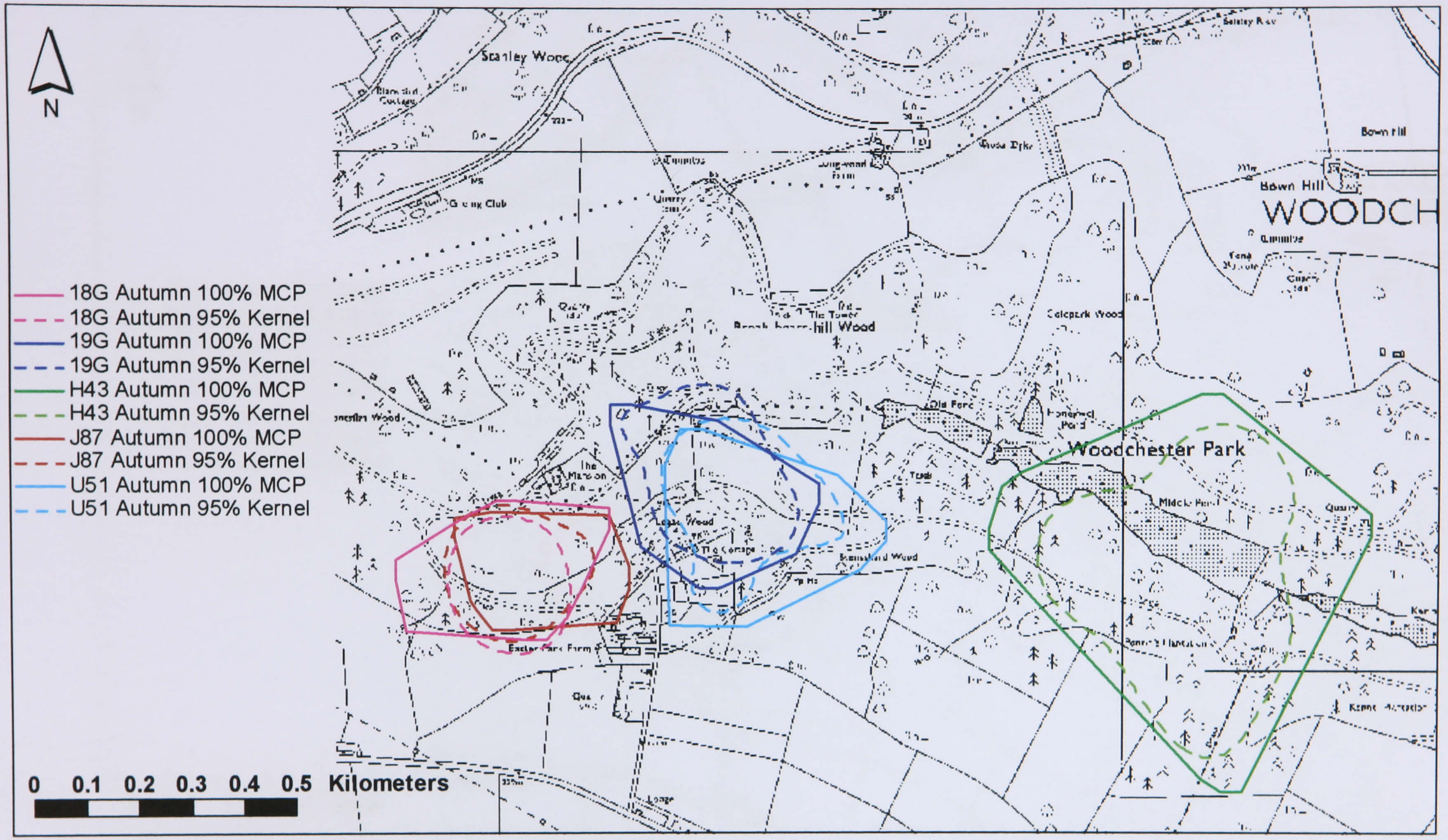


Figure 4.1. Diagrammatic representation of 100% MCP and 95% kernel estimates for all badgers whose home range had reached an asymptote for Autumn. Ranges are colour coded to represent social group membership; red – Beech, blue – Septic Tank, green – Wych Elm, yellow – Cedar.

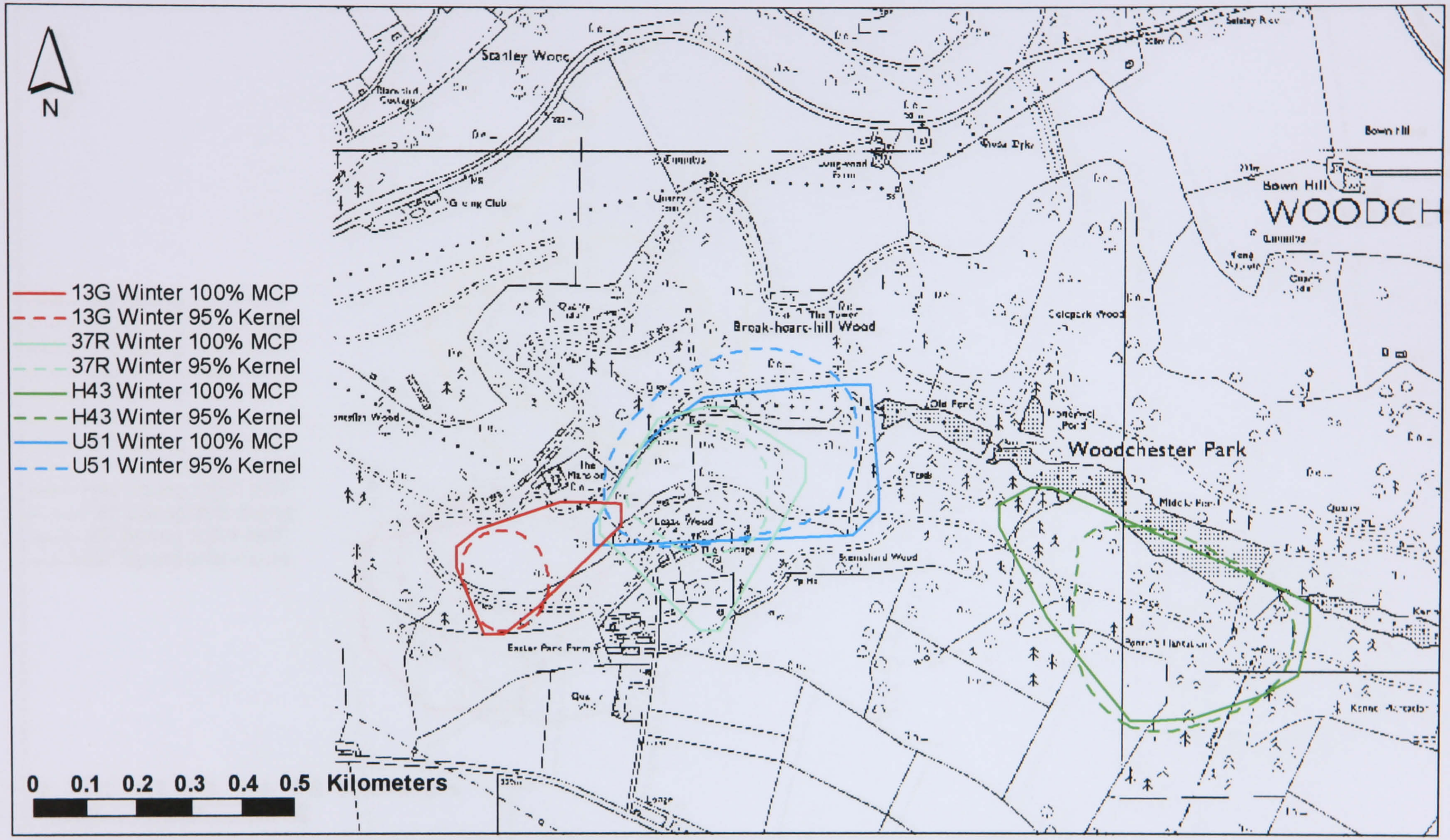


Figure 4.2. Diagrammatic representation of 100% MCP and 95% kernel estimates for all badgers whose home range had reached an asymptote for Winter. Ranges are colour coded to represent social group membership; red – Beech, blue – Septic Tank, green – Wych Elm, yellow – Cedar.

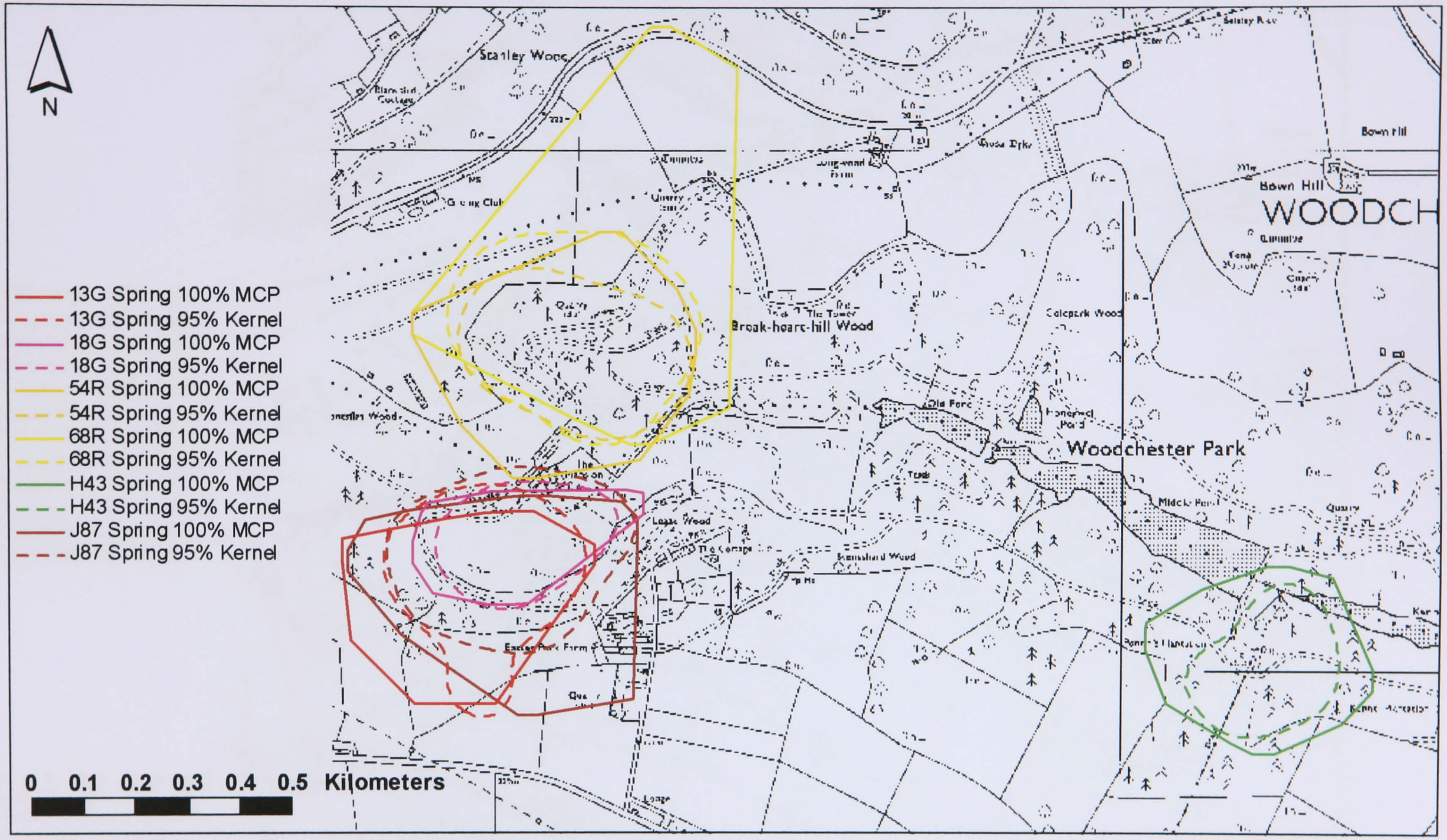


Figure 4.3. Diagrammatic representation of 100% MCP and 95% kernel estimates for all badgers whose home range had reached an asymptote for Spring. Ranges are colour coded to represent social group membership; red – Beech, blue – Septic Tank, green – Wych Elm, yellow – Cedar.

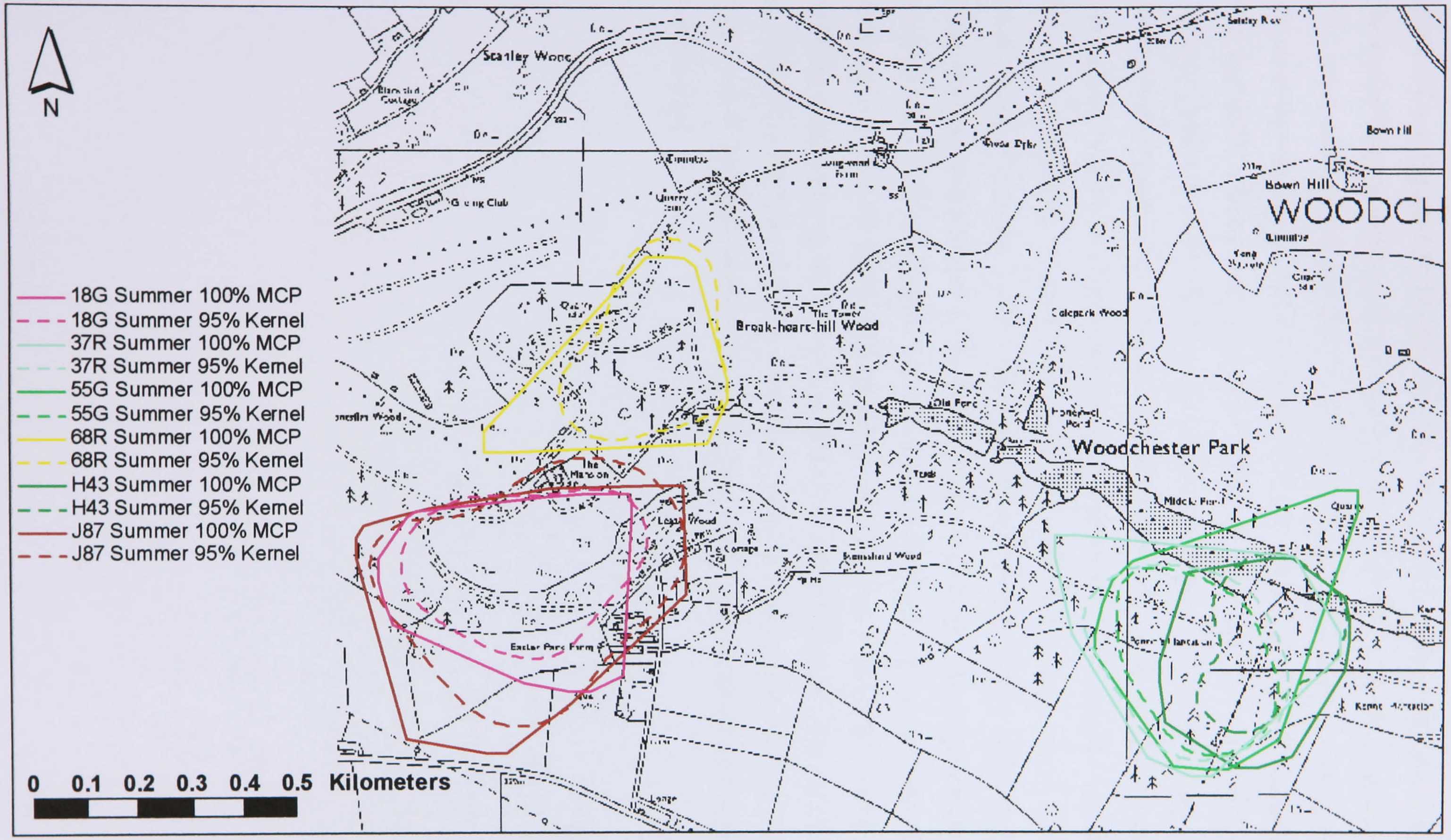


Figure 4.4. Diagrammatic representation of 100% MCP and 95% kernel estimates for all badgers whose home range had reached an asymptote for Summer. Ranges are colour coded to represent social group membership: red – Beech, blue – Septic Tank, green – Wych Elm, yellow – Cedar.

4.4.2 Core area sizes

Table 4.4 and Figure 4.5 to Figure 4.8 show the 70% kernel home range estimates per season for badgers with asymptotic home ranges. The 70% isopleth is used to delineate all core areas, and only kernels (not MCPs) are reported here to allow clarity in diagrams as the areas represented are relatively small, and because kernels are less sensitive to sample size than MCPs. Mean core area is 5.51 ± 0.62ha. Core areas show a slightly different seasonal pattern to 100% MCP and 95% kernel range sizes, with areas being smallest in Winter then Autumn, slightly larger in Spring, with Summer having the largest area. There were several visible patterns in the data: males again had slightly larger core areas than females (consistent with home range sizes), adults had larger core areas in all seasons apart from Spring. Core area sizes for badgers with and without TB were similar to home range sizes; badgers with a negative TB status had larger core areas in Spring and Summer whereas the TB positive badger had a larger core area in Autumn and Winter (Table 4.5). However, as with the home range estimates, no significant results were found with respect to home range size varying between seasons, sex, age or TB status, ($F_{season} = 0.6$, d.f. = 3,8, $p = 0.64$; $F_{sex} = 0.1$, d.f. = 1,6, $p = 0.81$; $F_{age} = 0.6$, d.f. = 1,6, $p = 0.47$; $F_{TBstatus} = 0.9$, d.f. = 1,6, $p = 0.37$ for 70% kernels). No interaction effects were investigated due to small sample sizes.

Badger ID	Autumn 70% Kernel	Winter 70% Kernel	Spring 70% Kernel	Summer 70% Kernel
13G		1.35	5.09	
18G	2.89		3.76	6.84
19G	4.28			
37R		2.83		6.15
54R			6.52	
55G				4.67
68R			8.20	5.24
H43	11.32	6.71	3.67	2.88
J87	2.88		6.45	12.38
U51	3.24	8.28		

Table 4.4. Core area estimates for badger home ranges that had reached an asymptote for that season. All core areas are represented by the 70% isopleth to allow comparisons between individuals, and the kernel home range estimator is used, values are in hectares.

		Autumn	Winter	Spring	Summer	Overall
Males	N	2	1	2	2	7
	70% kernel	3.06 ± 0.18	8.28	6.49 ±0.03	8.53 ± 3.86	6.35 ± 1.24
Females	N	3	3	4	4	14
	70% kernel	6.16 ± 2.61	3.63 ± 1.60	5.18 ± 1.06	5.28 ± 0.86	5.09 ± 0.70
Adults	N	3	2	2	2	9
	70% kernel	5.81 ± 2.76	7.50 ± 0.79	5.06 ± 1.39	7.63 ± 4.75	6.42 ± 1.21
Yearlings	N	2	2	4	4	12
	70% kernel	3.59 ± 0.70	2.09 ± 0.74	5.89 ± 0.95	5.73 ± 0.48	4.82 ± 0.56
TB -ve	N	4	3	5	5	17
	70% kernel	3.32 ± 0.33	4.15 ± 2.11	6.00 ± 0.75	7.06 ± 1.38	5.36 ± 0.65
TB +ve	N	1	1	1	1	4
	70% kernel	11.32	6.71	3.67	2.88	6.15 ± 1.91
Overall	N	5	4	6	6	21
	70% kernel	4.92 ± 1.62	4.79 ± 1.62	5.62 ± 0.72	6.36 ± 1.33	5.51 ± 0.62

Table 4.5. Summary mean core range sizes (±SEM) estimated using the 70% kernel for different badger categories (found from badgers with asymptotic home ranges only), values are in hectares.

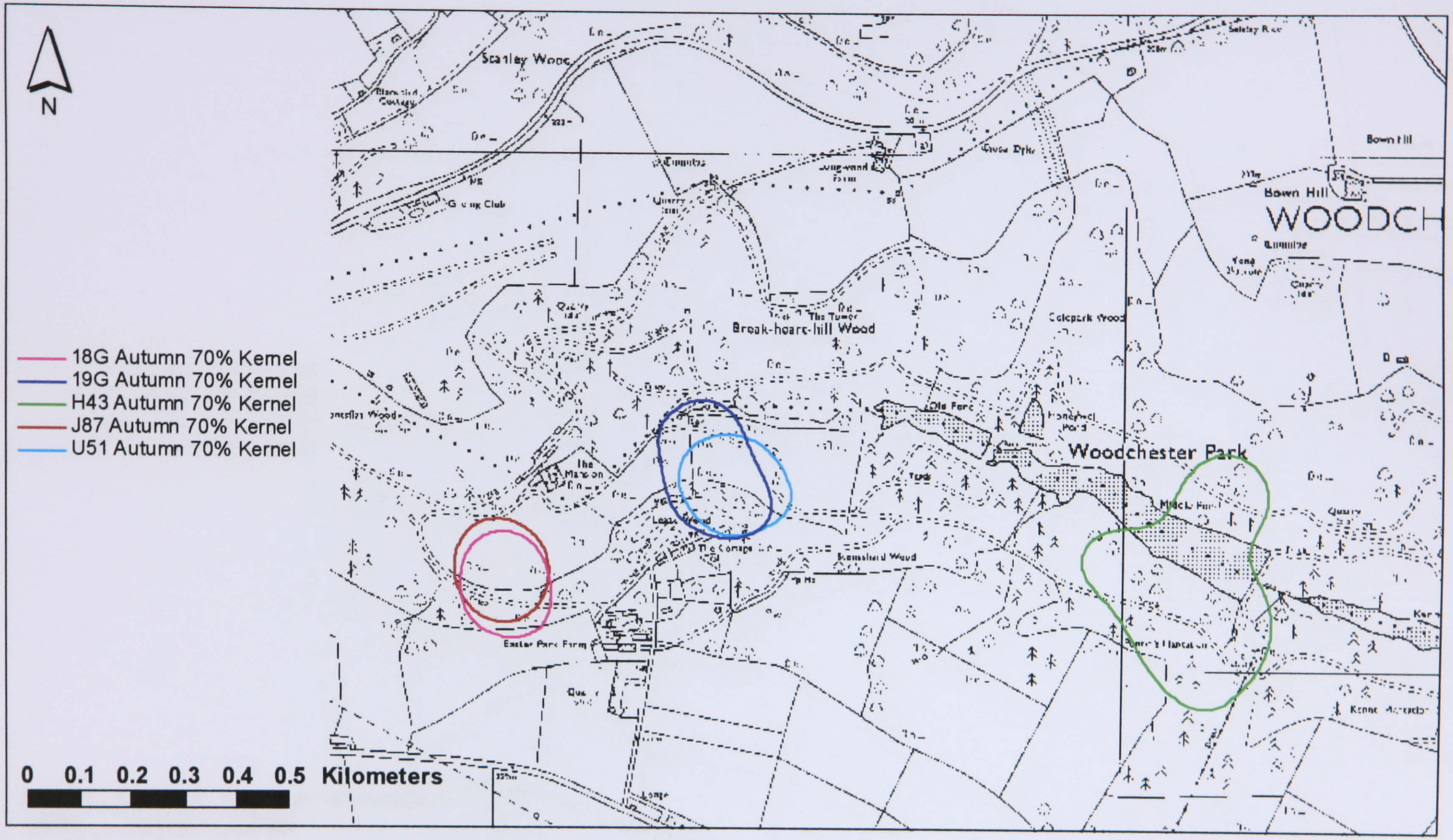


Figure 4.5. Diagrammatic representation of 70% kernel core area estimates for all badgers whose home range had reached an asymptote for Autumn. Ranges are colour coded to represent social group membership: red – Beech, blue – Septic Tank, green – Wych Elm.

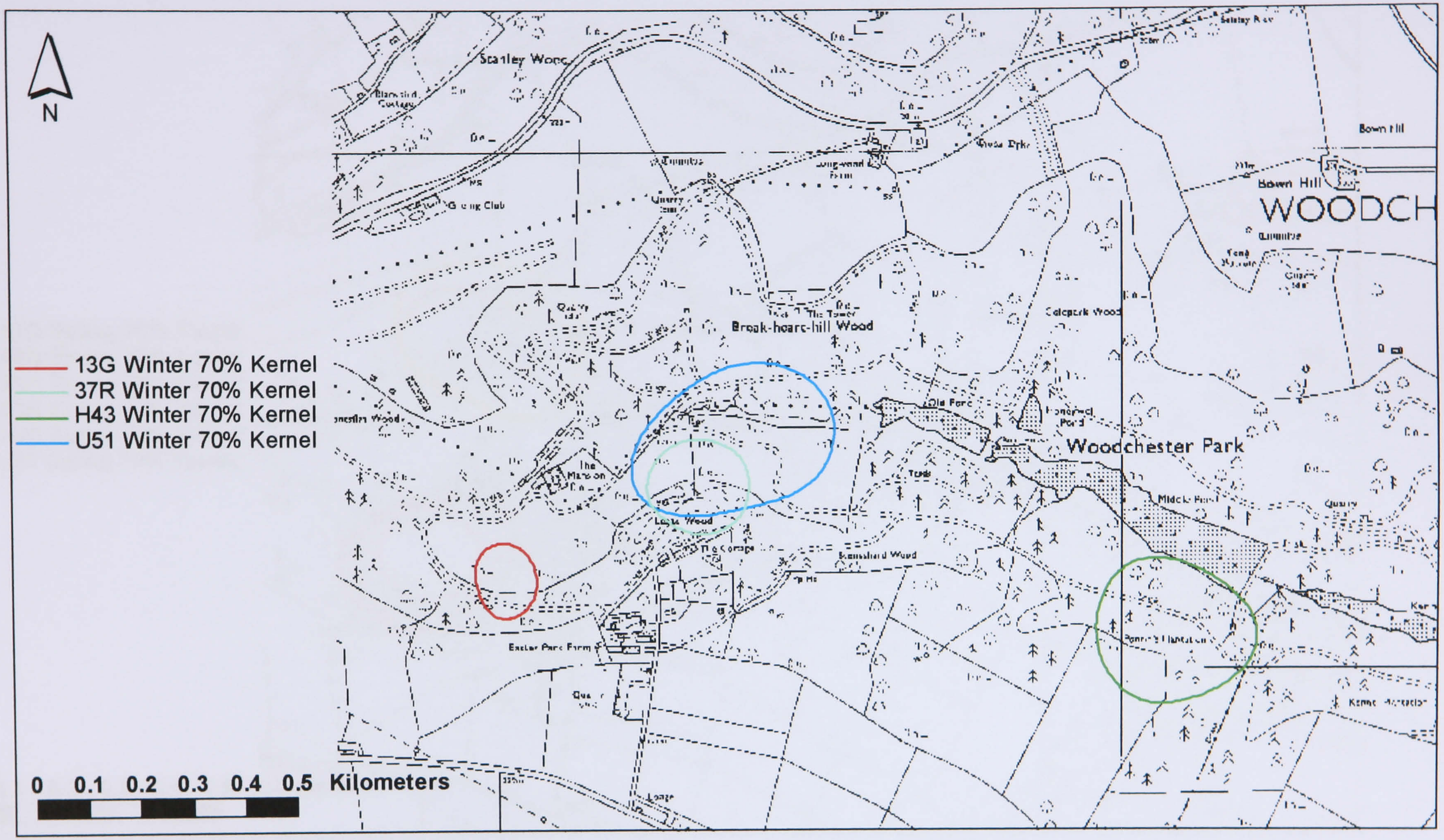


Figure 4.6. Diagrammatic representation of 70% kernel core area estimates for all badgers whose home range had reached an asymptote for Winter. Ranges are colour coded to represent social group membership: red – Beech, blue – Septic Tank, green – Wych Elm, yellow – Cedar.

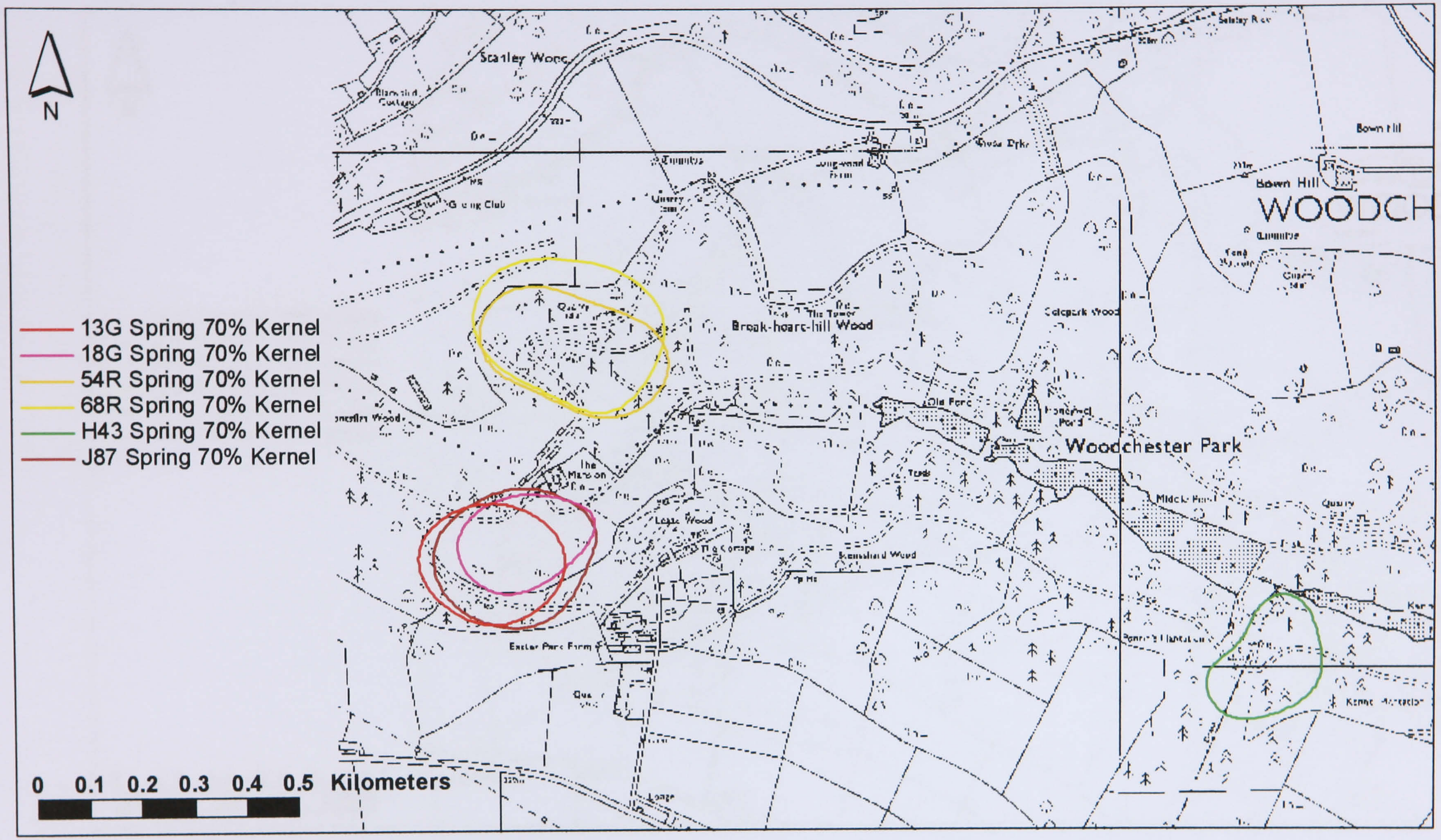


Figure 4.7. Diagrammatic representation of 70% kernel core area estimates for all badgers whose home range had reached an asymptote for Spring. Ranges are colour coded to represent social group membership: red – Beech, blue – Septic Tank, green – Wych Elm, yellow – Cedar.

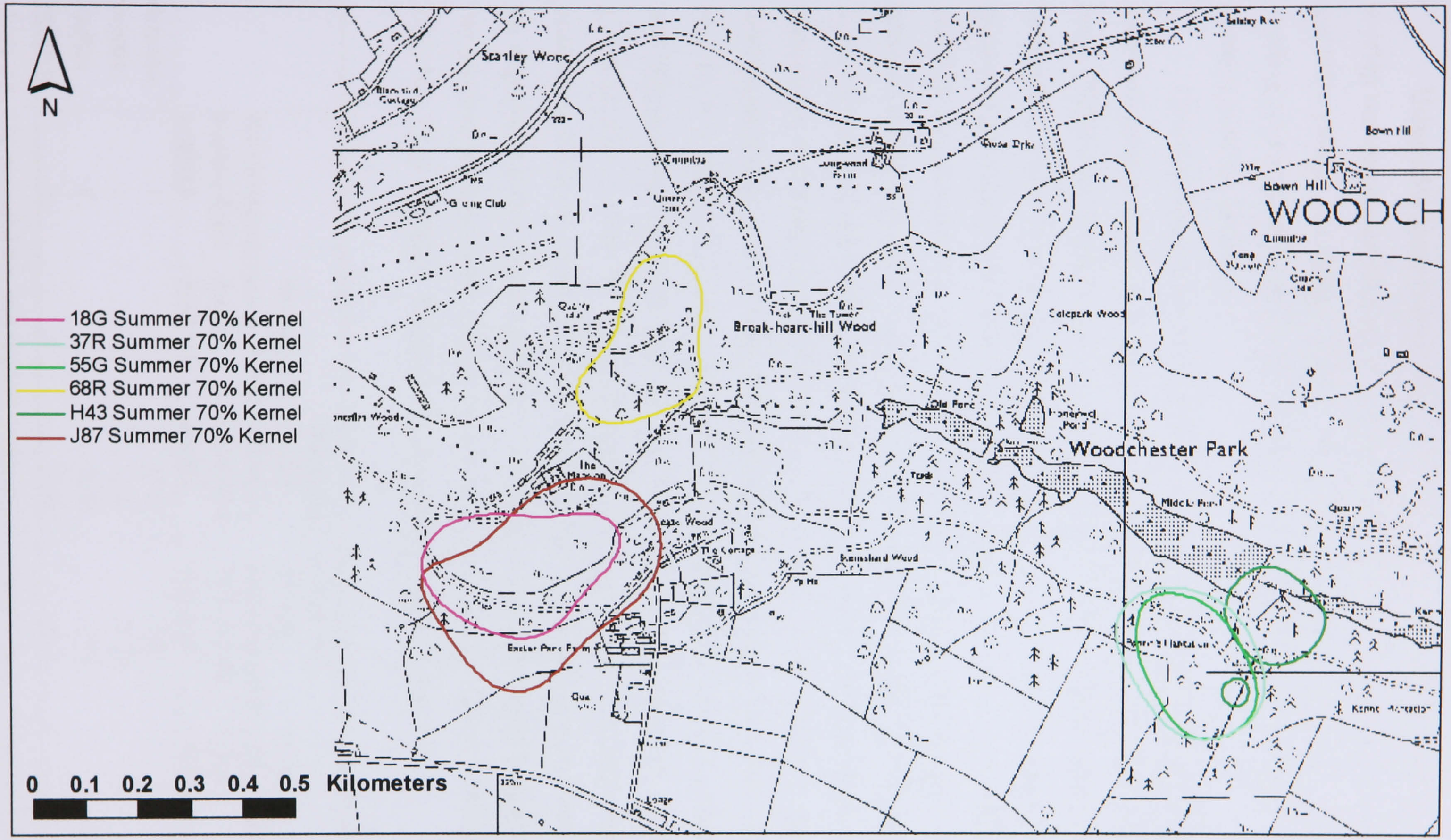


Figure 4.8. Diagrammatic representation of 70% kernel core area estimates for all badgers whose home range had reached an asymptote for Summer. Ranges are colour coded to represent social group membership: red – Beech, blue – Septic Tank, green – Wych Elm, yellow – Cedar.

4.4.3 Static Interaction

Using 95% kernel home and 70% kernel core range estimators, the proportion of overlap was calculated for badger dyads classified according to season, group (intra- and inter-group), sex (female-female, female-male and male-male), age (yearling-yearling, yearling-adult, and adult-adult) and TB status (negative-negative, negative-positive, positive-positive).

Overlaps were only observed between intra-group badger dyads even though there was greater potential in terms of numbers available for inter-group contacts to occur (Table 4.6). Home range overlaps were greatest in autumn, followed by summer then spring, with winter having the smallest overlap. Core area overlap also showed the greatest overlap in autumn, and the smallest in winter. However, with both 95% kernel and 70% kernel estimators there was no statistically significant difference in overlaps between seasons (Kruskal Wallis; $\chi^2 = 1.71$, d.f = 3, $p = 0.66$ for 95% kernels and $\chi^2 = 2.48$, d.f = 3, $p = 0.48$ for 70% kernels) (Table 4.6). Ignoring season as a factor, female-male dyads overlapped to a greater extent than female-female dyads (no male-male inter-group dyads were present) although this was non-significant (Mann-Whitney U; Z = -1.41, N = 11, $p = 0.22$), and adult-adult dyads overlapped to a lesser extent than yearling-yearling dyads and yearling-adult dyads (also non-significant, Kruskal Wallis; $\chi^2 = 0.51$, d.f = 2, p =0.78). There was however a significant difference when examining TB status dyads, with the proportion of overlap being significantly smaller for negative-positive dyads (0.009 ha) compared to negative-negative dyads (0.56ha) (no positive-positive dyads were present), for core areas only (Mann – Whitney U; Z = -2.12, N = 11, $p = 0.036$). These results are summarised in Table 4.7.

	No. intra-group overlap dyads available	No. intra-group overlap dyads observed	Proportion overlap estimated using 95% Kernel	Proportion overlap estimated using 70% Kernel core area	No. inter-group overlap dyads available	No. inter-group overlap dyads observed
Autumn	2	2	0.62	0.61	4	0
Winter	1	1	0.35	0.29	2	0[*1]
Spring	4	4	0.40	0.58	6	0
Summer	4	4	0.44	0.33	2	0

Table 4.6. The potential for, and realised numbers of overlaps between badger dyads, and the proportion of overlap estimated using both 95% and 70% core kernel home range estimates.

[*1] Using the MCP home range estimator, two inter-group overlaps were observed in Winter. These two overlaps gave a mean proportion of 0.02 (see figure 4.2 for diagrammatic representation).

Dyad category	Proportion overlap estimated using 95% kernels	Proportion overlap estimated using 70% kernel core area	N
Female / Male dyads	0.48 ±0.08	0.52 ±0.08	9
Female / Female dyads	0.33 ±0.08	0.25 ±0.19	2
Yearling / Yearling dyads	0.40 ±0.20	0.62 ±0.10	3
Yearling / Adult dyads	0.48 ±0.07	0.43 ±0.10	7
Adult / Adult dyads	0.35	0.29	1
TB –ve / TB-ve dyads	0.50 ±0.07	0.56 ±0.05	9
TB-ve / TB+ve dyads	0.24 ±0.01	0.04 ±0.01	2
Overall mean	0.45 ± 0.07	0.47 ±0.07	11

Table 4.7. Mean proportion overlaps between different badger dyads estimated using both the 95% kernel and 70% core kernel home range estimate. N is the number of different dyads observed across all four seasons.

4.4.4 Dynamic Interaction

Radio tracking data were collected for 54 dyads of badgers, consisting of 39 inter group dyads and 15 intra group dyads over 24 six-hour nights (six nights per season). In general, six badgers were radio tracked on any night (range 3 – 9), but it was not always possible to obtain a fix for every five-minute interval for every badger; separation distances have been calculated when the fixes were simultaneous. A total of 8337 simultaneous fixes were obtained (4656 inter-group dyad fixes and 3681 intra group dyad fixes). Simultaneous separation distances recorded between intra-group and inter-group dyads were significantly different (Mann-Whitney U test, Z = -62.406, N = 8337, $p < 0.001$) so were analysed separately. The mean intra-group separation distance was 102.36 ± 2.40 meters and the mean inter-group separation distance was 513.15 ± 3.93 meters (Table 4.8 and Table 4.9).

Intra-group and inter-group separation distances were square-root transformed prior to analysis. TB status of badgers with respect to separation distances was not considered because only two badgers were classed as positive, affecting only 10 badger dyads over all seasons.

Intra-group separation distances varied significantly between different age dyads ($F_{age} = 214.6$, d.f. = 2,3594, $p < 0.001$) with both yearling-adult and adult-adult dyads being significantly different from yearling-yearling dyads (the reference category). Intra-group separation distances also varied significantly with activity dyad ($F_{activity} = 247.5$, d.f. = 2,3594, $p < 0.001$), with inactive-inactive dyads having significantly smaller separation distances than active-active or active-inactive dyads. There was a significant interaction effect of intra-group activity dyad and different seasons ($F_{activity \times season} = 54.0$, d.f. = 6,3594, $p < 0.001$) with active-inactive dyads in winter differing from

active-active dyads in winter (the reference category), active-inactive and inactive-inactive dyads in spring and inactive-inactive dyads in summer were also significantly different. No other interaction effects could be investigated due to certain dyad categories missing in some seasons (Table 4.8).

Inter-group separation distances also varied significantly between different age dyads ($F_{age} = 14$, d.f. = 2,2617, $p < 0.001$); yearling-adult and adult-adult dyads were significantly different from yearling-yearling dyads (the reference category), but there was no significant difference between activity dyads. Only active-active and active-inactive dyads were used for inter-group analysis due to the large numbers of inactive-inactive fixes being large distances apart and because when both badgers are inactive it is highly unlikely there is potential for contact to occur. All activity dyad types (active-active, active-inactive and inactive-inactive) were included in intra-group separation distance analysis, because both badgers could be inactive but in the same location. There was however, a significant interaction effect between inter-group activity dyad and season ($F_{activity \times season} = 16$, d.f. = 3,2617, $p < 0.001$) with active-inactive dyads in summer being significantly different from active-active dyads in winter (the reference category) and between inter-group sex dyad and activity dyad ($F_{sex \times activity} = 3$, d.f. = 2,2617, $p = 0.045$) (Table 4.9).

The proportion of fixes occurring within the specified separation distance categories is shown in Table 4.10 (intra-group) and Table 4.11 (inter-group). There was a higher proportion of separation distances falling within the distance within which a contact was likely to occur between badgers from the same social group, and the proportion was highest in spring and smallest in summer (Table 4.10).

Inter-group badger dyads showed no contacts within 82 meters (the maximum distance a contact could occur in taking into account the error associated with radio tracking) in autumn. Spring and summer showed a very small proportion of separation distances occurring close enough for a contact to occur, whereas winter showed a slightly higher proportion. This was due to two female badgers from neighbouring groups (Septic Tank and Top) spending one night together (both inactive and active) in an outlying hole on the edge of the Top/Yew social group range.

Intra - group	Autumn	Winter	Spring	Summer	Overall
Male - Female	64.12 ±3.24 (2)	74.90 ±3.74 (3)	122.14 ±8.57 (5)	127.54 ±3.96 (4)	100.14 ±2.93
Female - Female	93.76 ±3.98 (2)	98.41 ±7.33 (2)	60.09 ±8.17 (2)	195.56 ±8.60 (2)	106.22 ±4.32
Male - Male				132.07 ±9.03 (1)	132.07 ±9.03
Yearling - Yearling	93.76 ±3.98 (1)	54.28 ±2.66 (1)	59.88 ±6.03 (1)	40.05 ±5.43 (1)	65.05 ±2.78
Yearling - Adult	64.12 ±3.24 (3)	126.95 ±6.44 (1)	817.16 ±12.07 (4)	144.48 ±6.75 (2)	147.80 ±5.60
Adult - Adult		55.65 ±4.81 (3)	57.68 ±3.91 (3)	145.90±4.12 (4)	84.87±2.69
Active - Active	87.92 ±9.20	156.58±21.59	101.21 ±6.70	140.46±4.68	125.90±3.75
Active - Inactive	94.49 ±4.00	116.37 ±7.81	222.60±19.90	163.94 ±6.66	147.06±5.80
Inactive - Inactive	53.37 ±3.27	67.11±3.81	47.91 ±9.00	104.43 ±7.59	64.55±2.99
Overall	73.52 ±2.61	82.80 ±3.51	109.85 ±7.11	139.37 ±3.48	102.36 ±2.40

Table 4.8. Mean intra-group separation distances between different badger dyad categories. Distances are in meters and numbers in brackets are the number of dyads that have contributed to the mean values.

Inter - group	Autumn	Winter	Spring	Summer	Overall
Male - Female	473.82 ±6.65 (3)	507.17 ±8.56 (6)	530.59 ±9.4 (6)	519.58 ±16.71 (6)	515.43 ±5.56
Female - Female	463.64 ±5.15 (2)	498.17 ±10.56 (7)	579.57 ±17.00 (4)	475.2 ±19.04 (3)	519.53 ±7.71
Male - Male	468.83 ±12.49 (1)	529.64 ±13.75 (1)	482.99 ±7.03 (3)	522.43 ±25.77 (5)	497.58 ±7.5
Yearling - Yearling	463.64 ±5.15 (2)	573.41 ±22.8 (4)	693.81 ±30.47 (2)		591.39 ±15.54
Yearling - Adult	473.82 ±6.65 (3)	463.13 ±5.99 (9)	494.94 ±3.83 (10)	505.71 ±13.33 (10)	487.12 ±3.45
Adult - Adult	468.83 ±12.49 (1)	592.11 ±13.65 (1)	560.54 ±25.00 (1)	550.06 ±28.04 (4)	549.31 ±9.46
Active - Active	462.32 ±10.62	522.12 ±20.9	607.19 ±15.54	575.99 ±19.67	576.47 ±10.64
Active - Inactive	470.48 ±4.58	504.28 ±6.42	486.88 ±4.74	487.67 ±14.75	489.9 ±3.55
Overall	468.83 ±4.24	506.16 ±6.15	534.29 ±6.98	511.76 ±12.14	513.15 ±3.93

Table 4.9. Mean inter-group separation distances between different badger dyad categories. Distances are in meters and numbers in brackets are the number of dyads that have contributed to the mean values. Inter-group dyads refer to neighbouring social groups only, inactive-inactive separation distances have been excluded from inter-group analysis of separation distances.

Separation distance (m)	Autumn	Winter	Spring	Summer	Yearly average
0 – 41	0.4066	0.5115	0.5862	0.2233	0.4319
– 82	0.5875	0.7542	0.7219	0.3399	0.6009
– 123	0.7976	0.8400	0.7998	0.4510	0.7221
– 200	0.9688	0.8714	0.8665	0.7392	0.8615
– 300	0.9999	0.9196	0.8988	0.9372	0.9389
– 500	0.9999	0.9747	0.9277	0.9966	0.9748
500+	1	1	1	1	1

Table 4.10. Cumulative proportion of frequencies of separation distances within specified distances for badgers belonging to the same social group.

Separation distance (m)	Autumn	Winter	Spring	Summer	Yearly average
0 – 41	0	0.0377	0.0019	0.0016	0.0103
– 82	0	0.0403	0.0044	0.0016	0.0116
– 123	0	0.0403	0.0044	0.0349	0.0199
– 200	0	0.0448	0.005	0.0571	0.0267
– 300	0.0103	0.0653	0.0619	0.0809	0.0546
– 500	0.6253	0.5723	0.6026	0.3757	0.544
500+	1	1	1	1	1

Table 4.11. Cumulative proportion of frequencies of separation distances within specified distances for badgers from neighbouring social groups.

4.5 Discussion

Relatively few studies have reported individual range sizes found by radio tracking for badgers in high-density populations. Most studies instead focus on group territory sizes, usually found by bait marking. Studies that have used radio tracking at Woodchester Park have focused on TB infection; they have found that badgers infected with TB have larger home ranges, and ranged over a greater proportion of their own territory, their ranges overlapped more with neighbouring ranges compared to uninfected badgers (Garnett 2002, Garnett et al. 2005). Badgers re-colonising areas previously cleared of badgers have larger home ranges compared to undisturbed badgers (Cheeseman et al. 1993, Tuyttens et al. 2000), and radio tracking has revealed that badgers visit cattle farms at night (Garnett et al. 2002). Where home range sizes have been reported in some of the above studies the mean size is approximately 15 hectares, which is in broad agreement with the results from this study. The mean individual home range size is however much smaller when compared to other badger populations with lower densities e.g. 34 or 77 hectares in a medium density population (Palphramand et al. 2007) and (Frantz 2004) respectively, and up to 412 hectares in a low density population (Revilla and Palomares 2002). Group territory sizes have remained relatively stable over the years at Woodchester Park, being approximately 35 hectares in size (Rogers et al. 1997). It is likely that several badgers from each social group contribute to their group range, whether badgers from the same social group have separate (but overlapping) areas that they use more, or whether all badgers use all of the group range would require more radio tracking. Radio tracking did reveal that individual ranges agreed with group ranges, i.e. individual ranges fell within group ranges, and often included part of the territory boundary as their boundary.

Although not significant, the patterns observed of seasonal home ranges being smaller in winter is consistent with other studies (e.g. (Neal and Cheeseman 1996)). Badgers do not hibernate in winter but are relatively inactive, and the reduced range size may be to reduce energy expenditure. Home ranges may be largest in summer due to badgers needing to seek a wider variety of food resources as the preferred food source of earthworms are harder to access because of hard dry ground (Roper 1994, Broseth et al. 1997), and ranges in other seasons may be affected by territorial defence, the seeking of a mate and reproduction.

Male badgers showed slightly larger (non-significant) home ranges, which is similar to findings in other studies at Woodchester Park (Rogers et al. 1997). The fact that no difference was found between TB infected and uninfected badgers should be treated with caution and may be due to small sample sizes. Only one badger (badger H43, an adult female from Wych Elm social group) was recorded as being positive; all other badgers were negative or exposed only. This positive badger showed somewhat erratic behaviour with a very large home and core range in autumn relative to other badgers, a slightly larger home range in winter and similar range sizes in spring and summer. Analysis of her core area revealed that she was not using the main sett of her social group for daytime resting and activity, but instead using an outlying hole between her social group and a neighbouring one. She was also trapped at this neighbouring social group in August 2005 instead of her own, and was later found dead in October 2005 in pasture on the edge of this neighbouring groups range. Such behavioural patterns may play an important part in the spread of disease, by either bringing the badger into closer contact with another social group, or by reducing contacts by spending time in outlying setts away from the main social group sett. None of the badgers from the neighbouring social group were fitted with a collar so their space use and movements are not known, and this badger's space use and movements cannot be determined in relation to them.

Another badger (badger 37R moving from Septic Tank to Wych Elm social group) also demonstrated behaviour worthy of note by moving to a different social group part way through the study. Previous radio tracking studies have suggested that movement between social groups is rare (Cheeseman et al. 1988a, Rogers et al. 1998), because dispersal is costly for the badger due to the potential aggressive behaviour that may be encountered (Kruuk 1978, Kruuk and Parish 1987). However analysis of trapping records of badgers at Woodchester Park suggest movements are more common than previously thought (Rogers et al. 1998). Rogers et al (1998), found that of the badgers trapped at Woodchester Park, 22.1% could be classed as permanent movers, which is how this move would be classed based on the trapping records and social group allocation (see chapter 2 for further details). Unfortunately insufficient radio tracking data were collected during the spring period when this particular badger moved social group to give an asymptotic home range, but the data that were collected revealed the badger was still associated with its initial social group. Intensive radio tracking of this badger during this period may have given some insight into how the move took place, i.e. if it occurred suddenly or if the badger went back and forth

between social groups. The badger must have crossed another different social group's territory at least once to reach its new social group. The trapping history for this badger reveals that it was only ever caught at its initial social group and the one it moved to. Whether this badger would move again or stay with its new group permanently cannot be determined as it was involved in a road traffic accident in October 2005. Studies have shown that when dispersal of badgers to other groups occur, badgers are more likely to move to social groups with fewer individuals (Woodroffe et al. 1995, Rogers et al. 1998), which, for females, may serve to increase their potential to breed. This badger did indeed move from a larger social group to a smaller one (refer to table 2.2 in chapter 2 for exact numbers).

This study was limited slightly by the small sample sizes, due to the time consuming nature of radio tracking, problems of collars dropping off or electrical failure and badgers dying. With advances in technology such as proximity collars or GPS collars, some of these problems could be overcome. This study also aimed to collect data on many individuals, with the aim to calculate separation distances (dynamic interaction) between as many badger dyads as possible, and to be able to geo-reference the locations with the proximity logger data (chapter 6), rather than more in-depth data for fewer animals. Radio tracking was also only conducted for six hours starting from dusk, which would mean behaviour occurring after this period would be ignored, although monitoring badgers at other times did not reveal any movements into areas not covered during the six hour period. The division of data into seasons is somewhat arbitrary (badgers do not conform to the Gregorian calendar system), and the dates on which badgers were radio tracked were not always evenly spread throughout the seasons. Localised climatic variations have been shown to affect activity levels of badgers e.g. (Cresswell and Harris 1988, Garnett et al. 2002, Roper et al. 2003a), in particular the rainfall in the previous 24 hours (Cresswell and Harris 1988). These localised effects may affect badger behaviour on the nights radio tracking took place and mask overall seasonal differences.

The initial error ratio calculated before the start of this study fell into the 0.010 – 0.049 category, defined by Moser and Garton (Moser and Garton 2007)), as implicit of a relatively inaccurate telemetry system, the actual error ratios calculated from mean MCP and 95% kernel estimates are 0.036 and 0.049 respectively. Although this is not the highest category this is probably a fair result because there is some inaccuracy associated with this method of radio tracking. Steps have been taken in this study to improve the accuracy

where possible, or account for the inaccuracy where possible. The reason MCP estimates are significantly larger than kernel estimates is likely due to a boundary strip being applied to the MCP estimate; the width of the boundary being based on the tracking resolution which was based on the radio tracking accuracy. The nature of the way the kernel home range is estimated and the smoothing factor applied will incorporate some level of inaccuracy from the data, but not to such an extent as the MCP boundary strip.

Analysis of the potential for interaction (static interaction) between badgers belonging to the same and different social groups revealed that there were no inter-group interactions observed when analysed using the 95% and 70% kernel home range method. This is consistent with results from bait marking studies that have found the Woodchester Park badger population has clearly defined boundaries that remain stable over many years (Delahay et al. 2000a, Tuyttens et al. 2000, Vicente et al. 2007). The presence of these distinct boundaries may negate the need for badgers to venture into other social groups' territories. Studies investigating badgers living at lower population densities have found varying levels of territoriality and overlap between social groups and individuals, e.g. (Kruuk and Parish 1987, Revilla and Palomares 2002) due to the flexible spatial organisation of the species (Johnson et al. 2000). Levels of inter-group overlap may be influenced by food resources (Kruuk and Parish 1987), mating opportunities (Revilla and Palomares 2002) or spatial perturbation caused by culling (Woodroffe et al. 2006a). Intra-group overlaps were observed, indicating that badgers belonging to the same social group do utilise the same areas and perhaps the same resources. Whilst static interaction analysis is a useful tool it is limited by the fact that differential levels of use within the home range boundary are not considered; the presence of core areas demonstrates that home range use in not random. A small overlap between two badgers that use an overlapping area frequently may have different consequences than a large overlapping area between two badgers that visit the overlapping area very infrequently.

Calculation of simultaneous separation distances showed that badgers belonging to the same social group had a higher proportion of shorter separation distances than badgers from neighbouring social groups. The very low proportions of small inter-group separation distances is consistent with the static interaction analysis of no inter-group overlaps compared to intra-group analysis. However, using data from more badgers for the separation distance analysis than the home range and static interaction analysis reveals that badgers from different social groups can come within close distances of each other. The

mean separation distance between badgers from different social groups was 513.15 meters. This corresponds well to the mean nearest neighbour distance between social group main setts at Woodchester Park of 595.28 meters (range 242-1176 meters) (Rogers et al. 1998).

The categorisation of separation distances into certain distance bands was necessary due to the error associated with radio tracking and even when separation distances were very small it does not necessarily mean that actual physical or close contact occurred between the two individuals. No information is available about the length of time individuals were in contact with each other or if more than two badgers were in contact with each other for example. These limitations can be overcome through the use of proximity loggers, as described in the next chapter.

4.5.1 Summary

Previous studies have revealed that the Woodchester Park badger population has stable group territories with distinct boundaries. This research supports these findings with individual badgers having home ranges comprising part of the social group range. The potential for badgers to interact in overlapping areas revealed little overlap between different social groups, but there were varying degrees of overlap between badgers belonging to the same social group. Simultaneous separation distances revealed badgers from the same social group were more likely to be at closer distances to each other than badgers belonging to different social groups and that close interactions between badgers from neighbouring groups were very rare.

Chapter 5 Consistency and reliability of proximity loggers under laboratory and field conditions

5.1 Introduction

5.1.1 Importance of understanding contacts in animals

Studying contacts between animals allows us to gain some understanding of species' behavioural ecology. For example, group formation may be affected by contacts between individuals, mating behaviour involves two individuals and thus contact between them, the foraging strategies of an individual or a group may be affected by contacts between the focal individual and others, predator-prey relationships may be affected by (inter-specific) contacts, and the use of areas or structures (e.g. den sites or corridors), spacing behaviour, and parental bonds are also affected by contacts. Contacts between individuals may also play a role in the transmission and spread of diseases or infectious agents.

5.1.2 Existing methods for quantifying contacts

Several different techniques have been used to attempt to quantify contacts with varying levels of success. The methods used have been limited by their accuracy and available technology; with the proximity loggers used in this chapter many of these problems are overcome. A brief outline of existing methods with their main advantages and shortcomings is given below.

Perhaps the simplest method of observing contacts is by direct observation of individuals. Direct observations are possible for species that are easy to observe, e.g. species that are large (Schneeberger and Jansen 2006) or that occupy open habitats (Schaller 1972), or species that habituate quickly to observers (Rood 1989). Where it is not possible to observe species in the wild, animals in captivity can be observed (Macdonald 1996, Day et al. 2000). However, captive animals often show abnormal behaviour which is not necessarily representative of wild behaviour (Lambrechts et al. 1999). Short-term direct observations may be possible for some species, for example, where a species may aggregate at a feeding site, be it natural (Cote 2000) or artificial (Totton et al. 2002). However, these results may be biased as they only provide a snapshot of activity, and if, for

example, a highly concentrated feeding site is supplied, unusual behaviours may be exhibited.

Radio-telemetry has been used to investigate contacts between individuals, either to take observers to the locations of species where they can then be observed directly (Baker and Harris 2000), or by simultaneously radio tracking several individuals and recording their locations with respect to each other (White and Harris 1994, White et al. 1995). Radio tracking has a certain level of error associated with position estimates of individuals (Chapter 3), and is very labour intensive. It is also usually only carried out for short periods of time and thus provides only a snapshot of the species' behaviour.

Passive integrated transponder (PIT) tags have been used in automatic acquisition systems to monitor individuals' proximity to certain structures or certain areas (Prentice et al. 1990, Rogers et al. 2002, Sutherland and Singleton 2003). However, they require high-powered readers for close range and so cannot be attached to small or medium-sized animals to investigate individual to individual contacts (Gibbons and Andrews 2004). Micro data-loggers have been used in biomedical and physiological telemetry applications, e.g. body temperature loggers (Woakes 1992) and depth recorders for sea mammals (Bodkin et al. 2007). However, they are not able to detect contacts between individuals or again, are too large for attachment to smaller species.

The MateID system is the forerunner to proximity loggers; one collar contains a VHF transmitter whilst another collar contains a low-power wideband VHF receiving device and data-logger (Ji et al. 1999). Collars are attached to individuals; usually a subset of the population or one gender wears one type of collar whilst another subset or gender wears the other type. Contacts can be estimated between the two groups wearing the collars, but not within the groups.

With the recent advances in technology the use of global positioning system (GPS) collars is becoming more common. Collars fitted to individuals can be programmed to either record their location onto the collar or relay the information to a satellite that can then be transmitted to a computer or mobile phone. Collars can be programmed to transmit locations at certain time intervals or to keep trying to transmit a fix until it has been successful. Under certain conditions many fix attempts are unsuccessful, e.g. up to <50% of fix attempts (Johnson et al. 2002, D'Eon 2003); factors such as vegetation cover and topography can introduce bias as they influence the success of the fix being obtained (Moen et al. 1996, Frair et al. 2004, Visscher 2006). When comparing locations between

individuals in order to compare contacts, there is still a certain level of error associated with the location recorded and it is unlikely that locations are synchronous between individuals. GPS collars have been used successfully to investigate contacts in deer (Schauber et al. 2007), but their large cost, relatively large size and weight and the fact they are not suitable for all species, e.g. species that live in unsuitable habitat or topographical conditions, means that their use is limited.

Finally, where contact rates have been used as a parameter in disease models, they have been estimated by experts in the field as best guesses (Smith and Wilkinson 2002), or derived from other model parameters (White and Harris 1995b).

5.1.3 The advantage of using proximity loggers to study contacts between animals

Proximity loggers are able to document contacts accurately and quantifiably. They provide an ideal method to record contacts between species that are secretive, nocturnal, cryptic or hard to observe directly. Their overall size and weight depends largely on the type of battery used; this means they can be adapted to fit a wide variety of species. The only limiting factor is that the species needs to be readably trappable as this is when the collar is fitted and proximity data downloaded. Proximity loggers are not limited to collars; they can also be mounted on a harness or glued on to the animal. If desired, they can also be mounted with a VHF antenna if the animal needs to be monitored remotely. Proximity loggers will record all contacts with other proximity loggers as and when they occur without the need for human presence.

5.1.3.1 The advantage of using proximity loggers specifically to study contacts between badgers

The European badger (*Meles* meles) is a crepuscular species, which makes it difficult to observe directly. It is also sensitive to the presence of humans, and may alter its behaviour when disturbed (Tuyttens et al. 2001). Badgers have a complex social system. In medium to high density populations they usually live in mixed age and mixed sex social groups of between three and 10 individuals, occupying a mutually defended territory (Neal and Cheeseman 1996). Badgers are widely considered to be a significant reservoir for *Mycobacterium bovis*; the causative agent of bovine tuberculosis (TB) (Krebs 1997), which can affect domestic animals of economic importance (Amanfu 2006). Studying contacts

between badgers will provide insight into how this disease and others (such as rabies) may spread. Additionally, badgers are relatively easy to trap (Tuyttens et al. 1999a). and can be fitted with a proximity logger collar and re-trapped to download the data without serious damage to their health (Woodroffe et al. 2005a). They are also large enough to be fitted with a proximity logger with a battery life of approximately a year that can be worn round the neck without serious detriment to the body condition of the badger over a long time period (Tuyttens et al. 2002).

5.1.3.2 Previous studies using proximity loggers to study contacts between animals

Published data exploring the use of proximity loggers to quantify contacts between wild animals include those by Ji et al. (2005); where the fore-runner to the proximity loggers was used to investigate contacts between possums (*Trichosurus vulpecula*) at three different sites in New Zealand. A very detailed study by Prange et al. (2006) investigated the behaviour of the proximity collars both in a laboratory environment and deployed on racoons (*Procyon loctor*) in the field. They investigated the distance at which contacts were initiated by collars at different orientations and different heights above ground. They also investigated how multiple collars behaved when placed together to record contacts over a longer time period. Swain and Bishop-Hurley (2007) used proximity loggers to quantify contacts between cattle, specifically to determine cow-calf (mother-offspring) pairs in herds.

5.2 Chapter aims

This study aimed to investigate the consistency and reliability of the data recorded by the proximity loggers both in a controlled environment and in a field setting. Two versions of proximity loggers were used in this study (version one, an older model, and version two, a newer model); the way in which the different versions behaved when they came into contact with other collars of the same and different model needed to be determined to ensure accurate and consistent results from the field. The distance at which contacts are detected (initiation distance), and the distance at which contacts end (termination distance) is investigated in detail

The results from the deployment of both models of the collars on badgers in the field are presented with respect to performance and functioning of the collars, and the steps necessary to produce accurate contact data suitable for further analysis are investigated.

5.3 Methods

5.3.1 Investigating the accuracy of the collars in a controlled environment

For details about the proximity collars used and their method of functioning refer to chapter 2 (section 2.4.5). The Ultra High Frequency (UHF) setting on the collars determines the distance at which collars can detect each other and can be altered by the user. In the first version of the collars (hereafter termed v.1) the UHF setting was set to 31 (the highest value and shortest detection distance available). The second version of the collars (v.2) had an extended range of UHF settings (up to UHF 62). Values up to 31 altered the receiver volume and values between 32 and 62 altered the transmission power; this was a modification to the collars designed to give greater control of distance settings (P. Sargisson, Sirtrack Ltd., *personal communication*).

This study aimed to determine the distance at which contacts were detected and lost in the field; the first version of the collars had already been deployed with a UHF setting of 31, so an equivalent UHF setting for the second version of collars needed to be found. Any discrepancies within and between the collars would also be detected.

The study was carried out outside, away from buildings and people in long grass with trees surrounding the site approximately 10 meters away in all directions. The observer was the only person moving about in the area and always tried to keep to the same movement route so as not to bias results or affect the radio wave propagation.

Collars were attached to clamp stands which were wrapped in bubble wrap insulation so that the clamp stands would not act as large aerials for the collars. The collars were held in a downward orientation to mimic the orientation they would be worn in around a badger's neck at approximately 10 centimeters off the ground – a similar height to when the collars are attached to badgers. A tape measure was used to measure the distance between two collars. In the first experiment (designed to investigate contact initiation) one collar was kept stationary whilst the other collar was moved towards the stationary collar in 10 centimetre increments every 60 seconds starting from a distance of 4 meters. In the second experiment (designed to investigate contact termination) one collar was kept stationary whilst the other collar was moved away from the stationary collar in 10 centimetre increments every 60 seconds, starting from zero centimeters (touching each other) up to a distance of 4 meters.

Each experiment was repeated ('run') four times at each of the UHF settings under investigation. Collars were selected randomly from those available for each experiment type (investigating v.1; 2 collars available, investigating v.2; 5 collars available). The data were downloaded from each collar after each run and the data deleted from the collar before being used again.

5.3.2 Field study methods

The study took place in Woodchester Park between September 2004 and November 2006. Collars were fitted to anaesthetised badgers according to the protocol described in chapter 2. Badgers were released at the sett they were caught at and left undisturbed to go about their daily activities apart from occasional radio tracking of some individuals (see chapter 4 for further details). Badgers that were not used in the radio tracking study were periodically located (using the VHF radio tracking signal) to check on the status of the collar.

Proximity data were downloaded from the collar when the badger was re-trapped or if the collar was located if it had fallen off in the field. During re-trapping, the condition of the collar was checked to determine it was working correctly and the health of the badger was checked to determine if wearing a collar was causing it problems. Collars were removed if they had failed, if they were affecting the badger, or if they had been worn for over a year (as the battery life would probably soon end). Collars that had fallen off in the field were retrieved where possible when they were above ground. The locations of collars that had fallen off badgers below ground were periodically monitored in case the collar was removed from the sett by the badger with part of its bedding or with soil from fresh excavations.

5.3.2.1 Validating the consistency and accuracy of collars returned from the field

Each time a badger was trapped or the collar retrieved from the field, and data were downloaded, was classed as a 'download event'. The success of each of these events, or the nature of the failure was noted. The number of contacts that were corrupt in some way was calculated as a proportion of the total number of contacts downloaded at each download event. At the time of download the clock time on the collar was compared to an

accurate time source to check how the clock was keeping to time, and any adjustments made if the collar was redeployed.

Contacts that occurred whilst the badger was being trapped were removed, as were any contacts that occurred within 24 hours of release after the second day of each two-day trapping session; this was to allow the badger to acclimatise to wearing a collar and recover fully from the anaesthetic. Where a trapped badger had come into contact with badgers that had not been trapped during the acclimatisation period, contacts were removed from both collars (where available) since the presence of a badger recently trapped may alter the behaviour of other badgers. Where contacts occurred on the night the badger was trapped there was the potential these might have occurred whilst the badger was in a cage, so these contacts were also removed (from 18:00 hours onwards).

Data were imported into a spreadsheet programme for further analysis. Example data obtained from each collar are shown in Table 5.1.

Data number	ID of badger being contacted	Date of contact	Time of contact	Duration of contact (seconds)
1	41	19/05/2006	22:31:35	18
2	33	20/05/2006	23:42:54	8
3	33	20/05/2006	23:43:27	1
..... etc.				

Table 5.1. Example data downloaded from each collar. In this example the collar is ID28, or badger U57, contacting badger ID41 (badger 53W), and ID33 (badger 52W). Although the collars record contacts with other badgers in ID numbers, badgers are referred to by their unique tattoo from here-on, to avoid confusion as several collars were re-used, and so have the same ID number.

5.4 Results

5.4.1 Investigating the accuracy of the collars in a controlled environment

The mean detection distances and termination distances of collars used under the different experimental conditions are shown in Table 5.2. The v.1 collars were set to the highest UHF setting available (UHF31) and were already deployed in the field at this setting so were not altered. The UHF settings of the v.2 collars were varied between UHF31 and UHF62 (the highest setting available). At a UHF setting of 57 the results became very variable and collars often failed to record any data on either one or both of the collars. At a UHF setting of 60 the collars recorded contacts very well inside but not in the experiment outside, and at a UHF setting of 62 no contacts were recorded at all. Within each run of the experiment the results varied with different collars as shown by the relatively large values for the standard error of the mean. Some collars appeared to perform better than others at both detecting and terminating contacts, but no patterns as to when and why this might occur were obvious. It became apparent from the results of the termination experiment that some collars were recording one long consistent contact with another collar whilst the reciprocal collar was recording several shorter duration 'broken' contacts. Version 1 of the collars recorded more broken contacts than v.2 (Table 5.2 and Figure 5.1 and Figure 5.2). This was supported with evidence from initial testing of v.1 of the collars in which four collars were placed together in a room overnight; all of them recorded broken contacts instead of one long contact. The time difference between the end of one broken contact and the start of the next contact was calculated and averaged for each run of the termination experiment. V.2 of the collars had a much more consistent time difference between broken contacts; always being between 17 – 21 seconds, compared to v.1.

There was no significant difference in values between collars that were kept stationary and collars that were moved in either the initiation (paired T-test, $t = 1.64$, d.f. = 27, $p = 0.11$) or termination experiment (paired T- test, $t = -0.8$, d.f. = 27, $p = 0.94$). There was a significant difference in the termination distances at different UHF settings (Kruskal Wallis $\chi^2 = 22.41$, d.f. = 6, $p = 0.001$), but not between initiation distances at different UHF settings (Kruskal Wallis $\chi^2 = 6.12$, d.f. = 6, $p = 0.41$).

UHF frequency/ Collar type	Average Initiation distance (m) (±SEM)	Average Termination distance (m) (±SEM)	Average number of broken contacts per collar (±SEM)	Average time difference between broken contacts (seconds) (±SEM)
UHF31 v.1	1.53±0.17	1.99±0.10	6.0±0.92	29.9±0.34
UHF31 v.2	1.85±0.14	3.14±0.17	1.3±0.31	18.4±0.05
UHF40 v.2	1.69±0.11	2.74±0.12	1.5±0.50	18.5±0.09
UHF45 v.2	1.47±0.13	2.67±0.22	1.5±0.65	18.4±0.18
UHF50 v.2	1.36±0.18	2.61±0.23	4.3±0.33	20.1±0.23
UHF55 v.2	1.42±0.20	1.98±0.32	3.1±0.26	21.0±0.17
UHF31 v.1/UHF45 v.2	1.56±0.11	3.12±0.08	5.4±0.57	25.8±0.24

Table 5.2. Mean initiation and termination distances for new and old versions of proximity collars at different UHF settings. V.1 are the older model of the collars, v.2 are the newer model, and v.1 and v.2 are where both models are tested together.

As a result of these findings a UHF setting of 45 was chosen for v.2 of the collars, representing the closest initiation distance to v.1 even though the mean termination distance was larger. However, not all of v.2 of the collars performed equally well, so three collars (out of eight) were set to UHF 40. At UHF 45 these collars gave very inconsistent results, whereas at UHF 40 they did usually detect contacts with other collars. These inconsistencies are due to individual variation in the output power of the UHF transmitters and receivers (Colin Hunter, Sirtrack Ltd., *personal communication*). Prange et al. (2006), also found individual differences in comprehensive testing of proximity collars, and they recommended testing each collar to determine the appropriate power setting for the desired detection distance.

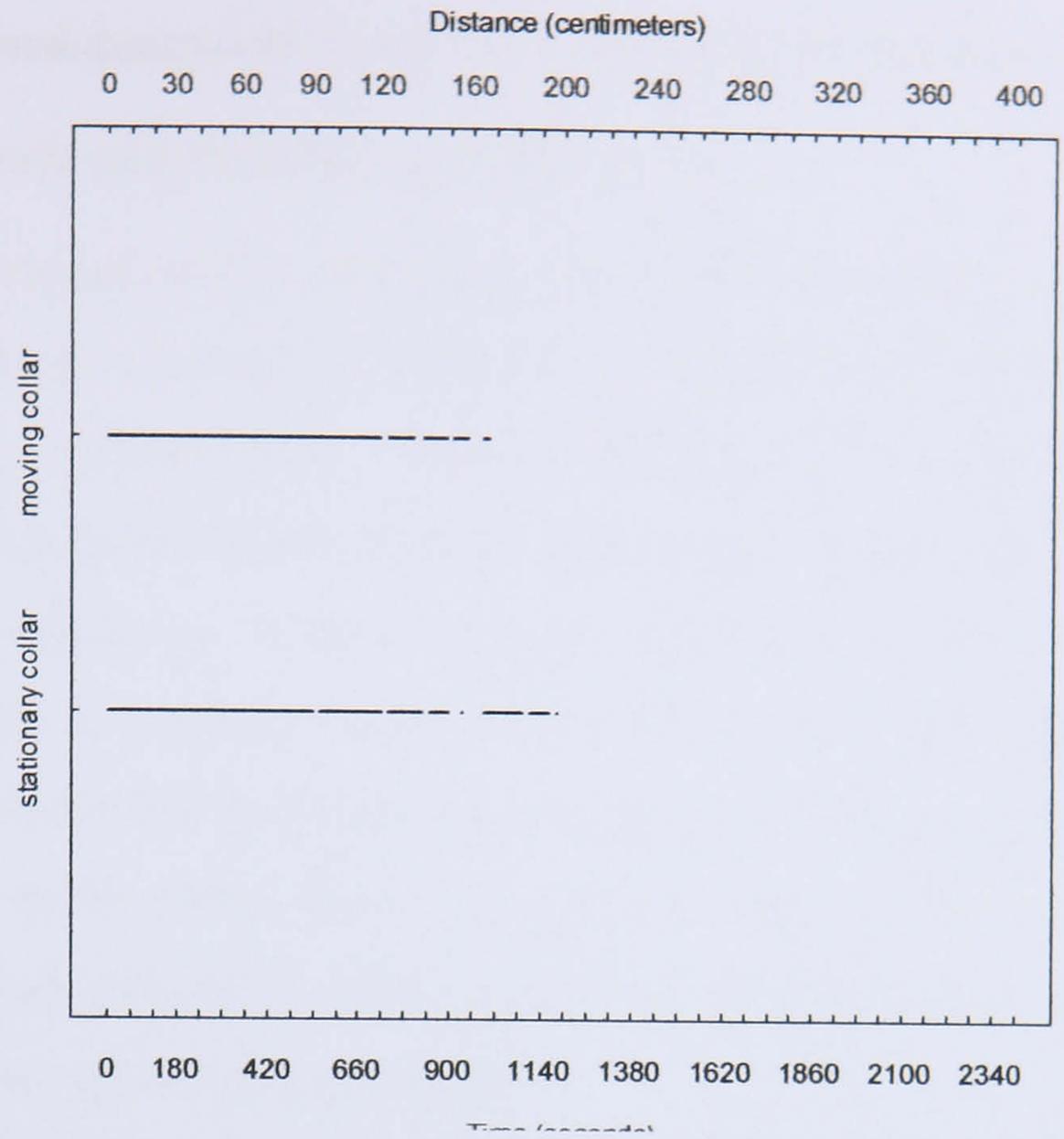


Figure 5.1. Example data obtained from the termination experiment with version 1 of the proximity collars (set to UHF31). The stationary collar recorded seven broken contacts whilst the moving collar recorded four. The average time between broken contacts was 28.6 seconds. The distance and time at which contacts were terminated are shown on the x-axis whilst the y-axis shows the two collars used in the experiment.

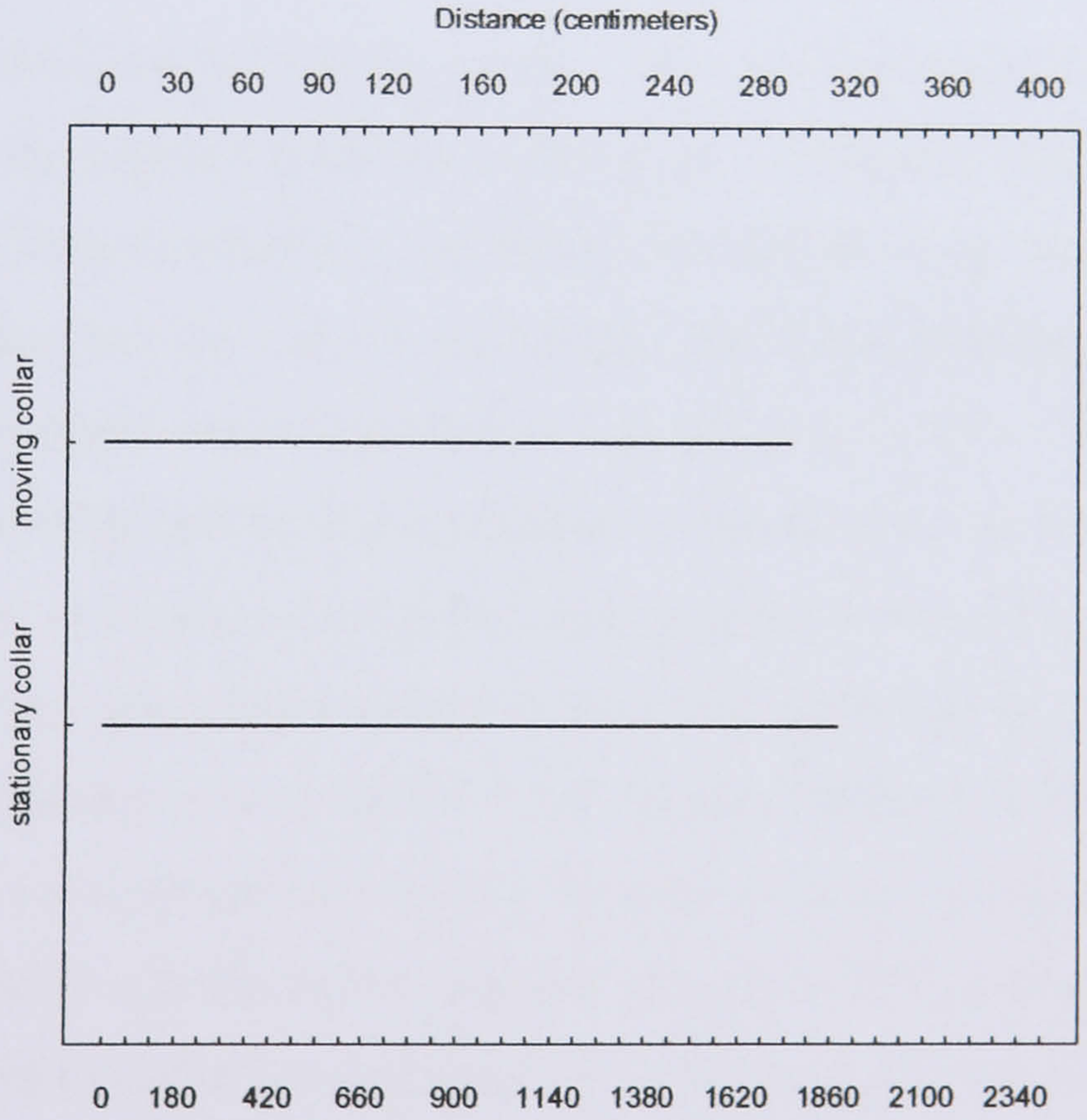


Figure 5.2. Example data obtained from the termination experiment with version 2 of the proximity collars (set to UHF45). The stationary collar recorded one contact with the moving collar, whilst the moving collar recorded two contacts 18 seconds apart with the stationary collar. The distance and time at which contacts were terminated are shown on the x-axis whilst the y-axis shows the two collars used in the experiment.

5.4.2 Validating the consistency and accuracy of the collars returned from the field

5.4.2.1 Downloading data and functioning of the collars

A total of 35 download events took place from 23 different collars: 23 download events were from 14 badgers wearing v.1 of the collars and 12 download events were from seven badgers wearing v.2 of the collars. From the 23 download events from v.1 there were five cases where data failed to download using the suggested method but downloaded instead using a full memory dump. There were three cases where data could not be downloaded due to the pin connections on the collars becoming waterlogged and damaged; sending the collars to Sirtrack Ltd for them to access the data directly on the micro-chip remedied this. With v.2 of the collars there were no cases where the data did not download using the upgraded software provided and the problem of the pins becoming damaged had been fixed by using a more secure protective cover.

With v.1 there was one case (badger 55G) where the collar failed to record contacts but continued to transmit contacts for the duration the collar was attached (contacts were detected by several other collars). There was also one case (badger 54R) where the collar worked as it should for the first six days then failed to record contacts for the rest of the duration (contacts were detected on another collar). This collar was left on the badger and functioned normally for the second period it was attached. It is highly likely that one collar (attached to badger H69) failed completely for the second period it was attached, neither recording nor transmitting contacts, and it is also highly likely that another collar (attached to badger 38R) failed completely after functioning normally for 20 days. These assumptions are based on other collars being attached to members of the same social group and functioning normally, or contacts previously being recording then stopping suddenly with no apparent reason (e.g. the battery should not be nearing the end of its life), or the badger being trapped/collar being retrieved from the field and found to be in a bad condition, e.g. the aerial very chewed and broken, the plastic casing cracked etc. With v.2 there were two periods (both with the collar attached to badger 39W) where the collar failed to record contacts but transmitted data that were picked up by several other collars. Table 5.4 summarises the data described here and in the following sections.

Determining whether the collar is functioning properly or not is not always possible. It is only possible to determine when a collar is only partly functioning, i.e. it is transmitting but not recording contacts when another collar is available that has recorded

contacts with this collar. Where no other collars are available it may be assumed that the badger is not contacting other badgers or the collar has failed completely. Likewise, determining whether the collar has failed completely is confounded by the problem of whether the collar has actually failed or the badger is just not contacting other badgers. The detection of a VHF signal (radio tracking signal) is not a good indicator of the functioning of the UHF proximity detecting part of the collar.

5.4.2.2 Corrupt contacts

Where contacts were corrupt it was most often due to a corrupt ID recorded of the badger being contacted, but occasionally a corrupt date or time occurred. Corrupt contacts gave nonsense data, e.g. IDs that did not exist, and so needed to be removed from the data. The average percentage of contacts that occurred per download event was 3.10 ± 2.20%, N = 31 (35 download events minus three events where the collar transmitted only and 1 event where the collar failed completely). V.1 recorded significantly more corrupt contacts than v.2; average 5.52 ± 3.23% (N = 21) versus an average of 0.11 ± 0.07% (N = 10), the difference between the two groups was significant ($Z = -2.01$, N = 31, $p = 0.048$). After these corrupt contacts and contacts when the badgers had been in traps had been removed from the data there were 120,456 contacts (from an initial 122,168 contacts), lasting for a total duration of 13,963,882 seconds – which is equivalent to 161 days, 14 hours, 51 minutes and 22 seconds.

5.4.2.3 Collar battery life and clock time keeping

The maximum period over which a collar was observed to record contacts or have contacts recorded with it if the memory was full was 419 days. The approximate battery life suggested by Sirtrack Ltd. was one year, however, they allow a 10% safety margin (SirtrackLtd. 2006b) and advise that battery life is affected by ambient temperature. Determining the average battery life is not possible because most collars were removed before they approached a year of use to avoid the battery failing whilst the collar was still attached to a badger and therefore being unable to locate the collar.

Clocks on the collars generally ran slightly fast, ranging from 02 minutes 21 seconds fast to 13 minutes 29 seconds fast for v.1 and 00 minutes 01 seconds to 04 minutes 19 seconds fast for v.2. This was over a minimum time period of 41 days and a maximum

of 500 plus days (the time between the collar first being fitted and data downloaded and clock checked). There was no obvious pattern between the length of time a collar was worn and the rate in discrepancy between real time and 'collar time'. No adjustment was subsequently made to the data; because it was not known at what rate the clocks changed, or whether it was related to the time over which the collars were worn or due to the battery decaying, and whether the change in time occurred suddenly or gradually over a longer period.

5.4.2.4 Removal of one-second contacts

120,456 contacts remained from 31 successful download events after corrupt contacts and 'trapped' contacts (contacts that occurred whilst the badger was in the process of being trapped) had been removed. Of these 120,456 contacts, 34.81% were contacts lasting one second in duration. V.2 of the collars had a slightly higher average percentage of one-second contacts (27.89%, N = 11) compared to v.1 (19.88%, N = 21), however the difference was not significant between the two versions of the collars ($Z = -0.04$, $N = 31$, $p = 0.98$). Previous work by Prange et al. (2006) and observations from laboratory testing of the collars, suggested that one-second contacts are likely to occur on the edge of the detection range of the collars at up to 0.5 meters from the continuous detection zone. The percentages of one-second contacts are also an underestimate of the real numbers because the percentages were calculated after corrupt and trapped contacts had been removed; the majority of corrupt contacts where the duration was not corrupt were one-second in duration. The numbers of two, three, four etc. second contacts were much more consistent with the rest of the data and did not bias the data as the one-second contacts did. As a result of these findings, all one-second contacts were removed from all download events. This left 78,523 contacts from 31 download events with a total duration of 13,921,889 seconds – which is equivalent to 161 days, 3 hours, 11 minutes and 29 seconds.

5.4.2.5 Combining broken contacts

The laboratory trials of the proximity loggers revealed a tendency for collars to record single contact periods as multiple shorter contacts (Table 5.2 and Figure 5.1 and Figure 5.2). Prange et al. (2006) found the tendency to record broken contacts was related to the separation time set on the collars. The separation time is the user-defined period that

a contact must not be detected during for that contact to be logged. Prange et al. (2006) found that more broken contacts were recorded when the separation time was shorter, and when more collars were available to be contacted. They found that when broken contacts were recorded, the time between the end of one contact and the start of the next contact was a function of the separation time, with the time between the broken contacts approximately equal to the separation time + 5 or 6 seconds. The separation time in this study was set to 15 seconds for all collars; the shortest time possible. In the laboratory trials described here the mean difference between broken contacts for both versions of the collars was 21.7 seconds (Table 5.2), this is similar to the mean time difference between broken contacts found by Prange et al. (2006) of 21.1 seconds. As a result of these findings contacts were combined if they were two seconds or longer (after removal of one-second contacts), and they occurred less than 21 seconds apart and they were from the same badger, i.e. if collar A recorded a contact with collar B, then another contact with collar B less than 21 seconds apart the two contacts were combined, but if collar A recorded a contact with collar B, then a contact with collar C within the 21 seconds, the contacts between collars B and C would not be combined). Successive contacts less than 21 seconds apart between the same badgers were all combined into one longer contact. 21 seconds was used instead of rounding up the average time difference between contacts to err on the side of caution. Combining contacts had the effect of reducing the number of contacts but increasing the duration of contacts. This left a total of 62,481 contacts from 31 download events with a combined duration of 14,139,146 seconds – which is equivalent to 163 days, 15 hours, 32 minutes and 26 seconds.

5.4.2.6 Removal of reciprocal contacts

Twenty-one datasets were recorded where contacts had been reciprocated between two collars, between 17 different badger pairs. Reciprocated data are duplicated data, and therefore the contact data from one badger of the pair needs to be removed. Data were removed from the badger that had recorded data over the shortest period (e.g. if the memory had filled up more quickly than the other badger in the pair – this was for consistency). If the period over which data were collected from the two collars was the same, the data from the collar that had recorded the shortest duration of contacts were removed.

Reciprocal data also allowed the consistency of the two collars to record contacts to be investigated. In theory, the data recorded on each collar should be exactly the same. Laboratory trials revealed discrepancies between the collars due to inherent differences in transmitter strength (Prange et al. 2006), so some variation may be expected (Section 5.4.1). For each pair the total number of contacts, the total duration of contacts, the average duration of contacts and the average time difference between successive contacts was calculated. Adjustments were made so that contacts were recorded over exactly the same time period. For example, if the memory on collar A became full before the memory on collar B, collar A could continue transmitting contacts but not record any more, whereas collar B could continue to transmit and record contacts with collar A. The time over which both collars could reciprocate contacts would be up to the point at which collar A's memory became full. Because the exact number of contacts that occurred cannot be determined, a measure of agreement was calculated for each of: the total numbers of contacts, total duration of contacts, average duration and average time difference using the following formula (equation 5.1);

$$\frac{A-B}{A}\times 100 \qquad \text{(Eqn. 5.1)}$$

Where A is the larger of number of contacts/duration of contacts etc. and B is the smaller. A value of 0 means perfect agreement between the two collars whereas a value of 100 indicates complete disagreement (a value of 50 means one collar has twice as many contacts/twice the duration etc. compared to the reciprocal collar). Of the 21 datasets, 11 were from v.1 with v.1 collars, one was from v.1 with v.2 and nine were from v.2 with v.2 collars. The results are shown in Table 5.3, broken down for each of the collar types, both for the original data (corrupt and trapped contacts removed), and for the adjusted data (one-second contacts removed and contacts less than 21 seconds apart removed).

The differences in numbers of contacts, durations of contacts, average durations and average time differences between the original data and adjusted data were compared but found to be not significant (Wilcoxon signed ranks; $Z = -0.36$, $N = 21$, $p = 0.72$; $Z = -0.78$, $N = 21$, $p = 0.43$; $Z = -0.45$, $N = 21$, $p = 0.65$; $Z = -0.17$, $N = 17$, $p = 0.87$ respectively). Combining the contacts and removing one-second contacts did generally lower (improve) the average reciprocal agreement between pairs of collars. The reciprocal calculation was generally low for most pairs of collars with all measures. One v.1 with v.1 pair did not agree particularly well over one period over which contacts were reciprocated, however.

after the second download event and a second period of reciprocated contacts, the collars were much more consistent. The reason for this is unknown. The one example where contacts between a v.1 and a v.2 collar were reciprocated showed the greatest disagreement of all of the pairs of collars; the v.1 collar recorded almost twice as many contacts (and therefore a much greater duration of contacts) as the v.2 collar. This may be due to individual variation in the collars, or due to v.1 and v.2 being on different UHF power settings.

After data that were reciprocated between pairs of badgers had been removed a total of 48,038 contacts remained lasting for 10,980,339 seconds – which is equivalent to 127 days, 2 hours, 5 minutes and 39 seconds.

	Total numbers of contacts		Total durations of contacts		Average duration of contacts		Average time difference between contacts	
	Original data	Adjusted data	Original data	Adjusted data	Original data	Adjusted data	Original data	Adjusted data
All data (N = 21)	11.32±2.98	9.85±2.41	17.83±5.45	17.80±5.43	22.64±4.94	20.54±5.84	19.47±4.35	16.10±3.09
V.1 with V.1 (N = 11)	11.50±3.40	10.75±3.18	9.59±2.21	9.61±1.92	18.35±3.78	13.84±4.75	23.24±6.71	19.08±6.07
V.1 with V.2 (N = 1)	48.02	37.24	79.61	79.83	60.78	67.85	48.88	38.72
V.2 with V.2 (N = 9)	7.01±3.64	5.71±2.33	21.03±10.06	20.91±10.07	23.65±9.87	23.48±9.71	10.41±2.80	9.03±3.34

Table 5.3. Agreement between reciprocal pairs of collars for the original data and the adjusted data (one-second contacts removed and contacts from the same badger occurring less than 21 seconds apart combined). Average time difference has a smaller sample size compared to the other measures (17, 9, 1, and 7 for all data, v.1 with v.1, v.1 with v.2 and v.2 with v.2 respectively) due to occurrences where only one contact is recorded between each pair of badgers; the time difference between successive contacts can not be calculated if there is only one contact.

Badger ID	Download event per badger	Initial number of contacts downloaded	Number of corrupt contacts removed	Number of trapped contacts removed	Number of 1 second contacts removed	Number of contacts remaining after 1s removed	Duration of contacts remaining after 1 s removed	Number of contacts combined	Number of contacts remaining after contacts combined	Duration of contacts remaining after contacts combined	Number of badgers contacted
13G	1	8190	13	27	2270	5880	1025124	1289	4591	1049967	2
18G	1	8190	30	0	2710	5450	1189419	1041	4409	1209605	3
37R	1	2221	20	207	710	1284	176140	169	1115	179414	4
37R	2	8190	0	16	3393	4781	729633	655	4126	742272	3
37R	3	7806	17	15	2404	5370	1152899	1176	4194	1175449	3
38R	1	2277	0	23	986	1268	253276	230	1038	257704	2
39W	1	1	0	0	0	1	5	0	1	5	1
39W	2	NA									
39W	3	NA									
43W	1	1538	0	28	395	1115	57809	87	1028	59540	1
44R	1	47	32	0	4	11	369	0	11	369	3
47R	1	18	0	12	2	4	61	0	4	61	2
50W	1	2	0	0	1	1	6	0	1	6	2
50W	2	1	0	0	0	1	9	0	1	9	1
52W	1	8188	15	195	2800	5178	912035	1045	4133	932058	5
52W	2	8189	13	146	3035	4995	738374	809	4186	753801	4
53W	1	8189	1	157	2979	5052	914206	865	4187	930657	4
54G	1	8188	2	7	2841	5338	819893	1056	4282	840108	4
54G	2	8189	3	34	3119	5033	655926	765	4268	670519	4
54R	1	1024	4	31	248	741	149579	113	628	151756	1
54R	2	5491	0	42	2068	3381	922892	463	2918	931818	1
55G	1	NA									
68R	1	8190	3	200	3619	4368	822780	1148	3220	844996	2
68R	2	8191	68	114	1646	6363	1054057	1954	4401	1017886	1
D19	1	1088	6	18	493	571	77397	113	458	79557	2
D59	1	5873	4	34	1790	4045	654149	1832	2213	670160	2
H43	1	596	4	24	173	395	48634	61	334	49818	4
H43	2	17	1	0	0	16	581	2	14	583	2
H43	3	18	0	3	0	15	852	4	11	919	2
H69	1	2245	1	20	1041	1183	252475	154	1029	255474	3
H69	2	NA									
J15	1	10	1	7	0	2	22	0	2	22	1
U51	1	8190	33	39	2855	5263	907508	684	4579	920681	1
U57	1	1794	13	24	348	1409	405585	327	1082	411853	5
U68	1	17	1	4	3	9	194	0	9	194	2
Total	35	122168	285	1427	41933	78523	13921889	16042	62473	14137261	

Table 5.4. Summary of data collected at each download event and how the different processes applied to the data affects the overall number and duration of contacts. NA = no data – collar failed; see section 5.4.2.1 for further details.

5.5 Discussion

The investigation of the behaviour of the proximity collars in a laboratory and field environment has given an indication of how the collars perform and allowed some aspects of their performance to be quantified. The proximity collars are a relatively novel technology so there will inevitably be initial teething problems to discover and overcome, and improvements are constantly being made by the developers. The second version of the collars was improved compared to the first version, in terms of a greater (decreased) UHF range, easier to use user interface and recording fewer corrupt contacts. However, as most of the badger proximity data were collected using v.1 collars, the v.2. collars needed to behave in a similar way to v.1. The initiation experiment suggested that a UHF setting of 45 may be the most similar to v.1, however, the termination distances were greater. Data collected from the field from badgers suggested v.1 and v.2 behaved in a similar way in terms of recording contacts and collected data. Only two badgers contacted each with one v.1 and one v.2 collar; in this case v.1 recorded many more contacts for a longer overall duration than v.2, suggesting that v.1 may detect contacts at a greater range or the individual variation in the collars was very large. As with the laboratory trials, larger sample sizes may give more conclusive results. The laboratory trials also revealed a large degree of difference between different collars at the same settings and also variation within the same collars.

These variations are probably due to radio wave propagation; ideally, the radiation pattern of the UHF transmitter should be symmetrical around the UHF antenna, meaning that whatever the orientation of the antenna, the distance the radio waves are transmitted should be the same. In reality, the radiation pattern is affected by many factors including the position, type and shape of the UHF antenna and the position of the detector. Other factors such as surrounding vegetation, metal objects, atmospheric moisture, standing water, height above ground, the uniformity of the terrain or the body mass of the animal can also affect the UHF field and either increase the signal or absorb it (SirtrackLtd. 2006b). This can result in discrepancies between collars even when set to the same power settings. In the trials conducted here only one orientation of the collars was used (two collars upright facing each other as they would hang around a badgers neck), and only one height above ground was tested. Both orientation and height have been shown to affect initiation distance (Prange et al. 2006), however, when the collars are worn by badgers they are likely

to stay in the same orientation around the neck (even though two badgers may not meet each other face on), and badgers are not an arboreal species so large height differences between collars are unlikely to be observed. Radio wave propagation may have been amplified in the laboratory trials due to the use of metal clamp stands to hold the collars, surrounding vegetation and varying weather conditions. Using an object to hold the collars that was more realistic in size, shape and body mass to a badger may have alleviated some of these problems. The specifics of the environment in which the trials were carried out will hinder comparisons between other studies; for example, collars were initially tested indoors and found to not terminate contacts until over four meters. This was due to the reflection and propagation of radio waves off many indoor surfaces in an enclosed environment; this will occur outdoors as well to varying degrees depending on the environment.

The termination effect revealed the effect of hysteresis, the potential need for greater distances to terminate than to initiate contact (Prange et al. 2006), which can be up to twice as great as induction distances (Colin Hunter, Sirtrack Ltd., *personal communication*). The hysteresis effect appeared to affect v.2 greater than v.1 of the collars, although the reason for this is not known. The termination experiment also highlighted that collars were often recording broken contacts instead of one longer duration contact. The time difference between broken contacts is a function of the separation time, the time specified by the user that designates a definite break in contact between individuals (SirtrackLtd. 2006b). If two individuals are in contact with each other, and then move apart for longer than the separation time, if they then move back into contact with each other, two contacts will be logged. However, if they move back into contact with each other within the separation time, then only one longer contact will be logged. The separation distance for the badger collars was set to the lowest time possible (15 seconds) so as to record as accurate contacts as possible. However, the termination experiment and reciprocal data retrieved from the field revealed that one collar may be recording a single long contact whilst the other collar records multiple contacts, when they should both be recording one long contact. This problem was overcome by combining broken contacts in the field data less than the separation time plus six seconds. Adding the extra seconds onto the separation time was to overcome in part, the three-second delay in signal detection following the transfer of data to permanent memory (Prange et al. 2006). Examination of the badger contact data after contacts had been combined revealed there were still many

contacts separated by 22 – 30 seconds, so perhaps a larger separation time could have been used. A better solution for future research would be to increase the separation time on the collar settings before deployment to the maximum separation time possible which does not result in the loss of meaningful biological data.

Recovery of data from the field demonstrated that collars were functioning as intended with only a small proportion of the data being corrupt or missing. The collars appeared to be robust enough to withstand the badgers' attempts to chew the collars, with the aerials being the worst affected by this, although this will affect the VHF signal more than the UHF signal. One collar continued to function and data could be downloaded after it had been run over by a car. The large quantity of one-second contacts recorded by the collars only became apparent from examination of the field data. These contacts usually occur when the collars are just beyond the continuous detection range (Prange et al. 2006), and comprised approximately 35% of the data. The suggested course of action is to remove these contacts, to better represent true contacts ((Prange et al. 2006); Trevor Jordan, Sirtrack Ltd., *personal communication*).

It is believed that the processing of the data (removal of corrupt contacts, removal of one-second contacts and combining contact between the same individuals occurring less than 21 seconds apart), gives a more accurate representation of the true numbers and durations of the contacts occurring without any prior assumptions about the behaviour of badgers. The distances at which contacts are recorded (initiated at approximately 1.5 meters), does not necessarily imply physical contact between animals, but at 1.5 meters it is highly likely that animals will be aware of each other, and does imply proximity rather than direct contact which is a very important biological event to investigate further.

5.5.1 Summary

The consistency and reliability of the proximity loggers has been investigated in this chapter, and whilst some processing of the data is required, only minor adjustments are needed to give accurate results that have biological significance.

The use of proximity loggers are a great technological advance; they allow interactions to be studied remotely and constantly, and to a higher degree of accuaracy than has previously been possible for relatively less cost and time, therefore, they are a considerable step forward in allowing us to investigate contacts between animals.

Chapter 6 Quantifying contacts between badgers in a high-density badger population

6.1 Introduction

This chapter describes the data collected by proximity data loggers attached to badgers in a high-density population. The functioning of the loggers is described in chapter 2, and laboratory trials investigating the accuracy and validity of the collars and steps necessary to obtain data suitable for analysis are described in chapter 5.

6.1.1 What constitutes a contact?

A contact can be defined as 'the state or condition of communicating or meeting' (Compact Oxford dictionary), in this chapter a contact is defined as having occurred when two or more individuals come within a distance of approximately one and a half meters of each other for a period of two seconds or longer. This is the approximate resolution of the proximity loggers at the UHF setting they were set to as determined by laboratory trials (section 5.4.1), and whilst there may be considerable variation in detection distances between collars, the majority of collars have to come within one and a half meters of each other for a contact to be detected. This distance does not necessarily represent physical contact occurring between two or more badgers, although it may well occur, but rather the close proximity of individuals. It is likely that at this close proximity distance, badgers will be aware of each other, through the senses of sight, smell, sound or touch, and will react to the presence of other individuals at this distance.

6.1.2 Importance of understanding contacts in animals

The frequency of contacts between individuals, the duration of contacts, when and where they occur play a vital role in many aspects of a species' behavioural ecology (Prange et al. 2006). Contacts are important in mating between individuals (Ramsey et al. 2002, Ji et al. 2005, Pimley et al. 2005), in social group formation (White and Harris 1994, Gehrt and Fritzell 1998), in foraging (Grenier et al. 1999, Totton et al. 2002), and additionally, are fundamental to understanding infectious disease transmission (McCallum et al. 2001, Lloyd-Smith et al. 2005). This last factor has received perhaps the most

attention. For directly transmitted wildlife diseases, the rate at which new infections occur in a population, or the rate at which an existing infection spreads through the population, is the product of the contact rate; the proportion of these contacts that are with susceptible individuals, and the proportion of these contacts that result in infection (McCallum et al. 2001). It is therefore the rate determining step in the spread of disease (White and Harris 1995b).

6.1.3 Importance of understanding contacts in badgers

The Eurasian badger was first identified as a wildlife host for bovine tuberculosis (TB) with the discovery of several tuberculous badgers in Gloucestershire in 1971 (Muirhead and Gallagher 1974). This is a disease of considerable economic importance to cattle in the UK, and much attention has been paid to the role of badgers as they are widely considered to be the main wildlife reservoir for the transmission of *Mycobacterium bovis* to cattle (Delahay et al. 2003). Disease transmission structure, operating through contact rate patterns and contact rate/density relationships, is a key factor influencing the dynamics of the disease (McCallum et al. 2001). However, uncertainty in the estimate of the disease transmission rate (both within and between species) and transmission structure, has resulted in considerable controversy surrounding management options (Smith 2001). Badgers are also relatively susceptible to infection with the rabies virus (Wandeler et al. 1974), and if an outbreak were to occur in the UK, the role of the badger as a potential vector and its contact probabilities needs to be understood (Smith and Wilkinson 2002).

6.1.4 Models of disease in badgers

Models formulated to predict dynamics of disease specifically in badgers can be split into those investigating TB and those investigating rabies. In both types, however, models lack accurate information on the contact rate and thus transmission rate. Contact rates have been derived from best guesses from expert opinions, e.g. (Smith and Wilkinson 2002) or derived from other model parameters e.g. (White and Harris 1995b). Models may be either deterministic (they use one set of fixed values), or stochastic (they incorporate a random element). The transmission function (the function that relates the contact or transmission rate, (the number of new infections per unit time) to the densities of susceptible and infectious or infected hosts), (McCallum et al. 2001) also affects the model

used; models usually assume either density-independent of density-dependent contact probabilities. Density-independent (also equivalent to frequency dependent) transmission assumes contact probabilities are constant at all densities, that is, each infected animal contacts the same number of healthy animals regardless of territory size (McCallum et al. 2001). This may occur with mating activity. Density-dependent probabilities assume that contact probabilities are an increasing function of density, that is, the number of contacts increases with density. This may occur with random movements (McCallum et al. 2001), but in territorial animals, animals may make a relatively fixed number of contacts regardless of the population density (Smith 2001). The relationship between contact rates and density may therefore be more complex and may not be linear. For example, (Caley et al.) (1998) and Ramsey et al., (2002), were able to manipulate possum density in New Zealand and investigate the effects of reducing density on contact rates; they found a non-linear relationship. With regard to badgers, Smith (2001) states that the relationship between contact probability and population density is unknown and requires further investigation.

Because so many models of TB in particular, but also of rabies, have been constructed, a brief review of the models is given below, with reference to the main features of the models, but specifically the contact rates in terms of how they were estimated within the models.

6.1.4.1 TB models

The first badger/TB model is that by Anderson and Trewhella (1985), who modelled density-dependent transmission and included pseudo-vertical (mother-cub) transmission in their model. These authors defined many population and disease parameters that are still being used today. This model was later extended by Bentil and Murray (1993) to include a class of badgers that could recover from the disease after infections, however, there has been little evidence to suggest this can occur. The original Anderson and Trewhella model was again extended by Ruxton (1996) to investigate seasonality and stochasticity. Barlow (1996), modelling TB in badgers and other diseases, took parameter values from the Anderson and Trewhella model and included density-dependent mortality, recruitment, or both, and examined both linear density-dependent transmission and non-linear transmission. Barlow (2000) found that disease heterogeneity

may occur as a result of the non-linear relationship between host density and disease contact rate, although he focussed mainly on possums and TB interaction. Swinton et al., (1997) revised the original Anderson and Trewhella model to examine density-dependent and frequency-dependent transmission and an increase in transmission as a result of social perturbation, a factor that has received more attention recently, e.g. (Woodroffe et al. 2006a, Woodroffe et al. 2006b, Carter et al. 2007).

White and Harris (1995b), produced a spatial stochastic simulation model of badger population dynamics and TB. In this model, dispersal and social perturbation was limited to adjacent social groups. They predicted a minimum social group size of about six adults and yearlings for TB to persist in the population, and at group sizes above this the disease would become endemic. Their model allowed for inter-group transmission between adult males, adult females and yearling males only. Greatest importance in transmission was given to adult males to other adult males, and they used a ratio of transmission processes of 4:2:1 for adult male: adult male, adult male: adult female and adult male: yearling male pathways. They also allocated different proportions of the annual infection probability to different seasons. This model was then used to evaluate different badger control options (White and Harris 1995a), and later modified to include fertility control as an option (White et al. 1997). However, when modelling different badger control strategies, these authors did not simulate the detection of disease in cattle, making reactive control policies unrealistic (Smith 2001).

Smith et al. (1995), determined that a group size of about eight badgers was needed to sustain endemic TB, similar to findings by White and Harris (1995b), and that a model which included differential transmission states (infectious and super-infectious) gave predictions closest to reality. This model was extended to investigate different control options (Smith et al. 1997, Smith et al. 2001a), and again to investigate sex differences in transmission and the transmission of TB from badgers to cattle herds (Smith et al. 2001b). More recently, focus has shifted to the effectiveness of different control methods, e.g. vaccination (Wilkinson et al. 2004). Potential control methods include lethal control, vaccination, fertility control or habitat manipulation of the wildlife host, or management of cattle, including vaccination, selective breeding or a change in farm management practices. Individual-based spatially-explicit models have been developed (Shirley et al. 2003), and a cost-benefit analysis of badger control strategies carried out (Smith et al. 2007).

6.1.4.2 Rabies models

Studies investigating rabies in the badger include models developed by Smith and Wilkinson (2002) and Smith (2002). In the first paper, the authors derived badger-to-badger contact rates using consensus expert opinion as no empirical data were available. Contact probabilities were determined for all individuals within the same social group, between males and females from different social groups, between same sex animals, between social groups and between adults and juveniles from different social groups for different seasons in a high-density badger population. They investigated both density dependent and density independent contact probabilities, and emphasised the knowledge gap in the understanding of contacts. The contact probabilities derived by Smith and Wilkinson (2002) are perhaps the most detailed contact probabilities published to date; these were compared to contact probabilities derived by radio tracking badgers in a moderate density population and found to be much higher (Newton-Cross 2003), although the study by Newton-Cross was limited in that contacts were only recorded between badgers when they were active and during a six hour period on each night they were radio tracked.

6.1.4.3 Summary regarding models of diseases in badgers with reference to contact rates

The most important point all these above models have in common is that they lack baseline field data, particularly regarding the variation of contact rates between badgers of different age, sex, and disease classes and at different population densities and in different seasons. Where different age/sex/season categories have been investigated, models have given the greatest importance to transmission in spring due to mating behaviour, and inter-group transmission between adult males, with very little consideration given to female badgers. Clearly, this requires further investigation.

6.1.5 Movements of badgers

As has been previously discussed (see chapter 1), at high densities, badgers form discrete, collectively defended social groups (Kruuk 1978, Rogers et al. 1997), believed to be formed by delayed dispersal of offspring (Kruuk and Parish 1982, Cheeseman et al. 1987, Da Silva et al. 1994), and it is thought that there are greater constraints on individuals from leaving their natal territory to breed independently at greater habitat saturations

(Woodroffe 1993). Previous radio tracking studies of high-density badger populations has shown that movement of badgers between social groups is rare. For example, Cheeseman et al., (1988a) at Woodchester Park, found males seldom dispersed but instead made temporary forays to adjacent social groups to mate with resident females, and no females were observed to disperse at all. Woodroffe et al., (1993) also observed low male dispersal rates at Wytham Woods (another high-density badger population), but they also observed female dispersal, which was slightly more common than male dispersal and often involved badgers moving in coalitions and to social groups that had fewer individuals. Christian (1995) also observed male badgers making temporary forays to mate with females, however, he also reports in another study more females than males making permanent moves to different social groups and subsequently breeding successfully (Christian 1994).

Results from a large-scale study of badger movements determined by trapping badgers rather than radio tracking, found that overall movement rates were higher than those observed by radio tracking, with approximately 50% of badgers captured moving at some point, although most movements were occasional movements where badgers visited only one or two social groups other than their main resident group (Rogers et al. 1998). Rogers et al. (1998) also found male badgers moved more often than females, and male badgers were more likely to move to groups with a higher proportion of females. Both males and females were more likely to move to smaller groups, and dispersal was more common in older and heavier badgers. Cubs were also found to move, a result that had not been observed before. As with previous studies, the majority of moves were observed between adjacent social groups (Rogers et al. 1998).

More recently, genetic studies have been used to investigate the mating system of badgers in a high density badger population (Woodchester Park) (Carpenter et al. 2005). Extra-group paternity has previously been reported (e.g. see above and also (Evans and Macdonald 1989, Domingo-Roura et al. 2003)), but the extent, and the distances over which it occurred, were unknown. Genetic analysis revealed roughly half of assigned paternity was attributed to extra-group males, the majority of which were from neighbouring groups, although one yearling male was found to have crossed social group boundaries. This high level of extra-group paternity is thought to contribute to reduced inbreeding.

6.1.5.1 Movement of badgers with respect to TB

Studies to date have shown a localized distribution of infection of *Mycobacterium bovis* in high-density badger populations, often with infected and uninfected social groups adjacent to each other. This had led to suggestions that the organisation of the population into social groups may limit the spread of TB; that there is limited evidence of transfer between social groups (Delahay et al. 2000c); and mating between social groups has not encouraged the disease to spread (Carpenter et al. 2005). Whilst the association of badgers belonging to the same social group in setts is thought to facilitate transmission within the group, movements of badgers between groups are likely to be important in the spread of infection within the population as a whole. Rogers et al., (1998) found that increases in the movements of individuals between groups are followed by a rise in the incidence of disease the following year. They also found that infection status did not affect movement. Vincente et al., (2007) also found the likelihood that an individual or a group was a TB incident case positively correlated with individual and group level movement.

Many of the control options for TB involve reduction in badger densities, by culling or other methods. However, culled badger populations experience social perturbation (defined as substantial disruption to the social organisation and behaviour patterns of individuals in a population (Carter et al. 2007)), such as enhanced movement, increased immigration into culled areas, disruption of territoriality, increased ranging and mixing between social groups (Cheeseman et al. 1993, Tuyttens et al. 2000, Carter et al. 2007). These perturbation effects appear to cause increased contact amongst badgers and hence elevated *Mycobacterium bovis* prevalence (Woodroffe et al. 2006a, Woodroffe et al. 2006b), increased opportunities for badgers to come into contact with cattle, and may increase the likelihood that infected individuals may become infectious through stress-induced immunosuppression (Gallagher and Clifton-Hadley 2000). In conclusion, it appears that culling causes increased movement, which in turn increases contact rates between badgers and exacerbates disease transmission.

6.2 Chapter aims

This chapter aims to quantify contacts between badgers in a high-density undisturbed badger population. This is the first time proximity loggers have been used on badgers in this way. An in-depth investigation into contact rates between individuals will be carried out and seasonal, sex, age, disease state and other patterns of contact will be investigated where possible. The average daily contact rate, average daily contact duration and frequency of contacts will be calculated between pairs of badgers and analysed at an intra- and inter-group level. This study will focus on direct contacts (as defined in section 6.1.1) between badgers. The main route of *Mycobacterium bovis* infections amongst badgers is thought to be by aerosol via the respiratory route (Cheeseman et al. 1989, Clifton-Hadley et al. 1993), or as a result of the injection of infected saliva when bite wounding occurs; both of which are likely to occur when badgers contact other badgers. An undisturbed badger population which has not been subject to culling is used in this study, although some members of the population are naturally infected with TB. This study will aid in the understanding and quantification of contact rate in an undisturbed population, allowing comparisons to be made with different density or culled populations at a later date.

6.3 Methods

The methods by which the proximity loggers function and the technology behind them is described in chapter 2 (section 2.4.5), and the performance and accuracy of the collars in recording contacts between badgers are described in chapter five. The proximity loggers record contacts between badgers when individuals wearing collars come within approximately one and a half meters or less of each other. The identities of the badgers contacting each other, the date and time of the start of the contact and the duration of the contact are logged onto the memory on the collar for later downloading. Downloaded data were treated as described in chapter five; corrupt contacts and contacts that occurred whilst the badger was being trapped and before the end of the acclimatisation period post trapping were all removed. One-second contacts were removed and consecutive contacts were combined if they were between the same badgers and occurred less than 21 seconds apart to alleviate some occurrences of broken contacts. Reciprocal data were removed.

6.3.1 Frequency of contacts

For each badger pair, the number of days on which contacts occurred between two badgers was calculated as a percentage of the total number of days during the study period on which contacts could occur.

6.3.2 Contact rate and contact duration

The average daily (24-hour) contact rate and average daily contact duration were calculated between each pair of badgers that contacted each other on a seasonal basis. This was determined by calculating the number (or duration, in seconds) of contacts that occurred within that season between pairs and dividing it by the number of days over which contacts could have occurred within that season. Seasons were defined as; Autumn (September to November), to cover the slightly less than spring peak of territoriality and mating activity; Winter (December to February), to cover the gestation period and the birth and rearing of cubs; Spring (March to May), to cover the main peak in territoriality and mating activity and cub emergence; and Summer (June to August), to cover the independence of cubs.

Where badgers were re-trapped within a season, the trapping days were removed as appropriate and if the data memory on the collar became full or the collar fell off before the end of the season, days were also removed as appropriate. The last date on which contacts could occur between two badgers when one or both of the badgers was not re-trapped was determined by taking the later of the last day the badger was radio tracked (and recorded as being active at some point during that night); or the last day on which contacts were recorded on that collar with another badger; or the last day another badger recorded contacts with that collar. This may result in an underestimate of the number of days over which contacts could have occurred in a few instances, because the date last radio-tracked or the date of last contact may not be the same as the date the collar fell off the badger. If no contacts occurred between two particular individuals within a season, but there was the potential for contacts to occur between this pair for 46 days or more (see section 6.4.3.1 for calculation of this cut-off period), the contact rate and duration was scored as zero.

6.3.2.1 Statistical analysis

Linear mixed-effects (LME) models were used to assess the effects of social group, sex, season and TB status on the average daily contact rate and duration for intra- and inter-group contacts. LME allows for hierarchically structured data and can include nested factors and/or repeated measures, as this can reduce the number of unknown regression components within the model (Zuur et al. 2007). Pair ID (an identifying number assigned to each different pair of badgers), year and season were treated as nested grouping factors, and a first order autoregressive structure was used to overcome time-dependence of the data between successive study periods.

6.3.3 Badger 37R as a case study

Badger 37R was a female badger fitted with a proximity logger. She made a permanent move from her natal social group to a different social group partway through the study and therefore demonstrates interesting behaviour worthy of further investigation. The badgers she contacts and the timing and duration of these contacts are looked at in-depth and displayed graphically.

6.3.4 Time of day contacts occurred

The time of day contacts occurred was found by calculating the frequency of contacts that occurred within each hour on a 24-hour basis, between each badger pair. The proportion of contacts within each hour was then determined by dividing the total in each hour by the total number of contacts. The average proportion within each hour was found for both intra-group and inter-group contacts separately.

6.3.5 Locations of contacts

The location of where contacts took place was found by investigating contacts that took place whilst badgers were being radio tracked (chapter 4); proximity data for badgers that had been radio tracked were analysed to see if contacts had occurred during the time period radio tracking took place. Data from other badgers that had recorded proximity data but were not radio tracked, were investigated to see if they had contacted individuals that had been tracked if no data were available for them. This allowed the locations of contacts to be plotted in ArcView GIS 3.3 (Environmental Systems Research Institute Inc.), and superimposed on top of the map of Woodchester Park, the bait marking map and badger home and core ranges as determined by radio tracking in chapter 4. Radio tracking location fixes were included if proximity data were recorded within the five-minute period between fixes.

6.3.6 Contact probabilities

Daily contact probabilities were calculated for different badger pair combinations in different seasons using the method described in White et al. (1995):

$$C_{prob} = 1 - (1 - C_{rate})^{ip}; (\text{maximum} = 1.0) \qquad \text{(Eqn 6.1)}$$

where C_{prob} is the contact probability over a specified period, C_{rate} is the contact rate (the number of encounters between any two animals in a given time period), and *ip* is the period in days, over which a contact probability is measured. The contact probabilities found in this study can be compared to those suggested by Smith and Wilkinson (2002), based on expert opinions for a high-density badger population, and those found by Newton-Cross (2003), based on simultaneous radio tracking of badgers in a moderate-density badger population.

6.4 Results

6.4.1 Overview of data collected

Twenty-nine badgers were fitted with proximity loggers at some point between September 2004 and November 2006. Proximity data were downloaded from 22 different collars (Table 5.4), but from these 22 collars, all badgers wearing collars (apart from one) were implicated in contacting at least one or more different badgers. The one collar that was not involved in contacting any other collars probably either failed or the badger wearing it moved away from the study site or died, because after the badger was radio tracked for one night, four nights after it was released, a VHF signal could never subsequently be found for it (after extensive searching) and the badger has not been trapped again since. It is possible that this badger may have just not contacted any other badgers, but this is highly unlikely when compared to data collected from the rest of the study. Thus, for the purpose of analysis, the collar is assumed to have failed the day after it was last radio tracked.

In theory, if all the collars had all been worn at the same time for the same duration, and they had all functioned, there is the potential for 405 pairs of contacts to occur. However, not all collars were fitted at once; collars functioned for different periods of time and some failed, complicating matters considerably. An overview of which badgers were fitted with collars at what time and for how long is provided in **Table 6.1**. The data are presented at a monthly resolution to provide an overview; this may mean that some data are over-represented, for example, if a badger was fitted with a collar in any given month it was recorded in that month, even if the collar failed or the memory filled up within a few days of that month. Because memory space on the collar was limited to approximately 8120 entries, some collars' memories filled up quickly and these collars acted only as transmitters once that had occurred; collars with memory spaces still available acted as both proximity transmitters and receivers, and the memory status of the seven collars not recovered from the field is unknown. In three instances, collars were recovered that had failed to record contacts onto the memory; these were deemed to be acting as transmitters only because other collars had logged contacts with these collars (see chapter 5 section 5.4.2.1 for further details). The mean duration a collar was worn for was 163.69 days (range 2 to 419 days), although this is probably a slight underestimate because when collars

dropped off in the field and were recovered, the exact date they fell off is unknown and the date of last contact or date last radio-tracked has been used as a surrogate date.

Once data had been processed as described in chapter 5, there were a total of 48,038 contacts lasting for 10,980,339 seconds (127 days, 2 hours, 5 minutes and 39 seconds) split between 42 different pairs of badgers. The number of contacts, duration of contacts and number of days on which contacts occurred varied greatly between different pairs of badgers. This variation was due mainly to the difference in the frequency and duration of contacts between badgers belonging to the same social groups and badgers belonging to different social groups. Intra- and inter-group contacts were subsequently analysed separately.

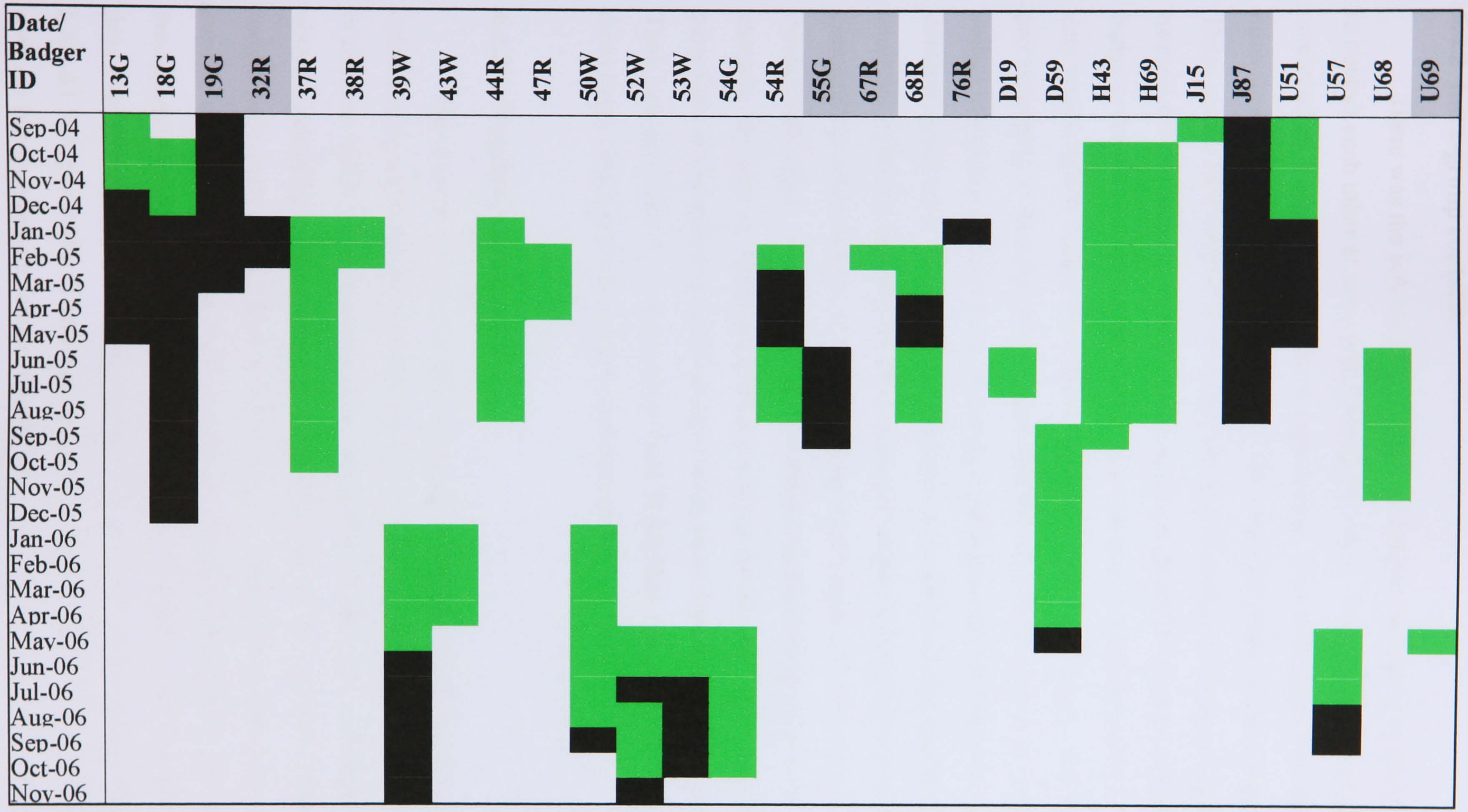


Table 6.1. Overview of which badgers were fitted with proximity loggers and how long for. A green bar means that the collar was able to both transmit contacts and record contacts in that month. A black bar means a collar was able to transmit contacts only. A grey bar in the badger ID row means data were not recovered from that collar so only its transmitting status is known from contacts recorded by other badgers.

6.4.2 Intra-group contacts

There was the potential for 24 pairs of badgers belonging to the same social group to contact each other at some point during the study. Twenty-one out of the 24 pairs contacted each other at least once in each season. Two of the pairs not contacting each other involved one badger (badger 44R) for which the status of the collar is uncertain. These results lend support to the proposition of the collar malfunctioning as it is very unusual for two badgers from the same social group not to contact each other (or any other badgers) for such a long period (in this case it was over a 50 day period). Therefore, the data involving this badger have been discounted from the analysis. The remaining badger pair belonging to the same social group that did not contact each other involved one of the collars in the pair failing within two days, meaning the period over which any potential contacts could occur was very short; this pair were therefore also discounted from the analysis. After discounting the above data, all badgers belonging to the same social group contacted all other badgers within that group where there was the potential for them to contact each other. This resulted in 23 different badgers being involved in intra-group contacts. In total, seven female:female pairs, ten female:male pairs and four male:male pairs from seven different social groups (seven pairs from Beech, three pairs from Septic Tank, one pair from Yew, seven pairs from Wych Elm, one pair from Cedar and one pair from Breakheart) were recorded as making contact.

6.4.2.1 Frequency of contacts

The number of days on which contacts occurred between badger pairs was calculated by dividing the number of days on which a contact occurred by the total number of days on which a contact could occur between each pair, then multiplying by 100 to obtain a percentage. On average, contacts occurred on 58.51±7.19% of days between badger pairs (range 3% of days to 99% of days). This does not take into account the number of contacts that occurred on each day they did contact each other or the duration they spent in contact with each other. There was no significant difference in the number of days over which contacts occurred between the different social groups (Kruskal-Wallis $\chi^2 = 5.42$, d.f. = 6, $p = 0.49$). There was also no significant difference in the frequency of contacts between female:female, female:male and male:male pairs (Kruskal-Wallis $\chi^2 = 0.075$, d.f. = 2, $p = 0.96$). The difference in contact frequency between pairs of animals of

different TB status (TB -ve:TB –ve, TB –ve:TB +ve and TB +ve:TB +ve) was not significant at the standard 5% level, although it was significant at the 10% level (Kruskal-Wallis $\chi^2 = 5.36$, d.f. = 2, $p = 0.07$). When TB status was re-coded to consider pairs as either having no potential to transmit TB, or pairs with potential to transmit or already transmitted TB (TB –ve:TB +ve and TB +ve:TB +ve considered as one category and TB –ve:TB-ve considered as one category), there was a significant difference at the 5% level (Kruskal-Wallis $\chi^2 = 5.35$, d.f. = 2, $p = 0.02$), with badgers pairs with TB potential (N = 7) contacting each less frequently than TB negative pairs (N = 14).

6.4.2.2 Contact rate and contact duration

The average daily contact rate between badgers belonging to the same social group was 33.23 ± 4.81 contacts/day (range 0.02 to 97.82) and the average daily duration was 7814.23 ± 1238.77 seconds/day (range 0.15 to 24535.00), which is equivalent to 2 hours, 10 minutes and 14 seconds (Table 6.2). However, these rates are average daily rates, and as section 6.4.2.1 shows, badgers do not contact each other every day, but on average on 59% of days. If the daily contact rate and duration are calculated only for days on which contacts occur the rates are higher; 50.52 ± 9.73 contacts/day (range 0.50 to 338.62), and 11509.97 ± 2293.24 seconds/day (range 2.0 to 78298.92), which is equivalent to 3 hours, 11 minutes and 50 seconds. The entire period (including days where no contacts were made) is used for future analysis as this is more representative of true contact patterns.

Average daily contact rate and duration between each badger pair for each season were normally distributed (Z = 1.01, N = 40, $p = 0.26$ for contact rate, Z = 1.29, N = 40, $p = 0.07$ for contact duration). Contact rate and contact duration were positively correlated (Pearson product-moment correlation $r = 0.97$, N = 40, $p < 0.001$) (Figure 6.1).

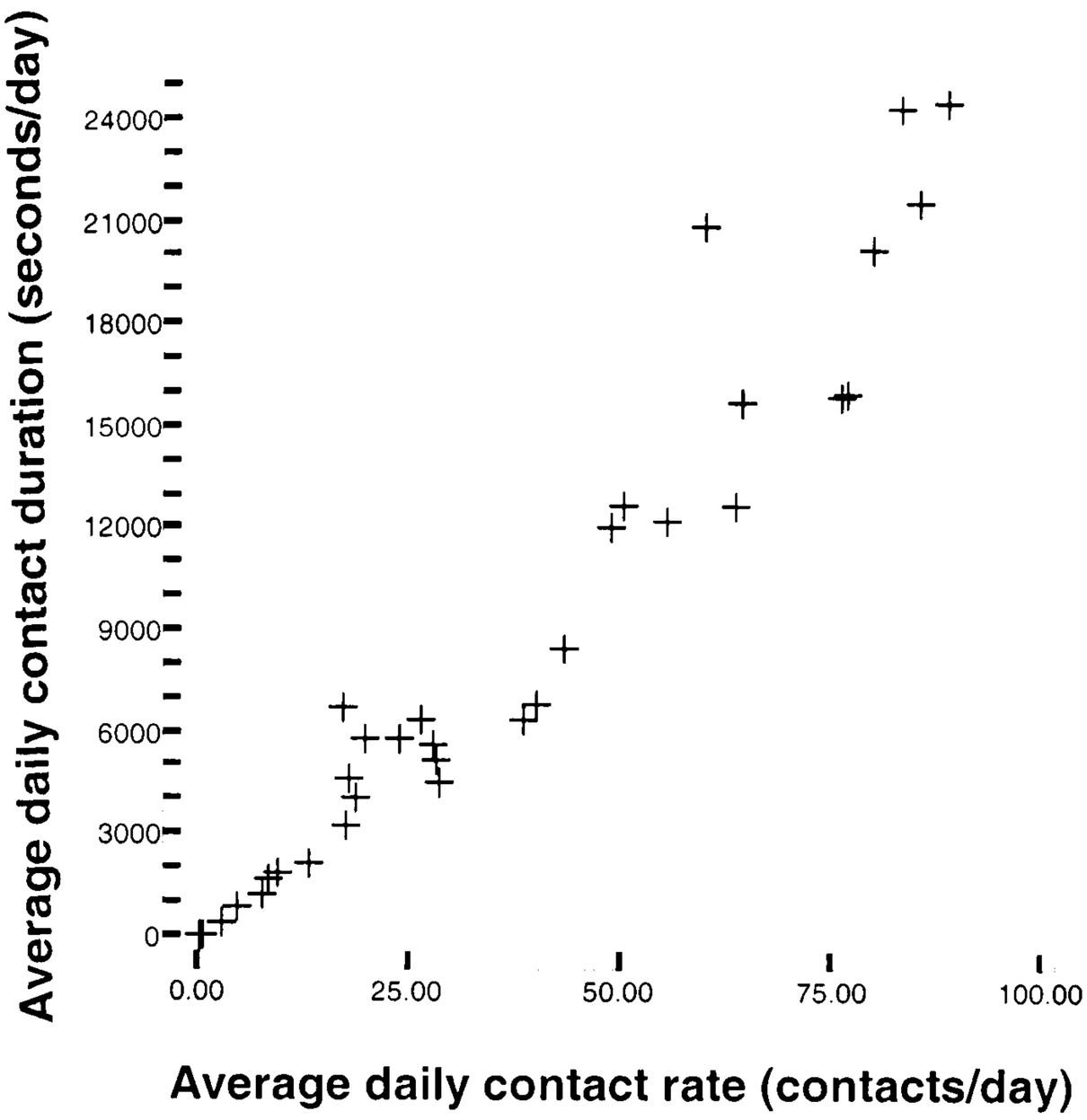


Figure 6.1. Correlation between average daily contact rate and average daily contact duration between badger pairs belonging to the same social group.

The factors of age, sex, disease status, season and social group and how they affect average daily contact rates and contact durations are summarised in Table 6.2. The design was not balanced: the number of pairs contacting each other within different social groups varied, and not all ages, sex and disease status categories were available in different social groups and in different seasons. These factors were analysed using linear mixed effect models for intra-group contact rates and contact durations separately (**Table 6.3**). Because of the lack of data the only interactions that could be investigated were disease status × season and disease status × sex. Only disease status had a significant effect on contact rate and contact duration (LME: $F_{\text{disease status}} = 8.4$, d.f. = 1,9, $p = 0.018$ (contact rate), and $F_{\text{disease status}} = 7.7$, d.f. = 1,9, $p = 0.021$ (contact duration)), although the interaction between disease status and season was significant at the 10% level for intra-group contact rate only ($F_{\text{disease status} \times \text{season}} = 2.7$, d.f. = 3,10, $p = 0.099$). Badger pairs with the potential to transmit TB (either one or both badgers in the pair classed as TB positive) had lower average daily contact rates and durations compared to badgers with no potential to transmit TB.

		Average daily contact rate (contacts/day)		Average daily contact duration (seconds/day))		Number of pairs
		Mean ± s.e	range	Mean ± s.e	range	
Season	Autumn	30.40 ± 7.95	0.04 - 83.19	7056.29 ± 2134.74	0.15 - 24348.46	11
	Winter	35.11 ± 8.83	1 - 85.36	8814.83 ± 2542.61	6.00 - 21578.79	11
	Spring	32.39 ± 12.85	0.03 - 88.46	7510.36 ± 3285.50	2.59 - 24535.00	8
	Summer	34.98 ± 11.11	0.02 - 97.82	7790.00 ± 2513.96	0.24 - 22619.69	10
Sex	Male:female	41.36 ± 8.58	0.02 - 97.82	9880.84 ± 2210.66	0.15 - 24535.00	10
	Female:female	17.44 ± 5.90	0.06 - 59.86	4889.96 ± 1855.88	6.0 - 20868.29	7
	Male:male	37.55 ± 7.12	3.00 - 76.08	7603.47 ± 1712.31	312.10 - 15910.92	4
Age	Adult:adult	20.59 ± 7.13	3.00 - 50.30	4657.02 ± 1846.94	312.10 - 12692.79	5
	Adult:yearling	29.08 ± 5.84	0.02 - 85.36	6354.95 ± 1411.35	0.15 - 24348.46	12
	Yearling:yearling	53.10 ± 11.25	1.00 - 97.82	13972.62 ± 2986.14	6.00 - 24535.00	4
Disease status	TB negative	39.53 ± 6.10	0.03 - 97.82	9803.84 ± 1601.53	2.59 - 24535.00	14
	TB potential	20.16 ± 6.55	0.02 - 76.08	3681.96 ± 1302.03	0.15 - 15910.92	7
Social group	Beech	31.29 ± 7.73	3.00 - 85.26	7826.73 ± 2224.45	312.10 - 21578.79	7
	Septic Tank	17.95 ± 9.73	0.03 - 63.74	3607.15 ± 1960.48	2.59 - 12676.58	3
	Yew	8.91 ± 8.34	0.57 - 17.25	3376.48 ± 3368. 84	7.64 - 6745.31	1
	Wych Elm	33.90 ± 7.41	0.02 - 83.19	7374.70 ± 1854.25	0.15 - 24348.46	7
	Peglars	50.30	NA	12692.70	NA	1
	Cedar	88.62 ± 5.27	79.58 - 97.82	22461.82 ± 1245.03	20230.77 - 24535.00	1
	Breakheart	1.00	NA	1.00	NA	1
Overall		33.23 ± 4.82	0.02 - 97.82	7184.23 ± 1238.77	0.15 - 24535.00	21

Table 6.2. Mean daily contact rates and contact durations for pairs of badgers contacting each other belonging to the same social group. Disease status has been classified as TB negative (both badgers are TB negative and there is no potential for disease transmission), or TB potential (one or both badgers are TB positive, so there is potential for disease transmission). NA means that only one pair of badgers from that social group contacted each other during one season only; therefore an average cannot be calculated.

Variable		Contact rate				Contact duration			
		d.f.	coefficient ± s.e.	t	*p*	d.f.	coefficient ± s.e.	t	*p*
Intercept		11	45.0 ± 11.0	4.08	0.0028	11	11145 ± 3040	3.67	0.0037
Season									
	Winter	11	7.9 ± 10.0	0.79	0.4453	11	1524 ± 2915	0.52	0.6116
	Spring	11	-1.9 ± 10.5	-0.19	0.8563	11	-741 ± 3082	-0.24	0.8144
	Summer	11	15.4 ± 10.8	1.42	0.1823	11	2039 ± 3232	0.63	0.5409
Social group									
	Septic Tank	8	-21.8 ± 14.4	-1.51	0.1692	8	-6614 ± 3931	-1.68	0.1309
	Yew	8	-26.4 ± 25.6	-1.03	0.3325	8	-6616 ± 6962	-0.88	0.4053
	Wych Elm	8	22.2 ± 16.3	1.36	0.2097	8	5628 ± 4442	1.27	0.2408
	Peglars	8	13.8 ± 26.9	0.51	0.6234	8	2325 ± 7393	0.31	0.7611
	Cedar	8	26.5 ± 23.8	1.54	0.1631	8	10376 ± 6382	1.63	0.1426
	Breakheart	8	-35.5 ± 26.9	-1.32	0.2234	8	1524 ± 2915	-1.40	0.1986
Sex									
	Female:Female	8	-16.4 ± 14.2	-1.15	0.2827	8	-2301 ± 3861	-0.60	0.5677
	Male:Male	8	-27.7 ± -60.9	-1.04	0.3267	8	-6627 ± 7121	-0.92	0.3793
Disease status									
	TB potential	8	-60.9 ± 21.4	-2.85	0.0216	8	-15227 ± 5916	-2.57	0.0329
TB status × season									
	TB potential × Winter	8	-4.6 ± 31.8	-0.14	0.8889	8	-1209 ± 8759	-0.14	0.8936
	TB potential × Spring	11	34.9 ± 16.4	2.13	0.0571	1	7966 ± 4908	1.62	0.1328
	TB potential × Summer	11	-4.9 ± 14.5	-0.24	0.7413	1	317 ± 4356	0.07	0.9432
Sex × TB status									
	Female:Female × TB potential	8	4.9 ± 31.8	0.15	0.8816	8	-409 ± 8586	-0.05	0.9631
	Male:Male × TB potential	8	43.9 ± 32.7	1.34	0.2157	8	9070 ± 8803	1.03	0.333

Table 6.3. Linear mixed-effects model for differences in the intra-group daily contact rate and intra-group daily contact duration. Results shown are relative to the reference category; season: Autumn, group: Beech, sex: male:female, disease status: TB –ve:TB –ve.

6.4.3 Inter-group contacts

Contacts were recorded between 22 pairs of badgers belonging to different social groups. Apart from one badger pair, contacts were only recorded between badgers belonging to neighbouring social groups. The pair of badgers that contacted each other that did not belong to neighbouring social groups were badgers 37R and H43; badger 37R subsequently moved to the social group to which H43 belonged (see section 6.4.4 "badger 37R case study"). Therefore, for subsequent analysis, only actual contacts, and the potential for contacts between badgers belonging to neighbouring social groups are considered. Not all badgers from different social groups contacted each other; there was the potential for 69 neighbouring pairs of badgers to contact each other, although the time periods over which the potential for contacts to occur varied greatly from just two days to 294 days.

6.4.3.1 Frequency of contacts

The frequency of inter-group contacts was much lower compared with intra-group contacts. Contacts occurred very rarely and not all badgers contacted each other. The maximum period over which there was the potential for contacts to occur between neighbouring badgers and contacts did occur was 294 days, in which contacts occurred on one day. The equivalent minimum period was 2 days, in which contacts occurred on one day (this does not take into account the number of contacts on that day or the duration). The maximum number of days on which contacts occurred between inter-group badgers was 21 days (out of a possible 100 days), i.e. on 21% of days. The maximum number of days over which no contacts occurred, although there was the potential for them to occur, was 194 days, and the minimum was zero contacts in two days. Based on the 22 pairs of badgers where contacts did occur, contacts occurred on 8.01 ± 2.34% of days. However, this value is heavily influenced by the pair of badgers that contacted each other once in two days (50% of days, and is not representative of the rest of the data), therefore, the median value is more characteristic; where contacts did occur between badgers belonging to neighbouring social groups they occurred on 4.38% of days.

Because inter-group contacts are very infrequent, the likelihood of any contacts occurring between neighbouring badgers within a short time-span such as two days is very unlikely. Therefore, where no contacts occurred between pairs of inter-group badgers, a

cut-off point of 46 days was chosen based on the median percentage of days; 4.38% is approximately equivalent to one contact every 23 days, and allowing an error margin of twice this is 46 days. Therefore, if within any given season there were no contacts recorded between pairs of badgers belonging to neighbouring groups, and the potential number of days over which contacts could occur within that season was less than 46, the data were excluded for that season. This left 40 pairs of badgers with the potential to contact each other, of which 21 pairs (excluding the non-neighbouring pair) did make contact.

6.4.3.2 Potential for contacts

Excluding pairs of badgers where no contacts were recorded between pairs when the potential for contacts to occur was less than the 46-day cut-off point, left 40 pairs of badgers from neighbouring social groups with the potential to contact each other. Twenty-one of these pairs did make contact. The number of pairs within each age group, each sex group, each disease state and between social groups is shown in Table 6.4, along with the total number of pairs that could make contact.

Between social groups:		**No. of pairs that made contact**	**No. of pairs with potential for contacts to occur**
Beech	Septic Tank	2	10
Beech	Larch	1	1
Beech	Cedar	0	2
Septic Tank	Yew	4	5
Septic Tank	Cedar	0	0
Septic Tank	Breakheart	0	2
Yew	Wych Elm	10	13
Yew	Peglars	0	2
Wych Elm	Peglars	3	4
Breakheart	Cedar	1	2
Between sexes:			
Male	Female	14	23
Female	Female	7	15
Male	Male	0	2
Between ages:			
Adult	Adult	4	7
Adult	Yearling	13	25
Yearling	Yearling	4	8
Between disease status:			
TB negative	TB negative	16	34
TB potential	TB potential	5	6

Table 6.4. Numbers of pairs of badgers that made contact between social groups, and the total number of pairs that had the potential to make contact between social groups. Pairs are included only if they either made contact, or did not make contact over a period of 46 days or more.

6.4.3.3 Contact rates and contact duration

Average daily contact rates and average daily contact durations between all badger pairs from neighbouring groups, where there was potential for contacts to occur over a period of 46 days or more, were not normally distributed ($Z = 3.61$, $N = 64$, $p < 0.001$ for contact rate and $Z = 3.88$, $N = 64$, $p < 0.001$ for contact duration). This was because of the large number of zero values where no contacts occurred between pairs of badgers. Contact rate and duration were significantly positively correlated (Spearman's rank correlation $r_s = 0.97$, $N = 64$, $p < 0.001$) (Figure 6.2).

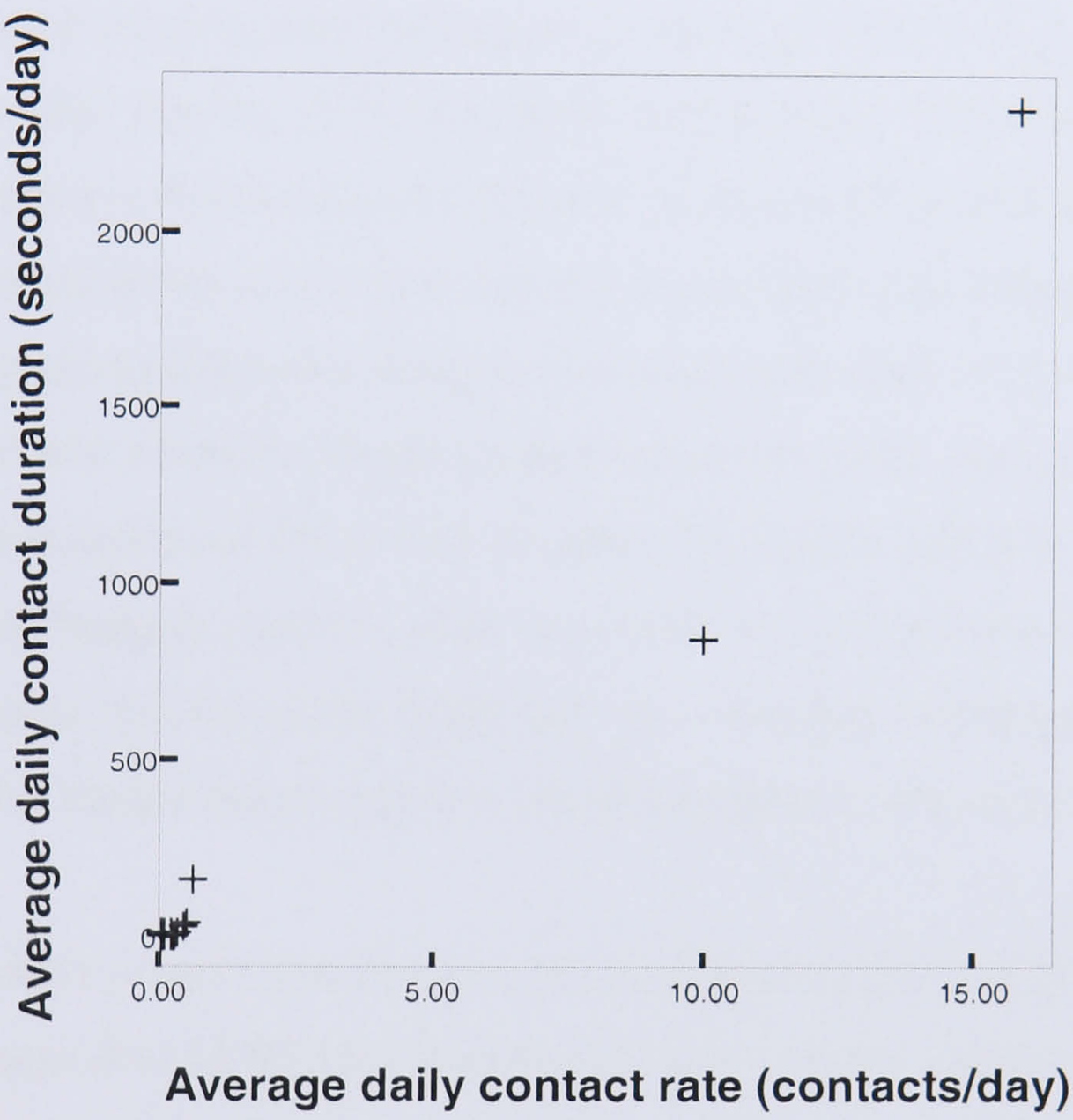


Figure 6.2. Correlation between average daily contact rate and average daily contact duration between badger pairs belonging to neighbouring social groups.

Figure 6.2 shows that there are two data points that have a much larger average daily contact rate and duration compared to the rest of the data. If these are removed the data are still significantly positively correlated (Spearman's rank correlation $r_s = 0.97$, $N = 64$, $p < 0.001$). These two data points are contacts between badgers 39W and 52W (the highest contact rate and duration of the two) and 52W and U69.

39W is a yearling female belonging to the Yew social group and 52W is a yearling male belonging to the Wych Elm social group. These two badgers contacted each other on

seven days out of a possible 14 days during the spring season, and made 222 contacts lasting a total of 32872 seconds (therefore average daily contact rate is 15.86 contacts/day and average daily contact duration is 2348 seconds/day). During the following summer and autumn periods the same two badgers contacted each other on six out of a possible 55 days in summer (average daily contact rate of 0.20 contacts/day and average daily contact duration of 2.58 seconds/day) and eight out of a possible 31 days in autumn (average daily contact rate of 0.48 contacts/day and average daily contact duration of 37.19 seconds/day). Therefore, during the spring period the contact rate and duration was much greater compared to other seasons.

52W is the same yearling male belonging to the Wych Elm social group described above and U69 is an adult female. U69 was caught in the Septic Tank social group when she was first fitted with a collar but had always previously, and has subsequently, been caught in the Yew social group, so for this analysis is considered as belonging to the Yew social group. During spring these two badgers contacted each other on one day ten times, for a total duration of 846 seconds. These contacts occurred on the day after she was released having been trapped and fitted with a collar. No further contacts were recorded with U69 by any other badgers, and her collar was never recovered from the field. We therefore have to assume that her collar either fell off or stopped working after the last contact recorded. This means the period over which contacts could occur is not very representative.

The average daily contact rate between all neighbouring pairs of badgers is 0.46 ± 0.29 contacts/day (range 0 to 15.86) and the average daily contact duration is 53.28 ± 38.20 seconds/day (range 0 to 2348). If however, average contact rates and durations are calculated without considering the two pairs mentioned above then the averages decrease significantly to 0.07 ± 0.16 contacts/day (range 0 to 0.61) and 4.29 ± 2.55 seconds/day (range 0 to 155.48). However, as with intra-group contacts these rates are daily rates averaged over a period of days on which contacts do not occur every day. Badgers from neighbouring social groups do not contact each other every day, but on approximately 4.38% of days (section 6.4.3.1). If the daily contact rate and duration are calculated only for pairs of badgers that do contact each other and based only on days on which contacts actually occur the rates are higher; 3.11 ± 0.99 contacts/day (range 0.50 to 31.71) and 274.32 ± 149.08 seconds/day (range 2.00 to 4696.00), which is equivalent to 4 minutes and 34 seconds. These rates and durations for inter-group pairs can be compared to the rates for

intra-group pairs, and are significantly different (Mann-Whitney test; Z = -5.7, N = 73, $p <$ 0.001 for contact rate and Z = -5.81, N = 73, $p < 0.001$ for contact duration). Therefore, on the days on which badgers from neighbouring social groups do contact each other, they make fewer contacts and for less time compared to days on which badgers from the same social group contact each other. As with intra-group contacts, the entire period including days where no contacts were made and including pairs where no contacts were made but there was potential for contacts to be made is used for future analysis, as this is more representative of true contact patterns.

The factors of age, sex, disease status, season and social group and how they affect average daily inter-group contact rates and contact durations are summarised in Table 6.5. As with intra-group contacts, the design was not balanced: the number of pairs contacting each other within different social groups varied, and not all ages, sex and disease status categories were available in different social groups and in different seasons. In order to analyse these factors, only contact data between pairs of badgers that made contact were used. If all pairs (including potential pairs where no contacts were recorded) were used the model assumptions were violated because there were too many values of zero. The contact rate and contact duration were log-transformed, and were analysed in separate models (Table 6.6). None of the factors investigated had a significant effect on contact rate or contact duration. There may be other factors that were not investigated that may affect contacts between badgers from neighbouring groups, or it may be because the sample size is too small.

		Average daily contact rate (contacts/day)		Average daily contact duration (seconds/day)		Number of pairs made contact	Potential number of pairs
		Mean ± s.e	range	Mean ± s.e	Range		
Season	Autumn	0.126 ± 0.044	0 - 0.484	4.187 ± 2.782	0 - 37.194	7	13
	Winter	0.033 ± 0.019	0 - 0.179	1.099 ± 0.486	0 - 3.821	5	9
	Spring	1.015 ± 0.707	0 - 15.857	123.281 ± 94.736	0 - 2348.00	12	27
	Summer	0.102 ± 0.042	0 - 0.607	11.447 ± 9/152	0 - 155.475	10	19
Sex	Male:female	0.614 ± 0.526	0 - 15.857	86.376 ± 78.167	0 - 2348.000	14	23
	Female:female	0.353 ± 0.302	0 - 10.000	26.452 ± 25.612	0 - 846.000	7	15
	Male:male	0.000	0.000	0.000	0.000	0	2
Age	Adult:adult	0.073 ± 0.037	0 - 0.333	1.056 ± 0.484	0 - 4.500	4	7
	Adult:yearling	0.338 ± 0.277	0 - 10.000	29.197 ± 23.739	0 - 846.000	13	25
	Yearling:yearling	0.946 ± 0.878	0 - 15.857	133.418 ± 130.285	0 - 2348.000	4	8
Disease status	TB negative	0.533 ± 0.356	0 - 15.857	63.359 ± 47.654	0 - 2348.000	16	34
	TB potential	0.099 ± 0.049	0 - 0.607	13.044 ± 11.876	0 - 155.475	5	6
Social group	Beech:Septic Tank	0.008 ± 0.006	0 - 0.078	0.156 ± 0.133	0 - 1.725	2	10
	Beech:Larch	0.286	NA	3.143	NA	1	1
	Beech:Cedar	0.000	0.000	0.000	0.000	0	2
	Septic Tank:Yew	0.054 ± 0.031	0 - 0.250	0.879 ± 0.459	0 - 3.821	4	5
	Septic Tank:Cedar	NA	NA	NA	NA	0	0
	Septic Tank:Breakheart	0.000	0.000	0.000	0.000	0	2
	Yew:Wych Elm	1.194 ± 0.759	0 - 15.857	142.313 ± 102.225	0 - 2348.000	10	13
	Yew:Peglars	0.000	0.000	0.000	0.000	0	2
	Wych Elm:Peglars	0.061 ± 0.050	0 - 0.407	1.4.247 ± 3.490	0 - 28.481	3	4
	Breakheart:Cedar	0.013 ± 0.013	0 - 0.038	0.551 ± 0.551	0 - 1.654	1	2
Overall		0.462 ± 0.285	0 - 15.857	53.296 ± 38.201	0 - 2348.000	21	40

Table 6.5. Mean daily contact rates and contact durations for pairs of badgers belonging to neighbouring social groups. Not all pairs of badgers that had the potential to contact each other did contact each other; the number of pairs that did make contact out of the total number of pairs that had the potential to make contact is shown in the last two columns. Disease status has been classified as TB negative (both badgers are TB negative and there is no potential for disease transmission), or TB potential (one or both badgers are TB positive, so there is potential for disease transmission). NA means that there were no pairs belonging to that category with the potential to contact each other.

Variable		Contact rate				Contact duration			
		d.f.	coefficient ± s.e.	t	*p*	d.f.	coefficient ± s.e.	t	*p*
Intercept		8	-1.373 ± 0.503	-2.737	0.0356	8	-0.040 ± 0.695	-0.06	0.955
Season									
	Winter	8	-0.021 ± 0.640	-0.032	0.9748	8	0.736 ± 0.878	0.84	0.4257
	Spring	4	-0.343 ± 0.395	-0.869	0.4338	4	-0.358 ± 0.632	-0.57	0.6009
	Summer	4	-0.022 ± 0.306	-0.072	0.9463	4	-0.297 ± 0.502	-0.59	0.5855
Social groups									
	Beech:Larch	8	0.835 ± 0.691	1.208	0.2616	8	0.537 ± 0.950	0.57	0.5872
	Septic Tank:Yew	8	-0.129 ± 0,493	9.263	0.7997	8	-0.503 ± 0.653	-0.77	0.4636
	Yew:Wych Elm	8	0.586 ± 0.420	1.397	0.2	8	0.770 ± 0.567	1.36	0.2115
	Wych Elm:Peglars	8	0.754 ± 0.574	1.314	0.2254	8	1.554 ± 0.782	1.99	0.082
	Breakheart:Cedar	8	-0.783 ± 0.574	-0.938	0.3757	8	-0.867 ± 1.125	-0.77	0.4628
Sex									
	Female:Female	8	0.393 ± 0.397	0.991	0.3507	8	0.392 ± 0.572	-0.06	0.955
Disease status									
	TB potential	8	-0.184 ± 0.527	-0.35	0.7355	8	-0.245 ±0.698	-0.35	0.7347
TB status × season									
	TB potential × Winter	8	-0.477 ± 0.991	-0.481	0.6433	8	-1.550 ± 1.328	-1.17	0.2768
	TB potential × Spring	4	0.032 ± 0.485	0.065	0.951	4	0.687 ± 0.800	0.86	0.4386
	TB potential × Summer	4	0.653 ± 0.374	1.744	0.1562	4	1.492 ± 0.663	2.25	0.0876
Sex × TB status									
	Female:Female × TB potential	8	-0.993 ± 0.359	-2.762	0.0507	8	-0.698 ±0.831	-0.84	0.4254
Sex × Season									
	Female:Female × Winter	8	0.385 ± 0.781	0.493	0.6353	8	-0.003 ± 1.080	0.00	0.9977
	Female:Female × Spring	4	-0.317 ± 0.501	-0.633	0.5613	4	-0.630 ± 0.815	-0.77	0.4827
	Female:Female × Summer	4	-0.993 ±0.359	-2.762	0.0507	4	-0.926 ± 0.615	-1.51	0.2067

Table 6.6. Linear mixed-effects model for differences in inter-group daily contact rate and inter-group daily contact duration. Results shown are relative to the reference category; season: Autumn, social groups: Beech:Septic Tank, sex: male:female, disease status: TB –ve:TB –ve. No male:male contacts were recorded. The model is based on pairs of neighbouring badgers that made contacts only.

6.4.4 Badger 37R case study

Badger 37R made a permanent move between two social groups part-way through the study, and provides us with a good insight into the process of movement between groups. Therefore, her life history, and the details of the contacts she made whilst moving, are presented in detail in this section.

Badger 37R was first caught at the beginning of June 2004 as a cub in the Septic Tank social group. She was caught twice more in 2004 at Septic Tank, before being caught on the 18th of January 2005, again at Septic Tank. She was now classed as a yearling and was fitted with a proximity collar. She was radio tracked on three nights in winter (22nd, 23rd and 24th January), and the radio tracking showed she was ranging in the Septic Tank territory. She was next radio tracked for one night in spring (19th May), and although not enough fixes were recorded to produce an asymptotic home range for her for this season, her movements were now in the Wych Elm social group. She was re-trapped in June at the Wych Elm social group; the proximity data were downloaded and she was released with her collar still attached. In the summer she was radio tracked on five nights (13th and 14th July and 8th, 9th and 10th August), and her behaviour showed she was associated with the Wych Elm social group. She was re-trapped in August at the Wych Elm social group and released still wearing the proximity collar. On the 26th of August she was found run over on a road that forms the lower boundary of the Yew social group (refer to figure 2.2 in chapter 2).

Therefore, based on the radio tracking data, we can deduce that she moved sometime between the 24th January and the 19th of May. The proximity data provide further insight into this, but are confounded by the fact that collars were fitted to different badgers at different times and collars fell off badgers at different times. Figure 6.3 shows the pattern of which other badgers 37R contacted and when, over the period that she wore a collar. She contacted six different badgers in all. Badgers: 19G (adult female) and U51 (adult males) were associated with the Septic Tank social group. H43 (adult female) and 55G (adult male) were associated with the Wych Elm social group. 13G (adult female) was a member of the Beech social group, which borders the Septic Tank territory and U68 (adult female) belonged to the Yew social group, which borders both the Septic Tank and Wych Elm social group (refer to figure 2.2 in chapter 2). There were no other badgers fitted with collars in the Septic Tank social group between the time 37R was fitted with a collar and died. There was a male yearling fitted with a collar at the Wych Elm social

group at the same time 37R was fitted with a collar, but it is thought this collar was only attached to this badger for 23 days (and it is before she moved to the Wych Elm social group). There were two other badgers in the Beech social group (a group that neighbours Septic Tank) and one in the Yew social group (the group that is between Septic Tank and Wych Elm) fitted with collars throughout this period. Figure 6.4 shows the same plot as Figure 6.3 but is annotated as to when the six badgers were available to be contacted and when trapping and radio tracking took place. For the first month or so, 37R contacts badgers 19G and U51 at Septic Tank only; one interesting thing to note is that she rarely contacts both badgers at the same time. Unfortunately no proximity data are available for U51 contacting 19G during this period, since although both badgers wore collars, the memories were full, so the collars were acting as transmitters only. However, we do know from proximity data for these two badgers from September, October and November in 2004 that they do contact each other (or at least they did during that time). 37R then goes through a short period where she contacts both 19G and U51 (Septic Tank), and H43 (Wych Elm), sometimes all on the same night, but not at the same time, and no contact data were recorded of H43 contacting 19G or U51. She then appears to contact all three badgers much less frequently than previously. She then contacts badger U51 and 13G (Beech) on the same night. She had not contacted 13G previously; radio tracking during spring shows this badger is associated with the Beech social group, which neighbours Septic Tank on the west, so it is likely she was in the Septic Tank social group territory, or had crossed the territory to meet the female Beech badger.

The last contacts she records with 19G and U51 and 13G are the last available data we have for those three collars, so for the purpose of calculating contact rates we have to assume that is the last date the collars were attached, although based on the period of time between the previous contacts, it is equally likely the collars could have remained on the badgers for a much longer period; they just were not contacted by other badgers. Once 55G (an adult male at the Wych Elm social group) was fitted with a proximity collar 37R contacted him frequently; of course we do not know how frequent contacts were before he was fitted with a collar. Badger U68 (an adult female at the Yew social group) was fitted with a collar at the same time, and 37R contacted her infrequently. The Yew social group is sandwiched between Septic Tank and Wych Elm, so it is likely that 37R had to cross this group's territory several times to make the contacts between the Septic Tank and Wych

Elm badgers. On the night that she was run over she made contact with U68 and she was run over on the boundary of the Yew territory so it is highly likely she was in this territory.

We can extract further information by investigating the time of day contacts occur between this badger and other badgers. The frequency of contacts occurring in each hour over a 24-hour period for each month was plotted for each badger that 37R contacted. In January (from the 20th (the start of the study) to the 31st), she contacts only 19G and U51, and the majority of contacts are during the middle of the day when she is most likely to be inactive (Figure 6.5; the legend also shows all other badgers available for contact in that month too including badgers she did not contact). In February, she contacts 19G, U51 and H43. The contacts with H43 are during the early or late hours in the day, whilst the contacts with U51 are mostly during the day. Interestingly, the contacts she makes with 19G are much less frequent and mostly during the early or late part of the day. In March she does not contact U51 at all, and when she does contact 19G and H43, it is in the early hours of the morning. In April she contacts H43 again infrequently and early or late in the day (not shown). In May she contacts U51 and 13G between midnight and one o'clock in the morning on the same day (the contacts are approximately six minutes apart so U51 and 13G may or may not have contacted each other as well). She also contacts H43 during the same hour, but on a different day within that month. June, July, August and September all show a similar pattern of a large number of contacts with 55G during the day and less during the night. When she contacts H43 and U68, it is always late in the day or early in the morning.

For the purpose of contact rate and duration analysis and categorising contacts as intra- or inter-group, 37R was treated as belonging to Septic Tank social group for winter and spring (January to May), and to Wych Elm social group for summer and autumn (June to October). This does however mean that the contacts between 37R and H43 are categorised as inter-group contacts in winter and spring but intra-group contacts in summer and autumn. These assumptions are based on the available data; the fact that she contacts a Beech badger during spring implies she is likely to be in the Septic Tank territory as the Beech territory borders this group.

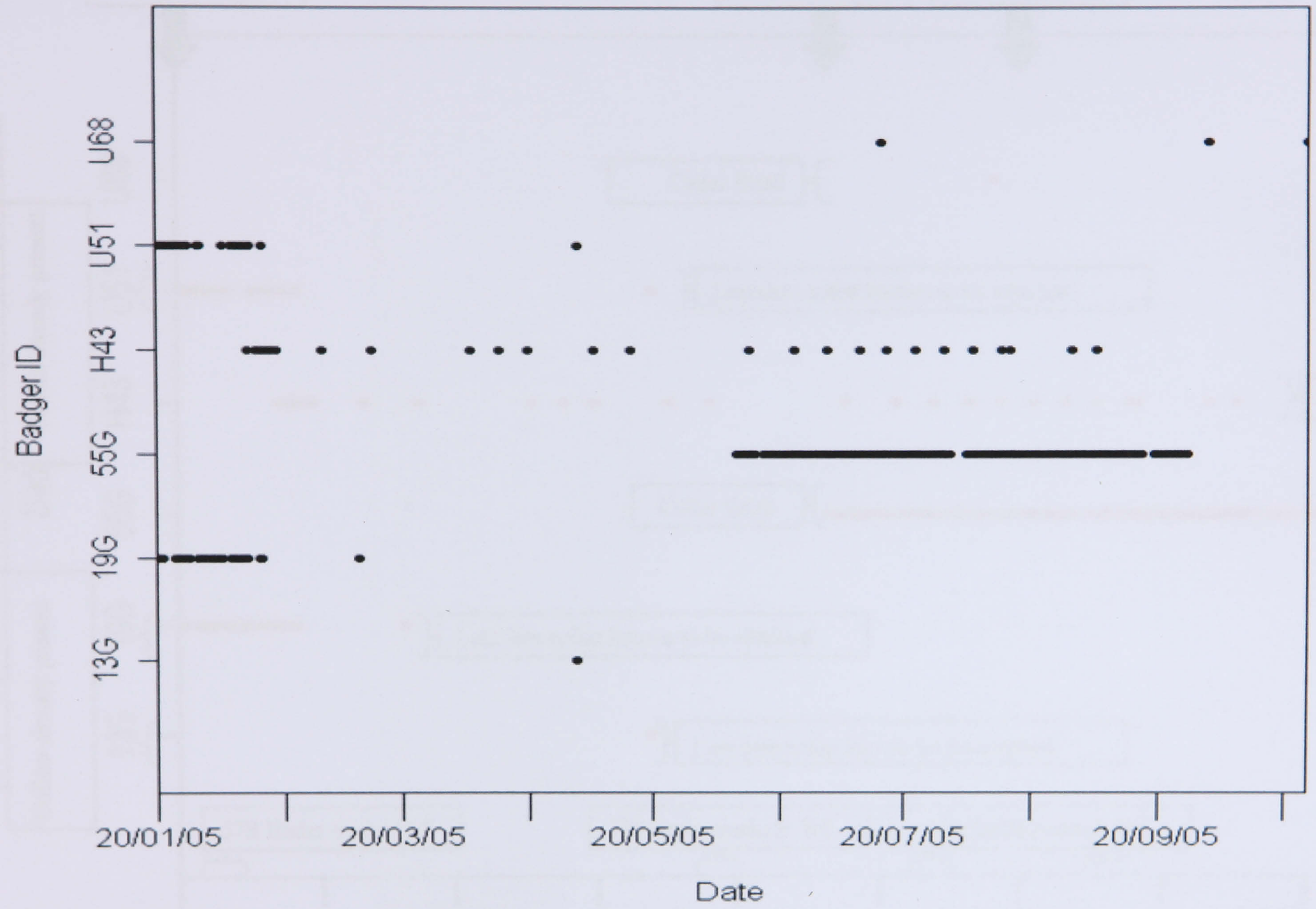


Figure 6.3. Contact pattern time-line for badger 37R over the period she wore a proximity collar. The badgers 37R makes contact with are labelled on the y-axis, and the time-line is shown on the x-axis.

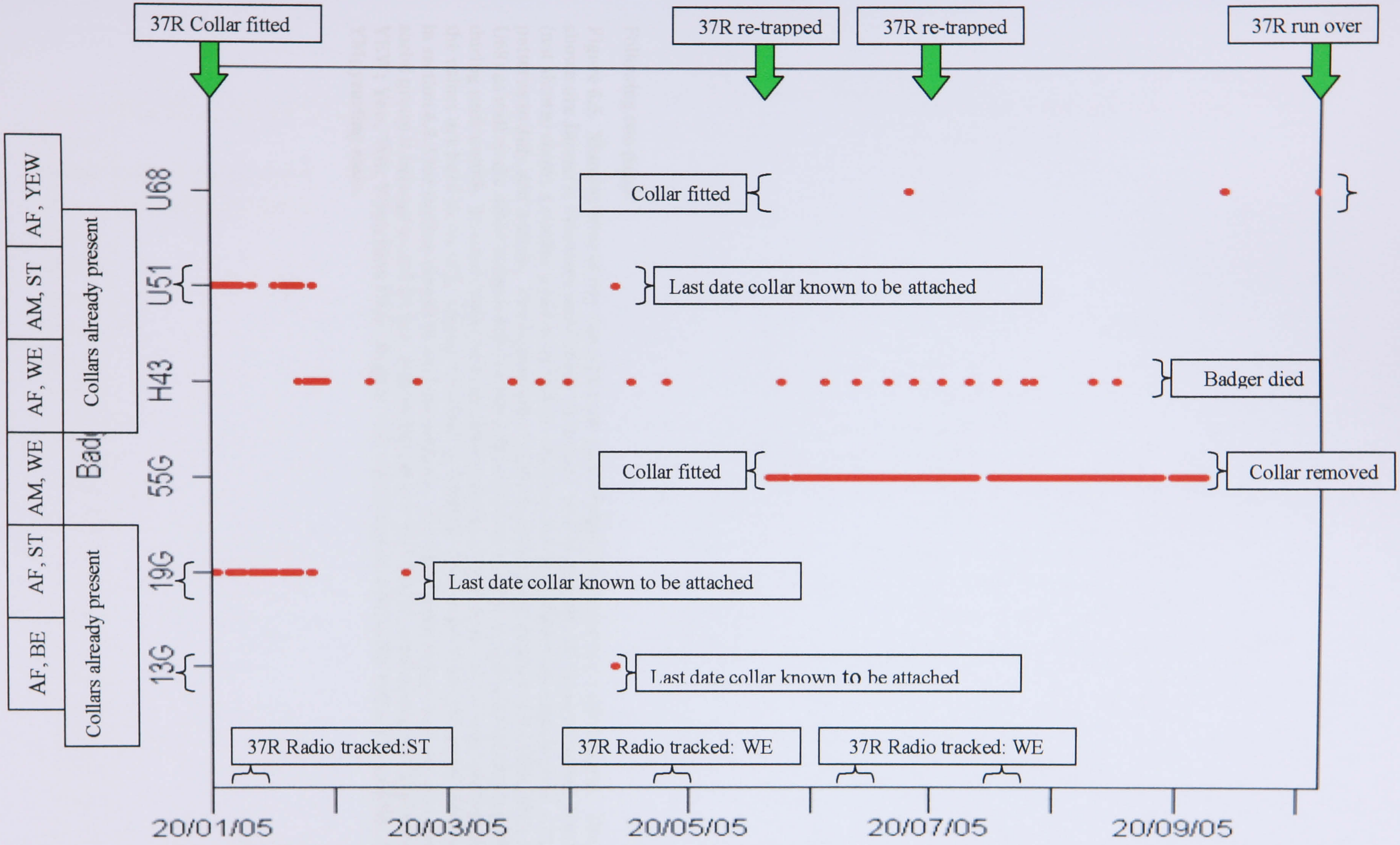
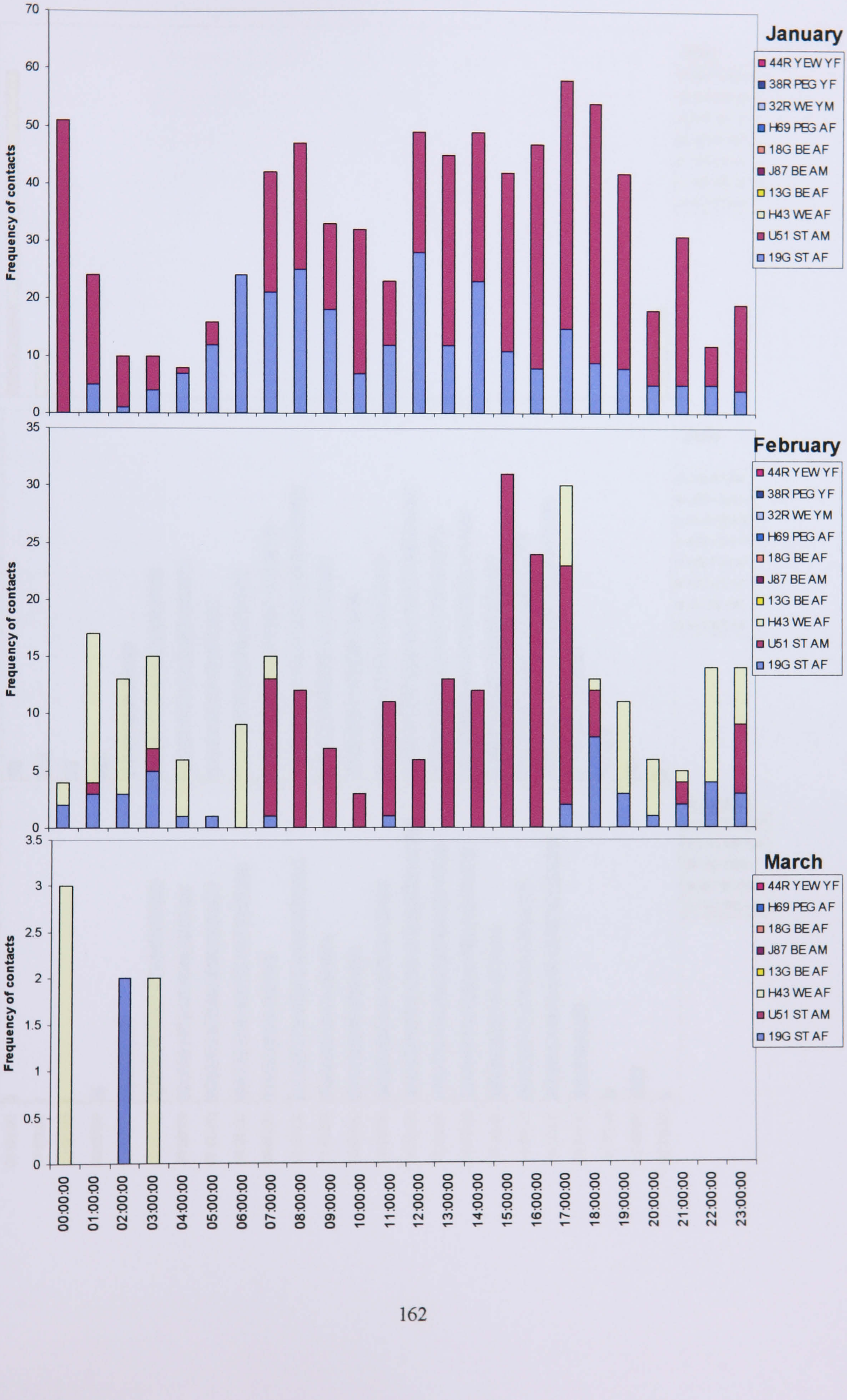


Figure 6.4. Annotated contact pattern time-line for badger 37R.

Following two pages:

Figure 6.5. Monthly time of day (on a 24-hour scale) badger 37R contacts other badgers. The months shown are January, February and March (first page) and May, July and August (second page). April (not shown) shows a similar pattern to March and June and September (not shown) show very similar patterns to July and August. The legend refers to the badgers she contacted (13G, 19G, 55G, U51 and U68) as well as the other badgers fitted with collars that she had the potential to contact but did not, during each month. In some cases she does make contacts with badgers but at very low frequencies, so the values are hard to see (e.g. August with H43 in 00:00:00 hours and 22:00:00 hours), refer to the text in section 6.5.3 for further details of who she contacts. The ID of each badger is given, along with the social group it belongs to and its age. Abbreviations are: BE; Beech social group, ST; Septic Tank, YEW; Yew, WE; Wych Elm, PEG; Peglars. AF; Adult female, AM; adult male, YF; yearling female, YM; yearling male.


January
Frequency of contacts
70
60
50
40
30
20
10
0
44R YEW YF
38R PEG YF
32R WE YM
H69 PEG AF
18G BE AF
J87 BE AM
13G BE AF
H43 WE AF
U51 ST AM
19G ST AF
February
Frequency of contacts
35
30
25
20
15
10
5
0
44R YEW YF
38R PEG YF
32R WE YM
H69 PEG AF
18G BE AF
J87 BE AM
13G BE AF
H43 WE AF
U51 ST AM
19G ST AF
March
Frequency of contacts
3.5
3
2.5
2
1.5
1
0.5
0
44R YEW YF
H69 PEG AF
18G BE AF
J87 BE AM
13G BE AF
H43 WE AF
U51 ST AM
19G ST AF
00:00:00
01:00:00
02:00:00
03:00:00
04:00:00
05:00:00
06:00:00
07:00:00
08:00:00
09:00:00
10:00:00
11:00:00
12:00:00
13:00:00
14:00:00
15:00:00
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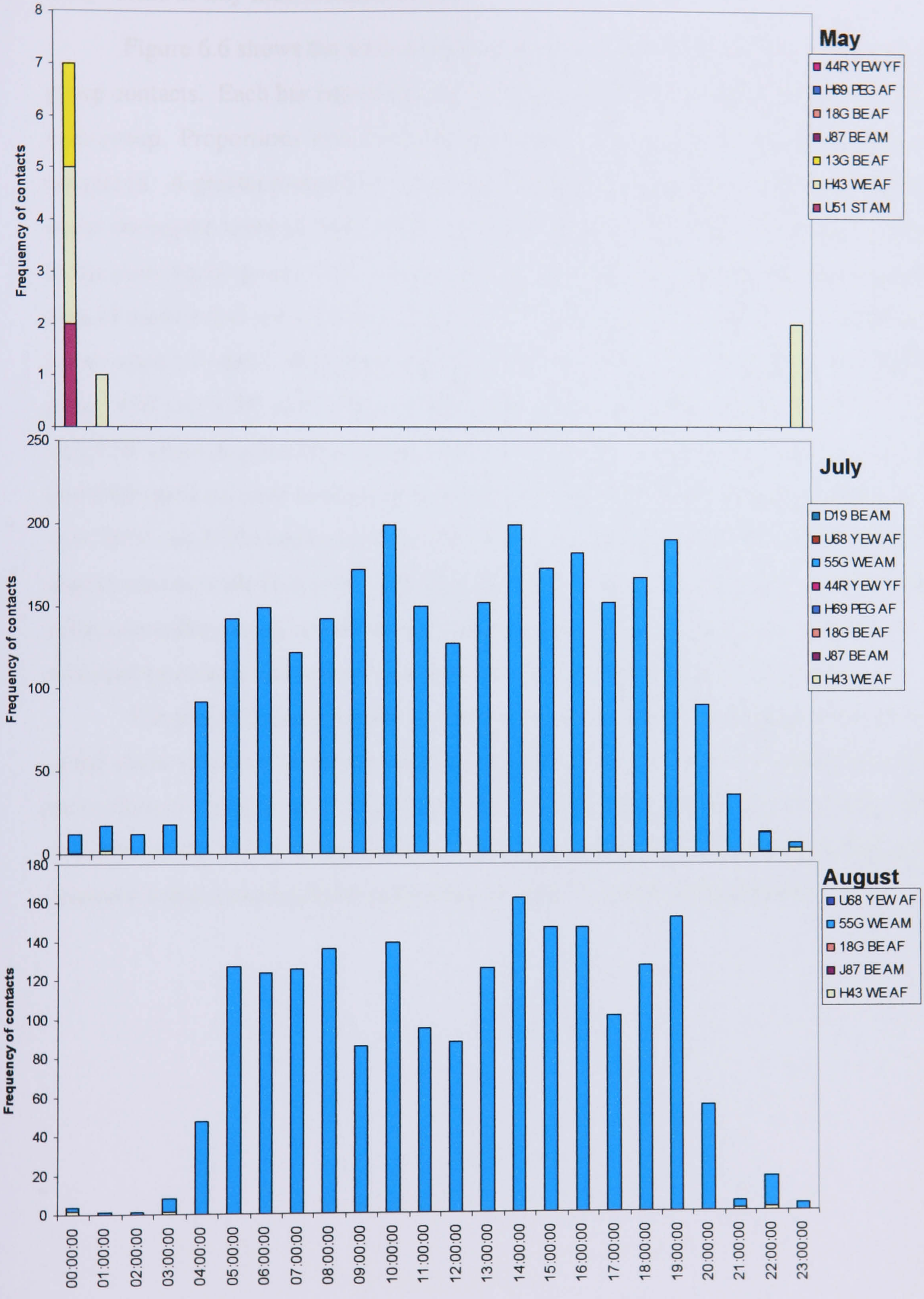
20:00:00
21:00:00
22:00:00
23:00:00


May
44R YEW YF
H69 PEG AF
18G BE AF
J87 BE AM
13G BE AF
H43 WE AF
U51 ST AM
Frequency of contacts
0
1
2
3
4
5
6
7
8
July
D19 BE AM
U68 YEW AF
55G WE AM
44R YEW YF
H69 PEG AF
18G BE AF
J87 BE AM
H43 WE AF
Frequency of contacts
0
50
100
150
200
250
August
U68 YEW AF
55G WE AM
18G BE AF
J87 BE AM
H43 WE AF
Frequency of contacts
0
20
40
60
80
100
120
140
160
180
00:00:00
01:00:00
02:00:00
03:00:00
04:00:00
05:00:00
06:00:00
07:00:00
08:00:00
09:00:00
10:00:00
11:00:00
12:00:00
13:00:00
14:00:00
15:00:00
16:00:00
17:00:00
18:00:00
19:00:00
20:00:00
21:00:00
22:00:00
23:00:00

6.4.5 Time of day that contacts occur

Figure 6.6 shows the time of day contacts occurred for both intra-group and inter-group contacts. Each bar represents the average proportion of contacts within that hour for each group. Proportions have been plotted to enable intra- and inter-group contacts to be compared. A greater proportion of contacts between badgers from neighbouring groups occur during the hours of dusk and dawn compared to contacts between badgers belonging to the same social group. The data have been combined to cover the whole year, so the time of sunrise and sunset will vary, but apart from one peak at midday, most contacts occur when it is dark. This peak between midday and one o'clock is due to two badger pairs, 39W and 52W, and 52W and U69 (mentioned previously in section 6.4.3.3). 39W and 52W spent daytime hours together on the 18th of May and the 19th of May, and 52W and U69 spent daytime hours together on the 18th of May. The contacts recorded by 52W with 39W and U69 overlap on the 18th of May, so it is highly likely that 39W and U57 were also in contact with each other, although we have do not have the contact data for either of these two collars so are unable to say conclusively. These badger pairs were the only pairs recorded to contact each other during the day from neighbouring social groups.

The proportions of contacts occurring between badgers belonging to the same social group occur relatively evenly throughout the 24-hour day. There is a slight dip in the proportion of contacts occurring in the hours of early evening and early morning, although contacts do still occur during the night. The biggest difference compared to inter-group contacts is that a much greater proportion of contacts occur during the day.

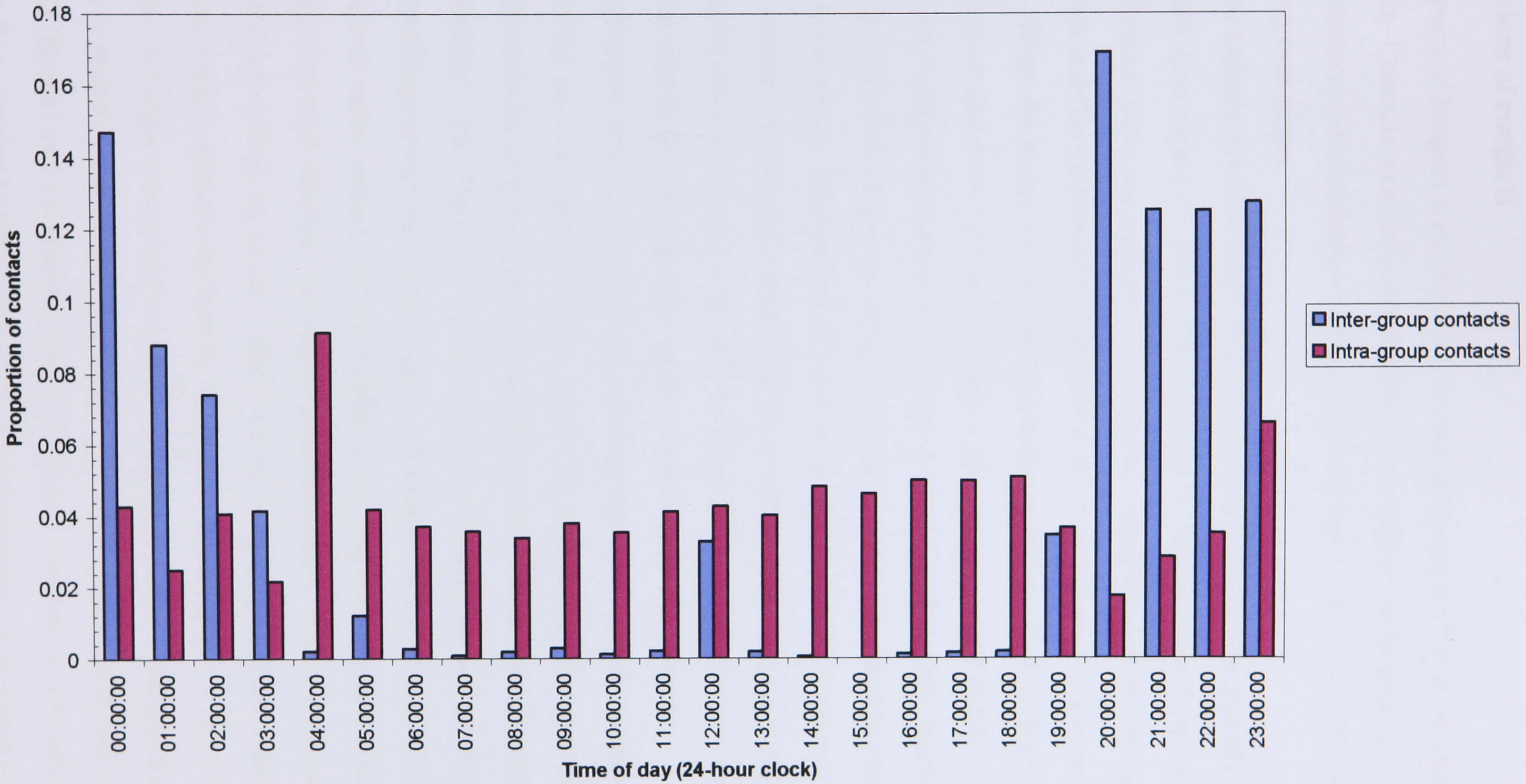


Figure 6.6. Average proportions of contacts showing the time of day during which contacts occurred. Average inter-group and average intra-group proportions are shown to allow comparisons to be made. Each hour represents the proportion of contacts occurring within that hour.

6.4.6 Locations of contacts

Six pairs of badgers were recorded as contacting each other whilst they were being radio tracked. Contacts were only recorded between badgers belonging to the same social group. No contacts between badgers from neighbouring social groups were recorded whilst radio tracking took place.

Three badgers from the Beech social group could be located spatially on five nights in autumn and three nights in winter. The majority of radio location fixes occurred when contacts took place when the badgers were inactive underground in the sett, and both the proximity data and the location data showed that all three badgers were in proximity of each other. When the badgers were recorded as being active, all of the location fixes apart from one were located within the social group's territory (as determined by bait marking), and the majority within the badgers' core areas (as determined by radio tracking). It is not possible to quantify this because not all of the badgers were radio tracked enough to find an asymptotic home range. The one fix that was not within the social group's territory was located just outside the boundary (within 20 meters of the boundary), although when taking into account the error associated with radio tracking (40.89 meters for the median error as determined in chapter 3), this may have been located within the territory.

Two badgers from the Septic Tank social group were located spatially on four nights in autumn and one night in winter. Again, the majority of fixes were whilst the badgers were recorded as being inactive, and the majority within the core area clustered around a subsidiary sett. Figure 6.7 shows the spatial location of badgers when they were recorded as making contact with other badgers. Badgers 13G, 18G and J87 belonging to the Beech sett all made contact with each other on five nights in autumn, and badgers 19G and U51 contacted each other on four nights, also in autumn. Active fixes are marked by triangles and inactive fixes by circles. The location of the main sett and other outlying, subsidiary and annexe setts are marked for reference. Not all inactive fixes are located close to setts. A badger was recorded as being inactive if it was underground, so this discrepancy is probably due to the inaccuracy of the radio tracking method used. The core areas of 18G (Beech) and 19G (Septic Tank) are shown; the core area is calculated based on all active fixes for that badger within that season (irrespective of whether it was radio tracked or not). All the inactive fixes are located within the core area. Spatio-temporal locations of contacts between badgers on nights in winter and summer followed similar

patterns to the data already described, in that the majority of contacts occurred within core areas between inactive badgers. However, on one night in January two badgers belonging to the Wych Elm social group (H43 and 32R) demonstrated interesting behaviour. Both H43 and 32R were tracked intermittently on the night of the 23rd of January, and contacts were only recorded intermittently between the two badgers, so relatively few locations could be plotted on a map. All the locations apart from one were clustered around setts in the Wych Elm social group territory. One location, however was recorded where the badgers were in the Yew social group's territory (Figure 6.8). The location recorded in the Yew territory was also inactive, and is within the median accuracy location error to be located in a sett. Figure 6.8 only shows the radio location fixes for H43, but 32R (with whom H43 made contact) was also located at the same time as H43 was recorded in the Yew territory. Two badgers from the Yew social group were fitted with proximity loggers on this night so could have potentially made contact with H43 but did not. We cannot determine, however, if H43 or 32R contacted any un-collared badgers in this social group. On subsequent nights both badgers were relocated in the Wych Elm social group, so this appears to be an occasional foray into a neighbouring territory, where perhaps both badgers were travelling together.

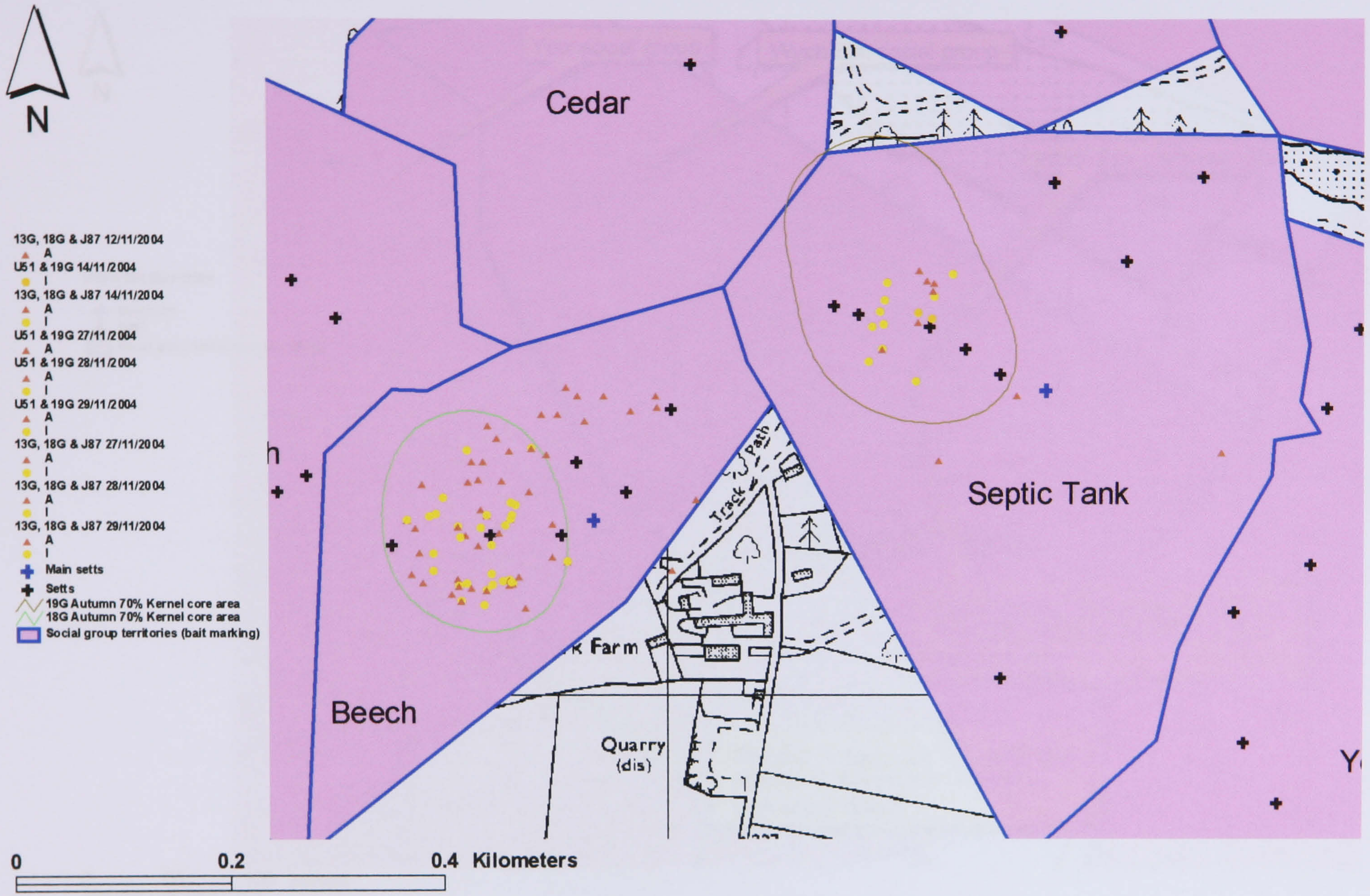


Figure 6.7. Locations of contacts recorded between three badgers belonging to the Beech social group (13G, 18G and J87), and two badgers belonging to the Septic Tank social group (19G and U51) on five nights in Autumn 2004. Fixes where the badgers were recorded as being active are denoted by triangles, and fixes where they are inactive denoted by circles. The location of the main sett within each social group's territory as well as any other setts are shown marked by crosses. 70% kernel core areas found by radio tracking are plotted for badgers 18G (Beech) and 19G (Septic Tank). Social group territory boundaries found by bait marking are also plotted.

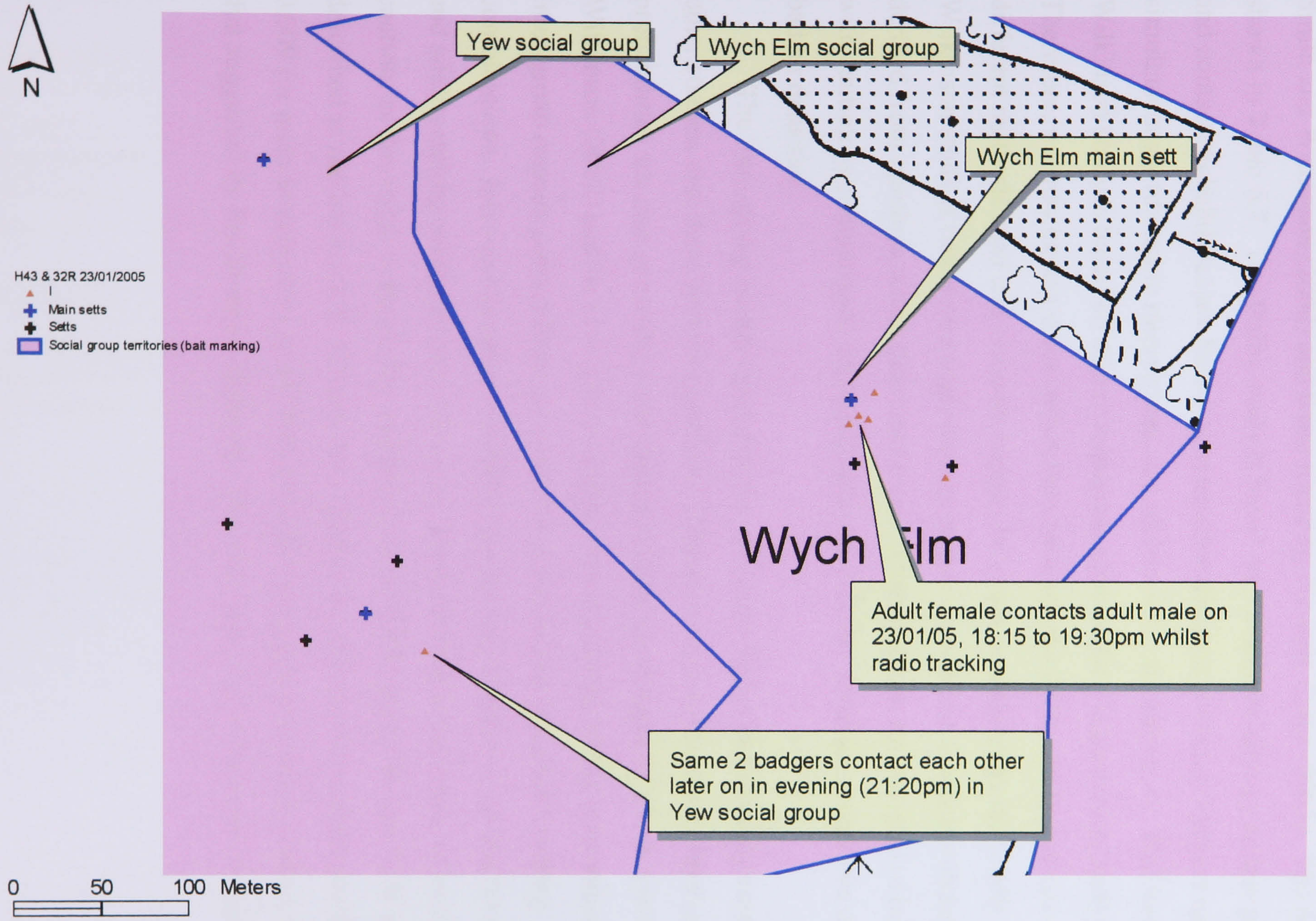


Figure 6.8. Locations of contacts recorded between two badgers (32R and H43) belonging to the Wych Elm social group on one night in winter. Annotations describe when contacts occurred. Fixes where the badgers were recorded as being active are denoted by triangles, and fixes where they are inactive denoted by circles. Main sett locations and other setts are marked by crosses. 70% kernel core areas found by radio tracking are plotted for badgers 18G (Beech) and 19G (Septic Tank). Social group territory boundaries found by bait marking are also plotted.

6.4.7 Contact probabilities

Daily contact probabilities were calculated based on the average daily contact rates for intra-group and inter-group contacts. The contact probabilities suggested by Smith and Wilkinson (2002) were converted from three-day contact probabilities to one-day contact probabilities to allow a comparison between those found in this study, those suggested by Smith and Wilkinson (2002) and those found by Newton-Cross (2003). The results are shown in Table 6.7. The Dalby study is based on a moderate-density badger population, and contact probabilities are based on separation distances between badgers radio tracked simultaneously (dynamic interactions; see section 4.1.5 in chapter 4). The Smith and Wilkinson study is based on expert consensus opinion for a high-density badger population. Therefore, we may expect some differences between the Dalby study and this study, due to different methods used and different badger densities, and although the Smith and Wilkinson study is based on a high-density badger population, contact probabilities are derived from opinions rather than field work. Therefore, the results need to be interpreted with caution as comparisons are based on three different methods across two different badger densities.

The intra-group contact probabilities are much higher in this study compared to both other studies, and there was no significant difference between seasons. Inter-group contact probabilities are also generally much higher than those estimated by both Smith and Wilkinson (2002) and Newton-Cross (2003). The exception to this is in winter, where inter-group contact probabilities are lower for male:female and adult:yearling combinations. Inter-group contact probabilities are much higher in spring for male:female and adult:yearling combinations. However, this particular result needs to be treated with caution, as this value is due to the contacts between 39W and 52W, and 52W and U69 as described in section 6.4.3.3. If these two badgers are omitted the contact probabilities are 0.009 for male:female pairs and 0.026 for adult:yearling pairs, which is much lower than that suggested by Smith and Wilkinson. The true value is probably somewhere in-between.

Pair combination	Autumn			Winter			Spring			Summer		
	This study	S & W	Dalby study	This study	S & W	Dalby study	This study	S & W	Dalby study	This study	S & W	Dalby study
Intra-group contacts												
All pairs	> 0.999	0.632	0.326	> 0.999	0.338	0.630	> 0.999	0.632	0.516	> 0.999	0.658	0.307
Inter-group contacts												
Male:Female	0.155	0.100	0.007	0.013	0.068	<0.001	>0.999	0.234	<0.001	0.185	0.068	<0.001
Same sex	M:M <0.001	0.100	M:M <0.001		0.068	M:M <0.001	M:M <0.001	0.234	M:M <0.001		0.100	M:M <0.001
	F:F =0.118		F:F =0.009	F:F =0.073		F:F <0.001	F:F =0.0697		F:F <0.001	F:F = 0.028		F:F =0.047
Adult:Yearling	0.077	0.068	0.010	0.042	0.068	<0.001	0.738	0.068	<0.001	0.111	0.068	<0.001

Table 6.7. Daily contact probabilities found from this study compared to those reported by Smith and Wilkinson (2002; "S&W"), and those found in Dalby forest (Newton-Cross (2003); "Dalby"). Sex combinations are M:M, male:male and F:F, female:female, where no value is given for M:M pairs there was no potential for contacts to be recorded.

6.5 Discussion

This chapter aimed to investigate patterns of contacts between badgers in a high-density badger population. Average daily contact rates and average daily contact durations were calculated, and the effects of sex, age, disease status, social group and season were considered. In addition, further exploration of when contacts occur and where they occur was completed. An in-depth investigation of one badger's contact patterns with other badgers was carried out, and contact probabilities were calculated, based on the contact rate data.

The use of proximity loggers to study contacts between individuals is a relatively novel technique, and whilst there are still some minor problems with the technology, the loggers have enabled contact data between badgers to be collected on a previously unrivalled scale. Existing methods to study contacts in free-ranging animals mainly involve direct observations of individuals or radio tracking, e.g. (White 1992, Doncaster and Macdonald 1997, Rhodes et al. 1998). Both observing animals and radio tracking are labour intensive and time consuming. They are also limited to studying a few animals at a time, and only during the period the observer is present. Recent technological advances in the field of global positioning systems (GPS) have lessened much of the time-consuming human element of radio tracking. GPS collars have been used to a limited extent to study interactions between animals (Schauber et al. 2007), but they are not without problems. GPS collars can be subject to error and bias (D'Eon 2003, Ganskopp and Johnson 2007), they are relatively expensive and they are not suitable for all species. Where species live in rugged terrain or densely vegetated areas, the success rate of securing a satellite signal can be quite low (Cain et al. 2005). Similarly, for species that spend a large proportion of their time underground, such as the badger, fix success will be low. The high-resolution fine-scale data that the proximity loggers are able to collect is therefore ideal for studying direct contacts between individuals.

This study investigated direct contacts between individuals, and for this study a contact was defined as occurring when individuals came into proximity of one and a half meters of each other. This distance was determined by the resolution of the proximity collars rather than being based on any biological reasoning. It is highly likely however, that at this distance badgers will be able to detect the presence of another badger. Palphramand and White (2007) and Palphramand (2005), were able to demonstrate, for

example, that badgers were able to detect the scent of other badgers within a distance of up to three meters. We are unable to determine the exact distance between badgers based on the proximity loggers, so we do not know if actual physical contact occurred, or what the nature of the contact was; whether affiliative or aggressive.

For the purpose of calculating contact rates and durations, average daily contact rates and durations were calculated on a seasonal basis. This means the contact rate and duration is averaged over the season. This methodology has the advantage that it provides a good overview of contact rates and can be easily compared to other studies. However, the disadvantage is that much variability in the data is lost. The definition of when a season starts and ends is also rather arbitrary to a badger. Badgers are more likely to respond to localised climatic conditions (Cresswell and Harris 1988), than human imposed calendar dates, although long-term trends should be detected.

An individual contact event was recorded as having occurred between two badgers when one of both collars recorded a contact that was 22 seconds apart or greater from other contacts. This separation time will affect the number of contacts recorded, and requires further investigation. Some badgers appeared to make repeated contacts with each other within a short space of time whereas other badgers made fewer, longer, contacts. These differences may be in part due to the separation time setting on the collar and variations in functioning between collars, or it may be due to badger behaviour.

One of the main hindrances to determining accurate contact rates and durations is not knowing the exact length of time each badger was wearing a collar for. Calculating the last day a collar is available for contacts, and hence the total number of days, is made more complicated by not knowing the exact date a collar remains attached until, if the badgers is not re-trapped with its' collar attached. If a collar falls off a badger, the date at which it becomes detached is unknown. In these circumstances, the date of last contact recorded with or by the collar, or the date radio tracked is used as a surrogate. This may increase contact rates because the period over which rates are calculated is shorter than reality. Conversely, some collars appeared to be functioning normally yet no contacts were recorded either by or with the collar when previously there had been frequent contacts. It may be that the collar ceased to function, and therefore contact rates and durations will be underestimated. The problems could be overcome to a certain extend by more regular monitoring by radio tracking and more regular trapping of badgers than was able to be carried out in this study. More frequent trapping would also prevent long periods of collars

acting as transmitters only because the memory was full, (setting the separation time to a longer duration would also help this too); trapping would enable the data to be downloaded and the memory to be cleared. However, the trapping regime should not be too frequent so as to disrupt the behaviour of the individual. Trapping badgers is time consuming and labour intensive, and is subject to ethical considerations (Powell and Proulx 2003), some individuals are more likely to be trapped than others (Tuyttens et al. 1999a), and some animals (although a minority) may become injured as a result of being trapped (Woodroffe et al. 2005a). The welfare of badgers wearing a radio collar has been investigated by Tuyttens et al. (2002), who found no significant effect on body condition for badgers wearing collars for over 100 days. In this study the mean period collars were worn for was 164 days, so the proximity loggers should not have a detrimental effect on body condition or behaviour. However, to overcome the problem of needing to re-trap an animal to download proximity data, a planned future development is the addition of base stations, to which data can be downloaded remotely. Base station units could be placed at locations frequently visited by animals, such as setts or feeding sites, and data could be downloaded every time the animal was within a specified distance of the unit.

Analysis of intra-group contact rates revealed no significant effect of season, social group or sex on average daily contact rates and average daily contact durations. Only TB status was found to significantly affect rates, with badgers with the potential to transmit TB having lower contact rates and durations between other badgers belonging to the same social groups compared to badgers with no potential to transmit TB. This has significant implications for the transmission of TB. Garnett et al. (2005) found that badgers infected with TB had significantly larger home ranges, and foraged further away from their own main sett than uninfected badgers. Cheeseman and Mallinson (1981) found badgers in the advanced stages of infection exhibited abnormal behaviour. It may be that badgers infected with TB have been ostracised from their main sett and social group by other badgers, and are therefore roaming more widely. Whilst the lower contact rate with badgers within the social group means there is less potential for disease transmission within that group, there may be greater potential for transmission to badgers within neighbouring groups, or even groups further afield. However, no significant difference was detected in contact rates between badgers with different disease status between neighbouring groups in this study. This may be due to small sample sizes, and the fact that not all badgers within the population were collared so many contacts were undetected.

Comparing contact probabilities found in this study to those suggested by Smith and Wilkinson (2002) and Newton-Cross (2003), suggests intra-group probabilities are much higher than previously estimated. Due to not all badgers within each social group being collared, these rates are probably an underestimate. The greater probabilities found here compared to the Dalby study can be explained by the differences in the methods used. The Dalby study was based on radio tracking data over a limited period on each night, and only fixes when the badgers were recorded as being active were included in the analysis. This is unlikely to be representative of true contact rates, as this study has shown from the locations of contacts recorded that badgers can often contact other badgers when they are inactive in the sett, and during the middle of the day, when they are most likely to be inactive. The Dalby study was also based on a moderate-density badger population whereas this is a high-density population. There may be some form of density-dependent contact rate differences between the two populations, although this is thought to be unlikely to occur in territorial animals (McCallum et al. 2001, Smith 2001).

The intimate association of badgers in communal setts would be expected to facilitate TB transmission within social groups (Delahay et al. 2000c), however, infection in badgers is often only detected in a small proportion of badgers within a social group (Delahay et al. 2000c). One hypothesis to explain this is that there may be individual variation in contact rates within the social group that vary according to denning preferences and social relationships. This area requires further investigation; denning preferences could be found by locating collared badgers by radio tracking frequently. Social relationships are harder to determine, some studies have suggested there is a dominance hierarchy within each social group (Minta 1993), whilst other studies have found no evidence (Macdonald et al. 2002).

Within inter-group contact probabilities, male:female contact probabilities were higher in all seasons apart from winter, and especially high in spring. As well as affording opportunities for disease transmission, this may also suggest extra-group mating is occurring. The peak mating season is during spring, and recent genetic studies have shown extra-group matings occur much more frequently than previously thought, with many cubs being sired by males from neighbouring groups (Carpenter et al. 2005).

No male:male inter-group contacts were observed, although there was little potential for this combination to occur. This is a result of more females being fitted with collars than males, which is because the population as a whole is slightly female biased due

to higher mortality rates in male badgers (Rogers et al. 1997). However, contact probabilities in the Dalby study also found a very low male:male contact probability. This has important implications for disease transmission models because previous models have given greatest importance to male:male transmission (White and Harris 1995b), and transmission in spring. Trapping data at Woodchester Park has shown male badgers are more likely to move than female badgers (Rogers et al. 1998), and males may be more likely to have contact with badgers from adjacent groups as they are believed to be more active in territorial defence (Brown 1993, Roper et al. 2003b). Males are also more likely to have bite wounds than females, and to have multiple bite wounds (Delahay et al. 2006b). Bite wounds are also more likely to occur between December to February; the peak breeding period and the time when the most territorial activity occurs (Delahay et al. 2006b). Contact patterns between males from different social groups therefore require further investigation, perhaps by concentrating effort to fitting males with proximity loggers.

The application of inappropriate contact probabilities within a model can dramatically alter the outcome of host-pathogen model predictions (White et al. 1995, Smith and Wilkinson 2002). A sensitivity analysis on the Smith and Wilkinson (2002) rabies model in badgers found model predictions would differ significantly when contact probabilities were more than ten times those estimated (Smith 2002). The contact probabilities determined in this study did vary more than ten times those estimated compared to the Smith and Wilkinson model for some classes (e.g. Spring inter-group contact probabilities); this may dramatically alter the outcomes of the model and have implications if the model is used to predict the success or failure of the implementation of any strategies to control TB. These contact probabilities are also probably an underestimate of the true number of contacts because the number of contacts with un-collared badgers is unknown. In order to get a true estimate of contact rates, saturation of the population with proximity loggers needs to occur (Prange et al. 2006).

The in-depth analysis of the contact patterns of one badger with other badgers (37R case study) provides a unique insight into an individual's behaviour. This level of detail of individual animals' lives over such a long time period is previously unheard of for nocturnal free-living animals such as the badger. Badger 37R demonstrates interesting behaviour in that she moves social groups partway through the study. The process of movement has previously been investigated by trapping (Rogers et al. 1998), and by radio

tracking (Roper et al. 2003b). Neither method can provide as much information compared to that collected by proximity loggers. Roper et al. (2003b), investigating the process of dispersal of badgers making permanent moves between social groups using radio tracking, suggested dispersal can be a lengthy process, taking between two and nine months, with badgers first making occasional forays into the new territory but returning to their original territory to sleep before gradually spending more time sleeping and foraging in the new territory. The proximity data recorded by 37R with other badgers suggest this is also the case with this badger.

Studies investigating dispersal have suggested males move more frequently than females (Rogers et al. 1998), but when females move they usually move to territories with fewer females (Rogers et al. 1998), they may also move as coalitions of females (Woodroffe et al. 1995). The numbers of badgers allocated to each social group based on the trapping data (section 2.4.4 and table 2.2 in chapter 2), suggest that 37R does move to a social group with fewer females. Investigation of the individual animals that comprise each estimate do not reveal any other badgers that move at the same time. Trapping success is high for this population (Rogers et al. 1997), so other movements are likely to be detected by trapping individuals, although there is a small probability an individual may go undetected. Movement of badgers between social groups is thought to be an important determinant of TB infection spread within the population (Delahay et al. 2000b). This is consistent with observations that the incidence of infected badgers increases following years of high inter-group movement (Rogers et al. 1998, Vicente et al. 2007). Badger 37R had tested negative for TB, so was unlikely to facilitate transmission in this case.

As mentioned above, contact rates may vary with social relationships. It may be that there are key individuals in a population who are responsible for the majority of a certain type or distribution of contacts, and this more sociable behaviour may be associated with other behavioural patterns. A network analysis approach to understanding contact rates may reveal patterns and trends not picked up otherwise, and can be used to predict patterns of disease transmission (Corner et al. 2003, Christley et al. 2005). Genetic evidence from this badger population has suggested that roughly half of assigned paternity could be attributed to extra-group males, and the majority of extra-group males were from neighbouring social groups (Carpenter et al. 2005). The proximity loggers allow us to gain further information about contacts. Because not all matings will be successful, there may be many more contacts than those predicted from genetics.

Recent work investigating the effect of culling badgers on spatial perturbation has found that culling causes immigration of badgers into culled areas, along with disruption of social and territorial organization, which leads to increased contact among badgers and hence elevated TB prevalence (Woodroffe et al. 2006a, Carter et al. 2007). Quantifying the contacts between badgers in a disturbed population through the use of proximity loggers would be the next logical step.

6.5.1 Summary

This study has enabled quantification of contact rates and durations between badgers in a high-density badger population. The results have revealed that badgers belonging to the same social group contact each other very regularly, whilst contacts between social groups are less frequent but do still occur. The level of detail provided by the proximity loggers over such a long time period for nocturnal free-living animals such as badgers is unique. Whilst it is useful to categorise contact data into different sex, age, etc. groups, the continuous data from the loggers show us that the real pattern at an individual level is much more complex than such categorisations suggest.

Chapter 7 Discussion

7.1 Summary of thesis aims and results

This study aimed to quantify interactions between badgers in a high-density population. By using radio tracking to study space use and movement patterns of badgers, the movements of badgers with respect to each other, and the potential for direct and indirect interactions to occur in areas of shared space could be determined. By using proximity loggers, direct interactions between badgers could be recorded remotely, and contact rates and durations calculated.

Chapter two described the study site and the main methods used to study badgers at the study site. Novel proximity logging devices to record direct contacts between individuals were introduced, and the means by which they function described.

Chapter three investigated the accuracy of radio tracking using the homing-in method to locate animals. No such large-scale in depth study has been completed before using this method. Recording animal locations is often regarded as exact and error-free, whereas this study has shown that not always to be the case. Triangulation is more commonly used in radio tracking studies than the homing-in method, and the importance of reporting error has been stressed (Saltz 1994, Powell 2000) when using this method. The same applies to studies using the homing-in method; in order to enable comparisons to be made between studies, the level of error needs to be investigated and reported.

Observer experience and the distance the observer was from subject were found to have the most influence on the accuracy of recording locations. This has implications for studies such as this one that rely on volunteers to carry out radio tracking. There is often a high turnover of personnel, which means there is little time to build up the necessary skills and experience. Some species are secretive and sensitive to the presence of humans, and some species roam widely or cover large distances quickly, making it hard to get to within a certain distance of them. In some of these cases triangulation may be a more appropriate method to record these animals' locations, but in order to carry out accurate triangulation more observers are needed to be able to take simultaneous location fixes on each animal being studied. If this is not possible, the movement of animals between successive triangulations cannot be accounted for, and this has been shown to greatly affect the accuracy of this method (Schmutz and White 1990).

Chapter four investigated the social and spatial organisation of badgers determined by radio tracking. Home ranges, core area sizes and levels of intra-group overlap did not vary significantly with respect to different seasons, or between badgers of different ages, sexes or disease status. The areas of home range overlap between badgers belonging to the same social group were relatively large, whereas shared home range areas between badgers belonging to different social groups were virtually non-existent. Areas of overlap between individuals indicate potential areas in which interactions can occur, although make no indications about whether interactions actually occur. The lack of overlap of shared areas between badgers from different social groups is consistent with studies using bait marking to delineate social group territories. Studies have found discrete territories and boundaries between social groups, both at this study site and at other high-density areas (Roper et al. 1993, Rogers et al. 1997, Delahay et al. 2000a, Delahay et al. 2006a).

Individual movement patterns of badgers indicated badgers belonging to the same social group spend time within close distances of each other, and at distances within which they have the potential to interact. Movement patterns of badgers from different social groups revealed that most of the time badgers are active they are separated by distances over which it would not be possible for them to interact with each other. Although radio tracking may indicate animals are within certain distances of each other, the resolution of the data is too large to be able to infer animals are definitely interacting, even at very close distances. This is due to the inaccuracy associated with radio tracking, even though steps were taken to improve the accuracy or account for it where possible.

Previous studies investigating individual home range patterns in badgers have found seasonal difference in home range sizes, mainly thought to be due to food availability and breeding opportunities (Revilla and Palomares 2002, Kowalczyk et al. 2004, Palphramand et al. 2007). These studies involve badgers in low or moderate density populations. However, little attention has focussed on individual seasonal home range differences in high-density populations. Instead focus has been at the group level, where territories remain relatively stable in size over many years (Kruuk and Parish 1982, Cheeseman et al. 1987, Rogers et al. 1999). The lack of any significant seasonal differences in home and core area sizes may be because the badger population is at such a high-density; alternatively it may be due to the small sample sizes used in this study. Garnett et al. (2005) found badgers infected with TB had significantly larger home ranges and they ranged over a greater proportion of their own, and neighbouring territories. This behaviour was studied

by radio tracking and involved badgers in Woodchester Park so is comparable to this study. however, in this study these differences were not observed. This is probably due to small sample sizes again, as only one badger infected with TB was radio tracked for a significant length of time to accurately quantify patterns of home range size and use.

Chapter five presented results from laboratory and field trials of proximity loggers. Overall, the consistency and accuracy of the proximity loggers was fairly good and they performed well. The proximity collars are a relatively novel technology so some minor teething problems can be expected. Some problems were collars transmitting only and not recording contacts, recording large numbers of one-second contacts and variations in contact detection and termination distances between collars. The majority of these problems could be overcome to a certain degree by manipulation of the data after it had been collected and before analysis. The newer version of the collars used on badgers in the latter half of the study were much improved in terms of construction, design and functioning compared to the original version of the collars, indicating that improvements are being made, and further modifications to these collars are planned by Sirtrack Ltd., which will enhance the performance of the collars. Overall, the proximity loggers were able to provide relatively accurate and reliable data, and future developments to the technology and the collars will improve this even more. The current main advantage of the proximity loggers, however, is the ability to collect data that we have not been able to gain previously.

For this study, contacts between badgers were defined as occurring when two badgers came within approximately one and a half meters of each other. This distance was determined by the resolution of collars rather than being based on biological reasoning, and does not necessarily imply direct physical contact has occurred. However, within this distance badgers will be able to directly interact with each other as their senses of eyesight, smell and hearing are thought to be sufficiently developed (Neal and Cheeseman 1991).

Chapter six quantified direct interactions between badgers using proximity loggers. Contact rates and contact durations between badgers belonging to the same social group were high and frequent, whilst contacts between badgers from neighbouring groups were less common, and contacts between badgers from non-neighbouring groups were very rare. Intra-group contacts occurred at any time of day, whereas inter-group contacts occurred mainly during the hours of darkness, when badgers are most active (Neal and Cheeseman 1996).

Intra-group contacts occurred mostly within the vicinity of the sett, and the majority of intra-groups contacts were within the badgers' social group territory. Contact rates did not vary significantly with respect to season, sex or age for both intra- and inter-group contacts, however, contact rates between badgers with the potential to transmit TB to other badgers, or already infected with TB, were lower compared to contact rates between badgers with no potential to transmit TB. This has important implications for the spread of TB within badger populations.

Contact probabilities for badgers within the same social group were much higher than previously found through both estimation and field data, and contact probabilities for badgers between neighbouring groups were also generally higher in all seasons apart from winter, and especially high in spring for male:female inter-group pairs. This is consistent with findings from genetic studies that extra-group paternity is much higher than previously thought (Carpenter et al. 2005), as spring is the peak breeding season (Neal and Cheeseman 1996) and period of most territorial activity (Delahay et al. 2000a). Extra-group breeding may help reduce inbreeding in the population, potentially making philopatry a less costly strategy (Woodroffe et al. 1995).

7.2 Summary of methods used to study interactions in this thesis

The majority of the methods used in the thesis are established methods used to study wildlife. The exception to this is the use of the proximity loggers, which are a relatively novel technology and to date have only been used in a handful of studies (Ji et al. 2005, Prange et al. 2006, Swain and Bishop-Hurley 2007). Chapter two described the methods used to trap and sample animals, and social group territory delineation found by bait marking. All trapping is carried out with great consideration for the welfare of the animals concerned, and steps are taken to minimise any negative effects trapping may have (Powell and Proulx 2003, Woodroffe et al. 2005a). The effects of trapping on badgers is unknown, as it is hard to measure without trapping the animal, but badgers trapped repeatedly do not appear to suffer any loss in body conditions compared to badgers trapped only occasionally (Tuyttens et al. 1999a). Bait marking is frequently used to determine the territorial configuration of social groups (Delahay et al. 2000a), and provides a reliable comparison between study sites and populations provided the same amount of effort is put into locating latrines between sites (Delahay et al. 2000a). Baits can also be used to deliver

oral vaccines (Olson et al. 2000) or fertility control agents (Cagnacci et al. 2005), which may prevent the spread of diseases (Eisinger et al. 2005). Chapters three and four used radio tracking to study indirect and direct interactions between individual badgers. Radio tracking is a very common technique in the study of animal ecology and behaviour, and the advantage of using it is that it is relatively easy to obtain detailed information about individual animals. It is relatively inexpensive and because so many studies have used it, comparisons can be made between studies. However, radio tracking has been a target for criticism, mainly because of the error associated with recording locations of animals; locations found by radio tracking are often reported as error-free exact locations and this is not the case (Harris et al. 1990, Saltz 1994, Powell 2000). Chapter three investigated some of the sources of error associated with radio tracking, so when radio tracking is used in chapter four to study badgers, an accurate assessment of the error can be provided. The choice of appropriate home range estimator is also subject to debate (Powell 2000). In this study both minimum convex polygons (Mohr 1974a) and kernel (Worton 1989) home range estimators are used to enable comparisons with other studies. However, some home range estimators are more sensitive than others to sample size and differences in settings chosen (Seaman et al. 1999, Gitzen and Millspaugh 2003), so conclusions drawn from comparisons of different studies must be treated with caution. Radio tracking is considered the best available method for studying movement patterns of individual badgers (and also interaction; although the use of proximity loggers improves on this), as GPS collars are unsuitable due to badgers spending a large amount of time underground when resting (Roper et al. 2001), and often in dense vegetation when foraging (Neal and Cheeseman 1996) where GPS location fix success would be low (Frair et al. 2004, D'Eon and Delparte 2005, Visscher 2006). The effects of radio collars on badgers has been investigated by comparing body condition and reproduction success of badgers fitted with radio collars compared to those not fitted with collars by trapping and sampling badgers (Tuyttens et al. 2002). After an acclimatisation period, there were no significant negative impacts on badgers. The effects of proximity loggers are expected to be the same as those of radio collars, as they are very similar in size, shape and weight (SitrackLtd. 2006).

Chapters five and six used proximity loggers to investigate first their suitability for recording contacts between animals and their accuracy, and then applied this to the Woodchester Park badger population. Laboratory and field trials demonstrated that for the majority of the collars and for the majority of time the collars were performing as intended.

Some minor processing to the data once it had been downloaded further improved the accuarcy and reliability of the collars. As all collars can both receive and transmit contacts and log the data onto the memory there is potentially duplicated data. This is good because it provides a back up in the system; not all the collars need to be recovered to gain all the contact data. However, no interaction patterns can be inferred between badgers whose collars are not recovered. In the field study, not all collars were recovered; some fell off, probably due to a very dry summer that meant food availability was low and badgers lost weight (P. Spyvee, *personal communication*). When collars fell off underground they were not retrievable, although some collars were later found in spoil heaps outside entrances to the setts, presumably badgers had removed them along with bedding or excavated soil.

Average contact rates and durations were calculated from the contact data. Whilst this method provides a good way to compare contact rates, durations and patterns of interactions between different individuals and groups of individuals, a large amount of variability is lost in the data. The amount of data on interactions that the proximity loggers can collect at the level of the individual is unprecedented, and the analysis of this data has not been realised to its full potential in this thesis.

Prange et al. (2006) have suggested that in order to accurately quantify contact rates between animals the population needs to be saturated with proximity loggers. In this study this was not the case, as will occur with most studies. Budgets and resources will limit the availability of collars, and it is not possible to guarantee that 100% of the population will be trapped or caught to enable a collar to be fitted. In the badger population at Woodchester Park where trapping success is high, it is thought that approximately 92% of animals are caught at some point in their life (Hounsome et al. 2005); this still means 8% of animals go undetected. Furthermore, unless the population is completely closed, there will be immigration and emigration of animals from and to, surrounding populations.

7.3 Implications

The findings from this study demonstrate that badgers in this high-density population occupy distinct territories with little temporal or spatial overlap between social groups. Interaction rates within social groups are high; they have both a large potential to interact with other members of the same social group due to shared territorial areas, and they realise this potential to interact, in terms of frequency of interactions, the number of

interactions and the duration. The large numbers of contacts show that intra-group interactions are important in the maintenance of social cohesion within social groups. Locating some of these intra-group interactions both spatially and temporally showed that badgers contact each other mainly in the vicinity of the main sett, but also within other areas of the shared territory.

Inter-group contacts between badgers occurred occasionally between badgers from neighbouring groups, and very rarely between non-neighbouring groups. The nature of interactions, whether they are aggressive or affiliative cannot be determined, but the higher rates of contact in Spring between male:female pairs may indicate they are important in mating, and play a role in reducing inbreeding in social groups and maintaining genetic diversity.

With regard to TB in badgers, the results from this study are consistent with findings that TB is aggregated in social groups and that spread of infection between badgers in different social groups is limited, because it does not happen sufficiently often to synchronise the course of disease in neighbouring groups (Delahay et al. 2000b).

However, as is the case with many wildlife studies, the relatively small sample sizes means the capacity to draw solid conclusions is somewhat limited. However, an advantage of using proximity loggers to study contacts is that variations in complex behaviour of individual animals can be detected; whether these differences are due to individual behaviour or are due to a group effect or pattern is currently harder to detect.

7.4 Further applications

The success of proximity loggers at recording interactions between badgers has been demonstrated in this study. The Woodchester Park badger population is a high-density population, and to investigate how contact rates vary with different densities, proximity loggers should be fitted to other populations in other areas, as it is thought that interaction rates may vary at different spatial scales (Newton-Cross 2003).

Proximity loggers could also be used to quantify interactions between badgers that have been subjected to bovine TB control operations. Culling or removal of badgers is thought to cause social perturbation in badger populations. The spatial organisation and population density is disrupted, which may result in increased immigration of badgers into culled areas, disruption of territoriality, increased ranging and increased interactions

between social groups, therefore increasing the rate of contacts between cattle and infected badgers, and between infected badgers and uninfected badgers (Woodroffe et al. 2006a, Carter et al. 2007). Proximity loggers will enable these theories to be investigated directly with quantifiable results, and results can be compared to undisturbed badgers populations such as the one at Woodchester Park.

Proximity loggers are not restricted so studying contacts between one species only. Inter-species interactions can be studied, for example between wildlife and livestock, or between different wildlife species. Inter-specific interactions influence community structure, species coexistence and biodiversity (Caley and Hone 2004). Inter-species interactions are also important in transmission of diseases in multi-species host assemblages, and in animals of economic and conservation concern (Randall et al. 2006, Pedersen et al. 2007).

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