How does the Spatial and Social Dynamics of the Natterer's Bat Myotis Nattereri affect disease transmission and conservation?

Submitted by Simone Mordue as a thesis for the degree of Doctor of Philosophy in Biology at Newcastle University

Abstract

Natterer's bats (Myotis nattereri) are typical of many Bat species in that they participate in a variety of distinct seasonal communities and behaviours. In summer adult females are thought to be largely philopatric to their natal community/landscape where they rear their young and form largely matrilineal communities. Bat foraging behaviour and social participation is largely unquantified, as is our understanding of how age/maturity and sex may mediate their social behaviour. Crucially, the rate of female dispersal between communities is completely unquantified. A much better understanding of bat spatial and social dynamics is necessary to inform statutory functions, effective conservation and epidemiological modelling. We have mapped and quantified the spatial and social dynamics of three communities of Natterer's bats. Uniquely our roost switching data comes from a community roosting entirely in natural roosts. Radio-tracking, ringing and DNA evidence can be combined at one site, whilst ringing and DNA can be combined at two others. In addition, DNA samples from a further two sites could be included to complete the comparison of 183 Natterer's bats from 5 sites. Microsatellite data (based on 15 markers) was used to describe relatedness at two functional scales (between roosts within a community and between communities). Relatedness and population structure was also compared to home range analysis and roost use to determine if related individuals forage close to each other or share a roosts more frequently than unrelated individuals. Novel descriptions of demographic and epidemiological rates for this species were determined, which has been incorporated into predictive models of how both the community may respond to changes in the environment, or diseases may spread within the community which will help improve bat Conservation.

Acknowledgements

This work would not have been possible without the help of a wide range of people. I would like to thank my family including my husband Paul, my two children Lily and Poppy and my mother in law Isabell for all the emotional and practical support they have given me through long periods of nocturnal field work and then writing up. Without their help and support I would not have been able to do this.

I would also like to thank all my supervisors including Dr. Aileen Mill, Dr James Aegerter and Prof. Steven Rushton for their support, training, guidance, understanding and input into my work. Thank you to James for his patience and excellent teaching skills with my field work and to Aileen for all the help with analysis and navigating through university paperwork.

I would like to extend special thanks to Dr. Mark Shirley who has helped me significantly understanding and implementing R code and taught me a huge amount of programming skills whilst saving me from long periods of debugging.

Thank you to Dr. Debrorah Dawson, Dr. Helen Hipperson and all the staff at the NERC biomolecular lab in Sheffield for your help and support carrying out genetic microsatellite analysis and to Dr. Kirsten Wolf and Dr. Samuel Logan for help with the analysis and lab work back in Newcastle.

Also thanks to all the other PhD students at Newcastle whose help and friendship have been invaluable and kept me sane.

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Chapter 1. Introduction

1.1 Introduction

Bats are the most diverse order of mammals and account for one in five mammal species (Altringham, 2011). They are known to provide many benefits to ecosystem services including pollination (Kunz et al., 2011), arthropod suppression (Maas et al., 2013), acting as bio-indicators (Park, 2015, Jones et al., 2009) and due to their ability to fly, they are suggested to be responsible for recolonisation of tree species in tropical fragmented forests when other less mobile mammals are no longer present (Melo et al., 2009). Despite this, bats like much life on earth are under threat from increasing human pressure which leads to habitat fragmentation and loss. Due to their life history strategies , such as slow reproductive rate and tendency to form large aggregations for breeding and hibernating (Kunz, 2014a), they are particularly vulnerable to unique problems which will be outlined in this chapter.

Over the last couple of decades, bats have been found to be an important source of disease causing pathogens including Rabies, Nipah, Hendra, SARS and Ebola (Calisher et al., 2006). Increasing anthropogenic pressure on bat populations, which puts bats and humans in closer proximity, is thought to be one of the main causes of outbreaks of these diseases in humans which have caused large numbers of fatalities and high economic losses. At present little is known about how bats within populations (communities) interact during the spring/summer period, how different communities might interact during autumn swarming (Rivers et al., 2006), or how this behaviour might affect disease transmission and conservation of bats.

One possible model describing the operation of bat communities during the spring/summer period is that they live in social or semi-social community groups, continually re-arranging themselves across a network of roosts e.g. (August et al., 2014). A number of hypotheses have been proposed to explain the continual movement of bats between their roosts; predation (Lausen and Barclay, 2002), parasites or other epidemiological drivers (Reckardt and Kerth, 2006), to manage their energy budget (Kunz, 1980), sociability (Willis and Brigham, 2007) or epidemiological control (Willis and Brigham, 2004, Reckardt and Kerth, 2007, Kashima et al., 2013, Bartonicka et al., 2008). A network of roosts has previously been described for the Natterer's bat (August et al., 2014, Smith, 2000, Rhodes et al., 2006, Johnson et al., 2012) and all other Vespertilionids show evidence of similar roosting behaviour with no evidence to contradict this model. Supportive evidence that bats move across networks of roosts includes:

- strong roost philopatry by key classes (Thompson, 1992, Kerth et al., 2001a)
- a more general philopatry to natal landscapes by most/all classes (Thompson, 1992, Kerth et al., 2002b, Hillen et al., 2010)
- consistently short roost residency times (Russo et al., 2004, Reckardt and Kerth, 2007, Kashima et al., 2013, Feyerabend and Simon, 2000, Bartonicka et al., 2008)
- The frequent description in many radio-tracking studies of the use of an extensive network of roosts by individuals (Hale et al., 2012, Patriquin et al., 2010, Kerth et al., 2011, Johnson et al., 2013, August et al., 2014)

Very few studies have involved roosts in only natural woodland settings, where we might consider the majority of bats to live and the previous studies have only outlined the scale of the communities resulting in significant gaps in our understanding of the community structures and processes driving the spatial and social dynamics of bats. Similarly, we have no insight at all into the key rates used to describe how a bat community operates (e.g. contact rates between individuals or between classes or between communities). Extrapolating the existing evidence summarising bat social and spatial dynamics into a natural context may result in a poor generalisation of the dynamics of most bats and act as a poor foundation for our understanding of their population processes or epidemiology, leading to inaccurate policy recommendations and conservation prescriptions.

There is now therefore an urgent need to consider how the conservation of bats can be managed to reduce bat/human interactions and to preserve bats in their natural habitats along with a better understanding of how a community of bats operates in order to inform disease management policy.

This chapter aims to review the current threats to bats and their conservation including emerging infectious diseases and to describe their ecology and social behaviour. The aims and objectives of the thesis will be put into context and presented at the end of the chapter.

1.2 Threats to bat populations

Of over 1,000 species of bat, almost a quarter are threatened world-wide (IUCN, 2017) as a result of a growing number of factors, including disease, habitat loss and fragmentation, disturbances to roosts, exposure to toxins, human hunting pressures and introduced predators (Fenton et al., 1994, Boyles et al., 2011, Agosta, 2002). Many of the threats to bats can be directly related to increasing human populations that bring extra demands for land, food and other resources that ultimately results in the degradation or destruction of habitat for bats and other organisms (Mickleburgh et al., 2002). The wide variety of threats and wide diversity of species makes it difficult to draw general conclusions about bat conservation, which may require species-specific conservation plans (Fenton, 1997). Current threats to bat populations are outlined in more detail below.

1.2.1 Habitat loss

Urbanisation along with agricultural expansion are thought to be the biggest threats to bat populations worldwide (Russo and Ancillotto, 2015) and have led to the loss of vast areas of natural habitat throughout the different taxa (Jung and Threlfall, 2016). In Britain, increasing anthropogenic pressures and changing agricultural practices have greatly altered the habitat composition of most landscapes during the past century. In some regions up to 30% of broadleaved woodland has been lost since 1945 due to forest clearance, conifer conversion and urbanisation (Walsh and Harris, 1996b). As a direct consequence of the loss of habitat globally, many bat species have declined resulting in many species listed as threatened, 42 of which are European species (IUCN, 2017). Agricultural intensification, has directly attributed to the loss of woodland and many other bat habitats with negative impacts on bat populations (Park, 2015). Although there is growing concern of the negative impacts of intensive agriculture on biodiversity, resulting in increased interest in more sustainable methods of farming, there is little evidence of the benefits that this affords bats (Park, 2015).

1.2.2 Human-bat conflict/destruction of roosts

Bats and people are known to have shared dwellings for thousands of years. This is largely due to the decline in natural roosting sites and the increase in anthropogenic roosts in the form of houses, bridges, mines, barns and icehouses. However, even these man-made roosts are now under threat; demolition of old buildings, renovations, changes in use, artificial lighting and the move towards air-tight buildings, all have implications for bat populations using buildings (BCT, 2016). Where roosts in buildings need to be destroyed they are replaced with artificial roosts but the effectiveness of this mitigation has rarely been studied (Stone et al., 2013). There is also an increasing area of conflict where bats roost in large numbers in churches (Zeale et al., 2016, Hales, 2014). Although bats often go unnoticed, some churches experience problems which restrict the use of the church and / or affect its maintenance. As bats and their roosts are legally protected in Europe, they cannot be excluded from their roost site or removed without mitigation if this is thought to affect their Favourable Conservation Status (92/43/EEC, 2002). Conservation status will be taken as ‘favourable’ when: population dynamics data on the species concerned indicate that it is maintaining itself on a long term basis as a viable component of its natural habitats, and the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long term basis (92/43/EEC, 2002).

This has led to research by the University of Bristol to understand how and why bats use churches, and find solutions to these problems. 'Boxing-in' roosting areas around bats' entry points into a church has provided a promising solution, retaining roosting space for the bats but preventing access (and therefore deposition of droppings and urine) to the rest of the church interior, ongoing surveillance is still continuing in this area (Zeale et al., 2016).

1.2.3 Wind power

Wind energy continues to be one of the fastest growing renewable energy sources and although it is a clean energy source, it is not environmentally neutral. Large numbers of bats are being killed at wind energy facilities worldwide, raising concern about cumulative impacts of wind energy development on bat populations (Arnett et al., 2016). Studies have been carried out over the last decade or so to estimate how many bats are killed by turbines (Table 1) , for example in Africa up to 18 bats per turbine are killed each year (Rodrigues et al., 2008), whilst a recent study in Canada estimates that around 15 bats per turbine are killed per year. Installed wind capacity is growing rapidly worldwide, and is predicted to increase approximately 3.5-fold over the next 15 years, which could lead to direct mortality of approximately 166,000 bats/year in Canada alone (Zimmerling and Francis, 2016). Population-level impacts may become an issue for some bat species as numbers of turbines increase. These figures could also be an underestimate of the number of bats killed as they are based on carcasses found on site with the majority killed by impact with wind turbine blades. Barotrauma is also responsible for multiple bat mortalities at wind farm sites, (Grodsky et al., 2011). It is likely that some bats don’t die immediately from the effects of Barotrauma but may travel some distance before death therefore their carcasses would be undetected (Lintott et al., 2016). Either way it is evident that a large number of bats are being affected by wind turbine sites and these effects are only being noticed after the installation of the wind turbines. It is possible that many more fatalities are occurring during construction or that bat populations are being displaced as a consequence of construction. Research is urgently needed in this area to address population level effects of wind farms and these studies should include pre-construction assessments.

Table 1 Reports of multiple bat fatalities at wind farms modified from (O'Shea et al., 2016)

Region	Average no of fatalities per turbine per year	Source
Africa	18	(Rodrigues et al., 2008)
Australia	11	(Hall and Richards, 2000)
Canada	15	(Zimmerling and Francis, 2016)
Europe	4	(Rodrigues et al., 2008, Rydell et al., 2010, Brinkmann et al., 2006, Seiche et al., 2008, Silva et al., 2008, Trille et al., 2008, Rico, 2016)
United States of America	5	(Young et al., 2003, Erickson et al., 2008, Gruver, 2002, Howe et al., 2002, Krenz and McMillan, 2000, Brown and Hamilton, 2002)
South America	5	(Barros et al., 2015)

1.2.4 Toxins

Pesticides and agrochemicals can have both direct and indirect effects on bat populations (August, 2012, Bayat et al., 2014, Valdespino and Sosa, 2017) by either directly poisoning bats which ingest the chemicals or by reducing the abundance of prey species. Although pesticide use in agriculture in the developed world has recently moved towards chemicals with reduced mammalian toxicity, highly toxic alternatives such as dichlorodiphenyltrichloroethane (DDT) are still used in developing countries and they have been implicated in the decline of bat populations in the USA and Australia and Zimbabwe (Fenton and Rautenbach, 1998),

DDT is thought to be no longer a threat in the UK and organochlorides, used to treat timber and potentially fatal to bats, have been replaced with more suitable chemicals. However, low levels of mercury, lead and cadmium have been found in some bat species (Hernout et al., 2016, Hernout et al., 2015) and exposure to DDT still occurs from remaining residues many years after the compounds have been actively used.

1.2.5 Hunting

Bat hunting for consumption as bush meat and medicine is widespread globally and affects at least 167 species of bats (Mickleburgh et al., 2009). Bats are particularly vulnerable to the effects of hunting for a number of reasons including their slow reproductive rates (McCracken and Wilkinson, 2000). Mortality due to hunting may also have strong negative effects on ecological communities and ecosystem functions not only to natural ecosystems but also to human communities. As previously discussed, bats in their natural ecological roles perform valuable ecosystem services beneficial to humans therefore, reductions in bat populations as a result of hunting could have expensive consequences on local communities' water supplies, agriculture, and eco-tourism industries (Mildenstein et al., 2016). The hunting of bats may also expose human communities to potentially zoonotic pathogens including EIDs (Kamins et al., 2011, Jenkins and Racey, 2008, Harrison et al., 2011). For example, it has been suggested that the 2007 emergence of Ebola virus in the Occidental Kasai province of DRC could be attributable to the consumption of freshly killed bats (Leroy et al., 2009).

Although human communities have long exploited bat populations for consumption, current hunting pressure is likely to be much greater than previously with increases in human population density, greater accessibility to natural areas, technological advances in bat capture methods and transport options, and relaxed adherence to cultural taboos (Brooke and Tschapka, 2002). Therefore, bat hunting is likely to be unsustainable. The general consensus among biologists and managers is that hunting is a now a major conservation threat and to evaluate the impacts on bat populations research should compare the direct and indirect mortality rates of hunting with the population's capacity for growth (Mickleburgh et al., 2009).

1.3 Disease

Bats are well known for carrying disease of concern to human health (Daszak et al., 2000). Indeed, Emerging infectious diseases (EID's) where bats have been implicated e.g. Ebola (Leroy et al., 2009) and Hendra virus (Daszak et al., 2006) have been highly publicised raising concerns on the prevention of human disease from spillover events. Most of the recent bat borne EID's can be attributed to increased bat-human contact, usually due to some form of habitat degradation or reduction (Daszak et al., 2001).

One Health, recognises this, that the health of humans, animals and ecosystems are all interconnected. The initiative plays a significant role in the prevention and control of zoonoses (Bidaisee and Macpherson, 2014). It acknowledges that disease spillover from animals to humans gets progressively worse as humans successively alter the environment and impinge upon ecosystems and the species they support (Zinsstag et al., 2012, Narrod et al., 2012, Lu et al., 2016). It also states that zoonoses should be considered to be the most important factor to human health and well-being (Lu et al., 2016).

In addition to the threats to human health and unlike well known threats to bats such as those already mentioned in section 1.2, the impact of disease on bat populations is rarely considered, with the exception of large scale epidemics such as White Nose Syndrome (WNS) (Wilder et al., 2015, Wibbelt et al., 2011, Warnecke et al., 2012, Vonhof et al., 2016, Powers, 2016, Miller-Butterworth et al., 2014, Coleman et al., 2015). However diseases other than WNS, are a major cause of mortality in bat populations (Mühldorfer et al., 2011) and should be considered in conservation plans. Many historical records of mass bat mortalities caused by disease are directly attributable to anthropogenic change (Pierson and Rainey, 1992, King et al., 1994, Flannery, 1989) in agreement with the One Health philosophy, therefore protecting natural bat habitats and populations is not only important for bat conservation but also for public health. A challenge now exists in balancing public health measures to prevent human disease and protecting bat populations (Kunz and Fenton, 2005).

1.3.1 Diseases of concern to bat populations

One of the most recent well studied diseases of conservation concern to bat populations is white-nose syndrome (WNS) caused by the fungus *Pseudogymnoascus* destructans (formally Geomyces destructans destructans); which is thought to be transferred by bats and humans (Coleman et al., 2015). The disease has led to massive declines of bat populations in the eastern United States and Canada since its discovery in 2006. To date, over one million bats have died, and winter colony declines in the most affected region exceed 70% (Frick et al., 2010). Populations of at least one species (little brown bat, *Myotis lucifugus*) have declined so rapidly that regional extinction has been predicted (Frick et al., 2010, Boyles et al., 2011). The fungal pathogen, infects the wings, ears and nose of bats in winter and causes premature and repeated emergence from hibernation throughout the winter period, leading to dehydration, emaciation, depletion of fat stores, and often death (Powers, 2016). It is now established that *P. destructans* occurs at low levels on bats throughout Europe, where it has been isolated from eight Myotis spp., but with no evidence of mass mortality (Wibbelt et al., 2011). The absence of mortality observed among European bats infected with *P. destructans* is thought to reflect different physiological and behavioural responses of European versus North American bats, it has also been suggested that *P. destructans* may have impacted European bat populations in the past (Wibbelt et al., 2011) and that bats in Europe have coevolved resistance to or tolerance to infection with *P. destructans* (Warnecke et al., 2012). Either way it currently does not appear to pose a significant threat to European bat species but does highlight how an apparently minor shift in host range or environmental context may turn a cryptic pathogen into a significant problem.

In addition to WNS, other diseases are also a threat to bat populations. Mühldorfer et. al (2011), considered the impact of disease on 19 European Vespertilionid species using 486 bat carcasses collected from six regions in Germany and discovered that disease caused over 30% of fatalities. Bacterial disease attributed to approximately 18% of these disease related fatalities, and viruses including European bat lyssavirus and bat Adenovirus caused approximately 2%. In addition to this, a review by O'Shea et. al (2016), lists 25 mass mortality events of bats caused by disease concerning 14 different species of bat with the majority of deaths caused by Lagos virus, Bunyavirus and Lyssavirus. Few other studies have considered the impact on bat populations from disease outbreaks or how disease might spread within or between natural populations therefore this is an area that requires more research.

1.3.2 Emerging infectious diseases

Bats have many features which may attribute to their importance in EID transmission and maintenance, such as high species diversity, mobility, longevity and sociality (Kuzmin et al., 2011). Despite these attributes, there is little evidence to suggest that any major bat associated EID's persist within hosts and therefore it is likely that the viruses are maintained in nature within and between bat colonies (Kuzmin et al., 2011). There are many different zoonotic viruses- those that can be transmitted between non-human animals and humans including; Marburg virus, Nipah virus, Hendra virus, Rabies virus, and coronaviruses (Calisher et al., 2006). The drivers of bat associated EIDs include overpopulation, environmental degradation and socio-economic factors which put increasing pressure on natural populations (Kuzmin et al., 2011). An example of one such outbreak is the recent outbreak of Ebola, thought to be attributable to increased pressure on natural bat populations which had a significant impact on human health, and on the sustainability of agricultural systems. Many human deaths were attributed to Ebola along with a drastic increase in cocoa prices (Wallace et al., 2016, Obilade, 2015). By studying EID events from bats it may be possible to identify trends in the conditions surrounding disease spill over (August, 2012) in order to better manage habitats for bats or prevent future outbreaks. While many studies have focused on the highly human-pathogenic bat viruses in tropical regions, little is known about similar human-pathogenic viruses that may be present in European bats and further studies are needed (Kohl and Kurth, 2014).

Rhabdoviruses of the genus Lyssavirus have been detected in Europe and are harmful and zoonotic agents, always thought to cause the death of unvaccinated humans if not treated before onset of the rabies disease (Johnson et al., 2010). However, even though bat-transmitted lyssaviruses have a fatality rate of 100%, the reported total number of human fatalities in Europe is low (n = 2–5 since 1963) (Racey et al., 2013). This recent emergence of lyssaviruses in Europe has encouraged interest in understanding the community dynamics of bat populations to inform zoonotic disease prediction, prevention and potential options for policy responses. Natterer's bat *Myotis nattereri* is a widespread European bat which has been suggested to be a reservoir host for Bokeloh bat lyssavirus (Picard-Meyer et al., 2013, Nolden et al., 2014, Freuling et al., 2011) a novel lyssaviruses identified only in *M.nattereri*.

As all principle bat hosts of European bat lyssaviruses (EBLV-1; Serotine (E. serotinus), EBLV-2; Daubenton's bat (M. daubentonii) and Bokeloh; Natterer's bat (M. nattereri)) share their habitats with humans, spill-over of lyssaviruses prevalent in European bats is considered to pose a significant risk to public health, and preventive measures or policies have already been implemented by many European countries for decades (e.g., surveillance, vaccination plans, and post exposure prophylaxis) (Racey et al., 2013). Although lyssavirus prevalence is usually considered to be low (e.g.(Harris et al., 2006) changes in bat behaviour as a result of climate or landscape change as well as other changes in the relationship between bats and man may make it more likely to bring bats into contact with humans. This therefore requires a better mechanistic understanding of the epizootiology of lyssaviruses in bats in order to better predict the risks to man (Müller et al., 2007). However, despite the risk being relatively low (five fatal cases during the last 38 years out of 590 million people living in Europe) and the suggestion that the risk would disappear if people were educated appropriately (Racey et al., 2013), rabies as a normally fatal zoonosis inevitably draws policy attention. Relocation or culling of bat colonies has been studied in the context of bat disease, (Streicker et al., 2012a), although both were problematic and potentially ineffective for the management of rabies in vampire bats. Nevertheless, the increasing public fear of bats and their viruses poses a threat to their protection. Educating the public regarding bat lyssaviruses might result in reduced threats to both the public and the bats (Kohl and Kurth, 2014). However, we still need detailed information on how a disease might travel within and between populations of bats in order to effectively manage their conservation and to inform Government decision-making.

1.4 Conservation status of Vespertilionids

Effective and efficient species conservation in a context of competing policy demands and limited funding requires a good knowledge of bat ecology, population dynamics, behaviour and habitat requirements along with an understanding of how threats affect their essential requirements and processes. A good working knowledge of current conservation legislation is also needed to gain an insight into potential mitigation options where bat-human conflicts arise so any gaps in protection can be lobbied for with the aim for improving protection for vulnerable species. Current legislation, threats facing bats and tools to understand bat ecology are considered below.

1.4.1 European Conservation legislation

A significant proportion of current domestic environmental law derives from European Union (EU) Regulation and EU Directives. Across the UK all bats are legally protected both by national or devolved legislation, principally the Wildlife and Countryside Act 1981 and the Habitats regulations (2010), the later completing the transposition of EU 92/43/EEC into law. Favourable Conservation Status (FCS) is central to the application of EC Habitats Directive 1992 currently in force in the UK, and this legislation summarises three requirements for a species to be considered as achieving and maintaining FCS (Directive, 1992);

1. Long term population viability
2. Maintenance of the natural range of the species
3. Large enough habitat for the species

However, the application of FCS and especially the requirement to predict its maintenance is likely to become more complicated given ongoing climate and land-use change including the spread of activities known to disrupt bat populations (e.g. roads, wind power, building & development) (Altringham and Kerth, 2016, Arnett et al., 2016). Problems arise in conserving many species of bat when bat-human conflict requires mitigation, for the mitigation of conflict to be proportionate to its effects on bat populations, it may be necessary to recognise that heterogeneous landscapes will lead to a variation in the importance of specific roosts and require spatially specific predictions for FCS and local solutions to conflict. The quantitative assessment and prediction of the three requirements of FCS using agreed methodologies and robust data would help inform decision-making in this context. What is needed for any quantitative approach is an appropriate description of the unit of space, and by extension, a unit of population at which to model and predict population dynamics.

1.4.2 Bats and Natural Capital

It is possible that bats will gain protection when valued as 'Natural Capital', due to their natural pest control. In 2012, the Natural Capital Committee (NCC) was established in the UK in response to the governments 2011 Natural Environment White Paper 'The Natural Choice: Securing the Value of Nature (GOV.UK, 2011)'. The role of the NCC is to

- help the Government better understand how the state of the natural environment affects the performance of the economy and individual wellbeing in England;
- advise the Government on how to ensure England's "natural wealth" is managed efficiently and sustainably, thereby unlocking opportunities for sustained prosperity and wellbeing.

The study aimed to assign a value to nature so that it may be considered in economic terms when decisions are being made. This approach may afford some benefits to bats and their habitats as bats have been described as important to global ecosystems as primary, secondary, and tertiary consumers that support and sustain both natural and human dominated ecosystems (Kunz et al., 2011). For example, insectivorous bats are major consumers of nocturnal insects, many of which are economically important pests. In the US alone, the value of this natural form of pest control is estimated to be around $3.7 billion/year (Boyles et al., 2011).

Although there is evidence of both ecological and economic rationales for bat protection (Grinnell, 1918; Constantine, 1970; Whitaker, 1995; Pierson, 1998), it is not clear whether valuing nature in this way would be beneficial to bat conservation. In terms of planning development mitigation, if a cost benefit analysis is done of the natural habitat to be removed, it may be possible that the economic benefit of providing a larger new area of habitat after removing an existing habitat for development may be considered to be more beneficial overall to a nations natural capital. This does not account for the age of the habitat removed or its diversity and value to the species it may already support. Unless a very broad understanding of the terms are applied and sufficient surveys are carried out, valuing nature in this way could therefore be detrimental to biodiversity and ultimately cause a decline in bat species. Alternatively, if the importance of bats as ecosystem providers or bioindicators is highlighted along with the value of their irreplaceability and we have further evidence regarding their required roosting, foraging and habitat requirements, it may be that including their value in this way in economic considerations could afford them a high level of protection, perhaps similar to that afforded by the EC Habitats directive. Until the paper begins to be implemented it is difficult to know how it will be interpreted but information regarding the natural range, roosting and habitat requirements of bats is still crucial in order to protect them and our biodiversity.

1.5 Bat Ecology

1.5.1 Bats and Society

Evidence of society

Society or social structure in animals can be defined as “a group of animals belonging to the same species and consisting of individuals beyond the family unit, who perform specific tasks, spend distinctly more time together and interact much more within the group than with members of the same species outside of that group. ” (De Waal and Tyack, 2009). It is founded on and measured by, behavioral interactions among individuals (Whitehead, 2008).

Evidence of social structure has been shown in many different taxa including birds (e.g. Passerines (Beecher and Burt, 2004, Oh and Badyaev, 2010)), insects (e.g. Fewell (2003) and Bonabeau et al. (2000)) and mammals (e.g. Sperm Whales (Whitehead et al., 2012), baboons (Silk et al., 2010), elephants (De Silva and Wittemyer, 2012), primates (Dunbar, 2013)). Worldwide, bats also show diverse and powerful evidence of social behaviours and society.

Calls recognizable by conspecifics are one indication of social structure in bats and are known to serve a number of functions within bat communities, from identifying occupied roost sites (Schöner et al., 2010, Furmankiewicz et al., 2011, Carter et al., 2012), eavesdropping on productive foraging areas (Übernickel et al., 2013, Jones et al., 2014, Dechmann et al., 2009, Balcombe and Fenton, 1988) and identifying individuals (Kastein et al., 2013, Siemers and Kerth, 2006, Pfalzer and Kusch, 2003, Voigt-Heucke et al., 2010). Many species are also philopatric (Thompson, 1992, Rivers et al., 2005, Kerth et al., 2002b, Kerth et al., 2001a, Burland et al., 2001, Kerth and Van Schaik, 2012, Dixon, 2011, Chaverri and Kunz, 2011), with bat communities returning to the same roosting area each year and roosting with the same individuals, despite evidence of them leaving these sites for mating or hibernation (Veith et al., 2004, van Schaik et al., 2015, Rivers et al., 2006).

Society and socially driven processes have also been described in species or contexts similar to the study focus. For example Bechstein bats (*Myotis Bechsteinii*) are able to maintain long term relationships over at least five years (Kerth et al., 2011), many European species have been shown to be loyal to roosting areas (Thompson, 1992, Kerth and Reckardt, 2003, Kapfer et al., 2008, Feyerabend and Simon, 2000, Encarnacao et al., 2005, Boonman, 2000, August et al., 2014) or to transfer information about food (Kerth et al., 2001a, Rossiter et al., 2002) or to regularly associate together over time forming social networks e.g. (Kerth et al., 2011, August et al., 2014). Natterer's bats like many other European species have also been shown to exhibit this social behaviour. Indeed, long term relationships were shown in Natterer's bats caught in Wytham woods (August et al., 2014), Natterer's are able to recognise calls from conspecifics (Schöner et al., 2010) and they also exhibit roost philopatry (Smith, 2000, Rivers et al., 2005, Mortimer, 2006), we can therefore assume that they do have a level of social structure.

In species whose colony members are faithful to individual foraging areas, such as Natterer's, information transfer about food seems to be restricted to mother-daughter pairs (Kerth et al., 2001a, Rossiter et al., 2002). As such it's possible Natterer's show a learned behaviour whereby a mother would show her young where she forages but due to possible social structure this area may have been previously determined by her position within the social hierarchy. Thus it might be speculated that habitat preferences previously described in the literature, may include not only the preferred habitat of choice by dominant bats and their off-spring, but also areas of sub-optimal foraging used by subordinate individuals. Therefore, a detailed understanding of Natterer's individual foraging preferences and whether these are translatable to the whole community or specific to individuals is needed to better inform conservation management.

Evolution of society in bats

It is thought that bat sociality has evolved, both due to individual longevity and philopatry, which paved the way for stable groups that include related individuals (Kerth, 2008). Stable group structure is known to lead to the evolution of cooperation, which is an important benefit of sociality (Clutton-Brock, 2009). Female bats nurse their young until they reach almost the size of the mother; the spectacular growth pups show is energy-demanding and providing for it dominates the most significant season for adult female bats. This has been used to explain communal breeding among bats is thought to be beneficial because it facilitates mutual warming (Willis and Brigham, 2007), cooperative nursing (McCracken and Wilkinson, 2000) and safety from predators (Fenton et al., 1994). Benefits from communal breeding can explain why sociality in bats is more common in females than in males, which normally provide no paternal care (Kerth, 2008). Indeed in all temperate bat species females form maternity colonies to raise their young whilst males are mostly solitary, occasionally forming male only groups or or joining non-breeding females (McCracken and Wilkinson, 2000, Safi et al., 2007). Group decision making may also be necessary, to coordinate the reproduction of group members in situations in which individuals benefit from synchronized breeding, either because synchronization reduces predation or because it offers energetic benefits through mutual warming. Each of these situations which require group decision making occur in bats (Kerth et al., 2006, Fleischmann and Kerth, 2014) and any further social research might look to see how group decisions are made.

1.5.2 Roosting behaviour of bats

Roost switching or philopatry?

Although many authors have described temperate bats as philopatric to their natal sites (Burland et al., 1999), others have shown that they switch roost approximately every 3 days and use an average of 30 roosts per community (Table 2). One conceptual model that helps resolve this paradox involves bat communities being faithful to roosting *areas*, whilst they re-sort themselves across a constrained network of roosts each summer (Johnson et al., 2013, Chaverri, 2010, Fortuna et al., 2009, August et al., 2014). The day-to-day dynamics of this process have been labelled as fission-fusion dynamics where individuals frequently switch roosts in such a way that groups split apart and recombine (Kurta and Kunz, 1988, Rhodes, 2007, Metheny et al., 2008, Kerth et al., 2011, Kerth and König, 1999, Kashima et al., 2013, Fleischmann and Kerth, 2014). However, less attention has been made to describing the properties of the entity within which fission-fusion occurs: the size and demographic structure of the bat community as a functional unit, its geography and its spatial dynamics. Thus workers have explored or speculated on whether fission- fusion behaviour requires special communication, decision making, and cognitive skills (Aureli et al., 2008).

Natterer's bats amongst other species, switch roosts frequently and use contact calls to coordinate reunions at new roosting locations (Carter et al., 2012). In Bechstein's bats *Myotis bechsteinii*, there is evidence that reproductive status and relatedness explain which individuals roost together (Kerth et al., 2001a, Kerth et al., 2011). However, at present little is known about the relatedness of Natterer's roost mates.

Table 2 Evidence of roost switching behaviour in temperate bats

Species	No of roosts used	No of bats followed	Range of residency times (days)	Average residency times (days)	Reference
Barbastella barbastellus	33	25	1 to 6	2.6	(Russo et al., 2004)
Barbastella barbastellus	27	40	1 to 4	1.6	(Kerth and Melber, 2009)
Barbastella barbastellus	46	13	1 to 4	2	(Hillen et al., 2009)
Myotis bechsteinii	23	10	2 to 8	7.8	(Kerth and Morf, 2004)
Myotis bechsteinii	78	47	1 to 4	1.5	(Dietz and Pir, 2009)
Myotis daubentonii	4	7	1 to 10	3.8	(Kapfer et al., 2008)
Myotis mystacinus	7	13	1 to 5	1.7	(Buckley et al., 2013)
Myotis nattereri	25	38	1 to 12	3	(Smith, 2000, August et al., 2014)
Myotis nattereri	37	20	1 to 6	2.5	(Mortimer, 2006)
Nyctalus leisleri	28	15	1 to 17	2.6	(Spada et al., 2008)
Pipistrellus nathusii	28	14	1 to 8	3.3	(Flaquer et al., 2009)

Benefits of social roosting

The energetic costs of roosting at different temperatures is not known for Natterer's bats but the thermal neutral zone for another Myotis sp., *Myotis lucifugus,* is thought to be 27-29^{o}C (Kurta and Kunz, 1988) and the maximum body temperature recorded of a roosting Natterer's is 37.6^{o}C which suggests roosting at this temperature may be energetically costly for the bat. Temperate bats might choose between behavioural thermoregulation (switching roosts or clustering, or moving within roost) and / or the use of torpor to reduce energy costs associated with thermoregulation. This choice is likely to be influenced by ambient temperature and reproductive status, torpor use by bats prolongs gestation (Chruszcz, 1999) and could be used as a strategy to delay birth for a particular reason such as short food supply, or the increased temperature gained from clustering with other females may help speed up gestation. Another possible suggestion for roost switching could be to avoid large populations of ectoparasites, by deserting an infected roost before the eggs hatch or to avoid pathogens caused by a build-up of urine/faeces (Smith, 2000). Further work is again needed in this area to get a better understanding of which factors drive roost switching.

Roosting behaviour of Natterer's bats

The high home range densities (7-15 roosts sq.km) of day roosts in the Natterer's colonies in Smith's study (2001) suggests that a large number of roosts are needed to sustain a population. At present little is known about the importance of particular roosts to individuals and whether they act as social hubs for information transfer. Information transfer about roost sites is known to occur in species which switch their day roosts regularly (Kerth and Reckardt, 2003) and swarming behaviour at emergence and re-entrance to roosts is thought to be a possible time for information transfer or to act as a reinforcement of social bonds (Wilkinson, 1992). The idea that Natterer's use a network of roosts (August et al., 2014) and switch roosts regularly may suggest that a community is relatively stable to the loss of some roosts, however this depends of the function of the removed roosts. A simulated removal of roosts used by the Northern Long Eared Bat *Myotis septentrionalis* in the US showed that when a threshold of more than 20% of roosts are removed, the social network of the community starts to fragment (Silvis et al., 2014a), which would possibly result in negative fitness consequences for the community. However, if one roost in the network is key for pup raising, the loss of a single roost could have substantial negative impacts on the long term survival of the community.

1.5.3 Life cycles of temperate bats

Temperate bats can form summer nursery colonies comprising large numbers of adult females in buildings (Stebbings, 1991) trees or caves and males are known to be either solitary or form small summer groups from 8-28 bats (Swift, 1997). Roosts used by a Natterer's maternity colony have been shown to be exclusive to that colony despite close proximity of other colonies (Smith, 2000, August et al., 2014) and females demonstrate strong philopatry returning each year to the same roosts. At present it is unclear if, or how often females switch their nursery sites, little is known about why female bats rarely switch maternity colonies, or how new colonies are formed. Further work describing colony foundation / establishment is likely to be important in the long term conservation of bats.

Temperate bats are relatively long lived compared to other mammals of a similar size and usually give birth to a single pup per year ((McCracken and Wilkinson, 2000). This low birth rate results in relatively slow population growth and populations are therefore at higher risks of population crashes and local extinctions than other small mammals. Many temperate species occupy different winter and summer landscapes, with winter hibernation in roosts that are typically distinct from their summer roosting sites (McCracken and Wilkinson, 2000) where they also give birth in early summer. Mating occurs in the late summer at autumnal swarming sites, which often double as their winter hibernation sites, where large numbers of bats from surrounding areas congregate (Rivers et al., 2006). This swarming behaviour is thought to facilitate increased gene flow between populations and limit inbreeding depression (Rivers et al., 2005). There is some debate about how far temperate bats may migrate from their winter to summer sites and it appears to be species specific. Banded Indiana Bats *Myotis sodalis* migrate over 500Km between sites in the US and Canada (Kurta and Murray, 2002), Little Brown bats *Myotis lucifugus* have been shown to migrate up to 647Km between winter and summer sites (Norquay et al., 2013), whereas Natterer's bats in the UK have been observed migrating up to 63Km between sites in one study (Rivers et al., 2006) and only up to 26.7Km in another (Parsons and Jones, 2003).

However, the paucity of bat ringing programmes, associated with the almost non-existent knowledge of the locations of most autumnal swarming sites, suggests that these estimates represent a significant underestimate of the true distance they may migrate. Some species may also vary in their migratory patterns depending on their geography e.g. Noctule bats are not known to migrate in the UK (AIEEM et al., 2009) but migrate large distances in Europe (Petit and Mayer, 1999). It is also unclear whether temperate bats are faithful to their swarming sites and if so this could result in regional meta populations of bats which could have impacts on disease flow or conservation should the swarming site be lost or disturbed (Rivers et al., 2005).

1.6 Tools for effective conservation

FCS can be used as a proxy for the quantitative description of the current state of a bat population. It requires the same fundamental measures as any quantitative approach for the conservation of bats, an appropriate description of the unit of space (the foraging areas/the roosts) and a unit of population at which to measure, model and predict population dynamics. However, it is not clear how we define a “healthy” population of bats. This could include size of population, reproductive output or access to feeding areas. It is inevitable that different species will require different conservation prescriptions and likely that the same species in different settings may also require different approaches to their conservation. A range of research and analytical tools are currently in use to address these problems.

1.6.1 Habitat analysis

Quantitative studies of habitat selection have been used in the design of conservation management guidelines for many bat species e.g. (Zeale et al., 2012, Smith and Racey, 2008, Russo et al., 2005, Russo et al., 2002, Razgour et al., 2011, Nicholls and A Racey, 2006, Flaquer et al., 2009, Dietz and Pir, 2009). The need for such an approach to protect bat populations has recently been acknowledged in the Agreement on the Conservation of Bats in Europe (EUROBATS) under Article 4 of the Bonn Convention and all species of bat and their roosts are legally protected in the UK, as is significant disturbance to their foraging habitats. However, several different methods are in use to define bats foraging area, and it is not clear which is best to clearly define a functional description of bat foraging behaviour as well as attempting to measure the relative importance of different habitats to bats. In addition to this, the value of the habitats in Britain is still largely unquantified (Walsh and Harris, 1996a). Further work needs to be done in this area.

When determining habitat use of bats, many studies use radio tracking as a source of data (Encarnacao et al., 2005, Bontadina et al., 2002). Compositional analysis, first described by Aebischer et al (1993), can then be used to address the question of the relative preferences bats may show for habitats (Zeale et al., 2012, Walsh and Harris, 1996b, Smith and Racey, 2008, Robinson and Stebbings, 1997, Kniowski and Gehrt, 2014). The analysis compares 'available habitat', often computed by using all the points gathered by radio-tracking and encompassing them into a minimum convex polygon (MCP) and then considers 'used habitat' often computed by the use of Kernel density methods. This involves creating a grid over the tracking area, calculating the density of points over the grid and then using the area that has 50% densest points as the 'core foraging area'. The used habitat is then compared to the available habitat proportions to see if it is used more of less than what is available and to rank habitat types in order of preference. Common aims are to determine whether a species uses habitats available to it at random, to rank habitats in order of relative use, to compare use by different groups of animals, e.g., males and females, to relate use to variables such as temperature and food abundance, or to examine the effects of habitat on movement and home range size (Walsh and Harris, 1996b). The Manly selection ratio (Manly et al., 2007) attempts to achieve a similar goal though using a different mathematical approach. Although effective tools in addressing overall habitat use, both analytic methods suffer similar drawbacks based on their common assumptions. Firstly, it should always be remembered that such techniques reveal relative preferences, but may miss descriptions of use e.g. within group variation of habitat use, or the contribution apparently dis-favoured areas make to the fitness of an animal or group. In addition, both methods make explicit assumptions that; (i) animals are independent and (ii) all animals are selecting habitat in the same way (Calenge, 2011). Therefore the emerging perception that bats show territoriality (Nicholls and Racey, 2006, Encarnacao et al., 2005), or the suggestion that juveniles may forage close to their mothers, would violate the strict assumption of independence. Similarly, it has also been suggested that bats show individual specialization in their habitat choice

(Cryan et al., 2012) resulting in a contrasting use of a number of different habitats by habitat specialists within a group. Therefore, analyses which suggest a single ‘mean’ population preference for a particular habitat across the range used by a number of individuals, may not correctly capture the most important habitats for the colony.

Another problem with movement data (either collected by radio tracking or global positioning systems) is that fixes are not independent samples which can violate assumptions of traditional habitat use analyses (Wakefield et al., 2009). Recent work has seen a shift from traditional compositional analysis to the use of alternative analysis of movement data which account for within group variation and individual specialisation and might include Generalised linear mixed effect modelling (Wakefield et al., 2015) or measuring individual niche factor analysis (Bolnick et al., 2002) and state space models (for review see Wakefield et al. (2009)). Many populations have been found to comprise specialist individuals who select specific habitat types regardless of their availability (Bolnick et al., 2002, Layman et al., 2015). R packages (R Core Team, 2016) now exist to aid in the analysis of individual specialisation and habitat use (Zaccarelli et al., 2013).

At present many conservation prescriptions for bats considers species as a whole without factoring in specialists within populations or considering that bats may adapt their habitat use in different areas. Further work needs to address this as we may need to consider protecting a wide variety of habitat types for a single species.

1.6.2 Social Network Analysis (SNA)

At present we have a poor understanding of many aspects of bat populations, either their demographic structures or social processes (the social interactions which occur over time), which makes prescribing effective and successful mitigation and conservation management plans difficult. This poor understanding also makes it difficult to predict the impacts of anthropogenic activities (August, 2012, Mickleburgh et al., 2002). One tool used to describe and then explore the social and demographic structures present in bat populations and communities is social network analysis (SNA) which produces networks of individuals connected by their social ties (Wey et al., 2008). An abstract social network is composed of two elements, nodes and edges. Bat researchers commonly describe nodes as individuals or roosts, while edges may represent connections or associations between individuals or movements between roosts (Johnson et al., 2013) . Social networks have local and global properties that can be understood by a set of metrics describing the connectedness, closeness, and centrality of nodes. These metrics allow us to define social groups , identify important individuals and their structural roles, understand flow of disease and information, and quantify anthropogenic effects on animals (Wey et al., 2008). In addition, they allow us to abstract and model societies and social processes. For example, SNA may highlight individuals in the population which are disproportionally important for group reproductive success (Cheney et al., 2016) which may aid in prescribing conservation measures, or alternatively, produce strong epidemiological consequences. SNA therefore can be a useful tool that enables societies to be characterized and compared (Pinter-Wollman et al., 2014). It may also enable relationships, and interactions, to be evaluated e.g. (Patriquin et al., 2010, Lusseau and Newman, 2004, Hamede et al., 2009, Cheney et al., 2016, Chaverri, 2010) be used to understand responses to environmental and anthropogenic disturbances (Wey et al., 2008) or predict the spread of disease within or between communities (Shirley and Rushton, 2005, Rushmore et al., 2013, Perkins et al., 2009, Ortiz-Pelaez et al., 2006). Once a Social network is mapped, the effects of removing key individuals or roosts from natural populations can be assessed (Silvis et al., 2015) and by doing so the effect on social systems to inform disease management or conservation management plans can be determined. Doing so physically in natural populations is not easily attainable due to both the difficulty in re-catching marked individuals or due to the protected status of European bats.

At present there have only been a few studies on the social networks of temperate bats (Kerth et al., 2011, Hale et al., 2012, August et al., 2014, Rigby, 2010) showing that bats form tight social groups often of highly related individuals. The roost networks described consist of roosts which probably vary in their eco-physical properties and individual bats exploit these in response to their changing physiological demands, weather, or the season (Kerth et al., 2011). It is assumed that all members of the community know about all network roosts and use social processes to help determine their roost each time they switch (Kerth et al., 2006). However, robust descriptions of communities' foraging areas or descriptions of the communities living in networks are lacking. Also, little has been done to model disease flow through a bat community or look specifically at conservation questions related to number of roosts needed for a community or to model dispersal between communities and their long term viability. Tools such as SNA will likely be used more in the future, in particular in relation to the conservation of bats, where predictions of management outcomes on the FCS of populations may be required. However, SNA does have a number of challenges associated with its use, including a demand for a substantial amount of descriptive data (e.g. requiring a number of repeat observations of a large number of individuals) which can be difficult to obtain from wild populations of bats as they are often hard to observe and difficult to catch (August, 2012). Therefore, it is possibly unsurprising that most previous studies of using SNA in temperate bats have studied their use of artificial roosts. There is therefore a significant gap in our understanding of bat social dynamics in their most common and important context; their natural state. There is thus a need to study natural roosts to inform accurate decision making and conservation plans.

1.7 Habitat preferences of temperate bats

Walsh and Harris (1996) used volunteers to undertake a significant structured acoustic survey (2700 hours) across the UK looking at general descriptions of foraging preferences of temerpate bats. They suggested that woodland edge, hedgerows, tree lines and water bodies were important foraging areas for bats but pointed out that these 'optimal' foraging areas are patchily distributed within the landscape. The strongest selection was shown for semi-natural broad leaved woodland, which they assumed to accommodate higher insect densities and a preferred low clutter flying zone. They also inferred a lack of preference for water bodies in intensively managed agricultural areas, which they speculated was due to higher levels of insecticide runoff from surrounding fields reducing the value of these feature in producing bat food. Their study also discovered that Myotis sp. and other small bats preferred to commute along linear elements and suggest this could be due to a higher level of prey availability, shelter from the wind and shelter from predation, also orientation within the landscape. However, their methodology created substantial biases in the representation of non-edge elements in the landscape and their methodology, whilst robust at drawing out national scale comparisons between broad land use classes would now not be considered as a robust method to describe fine-scale geographical comparisons in activity.

Before the studies of (Smith, 2000) little work had reported the habitat preferences of *Myotis* bats , and none had use more modern analytical quantitative approaches to describe habitat preference or the structural description of exploited land-uses. Smith studied habitat preference, range use and roosting ecology of Natterer's bats *Myotis natterei* on the border of England and Wales in a grassland/woodland landscape using radio tracking. He tracked 34 females and 9 male Natterer's bats over 2 summers and formulated a minimum convex polygon (MCP) which encompassed all the fixes of foraging bats which he assumed represented the colony home range and habitat data within this range was quantified. He then used compositional analysis and concluded that semi-natural broadleaved woodland and open water, particularly tree lined river corridors were preferred habitats and that coniferous plantations and arable land were avoided. He also observed bats foraging in the open in semi-improved grasslands rather than along field boundaries, particularly in fields which had sheep, cattle or horses or those that were due to be cut for hay or silage. This is in contrast to previous work which suggested Natterer's would require cover from predation (Walsh and Harris, 1996b). Smith's work did not consider that MCP's encompass large areas between fixes which were probably not used regularly by the bat. After Smith, Parsons and Jones (2003) used kernel methods to reduce the biases caused by the inclusion of un-utilised areas by measuring utilized habitat v available habitat of 50% and 80% utilization distributions calculated using the Kernel method which aimed to identify core areas of activity and reduce errors due to areas little used by the bats. This work reinforced the work by Smith 2001, that Natterer's preferred woodland, pasture and open water habitats for foraging and reinforced the suggestion that Natterer's display considerable fidelity to feeding areas. In addition, habitat selected by Natterer's bats differed significantly from that available around the roosts in Parson's (2003) work, indicating that certain habitats were selected for feeding. The home range was defined to be a 2km buffer radius from the most used roost of the individual bat, with the roost as a centre point and with all land types within this buffer presumed to be available to the bat. Although the distance used for the buffer was relevant (mean home range for the colony was estimated to be 1.9km from the roost), it is possible that each individual’s most used roost may not have been central to the home range in question, and certainly roosts have found not to be centrally located in feeding areas in other studies, with Natterer’s returning to their feeding area regardless of where they choose to roost (Smith, 2000, Mortimer, 2006). It is also possible that not all the habitat types within the buffer are available to an individual due to intraspecific competition or overlapping territories. This highlights one of the problems in habitat analysis, that of defining ‘available’ habitat for the subject species.

In addition to radio-tracking studies, some authors have used trapping and acoustic surveys to determine temperate bat habitat use e.g. (Kirkpatrick et al., 2017, Fuentes-Montemayor et al., 2013). Fuentes-Montemayor (2013) who studied bat activity and abundance in woodland patches and surrounding landscape in agricultural land in Scotland, agreed with others (Walsh and Harris, 1996b, Smith and Racey, 2008, Parsons and Jones, 2003) that woodland was important for both *Pipestrellus sp.* and *Myotis sp* with both genera preferring woodlands with grazing. Differences were found in regards to tree denisties with *Pipestrellus sp* abundance and activity levels lower in woodlands with high tree denisties, and *Myotis sp* abundance and activity levels higher, possibly reflecting *Myotis sp* (particularly *Myotis nattereri*) ability to glean invertebrates from vegetation (Swift and Racey, 2002, Siemers, 2001b, Siemers and Schnitzler, 2000, Melcón et al., 2007, Siemers, 2001a, Arlettaz, 1996). Fuentes-Montemayor also considered the surrounding landscape on bat activity levels in addition to the immediate roosting habitat where *Myotis sp* preferred landscapes with water within 1500m but a negative association with woodland proximity They also note that woodland in the surrounding landscape was primarily coniferous and suggest coniferous woodland might be lower quality habitat for bats. Kirkpatrick (2017) supports this idea with limited activity of *Pipestrellus* and *Myotis sp* within coniferous stands and higher activity levels on plantation edges, although it should be noted here that both Fuentes-Montemayor and Kirkpatrick used only trapping and acoustic surveys for their work with microphones mounted at a height of only 1m. It is possible that bats foraging at canopy level within the plantation (up to 20m in coniferous plantations) may have been under-recorded before flying at a lower height on emerging from the plantation to feed on lower vegetation increasing their detectability. Indeed Mortimer (2006), using radio-tracking, provided evidence of

Natterer's both roosting and foraging in conifer plantations. Even though most of the roosts used were artificial, this contradicts the idea that coniferous woodlands are of limited value to bats.

Although Fuentes-Montemayor (2013) reported that *Pipestrellus sp* were only marginally affected by surrounding landscape properties, the surrounding landscape properties were the most important variable for *Myotis sp* activity and they suggest that the wider landscape (within 4km) is more important for *Myotis sp* than smaller spatial scales due to their ability to fly long distances from their roosts to foraging areas. This highlights the need for conservation managers to take into account the surrounding landscape around roosts for more mobile bat species when prescribing conservation plans rather than focusing on roosting habitat.

To conclude this section on habitat preferences, most authors have noted a preference of woodland for temperate bats, particularly around their roosting areas. However, use of the broader landscape is not yet fully understood. Different methods of detection and assessing abundance (radio-tracking v acoustic and trapping) may result in biases for certain habitat types or areas where bats are easier to catch. No work has been done to combine the spatial and compositional descriptions of bat foraging or explore how these foraging selections are made or maintained. Further work is also required to determine how individual feeding areas/ site or habitats are selected e.g. Do dominant females select the optimum feeding areas which are then passed on through information transfer to their young? If individual feeding areas overlap with con-specifics are these bats related? Do bats display aggression to defend their feeding grounds?

1.8 Thesis Aims

This work aims to provide a focused and detailed study describing in the closest possible detail the size, shape and function of a community of bats. This will be undertaken on Natterer's bats *Myotis nattereri*, primarily because of epidemiological interest associated with the discovery of a new European lyssavirus (Bokeloh) in the species and an interest in how it might circulate or be maintained; but also because a thorough understanding of the social and spatial dynamics of Natterer's bats is central to their effective management particularly when they come into conflict with humans.

Both direct and indirect methods (capture, observation and ringing / genetic) will be used, to assess how the spatial and social dynamics of Natterer's bats in natural and anthropogenic settings affects disease transmission, the conservation of the Natterer's bat and, by inference, other temperate bat species.

The thesis will present data collected from six populations of Natterer bats in England at their summer roosts and in the surrounding area. Specific aims are outlined below.

1. To investigate spatial foraging patterns and habitat preferences of *M.nattereri* (Chapter 2);
    a. Does M.natteeri exhibit forgaing fidelity over days/months/years?
    b. Do *M.nattereri* show individual specialisation in their habitat choice?
    c. Does *M.nattereri* conform to optimal foraging theory?
    d. Does *M.nattereri* have a preferred habitat type?
2. To investigate whether current methods of radio tracking bats are sufficient to infer an individual bats use of space over time (chapter 3);
    a. Is a whole night of data needed to capture an individual's foraging strategy and habitats used by an individual?
    b. Is one whole night of radio tracking data enough to describe an individual's foraging strategy?
3. To determine the genetic population structure of Natterer's bats in Northern England (Chapter 4);
    a. Are the sampled communities in Northern England distinct, are there regional differences or are they all part of a meta community?
    b. Do the sampled communities have viable populations of Natterer's bats?
    c. How much gene flow is there between the different sites?
    d. Are the Natterer's bats sampled in Northern England genetically similar to the Natterer's bats in Northern Europe or a distinct sub species?
4. To investigate the social structure of Natterer's bat populations at Wallington, Northumberland in natural roosts and Wytham Woods, Oxfordshire in artificial roosts and then model conservation scenarios and disease spread within and between populations (Chapter 5)
    a. Is there evidence of society within the two sampled communites?

    b. Are there differences between the natural and artificial roost networks in terms of information flow and social cohesion?
    c. Do related bats roost together more often than unrelated bats?
    d. How robust are the roost networks to potential roost loss?
    e. How resilient are the social networks at both sites to disease outbreaks?

5. To discuss our findings in relation to disease management and conservation policy.

Collectively this thesis aims to characterise a natural population of Natterer’s bats for the first time and identify which unit of space is necessary to protect to enable them to achieve long term population viability. It also aims to understand how disease might spread within or between populations of bats both in natural and anthropogenic settings. Both of these broad aims could then be applied to alternative species or other EID’s not only to conserve bats, our global biodiversity and the many ecosystem services they provide but also predict and prevent further outbreaks of EID’s and as a consequence protect public health.

Chapter 2. Foraging fidelity and individual specialisation in a temperate bat Myotis nattereri

2.1 Introduction

Globally bat populations have declined considerably over the last century largely due to habitat loss, hunting, or disease (Mickleburgh et al., 2002) with recovery predicted to be slow (Jones et al., 2003). Determining habitat types required for effective conservation of bats can be difficult compared to terrestrial mammals of similar size, due to their ability to fly, which enables them to travel long distances, allowing use of a wide range of resources across a wider variety of habitats. In summer bat roosts and individual foraging areas can be kilometres apart permitting them to assemble widely dispersed resources they require for survival and reproduction from across extensive landscapes (Rainho and Palmeirim, 2011).

However, flight and the large areas it allows bats to exploit, can expose them to nightly contact with a range of anthropogenic threats such as development (inc. residential, commercial and infrastructure) or sources of mortality such as wind-turbines (Zimmerling and Francis, 2016, Rydell et al., 2010, Horn et al., 2008, Cryan and Barclay, 2009, Baerwald et al., 2008, Arnett et al., 2016) and roads (Lesiński, 2008, Kitzes and Merenlender, 2014, Berthinussen and Altringham, 2012, Altringham and Kerth, 2016), which can also affect roosts, reduce or degrade available foraging habitat or interfere with the connectivity between habitats (Mickleburgh et al., 2002). Although the conservation of roost sites is important for the maintenance of bat populations e.g. (Kapfer et al., 2008), roost provision or the mitigation of roost loss is already common in the management of bat populations. In addition to this many species use a network of alternative roosts and cope with the loss of a few (Rhodes et al., 2006, Johnson et al., 2012, Silvis et al., 2015, August et al., 2014) . Conversely, bats appear loyal to their foraging sites despite roost loss (Silvis et al., 2015). Hence, the conservation of foraging sites/areas (rather than just habitats) may be as important as roost sites in the conservation of the species, although rarely considered. Further, it is not clear that there are tools to confidently identify the most important foraging areas in the landscape (rather than particular habitat types). This is of some concern especially as determining priorities for policy led management of habitats requires a robust understanding.

It is not clear whether site fidelity in bats (Kapfer et al., 2008, Hillen et al., 2010) is specific to temperate forest bats or a more general behaviour found in other species or why it is exhibited. Foraging animals are expected to make choices in order to minimise energy expenditure whilst maximising energy intake, therefore site fidelity may be a way of saving energy in the decision of which habitat to use next (Arthur et al., 2015) e.g. a previously beneficial habitat may have a higher probability of providing sufficient resources than an unexplored new habitat (Call et al., 2008). More recently the idea of bats exhibiting site fidelity has been extended to suggest the territorial defence of feeding areas through the use of social calls (Luo et al., 2017, Gadziola et al., 2012). Territorial defence of food resources is thought to minimize feeding competition (Wrangham, 1979), maximize feeding efficiency through familiarity with the distribution of food resources (Pusey et al., 1997, Hillen et al., 2009) or directly impact reproductive success (Thompson et al., 2007). Site fidelity or territoriality could have significant impacts on conservation and management objectives as well as the tools and measures used to describe bats use of space.

Studies to support bat conservation may need to shift from general descriptions of habitat preferences and the assumptions that as long as these are accessible FCS can be maintained at specific sites, to considering other aspects of behaviour. Bats like many other mammals may have individual preferences (Araújo et al., 2011, Cryan et al., 2012) and this may interact with the emerging study of bat sociality, such that dominant females have preferential access to the best resources (Honer et al., 2010), maternal inheritance of foraging sites occurs, or bats exhibit territoriality or personality (Patrick and Weimerskirch, 2014) which affects their access to foraging sites. Sexual segregation may also occur with females only utilising more favourable habitats to the exclusion of males who may be found more abundantly in marginal habitats (Angell et al., 2013). Alternatively, foraging variation may occur due to 'individual specialisation', such that individuals differ significantly in their prey or habitat utilisation, independent of class-effects (Bolnick et al., 2002).

Individual specialisation has important evolutionary (Bolnick et al., 2002), ecological and management implications as interactions between individuals and environment are not uniform across a landscape (Thiemann et al., 2011). If bats do exhibit individuality in their habitat choice, then there may not be a preferred habitat per species of bat as is often referred to in the literature e.g. (Catto et al., 1996, Robinson and Stebbings, 1997, Arlettaz, 1999, Russo et al., 2002) but instead a mosaic of habitats may be critical to their conservation. Therefore, the influence individual expressions of behaviour may have on our understanding of species requirements should be accounted for in measures of resource use and considered in conservation planning and management.

Here the aim is to produce authoritative and robust descriptions of where individual bats forage and the habitats they use. It is also to explore the fidelity individual bats show in their foraging choices and the possibility that Natterer's bats in this study show individual specialisation in their foraging habits. The consequences of the observed behaviour and the implications for conservation management are then discussed.

2.2 Materials and Methods

Natterer's bats from two sites in Northern England were radio tracked and continuous contact with each bat for full nightly foraging trips was achieved, from dusk to dawn. Foraging site fidelity of individual bats was measured by the degree of spatial overlap of data collected at varying intervals (days, months and years) to determine the potential data collected over a single night has to represent a more substantive and general description of individual behaviour.

2.2.1 Study sites

Natterer's bats *(Myotis nattereri)* were caught at a roost in a church at Low Catton, East Yorkshire, UK (53.98° N, 0.93° W: altitude 15m) between May and August in 2003 and from woodlands on the Wallington Estate, Northumberland, UK (55.15° N, 1.96° W: altitude 160-200m) between May- September of 2013, 2014 and 2015 (Supplementary section 1). Low Catton is a very small rural village in a mixed agricultural landscape typical of lowland England (mainly arable though with some pasture and small scattered parcels of woodland). Wallington Estate is a patchwork of parkland, lakes and woodland, within a mixed pastoral landscape including arable and woodland components as well as open moorland; typical of an upland agricultural landscape in England.

2.2.2 Bat capture and radio-tracking

Bats were captured on an approximately weekly schedule at roosts using a static hand net or harp trap attached to an extendable pole. The frequent roost switching behaviour of the bats at Wallington also required their capture from free flight, using mist nets or harp traps, and an acoustic lure. All disturbances at roosts, as well as the capture, handling and marking of bats were carried out under licence from Natural England. Captured bats were described noting; sex, age (adult/juvenile), reproductive condition (pregnant or lactating; by palpation of the abdomen), forearm length (0.1mm) weight (to 0.1g) and any existing mark. Unmarked bats were marked with a unique ring (2.9mm Alloy; BCT, England). Selected bats were fitted with radio transmitters (Pip AG317; Biotrack, Essex, England) attached to the skin between the scapulae using a hypoallergenic dermal adhesive. A small patch of fur was trimmed at the point of attachment to ensure reliable adhesion. A maximum of two bats were marked with transmitters in one tracking session to ensure that a complete and continuous night of data could be collected from all deployed tags within the short duration of their batteries (7-10days). Forecasts of inclement weather were considered to ensure the timing of tag deployment could always yield robust data.

Individual bats were usually radio-tracked by single workers using the close approach method (White and Garrott, 1990) using a Telonics TR-4 receiver (Telonics, Arizona, USA) attached to three-element flexible Yagi antenna or vehicle mounted omni-directional antennae (Kenward, 2001). Bats were tracked from their emergence from roosts until their return, with their locations recorded at 10 minute intervals. 10 minute intervals were selected to prevent temporal correlation between consecutive fixes whilst still recording regular movement patterns (Kenward, 2001).

Due to the difficulty in obtaining triangulations from fast flying animals (Mackie and Racey, 2007) especially within undulating terrain such as that of our field site at Wallington, approximate locations of bats were inferred using the strength, direction and variability of signal and recorded onto a large-scale map as polygonal observations, excluding areas outside the signal range, encompassing an area containing the bat's true location, to be later used in determining their foraging sites. Although this resulted in polygons rather than tradition points obtained from triangulation, points would have had a large error polygon associated with them due to the difficulty of communicating between observers when attempting triangulation within difficult landscapes. Tracking was undertaken in two phases. In the first, priority was given to simply maintaining contact with the bat and establishing its general foraging strategy (i.e. commuting routes, approximate location of its favoured foraging patches and the schedule of behaviours); trackers commonly stayed closer to access routes and vehicles to ensure a rapid response to unexpected bat movement; though this often resulted in more uncertain estimates of location. In the second phase, once it was felt that the general strategy used by that animal was known, trackers planned to optimise the quality of data by anticipating bat behaviour, and committing themselves to closer approaches on foot where this was possible. However, the intention was always to ensure continual contact with the bat throughout its period of activity. Data was only collected from tracking in the second phase of work for every bat and a complete night of data was only considered to have been recorded if continual contact with the bat was maintained and the night was not unexpectedly interrupted by inclement weather (not uncommon at these locations). For most bats a single complete night of data was collected during the second phase, although some were re-tracked at varying intervals either within a summer season or between years. The minimum time between tracking periods was one night. Phase 1 tracking often took 2-3 nights (for bats travelling long-distances quickly or those traversing difficult to cross barriers in the landscape such as rivers), and at least one additional night of effort to secure a complete, continuous and uninterrupted night of foraging data. A number of different trackers were used to establish general foraging strategies (phase 1 tracking), especially where a number of bats were tagged simultaneously. However, the same tracker (SM at Wallington, JA at Low Catton) undertook all data collection during phase 2 to ensure a consistency in the inference of location and the confidence of its recording. Nights of tracking data with continuous gaps of more than 20 minutes were excluded from the analysis. All roost positions were recorded using a handheld GPS device. Observations were digitised using ArcGIS (v.10.2; ESRI). Subsequent analysis was carried out in R (v. 2.1).

Core foraging patches representing areas of high use were described for each complete bat-night and used to inform spatial analyses. Observations were transformed into clouds of points by placing a single spatially randomised point into each polygonal description of location. Cores were then identified using a non-parametric clustering approach (clusthr function in adehabitatHR: 95% inclusion). This was repeated 5 times and the resulting cores were then intersected to find the areas common to all 5 iterations by sorting and overlaying each (gIntersection function in rgeos). These core patches used by bats on any given night represent locations that include the centres of high-density use and the area most exploited for foraging. They also represent the statistical unit in all subsequent analyses.

2.2.3 Data analysis

2.2.4 Exploring habitat use

Core patches for each individual were intersected with a land cover layer, LCM2007; (Morton, 2011) to describe the composition of the habitats most used by the bats. To quantify individual specialization using proportion data, Roughgarden's index (1972) was used which compares within-individual components of niche width (WIC) to the total niche width exhibited by a population (TNW). Calculations of WIC and TNW were carried out in R (RinSp using the 'PSicalc' function). For each individual, the proportional similarity index (PS_i) was calculated following Fodrie et al. (2015) based on habitat deviations in an individual's habitat use relative to population level, average habitat use (approaching 1 = more generalist; approaching 0 = more specialised). Mean PS_i among individuals was used to determine the average amount of specialisation in habitat use across all bats in this study and individuals were deemed to be specialists if their PS_i value was below the mean population Ps_i value. Monte Carlo permutations were run with 999 replicates to test whether observed WIC/TNW and PS_i values differed significantly from a random distribution of values subsampled from the population.

2.2.5 Foraging fidelity

The potential of a single complete night of radio-tracking data to act as a proxy for the long-term description of an individual's foraging strategy was explored. Pairwise comparisons were carried out for all bats including those tracked only once and those tracked repeatedly, either within the calendar year, or between years to describe the similarity of foraging strategies across differing intervals. The core area for each bat was compared between nights and the proportion of area overlap was calculated for each (using the gIntersection function in the rgeos package). This was compared to the proportion of overlap with every other bat core foraging site. Multiple-response permutation procedure (function MRPP, in the vegan package) analyses were conducted using the Euclidian distance metric and 1,000 iterations with individual proportion overlap as the response variable. To explore whether individual behaviour measured at varying intervals was repeatable foraging distance (from roost to the most heavily used core) was compared to foraging schedule (time from emergence to arrival at the most heavily used core) across all of the data with observations of the same bat compared to observations of different bats (using the rpt function in package rptR, with 1000 permutations) with individual distance and foraging schedules as the response variables. To determine whether individuals had similar foraging strategies and adhered to the optimal foraging theory, the relationship between distance travelled to the most used foraging patch was assessed along with the speed at which they travelled there using a linear model (lm) with Distance as the response variable and Speed and Site (Wallington/Low Catton) as the predictors.

2.3 Results

Thirty-four individual bats were tracked for at least one full night, 17 from Wallington and 17 from Low Catton (Supplementary 1). Six bats were tracked over repeated years, and 24 bats were tracked twice during the same year (Table 3). This produced 29 nights of data available for pairwise comparisons of foraging site fidelity at Wallington and 32 nights at Low Catton. Each night had an average of 32 observations (range 16-46) at an average of 20 different foraging patches (range 8-44) resulting in a mean foraging period of 5.3 hours (tracking usually represented most, if not all, of the period of dark at 55° N in summer (Table 4). At Wallington the majority of bats foraged at more than one patch (nine/17) although the proportion was slightly lower at Low

Catton (six/17). Some bats foraged at up to four discrete patches. Very few bats were recorded night roosting, and then only occasionally and for a few minutes at a time. As all 10 minute observations could describe foraging activity we assume for the purposes of this study that all observations carry the same weight.

Table 3. Number of individual bats tracked by site and year used to estimate foraging habitat overlap at two temporal scales, within-year (multiple foraging trips by one bat in one year) and between-year (one bat over multiple years).

Site	Year	Bats tracked	
		Fidelity level	
		Within-year	Between-year
Low Catton	2003	17	No
Wallington	2013	4	Yes (4)
	2014	2	Yes (4)
	2015	1	Yes (2)

Between-year fidelity (Yes or No) indicates for which years multi-year animals were tracked with the number of individuals in each of those years in brackets.

Table 4 Mean Radio tracking observations, locations and time spent foraging of Natterer's bats tracked at Low Catton (LC) and Wallington (W)

	Site	Mean	Range
Observations	LC	30	16-46
	W	34	25-41
Locations	LC	25	12-44
	W	14	8-23
Foraging time (hours)	LC	5.0	2.66-7.66
	W	5.66	4.16-6.83

In order to describe the range of strategies used by individuals at both sites, movement dynamics were explored. Of most interest here is a relationship between the distance between the roost of departure and the most used patch as well as the speed between the two, which represent independent choices (Figure 1). Some bats choose to travel long distances and some bats choose to travel quickly but there does not appear to be a consistent relationship between the two (R^2 = 0.217, F(3, 30)=4.062, p=0.95) which suggests the hypothesis that bats exhibit optimal foraging strategy can be rejected.

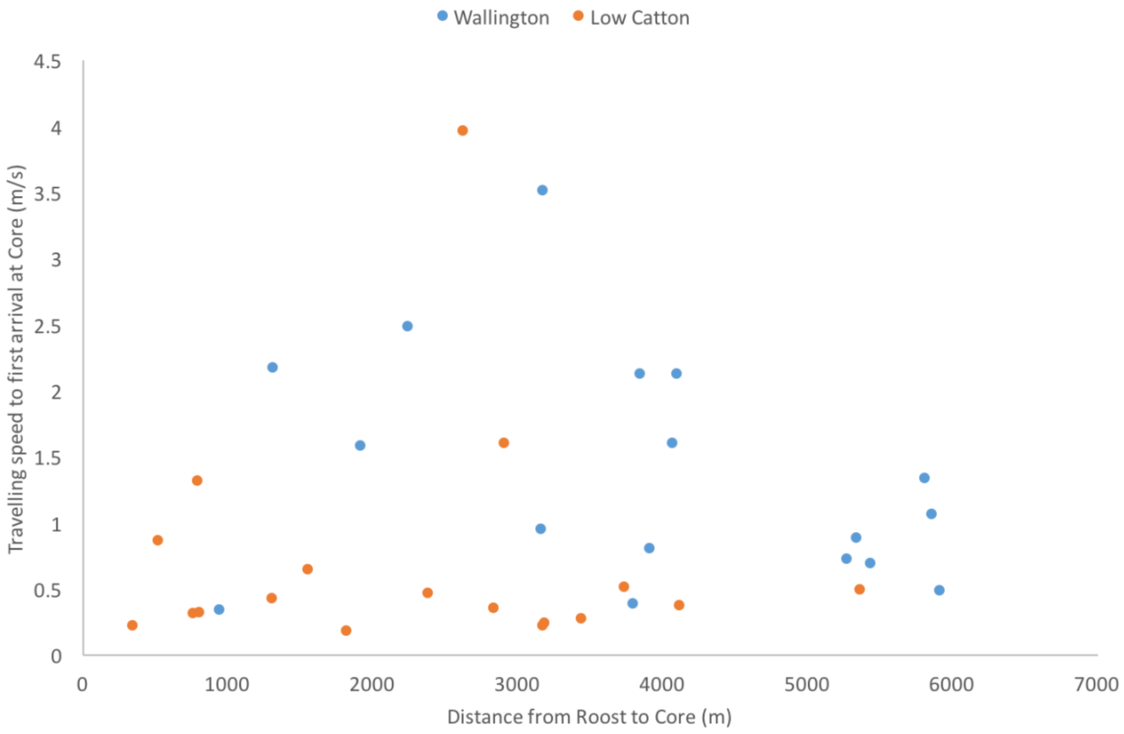

Figure 1 Distance from roost to core foraging site and speed for bats tracked at Wallington and Low Catton

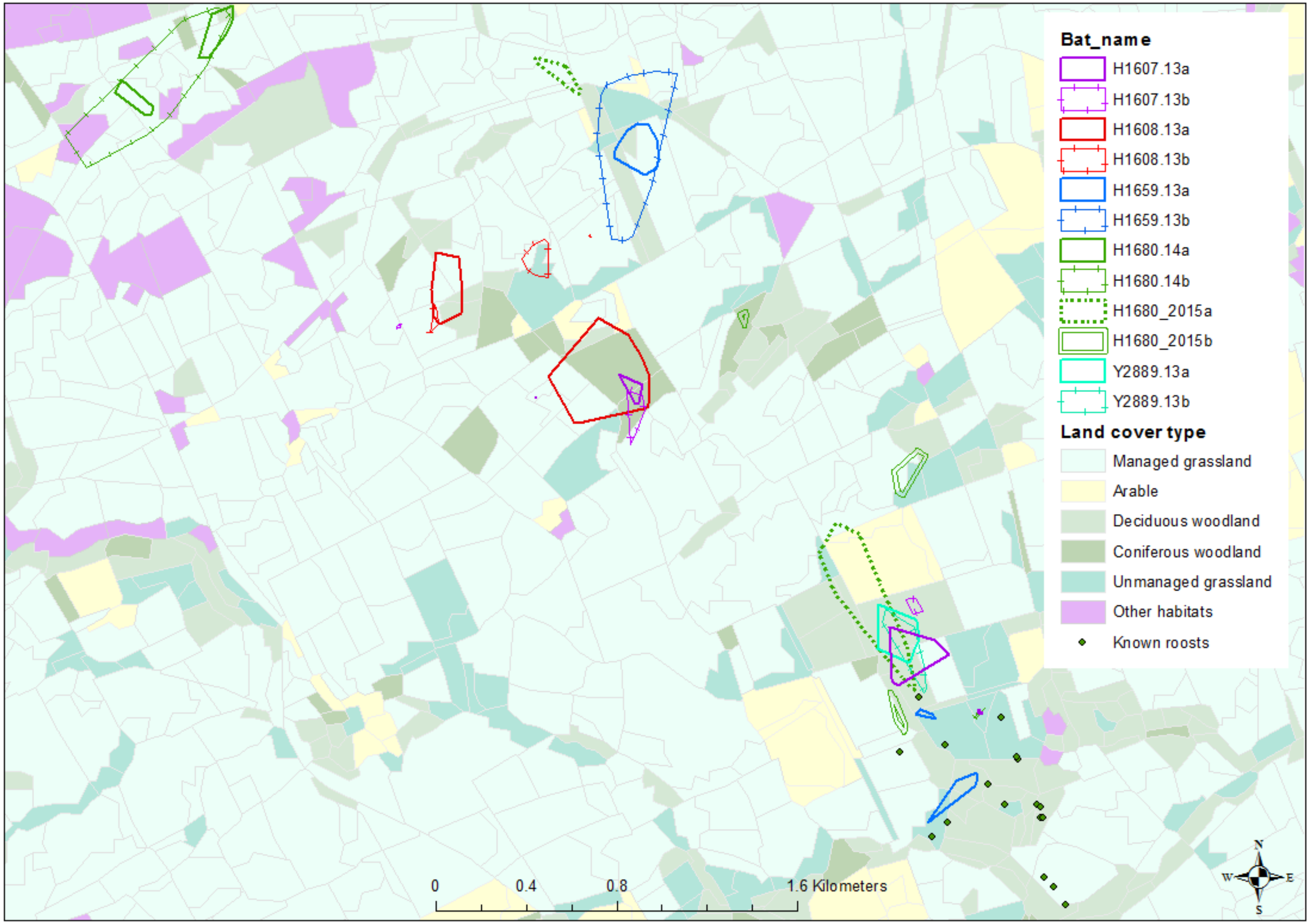

Figure 2 Foraging cores of bats tracked repeatedly at Wallington within the same year with 2007 Land cover data and roost locations

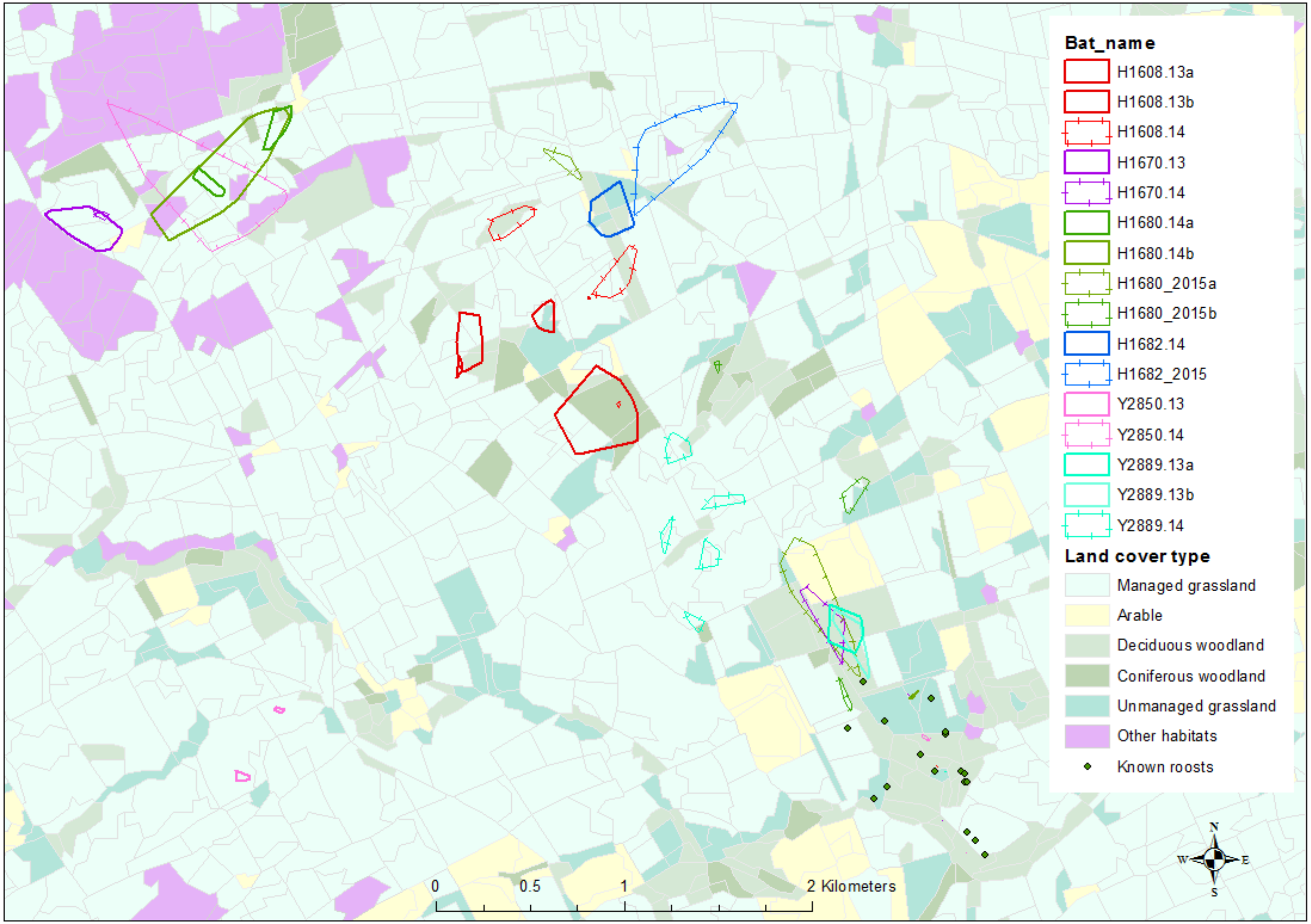

Figure 3 Foraging cores of bats tracked repeatedly at Wallington between years with 2007 Land cover data and roost locations

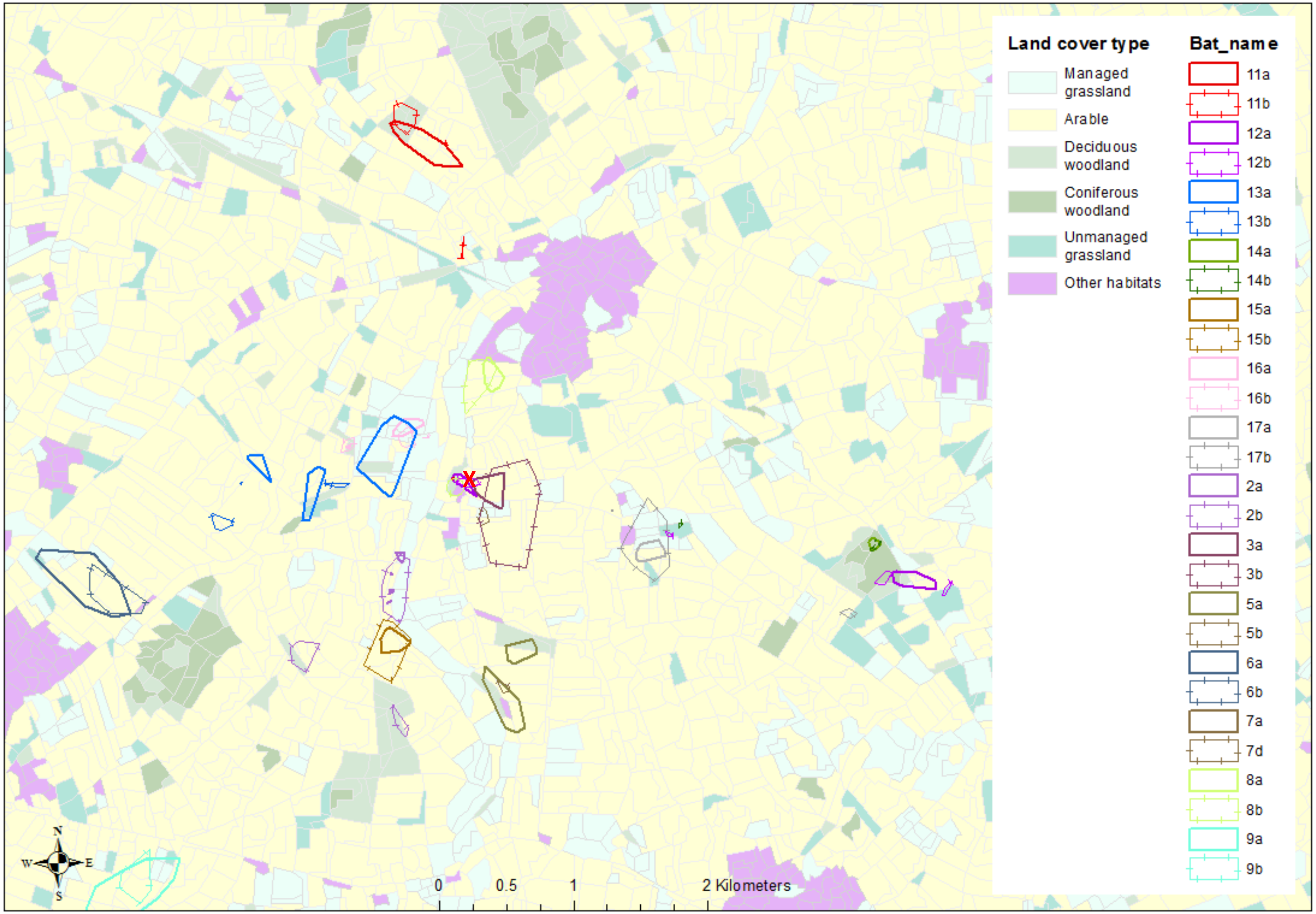

Figure 4 Foraging cores of bats tracked repeatedly at Low Catton within the same year with 2007 Land cover data, Church roost is marked with an X symbol

2.3.1 Foraging site fidelity

At both Wallington and Low Catton, a greater degree of foraging site overlap was observed within than between individuals tracked multiple times during the same year (Figure 2,Figure 4,Figure 5; post hoc Tukey tests P<0.01, P=0.02; Low Catton within individuals mean 0.92 ± 0.02(range 0.66- 1); Wallington within individuals mean 0.92 ± 0.06 (range 0.57- 0.9); Low Catton between individuals mean 0.29 ± 0.01 (range 0-1); Wallington between individuals mean 0.62 ± 0.02 (range 0.25- 0.99)).

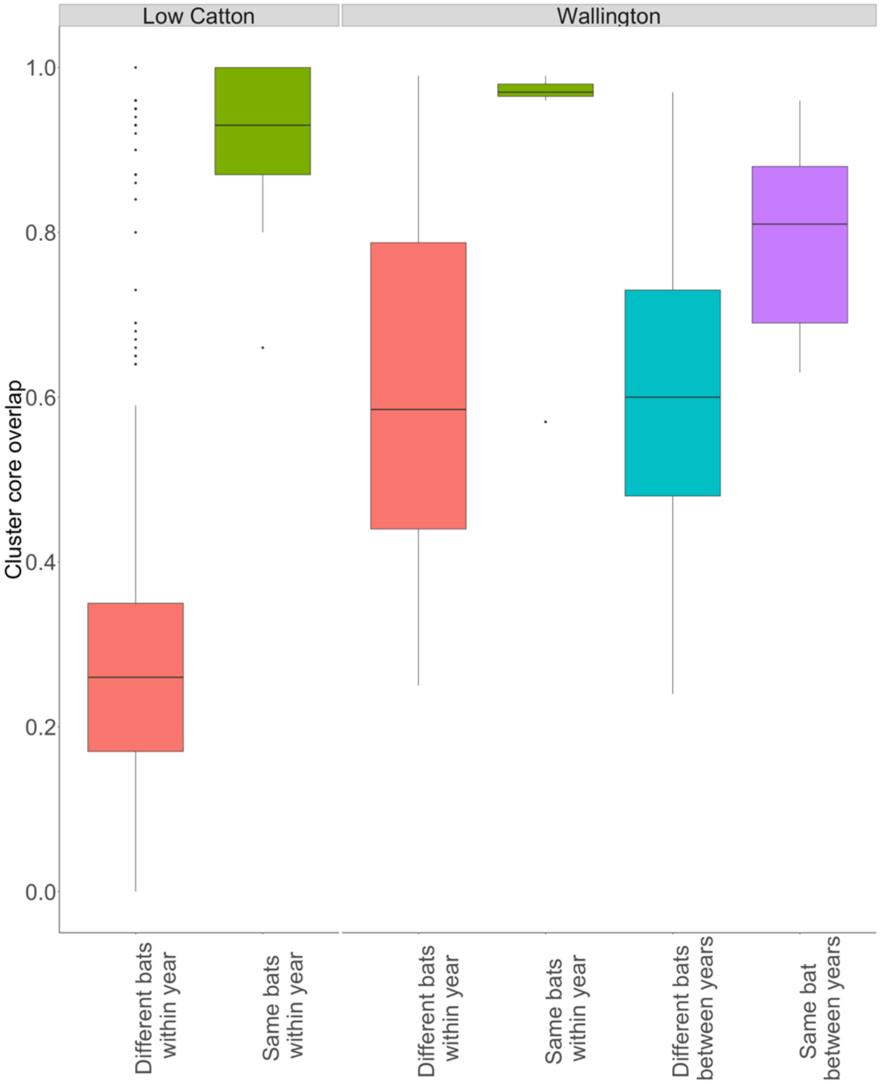

Figure 5 The proportion of overlap of 95% cluster areas for the same bat and different bats within and between years at Wallington and Low Catton. Scores close to 1 indicate 100% overlap of cluster areas whilst scores close to zero indicate independent use of space

There was also a higher degree of spatial overlap within individuals tracked over different years than between individuals at Wallington (Figure 3, Figure 5; post hoc Tukey tests P=0.02; within individuals mean 0.80 ± 0.03 (range 0.63- 0.96); between individuals mean 0.61 ± 0.01 (range 0.24- 0.97)). Individual bats tracked repeatedly also showed significantly more consistency in their foraging strategy (distance to most used foraging core and time taken to travel to most used foraging core) at both sites than pairwise comparisons with other individuals (Table 5).

Table 5 Repeatability score (± s.e.) of foraging characteristics of bats tracked at Wallington and Low Catton calculated from 'rptR' R package. * indicate repeatability scores significantly higher than random permutations

	Wallington	Low Catton
Distance to most used foraging core	0.979* ± 0.011	0.948* ± 0.027
Time to most used foraging core	0.698* ± 0.132	0.57* ± 0.149

2.3.2 Individual specialisation and habitat use

Overall managed grassland was the most utilised habitat at Wallington and arable at Low Catton (Figure 6). However, there was variability in the habitats used by individuals at both sites, for example the proportion of managed grassland within an individual's core foraging patches at Wallington ranged from 10% to 98%. The population level measure of individual specialisation (WIC/TNW) suggested that, on average, individual bats used a moderate fraction of the total population niche space (0.63 Wallington, 0.69 Low Catton). Monte Carlo analyses of individual versus population niche variation suggested that bats were more specialised than would be expected by chance at both sites ($P < 0.001$ Wallington, $P<0.001$ Low Catton) and the with some individual bats showing very different use of habitat types to others. At Wallington six bats can be contrasted (H1607, H1608, H1609, H1679, H1680, Y2889) which either combine unusual habitats or exploit habitats differently to most of the group (Figure 6) and have PS_i values below the population mean. At Low Catton the majority of individuals had large proportions of arable in their core foraging patches (which was the most dominant habitat type in the area) except for four individuals who showed unique habitat use specialisation (Y2049, Y2106, U8558, U3941) and had large areas of unmanaged grassland, managed grassland, coniferous woodland and a mixture of habitat types respectively (Figure 6).

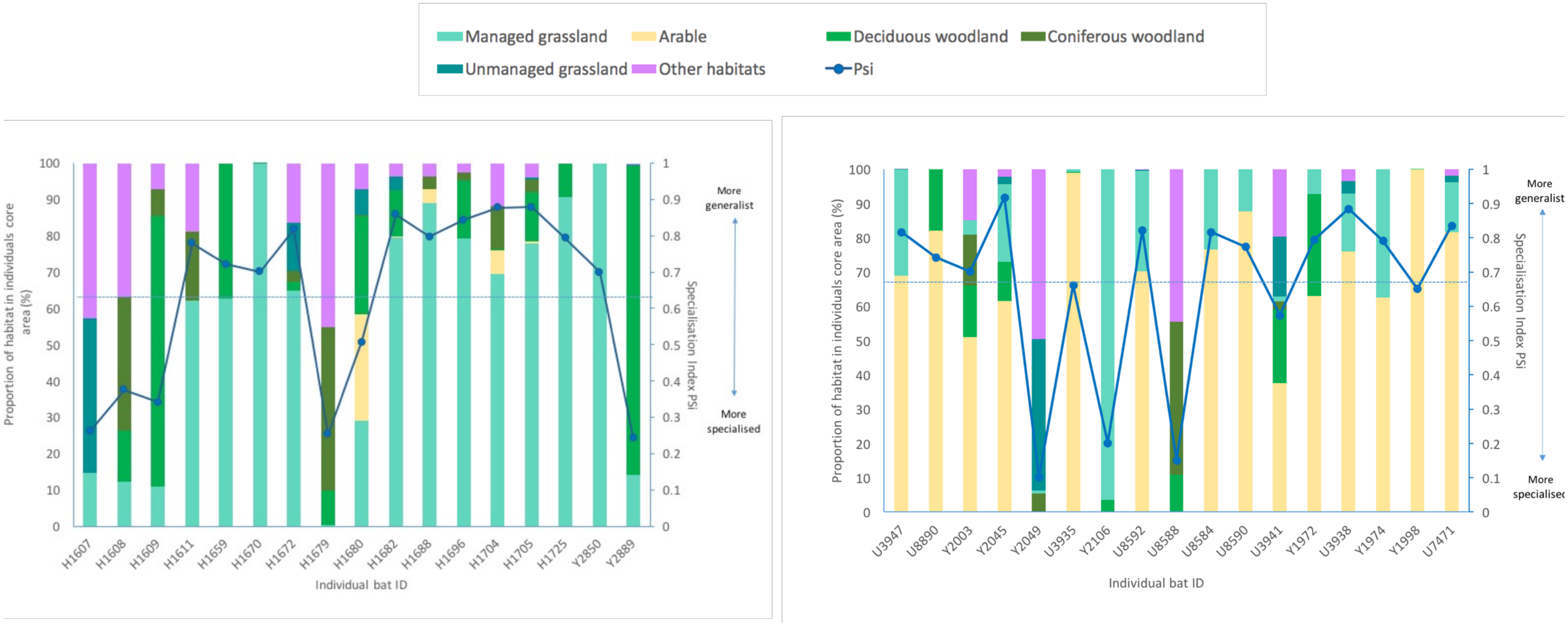

Figure 6 Individual variation in habitat use between bats tracked at Wallington(left) and Low Catton (right). Each individual (x-axis) is represented by a vertical bar, subdivided by the proportion of recordings in each habitat type in relation to the individual's total cluster core area and the specialization index PSi (blue dots; 0 = more specialized; 1 = more generalist) along with the mean colony Psi (dashed line).

2.4 Discussion

2.4.1 Foraging fidelity

Individual foraging fidelity has previously been reported or suggested for a few species of temperate bat (Kapfer et al., 2008, Hillen et al., 2009, Kerth et al., 2001a, Siemers et al., 1999) albeit with variable strength of evidence. Here, in common with Kerth et al. 2001, statistically robust quantitative evidence is provided of the re-use of the same locations and habitats by individuals, this fidelity appears consistent across a range of intervals (months and years) and extends beyond the immediate period of re-tracking defined by the life of currently available radio-transmitters (typically < 10 days for small and medium sized species). Fidelity also appears stable, despite contrasting seasonal contexts (Hillen et al., 2010). This is potentially good news for bat conservation. Firstly, a reliable understanding of the foraging requirements of bats requiring management or conservation is easier to plan for, and once understood, the long life of bats suggests that such areas are likely to remain valuable; validating any policy investment in protecting areas of the landscape. Secondly there is considerable value to scientists in knowing that descriptions of individual foraging strategies in adults represent long-lived behaviours, as this helps the integration of foraging choices into spatially explicit studies of the population dynamics of bats in anthropogenic landscapes.

2.4.2 Territoriality

The behaviour of individuals repeatedly exploiting specific foraging locations whilst also showing individual specialisation in their habitat use is consistent with the behaviour of a territorial species. Here it is shown that not only do some individuals show striking patch fidelity, but all appear to avoid overlap with other tracked bats which is generally considered to reflect territoriality (Chaverri et al., 2007).

This is not the first time that the apparent fidelity individual bats may show to their foraging sites suggests territoriality (Rydell, 1986, Chaverri et al., 2007, Rossiter et al., 2002), though the difficulties in studying individual bats have limited authors' confidence in describing this behaviour. It has most often been suggested for a number of bat species who have a strong connection with the underlying landscape, and therefore presumably keen to defend a static resource i.e. gleaners or those predating weak flying prey (Reyes-Garcia et al., 2008, Gerell and Lundberg, 1985). The suggestion of territoriality has often been associated with studies of Daubenton's bats foraging over still water e.g. (Kapfer et al., 2008). For Daubenton's bat, this speculation is supported by their use of a very specific and easy to map landscape feature as well as workers' subsequent confidence in the interpretation of spatial location from radio-tracking, along with the ability to directly observe foraging behaviour of some individuals. This includes the repetitive use of space and the presence of social interactions (social calls and chasing). Finally, it should be noted that the sociality of temperate bats is also becoming widely recognised (Silvis et al., 2015, Silvis et al., 2014c, Siemers and Kerth, 2006, Patriquin et al., 2010, Park et al., 1998, Kerth et al., 2011, Kashima et al., 2013, Johnson et al., 2013, Gerell and Lundberg, 1985, Entwistle et al., 2000, August et al., 2014, August, 2012, Altringham and Senior, 2005) and the identification of social hierarchies within groups is anticipated (Fleischmann and Kerth, 2014). Whilst social dominance might only be expressed in the choice of roost (Fleischmann and Kerth, 2014) or the position within the roosting group, it could also be expressed in other key activity bats undertake e.g. foraging; with dominant individuals choosing and maintaining their preferred locations whilst sub-dominant bats may be left with less productive foraging choices. If social dominance does occur, understanding its effects will be important in the management or conservation of bats where pup production is affected by the quality of the foraging resource (Arlettaz et al., 2017). In the future workers may need to identify and protect the most productive areas of a landscape and distinguish this from the location of preferred habitats, or those habitats used by inefficient or submissive individuals. It should be noted that only approximately half of each social group under study were tracked and there is no evidence of the functional definition of territory defence i.e. observations of antagonistic behaviour between individuals at potential territory sites.

2.4.3 Behavioural flexibility and individuality

This study suggests that individual bats can demonstrate distinct and divergent foraging choices compared to their peers, specifically in their choices of foraging habitats. In addition, this flexibility in strategy seems to have extended into groups adopting site-specific responses (or traditions) to the contrasting compositions and configurations of the habitats at our two study sites, e.g. the large use of managed grassland at Wallington compared to the use of Arable at Low Catton. Further, our demonstration of foraging site fidelity suggests that these individual differences are likely to be long-lived and may represent either differences in personality or tradition in wildlife species, examples of which are now reported for bats (Cryan et al., 2012) as well as other wildlife (Patrick and Weimerskirch, 2014, Knudsen et al., 2010, Araújo et al., 2011, Robertson et al., 2014). Alternatively, individual habitat choice may just represent individual preference across the broad menu offered by these mixed landscapes, and it should be noted that usually, Natterer's bat is thought to be proficient at both aerial hawking and gleaning (Swift and Racey, 2002, Siemers and Schnitzler, 2000) and is therefore able to develop almost unconstrained preferences in prey. However, further work is needed in this area for firm conclusions. These findings of individual specialisation may also be due to artefacts of the methodology used to defining foraging areas. For example, generalist individuals may have had larger errors around their foraging areas than specialists due to less certain radio tracking ellipses which may have resulted in the apparent use of more 'open ground' habitats. This could be tested by assessing whether the degree of specialisation was linked to home range size in further work.

The idea that Natterer's may show individual specialisation in their habitat choice and that this varies by site, highlights the need to protect a range of habitats types rather than presuming a preferred habitat type for the species globally or nationally. However to ensure that the level of diversity in habitat choice was not a methodological artefact, further work could include comparing measures of habitat diversity within individual foraging cores to that in the available habitat.

2.4.4 Implications for conservation and management

Effective decision-making for conservation and management relies on strong evidence. Here it is shown that individual bats forage at specific core locations, to which they repeatedly return. Whilst it is easy to simply collate the land-cover or habitat types represented within each core into simplistic descriptions of group behaviour, this data suggests that individuals differ greatly and show specialisation in their foraging choices, and that for some common habitats, the choice of core location is unique and important and may not be replaceable at another location, even if the habitat appears the same. Thus studies designed to inform conservation and management of temperate bats should attempt to maximize the number of individuals from which movement data is sought, but ensure that data represent a coherent and meaningful measure of behaviour. Further, it is not clear that any of the specific foraging strategies observed at one site (such as commuting style or habitat choices) could transfer to the second, and that our observed behaviours are sensitive to the characters of their landscapes, or the traditions of their communities.

Our finding that the strong foraging site fidelity by Natterer’s bats and our speculation that this may represent some type or territorial behaviour may off-set some of the effort required to collect a single full night of radio-tracking data, as a single full night of data may produce a long-lived and robust description of that bat’s behaviour; justifying the additional effort in field-work hours. It may therefore be a better solution in tracking studies to track many individuals for a single night rather than a few individuals for a longer time frame (Wakefield et al., 2015). However it raises the concern that many of the popular analytical methods frequently used by bat workers such as Compositional analysis (Aebischer et al., 1993) and selection ratios (Manly et al., 2007) may be inappropriate. Designing conservation strategies for the rapidly changing environment might then advocate protecting a mosaic of habitats to preserve the habitat specialisms of many individuals rather than choosing a single preferred habitat for a territorial bat which may only suit dominant few individuals.

Chapter 3. Data requirements for effective descriptions of space use by temperate bats

3.1 Introduction

Robust knowledge of bat foraging requirements and strategies for decision-making is necessary to support legislation. All European species (in Europe) are protected under the EC habitats directive 92/43/EEC, for which the concept of maintaining Favourable Conservation Status (FCS) is central to the directive. FCS summarises three requirements for a species to be considered as achieving and maintaining FCS (JNCC 2002); Long term population viability, maintenance of the natural range and sufficiently large enough habitat for the species. Similarly, in the US, thirteen species are protected under the Endangered Species Act of 1973 (e.g. *Myotis sodalis, Leptonycteris nivalis).* The act provides protection for the species listed but also aims to protect the ecosystems and habitats on which the protected species depend. Ensuring that protections are proportionate and fit-for-purpose (two common prerequisites of regulatory tools) requires evidence of the resources bats use. However, acquiring this evidence is problematic for animals that assemble their diverse resource requirements from across an extended and unbounded landscape.

Foraging data on large mammals is typically collected with the use of GPS tracking tags (Call et al., 2008, Arthur et al., 2015, Chilvers, 2008) however, no UK bat is considered to be able to bear the weight of current GPS technology, and conventional VHF radio tracking is often the only option to infer the use of space by individuals. Radio tracking bats involves making regular recordings of their location during their nocturnal period of activity, which is costly in terms of equipment and time. It appears that this task is often difficult (contact with bats being lost) and data collected may be incomplete or biased. In addition, little evidence is available to help researchers decide how many nights of tracking data are needed to generalise about the use of space for an individual, and as most bat foraging data come from individuals sampled in only one season or year, or under one set of environmental conditions it is unclear as to how much inference can be placed on this empirical data.

Here the evidence requirements to describe the foraging strategy of individual bats are examined. Data is presented from a radio-tracking study of the Natterer's bat *Myotis nattereri* collected at two sites in Northern England. The aim was to determine if a single night of good quality data could be deemed representative of the individual bats typical behaviour. Natterer's bats caught at two sites in N England were radio tracked and continuous contact was maintained with the bat and radio tracker from dusk to dawn. Previous radio-tracking studies were reviewed to determine the proportion of a night bats are typically tracked for in quantitative studies. Inferences were then compared between whole night and incomplete descriptions of space use by subsampling whole night's data. The aim was to produce authoritative and robust descriptions of where individual bats forage. As temperate bats are known to have a single foraging bout per night, leaving the roost around dusk and returning pre-dawn (Smith and Racey, 2008) whereas others have a bi-modal strategy (Maier, 1992), the appropriate time scale for bat foraging strategies is explored and it is hypothesised that unless a whole night's worth of data is collected, misleading inference might be drawn.

3.2 Materials and Methods

Radio tracking and creation of core foraging cores for individual bats was carried out at Wallington and Low Catton (2.3.1) as described in section 2.3.

3.2.1 Data analysis

Cores produced by whole night and continuous descriptions of nightly foraging (COMPLETE) were compared to cores derived from sub-sampled data to explore the validity of using more limited sequences of observations to make inference about foraging behaviour and strategy. Two different sub-sampling methods were used to produce our analytical treatments, both replicating the mean proportion of the night described by tracking data in previously published reports (i.e. 50%; S1) and used to infer behaviour. Data were either restricted to the continuous and complete first half of the night (BLOCK) or a random selection of observations from across the night (RANDOM). These methods were intended to simulate the common occurrence of following a bat from a roost but loosing contact with it partway through a night, and intermittent contact with a bat producing gaps in records. To ensure sample sizes remained the same between comparisons and determine whether representative sampling throughout the night is better than focusing the same amount on effort on the first half of the night, BLOCK was compared to RANDOM. To assess whether an increase in the number of observations per night affected the perceived use of space by bats, COMPLETE data was compared to RANDOM. Each night of radio tracking was treated as an independent variable for the purposes of data analysis with our treatments represented by data representing COMPLETE, BLOCK or RANDOM foraging data.

3.2.2 Exploring the use of subsampled data

A series of spatial and aspatial comparisons between treatments typical of the metrics often used in reports of bat foraging behaviour were undertaken, and the potential of using incomplete data to describe the foraging strategy of an individual bat was explored. For each individual bat-night this included the number of cores identified and quantitative spatial measures: distance to roost (Euclidian distance between roost of departure and centroid of the most distant core), total distance travelled per night (based on trajectory) and area of cores (sum of cores per night). R (R Core Team, 2016) was used to perform all statistical analyses. The lme4 package (Bates et al. 2014) was used to perform multiple linear mixed effects models of the relationship between treatments and various spatial measures. As responses, distance to roost, total distance travelled and size of core area were modelled. As fixed effects, treatment (COMPLETE/BLOCK/RANDOM) and site (Low Catton/Wallington) were included. As random effects, intercepts were included for site and bat ID. Post hoc contrasts between treatments were carried out (lsmeans in lsmeans package)**.** Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality and *P*-values were obtained by likelihood ratio tests of the full model against a model without the effect in question.

How the use of these alternative descriptions of core foraging sites might affect the habitat associations inferred for these bats was also investigated. Cluster core areas for each individual and treatment were intersected with a land cover layer, LCM2007; (Morton, 2011) to describe the composition of the habitats most used by the bats and pairwise quantitative comparisons were undertaken using compositional analysis (using the compana function in the adehaabitatHR package) between all three sampling regimes compared to available habitat. For this purpose, available habitat was defined by combining all polygon observations for each community and creating a minimum convex polygon (MCP) of 100%. The MCP was overlaid with the LCM2007 land cover map and the proportions of different habitat categories within the MCP were calculated. All habitat mapping was carried out in ARCGIS v. 10.1.

3.3 Results

A summary of bats caught and radio tracking details can be seen in section 2.4.

3.3.1 Subsampled data

First inspection of mapped cores indicated substantial qualitative differences between treatments illustrated by examples of individual bats from both sites (Figure 7).

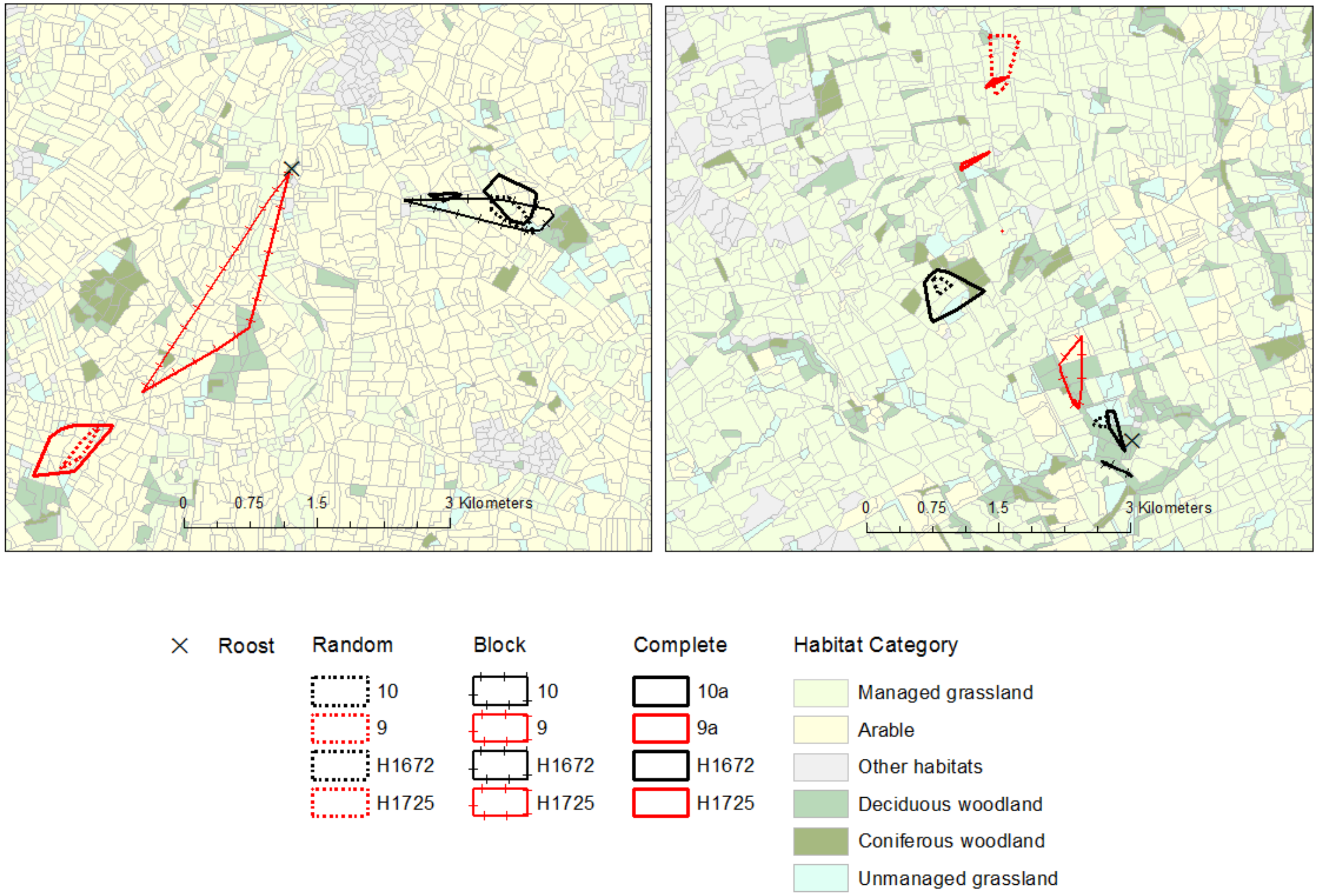

Figure 7 Examples of core areas of two bats tracked at Low Catton (left) and two at Wallington (right) with the land cover data.

The number, size and location of cores produced in the sub-sampled treatments differ obviously, both between themselves (BLOCK v RANDOM), suggesting that whole night sampling produces more accurate descriptions of space use than tracking for only the first half, and the RANDOM subsample also differs considerably from the COMPLETE treatment, suggesting that increasing the number of observations per night is also important. The differences in the size and location of cores consequentially produces striking qualitative differences in the habitats assumed to be exploited by individual bats and thus considered important to them.

Quantitative comparison of distance to roost, total distance travelled and core area size show that all were subject to significant differences between treatments, with one or both sub-sampled treatments seen to significantly over- or under-estimate these important metrics, or descriptions of their variance, compared to the COMPLETE data Figure 8; details of each of these results are given below. Similarly, the a-spatial analysis comparing the area of habitats used also showed differences in the ranking of habitat type and the significance of their pairwise comparisons. Very different inference might be drawn if sub-sampled data were relied upon.

3.3.2 Distance from roost to foraging core

Bats at Wallington flew significantly further from their roosts than those at Low Catton, (Wallington μ = 3.32Km, Low Catton μ= 2.09Km, Chi sq. (1) = 0.48, P=0.03). The model only considering the sampling method accounted for 15% of the variance, though this increased to 66% when including additional significant factors identified in the best-fit model (site and bat ID, ANOVA $P>0.01$).

Whole night v first half of night

There was no difference in the distance bats travelled to their foraging core from their roost at Low Catton between BLOCK and RANDOM treatments (Figure 8; $p<0.05$). At Wallington the BLOCK treatment significantly underestimated the total nightly distance travelled when compared RANDOM (Figure 8, $p>0.01$), suggesting that tracking for a whole night is important to understand the distances bats fly.

Increase in sample size

Increasing sample size to 100% (COMPLETE) compared to 50% (RANDOM) had no impact on the perceived distance bats may travel to their foraging cores at either Low Catton or Wallington (Figure 8; p<0.05).

Table 6 Mean (± SD) foraging trip characteristics of Natterer's bats tracked at Wallington and Low Catton under three different sampling regimes

	Wallington			**Low Catton**		
	COMPLETE (*n*=17)	BLOCK (*n*=17)	RANDOM (*n*=17)	COMPLETE (*n*=18)	BLOCK (*n*=18)	RANDOM (*n*=18)
Distance to roost (Km)	1.97 (0.18-4.74)	3.32 (0.84-5.40)	3.21 (0.53-5.38)	1.72 (0.01-4.65)	2.09 (0.32-5.33)	2.04 (0.28-4.69)
Total distance travelled (Km)	14.24 (5.80-20.79)	5.87 (2.11-8.94)	10.13 (4.17-16.28)	11.69 (6.38-17.19)	4.93 (0.88-7.78)	7.94 (2.59-15.07)
Area of cores (Km$_2$)	0.10 (>.00-0.46)	0.29 (>.00-4.23)	0.33 (0.001-5.65)	0.07 (0.004-0.43)	0.11 (>.00-0.91)	0.08 (>.00-0.68)

3.3.3 Total nightly distance travelled

Whole night v first half of night

BLOCK data resulted in approximately 40% shorter estimates of total distance travelled than RANDOM at both sites (P > 0.01). Here restricting the observations to only the first half of the night (BLOCK) can be seen to almost halve the trajectory flown by the bat (Table 6) implying that bats flew further in the second half of the night.

Increase in sample size

The RANDOM data significantly underestimated the total nightly distance travelled compared to COMPLETE data by approximately 30% (Figure 8:C; P > 0.01) at both sites. The model which best fit the total nightly distance travelled data included the subsampling type and site as fixed effects and bat ID as a random effect. Although bat ID explained around 50% of the variance of the data, the effect of subsampling the data still had a significant impact on estimating the total distance travelled by bats per night (ANOVA, F (2,68) = 101.6, P > 0.01).

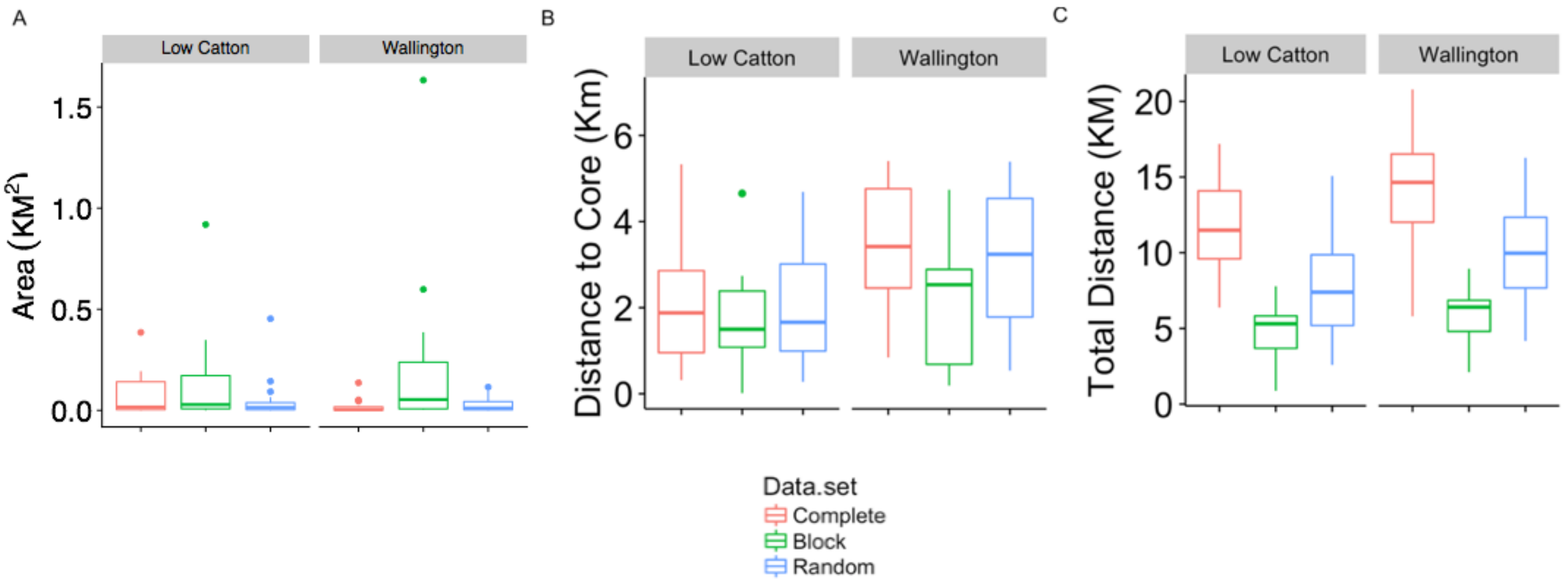

Figure 8 Spatial metrics measured from the first complete night of tracking data from bats tracked at Wallington and Low Catton for three different data sets. (A) Mean (±s.e) Cluster Core foraging site sizes (KM2), (B) Mean (±s.e) Distance (m) from Roost to core foraging site, (C) Mean (±s.e) total nightly distance travelled (KM)

3.3.4 Core Area Size

Whole night v first half of night

At Low Catton, treatment did not have significant effects on the mean area of foraging cores used by bats although at Wallington, RANDOM samples produced slightly larger (12%) cores than BLOCK ($p > 0.03$).

Increase in sample size

Increasing the sample size from 50% (RANDOM) to 100% (COMPLETE) had no effect on the core foraging area of bats at Low Catton or Wallington.

Overall bats did appear to respond to the contrasting landscapes at each site with slightly larger cores at Wallington (Wallington mean=0.7Km_2, Low Catton mean = 0.6Km_2). It should also be noted that these differences in the behaviour of the bats at the two sites interacted with subsampling to produce strong differences in the variance of core area seen at each site. At both sites BLOCK subsampling always increased the variance of the core area, this effect is particularly strong at Low Catton. The RANDOM subsampling produced contrasting results at the sites; greatly reducing the variance of core foraging site at Low Catton, whilst increasing the mean and variance of the cores at Wallington. The model which best described the differences in cluster core foraging site included a fixed effect of Site (Wallington/Low Catton) and a random effect of Bat ID.

3.3.5 Habitat composition

Compositional analysis using Wilk's Lambda revealed bats did not select the habitats exploited in their core areas at random. Wilk's lamda tests if there are differences between group means for a particular combination of dependent variables (habitat proportions). It measures the percent variance in habitat proportions not explained by differences in levels of the independent variable (between individual bats). It ranges from 0-1 and a value of zero means that all variance is explained by the independent variable and individuals are not selecting habitat at random. For all treatments at Wallington, bats preferred foraging in specific habitats (COMPLETE: Wilks Λ=0.058, P<0.01, BLOCK: Wilks ʎ=0.046, P>0.01, RANDOM Wilks ʎ=0.003, P>0.01). Similarly, at Low Catton the selection of preferred habitats was evident in all treatments except RANDOM (COMPLETE: Wilks ʎ=0.34, P =0.01, BLOCK: Wilks ʎ=0.139, P>0.01, RANDOM: Wilks ʎ=0.53, P=0.17).

Table 7 Habitat ranks from compositional analysis, comparing proportional use of habitat in colony home areas (100% MCP) vs. home-range cores (95% clusters) from both Wallington and Low Catton. A habitat preceding a ">" symbol was preferred to that immediately following the symbol and where ">>>" shows a significant selection between adjacent ranked habitats

Site	Data set	Habitat Ranking
Low Catton (*n*=17)	Complete	Arable > Managed grassland > Deciduous woodland > Other habitats > Unmanaged grassland > Coniferous woodland
	Block	Arable > Deciduous woodland > Managed grassland > Coniferous woodland > Unmanaged grassland > Other habitats
	Random	Arable > Other habitats > Managed grassland > Deciduous woodland > Coniferous woodland > Unmanaged grassland
Wallington (*n*=17)	Complete	Other habitats > Managed grassland > Coniferous woodland > Deciduous woodland >> Unmanaged grassland > Arable
	Block	Deciduous woodland > Managed grassland > Coniferous woodland > Unmanaged grassland >> Arable > Other habitats
	Random	Coniferous woodland > Other habitats > Deciduous woodland > Managed grassland >> Unmanaged grassland > Arable

Whole night v first half of night

Subsampling changed the rank order of habitat preference at each site (Table 7). At Wallington, the composition of habitats in the first half of the night (BLOCK) differed significantly from that in the second half (RANDOM (Wilks ʎ=0.232 P> 0.01)), e.g. Deciduous woodland was identified as the preferred habitat with the BLOCK data whilst Coniferous woodland was preferred with the RANDOM data. Similarly, at Low Catton there were significant differences in the habitat composition of core areas when comparing treatments RANDOM v BLOCK (Wilks= 0.33, p= 0.002), e.g. the order of habitat use varied although the preferred habitat (Arable) was the same.

Increase in sample size

Whole night data (COMPLETE) produced significantly different habitat compositions to that of the reduced sample data (RANDOM) at both Wallington (Wilks ʌ=0.232 P> 0.01)and Low Catton (Wilks ʌ= 0.26, P=0.002). Differences include a complete difference in rank order of preference for habitats (Table 7).

3.4 Discussion

3.4.1 Is a full night of data needed?

Misrepresentation of the true foraging strategy used by Natterer's bats is likely to occur when less than a full night of tracking data is obtained. Our comparisons show sub-sampled descriptions of individual foraging strategies produce bias or substantial error likely to confound robust inference including obvious qualitative differences in the maps of foraging cores produced for each bat and differences in a range of quantitative measures for communities (distance to roost, total distance flown, area of core). However, we should note here that due to the method used of sub-sampling the original data, sample sizes of the original polygonal descriptions of space use between COMPLETE and the other two treatments were not equal which may have influenced the resulting metrics used as response variables. Both RANDOM and BLOCK only included 50% of the original polygonal descriptions of the use of space which would have a direct impact on the measurement of apparent distance flown. However, here an attempt was being made to compare whole night data collection with part night data collection which would also have unequal sample sizes, so for this purpose the comparisons between COMPLETE and RANDOM should hold true.

Although total distance flow is rarely used in radio tracking studies involving bats except see Russo (2002), area of core and distance from roost to foraging site are commonly commented on (e.g. (Rossiter et al., 2002, Safi et al., 2007, Waters et al., 1999, Hillen et al., 2009), despite trackers not maintaining regular contact with individual bats in these studies. Our results support evidence provided by Nielson (Nielson et al., 2009) ,that important habitat types, areas of the landscape or foraging route choices may be missed if less than a full nights worth of data is collected. These foraging choices could be vital to the survival of the individual bat as they may represent areas of high prey density, areas of reliable access to prey or routes which enable the bat to avoid danger. The presence of bias was not affected by our contrasting study sites which differed in both landscape composition and configuration, as the misrepresentation of foraging habitats and metrics inferring use of space in our sub-sampled data were apparent at both sites. Therefore it is suggested that basic science, as well as applied decision-making reliant on robust descriptions of bat behaviour use only functionally complete data to describe bat movement; including trade-offs they may make in attending one or multiple foraging patches and the routes they use to get there. The ideal description of a foraging strategy should be derived from continuous tracking across a whole night, as this is an instantaneous, coherent and complete expression of the trade-offs bats make in order to survive and support reproduction (Lundy et al., 2012).

Metrics to inform decision-making include the distances bats fly. In Britain the Bat Conservation Trust promotes consideration of Core Sustenance Zones (CSZ) for impact assessment, expressed for a given species as the area surrounding the roost based on species specific average-maximum foraging radius e.g.(Froidevaux et al.) . Similarly, distance to forage sites significantly influences the quantitative predictions of preferred or exploitable resources of bats and should be specifically considered (Rainho and Palmeirim, 2011). A meaningful description of the distances bats fly, either across a foraging radius (as nominal central point foragers) or a flight trajectory, can only be achieved using a complete record of night-time behaviour. Sub-samples of a complete night-time flight trajectory may significantly underestimate both of these metrics and fail to capture some patches exploited by bats.

Another common application of bat foraging strategy data is in the description of preferred habitats and prescriptions for conservation. Here, the comparison between COMPLETE and sub-sampled tracking data show important qualitative differences in rank preferences and it is suggested that the use of tracking data representing substantially less than a complete night may produce potentially erroneous decision-making.

3.4.2 Inference from poorly sampled bat foraging strategies

The majority of studies of the movement and foraging in temperate bats have made inference from data representing less than a complete night of radio-tracking (S1).

Although reports usually indicate that a threshold number of fixes have been accumulated per individual to permit analysis e.g. (Bontadina et al., 2002, Gonsalves et al., 2013), this just implies that the size of home range is no longer increasing and although this may capture the area used by a bat it does not accurately describe the length of time an individual spends in each different habitat type within that area. In addition, few studies explicitly attempt or achieve coverage of a complete night and fixes are often constrained to particular periods (i.e. post-emergence from the roost), or easy to access locations or accumulated over a number of nights e.g. (Robinson and Stebbings, 1997, Kerth et al., 2001a, Rossiter et al., 2002, Safi et al., 2007, Russo et al., 2002). There is a clear balance to be made in reducing the error associated with recording bat locations and losing the fix on the bat: a short interval restricts the trackers ability to move and follow the bat resulting in missing data and low quality fixes due to the distance between recorder and constantly moving bat. This is especially problematic in difficult landscapes (i.e. undulating topography or extensive attenuating land-cover such as forest) where failing to stay close to a bat will result in its complete loss. Even with GPS tracking on larger animals detection frequency needs to be determined to capture the ecological processes of interest (Ryan et al., 2004) and a decision needs to made as to how often to record information. Frequency of detection in movement studies has been well discussed particularly in the context of GPS and home range estimation where discrepancies were shown e.g.(Girard et al., 2002). In addition, track length and speed estimates can be compromised by the frequency with which GPS tracks are sampled (Ryan et al., 2004) and estimated movement distance decreased exponentially as sampling frequency increased in a further GPS study (Mills et al., 2006). Whilst more difficult to obtain than *ad-hoc* fixes recorded at locations and times convenient to the tracker, an empirical approach can be systematised to produce data which supports robust inference. The sampling methodology here was in line with a number of other studies that suggest ten or fifteen minute sampling interval is optimal e.g. (Gonsalves et al., 2013).

Ad-hoc sampling of bat behaviour might permit robust inference if both bat movement and sampling were truly random. However individual behaviour and use of space appears well structured in Natterer's bats. Lundy showed the repeated sequential use of differing habitats while this data consistently describes a single foraging bout per night including visits to as many as four, distinct foraging patches consistently over time, behavior that has also been seen in other species (Araújo et al., 2011). In addition, the common practice of tracking bats from only the first part of the night from emergence from roost before losing touch, imposes a spatial structure to the periods of observation (close to roosts) and loss of data (further from roosts), further prejudicing strong inference derived from ad-hoc observations.

3.4.3 Single night as an experimental unit

A complete single night of data per individual appears to be the correct scale of natural experimental and statistical unit for the study of bat foraging behaviour. The behaviour of some bats (i.e. those without a distinct commuting behaviour and with a diffuse foraging style), foiled our attempts to reliably define comparative periods within a complete night, i.e. discrete commuting or foraging behaviour, resulting in the conclusion that the night could not be split into compartments easily and a full night should represent the lowest common denominator in the study of foraging strategies. It should also be noted that many of the bats in this study appeared to delay their progress towards their main foraging core (Figure 1), briefly exploiting opportunities to forage whilst moving, or alternatively, sampling an alternative habitat before progressing onto their principle foraging location. This sequential use of different habitats in different locations by Natterer's bats has also been reported in other work (Lundy et al., 2012). Assuming that individual's most heavily used core represents their most valuable foraging patch, any delay in reaching it, assumes an extended strategy and not one attempting to maximize the immediate rate of feeding. The sequence or progression of choices bats appear to make about foraging location across a single night become especially evident where distinct patches are well separated in the landscape and movement between them is rapid, as observed in this study. Here the drivers or consequences of these choices are not explored, but it is simply established that trade-offs in choice appear to be common for individuals, and that the temporal scale of this behaviour is at least a complete night. Whilst it is possible that trade-offs are made over longer timescales, this is unlikely in this study. Firstly, most of the bats tracked are reproductive female temperate bats foraging in an unpredictable climate at the cold edge of their range (8-10g, pregnant or lactating). The combination of substantial energetic demand, with the inability to carry much excess weight and a marginal energy budget associated with very unreliable access to prey (driven by frequent poor weather), argues against any longer term strategy reliant on stored reserves or compensatory foraging over successive nights. Secondly, strategies using trade-offs across longer timescales seem unlikely to result in the degree of foraging site fidelity observed here across days, months and years.

This study also illustrates why considering foraging across periods shorter than a complete night may also be inappropriate. Our total distance flown metric reaffirms our observation that sub-sampling a complete and continuous night of data yields a severe misrepresentation of the actual behaviour; both sub-sampled treatments consistently and significantly underestimate the distance flown compared to COMPLETE data. However, a comparison of the BLOCK treatment with COMPLETE describes an interesting additional phenomenon. At both sites, bats appear to have flown substantially greater distances in the second half of the night. This could be interpreted to represent one of two possible behaviours; either this is patch switching as a compensatory response to unsatisfactory early evening foraging, or this represents a bout of facultative alternative patch evaluation facilitated by better than expected early evening feeding. In either case, this supports the assumption that bats integrate decision-making across a single complete night-time period, continually calculating the trade-off in benefits from their attendance at one location against the potential at another.

3.4.4 Implications for conservation and management

Effective decision-making for conservation and management relies on strong evidence. Here the requirements to produce strong and unbiased descriptions of bat behaviour are starting to emerge; specifically, that quantifying their foraging strategies requires a full complete night of movement data. Thus studies designed to inform conservation and management of temperate bats should attempt to maximize the number of individuals from which movement data is sought, but ensure that data represent a coherent and meaningful measure of behaviour. Further, it is not clear that any of the specific foraging strategies observed at one site (such as commuting style or habitat choices) could transfer to the second, and that our observed behaviours are sensitive to the characters of their landscapes, or the traditions of their communities.

Chapter 4. Population genetic structure of Natterer's bats across Northern England

4.1 Introduction

The maintenance of genetic diversity in populations is highly important in conservation biology as it increases the ability of a species to adapt to environmental change (Lande, 1988). The general agreement is that populations with low genetic diversity have lower long term viability than populations of the same species with high diversity (Lacy, 1997). Gene flow helps maintains genetic diversity and is enabled by connectivity between populations across a species' distribution. It is therefore important for the persistence of those populations in the landscape and it also enables the recolonisation of available habitats where species have previously become extinct (Fischer and Lindenmayer, 2007). Understanding levels of gene flow and mixing between populations is therefore vital to enable accurate predictions of population viability for conservation management.

Mammals living in closed social groups such as many bat species e.g. (Kerth et al., 2000, Veith et al., 2004) are potentially more vulnerable to genetic and demographic effects than other species, largely due to natal philopatry and limited mixing of individuals between populations (Kerth et al., 2000). In addition to this, they face many anthropogenic threats which can lead to fragmentation, isolation and sub-division of population processes that can cause bottlenecks and declines in genetic diversity (Frankham et al., 2002) however, as they are relatively mobile and have long dispersal distances compared to more sedentary mammals, this may provide a potential buffer against fragmentation.

Bats are known to play ecologically pivotal roles within both natural and agricultural systems (Burland and Wilmer, 2001, Cleveland et al., 2006) however they also raise human concerns where they act as vectors of disease (Streicker et al., 2012a, Leroy et al., 2005, Li et al., 2005, Poel et al., 2006, Schneeberger and Voigt, 2016, Plowright et al., 2016, Johnson and Smith, 2017). Given bats importance in these two areas there is a need for a broad understanding of bat ecology and behaviour to inform conservation and disease management. Compared to species richness, bats have been underrepresented in behavioural ecology (Kerth et al., 2000), likely due to their features such as flight and nocturnality, making them difficult to study using traditional methods. Important aspects of behaviour and ecology therefore remain unknown for many species, reducing our ability to protect them effectively (Hutson et al., 2001) or predict disease transmission.

Molecular genetic techniques provide an invaluable resource for obtaining information about important bat species (Burland and Wilmer, 2001). Recently, they have been used to describe population structure (Rivers et al., 2005, Pritchard et al., 2000, Moussy et al., 2015, Entwistle et al., 2000, Burland et al., 1999, Atterby et al., 2010), dispersal rates (Meyer et al., 2009, Kerth et al., 2002a, Moussy et al., 2013, Vonhof et al., 2008, Kerth and Petit, 2005), mating systems (Storz et al., 2001, Heckel and Von Helversen, 2003, Rivers et al., 2005, Furmankiewicz and Altringham, 2007, Burland et al., 2001, Kerth and Morf, 2004) and distributions (Mayer and Von Helversen, 2001, Ruedi and Castella, 2003, Hulva et al., 2010, Ngamprasertwong et al., 2008) enabling researchers to assess the distribution and habitat utilisation of different species which should allow an improvement in broad scale conservation. They have also been used to further our understanding about how disease might move around the landscape (e.g. (Atterby et al., 2010, Halczok et al., 2017) which increases the ability of researchers to implement disease management strategies of those of both human and wildlife concern e.g. (Peel et al., 2016, Wilder et al., 2015).

Bats carry various diseases including Lyssavirus causing Rabies in humans (Smith et al., 2011, Rupprecht et al., 2011, Picard-Meyer et al., 2013, Nolden et al., 2014, Freuling et al., 2011). There are a few strains of lyssavirus, however, Bokeloh bat lyssavirus (BBLV) has only been found in European Natterer's bats *M. nattereri* (Picard-Meyer et al., 2013, Müller et al., 2007, Freuling et al., 2011) which suggests the species could be a reservoir for the virus. Bats infected with lyssaviruses pose a low but significant threat to both human health (Nolden et al., 2014) and the maintenance of viable populations of bats. Due to the widespread distribution of Natterer's bats in Europe, an understanding of the gene flow between populations could be utilised to target disease control interventions or to identify low-risk regions for special conservation measures (Vonhof et al., 2016).

The Natterer’s bat is a non-migratory, temperate Vespertilionid, widespread throughout Europe except for the Iberian and Italian peninsula and the South of France (Salicini et al., 2011). Most female temperate bats are faithful to summer colonies, although males are thought to disperse (Kerth et al., 2002a) and both sexes of temperate bat undertake annual autumn swarming events during which large numbers of bats from colonies from a wide geographical area meet prior to hibernation. Swarming is thought to be the main mating period, and it has been suggested that it could result in discrete breeding bat populations (Rivers et al., 2006) however this could have been an artefact of a limited number of sites being visited. As significant mating occuring during swarming is likely to have an important function in maintaining gene flow among individuals spatially segregated during the summer by enabling genetic exchange to occur between discrete summer bat populations (Burns et al., 2014).

Both male and female Natterer’s bats exhibit philopatry to their summer roosting sites although males leave their natal colony but may stay in its vicinity (Rivers et al., 2006). This suggests Natterer’s bats should have relatively strong population structure. However, there should be some degree of gene flow between populations due to swarming events. Although high levels of gene flow would be beneficial for bat populations in terms of long term population viability, routes of gene flow could also be routes of disease transmission (Halczok et al., 2017).

The aim of this chapter is to use microsatellite markers developed for *M. nattereri* (Rivers et al., 2005, Puechmaille et al., 2012, Scott et al., 2013) to characterise the genetic diversity and structure present in *M. nattereri* colonies in Northern England. In addition the aims are to assess the spatial population structure, its viability and levels of gene flow to enable disease spread within or between populations to be predicted. This will be used to inform management or conservation plans. To determine whether the species present in our study are similar to those from central and northern Europe, or a distinct sub-species (Salicini et al., 2013) sequencing data will be analysed. It is expected that the microsatellite data will support the hypothesis that there are distinct colonies in Northern England with limited dispersal between closed summer social roosting sites. Another hypothesis is that the main route of gene flow, is via mating at swarming sites rather than dispersal from nursery roosts.

4.2 Methods

4.2.1 Sample collection

Fifty-two individuals were captured from free flight or from known roosts (Table 8) at Wallington National Trust Estate, Northumberland during the summers of 2014–2015 using harp traps (Austbat), handmade Arial harp traps, mist nets and hand nets. All bats were identified to species and sex and classified as adults or juveniles where possible following Dietz *et al* (Dietz et al., 2009) (Supplementary section 2). A wing tissue sample was taken from all Natterer's bats caught using a 3mm biopsy punch and stored in 90% ethanol until DNA extraction. All bats were released within a few minutes of the procedure at their place of capture. All work was done with the approval of the ethical review bodies at APHA and Newcastle University and under licence from the UK Home Office (Animals in Scientific Procedures Act 1986) and Natural England (Habitats Regulations, 2010). Wing biopsies were also supplied for 119 individuals (Table 8) from a further four locations in Northern England, Wintringham, Wycoller, Harpham and Low Catton (Figure 9).

Table 8 Number of bats caught by different capture methods at five different sites in Northern England

Date	Capture method	Site	Region	*N*
18/06/2012	Church roost	Harpham	North Yorkshire	7
02/07/2012	Church roost	Harpham	North Yorkshire	25
24/07/2012	Church roost	Harpham	North Yorkshire	11
19/06/2003	Church roost	Low Catton	North Yorkshire	7
03/07/2003	Church roost	Low Catton	North Yorkshire	9
23/07/2003	Church roost	Low Catton	North Yorkshire	4
07/08/2003	Church roost	Low Catton	North Yorkshire	7
28/08/2012	Church roost	Wintringham	North Yorkshire	9
05/09/2012	Church roost	Wintringham	North Yorkshire	16
10/09/2012	Church roost	Wintringham	North Yorkshire	9
30/06/2013	Free flight	Wallington	Northumberland	2
17/06/2013	Free flight	Wallington	Northumberland	1
24/07/2013	Tree Roost	Wallington	Northumberland	5
07/08/2013	Free flight	Wallington	Northumberland	1
19/08/2013	Tree Roost	Wallington	Northumberland	10
03/09/2013	Free flight	Wallington	Northumberland	2
04/06/2014	Free flight	Wallington	Northumberland	1
12/06/2014	Tree Roost	Wallington	Northumberland	14
19/06/2014	Tree Roost	Wallington	Northumberland	11
13/07/2014	Free flight	Wallington	Northumberland	2
21/07/2014	Free flight	Wallington	Northumberland	3
22/07/2014	Free flight	Wallington	Northumberland	1
27/07/2014	Free flight	Wallington	Northumberland	1
05/08/2014	Free flight	Wallington	Northumberland	2
06/08/2014	Tree Roost	Wallington	Northumberland	7
12/08/2014	Free flight	Wallington	Northumberland	1
14/08/2014	Tree Roost	Wallington	Northumberland	31
09/06/2015	Free flight	Wallington	Northumberland	4
15/06/2015	Free flight	Wallington	Northumberland	2
23/06/2015	Free flight	Wallington	Northumberland	2
02/07/2015	Free flight	Wallington	Northumberland	5
27/06/2012	Church roost	Wycoller	Lancashire	10
18/07/2012	Church roost	Wycoller	Lancashire	9
15/08/2012	Church roost	Wycoller	Lancashire	9

4.2.2 Sample processing

Genomic DNA was extracted using the Dnamite kit for difficult cells (Micozone), (Robson et al., 2009). Twenty dinucleotide microsatellite loci were shown to amplify in

Natterer's bats (H19, D9, D15, E24, H29 in *Myotis myotis* (Castella et al., 2000), Paur03 and Paur06 from *Plecotus auritus* (Burland et al., 1999) B22 from *Myotis bechsteinii* (Kerth and Morf, 2004), Mnatt 1, 2, 3 (Boston et al., 2012). Mantt 4,5,6,7,8,9,10,11 (Scott et al., 2013), H4 (Jan et al., 2012). These loci were tested individually to determine their optimum annealing temperatures. However, after optimization five loci were removed due to either difficulties in amplification or difficulties in scoring, resulting in the remaining 15 loci (Table 9). Multiplex mixes were then created using Multiplex Manager (Holleley and Geerts, 2009) and amplified using the Qiagen Multiplex kit following the manufacturer's instructions and using various optimized primer concentrations (Table 1). Polymerase chain reactions (PCR) were then carried out in 5µl reactions with 2µl DNA and 3µl of the primer mix. Amplifications were performed in thermal cycler Applied Biosystems 2400 using one activation step (95°C/15 min) followed by 30 cycles (denaturation at 94°C for 30 s, annealing at 48°C (sets 1) or 55.9°C (sets 2,3) for 90 s, extension at 72°C for 90 s) and final extension step at 72°C for 30 min. PCR products were detected on an ABI 3130XL sequencer using 2 µl of amplified DNA and a mix of 10 µl of HiDi (Applied Biosystems, Foster City, California)/ROX 500 size standard (Applied Biosystems) at a concentration of 12:0.1. Genotypes were analysed using Genemapper 2.1 software. Only individuals that amplified at more than eight loci were included in the analysis.

4.2.3 Sequencing

Partial sequences were obtained for two mitochondrial DNA fragments, Cytochrome b (Cytb) and NADH dehydrogenase 1 (ND1) using Molcit-F (Ibáñez et al., 2006) Molcit-R (Salicini et al., 2011) and ND1F2 – ND1R (Kawai et al., 2002). After PCR amplification using MyTaq (Bioline) using manufacturer's instructions, the PCR product was purified using ExoSAP (Thermo Fisher) and sequenced using Big Dye terminator V3.1 (Applied Biosystems). Sequencing products were purified using ethanol precipitation and analysed on a ABI3130 Gene Analyser. Resulting sequences were analysed using Geneious V10 (Kearse et al., 2012). New mt DNA sequences were submitted to Genbank.

Table 9 Details of microsatellite markers used to Genotype Natterer's bats from all sites. Showing the forward and reverse primer sequences, PCR reaction conditions, allelic diversity, expected heterozygosity (H_E) and observed heterozygosity (H_O) values of the loci

Multiplex Number	Primer name	Forward and reverse primer sequence	Concentration in PCR (uM)	Annealing temperature	Mean Number of alleles	H_E	H_O	Allele size range (bp)	Reference 1
1	Mnatt-6	6-FAM-TTTCTCAGCCTCCATAATA ATAGCAAGGCAATAAAATA	0.6	48	7.6	0.748	0.854	275-291	Scott et al. 2013
	Mnatt-9	6-FAM-TCCCCAATATGATGTAGAAGTG GGCAATTTTTATCTCCCTTTTA	0.4	48	6.6	0.733	0.753	427-439	Scott et al. 2013
	Mnatt-11	HEX-ATAATATCCCAAGCCTCAAT CCTTTCTTCTATAGTGGATGC	0.2	48	10.2	0.811	0.902	216-248	Scott et al. 2013
	H29	6-FAM-TCAGGTGAGGATTGAAAACAC GCTTTATTTAGCATTGGAGAGC	0.2	48	5.4	0.634	0.631	171-189	Castella and Ruedi 2000
2	Mnatt- 2	6-FAM-ATTTATGAGGCCCCTGGTTT GCATGAGTGTTTATGTGGAGGA	0.2	55.9	7.8	0.794	0.854	278-316	Boston et al. 2012
	Mnatt-10	HEX-CCTCTTTCTTGCCCAAACTCAT AGGCCCTGGGTCATGTAGTCT	0.2	55.9	6.6	0.692	0.663	109-115	Scott et al. 2013
	D15	NED-GCTCTCTGAAGAGGCCCTG ATTCCAAGAGTGACAGCATCC	0.4	55.9	10.2	0.818	0.861	115-143	Castella and Ruedi 2000
	E24	HEX-GCAGGTTCAATCCCTGACC AAAGCCAGACTCCAAATTCTG	0.4	55.9	9.8	0.852	0.946	216-250	Castella and Ruedi 2000
	Mnatt- 1	NED-ACAATGGCTGGAAGGTGAAA GTCATTTTGTGGCTGGCTTA	0.2	55.9	5.4	0.716	0.71	207-239	Boston et al. 2012
	Mnatt-7	6-FAM-TAATCATGGAAAGTAAAAATAAAG TTTCGAGCAGCAAGTAGCATA	0.6	55.9	6.2	0.709	0.876	304-324	Scott et al. 2013

3	B22	6-FAM-CTGATGCAAGACCCCTTACAA ACGGCAGCAGTGAAATCAG	0.2	55.9	6.6	0.772	0.844	148-165	Kerth et al 2002
	D9	NED -TCTTTCCTCCCCTGTGCT TCTGGACCCAAAATGCAG	0.2	55.9	11.4	0.842	0.798	134-164	Kerth et al 2002
	H19	HEX-GGAATCCGAATCCCTGGC GACATCCCCTCACCCCAAC	0.4	55.9	10.4	0.86	0.923	85-116	Castella and Ruedi 2000
	Paur3	6-FAM-TTGCCCTTCAGTGATTTTGTTC TGAAAAGGCTGATGGTGGAG	0.4	55.9	5.4	0.565	0.599	216-224	Burland et al 1998

4.2.4 Statistical analyses

Genetic diversity

Data were prepared for analysis using GenAlex (Peakall and Smouse, 2006). Null allele frequencies were calculated using Cervus (Kalinowski et al., 2007). GenePop (Raymond and Rousset, 1995) was used to test loci for deviation from Hardy-Weinberg equilibrium and linkage disequilibrium. *P*-values were corrected for multiple tests (Verhoeven et al., 2005). Heterozygosities, number of alleles per locus, F_{IS} per sample site and pairwise F_{ST} estimates between sites (significance tested using 10,000 permutations) were estimated using Microsatellite Analyser (MSA) (Dieringer and Schlötterer, 2003). Differences in genetic diversity between sites were calculated using a one way ANOVA.

Relatedness

Relatedness was assessed using the R package 'related' (Pew et al., 2015). To determine which relatedness estimator was most appropriate, 100 individuals of known relatedness were simulated using the existing genotype data and the relatedness estimates for four different estimators was compared. The Pearson's correlation coefficient between observed and expected relatedness for each estimator was then calculated to determine best fit.

To determine if individuals at sample locations were more related than randomly distributed individuals, the average relatedness for each of the sites was estimated and compared to a simulated data set. The observed relatedness values were compared to the expected distribution of relatedness values for each site from the simulated data using the function 'grouprel'. For simulated data the group membership counts were preserved for each site but individuals were shuffled randomly across 1000 iterations, providing a distribution of expected relatedness assuming random distribution of individuals across sites. *P* values were calculated as the percentage of iterations where the expected relatedness was greater than or equal to the observed relatedness for a given site. Results were considered significant at the 5% level.

MLRelate (Kalinowski et al., 2006) was used to calculate the likelihood whether a pair of individuals was most likely unrelated, half sib, full sib or parent-offspring. All samples were included in one analysis. The number of pairs that were most likely full sibs or parent-offspring (first degree relatedness) within populations and between all populations were counted. This was expressed as a % of all possible pairwise comparisons (maximum number of pairs is N * (N-1) /2 within populations and N1 * N2 for between populations, with N1 being number samples in population 1 and N2 that in population 2).

Population Differentiation

The global null hypothesis of no population structure among sites was tested by conducting global tests of genetic differentiation. Hierarchical pairwise comparisons were then conducted between all pairs of sites at a local level and also at a regional level, by combining the three North Yorkshire sites (Harpham, Low Catton and Wintringham) and comparing those to the site at Lancashire (Wycoller) and the site in Northumberland (Wallington). Differentiation was assessed using a G-test implemented in 'Hierfstat' (Goudet, 2006). The G-test is thought to be more powerful than F_{ST} permutation tests for microsatellites (Goudet et al., 1996). Statistical significance was determined through 10,000 random permutations of the data set.

Population Structure

Two different clustering methods were used to determine if sites supported distinct populations of bats (Mira et al., 2017). The first was implemented using the program STRUCTURE 2.3.1 (Pritchard et al., 2000, Falush et al., 2003). The program uses Markov chain Monte Carlo sampling to find the most likely model describing the population structure. Estimates of the number of independent genetic clusters were obtained using the admixture algorithm, correlated allele frequencies and a separate alpha for each population with and without sampling location used as a prior. A burn-in of 1×10^4 followed by 1×10^6 permutations were input to test K=1 to K=10 with ten iterations each to calculate q, the membership coefficient. q Represents proportional individual memberships to different inferred population clusters, indicating if an individual showed admixture of two or more population clusters. STRUCTURE HARVESTER v 0.9.93 was then used to summarise the run statistics. To identify the likely number of clusters the ΔK method was applied. Finally, CLUMPP v.1.1.2 and DISTRUCT v1.1 were utilised to average individual and population membership q values over the ten runs and to visualise the Bayesian assignment. To identify admixed individuals, a threshold q-value of 0.8 was applied to assign an individual as belonging to a specific group. A q-value of less than 0.8 therefore indicated an admixed individual. The second method was implemented in TESS (Chen et al., 2007) with the correlated allele frequencies model and the spatial option. Ten independent runs of 1 X 10^6 MCMC iterations were performed with thinning set to 100. K values were set from 1 to 10. The most likely K value was decided based on the median K inferred in the models with the highest log posterior density. Finally TESS was run again with the same parameters as the spatial model but with the inferred K value fixed according to the most likely value, to accurately estimate the membership of each of the individuals.

Effective population size

Effective population N_e size of bats from each distinct population identified from STRUCTURE and TESS was calculated using NeEstimator software version 2.0.1 (Do et al., 2014), based on the linkage disequilibrium (LD) model. This estimate was calculated from the deviation of expected compared to observed degree of linkage disequilibrium in the populations. A Lincoln Peterson estimate (Nichols, 1992) of population size based on mark-recapture data was also calculated on those populations for which recapture data was available for comparison to the genetic methods.

Gene flow

The relative migration network was calculated using the function divMigrate of the diveRsity package (Sundqvist et al., 2016). The network was estimated using G_{ST} statistics. G_{ST} values could be interpreted as a measure of the level of allele fixation in populations and also reflect the population's demographic properties (e.g. the number of migrants per generation under assumed mutation rate) (Alcala et al., 2014). To test whether migration between populations was asymmetrical (significantly higher in one direction than the other), 95% confidence intervals were calculated from 50,000 bootstrap iterations.

Isolation by distance

Isolation-by-distance for all sites was tested via Mantel's test (Mantel, 1967) from the comparison of all pairwise $F_{ST}/(1-F_{ST})$ values with pairwise geographic distances using the R package 'ecodist' (Mira et al., 2017) with 10,000 permutations. The test was performed for the whole dataset as well as within the North Yorkshire region consisting of three populations (Harpham, Low Catton and Wintringham).

4.3 Results

4.3.1 Sequencing

Both the CytB abd the ND1 sequences confirmed that the samples are indeed the species *M. nattereri*. Cytb sequences (580 – 600bp) were obtained from 12 individuals (Wallington 3 and 6, Wintringham 5 and 8, Low Catton 17, Harpham 4, 8 and 15, Wycoller 6, 8, 9, 10) and three haplotypes were distinguished. Six individuals (four from Wycoller, one from Wallington and one from Low Catton) shared a haplotype, identical to six *M. nattereri* samples from France, Montenegro, Serbia and the UK on Genbank (e.g. JN591505.1,(Salicini et al., 2011)). A second haplotype was found in one individual from Wallington: it was very similar to the previous haplotype, with a T to C substitution at nucleotide 54. The third haplotype was shared by all three individuals from Harpham and the two from Wintringham: it was also very similar to the middle/northern Europe haplotype, but with a G to A substitution at nucleotide 237. ND1 sequences (600 – 650 bp) were obtained from fourteen individuals (Harpham 4, 7, 8, 10, 12, 14 and 16, Wallington 17, Wintringham 13, Wycoller 8 and Low Catton 4, 15, 16, 17). Two haplotypes were found. Again the majority haplotype (eleven out of fourteen samples) was identical to the haplotype found for *M. nattereri* by Salicini (Salicini et al., 2013) in France, Montenegro, Serbia and the UK (e.g. Genbank JN591538.1). A second ND1 haplotype was found in three of the seven Harpham samples, with a C to T substitution at nucleotide 204.

4.3.2 Genetic diversity

Tests for Linkage disequilibrium revealed significant linkage between 3 pairs of loci at Harpham and 1 pair of loci at Wallington (Table 10). However, as these loci were not linked in at least three out of the five populations they were kept in the rest of the analysis. Departure from Hardy-Weinberg equilibrium (HWE) (after Bonferroni correction) was low (F_{IS} = 0.052) over all loci (

Table 11). Departures were significant for locus Mnatt-10 in three out of five populations. However, Mnatt-10 was kept in the analysis as the locus appeared to have discriminatory power between populations. Other loci that deviated from HWE included Mnatt-11, D15 and Paur2-Mluc but these loci only deviated in one out of five of the populations, therefore were kept in the analysis.

Table 10 Pairs of loci showing Linkage disequilibrium. Test results from GenePop for Natterer's bats from 5 sites in Northern England, with standard error (*se*) and significance level (after adjusting for multiple tests using the False Control Discovery rate (FDR)

Pop	Locus 1	Locus 2	*p* value	*se*	corrected *p* value
Harpham	Mnatt9.	B22.	<0.01	0	<0.01
Harpham	Mnatt11.	D9.	<0.01	0	<0.01
Wallington	Mnatt11.	mnatt2.	<0.01	0	<0.01
Harpham	Mnatt11.	mnatt2.	<0.01	0	<0.01

Table 11 Hardy Weinberg P values for loci used to genotype Natterer's bats from 5 sites in Northern England. * indicate significant deviations from HW after P values were adjusted (FDR)

Locus	Harpham	Low Catton	Wallington	Wintringham	Wycoller
B22.	0.442	0.836	0.379	0.027	0.979
D15.	0*	0.791	0.541	0.496	0.421
D9.	0.99	0.066	0.238	0.143	0.695
E24.	0.1386	0.6696	0.2615	0.7322	0.1358
H19.	0.7253	0.6791	0.0111	0.472	0.4336
H29.	0.7808	0.0855	0.941	0.7525	0.4133
H4.	0.7988	0.1949	0.0012*	0.9402	0.7095
Mnatt-1.	0.1514	0.0671	0.0135	0.1161	0.0738
Mnatt-10.	0.4783	0.004	0*	0.0028*	0*
Mnatt-11.	0.9856	0.1199	0.0139*	0.0105	0.0372
Mnatt-2.	0.2137	0.2908	0.1852	0.0608	0.1313
Mnatt-6.	0.1372	0.19	0.4848	0.2907	0.0995
Mnatt-7.	0.3172	0.9106	0.1196	0.2187	0.3427
Mnatt-9.	0.3395	1	0.9468	0.9067	0.1812
Paur3-Mluc.	0.0045*	0.0731	0.2398	0.7146	0.2262

Genetic diversity, as measured by expected heterozygosity and number of alleles, was high at all sites (Table 12) mean (±SD) expected heterozygosity = 0.78±0.01) and there was no difference in the level of genetic diversity between sites (One - way ANOVA *F* =

0.12, *P* = 0.975). There was no evidence of inbreeding within sites (F_{IS} estimates for sample sites did not differ significantly from zero).

Table 12 Diversity statistics of Natterer's bats sampled from five sites in Northern England (mean number of alleles per locus (A), observed (H_O) and expected (H_E) heterozygosities and mean estimates of F_{IS}, with numbers of individuals included in analysis from each site

Site name	N	A	H_E	H_O	F_{IS}
Harpham	25	7.27	0.785	0.707	0.099
Low Catton	27	8.07	0.762	0.752	0.013
Wallington	38	8.2	0.779	0.765	0.018
Wintringham	34	7.4	0.79	0.731	0.075
Wycoller	28	8.07	0.801	0.751	0.062
Total	152				

When sites were considered independently, all pairwise F_{ST} values between sites were low but statistically significant from zero, ranging from 0.02–0.07 (Table 13). The highest genetic differentiations were between Harpham and Low Catton (pairwise F_{ST} = 0.07) and Harpham and Wallington (pairwise F_{ST} = 0.06), whilst the most genetically similar sites were Wintringham and Wycoller (pairwise F_{ST} = 0.02) (Figure 9). Despite evidence of some gene flow between sites, genotypes at different sites were significantly different from each other (Table 13). There was no evidence of genetic differentiation between regions (F_{ST} = 0.01, *P* = 0.08).

Table 13 Pairwise F_{ST} values (below the diagonal) and their significance (above the diagonal as P values) for all sites. Significant F_{ST} values are represented by a P value of <0.05. The highest F_{ST} values (>0.05) are indicated in bold

	Harpham	Low Catton	Wallington	Wintringham	Wycoller
Harpham		<0.01	<0.01	<0.01	<0.01
Low Catton	**0.073**		<0.01	<0.01	<0.01
Wallington	**0.064**	0.033		<0.01	<0.01
Wintringham	0.033	0.049	0.033		<0.01
Wycoller	0.041	**0.053**	0.048	0.021	

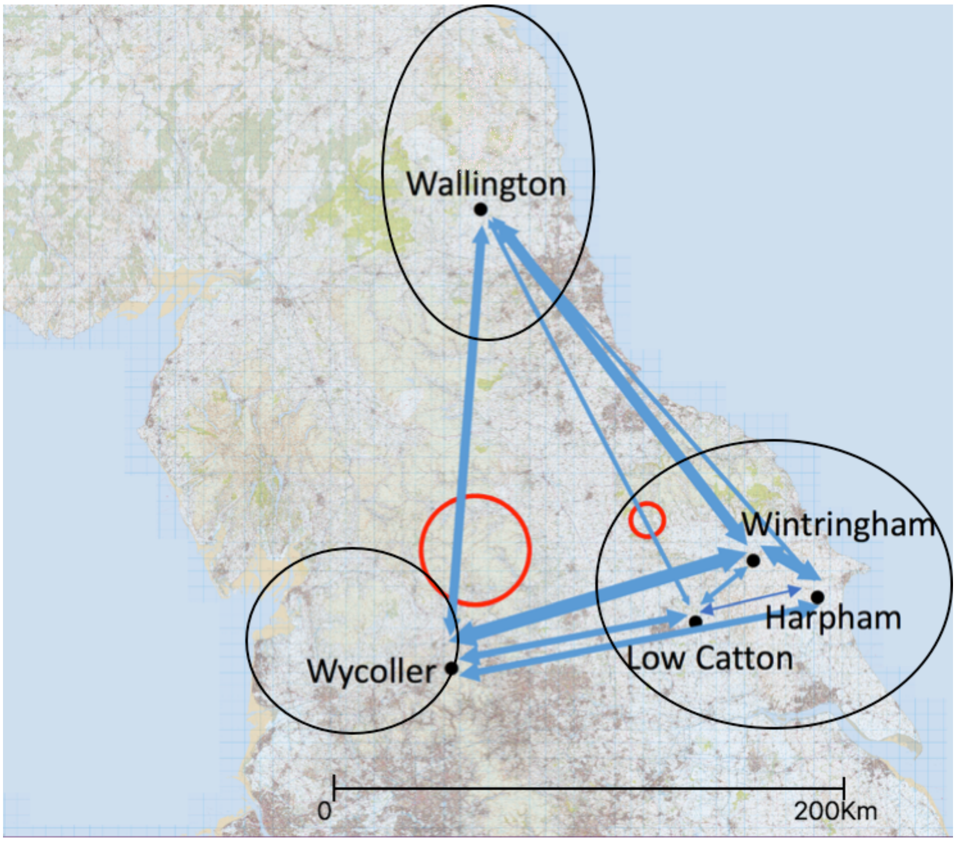

Figure 9 Sample sites, possible swarming sites and Population pairwise F_{ST} (genetic differentiation) of Natterer's bats sampled from 5 different sites in Northern England. Sample locations are represented by black dots, regional groups by black ellipses, known swarming sites (Rivers et al., 2006) are represented by red open circles. Lines represent genetic differentiation. Thicker lines represent lower F_{ST} values between sites. © Crown copyright database rights 2016 OS licence number 100051110

4.3.3 Relatedness

The Queller and Goodnight estimator (Figure 10) most closely correlated the observed values to the expected values of relatedness (e.g. 0.5 parent-offspring or full siblings, 0.25 half siblings, 0 unrelated) (correlation coefficient 0.88) and therefore was used in further analysis.

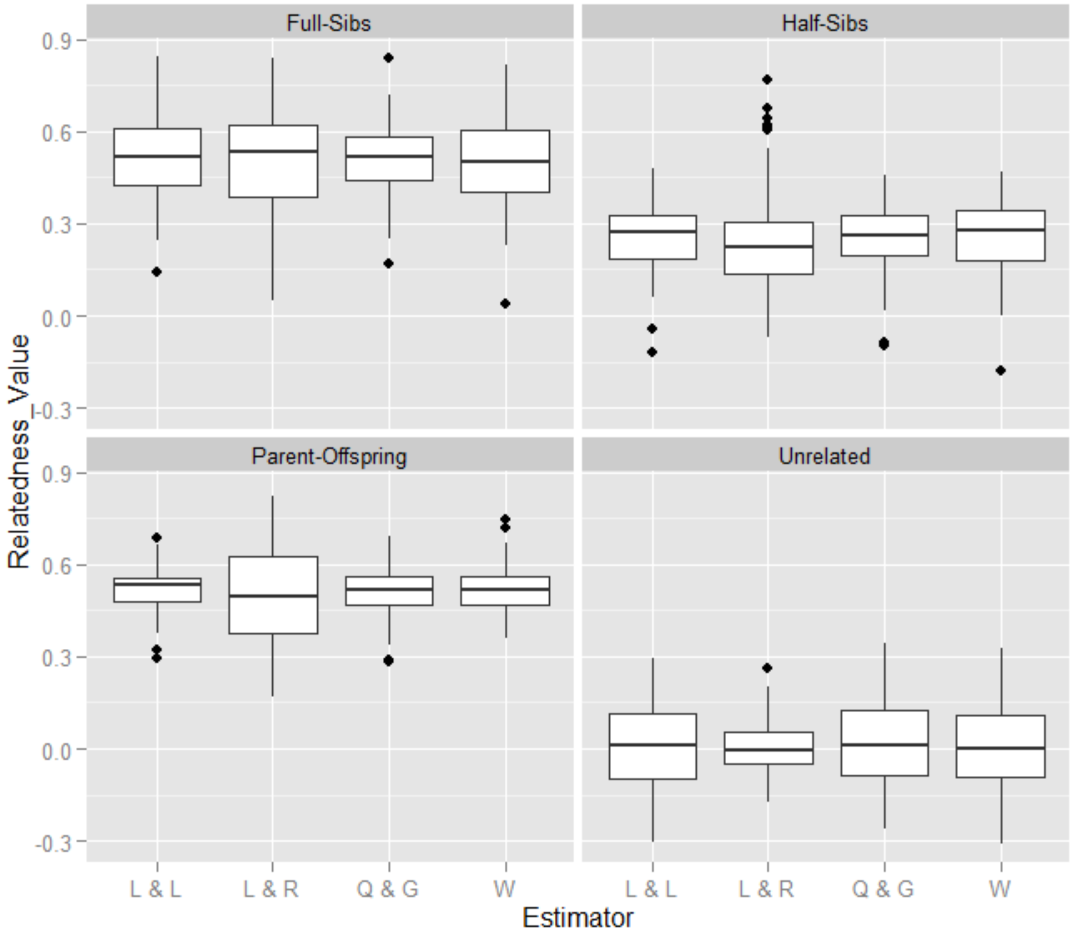

Figure 10 Relatedness estimates using four different estimators and simulated individuals of known relatedness. L & L = Lynch and Li estimator, L & R = Lynch and Rutland estimator, Q & G = Queller and goodnight estimator and W = Wang estimator

The likelihood of individuals having shared alleles through common decent was low due to the low average pairwise relatedness across all individuals from all sites (Table 14). Although pairwise relatedness was highly variable between all individuals sampled (-0.52 – 0.74), individuals within each site were more closely related to each other than would be expected by chance (*P<0*.001 at all sites). Harpham had the highest averaged relatedness followed by Wintringham, Low Catton and Wycoller. Wallington bats showed the least pairwise relatedness.

Table 14 Pairwise relatedness between individuals at sample sites

Sample Site	Average pairwise relatedness (Queller & Goodnight)	n	*P*
Harpham	0.13	25	<0.001
Low Catton	0.06	27	<0.001
Wallington	0.03	38	<0.001
Wintringham	0.08	34	<0.001
Wycoller	0.05	28	>0.001
All sites	-0.0005	152	

4.3.4 Population Differentiation

Hierarchical F-statistics revealed that overall genetic differentiation was low and not significant at the regional level ($F_{Region/Total}$ = 0.0005; p=0.082), while there was significant genetic differentiation at the sampling location level ($F_{Locality/Region}$ = 0.0196, *p*=0.009) suggesting that locality rather than region explained the distribution of genetic variability.

4.3.5 Population Structure

The optimal configuration determined from the STRUCTURE (Pritchard et al., 2000) analysis characterised individuals belonging to four groups based on the *ΔK* values (Figure 11: a) when sample site was not used as a prior. *K*-group assignment resulted in a structure where individuals from Wycoller, Harpham, Low Catton and Wallington formed four distinct groups with a small number of admixed individuals, whilst individuals at Wintringham seemed to be mostly admixed (Figure 12: a). When the sample sites were used as a prior, the optimal value for *K* was 2 (Figure 12: b) which grouped samples from Wallington and Low Catton together in one cluster and samples from Harpham, Wintringham and Wycoller in the other cluster (Figure 12:b). Further analysis with STRUCTURE on these initial two clusters identified 5 individual clusters representing the 5 sample sites (Figure 12:c). TESS analysis with the geographic locations resulted in the optimal value of K =5 (Figure 11:c,Figure 12:d) which corresponds with the site geographic locations. Overall, the different Bayesian clustering methods converged in identifying five distinct genetic units. The spatial models were the most consistent and meaningful geographically, and so were chosen for further analyses of genetic diversity including IBD.

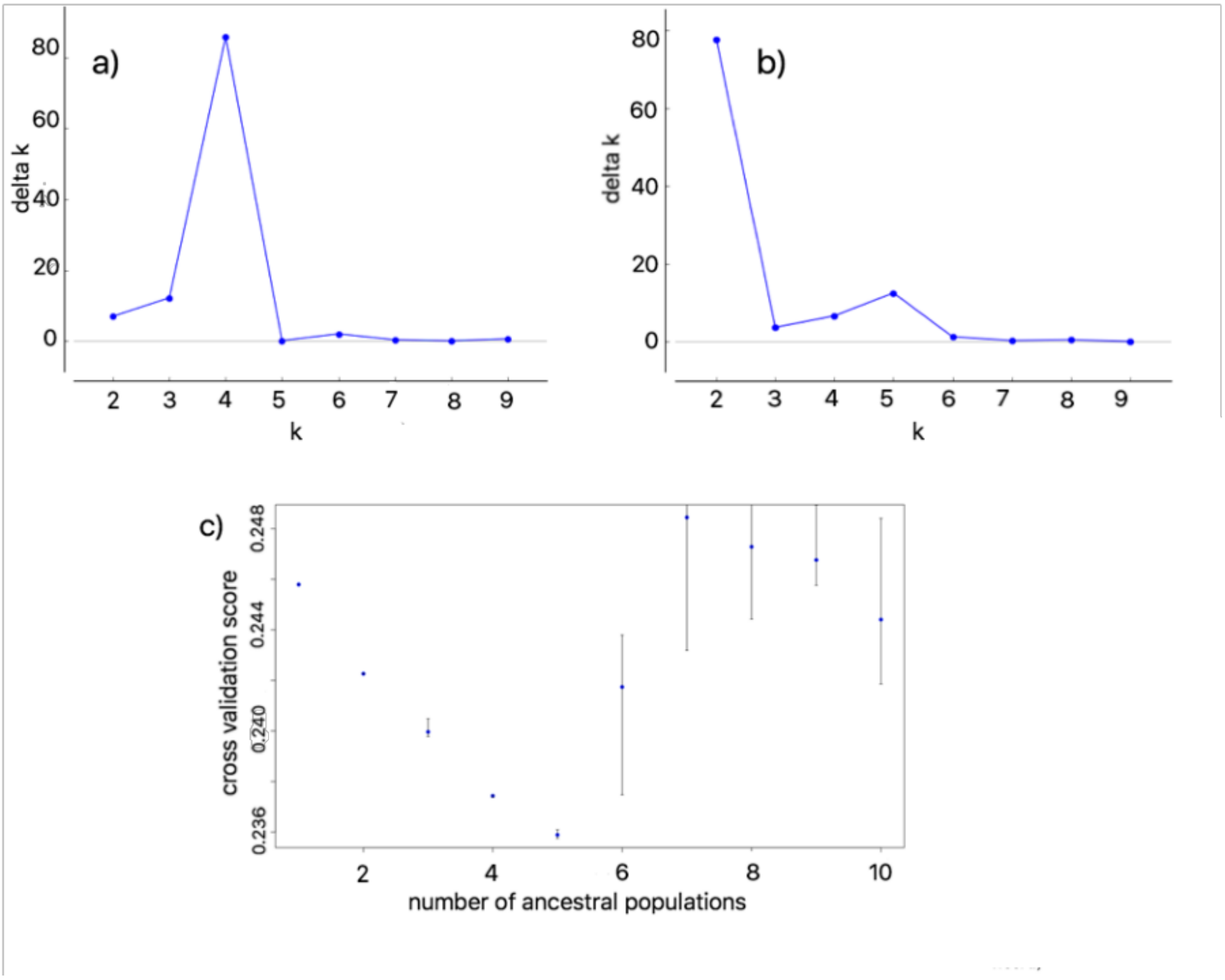

Figure 11 Optimal number of clusters in Natterer's bats genotypes sampled in Northern England using STRUCTURE and TESS a) ΔK plot showing the optimal number of clusters calculated by STRUCTURE not using pop info as prior b) ΔK plot showing the optimal number of clusters calculated by STRUCTURE using the pop info as a prior c) Optimal number of clusters calculated by TESS using the spatial model

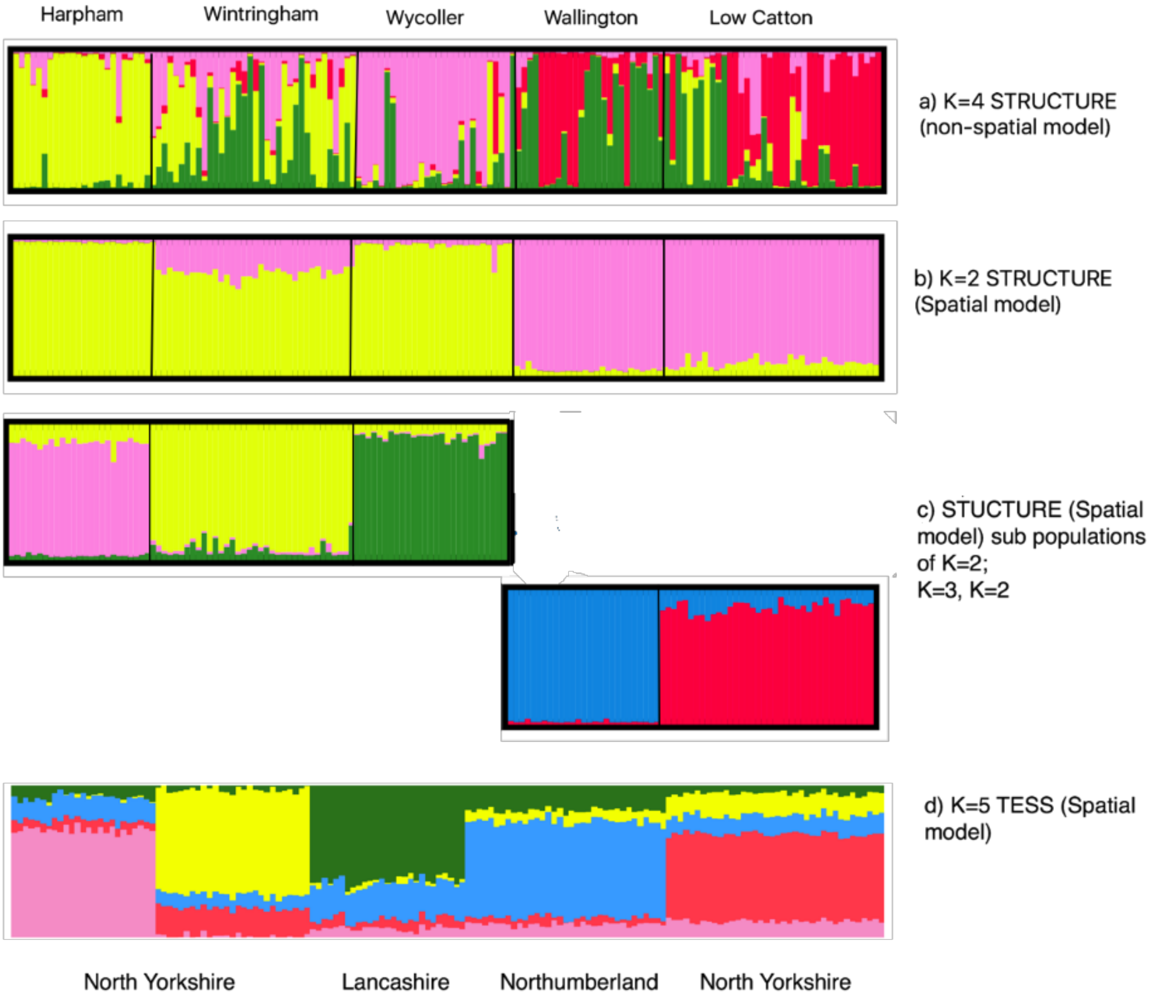

Figure 12 Bayesian posterior probability of membership of Natterer's bats from the 5 locations (Harpham, Wintringham, Wycoller, Wallington, Low Catton) to populations obtained by STRUCTURE without (a) and with a priori population info (b–c) and TESS spatial model (d). K= number of groups identified

4.3.6 Effective population size

Effective population size (N_e) ranged from 42.2 at Wallington with a 95% confidence interval (CI) of 29.2-69.9 to 101.2 (CI = 52.9-570.5) at Low Catton. The average N_e was 71.8 (CI = 66.2–77.4)(Figure 13). The large CI at Harpham and Low Catton are likely due to smaller sample sizes and therefore little inference can be gained from these estimates.

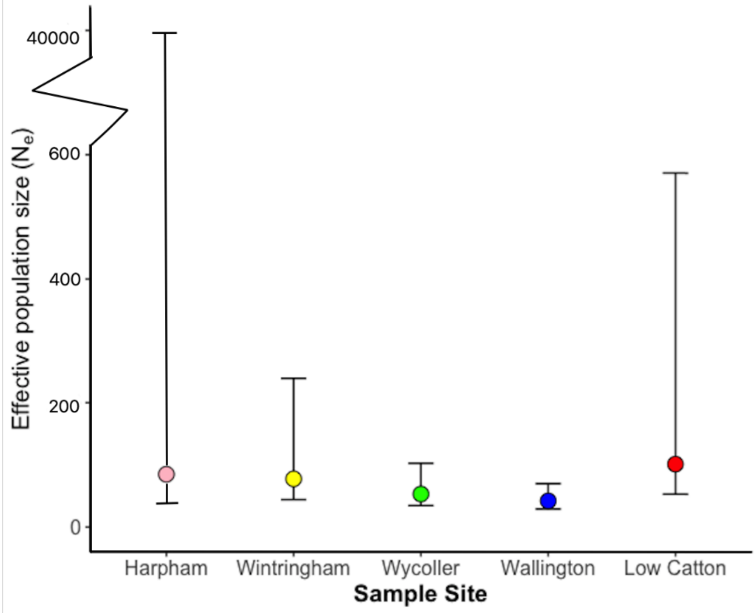

Figure 13 Mean effective population size N_e and 95% credible intervals of Natterer's bats at five sample sites in Northern England. Note the alternative scale for the Harpham site

4.3.7 Gene flow

On average relative migration rates were high (average: 0.611; range: 0.24–1) in the context of the estimation of demographic parameters. Analysis of the migration dynamics revealed migration flows (Figure 14,Table 15) between most populations, with high bidirectional flows between Wallington and Low Catton, and also between Wintringham and Wycoller. Wintringham was the only population that had relatively high (above 0.7 migration rates to or from all other populations). The only migration to or from Harpham above 0.7 was from Wintringham.

Table 15 Bidirectional estimate of relative migration rate based on the function divMigrate from the package of diveRsity (Sundqvist et al., 2016) G_{ST} values below the diagonal, p values of bidirectionality above the diagonal.

From\to	Harpham	Low Catton	Wallington	Wintringham	Wycoller
Harpham	-	0.3669332	0.604497	0.5894947	0.4517529
Low Catton	0.2474689	-	0.7863867	0.7686558	0.5788887
Wallington	0.3308921	0.8046213	-	0.6681537	0.4999109
Wintringham	0.7872422	0.5217214	1	-	0.9385223
Wycoller	0.4204555	0.467167	0.542148	0.847106	-

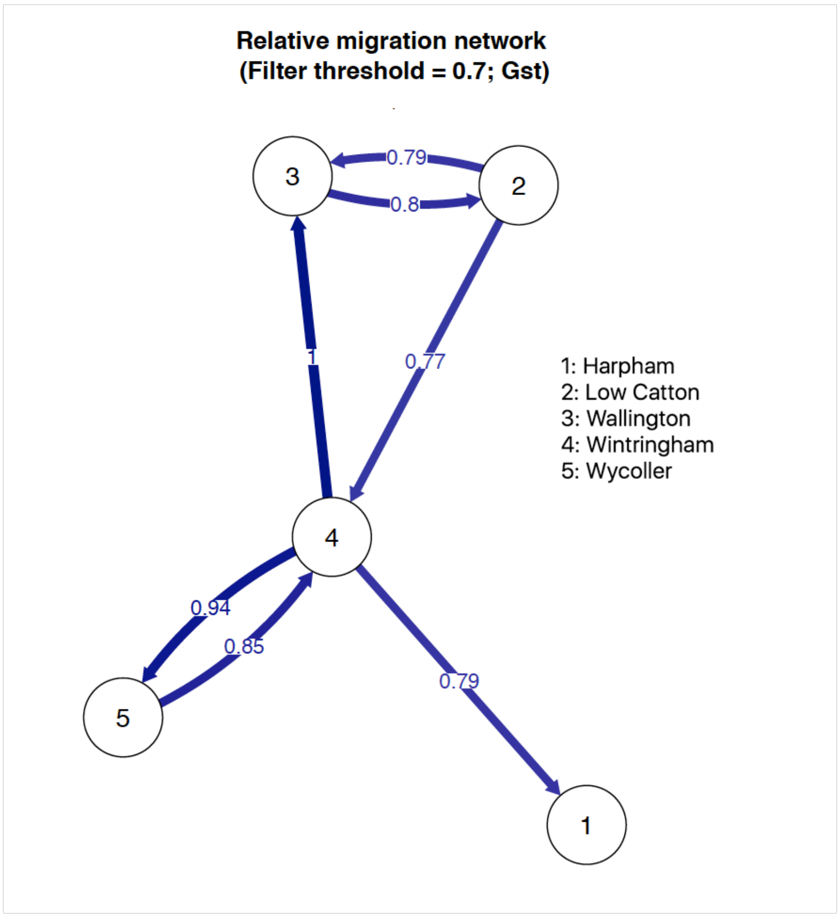

Figure 14 Directional relative migration of five populations of Natterer's bats estimated by divMigrate in r package 'diveRsity' with the filter threshold set to 0.7 to aid clarity

4.3.8 Isolation by distance

There was a slight positive correlation between genetic distance (F_{ST}) and geographic distance between all the sites (r= 0.14, *p*>0.01) and within the North Yorkshire region (r=0.35, *p*>0.01) indicating some support for isolation by distance. Due to the distinct cluster patterns it is likely that Natterer's bats follow the island model of migration £#

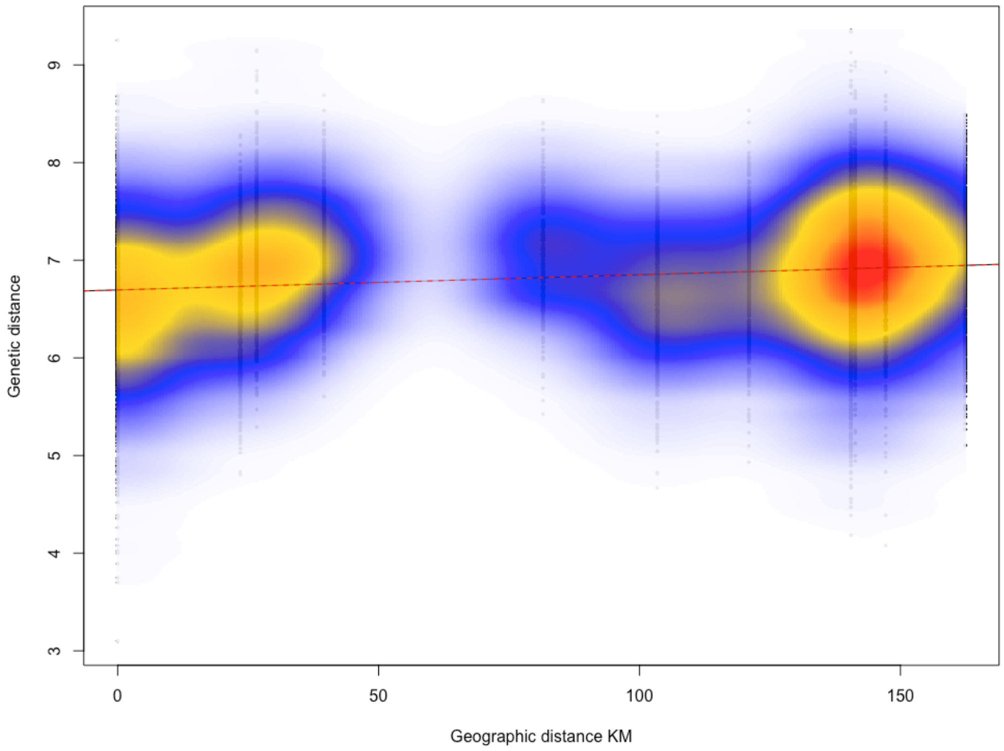

Figure 15 Geographic distance (KM) compared to genetic distance (Fst) of all sampled Natterer's bats.

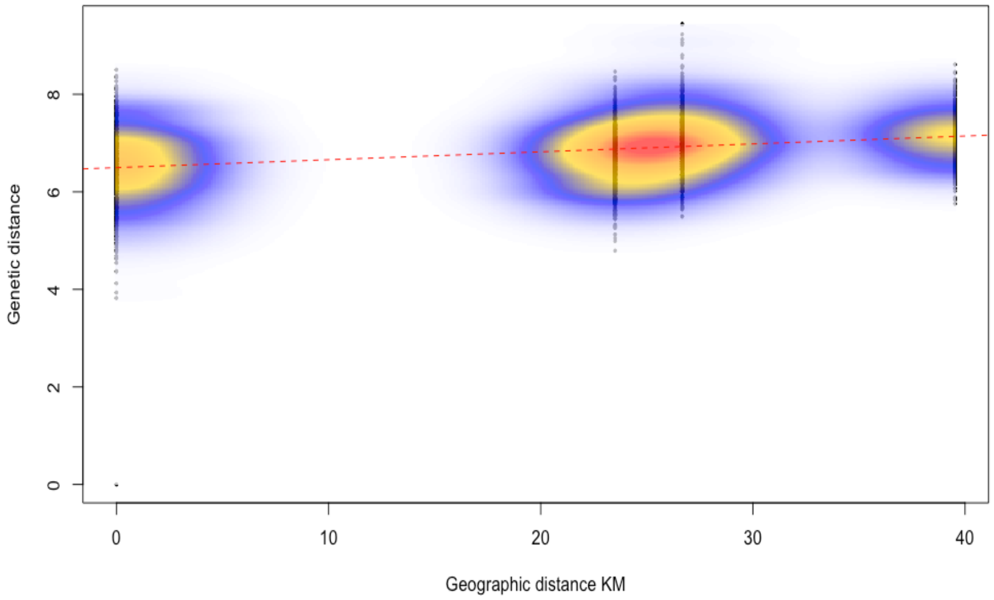

Figure 16 Geographic distance (KM) compared to genetic distance (Fst) of Natterer's bats sampled in North Yorkshire only (Harpham, Low Catton and Wintringham)

4.4 Discussion

The relatively high genetic diversity (mean 0.78) at all sample sites, coincides with previous studies on Myotis bats (Rivers et al., 2005, Atterby et al., 2010, Castella et al., 2000, Bogdanowicz et al., 2012) and could be expected in a highly mobile mammal such as Natterer's bats. High genetic diversity either supports the idea that Natterer's are able to travel to swarming sites to exchange genes (Rivers et al., 2006, Parsons and Jones, 2003, Halczok et al., 2017) or suggests male dispersal. There has been some debate as to whether male Natterer's bats disperse. Rivers et al (2005a), suggest the pattern of exchanging genes at swarming sites results in the same genetic pattern as permanent male dispersal and that males are also philopatric to their summer sites. However, Fairless (2013) provided evidence from a ringing study of limited male dispersal between sites up to 6.5km apart.

4.4.1 Is population structure due to gene exchange at swarming sites?

Both the results from the Bayesian clustering approach and the F_{ST} values support evidence of genetic structure at different sites, in contrast to previous work by Rivers et al(2005a) who suggested that mating at swarming sites creates a single population of large effective size. A higher number of loci (fifteen compared to seven) than Rivers were used here, which may have enabled finer scale genetic differences to be detected. The difference in the genetic structure shown here is likely to be due to differences in effective population size, male and female philopatry to summer roost sites combined with gene exchange at shared swarming sites and male dispersal.

It is likely that the strategy of swarming and gene exchange in large numbers has evolved to avoid inbreeding depression (Kerth et al., 2002a), in an otherwise philopatric species (Rivers et al., 2006). Although the philopatric nature of the bats to their summer sites may have evolved as a result of fragmented habitat and lack of alternative summer roosting sites (Sagot et al., 2016). Whatever the driver for the evolution of swarming events, the importance of swarming sites to Natterer's bats population viability cannot be underestimated. Swarming sites likely play a highly important role in maintaining high genetic diversity and therefore avoiding inbreeding depression. Although there are some well know swarming sites in Northern England for Natterer's bats, it is likely that many sites remain unknown and are therefore potentially vulnerable to disturbance or development which could then lead to the cut off of gene exchange between populations and the summer sites becoming isolated. It should be noted here that sample sites were not chosen randomly across the landscape. It is likely that there are many other populations of Natterer's bats between the sites sampled in this study which may enable individuals from Harpham to interact with in future and be less likely to become further isolated. However, at present the results suggest it is significantly isolated from the other populations.

4.4.2 Is population structure due to male dispersal?

Although the structure identified with Fst values was low but significant, the finding of statistically significant differences using Fst are not generally enough to make firm conclusions about population structure (Knutsen et al., 2011), with concern that non-random sampling or natural selection are responsible for generating the observed differentiation. Here these concerns have been dealt with by including bats from five different areas and randomly sampling those populations. In addition it should be noted that in *Myotis* bats males are thought to disperse (Rivers et al., 2005, Ruedi and Castella, 2003) which has the effect of maintaining high levels of gene flow as seen in this analysis. Indeed Ruedi and Castella (Ruedi and Castella, 2003) showed a strong difference in mtDNA results between populations of Myotis myotis ($\Phi ST = 0.384$) but only weak Fst values ($Fst= 0.010$) which they argue is to due to strong male-based dispersal. Here results also show this pattern of high relative migration values but low Fst so it is concluded that the population structure is due to male dispersal and swarming events. It could be possible that swarming sites provide male bats with the opportunity to follow others to new summer sites (Wilkinson and Wenrick Boughman, 1998).

4.4.3 Mitochondrial analysis

The mitochondrial analysis revealed that mitochondrial haplotypes were identical, or very similar, to those of Natterer's bats from middle and northern Europe (Salicini et al., 2013), including their two UK samples (Cumbria and Essex), and also the middle and northern European samples from their later studies, except Croatia and Greece.

All three individuals analysed from Harpham and the two from Wintringham share a new haplotype for CytB, with only one SNP different from the most common haplotype. This may indicate an exchange of females between Harpham and Wintringham as they share the new, unique, CytB haplotype and this is supported by the high relative migration values (G_{ST}) seen in the microsatellite analysis (Table 15).Three of the seven Harpham individuals have a new, unique, haplotype for ND1, differing by one SNP from the majority haplotype. This may indicate that there are fewer (or no) females moving from Harpham to Wintringham, which again is supported by G_{ST} values, but this needs larger sample sizes from Wintringham to confirm this. Both the Cytb and ND1 sequences indicate that Harpham is the most distinct population studied for their mitochondrial DNA, and may therefore be a 'sink' with limited outward gene flow which could suggest that it is particularly vulnerable to isolation and inbreeding, especially if the main swarming area used by bats at Harpham and Wintringham is compromised. Although the variation observed here is higher than observed by Salicini et al (2011), more samples from across the populations are necessary for firm conclusions.

4.4.4 Relatedness

Relatedness was significantly higher within colonies than between colonies supporting the hypothesis that Natterer's are philopatric to their summer sites. The mean within colony relatedness (0.07) is similar to other studies on temperate bats (Veith et al., 2004, Rivers et al., 2005, Kerth et al., 2002b, Burland et al., 2001) and although seems relatively low can be explained as Rivers suggested (Rivers et al., 2005), by lack of paternally related individuals even though there may be close matrilineal relatives in the colony. Large numbers of Natterer's bats congregate at swarming sites to mate and up to 300 males each night may be present, therefore females are unlikely to mate with the same male (Rivers et al., 2006) which results in low relatedness values.

4.4.5 Effective population size

It is likely that the effective population size estimates for Low Catton and Harpham are inaccurate due to the large confidence intervals, however the other estimates should be considered to be fairly accurate. Precise estimates of *Ne* can be obtained using 10-20 microsatellite loci and samples of at least 25-50 individuals when the effective population size is less than around 500, Waples and Do (2010). They also note that small populations are not likely to be mistaken for large ones. Wallington (the only samples from a naturally roosting population) appears to be much smaller than the others (sampled from church roosts) and this could be due to the limiting size of tree roosts compared to the larger space available for roosting in old churches (Moretto, 2017).

4.4.6 Isolation by distance and gene flow

The slight evidence for isolation by distance at both the regional and Northern England scale, coincides with previous work by Rivers to suggest some local bats may use a shared swarming site. The evidence of isolation by distance overall however is very weak which also suggests that some bats may travel further than previously thought to alternative swarming sites rather than visiting the closest. Although this ability to travel relatively large distances to mate is positive in terms of maintaining genetic diversity, this raises concerns for disease transmission. Despite the genetically distinct populations, disease transmission may be able to spread throughout Northern England relatively quickly. As lyssaviruses are thought to be spread through direct contact with con-specifics, via bites or scratches (Picard-Meyer et al., 2013) , the movement of Bokeloh lyssavirus across the landscape should mirror the movement of the bats. Therefore it could occur successively over large distances following the stepping stone model of gene transfer of the host via swarming sites (Halczok et al., 2017). This may result in small outbreaks of infection during the summer when communities are separate at their summer roost sites although should the virus still be present in the autumn, large numbers of bats aggregating could result in widespread infection of bat communities across the landscape.

It should be noted that it is possible that the Northern England study area was too small to detect strong isolation-by-distance or there were not enough sample sites. Indeed, within the UK, isolation-by-distance was not detected between summer colonies of Natterer’s bats unless distances exceeded 100 km (Rivers et al., 2005). However, this study extends the distance that Natterer’s bats are likely to travel to swarming sites, as significant gene exchange occurred between sites up to 200km apart. It should also be noted that it is likely that individuals do not necessarily use the swarming site closest to their summer roost site as higher genetic differentiation between adjacent sites (Low Catton v Harpham) compared to more distant sites (Wallington v Low Catton) was evident, which also supports the idea that individuals can travel further than previously thought and is good news in terms of conservation as it suggests distant sites may not become genetically isolated.

4.4.7 Conclusions

Our findings show significant population structure in Natterer's bats corresponding to the sample site locations. This suggests that disease transmission during the summer roosting period may be limited geographically to the site of origin. There will likely be less transmission between the two populations at the higher level (Wallington grouped with Low Catton | Wintringham, grouped with Wycoller and Harpham), compared to between the grouped sites due to some evidence of dispersal (e.g. Between Wallington and Low Catton). However, the relatively large distances Natterer's can travel to swarming sites suggests that monitoring for lyssaviruses should take place during the spring/summer months to detect lyssavirus within bat communities which may then be more easily isolated before transmission occurs across further bat communities in the Autumn swarming.

The presence of genetic structure at different sites, along with the relatively high genetic diversity, may suggest some local adaptations have taken place which is positive in terms of the long term viability of the species and its ability to adapt to climate change or further anthropogenic change. However, the importance of swarming sites again should be reinforced in order to prevent these genetically different sites from becoming isolated.

Chapter 5. Social Networks and disease modelling

5.1 Introduction

Across mammals there is a large diversity of social structure, differing in type, frequency and duration (Croft et al., 2008). Within a group sociality can be described as the frequency, temporal patterns and nature of interactions between individuals (Hinde, 1976) and is thought to have evolved for a number of reasons such as improved detection and defence against predators, benefits associated with social hunting (Dechmann et al., 2009), cooperating to rear young (Clutton-Brock, 2009) or to enable information transfer between individuals; all potentially increasing individual fitness and resulting in consistent interactions between individuals (e.g. associations or relationships). Examples of the benefits of relationships between social animals include longer life in high-ranking female Savannah baboons and increased reproductive success in feral horses who form stronger, more stable social bonds (Silk et al., 2010, Cameron et al., 2009). Understanding such relationships is important for conservation e.g. maintaining population viability;(Vucetich et al., 1997), because individual fitness, or group viability may be threatened if social dynamics are ignored or mis-understood (Courchamp et al., 2008). Classic examples include mis-understandings of mating or social systems which may interfere with in-situ conservation (Caro, 2007) or re-introduction (Gusset et al., 2009). However, here the interest lies in its fundamental role in mediating disease transmission (Rushmore et al., 2013, Ortiz-Pelaez et al., 2006, Hamede et al., 2009, Guimarães Jr et al., 2007), especially for contagious diseases where the epidemiological ‘contact rate’ is loosely associated with the behavioural association.

Bats are exceptional in the number of species considered to be social (Kerth, 2008). Despite their ability to fly, which allows them to disperse great distances, many species show strong philopatry in at least one sex (Burland and Wilmer 2001) and form group sizes from a few individuals to several million (McCracken and Wilkinson, 2000). This has driven the evolution of a large diversity of social structures in bat communities (McCraken and Wilkinson 2000) and which use social communication for a wide range of reasons which is only now being studied in earnest. Current themes in the study of bat social systems include the use of social calls and the distinct study of eavesdropping on the functional echolocation calls of others used to locate food patches e.g. (Übernickel et al., 2013, Jones et al., 2014, Dechmann et al., 2009, Balcombe and Fenton, 1988). Eavesdropping, or passive listening to feeding buzzes of conspecifics, is thought to decrease the amount of time a communally feeding bat needs to spend foraging. This is thought to be due to the patchiness of food resources dispersed with larger patches of poorer quality (Stephens and Krebs, 1986). By listening in to conspecifics, significant amounts of time and effort in foraging could be saved (Gillam, 2007). In addition, there is the emerging description of bat social geography and the coordination of roosting together e.g.(Silvis et al., 2014c, Kerth et al., 2011, Johnson et al., 2012) thought to be facilitated by social calls. Social calls enable individual recognition in bats and can help direct them to the location of roosts occupied conspecifics (Siemers and Kerth, 2006, Chaverri and Gillam, 2016, Chaverri et al., 2010).

Understanding links between sociality and disease transmission has become increasingly important as knowledge of bats as reservoir hosts of zoonotic disease has become more widely reported (Schneeberger and Voigt, 2016, Poel et al., 2006, Openshaw et al., 2016, Leroy et al., 2009, Kohl and Kurth, 2014). The virus of focus in this chapter is Bokeloh bat lyssavirus, which causes rabies and which has only been isolated in Natterer's bats suggesting the species is a reservoir for the virus (Picard-Meyer et al., 2013, Nolden et al., 2014, Freuling et al., 2011). Rabies is a deadly disease in humans causing in excess of 60,000 deaths globally (Singh et al., 2017) and bat rabies variants caused by various strains of Lyssavirus, are the leading source of rabies in humans in the United states (Birhane et al., 2017). It is therefore accepted that bats are the primary evolutionary hosts of lyssaviruses (Rupprecht et al., 2017). At present there have been only a small number of studies on rabies disease dynamics in natural bat populations, and excepting research on Vampire bats, much of the work has been theoretical e.g. (George et al., 2011). As the prevalence of rabies poses a serious public and animal health risk (Singh et al., 2017), further work in this area is urgently needed.

The social behaviour of bats is usually measured in terms of rates of association between individuals, whereby two individuals typically evidence that they were in the same place at the same time. Individuals sharing a roost at any given time would then be assumed be associated and have a relationship. Here we extend this to assume contact between associated individuals and use this as a quantitative description of the degree of epizootiological contact. Social relationships between individuals can then be expressed as links which join individuals together to form a social network (Scott, 2000), where individuals can be expressed as nodes and linkages as edges connecting those nodes (nodes may alternatively represent other entities such as roosts). The analysis of social networks (SNA) is a common, powerful tool used in many disiplines including transmission dynamics of diseases among wildlife species (Tompkins et al., 2011), to better understand observed social relationships by understanding the social contact of individuals and exploring various hypotheses e.g. the effect of removing key individuals (Lusseau and Newman, 2004), implications for disease transmission (Rushmore et al., 2013, Shirley and Rushton, 2005, Ortiz-Pelaez et al., 2006, Hamede et al., 2009), influence of individuals in group decision making (Kerth, 2010, Kerth et al., 2006, Fleischmann and Kerth, 2014) or the evolution of sociality (Wolf et al., 2007, McComb et al., 2001). SNA can also be used to determine factors influencing social structures of mammals, e.g. seasonal variation was present in the network structure of Bechstein bats *Myotis bechsteinii* (Kerth et al., 2011), individual traits affected social network structure in bottlenose dolphins *Tursiops spp*. (Lusseau and Newman, 2004) or the topological structure of the network can also affect social associations (e.g. David-Barett & Dunbar 2013) and should also be considered.

The structure of social networks, including the spatial pattern of associations can impact on disease dynamics considerably (Shirley and Rushton, 2005). For example, the degree to which the spread of disease occurs depends on the social relationships of animals. Craft et al (2009) provide evidence that outbreaks of canine distemper virus in Africa lion *Panthera leo* populations are a result of inter-specific interactions, whilst Hosseini et al (2004) suggest that strong seasonal aggregation of flocks of house finches *Carpodacus mexicanus* had a large effect on conjunctivitis transmission. In addition to this, identifying socially central animals in networks can help identify which individuals might be most influential in disease transfer which may in turn help with vaccination targeting. Scale-free networks can have large effects in disease transmission and are important to identify if disease management is to be considered.

Rhodes (2006) describes what is known as a ‘scale free network’ in a community of tree roosting white-striped freetail bats *Tadarida australis*, where a single tree was the hub of the network; nodes in this network where tree roosts and edges were bat movements between those roosts. The term “scale free” indicates that the structure and dynamics of those networks are independent of the scale of the network, and nodes are not randomly or evenly connected. Many nodes in scale free networks act as “hubs” that connect the rest of the nodes (Barabási, 2009) and may act as transmission points for disease. Where networks exhibit characteristics of being scale free, disease might persist longer and spread much more rapidly than expected in other networks (Leventhal et al., 2015) therefore, understanding whether networks follow this pattern is important in disease management and conservation. As all bats in Rhodes’ study at some time travelled through this key roost it highlights its importance not only for maintaining social cohesion of the group but also as a potential spreader of disease. Again, further work is needed to understand bat social systems in relation to disease flow to improve disease management prescriptions.

Many studies of social systems in temperate bats occur in anthropogenic settings where bats roost in boxes or use a combination of boxes and natural roosts (Kerth et al., 2011, August et al., 2014). As the loss of natural roosts is one of the major contributing factors to the decline of bat populations (Mickleburgh et al., 2002) and leads to bats roosting more commonly in areas where they have greater potential to come in contact with humans (Zeale et al., 2016), there is a need to better understand how bats behave in each setting in order to inform conservation as well as disease management and the management of bat/human conflict. There is little evidence to date of the difference between bat social networks in natural versus anthropogenic settings and the effect this may have on disease transmission rates or population longevity. Conversely, the lack of information about how bat societies operate in completely natural settings is also problematic, as this is probably how the bulk of the national population live, and as such the most important dynamic in the maintenance and spread of bat borne disease. Our lack of knowledge of the social and spatial dynamics of communities in natural contexts therefore limits our robust or accurate prediction of how disease may establish, spread or be maintained.

Natterer's bats appear to conform to the general pattern of roosting behaviours typical of many temperate species. Roosting colonies can be large, but many species have been shown to re-sort across a network of roosts and form smaller sub-groups (chapter 1 table 1), conventionally described as fission-fusion societies when considered over short temporal scales (Willis and Brigham, 2004, Silvis et al., 2014a, Rhodes, 2007, Kerth and Reckardt, 2003). For temperate bats, roosting together is thought to have evolved due to roost limitation (most bat species depend on refuges against weather or predators and most cannot build their own roosts (Kunz, 2014b)) and the benefits gained from thermoregulation (Willis and Brigham, 2007, Dzal and Brigham, 2013). Individuals are thought to gain long term social cohesion from this behaviour by having knowledge of a large number of individuals and roosts but relatively small daily subgroups, which also allows flexibility to respond to seasonally dynamic social drivers as well as ever-changing environmental conditions. This behaviour has been speculated to allow bats to avoid high parasite loads and reduce disease transmission between individuals (Popa-Lisseanu et al., 2008) whilst still gaining the benefits from group living. Less attention has been devoted to how to suitably abstract the daily fine-scaled details of bat social and spatial dynamics of these species across larger temporal and spatial scales, and what the population dynamics or epizootiology of these larger units may be.

For cave hibernating temperate species, such as the Natterer's bat, social behaviour may show a marked change in the autumn and winter. Two contrasting periods of social contacts in temperate bats can therefore be assumed, one during the summer months when bats live in a closed social system of predominately sexually segregated social contact with familiar individuals (Zeus et al., 2018, Senior et al., 2005, Encarnação, 2012, Altringham and Senior, 2005) but see Park (1998) and Angell (2013) for instances where males have been found roosting with females; and another period of significantly greater socio-sexual contact, during which large numbers of bats interact and mate (known and unknown individuals). The scant knowledge of bat behaviour at swarming sites results in considerable uncertainty over how distinct these two seasonal communities may be. Other than the obvious differences in their potential sizes; summer communities rarely exceed a few hundred bats (Kunz, 2014a), and are frequently much smaller, whilst autumnal swarming sites may serve 10,000s across an autumn (Rivers et al., 2006). However, whilst daily contacts within a summer community may include a substantial proportion of the total summer community at nursery sites, so little is known of the nightly behaviour at swarming sites that a number of equally likely possibilities exist. These involve combinations of specific behaviours none of which are well described for any single site or species, and for which a general behaviour can only be speculated.

In this chapter a network approach will be used to describe the social relationships within two Natterer's bat communities. Network characteristics will be assessed to determine how differences in roost settings (natural/anthropogenic) or sites, affect network structure and their vulnerability to roost loss.

Networks will then act as the base for an individual based disease model to simulate potential disease dynamics and by incorporating data from chapter 4 on the genetic relatedness and relative migration rates between communities in Northern England. Three hypothesis will be tested a) there is clear seasonality in disease transmission, with higher transmission rates in the autumn due to swarming ; b) higher immigration rates of individuals into summer roosting sites will lead to higher rates of disease transmission and c) disease transmission rates will be higher in the artificial roosts compared to the natural tree roosts.

5.2 Methods

5.2.1 Study sites

The two sites considered in this chapter are Wallington National Trust Estate, Northumberland and Wytham Woods, Oxford. The Wallington Estate (see 2.3.1) covers an area of 8,000 hectares, including farmland, moorland, woodland, lakes and mires, (Trust, 2018) with approximately 320 hectares of densely wooded amenity/ornamental woodland, composed of mature, and over-mature/veteran trees. Data was collected by Simone Mordue on roost switching behaviour from bats at Wallington where the bats exclusively used trees (Supplementary section 2). 42 Individual bats were sampled from a total of 24 natural tree roosts. Levels of relatedness within colonies and patterns of gene flow between colonies from this study were used to inform community structure (See 4.4.3).

Data from Wallington was compared to data provided by August *et al*. (2014) describing roost network structure and roost switching from an ongoing study at Wytham woods, Oxford, where bats occupy woodcrete bird boxes distributed thought the woodland. August's data included roost switching behaviour of 1303 individuals using a total of 329 bird boxes as roosts (Supplementary section 3). Wytham woods (Latitude: 51.7743, Longitude: −1.3379) is a 415-hectare site composed of semi-natural ancient deciduous woodland and 18th–20th century plantations. Over 1150 woodcrete bird boxes of very similar design are dispersed through the woods which are frequently used by bats from May up until mid-October.

5.2.2 Network Analysis

Roost networks (using both bats and roosts as nodes) and social networks (single network of bat nodes) were generated. Roost networks were used to assess patterns of roost use whilst social networks were used to assess social structure following (Silvis et al., 2014b) to provide a more generalised picture of how bats might associate across the roost network., To reduce bias from uneven tracking periods and observing only a proportion of the whole colony, multiple edge weights from the networks were removed, using the function 'simplify' following (Silvis et al., 2014a). A social interaction or association between individuals was defined when they were found roosting together. Individuals or roosts only observed or used once were not included in the analysis. All analysis was carried out in R V 3.3.1 (R Core Team, 2016) using custom scripts and the packages reshape2 v. 1.4.2 (Wickham, 2017, Wickham, 2007) and igraph v.1.0.1. (Csardi and Nepusz, 2006).

5.2.3 Network terminology

Network topology in this chapter was assessed with both node and group based metrics (

Table 16).

Table 16 Network Terminology - modified from Silk *et al* (2017)

Node based metrics

Closeness - is a measure of the degree to which a node (individual/roost) is near all other nodes in a network, and is important in determining the risk of exposure of an individual during an epidemic, especially in networks with greater substructure because individuals with high closeness tend to have connections that span between different modules or social groups

Betweeness (centrality) - the number of paths that pass through a node along the shortest path between all other nodes and is particularly valuable for measuring the importance of individuals in connecting different parts of the network. It can describe the ability of an individual to mediate the spread of infection during an epidemic, especially in networks with considerable substructure

Degree (centrality)- The degree of a node is the number of neighbours to which it is connected. Individuals with a high degree are more likely to be exposed to infection and will have greater opportunity for onward spread to a greater number of individuals

Eigenvector (centrality) - is a measure of the influence of a node in a network, individuals with higher eigenvector centrality are likely to be at a higher risk of exposure to infection and more important for its onward spread

Group based metrics

Average degree - The average number of neighbours per node for the whole network

Modularity - measures the strength of division of a network into modules/communities. Networks with high modularity have dense connections between the nodes within modules but sparse connections between nodes in different modules

Average transitivity - gives an indication of the clustering in the whole network and provides an idea of network substructure. For example, lower-density networks with high transitivity are likely to be more subdivided into different modules and therefore are likely to be less susceptible to disease spread

Density – the proportion of edges (connections/associations) in a network relative to the total number possible, disease transmission would be expected to occur more rapidly in networks with higher density. Value ranges from 0 to 1; the closer the value is to 0, the sparser the network is while the closer the value is to 1, the denser the network is.

5.2.4 Scale Free Network

To identify whether the social networks at Wallington and Wytham were scale free, the distribution of the network node degrees (degree distributions) were fitted to a power law distribution using the function 'fit_power_law' in the package 'igraph' (Csardi and Nepusz, 2006).

5.2.5 Comparison of natural v anthropogenic social networks

When comparing networks, randomisation techniques have been used (Croft et al., 2008) as they do not assume independent data points. However, the sample sizes must be equal. To compare the Networks from Wallington and Wytham where the sample sizes were different, Perkins *et al* (2009) was followed. A qualitative comparison of the networks using quantile-quantile plots (q-q plots) of degree distribution was carried out to determine whether the social network from the natural roost site (Wallington) had a different distribution to that from the artificial roost site (Wytham). As different network properties can affect disease spread (Shirley and Rushton, 2005), social network statistics were examined between the two data sets. Three network properties were measured relevant to disease dynamics, Closeness, Betweeness and Density (Table 16). Statistically significant differences in the properties of the networks using, closeness and betweeness separately as response variables and dataset (Wallington or Wytham) as the explanatory variable were assessed using one way ANOVA's. Scores were first normalised (such that the sum of the measured metric over all nodes/vertices equalled 1) to allow comparison between the networks.

5.2.6 Community detection

Various community detection algorithms exist to detect community structure in social networks (Yang et al., 2013). Key features of the algorithms considered here, modified from De Sousa and Zhao (2014) , are listed below;

- Cluster_fastgreedy – A hierarchical approach. It tries to optimize modularity in a greedy manner. Initially, every node belongs to a separate community, and communities are merged iteratively such that each merge is locally optimal. The algorithm stops when it is not possible to increase the modularity anymore.
- Walktrap_community –An approach based on random walks. Random walks are performed on the network graph. The walks are more likely to stay within the same community because there are only a few edges that lead outside a given community. Walktrap runs short random walks of 3-4-5 steps (depending on one of its parameters) and uses the results of these random walks to merge separate communities in a bottom-up manner.
- Leading.eigenvector.community- A top down hierarchical approach that optimizes the modularity function. In each step, the graph is split into two parts in a way that the separation itself yields a significant increase in the modularity. The split is determined by evaluating the leading eigenvector of the so-called

modularity matrix, and there is also a stopping condition which prevents tightly connected groups to be split further.

To decide which algorithm was most appropriate to describe community structure in Wallington and Wytham networks, various metrics were calculated. The number of communities detected, modularity score (*Q*) (which captures the degree of community fidelity when networks are robust) and a measure of certainty (R_{com}), to accompany the Q value for each algorithm were calculated for both the Wallington and Wytham using a script provided by Shizuka and Farine (2016). R_{com} permutes the community membership data and calculates how many times each individual appears in the same community to provide a metric between 0-1 for certainty. Values close to zero indicate that the individual was rarely assigned to the same community whilst values close to 1 indicate that the individual was always assigned to the same community. Social networks were then visualised using Gephi v. 0.9.1 (Bastian et al., 2009) and additional metrics were then calculated including Mean degree, Betweeness Centrality and Eigenvector centrality.

5.2.7 Network analysis and biometrics

Linear models of the relationship between node network measures (degree, betweeness centrality and eigenvector centrality) and biometric records from the Wallington site were modelled using lme4 package (Bates et al., 2014) with age and reproductive condition as fixed effects. Biometric data was not available for Wytham. As there were very few observations of males they were removed them from the analysis. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality and *P*-values were obtained by likelihood ratio tests of the full model against a model without the effect in question.

5.2.8 Roost Density

To estimate the roost density at Wallington (natural roosts) compared to Wytham (observations from nest boxes) roost locations were weighted by the number of bat-days used to represent the concentration of roost use (Popa-Lisseanu et al., 2008) raw data can be seen in supplementary sections 2 and 3.

5.2.9 Randomisation Techniques

To quantify social structure, field data / observations were tested against the hypothesis that associations of individuals are completely random. This was necessary to establish the statistical likelihood that observations are non-random and might act as a source of inference (Whitehead et al., 2005). Networks are based on non-independent observations of multiple individuals and small differences in how data are collected can easily generate patterns that appear as social structure. Therefore the random networks accounted for non-social factors which may have affected the co-occurrence of individuals (e.g. attraction to resources, ((Farine, 2017)). Our network data was compared to that produced by random networks following (Silvis et al., 2014a). Group sizes and number of individuals in the network were kept constant but associations were randomised. The original network matrices were each simulated 1000 times using the package ‘asnipe’ (Farine, 2013) and observed network metrics were compared to simulated metrics using two-tailed permutation tests.

5.2.10 Roosting association and relatedness

To determine whether related bats associated together more or less often than unrelated bats, relatedness at Wallington was determined using microsatellite analysis (see 3.2) and the package ML-relate (Kalinowski et al., 2006) with 10000 permutations. The social network of bat by bat connections was then weighted by relatedness and modularity scores were calculated for weighted and unweighted networks.

5.2.11 Removal simulation

The impacts of roost loss of the colonies at Wallington and Wytham were assessed using simulated roost removal. Random node removal simulations on the largest roost networks at each site were carried out using the single-node projection of the roosting network following Silvis (2015). For each random removal, a random selection of a set proportion of nodes was removed and each removal each repeated 100 times. The proportion of nodes removed was increased until only 20% remained. The mean number of remaining components (either a network or individual node) was then calculated for each proportion.

5.2.12 Disease modelling

An individual based simulation model was written in R with age (adult/juvenile), disease status (SEIR) and pregnancy status as state variables. Disease status was modelled with four stages, S; Susceptible, E; Exposed, I; Infected and R; Recovered. Bats are known to be able to become immune to the rabies after exposure and resistant to further exposure (George et al., 2011). In this case Recovered also included resistant individuals. The model was created with a weekly time step and run over a period of 5 years to capture disease dynamics at the summer roosting sites and later at autumn swarming and hibernation sites. Life history 'decisions' were made following a probabilistic approach (Shirley et al., 2003), where each individual had a chance it would become infected (after associating with another diseased bat), immune (after contact with a diseased bat but not succumbing to disease), die(either from natural or disease related mortality), or give birth. Only a proportion of adult females were expected to give birth (Table 18). The initial networks consisted only of female bats to represent the predominately female social networks observed at summer roosting sites. Each year was split into different seasons as detailed in Table 17.

Table 17 Seasons defined in model and the number of weeks over which the season is presumed to occur

Dates	Bat seasonal behaviour	Number of weeks
June -Sept	Summer roosting and birth (week 1)	16
Sept – Oct	Autumn swarming (dissolving of social network and increased random social contact with foreign infected bats)	4
Oct –Mar	Hibernation (slower infection rates and longer incubation periods)	20
Mar – May	Spring (reforming of pre-swarming social network and maturation of Juveniles)	12

The first phase of the model was the summer roosting season (June to September), representing the closed social groups at their summer sites and included processes to control birth, natural mortality, transmission of disease, incubation of disease, infection from disease, immunity from disease and death from disease. Life history and disease transmission parameters were obtained from the literature (Table 18). The social structure was modelled on the observed social networks from field data with the introduction of an infected bat at the start of the season in year 1. The second phase (September to October) represented the autumn swarming period and included all the processes included in phase one except birth, with the addition of a process to dissolve the social network structure to create random mixing with a number of new individuals (50x the number of individuals from the summer site), 10% of which were infected with disease. The third phase modelled was the hibernation period which included all the processes from the swarming period using the random association network. The final phase modelled was early spring (March to May) when all processes from the swarming stage (phase 2) were included with the addition of processes to govern maturation of juveniles to adults and reformation of the previous social structure to represent bats returning to their summer roosting sites. The model was run 1000 times and values were averaged over the runs.

Chapter 4 provides evidence of non-related bats at all five summer roost sites sampled in Northern England along with evidence of gene flow between sites. This suggests that individuals may move between colonies and that summer populations may not be closed. Here the model was used to test three different scenarios based on the observed gene flow to assess the potential impact on disease dynamics;

Base model: summer populations are closed to immigration

Early summer immigration model: summer populations receive immigrants at the start of the season (presuming individuals follow others back from the swarming/hibernation sites)

Random summer immigration model: summer populations receive immigrants at a random time during the summer season

There were a number of assumptions made when running the model. In addition to all individuals having the same values for the various disease parameters, e.g. length of incubation period etc., it was assumed that all adult females had a probability of giving birth, pups were linked to their mother and their mother’s neighbours, pups were born without immunity from disease and all pups were born within the same week.

Table 18 Model parameter values and associated references

Parameter	Value	Reference
Probability of pregnancy	0.8	Wallington field data
No of pups	1	(Stebbings, 1991)
Natural mortality - adult spring & summer	0.2	(Mortimer, 2006)
Natural mortality - adult autumn & winter	0.1	(Mortimer, 2006)
Natural mortality - juvenile spring & summer	0.6	(Mortimer, 2006)
Natural mortality – juvenile autumn & winter	0.4	Mortimer, 2006)
Incubation period – spring & summer	11 weeks	(George et al., 2011)
Incubation period – swarming period	11 weeks	(George et al., 2011)
Incubation period - hibernation	22 weeks	(George et al., 2011)
Infection rate	0.5	(George et al., 2011)
Length of infectiousness – spring & summer	2 weeks	(Amengual et al., 2007)
Length of infectiousness – swarming period	2 weeks	Assumed to be the same as summer due to high contact rates
Length of infectiousness - hibernation	4 weeks	(Amengual et al., 2007)
Probability of death after infection	0.5	Inverse of infection rate – all those who pass on the infection die

5.3 Results

The social networks at Wallington or Wytham do not fit power law distributions (Figure 17) (Wallington xmin = 47, and $\alpha = -0.33$, Wytham xmin = 2.87 $\alpha = -0.650$) therefore the hypotheses that the networks are scale free can be rejected.

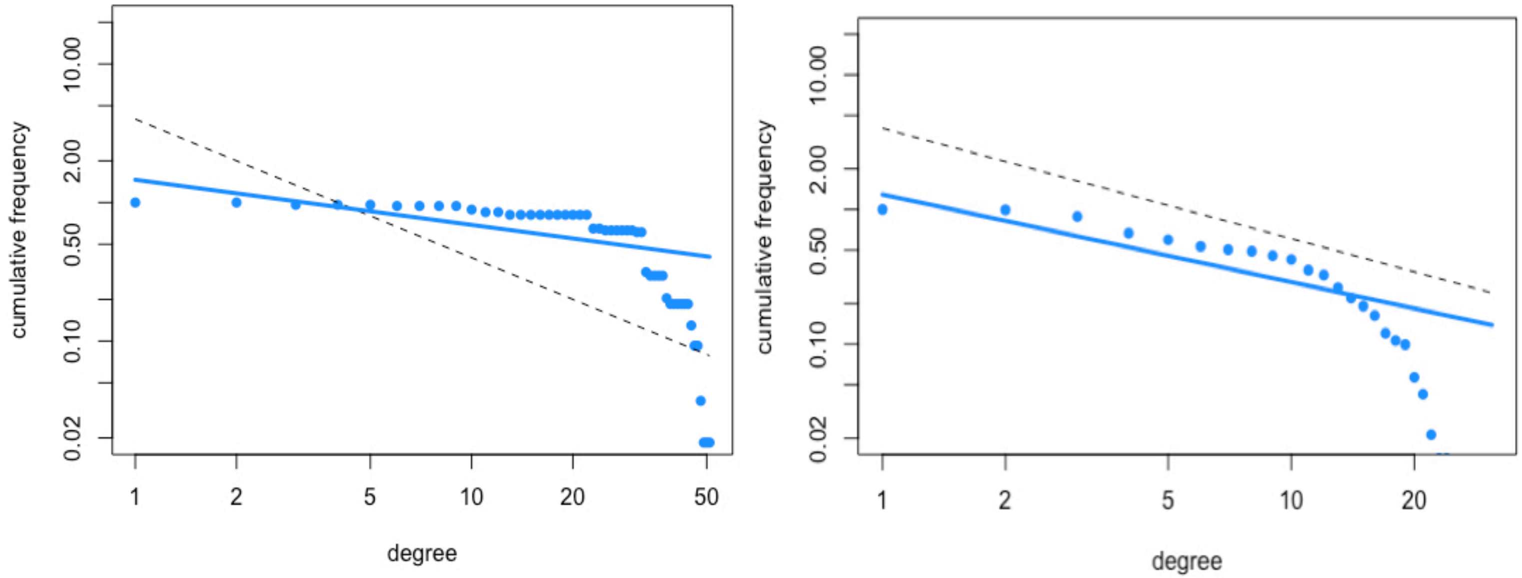

Figure 17 The cumulative degree distribution from the social network line of best fit (solid line) and power-law distribution fitted line (dashed line) for social network at Wallington (left) and Wytham Woods (right)

5.3.1 Network structure

There is evidence of significant structure in both the roost networks from Wallington and Wytham woods (Figure 18). Modularity was lower than random networks for both sites suggesting there was evidence of separation of groups of roosts, whilst degree, transitivity, betweeness and closeness were all higher than the randomised networks for both sites suggesting roost use was not random and particular roosts were more central or used more often than others.

The modularity scores from the social networks at both sites were no different than randomly generated networks suggesting the social networks contained no more or less separate communities than would be expected by chance. The scores for average degree, average transitivity, and closeness were all higher than expected suggesting bats were more highly connected and more clustered than randomly distributed individuals and some were more central to the networks (Figure 19). However, betweeness was no different to random indicating that no individual(s) acted as specific bridges between clusters than might be expected in a randomly distributed network.

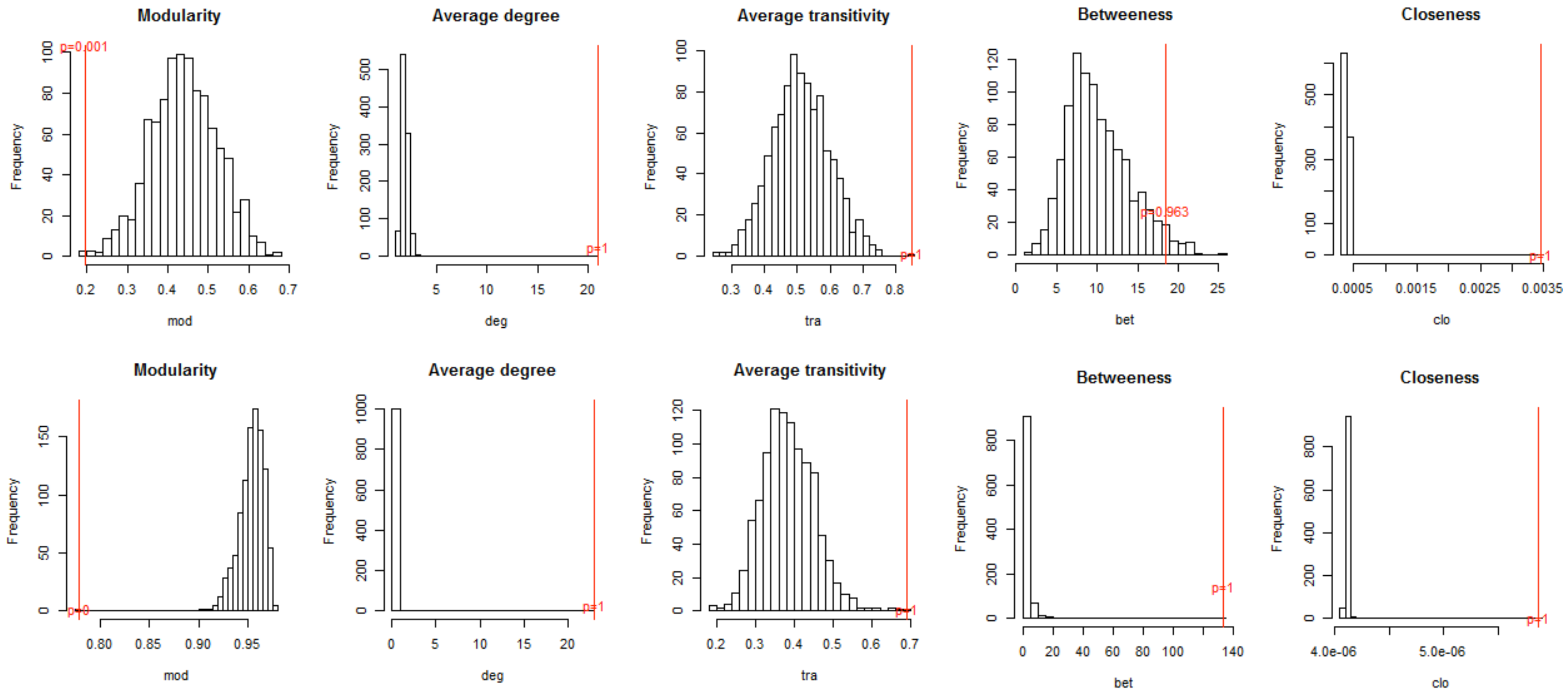

Figure 18 Comparisons of *roost* network metrics with random networks Metrics from 1000 permutations of random networks with actual network scores indicated by red line with the significance of the difference. Wallington *roost* networks (top row) and Wytham *roost* network (bottom row).

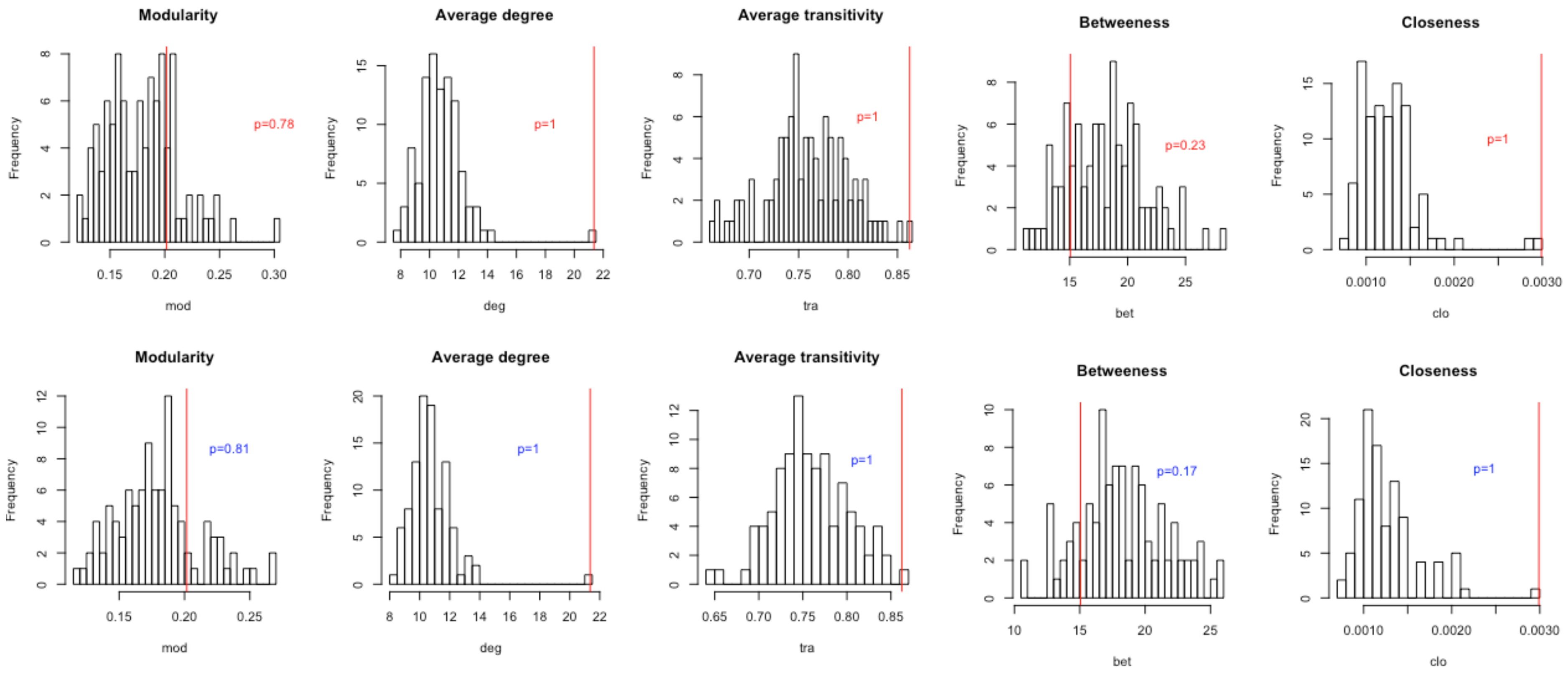

Figure 19 Comparisons of *social* network metrics with random networks. Metrics from 1000 permutations of random networks with actual network scores indicated by red line with the significance of the difference. Wallington *social* networks (top row) and Wytham *social* network (bottom row)

5.3.2 Comparison of natural v anthropogenic social networks

The social network at Wytham was much larger than that at Wallington (1303 bats compared to 42) but the Wallington network had a higher density of associations (Wallington = 0.554, Wytham = 0.017) (Table 19).

Table 19 Social network characteristics of bats from the Wallington and Wytham Networks Nodes are the number of bats, edges are the number of connections between bats, density is the proportion of completed edges in the network

	Wallington	Wytham
Nodes	42	1303
Edges	466	20167
Density	0.541	0.017

The social networks at Wallington and Wytham had different distributions (Figure 20), the number of contacts per individual observed in the Wallington network were much higher than the number observed in the Wytham data. In addition to this betweeness, and closeness were significantly higher at Wallington than Wytham after normalisation (Figure 21) (betweeness $F(1,1624)=218.55$, p = >0.001; closeness $F(1,1624=51430$, p = >0.001;) suggesting the social network at Wallington was better connected after accounting for differences in size.

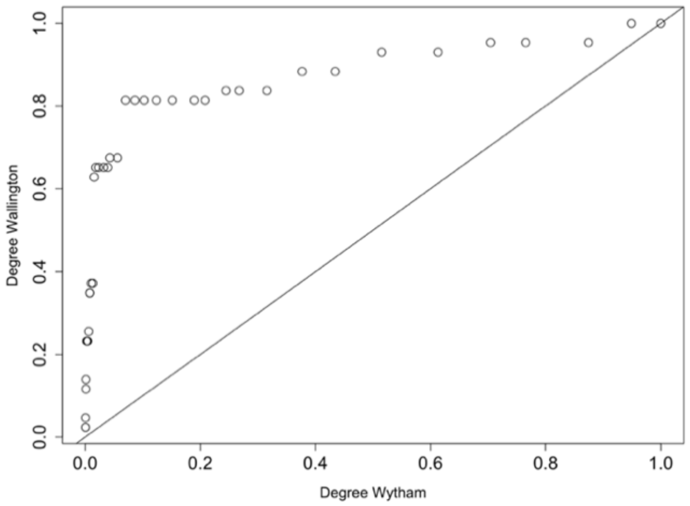

Figure 20 Quantile–quantile plots comparing the degree (contact) distributions derived from the social network at Wallington and the social network at Wytham. A 1:1 reference line is plotted

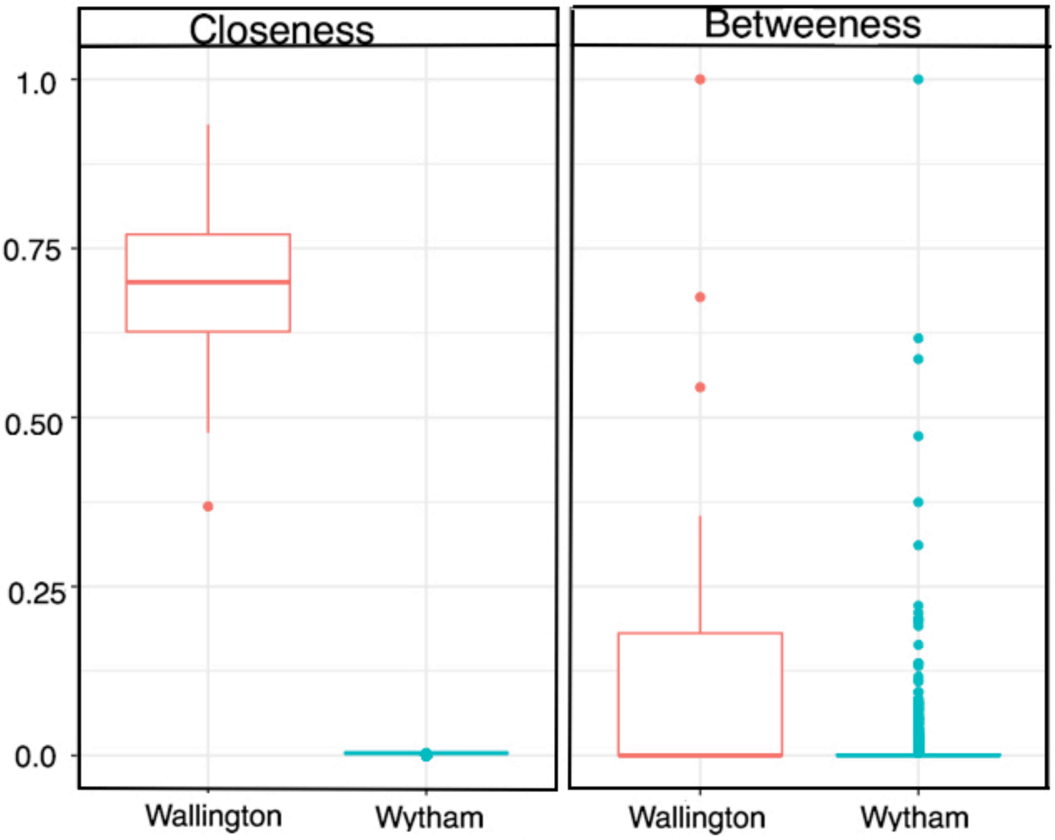

Figure 21 Normalised mean closeness and betweeness scores from social networks derived from the Wallington and Wytham datasets

5.3.3 Community detection

The most appropriate algorithm to use to describe both data sets was identified as 'cluster_fastgreedy' (Noack, 2009, Csardi and Nepusz, 2006) (Table 20). Wytham woods, with 18 communities (Figure 24), had a stronger level of community structure (Wytham Q = 0.86, Wallington Q = 0.26) and more robust data (Wytham rcom = 0.97, Wallington rcom = 0.36) than Wallington, suggesting that the number of communities found may be more stable over time. Although the algorithm suggested three groups at Wallington (Figure 22) it is likely that these are not separate communities but undergo a high degree of mixing due to the low modularity (Q =0.26) and robustness score (rcom =0.36) and are most likely part of one overall community, whereas the groups of bats at Wytham show higher community fidelity (Q=0.86) and are likely to be distinct.

Table 20 Comparison of community detection algorithms for Wallington and Wytham data (Q is the modularity index, and r_{com} is the assortivity index) * indicates selected algorithm based on highest r_{com} and *Q* values and most consistent number of communities)

Site	Algorithm	*c*	*Q*	r_{com}
Wallington	cluster_walktrap	5	0.19	0.38
	cluster_fastgreedy*	3	0.26	0.36
	cluster_leading_eigen	3	0.21	0.32
Wytham woods	cluster_walktrap	21	0.85	0.94
	cluster_fastgreedy*	18	0.86	0.97
	cluster_leading_eigen	18	0.85	0.95

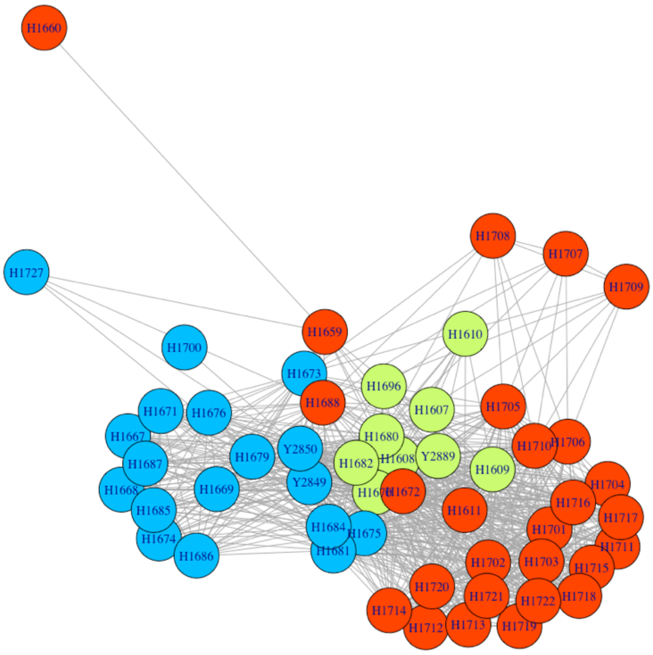

Figure 22 Social network diagram showing associated bats at Wallington as coloured nodes. Colours represent groups identified using 'igraph' 'cluster.fastgreedy'.

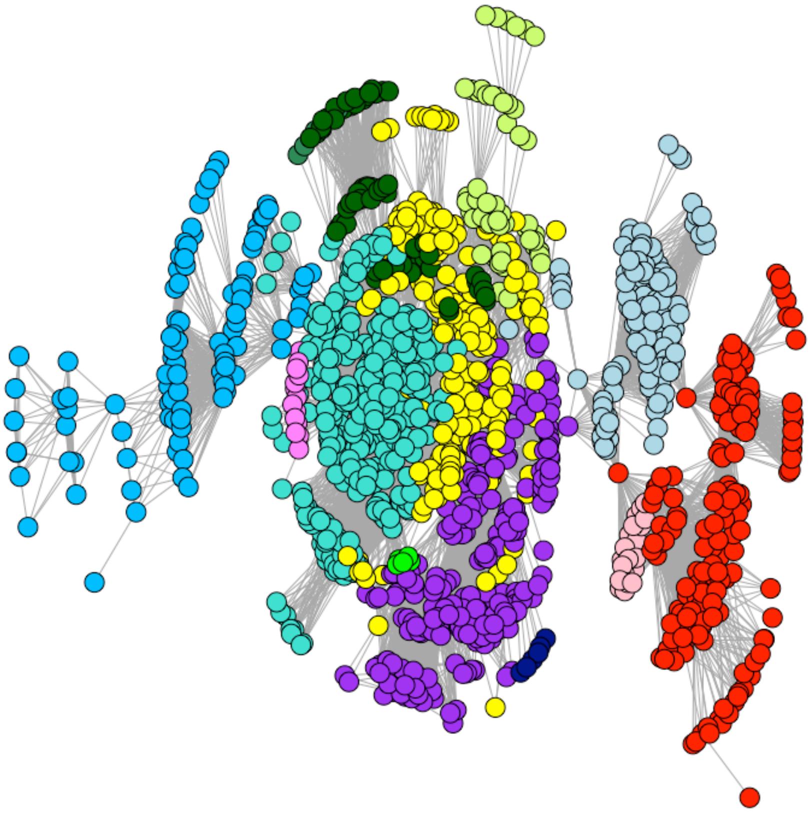

Figure 23 Social network diagram showing associated bats at Wytham woods. Colours represent distinct communities identified using 'igraph' 'cluster.fastgreedy'

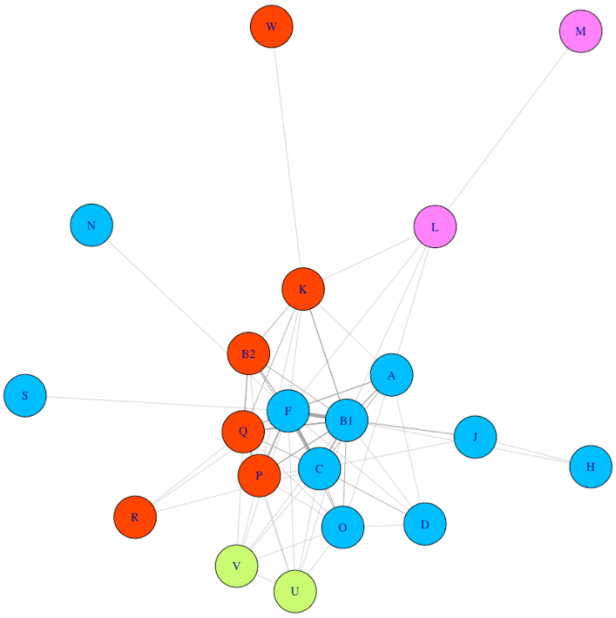

Figure 24 Roost network diagram showing associated roosts at Wallington woods. Colours represent distinct communities identified using ‘igraph’ ‘cluster.fastgreedy’. Nodes represent tree roosts

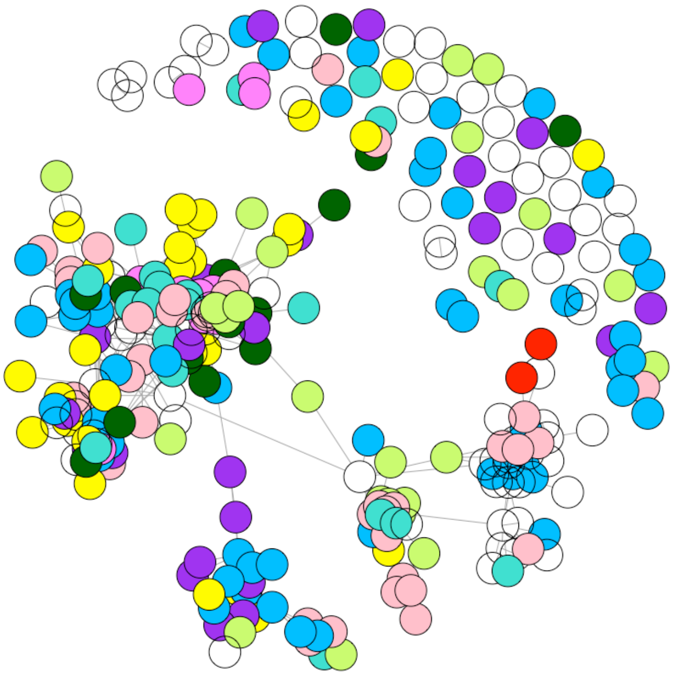

Figure 25 Roost network diagram showing associated roosts at Wallington woods. Colours represent distinct communities identified using ‘igraph’ ‘cluster.fastgreedy’. Nodes represent nest boxes, White nodes represent unconnected nest boxes.

5.3.4 Network structure and biometric data at Wallington

Degree centrality differed significantly as a function of reproductive condition, (Figure 26A: F(4,36) = 3.828, *p*=0.01) with lactating bats having fewer connections than others, but not as a function of age (Figure 26B: F(1, 39) = 3.289, p=0.08). A similar pattern occurred with lactating bats having low eigenvector centrality (little influence in the network) compared to others however the result was not significant (reproductive condition: Figure 26E: F(4, 36) = 2.99, *p*=0.08, age: (Figure 26F: F(1,39)=0.97, *p*=0.33). Betweeness centrality (the degree to which an individual acts as a contact between other members) did not differ by reproductive status (Figure 26C: F(4,36)= 0.398, *p*=0.808) or age class (Figure 26D: F(1,39)=0.963, *p*=0.332). More variance was observed in the adult data than juvenile data for all measures suggesting that adults vary more than juveniles in their level degree, betweeness and closeness.

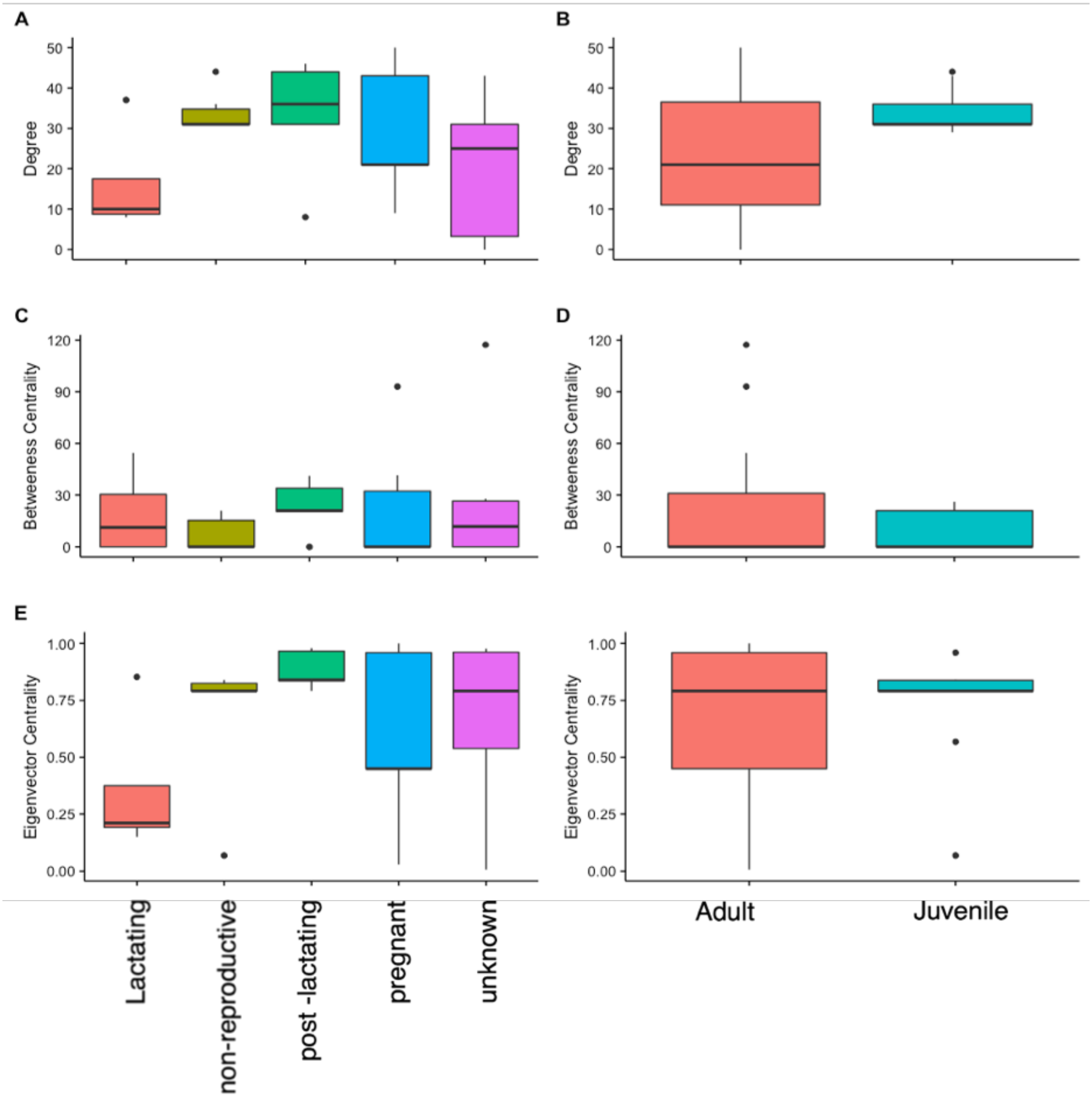

Figure 26 Mean ± se Degree, Betweeness Centrality and Eigenvector Centrality by Reproductive condition (A,C,E) and Age class (B,D,F) from the social network of female Simulated removal of roosts

5.3.5 Roosting association and relatedness at Wallington

Modularity was higher when vertices were not weighted by relatedness (Q unweighted 0.26, Q weighted 0.16) suggesting that individuals who roosted together more often (e.g. were in the same social group) were no more related than those in other groups (Figure 27). In some cases, siblings occured in three separate groups (e.g related individiauls H1680, H1720, H1679).

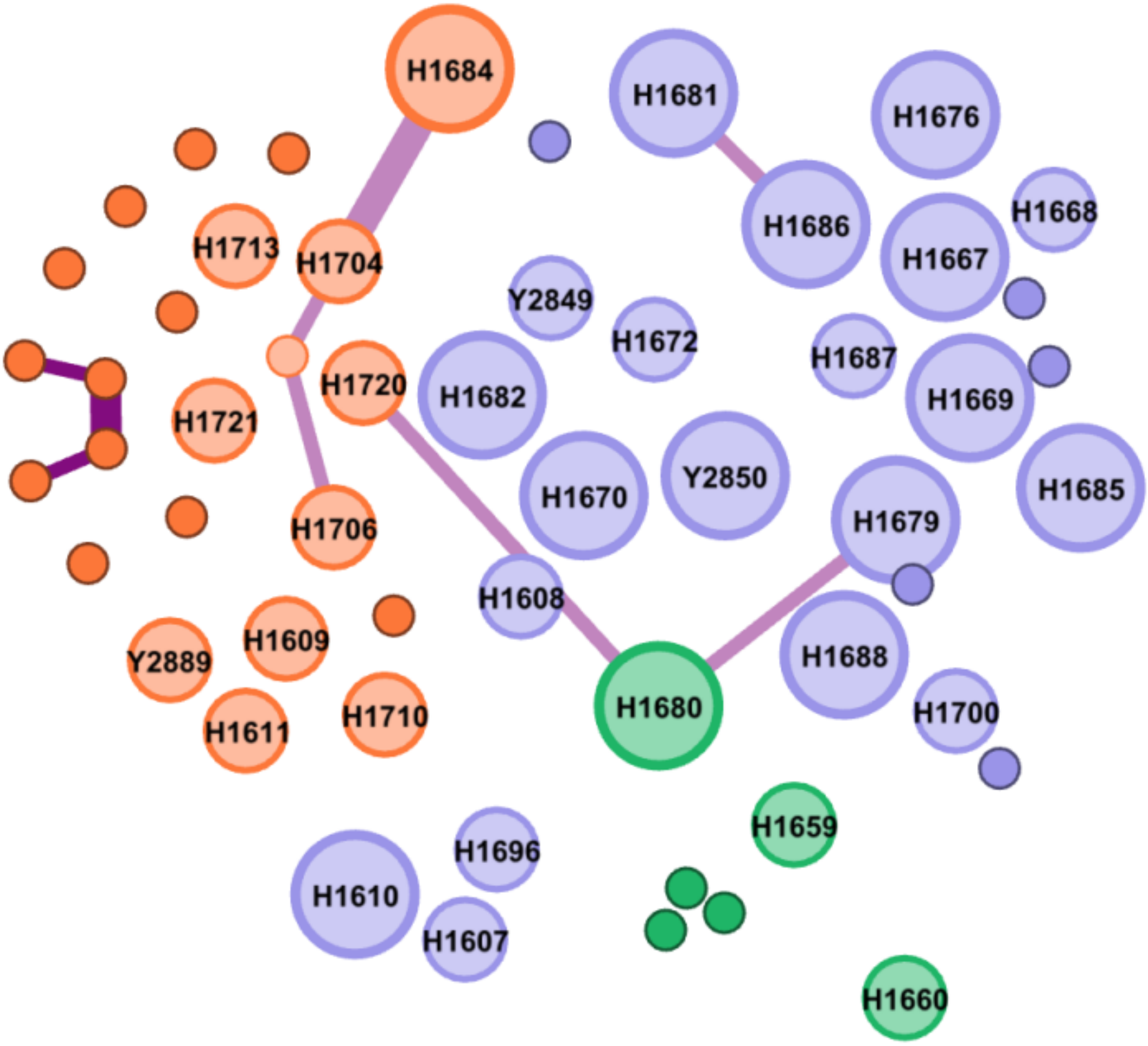

Figure 27 Social network diagram of relatedness. Thick lines indicate parent-offspring relationships; medium lines represent full sibling relationships. The absence of a line indicates that there was no relationship between individuals. Colours represent potential social groups. Large nodes represent pregnant females, medium nodes represent other adult females, small nodes represent juveniles and males

5.3.6 Roost density and removal simulations

The largest roost network at Wytham covered a larger area (31Km^2) than at Wallington (2.01km^2) and had a higher density of roosts used per Km^2 (18.86 Km^2 compared to 11.94Km^2) (Figure 28).

Figure 28 Roost locations for bats at Wallington (left) and Wytham woods (right). Roosts symbolised by red points and scaled by number of bat days used/10 to show the relative use by each community

Simulated roost removal on network fragmentation of the largest connected roost network at Wytham woods resulted in a linear increase in fragmentation from 10% until around 75% of the roosts had been removed (Figure 29). The roost network generated from the Wallington dataset began to fragment after around 25% of the roosts were removed; and once 75% of roosts the roosts were removed the network dissolved. Roost network division into two fragments required the simulated removal of 5% of the roosts at Wytham and 28% at Wallington.

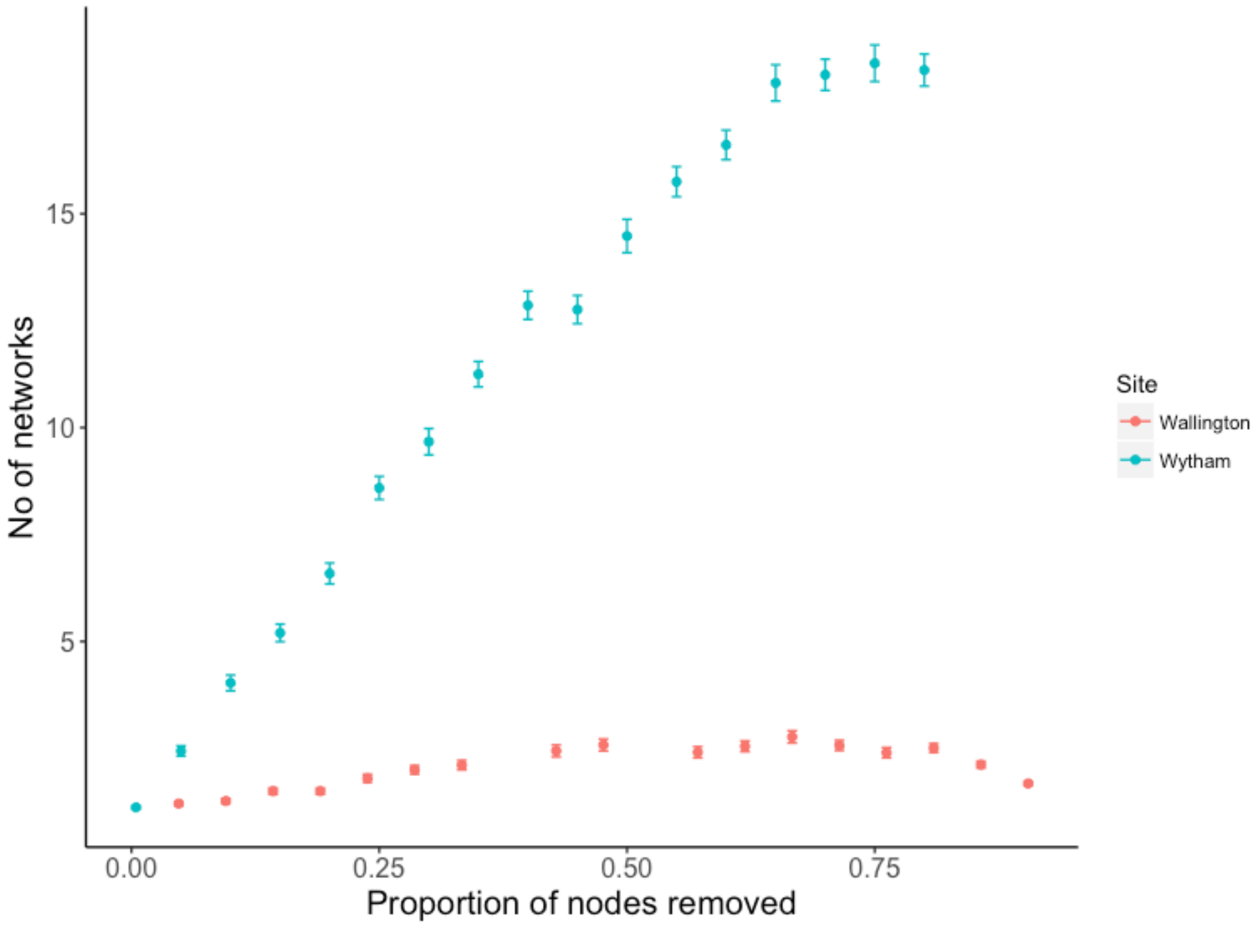

Figure 29 Simulated effect of node removal on the fragmentation of two roost networks. One sampled from Wallington, Northumberland and one sampled from Wytham Woods, Oxford. Random node removal was performed 100 times per proportion of nodes removed; mean and standard error of the number of resultant networks are presented

5.3.7 Disease modelling

When the base model was considered, the proportion of infected individuals dropped to a very low level during the summer seasons (weeks 1-16) and peaked during autumn swarming as a result of the breakdown of social structure into random associations and the addition of newly infected individuals (Figure 30). The mean proportion of exposed individuals in the Wallington network was higher than in the Wytham network, and the spread of disease was also quicker (exposure – panel E; Figure 12), however exposure to disease persisted longer in the Wytham network. At Wallington the proportion of exposed bats after 2 weeks was 62.15% ± s.d. 18.40, compared to only 27.75% (± 12.48) exposed after 9 weeks at Wytham. In addition, the mean proportion of infected individuals during the swarming periods was higher at Wallington than at Wytham (e.g. week 17; Wallington 26.94% ± 4.02, Wytham 8.08% ± 2.65).

The immigration models followed a similar pattern to the base model, but increased the mean proportion of exposed individuals at the start of the summer seasons in both networks. Aside from this they had little impact on the mean proportions of individuals infected or those who died from disease related mortality.

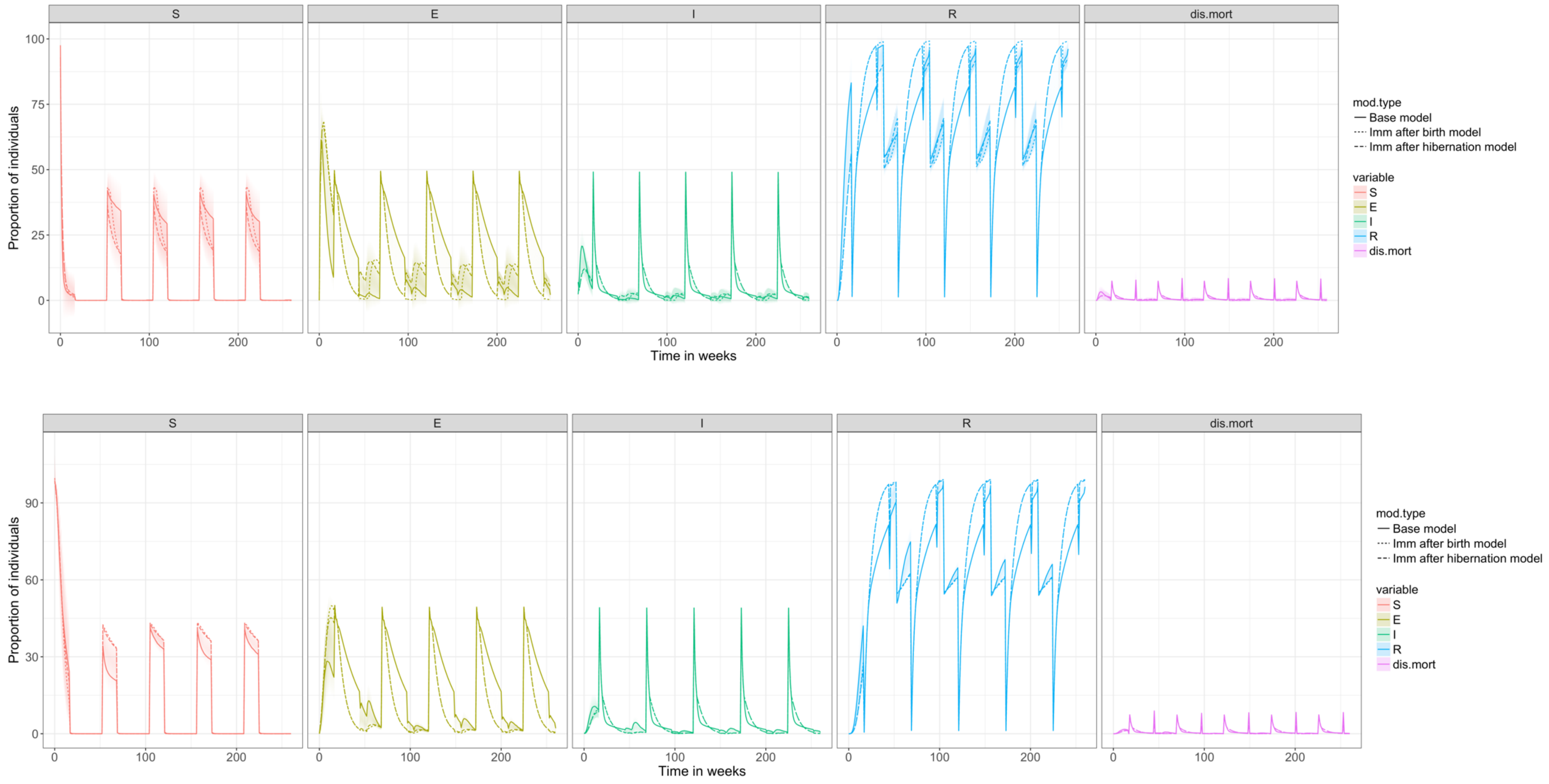

Figure 30 Base (solid line), Immigration after birth (dotted line) and immigration after hibernation (dashed line) models of disease dynamics from Wallington data (top) and Wytham (bottom). Simulated time series of mean proportion (± sd) of Susceptible (S), Exposed (E), Infectious (I) and Recovered (R) bats, along with numbers of bats dying died from disease related causes (dis.mort)) over 1000 runs of the model. Time series starts at week 1 of the summer season and runs for 5 year

Sensitivity analysis

The sensitivity of the model to its input parameters was investigated following Rushton *et al* (2000) by analysing the response to inputs of the total population size and the proportion of infected individuals in a simulated population of bats. The data from the sensitivity analysis were transformed into binary presence/absence of Bokeloh in a bat social group after 5 years. Latin hypercube sampling (LHS) was used to identify disease and population infection parameters to provide a range of input values for each variable that could occur in natural populations. The initial population was set to 43 individuals from the Wallington network. The effect on the proportion of infected individuals in the population was assessed by varying seven variables;

Length of infection during spring/summer

Length of infection during autumn swarming

Length of infection during hibernation

Incubation period during spring and summer

Incubation period during hibernation

Infection rate

Probability of disease related mortality

Each variable had 10 different values and the model was run 1000 times for five years with the final population size and proportion of the population infected as the outputs. The total population size was then correlated with the input variables in generalised linear models (GLMM) to investigate the effects of each of the input variables on population size. Partial correlation coefficients (PCC's) were calculated following Shirley *et al* (2003). PCC's reflect the contribution of that parameter to the outputs of the model, having partialled out the effects of the other variables in the model (Shirley et al., 2003). In addition to this, when modelling events of low probability such as the incidence of disease in natural populations it is likely that the frequency of animals predicted to have the disease will be low (Shirley et al., 2003) which may result in the presence of many zeros in the output data. Due to this, binary logistic regression analysis was used for the disease incidence data to identify variables contributing significantly to the presence of infected bats after 5 years.

Table 21 Partial correlation coefficients and associated F values after 1000 runs, relating the predicted total number of bats to the different life history parameters used in each model run

	PRCC	F - value	P - value
Probability of death after infection	-0.212	-21.687	0.000***
Infection rate	-0.009	-0.860	0.390
Incubation period hibernation	-0.007	-0.706	0.480
Length of infection during swarming	-0.007	-0.703	0.482
Length of infection during hibernation	-0.006	-0.609	0.543
Length of infection during spring/summer	-0.006	-0.595	0.552
Incubation period during spring/summer	-0.006	-0.550	0.583

The PRCC analysis suggest that the total population size was only significantly positively affected by decreasing the probability of death after infection (Table 21). The other variables had no detectable effect on total population size in the model.

Table 22 Significant predictors of Bokeloh persistence after five years from a binary logistic regression, arranged in order of importance (Z-value)

Predictor	Coefficient	Standard deviation	*Z* value	*P* value
Length of infection during swarming	-3.196	0.126	-25.278	0.000
Length of infection during hibernation	-2.916	0.132	-22.085	0.000
Probability of death after infection	-1.173	0.125	-9.416	0.000
Length of infection during spring/summer	-0.589	0.117	-5.017	0.000
Incubation period during hibernation	-0.474	0.131	-3.629	0.000

Of the seven variables described, only two were not significant predictors at the 5% level of the persistence of Bokeloh after 5 years in the simulation model—infection rate and the incubation period during spring and summer. Indicating that long term persistence of disease in the modelled bat population is mostly affected by the virus life history. There was 76% concordance between persistence of Bokeloh in the simulation model and the regression line fitted to it based on the five significant predictors (Table 22).

5.4 Discussion

5.4.1 Network structure

The evidence of social structure in the populations at Wallington and Wytham agrees with previous work that bats are social animals and use a network of roosts to which they return annually (Willis and Brigham, 2004, Webber et al., 2016, Park et al., 1998, Kerth et al., 2011, Kerth and Petit, 2005, Johnson et al., 2013, Entwistle et al., 2000, August et al., 2014, August, 2012, Altringham and Senior, 2005). Multiple roost use by bats is possibly a strategy for minimising exposure to parasites (Reckardt and Kerth, 2007), predator avoidance (Kunz, 2014b), thermoregulation or to maintain social structure (Willis and Brigham, 2004, Kerth and Reckardt, 2003, Kashima et al., 2013). It may also be an adaptive strategy to cope with unexpected roost loss (Silvis et al., 2014c). At both sites in this study the higher average degree, transitivity, closeness and betweeness of roosts compared to random roost networks, suggests that some roosts could be considered ‘primary’ and others ‘secondary’ based on the number of bats using them (Silvis et al., 2014c). Clusters of roosts exist within the networks and some roosts (those with high betweeness) could act as bridges between those clusters enabling the flow of information/transmission of disease/maintenance of social contact in an otherwise fragmented network.

The lower modularity score from the roost networks compared to random, suggests that roosts are not separated into different ‘communities’. Rather where modularity in roost networks is low, it is likely that all members of a population have knowledge of and use of all roosts which may make the network less vulnerable to roost loss (Silvis et al., 2015). Knowledge of roost location may be gained from previous experience, following conspecifics or perhaps via social calling (Schöner et al., 2010, Furmankiewicz et al., 2011).

In terms of disease transmission, according to network theory, higher degree (number of neighbours in a network) results in higher rate of disease transmission (Shirley and Rushton, 2005). Therefore, if the degree of roosts can be calculated or estimated based on the proportion of the population using them, one strategy to control the flow of disease within a population could be to limit access to the primary roosts (those with high degree) and effectively fragment the network. In this scenario, disease management and regulation supporting the maintenance of bat populations for conservation would need to be considered carefully along with the implications on network fragmentation. Although this might slow or prevent the flow of transmission it may effectively cause a fragmentation of the population or social perturbation (Carter et al., 2007) which may then cause individuals to disperse and recolonize another area (Weber et al., 2013, Silvis et al., 2014a) which could spread disease to new areas (Weber et al., 2013, Silvis et al., 2014a); rapidly spreading disease and potentially putting more bats into contact with more humans.

5.4.2 Social networks

Although the number of groups present in the social networks did not vary from random networks, there was still evidence of social structure at both sites suggesting that real bats preferentially associate with each other. There was also evidence that bats were more tightly connected and some bats played central roles in the networks suggesting at least two alternative hypotheses. That there could be a social hierarchy within the populations, or that bats may exhibit distinct personalities which mediate the degree of their social contact. Dominance hierarchy's in bats have been previously suggested (Kerth et al., 2003), however this phenomenon is difficult to study and to date small sample sizes have prevented definitive evidence being presented in the literature. Limited evidence to support this hypothesis is present within the Wallington data where lactating bats had significantly fewer connections than others at Wallington, although this could also be an artefact of the study, as lactating bats were particularly difficult to catch, possibly as a consequence of their behaviour being focussed on foraging or attending the pups in the roost limiting the number of associations recorded for them. Further evidence includes the large variance in the closeness and betweeness scores at Wallington (Figure 21) which suggests some individuals play more central roles in the network and the possibility of a social hierarchy – whilst other community members are only weakly connected to the society. In larger mammals this could be assessed more thoroughly with the use of proximity tags, which record incidences (time and location) of contact between two individuals. This technology is not small enough for use on temperate bats but an alternative could be to use new coded tags (Biotrack Ltd, Wareham. UK) which allow multiple tags to be detected on the same radio frequency but have an individual identifier. This would allow finer scale association data to be recorded that could be related to reproductive condition and age. In addition to coded tags, workers on tropical bats are currently developing custom tools to enable finer scale monitoring of small bats (Dressler et al., 2016).

The lack of evidence that bats within age classes at Wallington preferentially made connections with others in the same age class agrees with work by Silvis *et al. (Silvis et al., 2014c)* and suggests that the social structure of the network was not a result of segregation of roosts by age class but generated by adults and juveniles regularly associating with each other. It should be noted that the methodology used in this study did not consider changes in network structure over time, only the age and reproductive class at first capture. A more accurate representation of how age and reproductive condition affect network structure may be achieved if the change in network structure is considered over time; limited data prevented this at Wallington.

5.4.3 Natural v anthropogenic social networks

Although there was a higher number of bats and increased density of roosts at Wytham compared to Wallington, individuals at Wallington were better connected with lower modularity possibly due to the lack of separate communities which may have been enforced by the lack of available roosting sites. Although the perceived higher availability of roosts at Wytham, may have resulted in an artificially increased carrying capacity for the area, it is less clear whether roosts at Wallington were in fact limited. The character of the main roosting area described in section 5.2.1, included species known to produce substantial roosting opportunities (e.g. Oak – *Quercus sp*., Beech – *Fagus sylvatica*), suggesting that roosting opportunities may not have been limited. Indeed, it was a common occurrence during the radio-tracking to locate a bat hosting tree only to find that the visible lower quarter presented tens or hundreds of visible potential roost features (PRF), and that the emergence of the bat on subsequent nights was associated with obscured roosts higher up the tree. Thus the density of bats seen at Wytham may be driven by other environmental factors (e.g. climate, or availability of high quality foraging sites) and the local population has aggregated into multiple separate communities as an adaptive response to limit parasite load, predation or disease transmission (Reckardt and Kerth, 2007).

Although providing anthropogenic roosts for bats may increase numbers in vulnerable populations it should be noted that although separate communities are thought to be present at Wytham, there are links between those communities, either via shared roosts or individuals who spend time with more than one community. The higher density of bats present in a small area could therefore result in larger outbreaks in disease if strong links were present between communities. However, in the current description of bats at Wytham only weak links were present between communities, due possibly to individuals from different communities using a roost at a different time. In addition to this, there is limited evidence to support density dependant disease transmission in bat colonies (Streicker et al., 2012b). This could be explained by the presence of social structure in many bat communities which limits the number of contacts each animal has irrelevant of the total colony size. Further temporal analysis of the social network at Wytham would be useful to determine whether communities mix via direct contact between individuals or sites and to determine if social structure changes or remains stable over time. If individuals from different communities within the same area do not come into direct contact, then contagious disease would not be able to be transmitted to the wider population but may be contained within smaller communities and providing artificial roosts may be a good way of enabling vulnerable populations to recover.

5.4.4 Roost loss simulation

The roost network at Wallington was much less vulnerable to network fragmentation than the network at Wytham (Figure 29) indicated by the slightly lower betweeness and closeness scores (which represent decreased connectedness of the network) at Wytham along with the higher modularity score (number of separate groups of roosts,(Table 20; Wallington 0.2, Wytham 0.8). Where modularity is higher, there are more potential partitions in the network therefore the removal of those roosts which connect groups will more readily result in fragmentation. When the roost network becomes fragmented, social structure is also likely to be affected as individual bats will no longer encounter each other via shared roosts. This could result in small socially isolated and unviable communities which become locally extinct, or alternatively could be a mechanism driving the formation new communities and additional nursery sites. It has also been suggested that social association in bats is not limited to interactions in roosts but may occur while bats are foraging via social communication e.g. (Silvis et al., 2014c, Jonker et al., 2010, Wilkinson and Wenrick Boughman, 1998, Brooke, 1997). However, in Natterer's bats there was no supporting evidence of foraging site overlap between conspecifics of the same roosting colony (see 2.2.6) suggesting that social cohesion whilst foraging may be limited in this species. It is useful to speculate that social communication outside of the roost occurs (Naďo and Kaňuch, 2015, Naďo and Kaňuch, 2013). Communication outside of the roosts may enable colonies to stay together(Naďo and Kaňuch, 2015, Naďo and Kaňuch, 2013)and enables community cohesion despite losing primary roosts. The roost removal simulation carried out here was random and did not account for the relative use of the removed roosts, it is possible that the removal of more centralized roosts (those with a higher degree) would have a much more severe impact on the network fragmentation (Silvis et al., 2015).

5.4.5 Disease transmission

The differences between Wallington and Wytham, in the rate of spread of disease were notable. Spread was much quicker across the social network at Wallington and was probably due to the lower modularity, higher mean closeness and higher density of the single community at Wallington, in contrast to the highly modular Wytham Table 20. Faster spread in networks with low modularity has been described by Cross *et al.* (2009) who suggest the lack of substructure in networks with lower modularity makes them more susceptible to rapid spread of infection due to the limited connections present between the communities. Although the largest connected component was used from Wytham for comparison with the Wallington network, an alternative approach might have been to consider the structure of a random single community at Wytham for more consistent comparison to the single community at Wallington. Further work might consider the similarities and differences in the social structure of single communities of temperate bats at natural and anthropogenic sites. Particularly at sites where bats aggregate in large numbers such as in churches (Hales, 2014). It is likely that when transmission is a function of direct contacts, prevalence will increase with increased group size or density (McCallum et al., 2001). This was observed in a recent study on Big brown bats *Eptesicus fuscus* where modelled transmission of disease through a social network of bats roosting in a building occurred much more rapidly than in natural tree roosts (Webber et al., 2016).

Individuals with high closeness scores indicate those with multiple connections to others in the network and who might facilitate ‘super spreading’ of disease through a network (Craft and Caillaud, 2011). In addition, high network density which measures the fraction of all possible links that are realised within a network also explained the increased transmission rates in the Wallington model. Further modification to the model could identify closeness values of individuals and examine the speed of transmission when individuals are infected at the start of the model have varying values of closeness. It would be expected that where an individual with high closeness is infected at the start of the season, the disease would spread much more rapidly (Perkins et al., 2009). Management of disease spread in bat populations and other mammals could assess closeness values of individuals via SNA and then perhaps use this information to determine which individuals to vaccinate to limit the spread of disease.

The model only considered female bats during the summer season before random mating in the autumn. There was limited information available on males (due to few males being caught) during the summer season to be able to parametrise their inclusion in this part of the model. With finer scale association data, e.g. through the use of coded tags, then associations between males and female within the roost networks could be modelled. It is possible that males may be more susceptible to disease due to increased home range size e.g (Safi et al., 2007) which may increase exposure and increase their probability of being infectious. In addition to this male bats in summer may link otherwise separate female communities potentially transferring disease between communities in the summer. During autumn swarming males may also experience increased stress levels which along with the suppressive effect of testosterone on the immune system, which again may increase their susceptibility to disease (Zuk and McKean, 1996). It would be beneficial to be able to parameterise and further develop the model to include effects of increased male susceptibility in order to more effectively predict disease spread.

Model sensitivity

The only variable to affect population size in the simulated model was the probability of death after infection. This could be expected as the number of bats dying from disease will have a direct effect on the population size. It is surprising that the virus life history had no effect on population size and this could be due to the social structure of the bat populations acting as a barrier to disease spread (e.g. (Griffin, 2012, Calisher et al., 2006). The theory of social structure acting as a barrier to disease spread is further supported in this work as disease spread in the modelled population was not infected by infection rate. In addition to this, virus persistence in the modelled population was not affected by incubation period in spring and summer but an increase in incubation period during hibernation and swarming led to a decrease in virus persistence. Varying the life history effects of the virus during hibernation and swarming may have had more of an effect the during spring and summer due to the lack of social structure modelled during this time which would allow the virus to move freely between individuals rather than following the pathways of a social network. A lack of relationship between host density and rabies seroprevalance has previously been reported owing to the social structure of bat populations. This is likely due to bats having a limited number of neighbors even in very large colonies (Streicker et al., 2012b). It is also likely that bats and lyssaviruses have co-evolved strategies which allows the virus to persist in the population without having severe detrimental effects. The persistence of disease in the absence of pathology in bats is widely reported (Wang, 2011) and indicates a highly evolved relationship between host and pathogen. While long term survival of the virus can be achieved in the absence of disease or mortality, there may also be biological advantages to the bats who harbor disease, this could be via symbiotic enhancement of innate immunity (it prevents the bats from contracting other illnesses) or protection from predators e.g. a defensive biological weapon (Wang, 2011). One theory is that the virus may be released when there is an imminent threat of danger, indeed zoonotic spillover events from bats to livestock/humans seem to occur when bat populations are directly threatened via increased pressure on their natural habitats (Wood et al., 2012, Poel et al., 2006, Openshaw et al., 2016). This support the need for an integrated One Health Approach when considering disease management (Narrod et al., 2012, Lu et al., 2016, Coker et al., 2011, Bidaisee and Macpherson, 2014).

Chapter 6. General discussion

6.1 Introduction

The aim of this thesis was to better understand how the spatial and social dynamics of the Natterer's bat affects its successful conservation, efficient management where there is conflict with humans, and most importantly the epizootiology of associated disease. Understanding the mechanisms and drivers of bat populations to improve their viability is not only a legal requirement due to existing legislation (92/43/EEC, 2002) or solely important so that we may benefit from the ecosystem services they provide (Kunz et al., 2011, Ghanem and Voigt, 2012), it is also important due to potential disease spill over from bats to humans. One Health, recognises that the health of humans, animals and ecosystems are all interconnected. The initiative, which plays a significant role in the prevention and control of zoonoses (Bidaisee and Macpherson, 2014), acknowledges that disease spill over from animals to humans gets progressively worse as humans successively alter the environment and impinge upon ecosystems and the species they support (Zinsstag et al., 2012, Narrod et al., 2012, Lu et al., 2016),and that zoonoses should be considered to be the most important factor to human health and well-being (Lu et al., 2016). Bats carry many zoonotic diseases of concern both to human health and to the conservation of bat populations (Calisher et al., 2006). Therefore, by better understanding bats and their resource requirements, social structures and movements we can hopefully better conserve them and our ecosystems whilst at the same time preventing disease spill-over to humans.

It has been suggested that the population viability of wild populations strongly relies on their social structure (Snijders et al., 2017) which can be severely disrupted by anthropogenic changes to the landscape (Banks et al., 2007, Debinski and Holt, 2000). Habitat loss (the removal or degradation of roosts or foraging area for bats), might increase encounter rates with man due to a decrease in resources leading to the fragmentation of social structures or to individuals clumping together in areas where resources are still available e.g. large numbers of bats roosting together in churches (Zeale et al., 2016, Hales, 2014). Direct impacts, such as these scenarios will in turn impact disease transmission rates and pathways and understanding these underlying mechanisms is key to management.

The disease of focus in this study is Rabies caused by Bokeloh bat lyssavirus, thought to be carried predominantly by Natterer's bats (Picard-Meyer et al., 2013, Freuling et al., 2011). Disease transmission of Rabies from bats to humans is a growing health concern around the world and is one of the greatest causes of human rabies deaths in the United States (Lu et al., 2016). Unlike other animal vectors of rabies such as foxes (Freuling et al., 2013) and racoons (Rosatte et al., 2007), bat rabies is likely to be harder to control and much quicker to spread due to the flight ability of bats and their capacity for travelling large distances. For example the transcontinental spread of WNS in bats in North America (Coleman et al., 2015). In order to predict the spread of disease and put in management protocols for outbreaks, there is a need to better understand how bats utilise the landscape, both at a local scale (such as foraging and roost switching within a summer colony) and at a national scale (e.g. bat movements between sites or disease transmission to bats from neighbouring sites during autumn swarming).

Although a couple of studies have considered the roosting requirements or social structure of Natterer's bats (August et al., 2014, Smith, 2000) at present there is no information about Natterer's bats in entirely natural settings and limited information in general about temperate bats in natural settings, even though the majority of bats are likely to live in natural settings. Our data from Wallington, Northumberland attempts to address this by considering the social network of bats roosting entirely in trees. In addition to this, there is also limited evidence in the literature on the movements, either physical or genetic between bat populations which I also attempt to address (see 3.4).

This chapter summarises findings from the previous chapters where I have considered how the spatial and social dynamics and genetic structure of Natterer's bats may affect disease transmission in natural and anthropogenic settings and put my inference into a broader context of disease and conservation management advice.

6.2 Spatial dynamics

This study showed that bats at two contrasting sites in Northern England exhibit individual specialisation in their habitat choice. In contrast to previous work by Smith (2008) who suggested that Natterer's preferred semi-natural broad-leaved woodland and river corridors or conversely Mortimer (2006) who reported a preference for mature Corsican pines and water bodies, I suggest the idea of preferred habitat types for Natterer's bats should be rejected and conservation management plans should consider protecting a mosaic of habitat types per colony.

Individual specialisation in animals is a growing area of research and is evident in many taxa, see Bolnick *et al*. for review (2002). Group living, with individuals of similar reproductive condition, often results in increased competition for prey and the use of different foraging habitats may be one way in which individuals may decrease intraspecific competition whilst still gaining the benefits from group living (Rossman et al., 2015, Votier et al., 2017) e.g. increased reproductive success or decreased risk of predation (Wells, 2014). It is also possible that specialisation provides a route for evolutionary change which may enable species to more easily adapt to landscape or climate changes (Bolnick et al., 2002). Individual specialisation is rarely reported in temperate bats, (Cryan (2012)), although it is highly possible that it is a common phenomenon among other bat species. If only the average habitat choices of the colony are inferred e.g. with the use of compositional analysis (Aebischer et al., 1993), specialists' habitat choices may not be accounted for or protected which could result in a loss of specialists from populations. Although it is debatable whether pups learn where to forage directly from their mothers (Brigham and Brigham, 1989, Audet, 1990), there is growing evidence of social communication (Siemers and Kerth, 2006, Leonard and Fenton, 1984, Kastein et al., 2013) and social feeding (Übernickel et al., 2013, Jones et al., 2014, Gillam, 2007, Dechmann et al., 2009, Balcombe and Fenton, 1988) in bat species which suggests social learning within populations. Whether pups learn where or how to forage from their mothers or other members of the social group is irrelevant at the population scale, as some pups will undoubtedly follow the same habits of the specialists. Therefore, the loss of a few specialist bats from a population could result in the loss of specific foraging habits for generations. This could have negative impacts as the climate changes or the landscape is modified, as populations will no longer be able to adapt as easily to landscape or climate change. Further work on bats and habitat use should therefore first include an assessment of whether bats are exhibiting individual choice in their habitat requirements in order to effectively prescribe conservation management plans.

The finding that Natterer's bats are faithful to their foraging sites over time agrees with work by Hillen *et al* (2010) and Kapfer *et al* (2008) who describe foraging fidelity in *Barbastellus barbastellus* and *Myotis daubentonii*. With the addition of Natterer's bats, it is likely that this behaviour is common in many other species of temperate bat and further work should attempt to find more supporting evidence. Although fidelity to a particular area of the landscape potentially enables longer term conservation prescriptions and a good understanding of the areas where bats and humans may come into contact, it also causes concern as to the effect of landscape change on bat populations, both short term e.g. planting/removal of trees or long term effects associated with climate change. Returning to the concept of One Health, changes to the landscape where a bat population faithfully forages could result in colony fragmentation, local extinction or relocation which could have the effect of reducing long term population viability of the species and/or putting more bats into potential contact with humans. Therefore, a better understanding of how adaptable temperate bats are to changes in the habitat composition of their foraging areas and whether change in habitat composition results in population fragmentation or displacement is urgently needed both to conserve bat populations and mitigate the health risks associated with bat-human contact.

6.3 Genetic population structure

Although previous work on Natterer's bats has included assessment of genetic population structure both in the UK (Rivers et al., 2005) and Germany (Halczok et al., 2017), the two studies contradict each other somewhat in their findings. Rivers *et al*. (2005) suggest that mating at swarming sites results in a single effective population with high genetic diversity whilst Halczok *et al*. (2017) provides evidence of significant population differentiation across three regions. The samples analysed in the study by Rivers *et al*. (2005) where collected over a relatively small geographical area in the North of England including Yorkshire and County Durham, whilst the samples in Germany were collected over a broader geographic scale and analysed with a higher number of loci which may have enabled finer scale differentiation to be collected. The study by Halczok however did not include samples from within the same region to allow for comparison between regions and the study by Rivers perhaps did not use a large enough number of loci to differentiate populations within a region. Our work attempted to address the gap in knowledge to determine whether within and or between region genetic population structure exists in Northern England and relate that to potential disease transmission.

This study suggests for the first time that summer communities of Natterer's bats are genetically distinct from each other even if only a few tens of a kilometre apart. This conflicts with previous genetic work by Rivers et al (2005) but supports the concept that Natterer's are faithful to their summer roosting sites over a long period of time (Rivers et al., 2006). It Is known that genetic differentiation takes hundreds of years to become detected (Gauffre et al., 2008), therefore it can be assumed that the individuals in this study have been returning to their natal landscapes for many generations and highlights the importance of protecting those sites.

The genetic differentiation between sites could be one mechanism by which bats evolve to changes in the landscape or climate over time and indeed at the two sites from which habitat data was collected (Wallington and Low Catton), bats used their landscapes in very different ways, supporting this theory. In addition to this, the new haplotypes (which differed from European Natterer's bats) at one site in North Yorkshire which also had estimated low emigration rates, further supporting the theory of evolutionary change. Individual specialisation in habitat choices could be one mechanism driving evolutionary change which results in new mitochondrial haplotypes. Schreiber's' long fingered bat *Miniopterus schreibersii natalensis* consists of three distinct subpopulations, which are associated with distinct habitat types

(Miller-Butterworth et al., 2003). Further work might look to test this theory by examining habitat choices of individuals compared to other members of the population before carrying out mitochondrial analysis. This suggests that a new tool in the landscape scale conservation of bats may be to explore the genetic diversity of populations, and ensure that the most genetically diverse are conserved to provide the best opportunity to permit the evolution of new phenotypes or behaviours as climate change adaption. As the IUCN's current assessment for Natterer's bats is of 'Least concern' evidence of differentiated species could result in modifications to their threat status.

Surprisingly, a low level of within population relatedness was present at each of the five sites in this study. This could have been due to a lack of paternally related individuals (Kerth et al., 2002b) caused by random mating at autumn swarming sites (Rivers et al., 2005). However, as female Natterer's are known to philopatric to their summer sites, a high level of mother daughter pairs were expected which were not found at any sites, in contrast to Kerth *et al's.* work on *Myotis bechsteinii* (2002b). Sample sizes and number of loci used in Kerth's study and this study were similar (Kerth sampled 145 bats from four colonies with 11 loci, here 152 bats were sampled from 5 colonies with 15 loci) suggesting the difference is not related to sample size. Although previously it has been suggested that female temperate bats do not move between colonies (Kerth and Konig, 1999, Entwistle et al., 2000, Rivers et al., 2005), our data suggests that female immigration does occur between summer sites (Wilkinson, 1985). One theory to explain females moving colonies could be that poor quality habitat or difficult environmental conditions at sites in Northern England keeps the population below its carrying capacity. At the sites studied, Natterer's are very close to the cold 'northern' edge of their European range which I anticipate would produce erratic population dynamics and marginal Favourable Conservation Status. Certainly at Wallington, weather conditions throughout the reproductive period were often sub-optimal for night time foraging which could result in reduced reproductive success and in the population being well below its carrying capacity. Indeed, the estimated population size at Wallington (Northumberland) was much lower than the other sites slightly further south in North Yorkshire and Lancashire (with presumably more favourable foraging conditions). If this is considered in the context of the meta-population paradigm (Hanski and Gilpin, 1991), where summer communities are connected through dispersal across wider regional structures, with Philopatry to the natal community the default behaviour, and dispersal a consequence of over-crowding. Where conditions are optimal, perhaps further south or in a landscape with a high abundance of food, the sub-population(s) may periodically exceed carry capacity, which may drive dispersal into surrounding areas. These optimal sub-populations will be dominated by extensive matrilines which persist for many generations. This might explain why Kerth found a higher proportion of mother-daughters pairs in the South-Eastern forests of Germany (2002b) where weather conditions are more favourable. Conversely, sink sub-populations are consistently stressed by low reproductive success and maybe even higher rates of mortality and are often well below a notional carrying capacity. These areas receive and retain dispersing females from surrounding communities; producing the low rates of matrilineal relationships observed here. To confirm or refute this theory, a more complete survey of Natterer's bats in England could be carried out, including sites further south with warmer more stable weather conditions, or possibly large, apparently successful and numerous communities in churches. Habitat and weather quality of sites could be assessed along with levels of relatedness. It would be expected that higher levels of relatedness would be present at sites with more favourable conditions. This information could then be used to assess which variables make for more successful conservation management prescriptions. This further work on levels of relatedness across the UK would also provide information on the degree of interactions between bat communities and so that the geographic scales at which bats might move and disease might spread van be described.

The high genetic diversity in our data supports the idea of gene exchange at swarming sites, suggested by Rivers *et al* (Rivers et al., 2005) but this work extends the presumed distance Natterer's bats can travel to those sites. High genetic diversity is important to maintain in populations in terms of conservation as previously mentioned but the ability of bats to travel longer distances to mating sites raises concerns for disease transmission. An example of this can be seen with the Aids epidemic in Africa where increased road networks and movement along those roads had led to previously isolated communities experiencing outbreaks (Oster, 2012) or the spread of WNS throughout the USA (Coleman et al., 2015). Understanding the disease dynamics of bats should improve our ability to inform practical disease management solutions.

6.4 Social dynamics and disease transmission

Bats are known to be carriers or reservoirs for a wide range of zoonotic diseases, notably Rabies, Sars and Ebola. Although rabies is the disease of focus in this study, our results may be applied to other diseases of concern. Sylvatic or classical rabies (rabies lyssavirus - RABV) is known to cause 100% fatality in humans although there is an effective vaccine and with associated with effective post-exposure treatment is considered to be preventable (Tekki et al., 2013). However, it remains a significant cause of mortality in developing countries and this is thought to be due to a lack of coordination between scientists, veterinary and public health officials (Singh et al., 2017) with highlights the need for a One Health approach. Rabies control programmes are underway in some areas with the vaccination of carnivores including dogs and raccoons (Rupprecht et al., 2005), though in counties where it is also present in bats (e.g. USA) the fast long-distant flight of bats and their cryptic nature have deterred authorities from attempting vaccinations programs for bats. At present the epidemiology of RABV is largely unknown therefore to provide advice based on the One Health framework, modelling is essential to test various scenarios and hypothesis, e.g. targeted vaccination or roost size limitation. Our work attempts to better understand transmission of rabies in bat populations with the development of a base epidemiological model which may be then be modified and used to help make informed decisions for its control.

This study has addressed the two most likely transmission periods during a bat’s year, which vary greatly in the number of contacts.

1. Summer-continual short daily movements and resorting across a network of roosts in mostly closed populations
2. Autumn- Long distance movements with a very large number of potential contacts

Over winter hibernacula was also accounted for, with large numbers of contacts but reduced transmission rates owing to the bats being in torpor. The model developed predicts that autumn swarming enables virus maintenance and increased transmission owing to the large numbers of bats and random association patterns, highlighting the need to monitor summer populations of bats where the virus may be controlled before it reaches a much larger and widespread number of bats.

6.5 Zoonotic spill over to humans

An important aspect of zoonotic spill over from bats to humans is the change in social dynamics between natural and anthropogenic roosting structures. The loss of natural roost sites results in an increase in the colonisation of anthropogenic structures including buildings which house livestock or humans (Webber et al., 2016), for example bats roost in large numbers in Churches in the UK (Zeale et al., 2016, Hales, 2014). Although further contrasts between artificial and natural roosts are needed for firm conclusions, this study found a higher density of individuals at Wytham which had artificial roosting boxes compared to the natural roosts used at Wallington. This provides some support for evidence from Voigt *et al*. (2016) who suggest artificial roosts result in much higher densities of bats than natural settings. Higher roost fidelity and more consistent interactions between individuals such as those presumed to occur in buildings, could increase virus transmission and numbers of infected individuals through increased association rates. This, along with the increased proximity to humans could then result in a greater likelihood of spill-over to humans or livestock from contact with diseased bats. An example of where this has occurred is in Malaysia where increased agriculture led to an increase number of flying foxes (*Pteropus vampyrus*) roosting close to pigs which is attributed to the emergence and persistence of the Nipah virus. In addition to this an increase in agriculture in Australia is attributed to the Hendra virus spillover from bats to horses (Plowright et al., 2015).

Both of these diseases resulted in human deaths (Daszak et al., 2006). This highlights the importance of preserving and or enhancing natural roosting habitat for bats (Webber et al., 2016) to encourage them to remain in natural settings.

6.6 Artificial roosts and disease

If artificial structures are to be offered as bat roosts, e.g. bat boxes, it may be beneficial for them to be designed to prevent unnaturally high numbers of bats from roosting together to prevent or slow disease transmission. Although the model indicates a slower rate of transmission overall at Wytham, the largest connected component at Wytham was modelled which included several communities, whereas the Wallington model only consisted of a single community. It has been suggested that roost switching in bats is related to micro climate (Willis and Brigham, 2004, Kerth et al., 2001b, Boonman, 2000) therefore one way of doing so could be to vary the size of boxes used and/or vary the micro climate inside the boxes. A variety of boxes could then be used within an area resulting in a number of different microclimates being available to a population. This might more effectively mimic natural tree roosts and encourage frequent roost movements as seen in natural settings which may also have the added benefit of limiting disease transmission.

Buildings utilisied by bats typically have higher numbers of bats than natural settings although it is not clear if buildings provide multiple micro roosts with different micro climates inside a large space such as a loft and further work could involve tracking the movements of individuals inside loft spaces to see if they do indeed switch roost positions and or associations, perhaps with the use of coded nano-tags (Biotrack, Wareham. UK) and automatic receivers so as not to disturb the behaviour unduly. Coded tags, attached in a similar way to radio tags (see 2.3.2) would enable the tracking of many individuals at the same time, similar to the use of PITT tags however, they will also fall off the bat after 10-14 days as the fur grows back and are not regarded as an invasive procedure under the Animals in Scientific Procedures Act (ASPA) (Hollands, 1986). In addition to this they can be used with either mobile receivers attached to antennas from a distance, or static receivers left in situ. This association data could then be used to inform our epidemiological model of the social structure in a building and predict disease occurrence and the potential spill over to humans.

The bat colony in the artificial setting studied here had a higher number of groups and was more prone to fragmentation than the population at the natural site which may lead to an increase or decrease in virus prevalence or transmission, but further work on temporal network changes is needed to better understand this. Higher roost fidelity and more consistent interactions between individuals could increase virus transmission – then epidemics could occur and pass to humans or livestock in buildings (Daszak et al., 2001).

6.7 Further work

The lack of knowledge available about social interactions and therefore disease transmission in bat populations suggests the need for further work in this area, which may involve the collection of further data. However, there are a number of challenges associated with collecting such data. Our work was one of a limited number which have attempted to catch bats from an entirely natural setting of tree roosts. Although radio tracking along with catching from roosts was used here, ideally, to collect fine scale association data from natural roosts, PITT tagging would be used to monitor daily associations and roost switching. In order to do this and to gain an accurate representation of the population, a large enough sample size of bats would need to be caught and tagged. In this experience in areas of mature woodland, Natterer's bats, and likely many other species, fly much higher than standard mist net height and quite often at canopy level which make catching from free flight initially very difficult. It is also difficult to locate natural tree roosts, even with the use of thermal cameras and after radio tracking individuals back to individual trees, owing to foliage on trees and heights of roosts. If natural roosts are able to be found it is then a challenge to either catch from or attach a PITT tag reader close to the roost, without the use of tree climbers. Also due to the large numbers of roosts used by a single community (at least 24 trees at Wallington, some with more than one roost) and the frequent roost switching observed of movements every two-three days, a large number of PITT tag readers would need to be installed at considerable cost. Once installed, regular movements or additions would be needed as bats utilized new tree roosts. An alternative would be the use of nano-tags (Biotrack, Wareham. UK), previously discussed but as these only stay on until fur re-grows a large number of bats would need to be caught at once to facilitate the collection of association data, which would then be limited to a time scale of only up to 14 days. Perhaps a way forward would be to radio track a small number of individuals in order to locate a tree roost and then attempt to catch the majority of bats from the roost at emergence before attaching coded tags. This procedure could be repeated to build a longer scale pattern of associations, if contact with the community was maintained via radio tracking, providing the roosts the bats were occupying catchable from.

Collecting data from artificial roost sites should prove more achievable, especially at sites where large numbers of bats aggregate such as churches. Either PITT tags or nano tags could be used to monitor long term associations and social structure which may then be used to inform our model before suggesting disease management options. As bats in buildings result in an increased risk to human health this area of research should be a priority.

6.8 Policy implications

Although there is a desperate need to understand fine scale temporal data on both natural and artificially roosting populations of bats to inform one health, and technology is rapidly advancing to improve our ability to study animal movement, such a need should be balanced with conservation policy (McGowan et al., 2017) and objectives. It should be noted that whilst bats are currently protected under EU legislation (92/43/EEC, 2002), following a referendum in 2016, the UK has voted to leave the European Union and it is not known what this means for the future of nature conservation law in the UK because much depends on the type of post EU-UK relationship and the agreement that will be negotiated. However, it could be argued that, nature conservation may be more at risk, which may in turn alter licensing laws and potentially put bat populations at risk, particularly if there is suspected disease present. Collecting data on bat populations should be therefore be carefully assessed to check it will improve current knowledge before unduly disrupting them and modelling various hypothesis as done here, may serve as a better way to predict and manage disease transmission whilst preserving conservation status.

The current level of protection afforded to bats under EU legislation may be subject to change in the future. My findings from this work of individual specialisation in habitat use and perhaps local adaptations suggest that habitat mosaics should be protected in order to maintain FCS rather than considering temperate bats species to have preferred habitat types. I also found high occurrences of roost switching which is not currently considered in bat mitigation plans where planning applications are sought and should be written in future legislation to protect bats roosting networks. In terms of disease management, this work supports the current guidance on passive surveillance of bats (2018) as it is likely that social structure limits the spread of viruses in populations. Also, because a lack of, or disruption to social structure may increase the spread of disease within bat populations or even facilitate spillover to other animals and humans, I advocate an integrated One Health approach to future protective policy for bats to protect existing social structures are prevent spillover events.

Supplementary section 1 Radio tracking review and biometric data of radio tracked bats

Radio tracking review

The primary scientific literature was reviewed to determine the mean and range of the proportion of nights on which bats were reported to have been radio-tracked. Data collected included species, location of study (latitude and longitude), no of fixes per night and recording intervals, and these were combined to determine the proportion of a night represented by tracking data on a fixed date (30th June). In all cases choices have been made to maximise the assumed value of reported data despite limitations in the quality of their description. The date was chosen to represent a short night in the northern hemisphere during a period when bats were most likely to be reproductive and therefore active, regardless of latitude. It has also been assumed that nights were shorter still by assuming a two hour reduction in the period of dark (between sunrise and sunset times) to account for species specific preferences for emergence and return times. Both choices maximise the proportion of a night assumed to be represented by data, though in reality for some species (especially those which emerge in relatively high light levels at lower latitudes) the actual proportion of the night represented by data may be smaller than those calculated.

19 reports describing 18 species were used to determine the mean proportion of a nights represented by radio-tracking data. Of these studies only 5 reported the intention to track bats for a complete night, the rest reported data describing various proportions of a night Table 23. The mean proportion of nights bats were tracked for was 51%.

Table 23 Review of radio tracking literature for temperate bats

Bat Species	no of bats tracked	Full night of data	mean proportion of night tracked	ref
Rhinolophus hipposideros	8	yes	0.57	(Bontadina et al., 2002)
Myotis bechsteinii	10	no	0.72	(Kerth et al., 2001b)
Myotis bechsteinii	24	Yes	1	(Dietz and Pir, 2009)
P. pipistrellus & P. pygmaeus	12/14	no	0.83	(Nicholls and A Racey, 2006)
Rhinolophus ferrumequinum	14	no	0.05	(Rossiter et al., 2002)
P. pipistrellus & P. pygmaeus	23/23	yes	1	(Davidson-Watts and Jones, 2006)
Vespertilio murinus	18	no	0.37	(Safi et al., 2007)
Rhinolophus euryale	18	no	0.22	(Russo et al., 2002)
Nyctalus leisleri	8	no	0.3	(Waters et al., 1999)
Rhinolophus mehelyi & R. euryale	9/5	no	0.29	(Russo et al., 2005)
Tadarida teniotis	10	no	0.08	(Marques et al., 2004)
Barbastella barbastellus	28	no	0.95	(Zeale et al., 2012)
Myotis nattereri	35	yes	0.76	(Smith and Racey, 2008)
Barbastellus barbastellus	12	no	0.52	(Hillen et al., 2009)
Myotis nattereri	16	yes	0.9	(Lundy et al., 2012)
Pipistrellus nathusii	14	no	0.26	(Flaquer et al., 2009)
Plecotus austriacus	20	yes	1	(Razgour et al., 2011)

Biometric data of tracked bats

Table 24 Biometric data of bats tracked

Site	ID	Sex	Body mass (g)	Reproductive condition	Tracking date	No. of recordings	No. of locations
LC	U3935	F	7.5	Lactating	22/07/2003	33	20
LC	U3935	F	7.5	Lactating	24/07/2003	38	32
LC	U3938	F	7.9	pregnant	11/06/2003	30	18
LC	U3938	F	7.9	pregnant	12/06/2003	30	26
LC	U3941	F	8.1	pregnant	03/06/2003	29	17
LC	U3941	F	8.1	pregnant	04/06/2003	40	16
LC	U3947	F	8.2	Lactating	25/06/2003	25	20
LC	U3947	F	8.2	Lactating	26/06/2003	31	24
LC	U7471	F	7.9	non repro	24/06/2003	16	15
LC	U7471	F	7.9	non repro	25/06/2003	23	21

LC	U8584	F	7.4	unknown	20/05/2003	34	20
LC	U8588	F	7.4	unknown	15/05/2003	38	34
LC	U8590	F	6.3	non repro	29/05/2003	37	22
LC	U8590	F	6.3	non repro	05/06/2003	20	12
LC	U8592	F	8	nulliparous	05/08/2003	46	44
LC	U8592	F	8	nulliparous	06/08/2003	41	39
LC	U8890	F	7.5	Lactating	09/07/2003	35	31
LC	U8890	F	7.5	Lactating	10/07/2003	34	27
LC	Y1972	F	8.6	pregnant	11/06/2003	31	27
LC	Y1974	M	6.6	unknown	12/06/2003	29	20
LC	Y1974	F	6.6	unknown	16/06/2003	33	28
LC	Y1998	F	10.5	pregnant	25/06/2003	29	15
LC	Y1998	F	10.5	pregnant	26/06/2003	23	14
LC	Y2003	F	7.5	Lactating	08/07/2003	36	25
LC	Y2003	F	7.5	Lactating	09/07/2003	34	29
LC	Y2045	F	7.2	non repro	23/07/2003	36	31
LC	Y2045	F	7.2	non repro	24/07/2003	34	34
LC	Y2106	F	7	non repro	05/08/2003	36	34
LC	Y2106	F	7	non repro	07/08/2003	34	34
W	H1607	F	8.8	Lactating	26/07/2013	39	17
W	H1607	F	8.8	Lactating	28/07/2013	27	12
W	H1608	F	7.4	post lactating	30/07/2013	40	15
W	H1608	F	7.4	post lactating	31/07/2013	38	13
W	H1608	F	7.3	post lactating	30/07/2014	38	13
W	H1609	F	8.0	Pregnant	23/06/2015	35	10
W	H1611	F	7.8	post lactating	13/08/2014	39	12
W	H1659	F	8.7	lactating	08/08/2013	36	17
W	H1659	F	8.7	lactating	09/08/2013	36	15
W	H1659	F	9.1	post lactating	21/08/2014	44	23
W	H1670	F	8.2	post lactating	21/08/2013	44	17
W	H1670	F	9.4	pregnant	20/06/2014	33	16
W	H1672	F	9.2	post lactating	19/08/2014	39	18
W	H1679	F	9.1	pregnant	05/06/2014	27	11
W	H1673	F	8.0	Pregnant	15/06/2015	38	12
W	H1680	F	8.5	pregnant	17/06/2014	27	12
W	H1680	F	7.8	post lactating	06/08/2014	36	16
W	H1680	F	9.0	Pregnant	02/07/2015	36	14
W	H1682	F	8.9	pregnant	16/06/2014	27	13
W	H1682	F	8.5	Pregnant	09/06/2015	38	14
W	H1688	F	8.8	post lactating	22/08/2014	39	17
W	H1696	M	6.9	unknown	22/06/2014	26	11
W	H1700	F	7.6	Non repro	13/07/2014	37	15
W	H1704	F	8.2	Lactating	27/07/2014	34	16
W	H1705	M	6.8	unknown	05/08/2014	34	22
W	H1713	F	8.9	Pregnant	02/07/2015	36	17

W	Y2850	F	8.1	lactating	08/07/2013	25	13
W	Y2850	F	8.1	lactating	20/07/2014	34	15
W	Y2889	F	9.7	pregnant	19/07/2013	26	8
W	Y2889	F	9.7	pregnant	22/07/2013	25	9
W	Y2889	F	8.1	post lactating	18/08/2014	35	14

Supplementary section 2 Biometric data and capture method of bats caught in Northern England

Date	Location	Grid Ref	Roost or free flight?	County	Species	Ring	Sex	Age	Reproductive status	F/arm	Weight	Data collected by
07/02/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1433	F	Adult	Lactating	38.4	7.4	James Aegerter
07/02/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1434	F	Adult	Lactating	41.5	7.8	James Aegerter
07/02/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1436	F	Adult	Lactating	39.1	7.5	James Aegerter
07/02/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1437	F	Adult	Lactating	38.6	7.8	James Aegerter
07/02/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1439	F	Adult	Pregnant	37.3	9.1	James Aegerter
07/02/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1440	F	Adult	Lactating	39.6	7.6	James Aegerter
07/02/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1441	F	Adult	Lactating	39	7.3	James Aegerter
7/24/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1468	F	Adult	Lactating	39.6	7.8	James Aegerter
7/24/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1469	F	Adult	Lactating	39.4	7.6	James Aegerter
7/24/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1470	F	Adult	Lactating	39.4	7.7	James Aegerter

7/24/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1471	F	Adult	Lactating	39.8	8	James Aegerter
7/24/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1472	F	Adult	Lactating	39.2	7.7	James Aegerter
7/24/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1473	F	Adult	Lactating	39.1	7.2	James Aegerter
7/24/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1474	F	Adult	Lactating	39.4	7.6	James Aegerter
7/24/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1475	F	Adult	Not reproductive	38.3	7.6	James Aegerter
7/24/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1476	F	Adult	Lactating	38.1	7	James Aegerter
7/24/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1477	F	Adult	Lactating	39.2	7	James Aegerter
7/24/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	A1478	F	Adult	Lactating	39.7	8	James Aegerter
6/18/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	Y2793	F	Adult	Pregnant	39.6	8.4	James Aegerter
6/18/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	Y2794	F	Adult	Pregnant	40.5	9.1	James Aegerter
6/18/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	Y2795	F	Adult	Pregnant	39.3	8.6	James Aegerter
6/18/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	Y2796	F	Adult	Pregnant	39.5	9.1	James Aegerter
6/18/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	Y2797	F	Adult	Pregnant	38.8	7.3	James Aegerter

6/18/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	Y2798	F	Adult	Pregnant	40.6	9.7	James Aegerter
6/18/2012	Harpham	TA 09238 61582	Roost	East riding	Natterer's	Y2799	F	Adult	Pregnant	42.4	8.8	James Aegerter
6/19/2003	Low Catton	TA 09238 61582	Roost	East riding	Natterer's	A1401	F	Adult	Pregnant	40.8	8.4	James Aegerter
6/19/2003	Low Catton	TA 09238 61582	Roost	East riding	Natterer's	A1402	F	Adult	Pregnant	38.8	8.7	James Aegerter
6/19/2003	Low Catton	TA 09238 61582	Roost	East riding	Natterer's	A1404	F	Adult	Pregnant	41	7.5	James Aegerter
6/19/2003	Low Catton	TA 09238 61582	Roost	East riding	Natterer's	A1406	F	Adult	Not pregnant	38.8	7.1	James Aegerter
6/19/2003	Low Catton	TA 09238 61582	Roost	East riding	Natterer's	A1407	F	Adult	Pregnant	40.7	8.3	James Aegerter
6/19/2003	Low Catton	TA 09238 61582	Roost	East riding	Natterer's	A1408	F	Adult	Pregnant	40.7	8.2	James Aegerter
6/19/2003	Low Catton	TA 09238 61582	Roost	East riding	Natterer's	A1411	F	Adult	Pregnant	40.6	7.7	James Aegerter
07/03/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1442	F	Adult	Pregnant	39.7	9.4	James Aegerter
07/03/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1444	F	Adult	Lactating	40.9	7	James Aegerter
07/03/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1445	F	Adult	Lactating	39.9	8.6	James Aegerter
07/03/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1446	F	Adult	Not reproductive	40	8	James Aegerter

07/03/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1447	F	Adult	Lactating	39.1	6.8	James Aegerter
07/03/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1448	F	Adult	Lactating	37.7	8.9	James Aegerter
07/03/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1449	F	Adult	Lactating	38.7	7	James Aegerter
7/23/2003	Low Catton	TA 09238 61582	Roost	East riding	Natterer's	A1464	F	Adult	Lactating	38.5	7.7	James Aegerter
7/23/2003	Low Catton	TA 09238 61582	Roost	East riding	Natterer's	A1465	F	Adult	Lactating	37.6	7.3	James Aegerter
7/23/2003	Low Catton	TA 09238 61582	Roost	East riding	Natterer's	A1466	F	Adult	Lactating	40.2	7.5	James Aegerter
7/23/2003	Low Catton	TA 09238 61582	Roost	East riding	Natterer's	A1467	F	Adult	Lactating	40.9	9.8	James Aegerter
08/07/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1493	F	Adult	Post-lactating	40.3	8.6	James Aegerter
08/07/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1494	M	Adult	Unknown	40	7.1	James Aegerter
08/07/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1495	F	Adult	Post-lactating	40.5	8.3	James Aegerter
08/07/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1496	F	Adult	Lactating	38.7	8	James Aegerter
08/07/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1497	F	Adult	Lactating	39.2	8.1	James Aegerter
08/07/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	A1498	F	Adult	Post-lactating	39.9	8	James Aegerter

08/07/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	U3936	F	Adult	Unknown	41	7.8	James Aegerter
07/03/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	U8883	F	Adult	Lactating	39.7	7.7	James Aegerter
07/03/2003	Low catton	TA 09238 61582	Roost	East riding	Natterer's	U8890	F	Adult	Lactating	39	7.4	James Aegerter
30/06/2013	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	Y2849	F	Adult	hairless nipples	38.6	7	Simone Mordue
30/06/2013	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	Y2850	F	Adult	Pregnant	39.1	9.4	Simone Mordue
17/07/2013	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	Y2889	F	Adult	Lactating	39.4	7.7	Simone Mordue
24/07/2013	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1607	F	Adult	Lactating	39.9	8.8	Simone Mordue
24/07/2013	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1608	F	Adult	Post Lactating	37.1	7.4	Simone Mordue
24/07/2013	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1609	F	Adult	Lactating	39.3	8.1	Simone Mordue
24/07/2013	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1610	F	Adult	Unknown	38.5	7.9	Simone Mordue
24/07/2013	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1611	F	Adult	Lactating	39.5	8	Simone Mordue
07/08/2013	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1659	F	Adult	Lactating	40.3	8.7	Simone Mordue
19/08/2013	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1667	F	Adult	Unknown	38.9	7.7	Simone Mordue

19/08/2013	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1668	F	Adult	Unknown	38.9	8.1	Simone Mordue
19/08/2013	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1669	F	Juvenile	Unknown	38	6.6	Simone Mordue
19/08/2013	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1670	F	Adult	Post Lactating	38.4	8.2	Simone Mordue
19/08/2013	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1671	M	Juvenile	Unknown	40.8	7.6	Simone Mordue
19/08/2013	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1672	F	Adult	Post Lactating	38.9	9.5	Simone Mordue
19/08/2013	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1673	F	Juvenile	Unknown	40	8.1	Simone Mordue
19/08/2013	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1674	M	Juvenile	Unknown	40	8.1	Simone Mordue
19/08/2013	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1675	F	Juvenile	Unknown	38.5	6.7	Simone Mordue
19/08/2013	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	Y2849	F	Adult	Unknown	38.8	7.4	Simone Mordue
03/09/2013	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1676	F	Adult	Unknown	38.6	7.5	Simone Mordue
03/09/2013	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1677	M	Juvenile	Unknown	37.2	7	Simone Mordue
04/06/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1679	F	Adult	Pregnant	39.7	9.1	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1610	F	Adult	Pregnant	38.6	8.8	Simone Mordue

12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1669	F	Adult	Pregnant	38.3	6.4	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1676	F	Adult	Pregnant	38.7	8.5	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1679	F	Adult	Pregnant	39.8	8.8	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1680	F	Adult	Pregnant	38.4	8.5	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1681	F	Adult	Pregnant	40.2	9.4	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1682	F	Adult	Pregnant	40.6	8.9	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1683	F	Adult	Pregnant	40.5	8.4	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1684	F	Adult	Pregnant	41.4	9.5	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1685	F	Adult	Pregnant	39.3	8.7	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1686	F	Adult	Pregnant	41.1	8.4	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1687	M	Adult	Unknown	39.8	6.2	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	H1688	F	Adult	Pregnant	38.8	9.1	Simone Mordue
12/06/2014	Wallington	NZ 03072 84688	Roost B	Northumberland	Natterer's	Y2849	F	Adult	Pregnant	38.7	6.9	Simone Mordue

19/06/2014	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1609	F	Adult	Pregnant	39.7	9.7	Simone Mordue
19/06/2014	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1667	F	Adult	Pregnant	39.2	9.5	Simone Mordue
19/06/2014	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1670	F	Adult	Pregnant	38.2	9.4	Simone Mordue
19/06/2014	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1673	F	Adult	Pregnant	40.1	9.9	Simone Mordue
19/06/2014	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1686	F	Adult	Pregnant	39.2	9.2	Simone Mordue
19/06/2014	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1696	M	Adult	Unknown	39.4	6.9	Simone Mordue
19/06/2014	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1697	F	Adult	Unknown	39.8	7.2	Simone Mordue
19/06/2014	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1698	F	Adult	Pregnant	40.8	10	Simone Mordue
19/06/2014	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	H1699	M	Adult	Unknown	40.3	7.1	Simone Mordue
19/06/2014	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	Y2849	F	Adult	Unknown	38.7	7.1	Simone Mordue
19/06/2014	Wallington	NZ 03072 84688	Roost C	Northumberland	Natterer's	Y2889	F	Adult	Pregnant	39.4	9.7	Simone Mordue
13/07/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1700	F	Adult	Non-repro	40.9	7.6	Simone Mordue
13/07/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	Y2850	F	Adult	Lactating	39.5	8.1	Simone Mordue

21/07/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1701	F	Juvenile	Non-repro	38.9	5.8	Simone Mordue
21/07/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1702	F	Juvenile	Non-repro	38.8	6.5	Simone Mordue
21/07/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1703	M	Juvenile	Non-repro	35.2	6.2	Simone Mordue
22/07/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1704	F	Adult	Lactating	39.2	8.2	Simone Mordue
27/07/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1608	F	Adult	Post Lactating	37.05	7.3	Simone Mordue
05/08/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1680	F	Adult	Post Lactating	38.4	7.8	Simone Mordue
05/08/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1705	M	Juvenile	Unknown	39.1	6.6	Simone Mordue
06/08/2014	Wallington	NZ 03072 84688	Roost P	Northumberland	Natterer's	H1673	F	Adult	Post Lactating	40.08	8.2	Simone Mordue
06/08/2014	Wallington	NZ 03072 84688	Roost P	Northumberland	Natterer's	H1688	F	Adult	Post Lactating	38.9	8.3	Simone Mordue
06/08/2014	Wallington	NZ 03072 84688	Roost P	Northumberland	Natterer's	H1706	F	Adult	Post Lactating	39.8	7.3	Simone Mordue
06/08/2014	Wallington	NZ 03072 84688	Roost P	Northumberland	Natterer's	H1707	F	Juvenile	Non-repro	39.2	7.5	Simone Mordue
06/08/2014	Wallington	NZ 03072 84688	Roost P	Northumberland	Natterer's	H1708	F	Juvenile	Non-repro	38.8	7	Simone Mordue
06/08/2014	Wallington	NZ 03072 84688	Roost P	Northumberland	Natterer's	H1709	M	Juvenile	Non-repro	38.9	6.6	Simone Mordue

06/08/2014	Wallington	NZ 03072 84688	Roost P	Northumberland	Natterer's	H1710	F	Adult	Unknown	39.4	7.5	Simone Mordue
12/08/2014	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1611	F	Adult	Post Lactating	39.7	7.8	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1608	F	Adult	Post Lactating	37.14	7.2	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1609	F	Adult	Post Lactating	39.8	8.2	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1611	F	Adult	Post Lactating	39.6	8	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1672	F	Adult	Post Lactating	38.79	9.2	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1675	F	Adult	Unknown	38.6	8.2	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1680	F	Adult	Post Lactating	38.51	8.4	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1681	F	Adult	Post Lactating	40.05	8.2	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1682	F	Adult	Post Lactating	40.59	8.3	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1684	F	Adult	Post Lactating	41	8.6	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1701	F	Juvenile	Non-repro	41.17	7.2	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1702	F	Juvenile	Non-repro	40.69	7.7	Simone Mordue

14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1703	M	Juvenile	Non-repro	36.75	7	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1704	F	Adult	Post Lactating	39.45	8.8	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1705	M	Juvenile	Quick release	n/a	n/a	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1706	F	Adult	Post Lactating	39.85	7.5	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1710	F	Adult	Unknown	40.05	7.1	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1711	M	Juvenile	Non-repro	37.7	5.4	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1712	F	Juvenile	Non-repro	39.78	7.5	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1713	F	Adult	Post Lactating	39	7.9	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1714	F	Juvenile	Non-repro	40.66	8	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1715	F	Juvenile	Non-repro	38.89	7.5	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1716	M	Juvenile	Non-repro	39.04	6.5	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1717	M	Juvenile	Non-repro	39.07	7.3	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1718	M	Juvenile	Non-repro	39.78	7.1	Simone Mordue

14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1719	F	Juvenile	Non-repro	38.7	6.4	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1720	F	Adult	Unknown	39.75	6.9	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1721	F	Adult	Unknown	39.92	7.9	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	H1722	F	Juvenile	Non-repro	39.2	7.3	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	Y2849	F	Adult	Unknown	38.87	7	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	Y2850	F	Adult	Post Lactating	39.26	8.5	Simone Mordue
14/08/2014	Wallington	NZ 03072 84688	Roost F	Northumberland	Natterer's	Y2889	F	Adult	Post Lactating	39.46	8.1	Simone Mordue
09/06/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1682	F	Adult	Pregnant	40.77	8.5	Simone Mordue
09/06/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1697	F	Adult	Pregnant	38.9	7.3	Simone Mordue
09/06/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1698	F	Adult	Pregnant	40.8	8	Simone Mordue
09/06/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1710	F	Adult	Pregnant	40	7.8	Simone Mordue
09/06/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1716	M	Adult		39.2	6.8	Simone Mordue
15/06/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1673	F	Adult	Pregnant	40.04	8	Simone Mordue

15/06/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1723	F	Adult	Pregnant	38.9	6.9	Simone Mordue
23/06/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1609	F	Adult	Pregnant	39.45	8	Simone Mordue
23/06/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1724	M	Adult	Unknown	38.9	7	Simone Mordue
02/07/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1680	F	Adult	Pregnant	38.4	9	Simone Mordue
02/07/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1698	F	Adult	Pregnant	40.8	9.2	Simone Mordue
02/07/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1713	F	Adult	Pregnant	39	8.9	Simone Mordue
02/07/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1725	M	Adult	Unknown	38.2	7.5	Simone Mordue
02/07/2015	Wallington	NZ 03072 84688	Free flight	Northumberland	Natterer's	H1726	M	Adult	Unknown	38.5	6.6	Simone Mordue
8/28/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1491	F	Adult	Post-lactating	40.4	8.2	James Aegerter
8/28/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1492	F	Adult	Post-lactating	39.7	7.7	James Aegerter
8/28/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1493	F	Adult	Post-lactating	38.3	7.3	James Aegerter
8/28/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1494	F	Adult	Post-lactating	39.7	7.3	James Aegerter
8/28/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1495	F	Adult	Unknown	40.1	7	James Aegerter

8/28/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1498	F	Adult	Post-lactating	38.1	7.4	James Aegerter
8/28/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1499	F	Adult	Post-lactating	40.9	8.1	James Aegerter
8/28/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1500	F	Adult	Post-lactating	37.6	7.3	James Aegerter
8/28/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1501	F	Adult	Unknown	39.2	7.1	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1517	F	Adult	Unknown	38.3	7	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1519	F	Adult	Unknown	38	7.1	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1521	F	Adult	Unknown	39.1	6.4	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1522	F	Adult	Unknown	39.3	6.9	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1523	M	Adult	Unknown	37.7	6.3	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1524	F	Adult	Unknown	39.8	7.6	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1525	F	Juvenile	Unknown	39.5	7.2	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1526	F	Adult	Unknown	40.7	7.2	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1527	F	Adult	Unknown	39.1	7.6	James Aegerter

09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1528	F	Adult	Unknown	39.6	6.7	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1529	F	Adult	Unknown	38.9	6.8	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1530	F	Adult	Unknown	40.3	7.7	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1531	F	Adult	Unknown	38.4	7.4	James Aegerter
09/10/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1533	F	Adult	Unknown	41	8.2	James Aegerter
09/10/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1534	F	Adult	Unknown	39.4	7.4	James Aegerter
09/10/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1535	M	Adult	Unknown	38.1	6.5	James Aegerter
09/10/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1536	F	Adult	Unknown	40	7.5	James Aegerter
09/10/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1537	F	Adult	Unknown	41.1	7.4	James Aegerter
09/10/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1539	F	Adult	Unknown	39.6	7.2	James Aegerter
09/10/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1540	F	Adult	Unknown	38.3	6.7	James Aegerter
09/10/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	H1541	F	Adult	Unknown	38.2	6.7	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	U3995	F	Adult	Unknown	38.6	6.8	James Aegerter

09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	U8061	F	Adult	Unknown	39.1	7.4	James Aegerter
09/05/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	U8076	F	Adult	Unknown	37.4	6.1	James Aegerter
8/28/2012	Wintringham	SE 88704 73108	Roost	North Yorkshire	Natterer's	Y3701	F	Adult	Post-lactating	40.1	7.9	James Aegerter
27/06/2012	Wycoller	SD 93200 39317	Roost	Lancashire	Natterer's	A1422	F	Adult	Lactating	41.7	8	James Aegerter
27/06/2012	Wycoller	SD 93200 39317	Roost	Lancashire	Natterer's	A1423	F	Adult	Not reproductive	41	6.9	James Aegerter
27/06/2012	Wycoller	SD 93200 39318	Roost	Lancashire	Natterer's	A1424	F	Adult	Lactating	37.8	8.1	James Aegerter
27/06/2012	Wycoller	SD 93200 39319	Roost	Lancashire	Natterer's	A1425	F	Adult	Pregnant	40.7	9.8	James Aegerter
27/06/2012	Wycoller	SD 93200 39320	Roost	Lancashire	Natterer's	A1426	F	Adult	Not reproductive	39.2	7.4	James Aegerter
27/06/2012	Wycoller	SD 93200 39321	Roost	Lancashire	Natterer's	A1427	F	Adult	Not reproductive	38.7	7.9	James Aegerter
27/06/2012	Wycoller	SD 93200 39322	Roost	Lancashire	Natterer's	A1428	F	Adult	Pregnant	39.8	10.2	James Aegerter
27/06/2012	Wycoller	SD 93200 39323	Roost	Lancashire	Natterer's	A1429	F	Adult	Pregnant	40.2	9.9	James Aegerter
27/06/2012	Wycoller	SD 93200 39324	Roost	Lancashire	Natterer's	A1430	F	Adult	Not reproductive	40.7	7.7	James Aegerter
27/06/2012	Wycoller	SD 93200 39326	Roost	Lancashire	Natterer's	A1432	F	Adult	Not reproductive	39.5	7.4	James Aegerter

18/07/2012	Wycoller	SD 93200 39327	Roost	Lancashire	Natterer's	A1455	F	Adult	Lactating	41.5	8.8	James Aegerter
18/07/2012	Wycoller	SD 93200 39328	Roost	Lancashire	Natterer's	A1456	F	Adult	Lactating	40.5	7.7	James Aegerter
18/07/2012	Wycoller	SD 93200 39329	Roost	Lancashire	Natterer's	A1457	F	Adult	Lactating	39.7	8.4	James Aegerter
18/07/2012	Wycoller	SD 93200 39330	Roost	Lancashire	Natterer's	A1458	F	Adult	Lactating	42.1	8.2	James Aegerter
18/07/2012	Wycoller	SD 93200 39331	Roost	Lancashire	Natterer's	A1459	F	Adult	Lactating	40	8.4	James Aegerter
18/07/2012	Wycoller	SD 93200 39332	Roost	Lancashire	Natterer's	A1460	F	Adult	Lactating	40.1	8.3	James Aegerter
18/07/2012	Wycoller	SD 93200 39333	Roost	Lancashire	Natterer's	A1461	F	Adult	Lactating	39.7	8	James Aegerter
18/07/2012	Wycoller	SD 93200 39334	Roost	Lancashire	Natterer's	A1462	F	Adult	Lactating	40.6	8.6	James Aegerter
18/07/2012	Wycoller	SD 93200 39335	Roost	Lancashire	Natterer's	A1463	F	Adult	Lactating	40.8	8	James Aegerter
15/08/2012	Wycoller	SD 93200 39336	Roost	Lancashire	Natterer's	H1478	M	Juvenile	Unknown	41	7	James Aegerter
15/08/2012	Wycoller	SD 93200 39337	Roost	Lancashire	Natterer's	H1479	F	Adult	Unknown	39.8	8.1	James Aegerter
15/08/2012	Wycoller	SD 93200 39338	Roost	Lancashire	Natterer's	H1480	F	Juvenile	Unknown	41.1	7.8	James Aegerter
15/08/2012	Wycoller	SD 93200 39339	Roost	Lancashire	Natterer's	H1481	F	Juvenile	Unknown	39.5	7.4	James Aegerter

15/08/2012	Wycoller	SD 93200 39340	Roost	Lancashire	Natterer's	H1482	M	Juvenile	Unknown	39	6.6	James Aegerter
15/08/2012	Wycoller	SD 93200 39341	Roost	Lancashire	Natterer's	H1483	M	Juvenile	Unknown	40	6.5	James Aegerter
15/08/2012	Wycoller	SD 93200 39342	Roost	Lancashire	Natterer's	H1484	F	Juvenile	Unknown	40.2	7	James Aegerter
15/08/2012	Wycoller	SD 93200 39343	Roost	Lancashire	Natterer's	H1485	M	Juvenile	Unknown	38.1	6.7	James Aegerter
15/08/2012	Wycoller	SD 93200 39344	Roost	Lancashire	Natterer's	H1486	F	Adult	Unknown	42.3	7.6	James Aegerter

Supplementary section 3 Roost data of bats caught at Wytham Woods, Oxford. Data supplied by August (2014)

Date	Bat_ID	Box number	Site
10/09/2006	Y9019	CP113	Wytham Woods
10/09/2006	Y9020	CP113	Wytham Woods
10/09/2006	Y9018	CP134	Wytham Woods
10/09/2006	Y9050	CP117	Wytham Woods
10/09/2006	Z3239	CP105	Wytham Woods
12/09/2006	Z3132	O211	Wytham Woods
12/09/2006	Z3124	O30A	Wytham Woods
12/09/2006	Z3123	O30A	Wytham Woods
12/09/2006	Z3127	O218	Wytham Woods
12/09/2006	Z3122	O30A	Wytham Woods
12/09/2006	Z3121	O30A	Wytham Woods
12/09/2006	Z3133	O201	Wytham Woods
12/09/2006	Z3131	O211	Wytham Woods
12/09/2006	Z3130	O211	Wytham Woods
12/09/2006	Z3129	O211	Wytham Woods
12/09/2006	Z3128	O211	Wytham Woods
12/09/2006	Z3120	O258	Wytham Woods
28/09/2006	Z3178	C2	Wytham Woods
28/09/2006	Z3172	C25	Wytham Woods
28/09/2006	Z3173	C25	Wytham Woods
28/09/2006	Z3176	C2	Wytham Woods
28/09/2006	Z3177	C2	Wytham Woods
28/09/2006	Z3171	C141	Wytham Woods
28/09/2006	Z3179	C2	Wytham Woods
28/09/2006	Z3180	C2	Wytham Woods
28/09/2006	Z3181	C2	Wytham Woods
28/09/2006	Z3170	C141	Wytham Woods
28/09/2006	Z3174	C101	Wytham Woods
28/09/2006	Z3175	C2	Wytham Woods
28/09/2006	Z3186	C109	Wytham Woods
28/09/2006	Z3185	C113	Wytham Woods
28/09/2006	Z3184	C113	Wytham Woods
28/09/2006	Z3182	C124	Wytham Woods
10/10/2006	Z3234	W19	Wytham Woods
10/10/2006	Z3238	W34	Wytham Woods
10/10/2006	Y9022	W24	Wytham Woods
10/10/2006	Z3237	W19	Wytham Woods
10/10/2006	Z3231	W19	Wytham Woods
10/10/2006	Z3233	W19	Wytham Woods
10/10/2006	Z3235	W19	Wytham Woods
10/10/2006	Y9024	W24	Wytham Woods
10/10/2006	Z3232	W19	Wytham Woods

10/10/2006	Y9023	W24	Wytham Woods
10/10/2006	Z3236	W19	Wytham Woods
24/05/2007	Y9022	W8	Wytham Woods
24/05/2007	Y9024	W8	Wytham Woods
04/08/2007	Z3173	C41	Wytham Woods
04/08/2007	Z3184	C13	Wytham Woods
04/08/2007	Z3180	C136	Wytham Woods
04/08/2007	Z3177	C59	Wytham Woods
04/08/2007	Z3170	C35	Wytham Woods
04/08/2007	Z3174	C101	Wytham Woods
05/08/2007	Z4690	CP12	Wytham Woods
05/08/2007	Z4714	CP3	Wytham Woods
05/08/2007	Z4715	CP3	Wytham Woods
05/08/2007	Z4716	CP3	Wytham Woods
05/08/2007	Z4708	CP100	Wytham Woods
05/08/2007	Z4683	CP153	Wytham Woods
05/08/2007	Z4671	CP20	Wytham Woods
05/08/2007	Z4685	CP153	Wytham Woods
05/08/2007	Z4689	CP16	Wytham Woods
05/08/2007	Z4686	CP153	Wytham Woods
05/08/2007	Z4673	CP20	Wytham Woods
05/08/2007	Z4707	CP100	Wytham Woods
05/08/2007	Z4717	CP3	Wytham Woods
05/08/2007	Z4709	CP100	Wytham Woods
05/08/2007	Z4692	CP12	Wytham Woods
05/08/2007	Z4710	CP100	Wytham Woods
05/08/2007	Z4688	CP16	Wytham Woods
05/08/2007	Z4719	CP3	Wytham Woods
05/08/2007	Z4718	CP3	Wytham Woods
05/08/2007	Z4706	CP103	Wytham Woods
05/08/2007	Z4694	CP12	Wytham Woods
05/08/2007	Z4700	CP12	Wytham Woods
05/08/2007	Z4701	CP32	Wytham Woods
05/08/2007	Z4702	CP32	Wytham Woods
05/08/2007	Z4703	CP32	Wytham Woods
05/08/2007	Z4704	CP32	Wytham Woods
05/08/2007	Z4705	CP32	Wytham Woods
05/08/2007	Z4684	CP153	Wytham Woods
05/08/2007	Z4674	CP20	Wytham Woods
05/08/2007	Z4670	CP20	Wytham Woods
05/08/2007	Z4697	CP12	Wytham Woods
05/08/2007	Z4691	CP12	Wytham Woods
05/08/2007	Z4695	CP12	Wytham Woods
05/08/2007	Z4687	CP16	Wytham Woods

05/08/2007	Z4675	CP20	Wytham Woods
05/08/2007	Z4676	CP17	Wytham Woods
05/08/2007	Z4712	CP3	Wytham Woods
05/08/2007	Z4677	CP17	Wytham Woods
05/08/2007	Z4693	CP12	Wytham Woods
05/08/2007	Z4678	CP17	Wytham Woods
05/08/2007	Z4679	CP17	Wytham Woods
05/08/2007	Z4680	CP17	Wytham Woods
05/08/2007	Z4711	CP3	Wytham Woods
05/08/2007	Z4681	CP17	Wytham Woods
05/08/2007	Z4713	CP3	Wytham Woods
05/08/2007	Z4696	CP12	Wytham Woods
05/08/2007	Y9049	CP137	Wytham Woods
05/08/2007	Y9037	CP144	Wytham Woods
05/08/2007	Y9039	CP144	Wytham Woods
05/08/2007	Z4682	CP153	Wytham Woods
05/08/2007	Y9041	CP144	Wytham Woods
05/08/2007	Y9042	CP144	Wytham Woods
05/08/2007	Y9043	CP144	Wytham Woods
05/08/2007	Y9044	CP144	Wytham Woods
05/08/2007	Y9045	CP144	Wytham Woods
05/08/2007	Y9046	CP144	Wytham Woods
05/08/2007	Y9036	CP144	Wytham Woods
05/08/2007	Y9048	CP137	Wytham Woods
05/08/2007	Y9038	CP144	Wytham Woods
05/08/2007	Z4656	CP125	Wytham Woods
05/08/2007	Z4657	CP144	Wytham Woods
05/08/2007	Z4653	CP34	Wytham Woods
05/08/2007	Z4658	CP144	Wytham Woods
05/08/2007	Z4659	CP144	Wytham Woods
05/08/2007	Z4651	CP34	Wytham Woods
05/08/2007	Z4652	CP34	Wytham Woods
05/08/2007	Z4660	CP144	Wytham Woods
05/08/2007	Z4672	CP20	Wytham Woods
05/08/2007	Y9047	CP144	Wytham Woods
05/08/2007	Z4661	CP144	Wytham Woods
05/08/2007	Z4669	CP20	Wytham Woods
05/08/2007	Z4668	CP20	Wytham Woods
05/08/2007	Z4663	CP144	Wytham Woods
05/08/2007	Y9025	CP137	Wytham Woods
05/08/2007	Z4662	CP144	Wytham Woods
05/08/2007	Z4667	CP20	Wytham Woods
05/08/2007	Z4666	CP20	Wytham Woods
05/08/2007	Z5782	CP137	Wytham Woods

05/08/2007	Y9040	CP144	Wytham Woods
05/08/2007	Z4665	CP20	Wytham Woods
05/08/2007	Y9035	CP137	Wytham Woods
05/08/2007	Y9031	CP137	Wytham Woods
05/08/2007	Y9034	CP137	Wytham Woods
05/08/2007	Y9027	CP137	Wytham Woods
05/08/2007	Y9032	CP137	Wytham Woods
05/08/2007	Y9030	CP137	Wytham Woods
05/08/2007	Y9029	CP137	Wytham Woods
05/08/2007	Y9028	CP137	Wytham Woods
05/08/2007	Z4654	CP34	Wytham Woods
05/08/2007	Z4655	CP34	Wytham Woods
05/08/2007	Z4664	CP20	Wytham Woods
05/08/2007	Y9033	CP137	Wytham Woods
08/08/2007	Z4698	B32	Wytham Woods
08/08/2007	Z4726	B55	Wytham Woods
08/08/2007	Z4721	B55	Wytham Woods
08/08/2007	Z4722	B55	Wytham Woods
08/08/2007	Z4723	B55	Wytham Woods
08/08/2007	Z4725	B55	Wytham Woods
08/08/2007	Z4729	B55	Wytham Woods
08/08/2007	Z4733	B55	Wytham Woods
08/08/2007	Z4699	B136	Wytham Woods
08/08/2007	Z4736	B55	Wytham Woods
08/08/2007	Z4735	B55	Wytham Woods
08/08/2007	Z4720	B168	Wytham Woods
08/08/2007	Z4734	B55	Wytham Woods
08/08/2007	Z4732	B55	Wytham Woods
08/08/2007	Z4731	B55	Wytham Woods
08/08/2007	Z4724	B55	Wytham Woods
08/08/2007	Z4730	B55	Wytham Woods
08/08/2007	Z4728	B55	Wytham Woods
08/08/2007	Z4727	B55	Wytham Woods
09/08/2007	Z4824	P8	Wytham Woods
09/08/2007	Z4816	SW64	Wytham Woods
09/08/2007	Z4821	P16	Wytham Woods
09/08/2007	Z4820	P16	Wytham Woods
09/08/2007	Z4819	P16	Wytham Woods
09/08/2007	Z4822	P15	Wytham Woods
09/08/2007	Z4818	P16	Wytham Woods
09/08/2007	Z4817	P16	Wytham Woods
09/08/2007	Z4823	P3	Wytham Woods
12/08/2007	Z4855	SW20	Wytham Woods
12/08/2007	Z4856	SW20	Wytham Woods

12/08/2007	Z4827	SW28	Wytham Woods
12/08/2007	Z4826	SW31	Wytham Woods
12/08/2007	Z4825	SW62	Wytham Woods
12/08/2007	Z4851	SW20	Wytham Woods
12/08/2007	Z4852	SW20	Wytham Woods
12/08/2007	Z4853	SW20	Wytham Woods
12/08/2007	Z4854	SW20	Wytham Woods
12/08/2007	Z4857	SW109A	Wytham Woods
13/08/2007	Z4742	O211	Wytham Woods
13/08/2007	Z4747	O211	Wytham Woods
13/08/2007	Z4737	O33	Wytham Woods
13/08/2007	Z4738	O33	Wytham Woods
13/08/2007	Z4740	O33	Wytham Woods
13/08/2007	Z4741	O33	Wytham Woods
13/08/2007	Z4802	O217	Wytham Woods
13/08/2007	Z4808	O217	Wytham Woods
13/08/2007	Z4807	O217	Wytham Woods
13/08/2007	Z4806	O217	Wytham Woods
13/08/2007	Z4805	O217	Wytham Woods
13/08/2007	Z4804	O217	Wytham Woods
13/08/2007	Z3127	O217	Wytham Woods
13/08/2007	Z3123	O217	Wytham Woods
13/08/2007	Z4745	O211	Wytham Woods
13/08/2007	Z4803	O217	Wytham Woods
13/08/2007	Z4743	O211	Wytham Woods
13/08/2007	Z4809	O238	Wytham Woods
13/08/2007	Z4750	O217	Wytham Woods
13/08/2007	Z4749	O211	Wytham Woods
13/08/2007	Z4748	O211	Wytham Woods
13/08/2007	Z4746	O211	Wytham Woods
13/08/2007	Z4801	O217	Wytham Woods
13/08/2007	Z4744	O211	Wytham Woods
13/08/2007	Z3121	O217	Wytham Woods
13/08/2007	Z4810	O235	Wytham Woods
13/08/2007	Z4811	O235	Wytham Woods
13/08/2007	Z4812	O235	Wytham Woods
13/08/2007	Z4813	O235	Wytham Woods
13/08/2007	Z4814	O235	Wytham Woods
13/08/2007	Z4815	O235	Wytham Woods
13/08/2007	Z4739	O33	Wytham Woods
16/08/2007	Z4500	W93	Wytham Woods
16/08/2007	Z4486	W63	Wytham Woods
16/08/2007	Z4487	W63	Wytham Woods
16/08/2007	Z4488	W63	Wytham Woods

16/08/2007	Z4489	W63	Wytham Woods
16/08/2007	Z4490	W63	Wytham Woods
16/08/2007	Z4492	W63	Wytham Woods
16/08/2007	Z4497	W78	Wytham Woods
16/08/2007	Z4495	W74	Wytham Woods
16/08/2007	Z4499	W93	Wytham Woods
16/08/2007	Z4483	W63	Wytham Woods
16/08/2007	Z4496	W74	Wytham Woods
16/08/2007	Z4498	W78	Wytham Woods
16/08/2007	Z4476	W63	Wytham Woods
16/08/2007	Z4466	W63	Wytham Woods
16/08/2007	Z4467	W63	Wytham Woods
16/08/2007	Z4468	W63	Wytham Woods
16/08/2007	Z4469	W63	Wytham Woods
16/08/2007	Z4470	W63	Wytham Woods
16/08/2007	Z4471	W63	Wytham Woods
16/08/2007	Z4472	W63	Wytham Woods
16/08/2007	Z4485	W63	Wytham Woods
16/08/2007	Z4475	W63	Wytham Woods
16/08/2007	Z4484	W63	Wytham Woods
16/08/2007	Z4477	W63	Wytham Woods
16/08/2007	Z4478	W63	Wytham Woods
16/08/2007	Z4479	W63	Wytham Woods
16/08/2007	Z4480	W63	Wytham Woods
16/08/2007	Z4481	W63	Wytham Woods
16/08/2007	Z4482	W63	Wytham Woods
16/08/2007	Z4474	W63	Wytham Woods
16/08/2007	Z4473	W63	Wytham Woods
16/08/2007	Z4494	W74	Wytham Woods
18/08/2007	Z4877	W61	Wytham Woods
18/08/2007	Z4833	CP138	Wytham Woods
18/08/2007	Z4831	CP138	Wytham Woods
18/08/2007	Z4830	CP138	Wytham Woods
18/08/2007	Z4829	CP138	Wytham Woods
18/08/2007	Z4828	CP138	Wytham Woods
18/08/2007	Z4881	W51	Wytham Woods
18/08/2007	Z4880	W51	Wytham Woods
18/08/2007	Z4866	W68	Wytham Woods
18/08/2007	Z4878	W61	Wytham Woods
18/08/2007	Z4836	CP138	Wytham Woods
18/08/2007	Z4876	W53	Wytham Woods
18/08/2007	Z4875	W61	Wytham Woods
18/08/2007	Z4874	W61	Wytham Woods
18/08/2007	Z4873	W61	Wytham Woods

18/08/2007	Z4872	W53	Wytham Woods
18/08/2007	Z4871	W53	Wytham Woods
18/08/2007	Z4879	W61	Wytham Woods
18/08/2007	Z4843	CP135	Wytham Woods
18/08/2007	Z4865	W68	Wytham Woods
18/08/2007	Z4864	W68	Wytham Woods
18/08/2007	Z4863	W68	Wytham Woods
18/08/2007	Z4862	W68	Wytham Woods
18/08/2007	Z4861	W68	Wytham Woods
18/08/2007	Z4846	CP135	Wytham Woods
18/08/2007	Z4834	CP138	Wytham Woods
18/08/2007	Z4844	CP135	Wytham Woods
18/08/2007	Z4835	CP138	Wytham Woods
18/08/2007	Z4842	CP135	Wytham Woods
18/08/2007	Z4841	CP135	Wytham Woods
18/08/2007	Z4840	CP138	Wytham Woods
18/08/2007	Z4839	CP138	Wytham Woods
18/08/2007	Z4838	CP135	Wytham Woods
18/08/2007	Z4837	CP138	Wytham Woods
18/08/2007	Y9043	CP138	Wytham Woods
18/08/2007	Z4845	CP135	Wytham Woods
18/08/2007	Z4489	W68	Wytham Woods
18/08/2007	Z4652	CP34	Wytham Woods
18/08/2007	Z4660	CP135	Wytham Woods
18/08/2007	Z4658	CP135	Wytham Woods
18/08/2007	Z4657	CP135	Wytham Woods
18/08/2007	Y9029	CP135	Wytham Woods
18/08/2007	Z4492	W68	Wytham Woods
18/08/2007	Z4870	W53	Wytham Woods
18/08/2007	Y9031	CP135	Wytham Woods
18/08/2007	Z4669	CP21	Wytham Woods
18/08/2007	Z4486	W68	Wytham Woods
18/08/2007	Z4484	W68	Wytham Woods
18/08/2007	Z4483	W68	Wytham Woods
18/08/2007	Z4481	W68	Wytham Woods
18/08/2007	Y9036	CP135	Wytham Woods
18/08/2007	Z4478	W68	Wytham Woods
18/08/2007	Z4477	W68	Wytham Woods
18/08/2007	Z4490	W68	Wytham Woods
18/08/2007	Z4474	W68	Wytham Woods
18/08/2007	Z4832	CP138	Wytham Woods
18/08/2007	Y9046	CP138	Wytham Woods
18/08/2007	Z4868	W53	Wytham Woods
18/08/2007	Z4860	W44	Wytham Woods

18/08/2007	Z4859	W44	Wytham Woods
18/08/2007	Z4858	W44	Wytham Woods
18/08/2007	Z4850	CP34	Wytham Woods
18/08/2007	Y9027	CP135	Wytham Woods
18/08/2007	Z4847	CP34	Wytham Woods
18/08/2007	Z4661	CP135	Wytham Woods
18/08/2007	Y9040	CP135	Wytham Woods
18/08/2007	Y9039	CP135	Wytham Woods
18/08/2007	Y9038	CP135	Wytham Woods
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18/08/2007	Y9037	CP135	Wytham Woods
18/08/2007	Z5782	CP135	Wytham Woods
18/08/2007	Z4869	W53	Wytham Woods
18/08/2007	Z4849	CP34	Wytham Woods
18/08/2007	Z5001	CP34	Wytham Woods
18/08/2007	Y9047	CP135	Wytham Woods
18/08/2007	Z5005	CP21	Wytham Woods
18/08/2007	Z5003	CP34	Wytham Woods
18/08/2007	Z5006	CP21	Wytham Woods
18/08/2007	Z5002	CP34	Wytham Woods
18/08/2007	Y9049	CP135	Wytham Woods
18/08/2007	Z5004	CP21	Wytham Woods
18/08/2007	Y9045	CP135	Wytham Woods
22/08/2007	Z4953	E14	Wytham Woods
22/08/2007	Z4887	E6	Wytham Woods
22/08/2007	Z4975	E43	Wytham Woods
22/08/2007	Z4954	E14	Wytham Woods
22/08/2007	Z4955	E14	Wytham Woods
22/08/2007	Z4886	E6	Wytham Woods
22/08/2007	Z4888	E6	Wytham Woods
22/08/2007	Z4978	E43	Wytham Woods
22/08/2007	Z4999	E19A	Wytham Woods
22/08/2007	Z5045	E19A	Wytham Woods
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22/08/2007	Z4990	E35A	Wytham Woods
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22/08/2007	Z4956	E14	Wytham Woods
22/08/2007	Z4974	E43	Wytham Woods
22/08/2007	Z4993	E35A	Wytham Woods
22/08/2007	Z4994	E35A	Wytham Woods
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22/08/2007	Z4962	E37	Wytham Woods
22/08/2007	Z4895	E6	Wytham Woods

22/08/2007	Z4894	E6	Wytham Woods
22/08/2007	Z4893	E6	Wytham Woods
22/08/2007	Z4892	E6	Wytham Woods
22/08/2007	Z4891	E6	Wytham Woods
22/08/2007	Z4890	E6	Wytham Woods
22/08/2007	Z4897	E6	Wytham Woods
22/08/2007	Z4898	E12	Wytham Woods
22/08/2007	Z4961	E37	Wytham Woods
22/08/2007	Z4998	E19A	Wytham Woods
22/08/2007	Z4976	E43	Wytham Woods
22/08/2007	Z4995	E35A	Wytham Woods
22/08/2007	Z4963	E37	Wytham Woods
22/08/2007	Z4900	E14	Wytham Woods
22/08/2007	Z4964	E37	Wytham Woods
22/08/2007	Z4889	E6	Wytham Woods
22/08/2007	Z4965	E37	Wytham Woods
22/08/2007	Z4951	E14	Wytham Woods
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22/08/2007	Z4973	E43	Wytham Woods
22/08/2007	Z4992	E35A	Wytham Woods
22/08/2007	Z4952	E14	Wytham Woods
22/08/2007	Z4899	E14	Wytham Woods
22/08/2007	Z4473	E35A	Wytham Woods
22/08/2007	Z4987	E42	Wytham Woods
22/08/2007	Z4958	E14	Wytham Woods
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22/08/2007	Z4467	E35A	Wytham Woods
22/08/2007	Z4481	E35A	Wytham Woods
22/08/2007	Z4997	E19A	Wytham Woods
22/08/2007	Z4996	E19A	Wytham Woods
22/08/2007	Z4466	E35A	Wytham Woods
22/08/2007	Z4959	E14	Wytham Woods
22/08/2007	Z5000	E49C	Wytham Woods
22/08/2007	Z4991	E35A	Wytham Woods
22/08/2007	Z4486	E35A	Wytham Woods
22/08/2007	Z4487	E35A	Wytham Woods
22/08/2007	Z5048	E19A	Wytham Woods
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22/08/2007	Z4981	E43	Wytham Woods
22/08/2007	Z4885	E6	Wytham Woods
22/08/2007	Z4979	E43	Wytham Woods
22/08/2007	Z4980	E43	Wytham Woods
22/08/2007	Z5046	E19A	Wytham Woods
22/08/2007	Z4882	E6	Wytham Woods

22/08/2007	Z4957	E14	Wytham Woods
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22/08/2007	Z4982	E43	Wytham Woods
22/08/2007	Z4984	E43	Wytham Woods
22/08/2007	Y9023	E19A	Wytham Woods
22/08/2007	Z4983	E43	Wytham Woods
22/08/2007	Z4883	E6	Wytham Woods
22/08/2007	Z4884	E6	Wytham Woods
24/08/2007	Y9046	E47	Wytham Woods
24/08/2007	Y9030	E47	Wytham Woods
24/08/2007	Z4877	E15	Wytham Woods
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24/08/2007	Z5039	E15	Wytham Woods
24/08/2007	Z5038	E15	Wytham Woods
24/08/2007	Y9045	E55	Wytham Woods
24/08/2007	Z5041	E15	Wytham Woods
24/08/2007	Y9048	E55	Wytham Woods
24/08/2007	Y9033	W15	Wytham Woods
24/08/2007	Y9032	E55	Wytham Woods
24/08/2007	Z4684	W15	Wytham Woods
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24/08/2007	Y9038	E55	Wytham Woods
24/08/2007	Z4707	W15	Wytham Woods
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24/08/2007	Z4685	W26	Wytham Woods
24/08/2007	Y9028	E55	Wytham Woods
24/08/2007	Y9025	E47	Wytham Woods
24/08/2007	Z4661	E55	Wytham Woods
24/08/2007	Z5042	E15	Wytham Woods
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24/08/2007	Y9027	E55	Wytham Woods
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24/08/2007	Z5009	W26	Wytham Woods
24/08/2007	Z5024	W15	Wytham Woods
24/08/2007	Z4968	E49A	Wytham Woods
24/08/2007	Z5010	W26	Wytham Woods

24/08/2007	Z5023	W15	Wytham Woods
24/08/2007	Z4970	E49A	Wytham Woods
24/08/2007	Z5028	W15	Wytham Woods
24/08/2007	Z4969	E49A	Wytham Woods
24/08/2007	Z4865	W26	Wytham Woods
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24/08/2007	Z5020	W26	Wytham Woods
24/08/2007	Z4972	E49A	Wytham Woods
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24/08/2007	Z4862	W54	Wytham Woods
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24/08/2007	Z5013	W26	Wytham Woods
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24/08/2007	Z4836	E47	Wytham Woods
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24/08/2007	Z5035	W13	Wytham Woods
24/08/2007	Z5019	W26	Wytham Woods
02/09/2007	Z4778	W13	Wytham Woods
02/09/2007	Z4757	CP10	Wytham Woods
02/09/2007	Z3058	CP3	Wytham Woods
02/09/2007	Y9028	CP117	Wytham Woods

02/09/2007	Z4769	W13	Wytham Woods
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02/09/2007	Z4659	CP117	Wytham Woods
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02/09/2007	Z3057	CP3	Wytham Woods
02/09/2007	Z4777	W13	Wytham Woods
02/09/2007	Z4756	CP10	Wytham Woods
02/09/2007	Z4717	CP101	Wytham Woods
02/09/2007	Z4775	W13	Wytham Woods
02/09/2007	Z4765	W13	Wytham Woods
02/09/2007	Z4700	CP127	Wytham Woods
02/09/2007	Y9027	CP117	Wytham Woods
02/09/2007	Z4661	CP117	Wytham Woods
02/09/2007	Z4755	CP10	Wytham Woods
02/09/2007	Z3062	CP3	Wytham Woods
02/09/2007	Y9035	CP117	Wytham Woods
02/09/2007	Z4695	CP10	Wytham Woods
02/09/2007	Y9047	CP117	Wytham Woods
02/09/2007	Z4689	CP3	Wytham Woods
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02/09/2007	Y9034	CP117	Wytham Woods
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02/09/2007	Z3061	CP3	Wytham Woods
02/09/2007	Z4766	W13	Wytham Woods
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02/09/2007	Z3052	CP117	Wytham Woods
02/09/2007	Z3059	CP3	Wytham Woods
02/09/2007	Z3063	CP151	Wytham Woods
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02/09/2007	Z4692	CP127	Wytham Woods
02/09/2007	Z4758	CP10	Wytham Woods

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02/09/2007	Z4763	CP157	Wytham Woods
02/09/2007	Z5050	B206	Wytham Woods
02/09/2007	Y9042	CP117	Wytham Woods
02/09/2007	Y9043	CP117	Wytham Woods
02/09/2007	Z4771	W13	Wytham Woods
02/09/2007	Z5030	CP157	Wytham Woods
02/09/2007	Z5031	CP151	Wytham Woods
02/09/2007	Z4837	CP117	Wytham Woods
02/09/2007	Y9045	CP117	Wytham Woods
02/09/2007	Z5032	CP157	Wytham Woods
02/09/2007	Z5033	CP157	Wytham Woods
02/09/2007	Z4693	CP127	Wytham Woods
02/09/2007	Z4759	CP10	Wytham Woods
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02/09/2007	Z4752	CP10	Wytham Woods
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02/09/2007	Z5049	B206	Wytham Woods
02/09/2007	Z4779	W13	Wytham Woods
02/09/2007	Z5019	CP157	Wytham Woods
02/09/2007	Z4706	CP102	Wytham Woods
02/09/2007	Z3056	CP3	Wytham Woods
02/09/2007	Z5047	W13	Wytham Woods
02/09/2007	Z4751	CP10	Wytham Woods
02/09/2007	Z4684	CP151	Wytham Woods
02/09/2007	Z4828	CP117	Wytham Woods
02/09/2007	Z4707	CP157	Wytham Woods
02/09/2007	Z5018	CP151	Wytham Woods

02/09/2007	Z4753	CP10	Wytham Woods
02/09/2007	Z5017	CP151	Wytham Woods
02/09/2007	Z4709	CP151	Wytham Woods
02/09/2007	Z4710	CP151	Wytham Woods
02/09/2007	Z5016	CP157	Wytham Woods
02/09/2007	Z4682	CP157	Wytham Woods
02/09/2007	Z4690	CP10	Wytham Woods
09/09/2007	Z3067	O19	Wytham Woods
09/09/2007	Z3077	O77	Wytham Woods
09/09/2007	Z3078	O77	Wytham Woods
09/09/2007	Z3075	O77	Wytham Woods
09/09/2007	Z3076	O77	Wytham Woods
09/09/2007	Z3074	O77	Wytham Woods
09/09/2007	Z3068	O19	Wytham Woods
09/09/2007	Z3801	O231	Wytham Woods
09/09/2007	Z3073	O77	Wytham Woods
09/09/2007	Z3072	O19	Wytham Woods
09/09/2007	Z3069	O19	Wytham Woods
09/09/2007	Z3070	O19	Wytham Woods
09/09/2007	Z3066	O19	Wytham Woods
09/09/2007	Z3071	O19	Wytham Woods
09/09/2007	Z3065	O19	Wytham Woods
09/09/2007	Z4795	O240	Wytham Woods
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09/09/2007	Z4784	O253	Wytham Woods
09/09/2007	Z4782	O253	Wytham Woods
09/09/2007	Z4781	O253	Wytham Woods
09/09/2007	Z4783	O253	Wytham Woods
09/09/2007	Z4800	O240	Wytham Woods
09/09/2007	Z4799	O240	Wytham Woods
09/09/2007	Z4798	O240	Wytham Woods
09/09/2007	Z4796	O240	Wytham Woods
09/09/2007	Z4794	O240	Wytham Woods
09/09/2007	Z4793	O240	Wytham Woods
09/09/2007	Z4792	O240	Wytham Woods
09/09/2007	Z4790	O240	Wytham Woods
09/09/2007	Z4789	O240	Wytham Woods
09/09/2007	Z4788	O240	Wytham Woods
09/09/2007	Z4787	O240	Wytham Woods
09/09/2007	Z4786	O240	Wytham Woods
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09/09/2007	Z4797	O240	Wytham Woods
16/09/2007	Z5653	C32	Wytham Woods
16/09/2007	Z3095	C107	Wytham Woods

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16/09/2007	Z3084	C102	Wytham Woods
16/09/2007	Z3081	C37	Wytham Woods
16/09/2007	Z3098	C107	Wytham Woods
16/09/2007	Z3099	C107	Wytham Woods
16/09/2007	Z3083	C45	Wytham Woods
16/09/2007	Z5656	C32	Wytham Woods
16/09/2007	Z5654	C32	Wytham Woods
16/09/2007	Z3092	C107	Wytham Woods
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16/09/2007	Z3093	C107	Wytham Woods
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16/09/2007	Z3079	C152	Wytham Woods
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16/09/2007	Z3080	C152	Wytham Woods
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16/09/2007	Z3182	C152	Wytham Woods
16/09/2007	Z3180	C107	Wytham Woods
16/09/2007	Z3091	C107	Wytham Woods
16/09/2007	Z3173	C152	Wytham Woods
16/09/2007	Z3100	C107	Wytham Woods
16/09/2007	Z3181	C107	Wytham Woods
16/09/2007	Z3087	C103	Wytham Woods
16/09/2007	Z3184	C113	Wytham Woods
17/09/2007	Z5659	C24	Wytham Woods
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20/09/2007	Z5671	MP3	Wytham Woods
20/09/2007	Z5672	MP3	Wytham Woods
20/09/2007	Z5673	MP3	Wytham Woods
20/09/2007	X3202	MP76	Wytham Woods
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20/09/2007	Z5679	MP3	Wytham Woods

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21/09/2007	Z4742	O210	Wytham Woods
21/09/2007	Z4745	O210	Wytham Woods
21/09/2007	Z4746	O210	Wytham Woods
21/09/2007	Z3127	O227	Wytham Woods
21/09/2007	Z4801	O210	Wytham Woods
21/09/2007	Z5694	O27	Wytham Woods
21/09/2007	Z4808	O210	Wytham Woods
21/09/2007	Z4809	O210	Wytham Woods
21/09/2007	Z5687	O210	Wytham Woods
21/09/2007	Z5688	O210	Wytham Woods
21/09/2007	Z5689	O210	Wytham Woods
21/09/2007	Z5690	O227	Wytham Woods
21/09/2007	Z4749	O210	Wytham Woods
21/09/2007	Z3121	O210	Wytham Woods
21/09/2007	Z5692	O27	Wytham Woods
24/09/2007	Z5656	P23	Wytham Woods
24/09/2007	Z5696	P23	Wytham Woods
24/09/2007	Z5698	P23	Wytham Woods
24/09/2007	Z5697	P23	Wytham Woods
24/09/2007	Z5651	P23	Wytham Woods
24/09/2007	Z5652	P23	Wytham Woods
24/09/2007	Z5653	P23	Wytham Woods
24/09/2007	Z3087	P23	Wytham Woods

24/09/2007	Z5655	P23	Wytham Woods
24/09/2007	Z4816	P104	Wytham Woods
24/09/2007	Z3084	P23	Wytham Woods
24/09/2007	Z5708	P103	Wytham Woods
24/09/2007	Z5701	P23	Wytham Woods
24/09/2007	Z5699	P23	Wytham Woods
24/09/2007	Z5654	P23	Wytham Woods
24/09/2007	Z5700	P23	Wytham Woods
24/09/2007	Z5707	P23	Wytham Woods
24/09/2007	Z5702	P23	Wytham Woods
24/09/2007	Z5703	P23	Wytham Woods
24/09/2007	Z5705	P23	Wytham Woods
24/09/2007	Z5704	P23	Wytham Woods
24/09/2007	Z5706	P23	Wytham Woods
24/09/2007	Z5695	P23	Wytham Woods
24/09/2007	Z5661	P116	Wytham Woods
24/09/2007	Z3085	P23	Wytham Woods
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30/09/2007	Z5754	E39C	Wytham Woods
30/09/2007	Z5755	E39C	Wytham Woods
30/09/2007	Z5756	E39C	Wytham Woods
30/09/2007	Z5709	E41A	Wytham Woods
30/09/2007	Z5757	E39C	Wytham Woods
30/09/2007	Z5758	E39C	Wytham Woods
30/09/2007	Z5751	E39A	Wytham Woods
30/09/2007	Z5753	E39C	Wytham Woods
30/09/2007	Z5763	E62	Wytham Woods
30/09/2007	Z5710	E41A	Wytham Woods
30/09/2007	Z4469	E39A	Wytham Woods
30/09/2007	Z4969	E62	Wytham Woods
30/09/2007	Z4471	E39A	Wytham Woods
30/09/2007	Z5764	E62	Wytham Woods
30/09/2007	Z4492	E39A	Wytham Woods
30/09/2007	Z4476	E39A	Wytham Woods
30/09/2007	Z4490	E39A	Wytham Woods
30/09/2007	X3204	E4	Wytham Woods
30/09/2007	Z4484	E39A	Wytham Woods
30/09/2007	Z5759	E39C	Wytham Woods
30/09/2007	Z5762	E62	Wytham Woods
30/09/2007	Z5761	E62	Wytham Woods
30/09/2007	Z5760	E39C	Wytham Woods
30/09/2007	Z4991	E39A	Wytham Woods
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07/10/2007	Z3073	SW126	Wytham Woods

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07/10/2007	Z5723	SW103	Wytham Woods
07/10/2007	Z3177	SW103	Wytham Woods
07/10/2007	Z5715	SW19	Wytham Woods
07/10/2007	Z4853	SW19	Wytham Woods
07/10/2007	Z5727	SW103	Wytham Woods
07/10/2007	Z4857	SW109	Wytham Woods
07/10/2007	Z3077	SW126	Wytham Woods
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07/10/2007	Z5729	SW103	Wytham Woods
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07/10/2007	Z4856	SW19	Wytham Woods
07/10/2007	Z5724	SW103	Wytham Woods
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07/10/2007	Z5717	SW13	Wytham Woods
07/10/2007	Z5722	SW126	Wytham Woods
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13/10/2007	Z3064	W23	Wytham Woods
13/10/2007	Z4881	W52	Wytham Woods
13/10/2007	Z5765	W34	Wytham Woods
13/10/2007	Z4765	W3	Wytham Woods
13/10/2007	Z5735	W5	Wytham Woods
13/10/2007	Z5734	W5	Wytham Woods
13/10/2007	Z5733	W3	Wytham Woods
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13/10/2007	Z5731	W3	Wytham Woods
13/10/2007	Z5736	W5	Wytham Woods
13/10/2007	Z5730	W3	Wytham Woods
13/10/2007	Z5761	W5	Wytham Woods
13/10/2007	Z4483	W73	Wytham Woods
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13/10/2007	Z4469	W73	Wytham Woods
13/10/2007	Z5766	W34	Wytham Woods

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13/10/2007	Z5768	W34	Wytham Woods
13/10/2007	Z5029	W23	Wytham Woods
13/10/2007	Z5769	W34	Wytham Woods
13/10/2007	Z4674	W3	Wytham Woods
13/10/2007	Z4755	W5	Wytham Woods
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13/10/2007	Z5772	W52	Wytham Woods
13/10/2007	Z5739	W77	Wytham Woods
13/10/2007	Z3056	W34	Wytham Woods
13/10/2007	Z4757	W5	Wytham Woods
13/10/2007	Z5043	W52	Wytham Woods
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11/05/2008	Z5742	B213	Wytham Woods
11/05/2008	Z5741	B213	Wytham Woods
11/05/2008	Z5740	B213	Wytham Woods
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15/05/2008	Z5743	W93	Wytham Woods
15/05/2008	Z5748	W93	Wytham Woods
15/05/2008	Z5750	W93	Wytham Woods
15/05/2008	Z4874	W93	Wytham Woods
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15/05/2008	Z4867	W93	Wytham Woods
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17/05/2008	Z4694	CP153	Wytham Woods
17/05/2008	Z4668	CP153	Wytham Woods
17/05/2008	Z5773	CP153	Wytham Woods
17/05/2008	Z5775	CP153	Wytham Woods

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19/05/2008	Z4749	O223	Wytham Woods
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19/05/2008	Z5779	O223	Wytham Woods
19/05/2008	Z5778	O223	Wytham Woods
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19/05/2008	Z4804	O223	Wytham Woods
19/05/2008	Z4806	O223	Wytham Woods
19/05/2008	Z4807	O223	Wytham Woods
19/05/2008	Z4746	O223	Wytham Woods
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20/05/2008	Z4807	E2	Wytham Woods
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20/05/2008	Z5781	E2	Wytham Woods
20/05/2008	Z4808	E2	Wytham Woods
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07/06/2008	Z4656	CP110	Wytham Woods
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13/06/2008	Z5031	W16	Wytham Woods
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13/06/2008	Z4682	W16	Wytham Woods
13/06/2008	Z5015	W16	Wytham Woods
13/06/2008	Z5009	W16	Wytham Woods
13/06/2008	Z4763	W16	Wytham Woods
13/06/2008	Z4707	W16	Wytham Woods
13/06/2008	Z5783	E12	Wytham Woods
13/06/2008	Z5020	W16	Wytham Woods
16/06/2008	Z5787	MP68	Wytham Woods
16/06/2008	Z5788	MP68	Wytham Woods
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20/06/2008	Z5793	C135	Wytham Woods
20/06/2008	Z3171	C59	Wytham Woods
20/06/2008	Z5794	C135	Wytham Woods
20/06/2008	Z3175	C135	Wytham Woods
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20/06/2008	Z3182	C135	Wytham Woods
20/06/2008	Z3088	C59	Wytham Woods
20/06/2008	Z3083	C59	Wytham Woods
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24/07/2008	Z5840	C13	Wytham Woods
24/07/2008	Z5839	C13	Wytham Woods
24/07/2008	Z5838	C13	Wytham Woods
24/07/2008	Z3182	C39	Wytham Woods
24/07/2008	Z5836	C13	Wytham Woods
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24/07/2008	Z5792	C13	Wytham Woods
24/07/2008	Z5844	C39	Wytham Woods
24/07/2008	Z5837	C13	Wytham Woods
26/07/2008	Z4741	O239	Wytham Woods
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26/07/2008	Z4738	O239	Wytham Woods
26/07/2008	Z5845	O82	Wytham Woods
26/07/2008	Z5848	O24	Wytham Woods
26/07/2008	Z5846	O242	Wytham Woods
26/07/2008	Z5847	O232	Wytham Woods
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27/07/2008	Z5743	W41	Wytham Woods
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27/07/2008	Z4951	W103	Wytham Woods
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27/07/2008	Z5910	W103	Wytham Woods
27/07/2008	Z5750	W68	Wytham Woods
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27/07/2008	Z5744	W95	Wytham Woods
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27/07/2008	Z5776	W55	Wytham Woods
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27/07/2008	Z5038	W103	Wytham Woods
27/07/2008	Z5861	W42	Wytham Woods
27/07/2008	Z5851	W68	Wytham Woods
27/07/2008	Z5852	W68	Wytham Woods
27/07/2008	Z5853	W42	Wytham Woods
27/07/2008	Z5854	W42	Wytham Woods
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03/08/2008	Z5919	MP80	Wytham Woods
03/08/2008	Z5921	MP80	Wytham Woods
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03/08/2008	Z5923	MP80	Wytham Woods
03/08/2008	Z5924	MP80	Wytham Woods
03/08/2008	Z5003	MP76	Wytham Woods
03/08/2008	Z5916	MP80	Wytham Woods
03/08/2008	Z5885	MP76	Wytham Woods
03/08/2008	Z5879	MP76	Wytham Woods
03/08/2008	Z5880	MP76	Wytham Woods
03/08/2008	Z5881	MP76	Wytham Woods
03/08/2008	Z5882	MP76	Wytham Woods
03/08/2008	Z5877	MP76	Wytham Woods
03/08/2008	Z5883	MP76	Wytham Woods
03/08/2008	Z5878	MP76	Wytham Woods

03/08/2008	Z5884	MP76	Wytham Woods
03/08/2008	Z5886	MP76	Wytham Woods
03/08/2008	Z5888	MP76	Wytham Woods
03/08/2008	Z5889	MP76	Wytham Woods
03/08/2008	Z5887	MP76	Wytham Woods
03/08/2008	Z5876	MP76	Wytham Woods
09/08/2008	Z5931	P16	Wytham Woods
09/08/2008	Z5932	P16	Wytham Woods
09/08/2008	Z5927	P16	Wytham Woods
09/08/2008	Z5934	P16	Wytham Woods
09/08/2008	Z5933	P16	Wytham Woods
09/08/2008	Z5935	P16	Wytham Woods
09/08/2008	Z5829	P16	Wytham Woods
09/08/2008	Z5928	P16	Wytham Woods
09/08/2008	Z5930	P16	Wytham Woods
09/08/2008	Z5926	P16	Wytham Woods
09/08/2008	Z5929	P16	Wytham Woods
23/08/2008	Z4695	CP8	Wytham Woods
23/08/2008	Z4660	CP144	Wytham Woods
23/08/2008	Z4756	CP15	Wytham Woods
23/08/2008	Z5940	CP134	Wytham Woods
23/08/2008	Z4662	CP141	Wytham Woods
23/08/2008	Z4752	CP112	Wytham Woods
23/08/2008	Z4693	CP15	Wytham Woods
23/08/2008	Z5818	CP127	Wytham Woods
23/08/2008	Z5938	CP134	Wytham Woods
23/08/2008	Z4656	CP144	Wytham Woods
23/08/2008	Z5956	CP141	Wytham Woods
23/08/2008	Z4689	CP15	Wytham Woods
23/08/2008	Z5973	CP8	Wytham Woods
23/08/2008	Z4696	CP19	Wytham Woods
23/08/2008	Z5947	CP134	Wytham Woods
23/08/2008	Z4687	CP134	Wytham Woods
23/08/2008	Z4697	CP15	Wytham Woods
23/08/2008	Z4843	CP144	Wytham Woods
23/08/2008	Z5957	CP144	Wytham Woods
23/08/2008	Z4686	CP130	Wytham Woods
23/08/2008	Z4680	CP8	Wytham Woods
23/08/2008	Z4679	CP108	Wytham Woods
23/08/2008	Z9047	CP144	Wytham Woods
23/08/2008	Z5941	CP134	Wytham Woods
23/08/2008	Z5939	CP134	Wytham Woods
23/08/2008	Z4765	CP15	Wytham Woods
23/08/2008	Z4836	CP144	Wytham Woods

23/08/2008	Z4700	CP112	Wytham Woods
23/08/2008	Y9030	CP144	Wytham Woods
23/08/2008	Y9032	CP141	Wytham Woods
23/08/2008	Z5964	CP19	Wytham Woods
23/08/2008	Z5963	CP19	Wytham Woods
23/08/2008	Z5962	CP19	Wytham Woods
23/08/2008	Z5961	CP19	Wytham Woods
23/08/2008	Z5960	CP19	Wytham Woods
23/08/2008	Z5959	CP19	Wytham Woods
23/08/2008	Z5958	CP19	Wytham Woods
23/08/2008	Z4694	CP8	Wytham Woods
23/08/2008	Z5954	CP134	Wytham Woods
23/08/2008	Z5945	CP134	Wytham Woods
23/08/2008	Z5953	CP134	Wytham Woods
23/08/2008	Z4847	CP134	Wytham Woods
23/08/2008	Z5952	CP134	Wytham Woods
23/08/2008	Z5951	CP134	Wytham Woods
23/08/2008	Z5950	CP134	Wytham Woods
23/08/2008	Z5949	CP134	Wytham Woods
23/08/2008	Z5782	CP141	Wytham Woods
23/08/2008	Z5946	CP134	Wytham Woods
23/08/2008	Z5948	CP134	Wytham Woods
23/08/2008	Z5955	CP134	Wytham Woods
23/08/2008	Z5971	CP112	Wytham Woods
23/08/2008	Y9045	CP144	Wytham Woods
23/08/2008	Z5977	CP15	Wytham Woods
23/08/2008	Z5976	CP15	Wytham Woods
23/08/2008	Z4669	CP15	Wytham Woods
23/08/2008	Z5975	CP15	Wytham Woods
23/08/2008	Z3054	CP19	Wytham Woods
23/08/2008	Z5974	CP15	Wytham Woods
23/08/2008	Z5942	CP134	Wytham Woods
23/08/2008	Z5965	CP19	Wytham Woods
23/08/2008	Z5972	CP8	Wytham Woods
23/08/2008	Z5966	CP112	Wytham Woods
23/08/2008	Z5943	CP134	Wytham Woods
23/08/2008	Z5970	CP112	Wytham Woods
23/08/2008	Z5969	CP112	Wytham Woods
23/08/2008	Y9043	CP141	Wytham Woods
23/08/2008	Z5968	CP112	Wytham Woods
23/08/2008	Z5967	CP112	Wytham Woods
23/08/2008	Z5944	CP134	Wytham Woods
23/08/2008	Z4668	CP19	Wytham Woods
23/08/2008	Z4690	CP8	Wytham Woods

23/08/2008	Z5775	CP8	Wytham Woods
30/08/2008	Z4657	E51A	Wytham Woods
30/08/2008	Z4656	E51A	Wytham Woods
30/08/2008	Z5782	E51A	Wytham Woods
30/08/2008	Y9027	E51A	Wytham Woods
30/08/2008	Y9028	E51A	Wytham Woods
30/08/2008	Z4847	E55	Wytham Woods
30/08/2008	Y9033	E51A	Wytham Woods
30/08/2008	Y9043	E51A	Wytham Woods
30/08/2008	Y9045	E51A	Wytham Woods
30/08/2008	Z4756	E55	Wytham Woods
30/08/2008	Y9049	E51A	Wytham Woods
30/08/2008	Z5823	E63	Wytham Woods
30/08/2008	Z4871	E31A	Wytham Woods
30/08/2008	Z4660	E51A	Wytham Woods
30/08/2008	Z4842	E51A	Wytham Woods
30/08/2008	Z5000	E51C	Wytham Woods
30/08/2008	Z5828	E51B	Wytham Woods
30/08/2008	Z5786	E28	Wytham Woods
30/08/2008	Z6050	E47	Wytham Woods
30/08/2008	Y9047	E51A	Wytham Woods
30/08/2008	Z5982	E55	Wytham Woods
30/08/2008	Z5996	E51B	Wytham Woods
30/08/2008	Z4687	E47	Wytham Woods
30/08/2008	Z5995	E51B	Wytham Woods
30/08/2008	Z5994	E51B	Wytham Woods
30/08/2008	Z5993	E51B	Wytham Woods
30/08/2008	Z5992	E31A	Wytham Woods
30/08/2008	Z5991	E31A	Wytham Woods
30/08/2008	Z5990	E31A	Wytham Woods
30/08/2008	Z5989	E31A	Wytham Woods
30/08/2008	Z5988	E31A	Wytham Woods
30/08/2008	Z5987	E31A	Wytham Woods
30/08/2008	Z5985	E63	Wytham Woods
30/08/2008	Z4969	E63	Wytham Woods
30/08/2008	Z5983	E55	Wytham Woods
30/08/2008	Z5939	E55	Wytham Woods
30/08/2008	Z5981	E55	Wytham Woods
30/08/2008	Z5980	E55	Wytham Woods
30/08/2008	Z5979	E55	Wytham Woods
30/08/2008	Z5978	E55	Wytham Woods
30/08/2008	Z5974	E47	Wytham Woods
30/08/2008	Z5943	E63	Wytham Woods
30/08/2008	Z5945	E55	Wytham Woods

30/08/2008	Z5954	E55	Wytham Woods
30/08/2008	Z5953	E55	Wytham Woods
30/08/2008	Z5952	E55	Wytham Woods
30/08/2008	Z5951	E55	Wytham Woods
30/08/2008	Z5950	E55	Wytham Woods
30/08/2008	Z5948	E55	Wytham Woods
30/08/2008	Z5984	E63	Wytham Woods
30/08/2008	Z6013	E47	Wytham Woods
30/08/2008	Z4970	E55	Wytham Woods
30/08/2008	Z5001	E55	Wytham Woods
30/08/2008	Z5986	E62G	Wytham Woods
30/08/2008	Z6018	E51A	Wytham Woods
30/08/2008	Z6017	E47	Wytham Woods
30/08/2008	Z6016	E47	Wytham Woods
30/08/2008	Z6015	E47	Wytham Woods
30/08/2008	Z6014	E47	Wytham Woods
30/08/2008	Z6012	E47	Wytham Woods
30/08/2008	Z6011	E47	Wytham Woods
30/08/2008	Z6010	E47	Wytham Woods
30/08/2008	Z6009	E47	Wytham Woods
30/08/2008	Z6007	E47	Wytham Woods
30/08/2008	Z6006	E47	Wytham Woods
30/08/2008	Z6008	E47	Wytham Woods
30/08/2008	Z6005	E47	Wytham Woods
30/08/2008	Z6002	E47	Wytham Woods
30/08/2008	Z6003	E47	Wytham Woods
30/08/2008	Z6001	E47	Wytham Woods
30/08/2008	Z6004	E47	Wytham Woods
31/08/2008	Z6061	E10A	Wytham Woods
31/08/2008	Z6057	E10A	Wytham Woods
31/08/2008	Z5783	E10A	Wytham Woods
31/08/2008	Z6063	E10A	Wytham Woods
31/08/2008	Z6062	E10A	Wytham Woods
31/08/2008	Z6058	E10A	Wytham Woods
31/08/2008	Z4964	E10A	Wytham Woods
31/08/2008	Z6064	E10A	Wytham Woods
31/08/2008	Z6060	E10A	Wytham Woods
31/08/2008	Z6069	E10A	Wytham Woods
31/08/2008	Z6065	E10A	Wytham Woods
31/08/2008	Z6071	E10A	Wytham Woods
31/08/2008	Z6068	E10A	Wytham Woods
31/08/2008	Z6067	E10A	Wytham Woods
31/08/2008	Z4962	E10A	Wytham Woods
31/08/2008	Z6066	E10A	Wytham Woods

31/08/2008	Z6059	E10A	Wytham Woods
31/08/2008	Z4799	E8A	Wytham Woods
31/08/2008	Z6073	E19	Wytham Woods
31/08/2008	Z5804	E19A	Wytham Woods
31/08/2008	Z6085	E14A	Wytham Woods
31/08/2008	Z6084	E14A	Wytham Woods
31/08/2008	Z6083	E14A	Wytham Woods
31/08/2008	Z6082	E14A	Wytham Woods
31/08/2008	Z6081	E14A	Wytham Woods
31/08/2008	Z6079	E19A	Wytham Woods
31/08/2008	Z5798	E19A	Wytham Woods
31/08/2008	Z5796	E19A	Wytham Woods
31/08/2008	Z5752	E19A	Wytham Woods
31/08/2008	Z5749	E14A	Wytham Woods
31/08/2008	Z6077	E19A	Wytham Woods
31/08/2008	Z6076	E19A	Wytham Woods
31/08/2008	Z5806	E19A	Wytham Woods
31/08/2008	Z6053	E8A	Wytham Woods
31/08/2008	Z5041	E19	Wytham Woods
31/08/2008	Z6000	E8	Wytham Woods
31/08/2008	Z5999	E8	Wytham Woods
31/08/2008	Z5998	E8	Wytham Woods
31/08/2008	Z5997	E8	Wytham Woods
31/08/2008	Z6075	E19A	Wytham Woods
31/08/2008	Z6052	E8A	Wytham Woods
31/08/2008	Z6074	E19A	Wytham Woods
31/08/2008	Z6054	E8A	Wytham Woods
31/08/2008	Z6055	E8A	Wytham Woods
31/08/2008	Z4900	E8	Wytham Woods
31/08/2008	Z6056	E8A	Wytham Woods
31/08/2008	Z6072	E19	Wytham Woods
31/08/2008	Z6080	E19A	Wytham Woods
31/08/2008	Z6051	E8	Wytham Woods
31/08/2008	Z6078	E19A	Wytham Woods
31/08/2008	Z6070	E10A	Wytham Woods
08/09/2008	Z4668	W2	Wytham Woods
08/09/2008	Z5010	CP6	Wytham Woods
08/09/2008	Z5016	CP6	Wytham Woods
08/09/2008	Z5018	CP6	Wytham Woods
08/09/2008	Z3064	CP148	Wytham Woods
08/09/2008	Z5020	CP6	Wytham Woods
08/09/2008	Z5023	CP148	Wytham Woods
08/09/2008	Z5025	CP148	Wytham Woods
08/09/2008	Z4714	CP5A	Wytham Woods

08/09/2008	Z5026	CP148	Wytham Woods
08/09/2008	Z5029	CP6	Wytham Woods
08/09/2008	Z5030	CP6	Wytham Woods
08/09/2008	Z5009	CP6	Wytham Woods
08/09/2008	Z3089	W2	Wytham Woods
08/09/2008	Z5019	CP148	Wytham Woods
08/09/2008	Z4703	W2	Wytham Woods
08/09/2008	Z5871	W2	Wytham Woods
08/09/2008	Z5870	W2	Wytham Woods
08/09/2008	Z5977	CP5A	Wytham Woods
08/09/2008	Z4694	W2	Wytham Woods
08/09/2008	Z6101	CP148	Wytham Woods
08/09/2008	Z6100	CP148	Wytham Woods
08/09/2008	Z6099	CP148	Wytham Woods
08/09/2008	Z6098	CP6	Wytham Woods
08/09/2008	Z6097	CP6	Wytham Woods
08/09/2008	Z6096	CP6	Wytham Woods
08/09/2008	Z4688	W2	Wytham Woods
08/09/2008	Z5031	CP6	Wytham Woods
08/09/2008	Z4686	CP148	Wytham Woods
08/09/2008	Z6087	W2	Wytham Woods
08/09/2008	Z4716	CP5A	Wytham Woods
08/09/2008	Z6089	W2	Wytham Woods
08/09/2008	Z6094	W2	Wytham Woods
08/09/2008	Z6095	W2	Wytham Woods
08/09/2008	Z4682	CP148	Wytham Woods
08/09/2008	Z4684	CP148	Wytham Woods
08/09/2008	Z6088	W2	Wytham Woods
08/09/2008	Z6090	W2	Wytham Woods
08/09/2008	Z6086	W2	Wytham Woods
08/09/2008	Z5874	CP5A	Wytham Woods
08/09/2008	Z6091	W2	Wytham Woods
08/09/2008	Z5767	W2	Wytham Woods
08/09/2008	Z6103	CP5A	Wytham Woods
08/09/2008	Z5006	W2	Wytham Woods
08/09/2008	Z6104	CP5A	Wytham Woods
08/09/2008	Z6093	W2	Wytham Woods
08/09/2008	Z6092	W2	Wytham Woods
08/09/2008	Z4710	CP6	Wytham Woods
08/09/2008	Z4765	W2	Wytham Woods
08/09/2008	Z6102	CP5A	Wytham Woods
11/09/2008	Z5992	W10	Wytham Woods
11/09/2008	Z6113	W12	Wytham Woods
11/09/2008	Z6110	W12	Wytham Woods

11/09/2008	Z6112	W12	Wytham Woods
11/09/2008	Z6111	W12	Wytham Woods
11/09/2008	Z6007	W12	Wytham Woods
11/09/2008	Z5819	W10	Wytham Woods
11/09/2008	Z6109	W12	Wytham Woods
11/09/2008	Z6105	W12	Wytham Woods
11/09/2008	Z6115	W10	Wytham Woods
11/09/2008	Z6087	W12	Wytham Woods
11/09/2008	Z6108	W12	Wytham Woods
11/09/2008	Z3060	W10	Wytham Woods
11/09/2008	Z6114	W10	Wytham Woods
11/09/2008	Z5739	W10	Wytham Woods
11/09/2008	Z6106	W12	Wytham Woods
11/09/2008	Z6107	W12	Wytham Woods
12/09/2008	Z3184	C112	Wytham Woods
12/09/2008	Z3175	C3A	Wytham Woods
12/09/2008	Z3090	C3A	Wytham Woods
12/09/2008	Z5837	C114	Wytham Woods
12/09/2008	Z5839	C114	Wytham Woods
12/09/2008	Z3088	C3A	Wytham Woods
12/09/2008	Z6116	C116	Wytham Woods
12/09/2008	Z5836	C114	Wytham Woods
12/09/2008	Z5795	C3A	Wytham Woods
12/09/2008	Z6118	C114	Wytham Woods
12/09/2008	Z6120	C3A	Wytham Woods
12/09/2008	Z6117	C114	Wytham Woods
12/09/2008	Z6122	C3A	Wytham Woods
12/09/2008	Z6125	C3A	Wytham Woods
12/09/2008	Z6124	C3A	Wytham Woods
12/09/2008	Z6123	C3A	Wytham Woods
12/09/2008	Z6121	C3A	Wytham Woods
12/09/2008	Z5706	C21	Wytham Woods
12/09/2008	Z6119	C114	Wytham Woods
21/09/2008	Z6005	W17	Wytham Woods
21/09/2008	Z6004	W73	Wytham Woods
21/09/2008	Z4858	W17	Wytham Woods
21/09/2008	Z3065	O256	Wytham Woods
21/09/2008	Z4744	O256	Wytham Woods
21/09/2008	Z6027	W74	Wytham Woods
21/09/2008	Z3070	O256	Wytham Woods
21/09/2008	Z3071	O256	Wytham Woods
21/09/2008	Z6110	W17	Wytham Woods
21/09/2008	Z4785	O256	Wytham Woods
21/09/2008	Z4782	O256	Wytham Woods

21/09/2008	Z6028	W73	Wytham Woods
21/09/2008	Z6015	W17	Wytham Woods
21/09/2008	Z6026	W17	Wytham Woods
21/09/2008	Z6025	W17	Wytham Woods
21/09/2008	Z6024	W17	Wytham Woods
21/09/2008	Z6023	W17	Wytham Woods
21/09/2008	Z6022	W17	Wytham Woods
21/09/2008	Z6021	W17	Wytham Woods
21/09/2008	Z6020	W17	Wytham Woods
21/09/2008	Z6029	W73	Wytham Woods
21/09/2008	Z6030	W73	Wytham Woods
21/09/2008	Z6102	W17	Wytham Woods
21/09/2008	Z6019	W17	Wytham Woods
21/09/2008	Z3062	W17	Wytham Woods
21/09/2008	Z6033	O256	Wytham Woods
21/09/2008	Z6031	W73	Wytham Woods
21/09/2008	Z6034	O256	Wytham Woods
21/09/2008	Z6032	W73	Wytham Woods
21/09/2008	Z6035	O9	Wytham Woods
21/09/2008	Z6036	O9	Wytham Woods
21/09/2008	Z6037	O9	Wytham Woods
21/09/2008	Z5047	W17	Wytham Woods
26/09/2008	Z6042	MP11	Wytham Woods
26/09/2008	Z5883	MP11	Wytham Woods
26/09/2008	Z5938	MP3	Wytham Woods
26/09/2008	Z6046	B122	Wytham Woods
26/09/2008	Z6045	B122	Wytham Woods
26/09/2008	Z6126	MP3	Wytham Woods
26/09/2008	Z6043	MP11	Wytham Woods
26/09/2008	Z6041	MP11	Wytham Woods
26/09/2008	Z6040	MP11	Wytham Woods
26/09/2008	Z6039	MP11	Wytham Woods
26/09/2008	Z6038	MP11	Wytham Woods
26/09/2008	Z6044	B122	Wytham Woods
09/10/2008	Z4816	SW71	Wytham Woods
09/10/2008	Z4826	SW31	Wytham Woods
09/10/2008	X3222	SW35	Wytham Woods
12/10/2008	Z5661	B156	Wytham Woods
12/10/2008	Z6047	B57	Wytham Woods
15/10/2008	Z6128	E92	Wytham Woods
15/10/2008	Z6127	E89	Wytham Woods
15/10/2008	Z6048	E86	Wytham Woods
19/10/2008	Z5843	C139	Wytham Woods
19/10/2008	Z3083	C145	Wytham Woods

19/10/2008	Z6049	C123	Wytham Woods
04/05/2009	Z9501	SW55	Wytham Woods
05/05/2009	Z9505	O217	Wytham Woods
05/05/2009	Z9507	O217	Wytham Woods
05/05/2009	Z9508	O217	Wytham Woods
05/05/2009	Z9509	O217	Wytham Woods
05/05/2009	Z9510	O217	Wytham Woods
05/05/2009	Z9511	O217	Wytham Woods
05/05/2009	Z9506	O217	Wytham Woods
06/05/2009	Z5685	B91	Wytham Woods
06/05/2009	Z4699	B91	Wytham Woods
06/05/2009	Z5661	B91	Wytham Woods
06/05/2009	Z5663	B91	Wytham Woods
06/05/2009	Z5680	B91	Wytham Woods
06/05/2009	Z5681	B91	Wytham Woods
06/05/2009	Z5686	B91	Wytham Woods
06/05/2009	Z5890	B91	Wytham Woods
06/05/2009	Z5912	B91	Wytham Woods
06/05/2009	Z5913	B91	Wytham Woods
06/05/2009	Z5917	B91	Wytham Woods
06/05/2009	Z9522	B91	Wytham Woods
06/05/2009	Z9512	B91	Wytham Woods
06/05/2009	Z5922	B91	Wytham Woods
06/05/2009	Z9517	B91	Wytham Woods
06/05/2009	Z9518	B91	Wytham Woods
06/05/2009	Z9519	B91	Wytham Woods
06/05/2009	Z9513	B91	Wytham Woods
06/05/2009	Z9516	B91	Wytham Woods
06/05/2009	Z9520	B91	Wytham Woods
06/05/2009	Z9515	B91	Wytham Woods
06/05/2009	Z9514	B91	Wytham Woods
06/05/2009	Z5919	B91	Wytham Woods
06/05/2009	Z9521	B91	Wytham Woods
07/05/2009	Z9530	W64	Wytham Woods
07/05/2009	Z9531	W64	Wytham Woods
07/05/2009	Z4479	W64	Wytham Woods
07/05/2009	Z4469	W64	Wytham Woods
07/05/2009	Z4492	W64	Wytham Woods
07/05/2009	Z4487	W64	Wytham Woods
07/05/2009	Z4474	W64	Wytham Woods
07/05/2009	Z9532	W64	Wytham Woods
07/05/2009	Z4995	W64	Wytham Woods
07/05/2009	Z4992	W64	Wytham Woods
07/05/2009	Z4991	W64	Wytham Woods

12/05/2009	Z5794	C24b	Wytham Woods
30/05/2009	Z5749	W64A	Wytham Woods
30/05/2009	Z6091	W33	Wytham Woods
30/05/2009	Z9534	W64A	Wytham Woods
30/05/2009	Z6023	W33	Wytham Woods
30/05/2009	Z9536	W33	Wytham Woods
30/05/2009	Z9667	W64A	Wytham Woods
30/05/2009	Z9538	W33	Wytham Woods
30/05/2009	Z9540	O38	Wytham Woods
30/05/2009	Z3059	W33	Wytham Woods
30/05/2009	Z5765	W33	Wytham Woods
30/05/2009	Z9535	W33	Wytham Woods
30/05/2009	Z4873	W64A	Wytham Woods
30/05/2009	Z4870	W64A	Wytham Woods
30/05/2009	Z4765	W33	Wytham Woods
30/05/2009	Z9539	W33	Wytham Woods
30/05/2009	Z5995	W33	Wytham Woods
30/05/2009	Z5781	O38	Wytham Woods
30/05/2009	Z5852	W64A	Wytham Woods
30/05/2009	Z5776	W33	Wytham Woods
30/05/2009	Z5874	W33	Wytham Woods
30/05/2009	Z9537	W33	Wytham Woods
30/05/2009	Z5872	W33	Wytham Woods
30/05/2009	Z5871	W33	Wytham Woods
30/05/2009	Z5870	W33	Wytham Woods
30/05/2009	Z5896	W64A	Wytham Woods
30/05/2009	Z5898	W64a	Wytham Woods
30/05/2009	Z5891	W64A	Wytham Woods
06/06/2009	Z5662	MP5	Wytham Woods
06/06/2009	Z9529	MP5	Wytham Woods
06/06/2009	Z9528	MP5	Wytham Woods
06/06/2009	Z9527	MP5	Wytham Woods
06/06/2009	Z9526	MP5	Wytham Woods
06/06/2009	Z9525	MP5	Wytham Woods
06/06/2009	Z9524	MP5	Wytham Woods
06/06/2009	Z9523	MP5	Wytham Woods
06/06/2009	Z5918	MP5	Wytham Woods
06/06/2009	Z5923	MP5	Wytham Woods
06/06/2009	Z5920	MP5	Wytham Woods
06/06/2009	Z5924	MP5	Wytham Woods
06/06/2009	Z5921	MP5	Wytham Woods
06/06/2009	Z5660	MP5	Wytham Woods
17/06/2009	Z9599	CP32	Wytham Woods
17/06/2009	Z9544	CP32	Wytham Woods

17/06/2009	Z9597	CP155	Wytham Woods
17/06/2009	Z9598	CP155	Wytham Woods
17/06/2009	Z4714	CP155	Wytham Woods
17/06/2009	Z4719	CP155	Wytham Woods
17/06/2009	Z9600	CP32	Wytham Woods
17/06/2009	Z9542	CP32	Wytham Woods
17/06/2009	Z9543	CP32	Wytham Woods
17/06/2009	Z9552	CP124	Wytham Woods
17/06/2009	Z9551	CP32	Wytham Woods
17/06/2009	Z9550	CP32	Wytham Woods
17/06/2009	Z9549	CP32	Wytham Woods
17/06/2009	Z9548	CP32	Wytham Woods
17/06/2009	Z9546	CP32	Wytham Woods
17/06/2009	Z9545	CP32	Wytham Woods
18/06/2009	Z4477	W38	Wytham Woods
18/06/2009	Z4718	W2	Wytham Woods
18/06/2009	Z9562	W39	Wytham Woods
18/06/2009	Z5861	W39	Wytham Woods
18/06/2009	Z5991	W2	Wytham Woods
18/06/2009	Z9566	W45	Wytham Woods
18/06/2009	Z4880	W39	Wytham Woods
18/06/2009	Z5853	W39	Wytham Woods
18/06/2009	Z5858	W39	Wytham Woods
18/06/2009	Z4773	W2	Wytham Woods
18/06/2009	Z4775	W2	Wytham Woods
18/06/2009	Z4779	W2	Wytham Woods
18/06/2009	Z6019	W2	Wytham Woods
18/06/2009	Z9563	W39	Wytham Woods
18/06/2009	Z4860	W39	Wytham Woods
18/06/2009	Z9564	W45	Wytham Woods
18/06/2009	Z5862	W39	Wytham Woods
18/06/2009	Z5865	W45	Wytham Woods
18/06/2009	Z5866	W39	Wytham Woods
18/06/2009	Z5013	W38	Wytham Woods
18/06/2009	Z5031	W18	Wytham Woods
18/06/2009	Z5033	W18	Wytham Woods
18/06/2009	Z5035	W2	Wytham Woods
18/06/2009	Z9565	W45	Wytham Woods
18/06/2009	Z9557	W38	Wytham Woods
18/06/2009	Z9553	W2	Wytham Woods
18/06/2009	Z9554	W2	Wytham Woods
18/06/2009	Z9555	W2	Wytham Woods
18/06/2009	Z9556	W38	Wytham Woods
18/06/2009	Z6112	W2	Wytham Woods

18/06/2009	Z6099	W18	Wytham Woods
18/06/2009	Z9559	W39	Wytham Woods
18/06/2009	Z6080	W2	Wytham Woods
18/06/2009	Z9560	W39	Wytham Woods
18/06/2009	Z9561	W39	Wytham Woods
03/07/2009	Z6018	CP145	Wytham Woods
03/07/2009	Z4842	CP145	Wytham Woods
03/07/2009	Z4898	E13	Wytham Woods
03/07/2009	Z5905	E13	Wytham Woods
03/07/2009	Z5909	E13	Wytham Woods
03/07/2009	Z5044	E13	Wytham Woods
03/07/2009	Z6053	E13	Wytham Woods
03/07/2009	Z5901	E13	Wytham Woods
03/07/2009	Y9032	CP145	Wytham Woods
03/07/2009	Z4836	CP145	Wytham Woods
03/07/2009	Z4957	E13	Wytham Woods
03/07/2009	Z4954	E13	Wytham Woods
03/07/2009	Z4952	E13	Wytham Woods
03/07/2009	Z4900	E13	Wytham Woods
03/07/2009	Y9033	CP145	Wytham Woods
03/07/2009	Z4899	E13	Wytham Woods
03/07/2009	Z5956	CP145	Wytham Woods
03/07/2009	Z5850	E13	Wytham Woods
08/07/2009	Z5895	W102	Wytham Woods
08/07/2009	Z9583	W101	Wytham Woods
08/07/2009	Z9584	W105	Wytham Woods
08/07/2009	Z9585	W105	Wytham Woods
08/07/2009	Z9586	W105	Wytham Woods
08/07/2009	Z9587	W105	Wytham Woods
08/07/2009	Z4959	W105	Wytham Woods
08/07/2009	Z9582	W101	Wytham Woods
08/07/2009	Z9568	W101	Wytham Woods
08/07/2009	Z5891	W102	Wytham Woods
08/07/2009	Z5893	W101	Wytham Woods
08/07/2009	Z9593	W102	Wytham Woods
08/07/2009	Z9592	W102	Wytham Woods
08/07/2009	Z9588	W105	Wytham Woods
08/07/2009	Z5749	W101	Wytham Woods
08/07/2009	Z9667	W102	Wytham Woods
08/07/2009	Z9534	W102	Wytham Woods
08/07/2009	Z5745	W102	Wytham Woods
08/07/2009	Z9602	W102	Wytham Woods
08/07/2009	Z5904	W105	Wytham Woods
08/07/2009	Z9567	W101	Wytham Woods

08/07/2009	Z5748	W101	Wytham Woods
08/07/2009	Z5047	W105	Wytham Woods
08/07/2009	Z9601	W102	Wytham Woods
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08/07/2009	Z9595	W102	Wytham Woods
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08/07/2009	Z6076	W101	Wytham Woods
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08/07/2009	Z9596	W105	Wytham Woods
08/07/2009	Z9569	W101	Wytham Woods
08/07/2009	Z4867	W101	Wytham Woods
08/07/2009	Z9570	W101	Wytham Woods
08/07/2009	Z4870	W102	Wytham Woods
08/07/2009	Z9571	W101	Wytham Woods
08/07/2009	Z9591	W102	Wytham Woods
08/07/2009	Z4873	W102	Wytham Woods
08/07/2009	Z4877	W105	Wytham Woods
08/07/2009	Z9594	W102	Wytham Woods
09/07/2009	Z9607	C13	Wytham Woods
09/07/2009	Z9637	C122	Wytham Woods
09/07/2009	Z9610	C13	Wytham Woods
09/07/2009	Z6120	C102	Wytham Woods
09/07/2009	Z9614	C102	Wytham Woods
09/07/2009	Z3088	C13	Wytham Woods
09/07/2009	Z3171	C101	Wytham Woods
09/07/2009	Z9628	C122	Wytham Woods
09/07/2009	Z9636	C122	Wytham Woods
09/07/2009	Z9613	C102	Wytham Woods
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09/07/2009	Z9604	C13	Wytham Woods
09/07/2009	Z9638	C122	Wytham Woods
09/07/2009	Z3087	C122	Wytham Woods
09/07/2009	Z9605	C13	Wytham Woods
09/07/2009	Z9621	C101	Wytham Woods
09/07/2009	Z5842	C13	Wytham Woods
09/07/2009	Z9618	C102	Wytham Woods
09/07/2009	Z9633	C122	Wytham Woods

09/07/2009	Z9617	C102	Wytham Woods
09/07/2009	Z5840	C13	Wytham Woods
09/07/2009	Z9632	C122	Wytham Woods
09/07/2009	Z9620	C102	Wytham Woods
09/07/2009	Z5836	C13	Wytham Woods
09/07/2009	Z9609	C13	Wytham Woods
09/07/2009	Z9615	C102	Wytham Woods
09/07/2009	Z9627	C122	Wytham Woods
09/07/2009	Z9619	C102	Wytham Woods
09/07/2009	Z9608	C13	Wytham Woods
09/07/2009	Z5792	C102	Wytham Woods
09/07/2009	Z5791	C101	Wytham Woods
09/07/2009	Z9635	C122	Wytham Woods
09/07/2009	Z9616	C102	Wytham Woods
09/07/2009	Z6118	C102	Wytham Woods
09/07/2009	Z9624	C122	Wytham Woods
09/07/2009	Z3175	C102	Wytham Woods
09/07/2009	Z9629	C122	Wytham Woods
09/07/2009	Z9612	C102	Wytham Woods
09/07/2009	Z9630	C122	Wytham Woods
09/07/2009	Z9606	C13	Wytham Woods
09/07/2009	Z9623	C101	Wytham Woods
09/07/2009	Z9631	C122	Wytham Woods
09/07/2009	Z9580	C102	Wytham Woods
09/07/2009	Z9626	C122	Wytham Woods
09/07/2009	Z9622	C101	Wytham Woods
09/07/2009	Z9634	C122	Wytham Woods
09/07/2009	Z5696	C122	Wytham Woods
09/07/2009	Z5697	C122	Wytham Woods
09/07/2009	Z5700	C122	Wytham Woods
09/07/2009	Z9625	C122	Wytham Woods
09/07/2009	Z5702	C122	Wytham Woods
09/07/2009	Z9603	C13	Wytham Woods
11/07/2009	Z9648	SW124	Wytham Woods
11/07/2009	Z9502	SW124	Wytham Woods
11/07/2009	Z9647	SW124	Wytham Woods
11/07/2009	Z9644	SW124	Wytham Woods
11/07/2009	Z9646	SW124	Wytham Woods
11/07/2009	Z9645	SW124	Wytham Woods
11/07/2009	Z9649	SW124	Wytham Woods
11/07/2009	Z9640	O217	Wytham Woods
11/07/2009	Z9643	SW124	Wytham Woods
11/07/2009	Z9642	SW124	Wytham Woods
11/07/2009	Z4857	SW109	Wytham Woods

11/07/2009	Z9641	O217	Wytham Woods
11/07/2009	Z3121	O217	Wytham Woods
11/07/2009	Z9639	O217	Wytham Woods
11/07/2009	Z3133	O204	Wytham Woods
23/07/2009	Z5893	W52	Wytham Woods
23/07/2009	Z9653	W32	Wytham Woods
23/07/2009	Z5862	W58	Wytham Woods
23/07/2009	Z6073	W68	Wytham Woods
23/07/2009	Z5861	W58	Wytham Woods
23/07/2009	Z9651	W49	Wytham Woods
23/07/2009	Z6023	W68	Wytham Woods
23/07/2009	Z9655	W32	Wytham Woods
23/07/2009	Z5866	W58	Wytham Woods
23/07/2009	Z5867	W49	Wytham Woods
23/07/2009	Z9569	W52	Wytham Woods
23/07/2009	Z9656	W58	Wytham Woods
23/07/2009	Z9654	W32	Wytham Woods
23/07/2009	Z5971	W58	Wytham Woods
23/07/2009	Z9652	W49	Wytham Woods
23/07/2009	Z5873	W58	Wytham Woods
23/07/2009	Z9650	W49	Wytham Woods
23/07/2009	Z9558	W58	Wytham Woods
23/07/2009	Z9565	W32	Wytham Woods
23/07/2009	Z9673	W68	Wytham Woods
23/07/2009	Z9534	W52	Wytham Woods
23/07/2009	Z5995	W49	Wytham Woods
23/07/2009	Z4870	W52	Wytham Woods
23/07/2009	Z9672	W68	Wytham Woods
23/07/2009	Z9667	W52	Wytham Woods
23/07/2009	Z9668	W68	Wytham Woods
23/07/2009	Z9562	W58	Wytham Woods
23/07/2009	Z4713	W32	Wytham Woods
23/07/2009	Z4775	W49	Wytham Woods
23/07/2009	Z9566	W49	Wytham Woods
23/07/2009	Z9671	W68	Wytham Woods
23/07/2009	Z9589	W52	Wytham Woods
23/07/2009	Z9563	W58	Wytham Woods
23/07/2009	Z9670	W68	Wytham Woods
23/07/2009	Z5856	W58	Wytham Woods
23/07/2009	Z9560	W68	Wytham Woods
23/07/2009	Z5772	W68	Wytham Woods
23/07/2009	Z4860	W49	Wytham Woods
23/07/2009	Z9669	W68	Wytham Woods
23/07/2009	Z5038	W58	Wytham Woods

23/07/2009	Z4880	W58	Wytham Woods
23/07/2009	Z5855	W58	Wytham Woods
23/07/2009	Z5854	W49	Wytham Woods
23/07/2009	Z9657	W58	Wytham Woods
23/07/2009	Z9658	W58	Wytham Woods
23/07/2009	Z5852	W52	Wytham Woods
23/07/2009	Z9659	W58	Wytham Woods
23/07/2009	Z9660	W58	Wytham Woods
23/07/2009	Z5851	W52	Wytham Woods
23/07/2009	Z9661	W58	Wytham Woods
23/07/2009	Z9662	W58	Wytham Woods
23/07/2009	Z9674	W68	Wytham Woods
23/07/2009	Z9590	W52	Wytham Woods
23/07/2009	Z9666	W52	Wytham Woods
23/07/2009	Z9675	W68	Wytham Woods
23/07/2009	Y9023	W58	Wytham Woods
23/07/2009	Z9664	W58	Wytham Woods
23/07/2009	Z9561	W49	Wytham Woods
23/07/2009	Z5767	W32	Wytham Woods
23/07/2009	Z5766	W58	Wytham Woods
23/07/2009	Z9665	W58	Wytham Woods
23/07/2009	Z5746	W52	Wytham Woods
23/07/2009	Z9663	W58	Wytham Woods
26/07/2009	Z9679	MP54	Wytham Woods
26/07/2009	Z9680	MP54	Wytham Woods
26/07/2009	Z9681	MP54	Wytham Woods
26/07/2009	Z9682	MP54	Wytham Woods
26/07/2009	Z9683	MP54	Wytham Woods
26/07/2009	Z9684	MP54	Wytham Woods
26/07/2009	Z9678	MP54	Wytham Woods
26/07/2009	Z9686	MP54	Wytham Woods
26/07/2009	Z5920	MP54	Wytham Woods
26/07/2009	Z4699	MP54	Wytham Woods
26/07/2009	Z9687	MP54	Wytham Woods
26/07/2009	Z9688	MP54	Wytham Woods
26/07/2009	Z9689	MP29	Wytham Woods
26/07/2009	Z9690	MP29	Wytham Woods
26/07/2009	Z9685	MP54	Wytham Woods
26/07/2009	Z5917	MP54	Wytham Woods
26/07/2009	Z5788	MP67	Wytham Woods
26/07/2009	Z5787	MP65	Wytham Woods
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26/07/2009	Z5681	MP54	Wytham Woods
26/07/2009	Z5662	MP54	Wytham Woods
26/07/2009	Z5660	MP54	Wytham Woods
26/07/2009	Z5652	MP82	Wytham Woods
26/07/2009	Z5912	MP54	Wytham Woods
26/07/2009	Z5921	MP29	Wytham Woods
26/07/2009	Z5914	MP29	Wytham Woods
26/07/2009	Z9677	MP54	Wytham Woods
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26/07/2009	Z9514	MP54	Wytham Woods
26/07/2009	Z9518	MP54	Wytham Woods
26/07/2009	Z5922	MP54	Wytham Woods
26/07/2009	Z9520	MP29	Wytham Woods
26/07/2009	Z9521	MP29	Wytham Woods
26/07/2009	Z9522	MP29	Wytham Woods
26/07/2009	Z9523	MP54	Wytham Woods
26/07/2009	Z9528	MP54	Wytham Woods
26/07/2009	Z9676	MP54	Wytham Woods
30/07/2009	Z9693	SW63	Wytham Woods
30/07/2009	Z9696	SW63	Wytham Woods
30/07/2009	Z3071	O252	Wytham Woods
30/07/2009	Z3065	O252	Wytham Woods
30/07/2009	Z9694	SW63	Wytham Woods
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30/07/2009	Z9697	SW63	Wytham Woods
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30/07/2009	Z9692	SW63	Wytham Woods
30/07/2009	Z9698	SW63	Wytham Woods
30/07/2009	Z9699	SW63	Wytham Woods
30/07/2009	Z9699	SW63	Wytham Woods
30/07/2009	Z9695	SW63	Wytham Woods
30/07/2009	Z9691	SW63	Wytham Woods
30/07/2009	Z4784	O252	Wytham Woods
30/07/2009	Z4744	O252	Wytham Woods
30/07/2009	Z6033	O252	Wytham Woods
30/07/2009	Z9692	SW63	Wytham Woods
30/07/2009	Z9691	SW63	Wytham Woods
04/08/2009	Z9611	C124	Wytham Woods
04/08/2009	Z9703	C139	Wytham Woods
04/08/2009	Z9618	C26	Wytham Woods

04/08/2009	Z9702	C139	Wytham Woods
04/08/2009	Z9616	C124	Wytham Woods
04/08/2009	Z9613	C26	Wytham Woods
04/08/2009	Z9705	C139	Wytham Woods
04/08/2009	Z9706	C36	Wytham Woods
04/08/2009	Z9707	C58	Wytham Woods
04/08/2009	Z9704	C139	Wytham Woods
04/08/2009	Z9708	C26	Wytham Woods
04/08/2009	Z9610	C124	Wytham Woods
04/08/2009	Z9709	C124	Wytham Woods
04/08/2009	Z9608	C26	Wytham Woods
04/08/2009	Z9710	C124	Wytham Woods
04/08/2009	Z9711	C124	Wytham Woods
04/08/2009	Z9620	C124	Wytham Woods
04/08/2009	Z9712	C124	Wytham Woods
04/08/2009	Z9621	C58	Wytham Woods
04/08/2009	Z6120	C124	Wytham Woods
04/08/2009	Z9622	C139	Wytham Woods
04/08/2009	Z6118	C26	Wytham Woods
04/08/2009	Z9617	C58	Wytham Woods
04/08/2009	Z5836	C124	Wytham Woods
04/08/2009	Z3182	C36	Wytham Woods
04/08/2009	Z3179	C124	Wytham Woods
04/08/2009	Z3175	C58	Wytham Woods
04/08/2009	Z3174	C61	Wytham Woods
04/08/2009	Z3088	C58	Wytham Woods
04/08/2009	Z3081	C139	Wytham Woods
04/08/2009	Z5652	C119	Wytham Woods
04/08/2009	Z5671	C139	Wytham Woods
04/08/2009	Z5791	C58	Wytham Woods
04/08/2009	Z9609	C58	Wytham Woods
04/08/2009	Z5795	C139	Wytham Woods
04/08/2009	Z9701	C139	Wytham Woods
04/08/2009	Z5839	C36	Wytham Woods
04/08/2009	Z9580	C58	Wytham Woods
04/08/2009	Z5840	C124	Wytham Woods
04/08/2009	Z5841	C26	Wytham Woods
04/08/2009	Z9605	C26	Wytham Woods
04/08/2009	Z5842	C124	Wytham Woods
04/08/2009	Z5889	C124	Wytham Woods
04/08/2009	Z9607	C124	Wytham Woods
04/08/2009	Z9700	C139	Wytham Woods
04/08/2009	Z9603	C124	Wytham Woods
04/08/2009	Z9541	C43	Wytham Woods

11/08/2009	Z6101	CP124	Wytham Woods
11/08/2009	Z4694	CP118	Wytham Woods
11/08/2009	Z9451	CP35	Wytham Woods
11/08/2009	Z3054	CP118	Wytham Woods
11/08/2009	Z4667	CP35	Wytham Woods
11/08/2009	Z4680	CP118	Wytham Woods
11/08/2009	Z4687	CP35	Wytham Woods
11/08/2009	Z5018	CP124	Wytham Woods
11/08/2009	Z4689	CP118	Wytham Woods
11/08/2009	Z9455	CP35	Wytham Woods
11/08/2009	Z4696	CP118	Wytham Woods
11/08/2009	Z4697	CP118	Wytham Woods
11/08/2009	Z4700	CP118	Wytham Woods
11/08/2009	Z4847	CP35	Wytham Woods
11/08/2009	Z4970	CP35	Wytham Woods
11/08/2009	Z5001	CP35	Wytham Woods
11/08/2009	Z9452	CP35	Wytham Woods
11/08/2009	Z9461	CP35	Wytham Woods
11/08/2009	Z9469	CP118	Wytham Woods
11/08/2009	Z9468	CP118	Wytham Woods
11/08/2009	Z9467	CP118	Wytham Woods
11/08/2009	Z9466	CP117	Wytham Woods
11/08/2009	Z9465	CP124	Wytham Woods
11/08/2009	Z9464	CP144	Wytham Woods
11/08/2009	Z9453	CP35	Wytham Woods
11/08/2009	Z9462	CP35	Wytham Woods
11/08/2009	Z9454	CP35	Wytham Woods
11/08/2009	Z9460	CP35	Wytham Woods
11/08/2009	Z9459	CP35	Wytham Woods
11/08/2009	Z9458	CP35	Wytham Woods
11/08/2009	Z9457	CP35	Wytham Woods
11/08/2009	Z9456	CP35	Wytham Woods
11/08/2009	Z4690	CP118	Wytham Woods
11/08/2009	Z9463	CP35	Wytham Woods
11/08/2009	Z5942	CP35	Wytham Woods
11/08/2009	Z5993	CP35	Wytham Woods
14/08/2009	Z5896	W98	Wytham Woods
14/08/2009	Z9534	W61	Wytham Woods
14/08/2009	Z4870	W61	Wytham Woods
14/08/2009	Z4873	W98	Wytham Woods
14/08/2009	Z4875	W61	Wytham Woods
14/08/2009	Z9569	W61	Wytham Woods
14/08/2009	Z5898	W61	Wytham Woods
14/08/2009	Z9582	W61	Wytham Woods

14/08/2009	Z9591	W61	Wytham Woods
14/08/2009	Z9592	W61	Wytham Woods
14/08/2009	Z9667	W98	Wytham Woods
14/08/2009	Z9594	W61	Wytham Woods
14/08/2009	Z9595	W61	Wytham Woods
14/08/2009	Z9471	W98	Wytham Woods
14/08/2009	Z9470	W98	Wytham Woods
14/08/2009	Z5852	W61	Wytham Woods
14/08/2009	Z5746	W61	Wytham Woods
14/08/2009	Z5851	W61	Wytham Woods
14/08/2009	Z9666	W61	Wytham Woods
14/08/2009	Z9567	W61	Wytham Woods
22/08/2009	Z6067	E40	Wytham Woods
22/08/2009	Y9047	E48A	Wytham Woods
22/08/2009	Z5782	E48A	Wytham Woods
22/08/2009	Z9559	E16	Wytham Woods
22/08/2009	Z9769	E22	Wytham Woods
22/08/2009	Z9768	E22	Wytham Woods
22/08/2009	Z9759	E16	Wytham Woods
22/08/2009	Z9767	E16	Wytham Woods
22/08/2009	Z6070	E40	Wytham Woods
22/08/2009	Z9766	E16	Wytham Woods
22/08/2009	Z9763	E16	Wytham Woods
22/08/2009	Z9764	E16	Wytham Woods
22/08/2009	Z9751	E42A	Wytham Woods
22/08/2009	Z9761	E16	Wytham Woods
22/08/2009	Z9757	E16	Wytham Woods
22/08/2009	Z9762	E16	Wytham Woods
22/08/2009	Z9754	E40	Wytham Woods
22/08/2009	Z9760	E16	Wytham Woods
22/08/2009	Z9571	E22	Wytham Woods
22/08/2009	Z6066	E40	Wytham Woods
22/08/2009	Z9753	E40	Wytham Woods
22/08/2009	Z9752	E40	Wytham Woods
22/08/2009	Z9765	E16	Wytham Woods
22/08/2009	Z9774	E29	Wytham Woods
22/08/2009	Z5811	E31	Wytham Woods
22/08/2009	Z9663	E22	Wytham Woods
22/08/2009	Z5754	E31	Wytham Woods
22/08/2009	Z5048	E31	Wytham Woods
22/08/2009	Z5042	E16	Wytham Woods
22/08/2009	Z9776	E29	Wytham Woods
22/08/2009	Z4968	E22	Wytham Woods
22/08/2009	Z6001	E29	Wytham Woods

22/08/2009	Z9775	E29	Wytham Woods
22/08/2009	Z6065	E40	Wytham Woods
22/08/2009	Z4869	E16	Wytham Woods
22/08/2009	Z9755	E40	Wytham Woods
22/08/2009	Z6061	E40	Wytham Woods
22/08/2009	Z6058	E40	Wytham Woods
22/08/2009	Z6039	E16	Wytham Woods
22/08/2009	Z4962	E40	Wytham Woods
22/08/2009	Z9770	E22	Wytham Woods
22/08/2009	Z9773	E29	Wytham Woods
22/08/2009	Z5991	E22	Wytham Woods
22/08/2009	Z6075	E16	Wytham Woods
22/08/2009	Z9771	E29	Wytham Woods
22/08/2009	Z5990	E22	Wytham Woods
22/08/2009	Z9772	E29	Wytham Woods
22/08/2009	Z4778	E22	Wytham Woods
24/08/2009	Z9777	W52	Wytham Woods
24/08/2009	Z9779	W52	Wytham Woods
24/08/2009	Z9756	E33	Wytham Woods
24/08/2009	Z9780	W52	Wytham Woods
24/08/2009	Z9781	W95	Wytham Woods
24/08/2009	Z9778	W52	Wytham Woods
24/08/2009	Z9660	W52	Wytham Woods
24/08/2009	Z4875	W95	Wytham Woods
24/08/2009	Z4873	W52	Wytham Woods
24/08/2009	Z4867	W52	Wytham Woods
24/08/2009	Z6078	E33	Wytham Woods
24/08/2009	Z9666	W52	Wytham Woods
24/08/2009	Z5804	E33	Wytham Woods
24/08/2009	Z5895	W52	Wytham Woods
24/08/2009	Z9594	W52	Wytham Woods
24/08/2009	Z5851	W95	Wytham Woods
24/08/2009	Z9596	W52	Wytham Woods
24/08/2009	Z6072	W52	Wytham Woods
24/08/2009	Z5891	W95	Wytham Woods
24/08/2009	Z6076	W52	Wytham Woods
24/08/2009	Z5852	W95	Wytham Woods
24/08/2009	Z9581	W95	Wytham Woods
24/08/2009	Z9583	W52	Wytham Woods
24/08/2009	Z9592	W52	Wytham Woods
24/08/2009	Z5853	W52	Wytham Woods
24/08/2009	Z9534	W52	Wytham Woods
12/09/2009	Z9785	CP103	Wytham Woods
12/09/2009	Z9786	CP103	Wytham Woods

12/09/2009	Z9784	CP103	Wytham Woods
12/09/2009	Z9788	CP130	Wytham Woods
12/09/2009	Z9469	CP103	Wytham Woods
12/09/2009	Z9787	CP130	Wytham Woods
12/09/2009	Z9783	CP103	Wytham Woods
12/09/2009	Z9782	CP103	Wytham Woods
12/09/2009	Z5016	CP130	Wytham Woods
12/09/2009	Z4706	CP105	Wytham Woods
12/09/2009	Z4697	CP157	Wytham Woods
12/09/2009	Z4690	CP107	Wytham Woods
12/09/2009	Z9467	CP103	Wytham Woods
12/09/2009	Z5024	CP130	Wytham Woods
16/09/2009	Z9540	O223	Wytham Woods
16/09/2009	Z9641	O223	Wytham Woods
16/09/2009	Z9640	O223	Wytham Woods
16/09/2009	Z9505	O237	Wytham Woods
16/09/2009	Z9509	O237	Wytham Woods
16/09/2009	A1952	O223	Wytham Woods
16/09/2009	Z5709	O230	Wytham Woods
16/09/2009	A1968	O36	Wytham Woods
16/09/2009	A1970	O36	Wytham Woods
16/09/2009	A1971	O36	Wytham Woods
16/09/2009	A1972	O36	Wytham Woods
16/09/2009	A1973	O36	Wytham Woods
16/09/2009	A1966	O36	Wytham Woods
16/09/2009	Z5710	O223	Wytham Woods
16/09/2009	A1967	O36	Wytham Woods
16/09/2009	Z5694	O36	Wytham Woods
16/09/2009	A1950	O223	Wytham Woods
16/09/2009	Z4809	O230	Wytham Woods
16/09/2009	Z4804	O223	Wytham Woods
16/09/2009	Z4746	O230	Wytham Woods
16/09/2009	Z4743	O230	Wytham Woods
16/09/2009	Z5777	O223	Wytham Woods
16/09/2009	A1958	O237	Wytham Woods
16/09/2009	A1954	O223	Wytham Woods
16/09/2009	A1951	O223	Wytham Woods
16/09/2009	A1953	O223	Wytham Woods
16/09/2009	A1955	O223	Wytham Woods
16/09/2009	A1956	O230	Wytham Woods
16/09/2009	A1969	O36	Wytham Woods
16/09/2009	A1957	O230	Wytham Woods
16/09/2009	A1965	O36	Wytham Woods
16/09/2009	A1959	O237	Wytham Woods

16/09/2009	A1960	O237	Wytham Woods
16/09/2009	A1961	O237	Wytham Woods
16/09/2009	A1962	O237	Wytham Woods
16/09/2009	A1963	O237	Wytham Woods
16/09/2009	A1964	O36	Wytham Woods
24/09/2009	Z5767	W54	Wytham Woods
24/09/2009	A1978	W54	Wytham Woods
24/09/2009	Z9581	W54	Wytham Woods
24/09/2009	Z9760	W54	Wytham Woods
24/09/2009	Z9786	W54	Wytham Woods
24/09/2009	Z5766	W54	Wytham Woods
24/09/2009	A1979	W54	Wytham Woods
24/09/2009	Z9469	W54	Wytham Woods
24/09/2009	A1974	CP103	Wytham Woods
24/09/2009	A1975	W54	Wytham Woods
24/09/2009	A1976	W54	Wytham Woods
24/09/2009	A1981	W54	Wytham Woods
24/09/2009	A1985	W54	Wytham Woods
24/09/2009	A1980	W54	Wytham Woods
24/09/2009	Z9666	W54	Wytham Woods
24/09/2009	A1983	W54	Wytham Woods
24/09/2009	A1984	W54	Wytham Woods
24/09/2009	Y9023	W54	Wytham Woods
24/09/2009	A1977	W54	Wytham Woods
25/09/2009	Z9795	MP33	Wytham Woods
25/09/2009	Z9796	MP33	Wytham Woods
25/09/2009	Z9797	MP33	Wytham Woods
25/09/2009	Z9798	MP33	Wytham Woods
25/09/2009	Z9799	MP33	Wytham Woods
25/09/2009	Z9800	MP33	Wytham Woods
25/09/2009	Z9801	MP33	Wytham Woods
25/09/2009	Z9802	MP33	Wytham Woods
25/09/2009	Z9803	MP33	Wytham Woods
25/09/2009	Z9804	MP33	Wytham Woods
25/09/2009	Z9805	MP33	Wytham Woods
25/09/2009	Z9806	MP33	Wytham Woods
25/09/2009	Z9794	MP33	Wytham Woods
25/09/2009	Z9808	MP27	Wytham Woods
25/09/2009	Z9681	MP27	Wytham Woods
25/09/2009	Z9807	MP27	Wytham Woods
25/09/2009	Z9687	MP27	Wytham Woods
25/09/2009	Z9792	MP33	Wytham Woods
25/09/2009	Z9791	MP33	Wytham Woods
25/09/2009	Z9790	MP37	Wytham Woods

25/09/2009	Z9789	MP55	Wytham Woods
25/09/2009	Z9513	MP27	Wytham Woods
25/09/2009	Z9683	MP27	Wytham Woods
25/09/2009	Z3100	MP33	Wytham Woods
25/09/2009	A1986	MP67	Wytham Woods
25/09/2009	Z9793	MP33	Wytham Woods
03/10/2009	Z9812	MP96	Wytham Woods
03/10/2009	Z9813	MP96	Wytham Woods
03/10/2009	Z9814	MP96	Wytham Woods
03/10/2009	Z9811	MP96	Wytham Woods
03/10/2009	Z9816	MP96	Wytham Woods
03/10/2009	Z9815	MP96	Wytham Woods
03/10/2009	Z9810	MP96	Wytham Woods
03/10/2009	Z9607	C4	Wytham Woods
03/10/2009	Z9610	C4	Wytham Woods
03/10/2009	Z9615	C140	Wytham Woods
03/10/2009	Z9618	C4	Wytham Woods
03/10/2009	Z3184	C113	Wytham Woods
04/10/2009	Z9819	W55	Wytham Woods
04/10/2009	Z9818	W55	Wytham Woods
04/10/2009	A1985	W55	Wytham Woods
04/10/2009	Z9817	W55	Wytham Woods
09/05/2010	Z9528	MP8	Wytham Woods
09/05/2010	Z5918	MP8	Wytham Woods
09/05/2010	Z5917	MP8	Wytham Woods
09/05/2010	Z9826	MP8	Wytham Woods
09/05/2010	Z9526	MP8	Wytham Woods
09/05/2010	Z9679	MP8	Wytham Woods
09/05/2010	Z5663	MP8	Wytham Woods
09/05/2010	Z9523	MP8	Wytham Woods
09/05/2010	Z9517	MP8	Wytham Woods
09/05/2010	Z9827	MP8	Wytham Woods
09/05/2010	Z5912	MP8	Wytham Woods
09/05/2010	Z5681	MP8	Wytham Woods
09/05/2010	Z9808	MP8	Wytham Woods
09/05/2010	Z9514	MP8	Wytham Woods
09/05/2010	Z5680	MP8	Wytham Woods
09/05/2010	Z5920	MP8	Wytham Woods
09/05/2010	Z9527	MP8	Wytham Woods
09/05/2010	Z5660	MP8	Wytham Woods
09/05/2010	Z5922	MP8	Wytham Woods
25/05/2010	Z9831	O115	Wytham Woods
25/05/2010	Z5719	O115	Wytham Woods
25/05/2010	Z5718	O115	Wytham Woods

25/05/2010	Z9830	O115	Wytham Woods
25/05/2010	Z9829	O115	Wytham Woods
30/05/2010	Z5661	MP25	Wytham Woods
30/05/2010	Z5917	MP25	Wytham Woods
30/05/2010	Z9525	MP25	Wytham Woods
30/05/2010	Z4699	MP25	Wytham Woods
30/05/2010	Z5918	MP25	Wytham Woods
30/05/2010	Z5681	MP25	Wytham Woods
30/05/2010	Z9833	MP25	Wytham Woods
30/05/2010	Z9519	MP25	Wytham Woods
30/05/2010	Z9514	MP25	Wytham Woods
30/05/2010	Z9684	MP25	Wytham Woods
30/05/2010	Z9521	MP25	Wytham Woods
30/05/2010	Z9523	MP25	Wytham Woods
30/05/2010	Z9683	MP25	Wytham Woods
30/05/2010	Z5914	MP25	Wytham Woods
30/05/2010	Z9808	MP25	Wytham Woods
30/05/2010	Z5698	MP25	Wytham Woods
30/05/2010	Z9832	MP25	Wytham Woods
31/05/2010	Z9593	W64A	Wytham Woods
31/05/2010	Z5019	W14	Wytham Woods
31/05/2010	Z9582	W64A	Wytham Woods
31/05/2010	Z6098	W14	Wytham Woods
31/05/2010	Z4875	W64B	Wytham Woods
31/05/2010	Z9837	W14	Wytham Woods
31/05/2010	Z4682	W14	Wytham Woods
31/05/2010	Z5895	W64A	Wytham Woods
31/05/2010	Z5852	W64A	Wytham Woods
31/05/2010	Z9834	W14	Wytham Woods
31/05/2010	Z4870	W64B	Wytham Woods
31/05/2010	Z5024	W14	Wytham Woods
31/05/2010	Z9835	W14	Wytham Woods
31/05/2010	Z5025	W14	Wytham Woods
31/05/2010	Z5786	W14	Wytham Woods
31/05/2010	Z6100	W14	Wytham Woods
31/05/2010	Z4710	W14	Wytham Woods
31/05/2010	Z9836	W14	Wytham Woods
31/05/2010	Z3064	W14	Wytham Woods
31/05/2010	Z5010	W14	Wytham Woods
31/05/2010	Z6099	W14	Wytham Woods
31/05/2010	Z5018	W14	Wytham Woods
31/05/2010	Z5016	W14	Wytham Woods
31/05/2010	Z9591	W64A	Wytham Woods
31/05/2010	Z5030	W14	Wytham Woods

31/05/2010	Z6076	W64A	Wytham Woods
31/05/2010	Z9534	W64A	Wytham Woods
31/05/2010	Z5899	W64A	Wytham Woods
31/05/2010	Z4500	W64A	Wytham Woods
31/05/2010	Z5749	W64A	Wytham Woods
31/05/2010	Z5851	W64A	Wytham Woods
31/05/2010	Z5745	W64A	Wytham Woods
31/05/2010	Z5748	W64A	Wytham Woods
31/05/2010	Z9567	W64A	Wytham Woods
31/05/2010	Z5891	W64A	Wytham Woods
31/05/2010	Z5038	W64A	Wytham Woods
31/05/2010	Z5023	W14	Wytham Woods
04/06/2010	Z4689	W45	Wytham Woods
04/06/2010	A1987	W45	Wytham Woods
04/06/2010	Z4766	W45	Wytham Woods
04/06/2010	Z5873	W45	Wytham Woods
04/06/2010	Z5765	W45	Wytham Woods
09/06/2010	A1994	O255	Wytham Woods
09/06/2010	A1997	O255	Wytham Woods
09/06/2010	A1963	O221	Wytham Woods
09/06/2010	Z5842	C107	Wytham Woods
09/06/2010	A1999	O255	Wytham Woods
09/06/2010	A1996	O255	Wytham Woods
09/06/2010	Z9850	O255	Wytham Woods
09/06/2010	A1993	O255	Wytham Woods
09/06/2010	A1992	O255	Wytham Woods
09/06/2010	A1991	O255	Wytham Woods
09/06/2010	A1990	O255	Wytham Woods
09/06/2010	A1989	O255	Wytham Woods
09/06/2010	A1988	O255	Wytham Woods
09/06/2010	Z9849	O255	Wytham Woods
09/06/2010	A1998	O255	Wytham Woods
09/06/2010	Z4810	O221	Wytham Woods
09/06/2010	Z9901	O221	Wytham Woods
09/06/2010	Z9902	O221	Wytham Woods
09/06/2010	Z9903	O221	Wytham Woods
09/06/2010	Z4811	O221	Wytham Woods
09/06/2010	Z9904	O221	Wytham Woods
09/06/2010	Z9905	O221	Wytham Woods
09/06/2010	Z9510	O221	Wytham Woods
09/06/2010	Z9511	O221	Wytham Woods
09/06/2010	Z9906	O221	Wytham Woods
09/06/2010	Z9509	O221	Wytham Woods
09/06/2010	Z5841	C107	Wytham Woods

09/06/2010	A1962	O221	Wytham Woods
09/06/2010	Z9508	O221	Wytham Woods
09/06/2010	Z9506	O221	Wytham Woods
09/06/2010	Z9524	SW26	Wytham Woods
09/06/2010	Z4699	SW26	Wytham Woods
09/06/2010	Z5680	SW26	Wytham Woods
09/06/2010	Z9847	O255	Wytham Woods
09/06/2010	Z9848	O255	Wytham Woods
09/06/2010	A1958	O221	Wytham Woods
09/06/2010	A1995	O255	Wytham Woods
11/06/2010	Z9526	B45	Wytham Woods
11/06/2010	Z5923	B45	Wytham Woods
11/06/2010	Z9519	B45	Wytham Woods
11/06/2010	Z5920	B45	Wytham Woods
11/06/2010	Z5661	B45	Wytham Woods
11/06/2010	Z9529	B45	Wytham Woods
11/06/2010	Z9679	B45	Wytham Woods
11/06/2010	Z5918	B45	Wytham Woods
11/06/2010	Z9517	B45	Wytham Woods
11/06/2010	Z5912	B45	Wytham Woods
11/06/2010	Z5680	B45	Wytham Woods
11/06/2010	A1801	B45	Wytham Woods
11/06/2010	Z5663	B45	Wytham Woods
11/06/2010	Z9833	B45	Wytham Woods
11/06/2010	Z9524	B45	Wytham Woods
11/06/2010	Z5922	B45	Wytham Woods
11/06/2010	Z5660	B45	Wytham Woods
11/06/2010	Z9827	B45	Wytham Woods
11/06/2010	Z9521	B45	Wytham Woods
11/06/2010	Z9528	B45	Wytham Woods
11/06/2010	A1800	B45	Wytham Woods
11/06/2010	Z5890	B45	Wytham Woods
15/06/2010	A1964	O39	Wytham Woods
15/06/2010	A1966	O39	Wytham Woods
15/06/2010	Z3071	O20	Wytham Woods
15/06/2010	A1969	O45	Wytham Woods
15/06/2010	Z9907	O45	Wytham Woods
15/06/2010	Z9908	O45	Wytham Woods
15/06/2010	Z9917	O39	Wytham Woods
15/06/2010	Z9916	O39	Wytham Woods
15/06/2010	Z5694	O39	Wytham Woods
15/06/2010	A1967	O39	Wytham Woods
15/06/2010	Z9913	O39	Wytham Woods
15/06/2010	Z9912	O39	Wytham Woods

15/06/2010	A1965	O39	Wytham Woods
15/06/2010	Z9911	O39	Wytham Woods
15/06/2010	A1973	O39	Wytham Woods
15/06/2010	A1970	O39	Wytham Woods
15/06/2010	Z6127	O39	Wytham Woods
15/06/2010	Z9910	O39	Wytham Woods
15/06/2010	A1971	O39	Wytham Woods
15/06/2010	Z9909	O39	Wytham Woods
15/06/2010	Z9914	O39	Wytham Woods
15/06/2010	Z9915	O39	Wytham Woods
15/06/2010	Z5692	O39	Wytham Woods
18/06/2010	Z9525	MP35	Wytham Woods
18/06/2010	Z9832	MP35	Wytham Woods
18/06/2010	Z9529	MP35	Wytham Woods
18/06/2010	Z9687	MP35	Wytham Woods
18/06/2010	Z5914	MP35	Wytham Woods
18/06/2010	Z5890	MP35	Wytham Woods
18/06/2010	A1801	MP35	Wytham Woods
18/06/2010	A1802	MP35	Wytham Woods
18/06/2010	Z5918	MP35	Wytham Woods
18/06/2010	Z5681	MP35	Wytham Woods
18/06/2010	Z4699	MP35	Wytham Woods
18/06/2010	Z5923	MP35	Wytham Woods
18/06/2010	Z9522	MP35	Wytham Woods
23/06/2010	Z9924	E4	Wytham Woods
23/06/2010	Z9921	E4	Wytham Woods
23/06/2010	Z9922	E4	Wytham Woods
23/06/2010	Z4891	E4	Wytham Woods
23/06/2010	Z9920	E4	Wytham Woods
23/06/2010	Z4886	E4	Wytham Woods
23/06/2010	A1990	O57	Wytham Woods
23/06/2010	Z4892	E4	Wytham Woods
23/06/2010	Z4896	E4	Wytham Woods
23/06/2010	Z4897	E4	Wytham Woods
23/06/2010	Z9919	E4	Wytham Woods
23/06/2010	Z4890	E4	Wytham Woods
23/06/2010	A1989	O57	Wytham Woods
23/06/2010	A1997	O57	Wytham Woods
23/06/2010	Z9848	O57	Wytham Woods
23/06/2010	A1995	O57	Wytham Woods
23/06/2010	A1988	O57	Wytham Woods
23/06/2010	A1991	O57	Wytham Woods
23/06/2010	Z9923	E4	Wytham Woods
23/06/2010	Z4887	E4	Wytham Woods

23/06/2010	Z9918	E4	Wytham Woods
23/06/2010	Z9938	E11	Wytham Woods
23/06/2010	Z9946	E11	Wytham Woods
23/06/2010	Z9585	E11	Wytham Woods
23/06/2010	Z9937	E11	Wytham Woods
23/06/2010	Z9940	E11	Wytham Woods
23/06/2010	Z4952	E11	Wytham Woods
23/06/2010	Z9936	E11	Wytham Woods
23/06/2010	A1978	E11	Wytham Woods
23/06/2010	Z4953	E11	Wytham Woods
23/06/2010	Z9591	E11	Wytham Woods
23/06/2010	Z9939	E11	Wytham Woods
23/06/2010	Z4956	E11	Wytham Woods
23/06/2010	Z5850	E11	Wytham Woods
23/06/2010	Z5901	E11	Wytham Woods
23/06/2010	Z5909	E11	Wytham Woods
23/06/2010	Z9941	E11	Wytham Woods
23/06/2010	Z6060	E8	Wytham Woods
23/06/2010	Z5766	E11	Wytham Woods
23/06/2010	Z9935	E11	Wytham Woods
23/06/2010	Z9925	E4	Wytham Woods
23/06/2010	Z4900	E11	Wytham Woods
23/06/2010	Z4893	E4	Wytham Woods
23/06/2010	Z4898	E11	Wytham Woods
23/06/2010	Z4958	E11	Wytham Woods
23/06/2010	Z9931	E8	Wytham Woods
23/06/2010	Z4884	E4	Wytham Woods
23/06/2010	Z9926	E4	Wytham Woods
23/06/2010	Z4895	E4	Wytham Woods
23/06/2010	Z9933	E8	Wytham Woods
23/06/2010	Z9927	E4	Wytham Woods
23/06/2010	Z9934	E8	Wytham Woods
23/06/2010	Z9928	E4	Wytham Woods
23/06/2010	Z9929	E4	Wytham Woods
23/06/2010	Z6063	E8	Wytham Woods
23/06/2010	Z9755	E8	Wytham Woods
23/06/2010	Z9945	E11	Wytham Woods
23/06/2010	Z6068	E8	Wytham Woods
23/06/2010	Z5987	E11	Wytham Woods
23/06/2010	Z9754	E8	Wytham Woods
23/06/2010	Z9932	E8	Wytham Woods
23/06/2010	Z6067	E8	Wytham Woods
23/06/2010	Z6066	E8	Wytham Woods
23/06/2010	Z6065	E8	Wytham Woods

23/06/2010	Z6062	E8	Wytham Woods
23/06/2010	Z9942	E11	Wytham Woods
23/06/2010	Z9943	E11	Wytham Woods
23/06/2010	Z9944	E11	Wytham Woods
23/06/2010	Z9930	E8	Wytham Woods
02/07/2010	Z9831	SW9	Wytham Woods
02/07/2010	A1843	SW122	Wytham Woods
02/07/2010	A1844	SW122	Wytham Woods
02/07/2010	A1845	SW124	Wytham Woods
02/07/2010	A1846	SW9	Wytham Woods
02/07/2010	Z5718	SW9	Wytham Woods
02/07/2010	Z9829	SW9	Wytham Woods
02/07/2010	A1847	SW9	Wytham Woods
02/07/2010	Z5719	SW9	Wytham Woods
02/07/2010	A1848	SW9	Wytham Woods
02/07/2010	A1849	SW9	Wytham Woods
02/07/2010	Z9830	SW9	Wytham Woods
08/07/2010	Z9642	O48	Wytham Woods
08/07/2010	A1957	O87	Wytham Woods
08/07/2010	A1841	O87	Wytham Woods
08/07/2010	A1842	O48	Wytham Woods
08/07/2010	Z9647	O48	Wytham Woods
10/07/2010	Z5016	CP149	Wytham Woods
10/07/2010	Z9947	CP135	Wytham Woods
10/07/2010	Z9948	CP135	Wytham Woods
10/07/2010	Z5957	CP135	Wytham Woods
10/07/2010	Z9949	CP135	Wytham Woods
10/07/2010	Z9950	CP29	Wytham Woods
10/07/2010	Z9545	CP29	Wytham Woods
10/07/2010	A1700	CP149	Wytham Woods
10/07/2010	A1701	CP149	Wytham Woods
10/07/2010	Z5030	CP149	Wytham Woods
10/07/2010	Z6100	CP149	Wytham Woods
10/07/2010	Z4684	CP149	Wytham Woods
10/07/2010	Z6098	CP149	Wytham Woods
10/07/2010	Z6097	CP149	Wytham Woods
10/07/2010	Z9599	CP29	Wytham Woods
17/07/2010	Z5793	C56	Wytham Woods
17/07/2010	Z5671	C56	Wytham Woods
17/07/2010	Z9700	C56	Wytham Woods
17/07/2010	Z5795	C56	Wytham Woods
17/07/2010	A1706	C54	Wytham Woods
17/07/2010	Z3181	C56	Wytham Woods
17/07/2010	Z3182	C56	Wytham Woods

17/07/2010	A1702	C54	Wytham Woods
17/07/2010	A1703	C54	Wytham Woods
17/07/2010	A1704	C54	Wytham Woods
17/07/2010	A1705	C54	Wytham Woods
17/07/2010	Z5994	E50	Wytham Woods
17/07/2010	Z9620	C39	Wytham Woods
17/07/2010	Z4687	E58	Wytham Woods
17/07/2010	A1806	E58	Wytham Woods
17/07/2010	Z9457	E58	Wytham Woods
17/07/2010	A1805	E58	Wytham Woods
17/07/2010	A1804	E58	Wytham Woods
17/07/2010	A1803	E58	Wytham Woods
17/07/2010	Z4667	E58	Wytham Woods
17/07/2010	Z9938	E31	Wytham Woods
17/07/2010	A1840	E58	Wytham Woods
17/07/2010	A1720	C134	Wytham Woods
17/07/2010	A1719	C134	Wytham Woods
17/07/2010	A1718	C134	Wytham Woods
17/07/2010	A1717	C134	Wytham Woods
17/07/2010	A1716	C134	Wytham Woods
17/07/2010	Z5700	C134	Wytham Woods
17/07/2010	A1715	C39	Wytham Woods
17/07/2010	A1714	C39	Wytham Woods
17/07/2010	A1745	E31	Wytham Woods
17/07/2010	Z9819	E50	Wytham Woods
17/07/2010	Z9622	C56	Wytham Woods
17/07/2010	A1707	C56	Wytham Woods
17/07/2010	A1811	E50	Wytham Woods
17/07/2010	Z5001	E50	Wytham Woods
17/07/2010	A1810	E50	Wytham Woods
17/07/2010	Z5003	E50	Wytham Woods
17/07/2010	Z5948	E50	Wytham Woods
17/07/2010	A1807	E58	Wytham Woods
17/07/2010	A1835	E50	Wytham Woods
17/07/2010	A1743	E49C	Wytham Woods
17/07/2010	A1836	E50	Wytham Woods
17/07/2010	A1837	E50	Wytham Woods
17/07/2010	Z4970	E50	Wytham Woods
17/07/2010	A1838	E50	Wytham Woods
17/07/2010	Z5942	E50	Wytham Woods
17/07/2010	Z5940	E50	Wytham Woods
17/07/2010	A1808	E58	Wytham Woods
17/07/2010	A1839	E58	Wytham Woods
17/07/2010	Z6006	E50	Wytham Woods

17/07/2010	Z9611	C39	Wytham Woods
17/07/2010	Z9607	C39	Wytham Woods
17/07/2010	A1709	C39	Wytham Woods
17/07/2010	Z9708	C39	Wytham Woods
17/07/2010	A1710	C39	Wytham Woods
17/07/2010	A1708	C39	Wytham Woods
17/07/2010	Z6120	C39	Wytham Woods
17/07/2010	Z5792	C39	Wytham Woods
17/07/2010	A1711	C39	Wytham Woods
17/07/2010	A1744	E31	Wytham Woods
17/07/2010	Z9619	C39	Wytham Woods
17/07/2010	A1712	C39	Wytham Woods
17/07/2010	Z5840	C39	Wytham Woods
17/07/2010	Z9580	C39	Wytham Woods
17/07/2010	Z3175	C39	Wytham Woods
17/07/2010	A1713	C39	Wytham Woods
17/07/2010	Z5842	C39	Wytham Woods
18/07/2010	A1742	W68	Wytham Woods
18/07/2010	Z5856	W68	Wytham Woods
18/07/2010	Z6073	W68	Wytham Woods
18/07/2010	Z9590	W68	Wytham Woods
18/07/2010	A1741	W68	Wytham Woods
18/07/2010	Z5891	W63	Wytham Woods
18/07/2010	Z9656	W68	Wytham Woods
18/07/2010	Z9534	W63	Wytham Woods
18/07/2010	Z5899	W63	Wytham Woods
18/07/2010	Z5904	W101	Wytham Woods
18/07/2010	Z9588	W101	Wytham Woods
18/07/2010	A1726	W101	Wytham Woods
18/07/2010	A1727	W101	Wytham Woods
18/07/2010	Z5952	W101	Wytham Woods
18/07/2010	Z4997	W101	Wytham Woods
18/07/2010	Z5850	W101	Wytham Woods
18/07/2010	Z4869	W101	Wytham Woods
18/07/2010	A1729	W63	Wytham Woods
18/07/2010	A1730	W63	Wytham Woods
18/07/2010	Z5896	W63	Wytham Woods
18/07/2010	Z9593	W63	Wytham Woods
18/07/2010	Z5750	W63	Wytham Woods
18/07/2010	A1733	W63	Wytham Woods
18/07/2010	Z4868	W63	Wytham Woods
18/07/2010	A1734	W63	Wytham Woods
18/07/2010	A1725	W101	Wytham Woods
18/07/2010	A1735	W63	Wytham Woods

18/07/2010	A1731	W63	Wytham Woods
18/07/2010	Z5898	W63	Wytham Woods
18/07/2010	A1732	W63	Wytham Woods
18/07/2010	Z9780	W68	Wytham Woods
18/07/2010	Z5749	W63	Wytham Woods
18/07/2010	A1740	W68	Wytham Woods
18/07/2010	Z4870	W63	Wytham Woods
18/07/2010	Z5748	W63	Wytham Woods
18/07/2010	Z4500	W63	Wytham Woods
18/07/2010	A1736	W63	Wytham Woods
18/07/2010	A1737	W63	Wytham Woods
18/07/2010	Z9658	W68	Wytham Woods
18/07/2010	Z9659	W68	Wytham Woods
18/07/2010	Z9560	W68	Wytham Woods
18/07/2010	A1738	W68	Wytham Woods
18/07/2010	Z5854	W68	Wytham Woods
18/07/2010	Z4860	W68	Wytham Woods
18/07/2010	A1739	W68	Wytham Woods
18/07/2010	Z4873	W63	Wytham Woods
18/07/2010	A1721	W101	Wytham Woods
18/07/2010	A1724	W101	Wytham Woods
18/07/2010	Z4955	W101	Wytham Woods
18/07/2010	Z4899	W101	Wytham Woods
18/07/2010	Z5905	W101	Wytham Woods
18/07/2010	Z5908	W101	Wytham Woods
18/07/2010	Z4959	W101	Wytham Woods
18/07/2010	Z4900	W101	Wytham Woods
18/07/2010	A1722	W101	Wytham Woods
18/07/2010	Z9585	W101	Wytham Woods
18/07/2010	Z5907	W101	Wytham Woods
18/07/2010	Z9586	W101	Wytham Woods
18/07/2010	A1723	W101	Wytham Woods
18/07/2010	Z5909	W101	Wytham Woods
18/07/2010	A1728	W101	Wytham Woods
20/07/2010	A1749	W49	Wytham Woods
20/07/2010	Z9539	W49	Wytham Woods
20/07/2010	A1753	W49	Wytham Woods
20/07/2010	A1752	W49	Wytham Woods
20/07/2010	A1751	W49	Wytham Woods
20/07/2010	A1750	W49	Wytham Woods
20/07/2010	A1748	W49	Wytham Woods
20/07/2010	A1747	W49	Wytham Woods
20/07/2010	A1746	W49	Wytham Woods
20/07/2010	Z5870	W49	Wytham Woods

20/07/2010	Z9535	W49	Wytham Woods
20/07/2010	Z5871	W49	Wytham Woods
20/07/2010	Z5872	W49	Wytham Woods
20/07/2010	A1980	W49	Wytham Woods
20/07/2010	A1755	W49	Wytham Woods
20/07/2010	Z5776	W49	Wytham Woods
20/07/2010	A1987	W49	Wytham Woods
20/07/2010	Z9538	W49	Wytham Woods
20/07/2010	Z5873	W49	Wytham Woods
20/07/2010	Z5874	W49	Wytham Woods
20/07/2010	A1754	W49	Wytham Woods
21/07/2010	A1816	W31	Wytham Woods
21/07/2010	A1832	W22	Wytham Woods
21/07/2010	A1818	W31	Wytham Woods
21/07/2010	Z5024	W31	Wytham Woods
21/07/2010	A1817	W31	Wytham Woods
21/07/2010	Z9836	W31	Wytham Woods
21/07/2010	Z5022	W31	Wytham Woods
21/07/2010	A1759	W22	Wytham Woods
21/07/2010	A1819	W31	Wytham Woods
21/07/2010	A1824	W31	Wytham Woods
21/07/2010	Z3064	W31	Wytham Woods
21/07/2010	Z5786	W31	Wytham Woods
21/07/2010	Z6100	W31	Wytham Woods
21/07/2010	Z9835	W31	Wytham Woods
21/07/2010	Z9837	W31	Wytham Woods
21/07/2010	Z5019	W31	Wytham Woods
21/07/2010	Z4710	W31	Wytham Woods
21/07/2010	A1820	W31	Wytham Woods
21/07/2010	Z6098	W31	Wytham Woods
21/07/2010	A1763	W22	Wytham Woods
21/07/2010	Z5023	W31	Wytham Woods
21/07/2010	A1821	W31	Wytham Woods
21/07/2010	A1834	W22	Wytham Woods
21/07/2010	A1823	W31	Wytham Woods
21/07/2010	A1760	W22	Wytham Woods
21/07/2010	A1825	W31	Wytham Woods
21/07/2010	Z3231	W22	Wytham Woods
21/07/2010	A1826	W22	Wytham Woods
21/07/2010	A1827	W22	Wytham Woods
21/07/2010	A1828	W22	Wytham Woods
21/07/2010	A1829	W22	Wytham Woods
21/07/2010	A1830	W22	Wytham Woods
21/07/2010	A1831	W22	Wytham Woods

21/07/2010	A1833	W22	Wytham Woods
21/07/2010	A1756	W22	Wytham Woods
21/07/2010	A1757	W22	Wytham Woods
21/07/2010	A1758	W22	Wytham Woods
21/07/2010	A1762	W22	Wytham Woods
21/07/2010	A1822	W31	Wytham Woods
21/07/2010	A1815	W31	Wytham Woods
21/07/2010	A1814	W31	Wytham Woods
21/07/2010	Z5018	W31	Wytham Woods
21/07/2010	A1813	W31	Wytham Woods
21/07/2010	Z4685	W31	Wytham Woods
21/07/2010	Z5010	W31	Wytham Woods
21/07/2010	Z4682	W31	Wytham Woods
21/07/2010	A1812	W31	Wytham Woods
21/07/2010	A1761	W22	Wytham Woods
23/07/2010	A1816	W1	Wytham Woods
23/07/2010	Z5024	W1	Wytham Woods
23/07/2010	Z5786	W1	Wytham Woods
23/07/2010	Z6100	W1	Wytham Woods
23/07/2010	A1824	W1	Wytham Woods
23/07/2010	A1822	W1	Wytham Woods
23/07/2010	A1819	W1	Wytham Woods
23/07/2010	Z3064	W1	Wytham Woods
23/07/2010	Z4685	W1	Wytham Woods
23/07/2010	Z4710	W1	Wytham Woods
23/07/2010	Z9837	W1	Wytham Woods
23/07/2010	Z5022	W1	Wytham Woods
23/07/2010	Z5019	W1	Wytham Woods
23/07/2010	Z9836	W1	Wytham Woods
23/07/2010	A1812	W1	Wytham Woods
23/07/2010	Z6099	W1	Wytham Woods
23/07/2010	Z4682	W1	Wytham Woods
23/07/2010	Z9835	W1	Wytham Woods
23/07/2010	Z5023	W1	Wytham Woods
23/07/2010	A1818	W1	Wytham Woods
23/07/2010	A1766	W10	Wytham Woods
23/07/2010	Z9949	CP124	Wytham Woods
23/07/2010	A2102	CP102	Wytham Woods
23/07/2010	Z4842	CP124	Wytham Woods
23/07/2010	Y9046	CP124	Wytham Woods
23/07/2010	A1769	W10	Wytham Woods
23/07/2010	A1768	W10	Wytham Woods
23/07/2010	A1767	W10	Wytham Woods
23/07/2010	Z4774	W10	Wytham Woods

23/07/2010	Z5016	W1	Wytham Woods
23/07/2010	Z5765	W10	Wytham Woods
23/07/2010	Z6098	W1	Wytham Woods
23/07/2010	A2101	CP124	Wytham Woods
23/07/2010	Z6080	W10	Wytham Woods
23/07/2010	A2100	CP124	Wytham Woods
23/07/2010	A1765	W10	Wytham Woods
23/07/2010	A1764	W1	Wytham Woods
23/07/2010	A1813	W1	Wytham Woods
23/07/2010	Z5010	W1	Wytham Woods
23/07/2010	A1821	W1	Wytham Woods
23/07/2010	Z4672	W10	Wytham Woods
23/07/2010	Z6019	W10	Wytham Woods
23/07/2010	A1817	W1	Wytham Woods
23/07/2010	A1820	W1	Wytham Woods
23/07/2010	A1814	W1	Wytham Woods
23/07/2010	A1825	W1	Wytham Woods
26/07/2010	Z5038	W67	Wytham Woods
26/07/2010	Z9596	W67	Wytham Woods
26/07/2010	A1730	W67	Wytham Woods
26/07/2010	Z5851	W67	Wytham Woods
26/07/2010	Z5748	W67	Wytham Woods
26/07/2010	Z9590	W67	Wytham Woods
26/07/2010	A1741	W67	Wytham Woods
26/07/2010	A1729	W67	Wytham Woods
26/07/2010	A2104	W67	Wytham Woods
26/07/2010	A1731	W67	Wytham Woods
26/07/2010	Z4873	W67	Wytham Woods
26/07/2010	A1732	W67	Wytham Woods
26/07/2010	Z4875	W67	Wytham Woods
26/07/2010	A2103	W67	Wytham Woods
28/07/2010	Z9836	CP104	Wytham Woods
28/07/2010	A2102	CP104	Wytham Woods
28/07/2010	Z4682	CP104	Wytham Woods
28/07/2010	Z5786	CP104	Wytham Woods
28/07/2010	Z9466	CP117	Wytham Woods
28/07/2010	A1818	CP104	Wytham Woods
28/07/2010	A1824	CP104	Wytham Woods
28/07/2010	A1822	CP104	Wytham Woods
28/07/2010	Z6098	CP104	Wytham Woods
28/07/2010	A1701	CP104	Wytham Woods
28/07/2010	A1812	CP104	Wytham Woods
28/07/2010	Z5024	CP104	Wytham Woods
28/07/2010	Z6097	CP104	Wytham Woods

28/07/2010	Z5023	CP104	Wytham Woods
28/07/2010	Z9837	CP104	Wytham Woods
28/07/2010	Z5016	CP104	Wytham Woods
28/07/2010	Z5018	CP104	Wytham Woods
28/07/2010	A1700	CP104	Wytham Woods
28/07/2010	Z5031	CP104	Wytham Woods
28/07/2010	A1821	CP104	Wytham Woods
28/07/2010	Z5022	CP104	Wytham Woods
28/07/2010	Z4684	CP104	Wytham Woods
28/07/2010	A1825	CP104	Wytham Woods
28/07/2010	A1823	CP104	Wytham Woods
28/07/2010	Z5030	CP104	Wytham Woods
28/07/2010	A1814	CP104	Wytham Woods
28/07/2010	A1817	CP104	Wytham Woods
28/07/2010	A1816	CP104	Wytham Woods
28/07/2010	A1819	CP104	Wytham Woods
28/07/2010	Z4685	CP104	Wytham Woods
28/07/2010	Z5019	CP104	Wytham Woods
28/07/2010	A1813	CP104	Wytham Woods
28/07/2010	Z3064	CP104	Wytham Woods
28/07/2010	Z4710	CP104	Wytham Woods
28/07/2010	Z9835	CP104	Wytham Woods
31/07/2010	Z4842	CP24	Wytham Woods
31/07/2010	Z9759	W11	Wytham Woods
31/07/2010	Z9591	W11	Wytham Woods
31/07/2010	A1771	W11	Wytham Woods
31/07/2010	Z5821	W11	Wytham Woods
31/07/2010	Y9042	CP24	Wytham Woods
31/07/2010	Y9030	CP24	Wytham Woods
31/07/2010	A1772	CP24	Wytham Woods
31/07/2010	A1770	W11	Wytham Woods
31/07/2010	A1773	CP24	Wytham Woods
31/07/2010	A1768	W11	Wytham Woods
31/07/2010	A1757	W19	Wytham Woods
31/07/2010	A1774	W19	Wytham Woods
31/07/2010	A1763	W19	Wytham Woods
31/07/2010	A2105	W19	Wytham Woods
31/07/2010	A1831	W19	Wytham Woods
31/07/2010	A2106	W19	Wytham Woods
31/07/2010	A1827	W19	Wytham Woods
31/07/2010	A1756	W19	Wytham Woods
31/07/2010	Z4843	CP24	Wytham Woods
31/07/2010	A1758	W19	Wytham Woods
31/07/2010	Z5748	W11	Wytham Woods

31/07/2010	A1767	W11	Wytham Woods
31/07/2010	A1759	W19	Wytham Woods
31/07/2010	Z3231	W19	Wytham Woods
02/08/2010	Z9607	C104	Wytham Woods
02/08/2010	Z9622	C61	Wytham Woods
02/08/2010	A1715	C61	Wytham Woods
02/08/2010	A1833	CP2	Wytham Woods
02/08/2010	Z5841	C104	Wytham Woods
02/08/2010	Z3081	C151	Wytham Woods
02/08/2010	Z9621	C61	Wytham Woods
02/08/2010	A1707	C61	Wytham Woods
02/08/2010	Z3182	C61	Wytham Woods
02/08/2010	Z9702	C61	Wytham Woods
02/08/2010	Z3098	C104	Wytham Woods
02/08/2010	Z5840	C61	Wytham Woods
02/08/2010	A2111	CP2	Wytham Woods
02/08/2010	Z9611	C61	Wytham Woods
02/08/2010	A2108	CP2	Wytham Woods
02/08/2010	Z5671	C104	Wytham Woods
02/08/2010	A1757	CP2	Wytham Woods
02/08/2010	A2110	CP2	Wytham Woods
02/08/2010	A1762	CP2	Wytham Woods
02/08/2010	A2109	CP2	Wytham Woods
02/08/2010	A1758	CP2	Wytham Woods
02/08/2010	Z6120	C61	Wytham Woods
02/08/2010	Z3171	C61	Wytham Woods
02/08/2010	A2107	CP2	Wytham Woods
02/08/2010	Z6118	C104	Wytham Woods
02/08/2010	Z5793	C104	Wytham Woods
05/08/2010	A1799	MP30	Wytham Woods
05/08/2010	A2057	MP48	Wytham Woods
05/08/2010	A1711	MP30	Wytham Woods
05/08/2010	A1791	MP30	Wytham Woods
05/08/2010	A1793	MP30	Wytham Woods
05/08/2010	A1794	MP30	Wytham Woods
05/08/2010	A1795	MP30	Wytham Woods
05/08/2010	A1796	MP30	Wytham Woods
05/08/2010	A1789	MP30	Wytham Woods
05/08/2010	A1798	MP30	Wytham Woods
05/08/2010	A1788	MP30	Wytham Woods
05/08/2010	A2050	MP30	Wytham Woods
05/08/2010	A2051	MP30	Wytham Woods
05/08/2010	A2052	MP30	Wytham Woods
05/08/2010	A2053	MP48	Wytham Woods

05/08/2010	A2054	MP48	Wytham Woods
05/08/2010	A2055	MP48	Wytham Woods
05/08/2010	A1792	MP30	Wytham Woods
05/08/2010	A1797	MP30	Wytham Woods
05/08/2010	Z5914	MP54	Wytham Woods
05/08/2010	Z5788	MP66	Wytham Woods
05/08/2010	A1775	MP66	Wytham Woods
05/08/2010	Z9519	MP54	Wytham Woods
05/08/2010	A1776	MP54	Wytham Woods
05/08/2010	Z9523	MP54	Wytham Woods
05/08/2010	Z5922	MP54	Wytham Woods
05/08/2010	A1777	MP54	Wytham Woods
05/08/2010	A1790	MP30	Wytham Woods
05/08/2010	A1779	MP54	Wytham Woods
05/08/2010	Z9525	MP48	Wytham Woods
05/08/2010	Z5889	MP30	Wytham Woods
05/08/2010	A1780	MP30	Wytham Woods
05/08/2010	A1781	MP30	Wytham Woods
05/08/2010	A1782	MP30	Wytham Woods
05/08/2010	A1785	MP30	Wytham Woods
05/08/2010	A1786	MP30	Wytham Woods
05/08/2010	A1787	MP30	Wytham Woods
05/08/2010	A1778	MP54	Wytham Woods
05/08/2010	Z9827	MP48	Wytham Woods
05/08/2010	A2056	MP48	Wytham Woods
05/08/2010	Z9527	MP48	Wytham Woods
05/08/2010	A2063	MP48	Wytham Woods
05/08/2010	A2062	MP48	Wytham Woods
05/08/2010	Z9808	MP48	Wytham Woods
05/08/2010	Z5681	MP48	Wytham Woods
05/08/2010	A2061	MP48	Wytham Woods
05/08/2010	Z5912	MP48	Wytham Woods
05/08/2010	Z5890	MP48	Wytham Woods
05/08/2010	A2058	MP48	Wytham Woods
05/08/2010	Z4699	MP48	Wytham Woods
05/08/2010	A2060	MP48	Wytham Woods
05/08/2010	A2059	MP48	Wytham Woods
05/08/2010	Z5913	MP48	Wytham Woods
05/08/2010	Z9515	MP48	Wytham Woods
05/08/2010	A1800	MP48	Wytham Woods
05/08/2010	Z9833	MP48	Wytham Woods
08/08/2010	A2016	O9	Wytham Woods
08/08/2010	Z4744	O250	Wytham Woods
08/08/2010	A2017	O9	Wytham Woods

08/08/2010	A2015	O9	Wytham Woods
08/08/2010	Z9668	O9	Wytham Woods
08/08/2010	Z5999	O9	Wytham Woods
08/08/2010	A2013	O9	Wytham Woods
08/08/2010	A2014	O9	Wytham Woods
08/08/2010	Z6033	O250	Wytham Woods
08/08/2010	A2010	O9	Wytham Woods
08/08/2010	A2009	O9	Wytham Woods
08/08/2010	A1990	O13A	Wytham Woods
08/08/2010	A2007	O56	Wytham Woods
08/08/2010	Z5688	O56	Wytham Woods
08/08/2010	Z4784	O250	Wytham Woods
08/08/2010	A2011	O9	Wytham Woods
09/08/2010	A1727	O237	Wytham Woods
09/08/2010	A2020	O218	Wytham Woods
09/08/2010	A2021	O218	Wytham Woods
09/08/2010	A2064	O218	Wytham Woods
09/08/2010	A2066	O218	Wytham Woods
09/08/2010	Z9640	O42	Wytham Woods
09/08/2010	A2065	O218	Wytham Woods
15/08/2010	A2070	CP13	Wytham Woods
15/08/2010	Z4486	W22	Wytham Woods
15/08/2010	A2071	CP13	Wytham Woods
15/08/2010	A2121	W22	Wytham Woods
15/08/2010	A2122	W22	Wytham Woods
15/08/2010	Z4991	W22	Wytham Woods
15/08/2010	A2123	W22	Wytham Woods
15/08/2010	Z4485	W22	Wytham Woods
15/08/2010	A2124	W22	Wytham Woods
15/08/2010	A2119	W22	Wytham Woods
15/08/2010	Z4487	W22	Wytham Woods
15/08/2010	Z4468	W22	Wytham Woods
15/08/2010	A2126	W22	Wytham Woods
15/08/2010	Z4995	W22	Wytham Woods
15/08/2010	Z4752	CP13	Wytham Woods
15/08/2010	A2067	CP13	Wytham Woods
15/08/2010	A2068	CP13	Wytham Woods
15/08/2010	A2069	CP13	Wytham Woods
15/08/2010	Z4680	CP13	Wytham Woods
15/08/2010	A2125	W22	Wytham Woods
15/08/2010	A2113	W22	Wytham Woods
15/08/2010	Z4866	W22	Wytham Woods
15/08/2010	Z4474	W22	Wytham Woods
15/08/2010	A2112	W22	Wytham Woods

15/08/2010	Z4863	W22	Wytham Woods
15/08/2010	Z9556	W22	Wytham Woods
15/08/2010	Z4992	W22	Wytham Woods
15/08/2010	Z5013	W22	Wytham Woods
15/08/2010	A2120	W22	Wytham Woods
15/08/2010	Z4993	W22	Wytham Woods
15/08/2010	Z4694	CP13	Wytham Woods
15/08/2010	A2114	W22	Wytham Woods
15/08/2010	A2115	W22	Wytham Woods
15/08/2010	A2116	W22	Wytham Woods
15/08/2010	Z4477	W22	Wytham Woods
15/08/2010	A2117	W22	Wytham Woods
15/08/2010	A2118	W22	Wytham Woods
15/08/2010	Z4479	W22	Wytham Woods
15/08/2010	Z9531	W22	Wytham Woods
15/08/2010	Z5963	CP13	Wytham Woods
16/08/2010	Z5654	C129	Wytham Woods
16/08/2010	A2081	C129	Wytham Woods
16/08/2010	Z9619	C130	Wytham Woods
16/08/2010	A2083	C134	Wytham Woods
16/08/2010	A2082	C129	Wytham Woods
16/08/2010	A1705	C129	Wytham Woods
16/08/2010	Z5651	C129	Wytham Woods
16/08/2010	A2079	C129	Wytham Woods
16/08/2010	A2078	C130	Wytham Woods
16/08/2010	A2077	C130	Wytham Woods
16/08/2010	Z9610	C130	Wytham Woods
16/08/2010	Z9603	C130	Wytham Woods
16/08/2010	Z9580	C130	Wytham Woods
16/08/2010	A1708	C130	Wytham Woods
16/08/2010	Z5840	C134	Wytham Woods
16/08/2010	Z5841	C130	Wytham Woods
16/08/2010	A2084	C134	Wytham Woods
16/08/2010	Z3175	C134	Wytham Woods
16/08/2010	A2080	C129	Wytham Woods
17/08/2010	Z9708	C134	Wytham Woods
17/08/2010	A2085	C134	Wytham Woods
17/08/2010	Z9614	C134	Wytham Woods
17/08/2010	Z9618	C134	Wytham Woods
17/08/2010	Z9611	C134	Wytham Woods
21/08/2010	A2097	P23	Wytham Woods
21/08/2010	A2096	P23	Wytham Woods
21/08/2010	Z9634	P23	Wytham Woods
21/08/2010	Z9632	P23	Wytham Woods

21/08/2010	Z9637	P23	Wytham Woods
21/08/2010	Z9626	P23	Wytham Woods
21/08/2010	A1717	P23	Wytham Woods
21/08/2010	A1703	P23	Wytham Woods
21/08/2010	A2099	P23	Wytham Woods
21/08/2010	A2128	B159	Wytham Woods
21/08/2010	A2098	P23	Wytham Woods
21/08/2010	A3550	P23	Wytham Woods
21/08/2010	A2089	P5	Wytham Woods
21/08/2010	A2131	P5	Wytham Woods
21/08/2010	Z9697	P5	Wytham Woods
21/08/2010	A2130	P5	Wytham Woods
21/08/2010	A2129	P5	Wytham Woods
21/08/2010	A2095	P5	Wytham Woods
21/08/2010	Z4825	P5	Wytham Woods
21/08/2010	A2094	P5	Wytham Woods
21/08/2010	A2093	P5	Wytham Woods
21/08/2010	A2092	P5	Wytham Woods
21/08/2010	Z9692	P5	Wytham Woods
21/08/2010	Z9696	P5	Wytham Woods
21/08/2010	A1719	P23	Wytham Woods
21/08/2010	A2090	P5	Wytham Woods
21/08/2010	Z9638	P23	Wytham Woods
21/08/2010	Z9691	P5	Wytham Woods
21/08/2010	Z9695	P5	Wytham Woods
21/08/2010	A2088	P5	Wytham Woods
21/08/2010	A2087	P5	Wytham Woods
21/08/2010	A2086	P9	Wytham Woods
21/08/2010	A2133	P5	Wytham Woods
21/08/2010	A2135	P5	Wytham Woods
21/08/2010	A2134	P5	Wytham Woods
21/08/2010	A2136	P5	Wytham Woods
21/08/2010	A2137	P5	Wytham Woods
21/08/2010	A1704	P23	Wytham Woods
21/08/2010	Z9631	P23	Wytham Woods
21/08/2010	A2091	P5	Wytham Woods
21/08/2010	A2054	B177	Wytham Woods
21/08/2010	Z9517	B46	Wytham Woods
21/08/2010	Z5680	B177	Wytham Woods
21/08/2010	A2062	B177	Wytham Woods
21/08/2010	Z5918	B177	Wytham Woods
21/08/2010	Z5890	B177	Wytham Woods
21/08/2010	A1779	B177	Wytham Woods
21/08/2010	Z9832	B177	Wytham Woods

21/08/2010	Z5660	B177	Wytham Woods
21/08/2010	A2063	B177	Wytham Woods
21/08/2010	Z9515	B46	Wytham Woods
21/08/2010	A3551	B177	Wytham Woods
21/08/2010	A2058	B177	Wytham Woods
21/08/2010	Z5685	B177	Wytham Woods
21/08/2010	A2139	B177	Wytham Woods
21/08/2010	Z5664	B177	Wytham Woods
21/08/2010	Z5913	B177	Wytham Woods
21/08/2010	A2138	B177	Wytham Woods
21/08/2010	A2059	B177	Wytham Woods
21/08/2010	Z9827	B177	Wytham Woods
21/08/2010	Z5661	B46	Wytham Woods
21/08/2010	A2132	P5	Wytham Woods
21/08/2010	Z9679	B46	Wytham Woods
21/08/2010	Z9528	B177	Wytham Woods
24/08/2010	Z6133	O245	Wytham Woods
24/08/2010	Z6129	O245	Wytham Woods
24/08/2010	Z6130	O245	Wytham Woods
24/08/2010	Z6134	O245	Wytham Woods
24/08/2010	Z5709	O247	Wytham Woods
24/08/2010	Z6135	O44	Wytham Woods
24/08/2010	Z6136	O44	Wytham Woods
24/08/2010	Z6137	O44	Wytham Woods
24/08/2010	Z6132	O245	Wytham Woods
24/08/2010	Z6131	O245	Wytham Woods
01/09/2010	Z9570	W87	Wytham Woods
01/09/2010	A2141	W200	Wytham Woods
01/09/2010	Z9588	W200	Wytham Woods
01/09/2010	A1736	W200	Wytham Woods
01/09/2010	A1978	W103	Wytham Woods
01/09/2010	Z9592	W87	Wytham Woods
01/09/2010	A1730	W87	Wytham Woods
01/09/2010	A1731	W87	Wytham Woods
01/09/2010	A1735	W87	Wytham Woods
01/09/2010	Z9567	W87	Wytham Woods
01/09/2010	A2142	W87	Wytham Woods
01/09/2010	A1732	W87	Wytham Woods
01/09/2010	A2143	W87	Wytham Woods
01/09/2010	A2145	W65	Wytham Woods
01/09/2010	A2140	W200	Wytham Woods
01/09/2010	A1737	W87	Wytham Woods
08/09/2010	A2117	E21	Wytham Woods
08/09/2010	A2158	E51A	Wytham Woods

08/09/2010	A2157	E21	Wytham Woods
08/09/2010	A2153	E14A	Wytham Woods
08/09/2010	A2125	E21	Wytham Woods
08/09/2010	Z9531	E21	Wytham Woods
08/09/2010	A2120	E21	Wytham Woods
08/09/2010	A2113	E21	Wytham Woods
08/09/2010	A2123	E21	Wytham Woods
08/09/2010	Z4995	E21	Wytham Woods
08/09/2010	A2116	E21	Wytham Woods
08/09/2010	A2121	E21	Wytham Woods
08/09/2010	Z4479	E21	Wytham Woods
08/09/2010	A2149	E14A	Wytham Woods
08/09/2010	Z4467	E21	Wytham Woods
08/09/2010	Z4992	E21	Wytham Woods
08/09/2010	A2146	E14A	Wytham Woods
08/09/2010	A2148	E14A	Wytham Woods
08/09/2010	A2150	E14A	Wytham Woods
08/09/2010	A2151	E14A	Wytham Woods
08/09/2010	Z9557	E21	Wytham Woods
08/09/2010	A2154	E14A	Wytham Woods
08/09/2010	A2155	E14A	Wytham Woods
08/09/2010	A2156	E21	Wytham Woods
08/09/2010	Z4486	E21	Wytham Woods
08/09/2010	A2152	E14A	Wytham Woods
08/09/2010	A2147	E14A	Wytham Woods
10/09/2010	A2163	B92	Wytham Woods
10/09/2010	A2162	B92	Wytham Woods
10/09/2010	A2160	B92	Wytham Woods
10/09/2010	A2159	B192	Wytham Woods
10/09/2010	A2161	B92	Wytham Woods
12/09/2010	A1842	SW121	Wytham Woods
12/09/2010	A3507	SW121	Wytham Woods
12/09/2010	Z4826	SW31	Wytham Woods
12/09/2010	Z9647	SW121	Wytham Woods
12/09/2010	A3500	SW121	Wytham Woods
12/09/2010	A3501	SW121	Wytham Woods
12/09/2010	A3502	SW121	Wytham Woods
12/09/2010	Z9648	SW121	Wytham Woods
12/09/2010	A3503	SW121	Wytham Woods
12/09/2010	A3504	SW121	Wytham Woods
12/09/2010	A3505	SW121	Wytham Woods
12/09/2010	A3506	SW121	Wytham Woods
12/09/2010	Z9502	SW121	Wytham Woods
14/09/2010	A3516	W29	Wytham Woods

14/09/2010	Z9557	W45	Wytham Woods
14/09/2010	A1751	W29	Wytham Woods
14/09/2010	A2123	W45	Wytham Woods
14/09/2010	A1753	W12	Wytham Woods
14/09/2010	Z4485	W45	Wytham Woods
14/09/2010	A3515	W28	Wytham Woods
14/09/2010	A3519	W45	Wytham Woods
14/09/2010	Z4476	W45	Wytham Woods
14/09/2010	A2117	W45	Wytham Woods
14/09/2010	A3520	W45	Wytham Woods
14/09/2010	Z4992	W45	Wytham Woods
14/09/2010	A3514	W12	Wytham Woods
14/09/2010	Z4479	W45	Wytham Woods
14/09/2010	A3517	W45	Wytham Woods
14/09/2010	Z4863	W45	Wytham Woods
14/09/2010	Z4474	W45	Wytham Woods
14/09/2010	Z4487	W45	Wytham Woods
14/09/2010	A2113	W45	Wytham Woods
14/09/2010	Z5013	W45	Wytham Woods
14/09/2010	A2121	W45	Wytham Woods
14/09/2010	Z9531	W45	Wytham Woods
14/09/2010	A2122	W45	Wytham Woods
14/09/2010	Z4991	W45	Wytham Woods
14/09/2010	A2164	W45	Wytham Woods
14/09/2010	Z9556	W45	Wytham Woods
14/09/2010	Z9759	W12	Wytham Woods
14/09/2010	A1752	W12	Wytham Woods
14/09/2010	A3518	W45	Wytham Woods
14/09/2010	A1769	W12	Wytham Woods
14/09/2010	A3513	W12	Wytham Woods
14/09/2010	A3512	W12	Wytham Woods
14/09/2010	A3558	W12	Wytham Woods
14/09/2010	A3511	W12	Wytham Woods
15/09/2010	A2163	MP7	Wytham Woods
15/09/2010	A2057	MP77	Wytham Woods
15/09/2010	Z4699	MP27	Wytham Woods
15/09/2010	A1800	MP27	Wytham Woods
15/09/2010	A1777	MP27	Wytham Woods
15/09/2010	A3521	MP7	Wytham Woods
15/09/2010	A2060	MP27	Wytham Woods
15/09/2010	A3541	MP27	Wytham Woods
15/09/2010	A3540	MP27	Wytham Woods
15/09/2010	Z9832	MP27	Wytham Woods
15/09/2010	Z5681	MP27	Wytham Woods

15/09/2010	Z9684	MP27	Wytham Woods
15/09/2010	A1776	MP27	Wytham Woods
15/09/2010	Z9515	MP27	Wytham Woods
15/09/2010	Z9523	MP27	Wytham Woods
15/09/2010	A2138	MP27	Wytham Woods
15/09/2010	A2061	MP27	Wytham Woods
15/09/2010	Z9525	MP27	Wytham Woods
15/09/2010	Z9527	MP27	Wytham Woods
15/09/2010	A3538	MP7	Wytham Woods
15/09/2010	A1778	MP22	Wytham Woods
15/09/2010	A2056	MP27	Wytham Woods
15/09/2010	A3539	MP7	Wytham Woods
15/09/2010	A3522	MP7	Wytham Woods
15/09/2010	A3537	MP7	Wytham Woods
15/09/2010	A3536	MP7	Wytham Woods
15/09/2010	A3535	MP7	Wytham Woods
15/09/2010	A3534	MP7	Wytham Woods
15/09/2010	A3533	MP7	Wytham Woods
15/09/2010	A3532	MP7	Wytham Woods
15/09/2010	A3525	MP7	Wytham Woods
15/09/2010	A3531	MP7	Wytham Woods
15/09/2010	A3524	MP7	Wytham Woods
15/09/2010	A3526	MP7	Wytham Woods
15/09/2010	A3523	MP7	Wytham Woods
15/09/2010	A3527	MP7	Wytham Woods
15/09/2010	A3528	MP7	Wytham Woods
15/09/2010	A3529	MP7	Wytham Woods
15/09/2010	A3530	MP7	Wytham Woods
16/09/2010	Z9570	W91	Wytham Woods
16/09/2010	A2174	E104	Wytham Woods
16/09/2010	A2169	E104	Wytham Woods
16/09/2010	A1988	E120	Wytham Woods
16/09/2010	A1998	E120	Wytham Woods
16/09/2010	A1992	E120	Wytham Woods
16/09/2010	A2167	E106	Wytham Woods
16/09/2010	A2168	E105	Wytham Woods
16/09/2010	A1730	W91	Wytham Woods
16/09/2010	A2170	E104	Wytham Woods
16/09/2010	A2171	E104	Wytham Woods
16/09/2010	A2178	E104	Wytham Woods
16/09/2010	A2173	E104	Wytham Woods
16/09/2010	A2175	E104	Wytham Woods
16/09/2010	A2176	E104	Wytham Woods
16/09/2010	A2177	E104	Wytham Woods

16/09/2010	A1735	W91	Wytham Woods
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14/10/2010	A3674	CP19	Wytham Woods
14/10/2010	A3672	CP6	Wytham Woods
14/10/2010	Z5019	CP152	Wytham Woods

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