Mechanisms of space use in the wood mouse, *Apodemus sylvaticus*

Benedict John Godsall

2015

Imperial College London

Faculty of Natural Sciences

Division of Biology

A thesis submitted for the degree of Doctor of Philosophy

Author's declaration

I declare that this thesis is my own work and that all else is appropriately referenced.

Copyright Declaration

Abstract

"Space use” describes a wide set of movement behaviours that animals display to acquire the resources necessary for their survival and reproductive success. Studies across taxa commonly focus on the relationships between space use and individual-, habitat- and population-level factors. There is growing evidence, however, that variation in space use between individuals can also occur due to differences in 'personalities' and genetic variation between individuals.

Using a wild population of the European wood mouse, *Apodemus sylvaticus*, this thesis aims to: i) investigate the roles of individual-level (body mass, body fat reserves and testosterone), habitat-level (*Rhododendron* and logs) and population-level (population density, sex ratio and season) factors as drivers of individual variation in the emergent space use patterns of individual home range size and home range overlap, estimated using spatial data collected in a mixed-deciduous woodland over three years. ii) Establish a link between genes and space use through the heritability and response to selection of phenotypic traits linked to individual variation in space use. A pedigree of the population is reconstructed from microsatellite data. Individual reproductive success is estimated from it and used to estimate selection gradients for three phenotypic traits. Heritability estimates are calculated using the animal model and together with selection gradients are used to predict the generational change in the population mean of traits using the Breeders equation.

The results of this thesis suggest that the mechanism behind space use in this population of *A. sylvaticus* involves interactions between season, habitat, sex and the three individual-level factors (body mass, body fat and testosterone). The heritability of traits linked to emergent space use patterns suggests indirect effects of genes on individual variation in space use. Small responses to selection for traits suggests that gene-driven changes to space use patterns will most likely be indistinguishable between generations.

Acknowledgements

First and foremost I would like to express my special thanks to my supervisors, Prof. Timothy Coulson and Dr. Aurelio Malo. I am very grateful, and feel privileged to have had the opportunity to work with and be mentored by both of them. The support and encouragement Tim and Aurelio provided throughout my thesis was invaluable. I have enjoyed being a part of the relaxed environment of the Coulson group, and it has been a real honour to be Dr. Malo's first PhD student.

Severin Dreβen, a fellow PhD student, deserves special thanks for his hard work and efficiency in helping collect data during long days in the field, developing the GIS map of the study site, and introducing me to DTT. I am also extremely grateful to Jacques Deere and his wife Sam Hopkins, who showed me an abundance of generosity by giving me a hot meal, a warm bed and good company on the evenings preceding fieldwork.

I thank all of the Masters students who worked for the project over the years for their efforts in data collection: C. Weevil, S. McCandless, T. Powell, G. Kingcome, M. Brouard, R. Moorhouse-Gann, O. Hicks, L. Sandbach, R. Barker, S. McLoughlin. A special thanks also goes to Michael Massam for his hard work as a volunteer.

The genetic elements of this thesis would not have been possible without the help of Martyn Powell, who taught me how to extract DNA, and especially Helen Hipperson, who gave a lot of her time to patiently instruct me how to perform PCRs with microsatellites.

Most of the genetic work was performed at the NERC Biomolecular Facility at Sheffield University. I would like to thank Prof. Terry Burke for giving me the opportunity and funding to work in his group and provide advice on pedigree reconstruction. Deborah Dawson, Andy Krupa and Gavin Horsburgh were exceptionally helpful in providing instruction and advice throughout my time in the lab, and I am extremely grateful to them for their help.

Mike Francis of Francis Scientific Instruments Ltd. built the pit-tag recording stations used to collect the spatial data in this thesis. The volume and quality of data collected during this project could not have been achieved without his support. I would also like to thank Igor Lysenko for his assistance in originally developing the digital map of the study site in GIS.

Finally, but by no means least, I would like to say a huge thank you to Helen Meredith for her understanding, patience and support throughout the last 5 years, which at times must have required a lot of energy to maintain.

Table of contents

Chapter 3: Habitat interacts with phenotypic traits to determine home range overlap 64

List of figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

List of tables

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Appendix

Chapter 1

An overview of animal space use

Introduction

In order to survive and reproduce, all animals must acquire the resources necessary for them to do so, including food, shelter and mates. As these resources are spatially and temporally distributed over landscapes, animals acquire them by utilising their environment. There are costs associated with the search for and acquisition of resources, however, and animals should attempt to minimise these costs in order to improve their chances of survival and reproduction (Gaines & McClenaghan 1980; Krivan 1997). "Space use" is a broad term which describes a wide set of behaviours that are influenced by individual-, population- and environment-level factors. Variation in the distribution of resources, and between the needs and ability of individuals to seek and acquire resources, leads to variation in patterns of individual space use. Understanding how and why variation in space use arises, as well as the consequences of it, are central to many important processes in Ecology. In order to effectively manage and conserve species and habitats, it is necessary to understand the driving forces behind key interactions between animals and their environments (Donovan *et al.* 2011; Coleman *et al.* 2013). The space use of individuals and their facilitation of the environment (the changes to resource abundance or habitat structure resulting from an individual's use of the environment) affects the distribution and abundance of resources (Mitchell & Powell 2004; Gautestad & Mysterud 2010a), ecosystem community structure

(Danielson 1991; Fagan, Lutscher & Schneider 2007), the social organisation within a population (VanderWaal *et al.* 2014), and the spatio-temporal distribution of populations (Fahrig 1988; Morris 2003; Wang & Grimm 2007). Immigration and emigration of individuals between populations have important consequences for population and meta-population dynamics (Gaines & McClenaghan 1980; Pulliam 1988; Byrom 2003), disease spread (Russell *et al.* 2004; Kenkre *et al.* 2007) and gene flow (Sugg *et al.* 1996; Lenormand 2002; Booth, Montgomery & Prodöhl 2009). Ultimately, the variation in fitness that arises from individual variation in space use results in selection on behavioural and physical phenotypic traits relating to variation in space use, which may lead to the evolution of these traits (Morris 2003; Olsson *et al.* 2008; Marmet *et al.* 2012).

The importance of understanding rodent space use

There are approximately 1700 rodent species worldwide, 5-10% of which are considered to be significant pest species due to their role in disease spread and agricultural losses (Stenseth *et al.* 2003). Across the globe, rodents are responsible for the transmission of over 60 known diseases to man and livestock, many of them fatal, either through direct transmission (via bites or contamination of food by faeces) or by harbouring other vectors of disease, such as ectoparasites (Meerburg, Singleton & Kijlstra 2009).

Estimates of rodent-related agricultural losses are staggering. Singleton (2003) reviewed the impacts of rodents on agricultural losses in Asia, where preharvest losses of rice production by rodents in traditional farming systems are typically 5-20% and postharvest losses even higher (20-30%). To put this into perspective, Singleton (2003, p.1) states:

> "*In Asia, a loss of 5% of rice production amounts to approximately 30 million [tons]; enough rice to feed 180 million people for 12 months.*"

These percentage losses are similar to other continents, where the economic price-tag of rodent-related losses commonly reaches tens to hundreds of millions of dollars per year (Stenseth *et al.* 2003)

Rodent control strategies are commonly based around the use of lethal poisons - rodenticides (Singleton *et al.* 2007). Rodenticides may be effective in the short term (Hygnstrom *et al.* 2000), but are not effective over the long term due to the ability of rodent populations to rapidly rebound from culls (Barnett & Bathard 1953). The use of rodenticides also results in the mortality of non-targeted species (Brown & Lundie-Jenkins 1999). These unintended environmental consequences, combined with their long term inefficiency, mean that lethal control strategies are not economically or ecologically sustainable. A growing body of literature has been developed showing that the impacts of rodents can be mediated through 'ecologically-based management' (Singleton *et al.* 1999). These bespoke management strategies incorporate knowledge of habitat use and population dynamics of pest species to improve the effectiveness, economic costs and environmental effects of lethal strategies (Singleton *et al.* 1999, 2003, 2005; Brown *et al.* 2006).

Their associations with disease and crop losses has given humanity a negative perception of rodents. Despite their sins in the eyes of humanity, rodents can also play important roles within natural ecosystems, acting as seed dispersers (Jensen & Nielsen 1986), controllers of insect pests (Stuart *et al.* 2007) and food supply for species of higher trophic levels (Pavey, Eldridge & Heywood 2008). It is therefore important to understand the drivers and consequences of space use in rodents, to both improve our ability to control them as pests while protecting populations involved in the functioning of natural ecosystems.

Quantifying space use: the 'home range' concept

When studying space use, scale is vitally important to interpret results. The scale selected to analyse space use data can greatly affect the interpretation of habitat selection patterns, population structure and behaviours such as dispersal (Bowler & Benton 2005). It is therefore necessary that the spatial and temporal scale used in a study is well defined and remains constant between individuals (Laver & Kelly 2008; Fieberg & Börger 2012).

Throughout this thesis the scale of animal space use used in analysis is the 'home range'. Home ranges are emergent spatial patterns that result from a combination of underlying movement, foraging, social and reproductive behaviours of individuals (Börger, Dalziel & Fryxell 2008; Fieberg & Börger 2012). The most frequently cited definition of a home range is also the earliest, given by Burt (1943, p.351) as:

> *“that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range.”*

As the methods used to estimate home ranges became more sophisticated, researchers sought a more quantifiable definition. White & Garrott (1990) suggested a home range to be the smallest bounded area in which there is a 95% probability of finding the animal. Kernohan, Gitzen & Millspaugh (2001, p.126) gave their definition as “the extent of area with a defined probability of occurrence of an animal during a specified time period”. A further defining aspect of a home range that distinguishes it from other space use patterns, such as dispersal or migration, is that home ranges are stationary in space over a given time period (Laver & Kelly 2008; Börger *et al.* 2008).

'Home range' should not be confused with “territory”, as the processes which determine the size and shape of each are different (Börger *et al.* 2008). A territory is a defended area where conspecifics are actively excluded in an effort to protect resources, offspring or a home site (Maher & Lott 1995, 2000). An animal’s territory will occur within its home range, and could form the entire home range or just a smaller, focused area around a home site (Burt 1943; Börger *et al.* 2008). Whereas use of a territory is restricted to the owner, home ranges may extensively overlap (Brown & Orians 1970). Home ranges are dynamic over time in relation to changes to the environment (Börger *et al.* 2006, 2008; Beyer *et al.* 2010; Volampeno, Masters & Downs 2011), whereas territories are considered to be more fixed around a specific location, but can still vary in their location depending on interactions with neighbouring individuals (Burt 1943; Maher & Lott 1995; Börger *et al.* 2008).

Throughout this thesis I quantify individual home ranges using kernel density estimation (Worton 1989). This method assumes that location data collected for an individual is sampled from an underlying probability distribution (Worton 1989; White & Garrott 1990; Kernohan *et al.* 2001). The home range is estimated from a probability density function by fitting a statistical kernel to the location data, resulting in an animal's utilization distribution. The utilization distribution shows the proportion of time an animal spends in each area of its home range, and the outer boundary is typically set at 95% to allow for exploratory movements outside the usual home range (Burt 1943; White & Garrott 1990). Kernel methods are often preferred as they free the utilization distribution estimate from the parametric assumptions required by other statistical methods (Worton 1989), but are highly sensitive to the choice of smoothing parameter, or bandwidth selection (Worton 1989; Gitzen, Millspaugh & Kernohan 2006; Laver & Kelly 2008; Cumming & Cornélis 2012). The purpose of smoothing the data is to minimise the error between the estimated and true utilization distributions at the cost of bias (Worton 1989; Matthiopoulos 2003a; Fieberg 2007). Numerous smoothing methods have been developed (Wand & Jones 1995), but simulations have shown that with the appropriate data-based selection of smoothing parameter (e.g. plug-in or solve-the-equation methods), kernel methods provide a reasonably unbiased means of producing animal utilization distributions for use in home range studies (Horne & Garton 2006; Fieberg 2007; Laver & Kelly 2008).

Drivers of space use

Both the biological needs of individuals and the environment can change over space and time, leading to variable space use patterns between individuals (Mauritzen *et al.* 2003; Godvik *et al.* 2009; Bjørneraas *et al.* 2012). The environment can change seasonally and annually in response to abiotic climatic factors such as photoperiod, temperature and rainfall. Habitat facilitation (the use of habitat) by species can also alter the state of the environment through the removal of resources or changes in its structure (Arsenault & Owen-Smith 2002; Gautestad & Mysterud 2010a). In this chapter I refer to 'individual state', which I define as a multidimensional physical, physiological and neurological state that affects an individual's ability and motivation for movement (Nathan *et al.* 2008). Each individual's state is affected by numerous individual-level factors, including sex, life history, body size and physiology, which can themselves be affected by environmental factors (Perret & Aujard 2001; Bartness, Demas & Song 2002). The behaviour an individual displays in order to meet its needs, for example, foraging, mate-seeking, or dispersal, are a response to that individual's state (Bowler & Benton 2005). The same is true for each individual from any species in a community, so the distribution, density and actions of conspecifics or heterospecifics affect both the state of the environment and the fitness consequences for each individual (Danielson 1991; Landman, Schoeman & Kerley 2013; Wakefield *et al.* 2013).

A landscape can be divided into a complex network of distinct habitats, and each habitat into a matrix of patches distinguished by differing physical structure, community composition, resource abundance or other characteristic (Danielson 1991; Pulliam, Dunning & Liu 1992; Bailey *et al.* 1996). The factors, or 'drivers', which govern individual variation in space use operate across a range of spatial and temporal scales (Johnson 1980). Drivers at smaller spatial scales, including the quality or abundance of patch resources, habitat structure and the presence of conspecifics or predators can influence an individual's decisions regarding patch selection and within- or between-patch movements (Charnov 1976a; b; Benhamou & Bovet 1989; Bailey *et al.* 1996; Nonacs 2001; Mueller & Fagan 2008). An animal’s sensory-motor mechanisms - its ability to both perceive and move through its surrounding environment - can therefore influence space use in conjunction with environmental drivers (Sinsch 1990; Mueller & Fagan 2008; Nathan *et al.* 2008). At larger spatial and temporal scales, i.e. beyond the sensory range of an individual and over longer time periods, an individual's memory of patch quality and the location of predators and conspecifics can also act as a driver of space use (Stamps 1995; Bailey *et al.* 1996; Mueller & Fagan 2008; Gautestad & Mysterud 2010a; b).

Regardless of the spatio-temporal scale over which space use occurs, individual variation in space use is driven by a combination of individual- population- , interspecific- and habitat-level factors. In order to understand the dynamics of space use, it is necessary to understand the multitude of interactions between the different levels of drivers occurring across different spatio-temporal scales.

Habitat and resource distribution

Habitat selection is the process whereby individuals use or avoid specific patches or habitats non-randomly because their properties can improve or reduce individual fitness (Johnson 1980; Morales & Ellner 2002; Morris 2003; Rhodes *et al.* 2005). Some habitat patch characteristics, for example the abundance of food resources, are dynamic over time and space, while others such as topographic features remain relatively constant. Dynamic variation in patch characteristics may mean that an animal is forced to shift its location and select new patches or habitats in order to maximise its fitness (Charnov 1976b; Stephens & Charnov 1982; Pyke 1984; Arditi & Dacorogna 1988). Resource abundance across a landscape may change seasonally or annually (Volampeno *et al.* 2011), whereas at a smaller spatiotemporal scale resource levels might change through their depletion by animals (Gurnell 1993; Mitchell & Powell 2004; Fagan *et al.* 2007). The physical structure of habitat determines the availability of suitable nesting or home sites (Timoney 1999; Rosalino *et al.* 2011a), predation risk (Kotler, Brown & Hasson 1991; Roos 2002) and foraging (or hunting) efficiency (Ziv *et al.* 1995; Jenkins 2000). Habitat structure can change over long time periods through vegetation succession and change seasonally with changes in community structure and new growth. Over shorter time scales habitat structure can be altered by animals or humans (Hobbs 1996). Individual space use should therefore reflect the spatial and temporal distributions of food resources and preferred habitat across a landscape.

Climatic and other abiotic factors can lead to alterations in space use behaviour, through interactions with habitat, by altering the effectiveness of certain habitat patches to provide shelter, protection or hunting opportunities (Stokes, Slade & Blair 2001). Rainfall or wind, for example, can reduce prey detection rates by predators relying on acoustic cues by creating background noise or removing scent trails (Vickery & Bider 1981). Heavy rainfall could have a negative impact on foraging efficiency by increasing the energetic cost of thermoregulation (Cuyler & Oritsland 2004). Moonlight can increase the risk of predation by facilitating the visual location of prey by predators (Kotler *et al.* 1991; Bowers & Dooley 1993; Diaz *et al.* 2005). Short term changes in weather may therefore affect habitat selection at small spatiotemporal scales if the resulting change in space use improves an individual's chances of gathering resources or reduces energetic costs. Longer term, seasonal changes in weather patterns may therefore result in larger scale shifts in space use (Börger *et al.* 2006).

In nature, resources are often limited and heterogeneously distributed, so individuals must compete for them (Tilman 1994; Ryabov & Blasius 2014). Individuals vary in their ability to detect and compete for resources, and this will be reflected in the variation in space use between individuals. Furthermore, populations are composed of individuals at different life history stages with differing biological requirements, which consequently also lead to variation in space use (Bowler & Benton 2005). Therefore, although habitat factors are important drivers of space use, they cannot fully explain why and how individuals show variation in space use.

The state of the individual

An animal's state at any point in time is influenced through a number of individual, social and environmental factors. An individual's state governs its biological requirements, which determine the behaviours performed to satisfy them, ultimately affecting the individual's space use (Ims 1987a; b, 1989; Bowler & Benton 2005). Furthermore, individual-level variation between animals in their ability to perceive, evaluate, memorise and move through the environment, acquire resources and compete with others can also result in differences in the spatial organisation and space use behaviour observed between individuals (Sinsch 1990; Stamps 1995; Bailey *et al.* 1996; Hurst *et al.* 1996; Mueller & Fagan 2008;

Nathan *et al.* 2008). In fact, Morales & Ellner (2002) even argue that the effects of individual-level factors on space use may be of greater importance than habitat-level effects.

Two examples of how individual-level factors affect space use in conjunction with environmental factors are sex and body size. These are two of the most commonly tested individual-level drivers of space use in the literature. Sex has been found to play a significant role in explaining variation in space use between individuals across taxa, including mammals (Swihart & Slade 1989; Lurz, Garson & Wauters 2000; Dahle & Swenson 2003), birds (Gray *et al.* 2009; Fernández & Lank 2012; Campioni *et al.* 2013), amphibians (Donnelly 1989; Pröhl & Berke 2001; Ekdahl, Malmgren & Andersson 2007) and reptiles (Pounds 1988; Carfagno & Weatherhead 2008; Carrière, Bulté & Blouin-Demers 2009). Differences in space use between sexes occur because males and females require different resources in order to maximise their reproductive fitness (Gaulin & FitzGerald 1986, 1989; Clutton-Brock 1989; Ecuyer-dab & Robert 2004). These differences in requirements are linked to the energetic and parental investment in reproduction made by each sex, which is related to the reproductive rates of each sex (Clutton-Brock & Vincent 1991), and ultimately the mating system of the population (Emlen & Oring 1977; Ostfeld 1985; Ims 1987b; Clutton-Brock 1989). In mammals, for example, females typically invest a greater amount of time and energy in the gestation and nurturing of offspring compared to males, and have a slower rate of offspring production as a result (Clutton-Brock & Vincent 1991). During breeding periods, females maximise their fitness by increasing their offspring's probability of survival, which can be achieved by securing nesting or home sites in habitats with high quality nutritional resources and low predation-risk (Ostfeld 1985, 1990; Clutton-Brock 1989). Male mammals, on the other hand, commonly invest less time and energy in reproduction and have higher reproductive rates (Clutton-Brock & Vincent 1991). Their biological needs (to maximise their reproductive success) are different to females as a result, and consequently their patterns of space use may differ from females during breeding periods depending on the mating system (Emlen & Oring 1977). In monogamous mating systems, males maximise their reproductive success by securing high-quality resources that attract females, and space use may be similar between males and females, although females are more likely to be the dispersing sex (Johnson & Gaines 1990). In polygamous mating systems, however, males maximise their reproductive success by mating with multiple receptive females, which become the resource males compete for. Male space use is then driven by the spatial distribution of females and the ability of males to successfully compete for access to them (Emlen & Oring 1977; Ims 1987b; Clutton-Brock 1989; Ostfeld 1990).

Body size has been linked to individual variation in space use both within and between species (Johnson & Gaines 1990; Bailey *et al.* 1996; Kelt & Van Vuren 2001; Jetz *et al.* 2004; Bowler & Benton 2005; Fokidis, Risch & Glenn 2007; Schradin *et al.* 2010). Intraspecific variation in home range size can occur as larger species have greater net energetic demands, requiring greater resource acquisition, and may therefore allocate more time to travel (over greater distances) and forage relative to other activities (Swihart, Slade & Bergstrom 1988; Bailey *et al.* 1996; Fernández & Vrba 2005; Woodward *et al.* 2005). Body size has also been linked to individual competitive ability due to its relationship with individual strength (Nakano 1995; Briffa & Sneddon 2007; Arnott & Elwood 2009). Intraspecific variation in home range size may occur if larger individuals are more dominant and therefore more likely to outcompete conspecifics for access to habitat patches containing high quality resources or mates (Nakano 1995; Jennings *et al.* 2010; Huang, Wey & Blumstein 2011). Smaller, less dominant individuals may be forced to disperse (Stephens & Charnov 1982; Nakano 1995; Bowler & Benton 2005). In this example, the distribution of high quality resources determines the attractiveness of habitat patches, while the relative sizes of conspecifics within a population determines which individuals successfully acquire them, and which are forced to disperse. Other individual-level factors associated with competitive ability, such as weaponry (Sneddon, Huntingford & Taylor 1997), stamina (Mowles & Briffa 2012), experience (Stuart-Fox & Johnston 2005) and physiological state (Poole 1989; Marden & Rollins 1994; Zamudio, Huey & Crill 1995) may play similar roles in determining the spatial organisation of individuals.

Variation between individuals in their 'personalities' - defined as consistent or predictable differences in behaviour between individuals over time or for a given context (Sih *et al.* 2004; Réale *et al.* 2007) - has also been shown to correlate with variation in space use patterns (Dingemanse *et al.* 2003; Boon, Reale & Boutin 2008). For example, in both Siberian chipmunks (*Tamias sibiricus*) and North American red squirrels (*Tamiasciurus hudsonicus*), individuals with more active, exploratory or aggressive personalities were found to be more frequently trapped and trapped over a wider area than those with less active, more shy personalities (Boon *et al.* 2008; Boyer *et al.* 2010). In great tits, *Parus major*, personality differences relating to the speed of exploration were found to affect the foraging strategy for juvenile birds (van Overveld & Matthysen 2010) and dispersal distance of post-fledging offspring (Dingemanse *et al.* 2003). Individual differences in behaviour can therefore potentially explain some of the observed variation in emergent spatial patterns, such as home ranges, between individuals.

More recently, there has been increasing interest in the role of endocrine and neuropeptide systems in space use behaviour. In laboratory studies, mice bred to lack a specific noradrenalin receptor, for example, were less cautious, more active and more interested in novel objects than control mice, but were unable to learn spatial tasks (Spreng, Cotecchia & Schenk 2001). Studies on the role of vasopressin in social and reproductive behaviour have shown that individuals with higher numbers of receptors in the brain for this neuropeptide show more monogamous behaviour in several rodent species (Young *et al.*

1999; Pitkow *et al.* 2001; Fink, Excoffier & Heckel 2007), which may have implications for conspecifics attraction and patch selection in the wild.

Gonodal hormones in particular have received increasing attention in both the lab and studies on wild populations. These hormones are known to drive aggressive and reproductive behaviours (Drickamer 1996; Ryan & Vandenbergh 2002), but there is increasing evidence from laboratory and experimental studies that suggests variation in space use behaviour is also, to some extent, affected by individual-level variation of these hormones. Individual variation in gonodal hormone levels can occur via the prenatal intrauterine position of individuals, with foetuses flanked by male siblings exposed to a higher concentration of testosterone compared to those with neighbouring females (vom Saal & Bronson 1980; vom Saal & Dhar 1992; Vandenbergh & Huggett 1995; Ryan & Vandenbergh 2002). A study of wild house mice, *Mus musculus*, in small experimental enclosures, showed males exposed to greater concentrations of testosterone *in utero* were more aggressive, more likely to disperse and had larger home ranges (Drickamer 1996). Further study showed that areas containing scent marks from mice were actively selected or avoided by other mice depending on their relative levels of exposure to testosterone *in utero* (Drickamer, Robinson & Mossman 2001). In meadow voles, *Microtus pennsylvanicus*, females with high oestradiol levels were poorer at retaining learned spatial information than females with low oestradiol levels or males (Galea *et al.* 1995; Galea, Kavaliers & Ossenkopp 1996). Testosterone also plays a role in aggression towards conspecifics (Drickamer *et al.* 2001) which can affect an individual's competitive ability and therefore access to patches containing females and abundant resources (Jennings *et al.* 2010; Huang *et al.* 2011). Recent studies on yellow-bellied marmots, *Marmota flaviventris*, in the wild have corroborated the findings of some laboratory studies (Monclús & Blumstein 2012; Monclús, Cook & Blumstein 2012). A greater number of males in a litter increased the androgenisation of females (due to exposure to higher prenatal levels of testosterone). These females displayed more masculine social behaviour and were more likely to disperse than less androgenised females (Monclús & Blumstein 2012; Monclús *et al.* 2012). These findings not only encourage new areas for research into individual variation in space use, but also suggest that the experimentally induced effects of neuro-endocrine mechanisms on space use behaviour observed in the laboratory could reflect natural processes occurring in wild populations.

Population density, sex ratio and interspecific competition

As well as the density of resources, conspecific density can influence the attractiveness of a habitat patch and therefore the probability of its use by an individual (Brown & Orians 1970). Attraction towards conspecifics may occur due to the fitness benefits arising from reduced individual predation risk at higher densities, group territory defence or the improved probability of finding a mate (Lima & Zollner 1996; Muller *et al.* 1997; Bowler & Benton 2005). The density of conspecifics in a patch can also indicate the quality or abundance of resources in that patch either directly through communication or indirectly simply by the numbers present (Muller *et al.* 1997; Wakefield *et al.* 2013).

At high densities (determined by the carrying capacity of a patch), however, the abundance of resources becomes limiting, resulting in density-dependent movement out of the patch due to competition or aggressive interactions (Brown & Orians 1970; Albon *et al.* 1992; Clutton-Brock, Rose & Guinness 1997; Kie & Bowyer 1999; Wakefield *et al.* 2013). Which individuals remain and which leave a patch partly depends on each individual's competitive ability as well as their experience and knowledge of the quality of the surrounding environment (Jennings *et al.* 2010; Huang *et al.* 2011). Density-dependent competition can be exploitative, i.e. conspecifics deplete resources making fewer available overall (Alatalo *et al.* 1987), or can occur through interference, in which the density of conspecifics makes it more difficult to acquire resources or mates (Berger & Gese 2007). When the competition for resources, space or mates is so high that some individuals are unsuccessful in foraging or mating, those individuals are forced to disperse (Brown & Orians 1970; Andreassen & Ims 2001; Bowler & Benton 2005).

The sex-ratio of a population can influence space use, particularly during breeding periods, when within-sex competition is highest (Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996). Spatio-temporal variation in the relative densities of males and females leads to variation in the probability of encountering potential mates versus competitors, which can have consequences for the spatial organisation of individuals within a population, the nature of the mating system (Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996) and dispersal rates (Bowler & Benton 2005).

Interspecific interactions can influence individual space use through predation (Kotler *et al.* 1991; Longland & Price 1991), competition for space or resources (Reichard, Jurajda & Smith 2004; Berger & Gese 2007) or, occasionally, mutualism (Bshary & Noe 1997; Majolo & Ventura 2004). The role of interspecific interactions in determining space use can be similar to the influence of intraspecific effects. One species may influence the way another species uses space by utilising habitat patches and, in doing so, make them more or less attractive (Brown & Orians 1970). As with conspecific attraction, the presence of a different species in a patch may signal the patch's quality, but there are also examples of more direct fitness benefits from the presence of another species when a mutualistic relationship is formed, either by reducing predation risk or improving foraging success (Bshary & Noe 1997; Majolo & Ventura 2004).

If different species compete over space or resources (or one predates upon another), the presence of one species may decrease the attractiveness of a habitat patch to another. As with intraspecific competition, interspecific competition can occur through resource depletion, interference or costly aggressive encounters (Schoener 1974). Competition theory predicts that the more ecologically similar the species are, the greater the competition between them, and consequently the outcompeted species should differentiate its use of space and resources from the more dominant one (Schoener 1974; Schoener & Schoener 1982). The distribution and abundance of one species can therefore influence the space use and distribution of other species across a landscape (Landman *et al.* 2013).

Genes and space use

There are increasing examples from laboratory studies that demonstrate the influence of genes on space use behaviours (Sokolowski 2001). Unfolding the nature of the relationship between genes and behaviour is complex. Although genes cannot determine exactly when or where certain behaviours will be performed by an individual, they do govern the development and functioning of the brain (in conjunction with an individual's developmental environment), which organizes behaviour. An individual's genotype can therefore influence the disposition of that individual towards certain spatial behaviours (Heisenberg 1997). Although there is evidence of specific genes governing specific behaviours (Sokolowski 1980), it is more commonly hypothesised that genes have pleiotropic effects and play a role within a complex genetic architecture that influences behaviour (Sokolowski 2001). Variation in gene expression may also cause behavioural variation seen in the laboratory (Heisenberg 1997).

Until recently, studies linking behaviour with specific genes had been confined to the laboratory due to the necessity to knock-out or manipulate the target gene’s expression in order to link functionality to the expressed behaviour (Fitzpatrick *et al.* 2005). Classic laboratory examples of genes that affects behaviour come from studies of *Drosophila*.

Perhaps the most striking example of a gene's effect on spatial behaviour is from mutations in the *foraging* (*for*) gene. Two general behavioural phenotypes exist in *Drosophila* that relate to space use. One phenotype, 'rovers', display longer movement paths when foraging as well as a greater propensity to leave a patch compared to the other phenotype, 'sitters'. Variation between these two phenotypes can be explained by a mutation in this single *for* gene (Sokolowski 1980). Recently an ortholog of the *for* gene, *Amfor*, has been discovered in the honeybee, *Apis mellifera*. Manipulating the expression of this single gene was sufficient to cause a shift in behaviour in individual bees from within-hive tasks, such as nursing, to foraging, which resulted in a completely different use of space (Ben-Shahar *et al.* 2002).

A second example from *Drosophila* is a mutation in the *period* (*per*) gene, which regulates circadian rhythms. Three mutations of this gene were discovered by Konopka & Benzer (1971) which caused either a lengthening or shortening of the normal activity period of flies, or a loss of rhythmicity of their activity. This genetic influence on circadian rhythms has more recently been confirmed in higher order organisms as well. Laboratory mice bred to have a semi-dominant mutation in the *Clock* gene, which regulates both the circadian period and circadian rhythmicity in mammals, displayed an extended circadian period but lacked the persistent circadian rhythmicity seen in normal individuals (Vitaterna *et al.* 1994). These findings suggest that genes play a role in determining the period and duration of space use behaviours.

The role of genes in complex behaviours was investigated in a recent study by examining differences in the burrowing behaviour of oldfield mice, *Peromyscus polionotus*. Burrowing behaviour was tested for a genetic basis using quantitative trait locus analysis (Weber, Peterson & Hoekstra 2013). Three independent genetic loci were found to be linked to burrow length and a single locus to the presence of an escape tunnel. This example, along with those above, provides evidence that genetic variation can have a seemingly direct effect on space use behaviour.

More recently, studies linking genes with behaviour in wild populations have, similar to laboratory studies, revealed the effects of single genes on behaviours relating to space use patterns. Studies on the Glanville fritillary butterfly (*Melitaea cinxia*) have shown that individual genotypic variation of the *phosphoglucose isomerase* (*Pgi*) gene relates to individual variation in the frequency of patch emigration (Zheng, Ovaskainen & Hanski 2009), flight physiology and movement behaviour at the landscape level (Niitepõld *et al.* 2009), and lifespan in females, which is correlated with their distance travelled between consecutive censuses (Klemme & Hanski 2009). A study of wild red deer on the Isle of Rum tested the heritability of home ranges within the population, but found very little evidence of heritability after including spatial factors in their models (Stopher *et al.* 2012).

Phenotypic drivers of space use also have a genetic basis, but whether individual genetic variation for these has a strong enough effect to directly influence individual space use is yet untested. Studies on invertebrates and rodents have concluded that the expression of certain genes is essential in facilitating long-term memory (Silva *et al.* 1998; Alberini 1999). Individual differences in hormones and neuropeptides are governed by genotype and variation in gene expression (Young *et al.* 1999; Insel & Young 2000; Pitkow *et al.* 2001; Spreng *et al.* 2001; Fink *et al.* 2007; Landgraf *et al.* 2007). Evidence for genetic effects on visual (Kaczmarek & Chaudhuri 1997) or olfactory sensory mechanisms (Zhang & Firestein 2002) may also contribute to different space use between individuals. There is also some evidence for genes governing body size in laboratory mice (Zhang *et al.* 1994; Trumpp *et al.* 2001).

Evidence is therefore growing that genetic variation between individuals can lead to differences in space use behaviour, but our knowledge of the extent to which genotypes play a role in explaining variation in space use behaviour in the wild is still limited to a few studies (Klemme & Hanski 2009; Niitepõld *et al.* 2009; Zheng *et al.* 2009; Stopher *et al.* 2012). A trait is under selection when its phenotypic variance translates into variance in fitness between individuals within a population (Kingsolver & Pfennig 2007). The allelic frequencies governing such traits should then increase in frequency within the population. If these alleles influence space use, then space use should change over successive generations as a response to the selective pressures suffered by the population each generation. Quantitative genetics is a field of research concerned with the ways in which genotypes and the environment contribute to individual phenotypic variation (Falconer & Mackay 1996). This does not require explicit knowledge of a phenotypic trait's genetic architecture, but instead assumes that genetic variance in the value of a phenotypic trait is governed by the summed contribution of many genes of small effect (Hazel 1943; Henderson 1976; Lande 1979). As related individuals share more genes than unrelated individuals, the additive genetic variance of a trait can be calculated using knowledge of the relatedness between individuals. The proportion of total phenotypic variance explained by additive genetic variance gives an estimate of a trait's heritability (Jacquard 1983). The heritability estimate of a trait therefore provides evidence of a genetic influence on trait values. If variance in the value of a trait between individuals leads to variance in space use, and that trait is heritable, then there is evidence of an indirect effect of genotype on space use behaviour. How the distribution of trait values within a population changes over successive generations can then be predicted using a trait's heritability and a measure of the strength and direction of selection upon that trait (Lande 1976; Lande & Arnold 1983).

Study species: the European wood mouse, *Apodemus sylvaticus* (L.)

The European wood mouse is one of the most common species of small mammal in Britain, inhabiting both woodland (Watts 1969) and arable environments (Tew & Macdonald 1994). Wood mice are predominantly granivorous, but also feed on invertebrates when seeds are in short supply during spring, before trees begin to drop their seeds or fruit from mid to late summer (Watts 1968; Hansson 1985; Jensen 1993). This is a nocturnal species, with individuals making several outings each night from subterranean nests which are strongly related to the timings of sunrise and sunset (Greenwood 1978; Wolton 1983). Populations of *A. sylvaticus* undergo distinct seasonal cycles (Kikkawa 1964; Flowerdew 1985). These cycles are characterised by an increase in population density at the end of the breeding season from mid to late autumn as aggression and territoriality decline. Males enter reproductive condition before females in early spring (Clarke 1985), leading to a decline in population density as aggression and territoriality increase (Gurnell 1978), and less dominant individuals are forced to disperse (Malo *et al.* 2013). Peak reproductive periods are typically between June and September, but may occur earlier or later depending on food availability (Clarke 1985). Individuals typically live for over a year, being born during a breeding season, maturing through the winter and reproducing in the following breeding season, then dying the following winter (Flowerdew 1985). The life cycle of mice in the study system used in this thesis followed this pattern.

A. sylvaticus occupy home ranges which have been shown by previous studies to vary in size between habitats (Corp, Gorman & Speakman 1997; Macdonald *et al.* 2001), seasons (Wolton & Flowerdew 1985; Corp *et al.* 1997) and between the sexes, with male home ranges being approximately twice as large as females (Wolton 1985; Wolton & Flowerdew 1985; Tew & Macdonald 1994; Macdonald *et al.* 2001; although not all studies corroborate these findings - see Rosalino *et al.* 2011b). Estimates of home range size for *A. sylvaticus* vary considerably between studies, from the smallest reported area of $950m^2$ (Tew & Macdonald 1994) up to $37420m^2$ (Rosalino *et al.* 2011b).

Study site

The study site was a 2.4ha region of Nash's Copse at Imperial College London's Silwood Park campus, near Ascot, UK (51° 24' 50.3542"N, -0° 38' 43.4816"E). The study area was a mixed deciduous woodland most consistent with the W11 category of the National Vegetation Classification system (Fig. 1.1). The canopy was dominated by birch trees (*Betula pubescens*), with less common presence of European beech (*Fagus sylvaticus*) and sycamores (*Acer pseudoplanatus*). Rarer (n<5) tree species included common oaks (*Quercus petraea*), ash (*Fraxinus excelsior*) and common alder (*Alnus glutinosa*). Coppiced hazel trees (*Corylus avellana*) and a species of *Rhododendron* dominated the understory and shrub layer respectively. A single patch of invasive bamboo was also present. Ground cover was dominated by bluebells (*Hyacinthoides non-scripta*) during spring and bracken (genus *Pteridium*) during summer and autumn. Wood sorrel (*Oxalis acetosella*) and several moss and bryophyte species were also present. In winter, the dominant ground cover was leaf litter.

Other small mammal species present at the study site were yellow-necked mice (*Apodemus flavicollis*), bank voles (*Myodes glareolus*) and the common shrew (*Sorex araneus*). These species are also insectivorous and granivorous (excluding shrews) and occupy similar ecological niches to *A. sylvaticus* (Watts 1968; Hansson 1985; Wolton & Flowerdew 1985), potentially resulting in interspecific competition with wood mice for food resources or home sites. Predators observed at the study site included the red fox (*Vulpes vulpes*), the European badger (*Meles meles*) and tawny owls (*Strix aluco*).

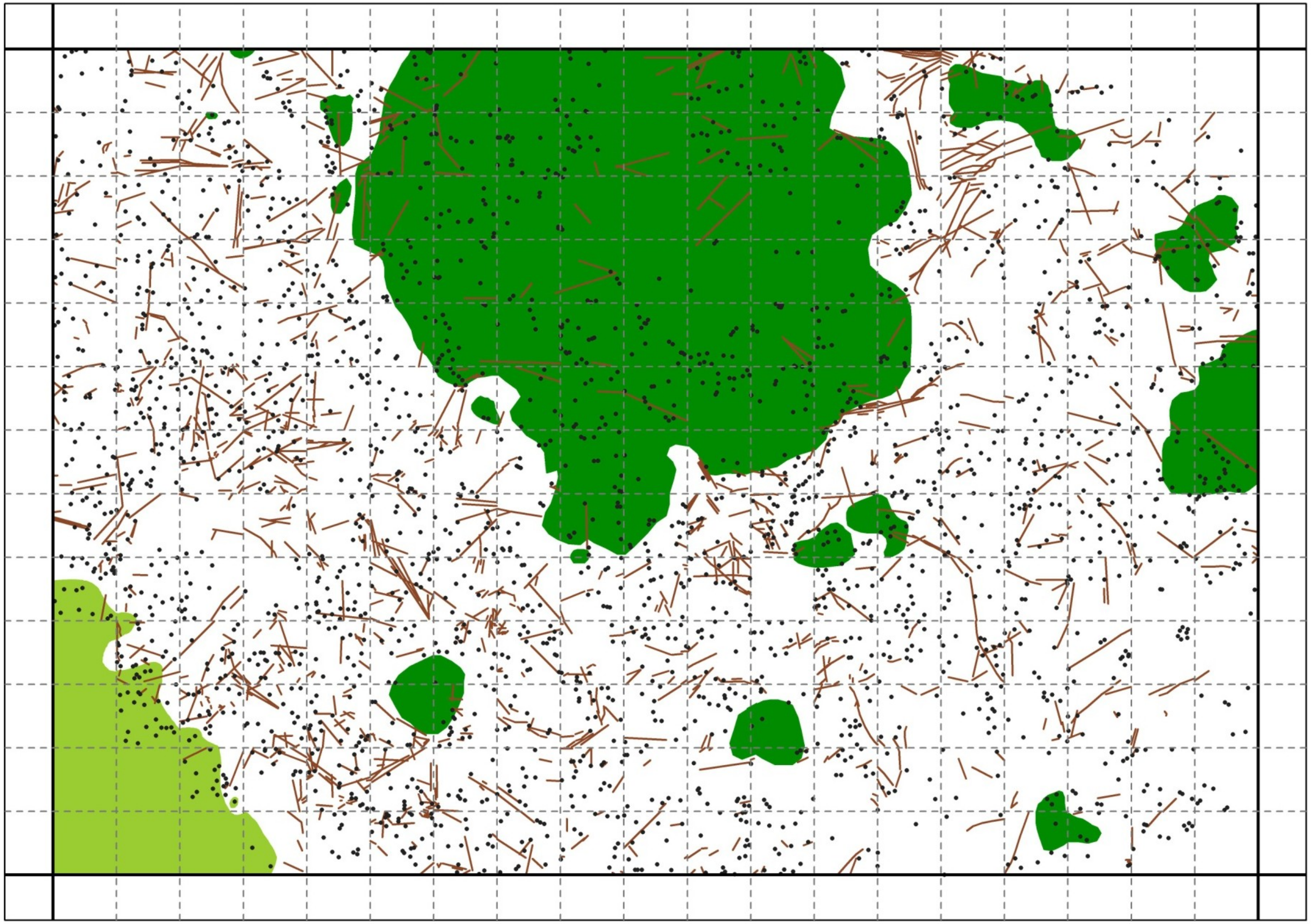


Figure 1.1: Map of the study site at Nash's Copse, Silwood Park showing Rhododendron (dark green), bamboo (light green), trees (●) and logs (brown lines). Dotted lines represent the 10 x 10m quadrates used for trap and pit-tag recording station placement.

The study site was bordered along the lower edge (according to the orientation of the map in Fig 1.1) by a stream, on the other side of which was open woodland with a lower tree density that the study site and dominated by oak (*Q. petraea*) and birch (*B. pubescens*). This area had very little ground cover and no *Rhododendron*. The left-hand edge of the study site bordered more open woodland (approximately 50m x 90m) composed of the same tree and ground cover species as the study site, but without *Rhododendron*. The top edge of the study site bordered a fence and public footpath, with open grassland on the other side of the footpath. The right-hand edge of the site was also adjacent to a fenced public footpath, on the other side of which was a patch of open woodland similar in composition to the study site and approximately half the size of the study site. Within this area there was a large patch of *Rhododendron*.

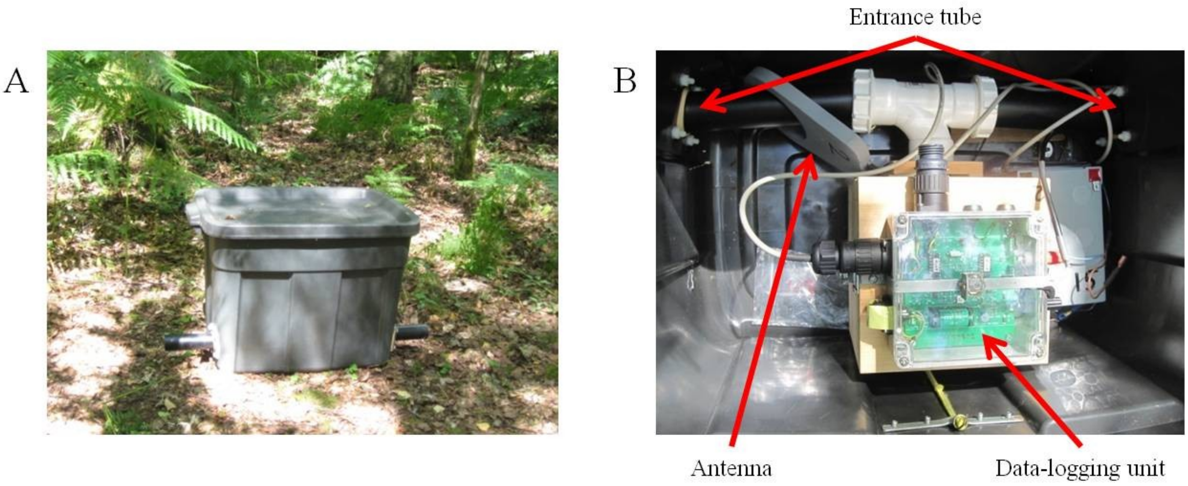
Live trappings conducted in 2010 in each neighbouring area (40 traps per area) around the study site did not result in the capture of *A. sylvaticus* in neighbouring habitat to the bottom, left or top of the study site (Fig. 1.1). Trappings conducted in the habitat to the right of the study site (open woodland and large patch of *Rhododendron*, hereafter referred to as the 'lake site') did result in captures of *A. sylvaticus*, however, and revealed that some individuals were being caught in both the study site and this area. The lake site was trapped a further 5 times between 2010 and 2013, using 40-60 traps arranged in a grid and spaced at 10m intervals during each trapping session. A total of 27 different *A. sylvaticus* were caught during these trappings sessions. Of these, 22 were also caught in the study site. Only five individuals were exclusively trapped outside the study site. Given the high number of individuals within this sample caught at both the study and lake sites, it is likely that the mice at both sites were part of the same local population. Although the boundaries of the study site (and therefore data collection) did not encompass the entire local population of *A. sylvaticus*, the trapping results from the lake site suggested that data collection efforts within the study site encompassed the great majority of the local population, and only a low proportion was excluded. I believe that a sufficient proportion of the population was caught, measured and tracked in order to be representative of the population as a whole. All 27 individuals caught at the lake site were excluded from analyses of home range size (Chapter 2) and home range overlap (Chapter 3).

Previous studies on *A. sylvaticus* in deciduous woodland ecosystems similar to this study site have reported population densities of between 4 and 50 mice per hectare (Watts 1969; Montgomery 1989; Unnsteinsdottir & Hersteinsson 2011). The population density of mice at this study site during the spatial data collection period (March 2010 - March 2013) varied between 12 and 67 mice per hectare, suggesting that the study population attained higher densities than other study systems at times, but was largely in line with the densities of other study populations.

Spatial data collection: using RFID PIT-tags to track individuals

Mice were caught during regular trapping sessions (described in Chapter 2) using Sherman traps. Individual-level data was collected during these trapping sessions, but the spatial data used to estimate each individual's home range was collected by the novel method of using a radio frequency identification (RFID) system with passive-induced transponder (PIT) tags. A PIT tag is a small 12mm long, 2mm wide cylinder that, when scanned by an radio frequency antenna, transmits a unique 10-digit identification number.

When first caught, all mice >15g in weight had a PIT tag inserted under the skin at the scruff of the neck behind the head. Each PIT tag provided a unique identification code for individual mice. Spatial location fixes for each PIT-tagged individual could then be collected using ten mobile recording stations (Fig. 1.2A). Recording stations were constructed from plastic crates (60cm L x 39cm W x 42cm H) with a 45mm diameter tube running through the inside providing two entrances on opposite sides through which a mouse was able to pass freely into the crate. Inside the crate, the tube fed into in a wooden box where wood chippings were placed to help soak up urine, and a single peanut was placed as a minor reward (approximately 11% of the daily energy budget reported by Corp, Gorman & Speakman 1997). An antenna, connected to a recording unit (Francis Scientific Instruments Ltd.) on top of the wooden box, was fastened in place around the tube where it entered the wooden box (Fig. 1.2B). When a PIT-tagged individual entered the wooden box, the unique PIT tag number (mouse identity) and the time was recorded to under a one second resolution by a data-logging unit, powered by a 12 volt battery.



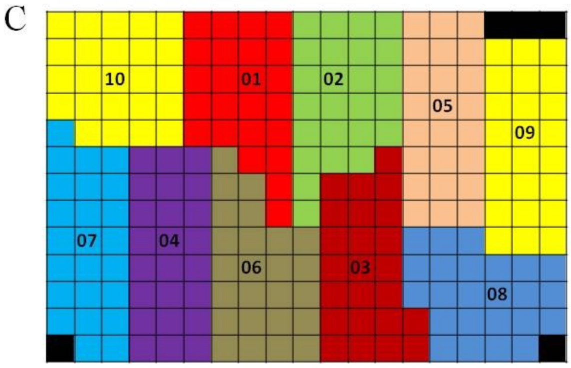


Figure 1.2: A) Exterior view of a recording station showing the entrance tubes extending out of the crate on both sides. B) Bird's-eye view of the inside of the recording station crate: an antenna surrounds the entrance tube and feeds the unique PIT tag identity of a mouse that has entered the recording station to a data-logging unit on top of a wooden box containing wood chippings and a single peanut as a minor reward. C) The study site divided into ten different regions, one per recording station.

In order to adequately sample the full study site, the ten recording stations were moved to new locations daily by hand, where they remained for a 24h period before being moved again (5 times per week). The study site was divided into ten equal-sized 0.24ha regions - one region for each recording station (Fig. 1.2C). Within each region, a recording station was randomly moved between 10 x 10m quadrates (Fig. 1.1) each day, and placed at a random $1m^2$ coordinate within that quadrate. After all quadrates (n = 24/region) within a territory had been sampled, the list of quadrates was re-randomised and the process restarted. A pilot study into the use of the recording stations found that a minimum distance of 30m between different recording stations was sufficient to negate unnatural influences on space use that may have arisen from their presence. The resulting data yielded a spatial location accurate to ±1m, the time of presence in the recording station and the identity of the individual.

Aims and outline of the thesis

This thesis aims to investigate the roles of individual-level (body mass, body fat reserves and testosterone), habitat-level (*Rhododendron* and logs) and population-level (population density, sex ratio and season) factors as drivers of space use in a wild population of *Apodemus sylvaticus*. Seasonal home ranges were estimated for individuals and individual space use quantified as both home range size and the degree of home range overlap with members of the same and opposite sex. Seasons were selected to represent the different space use patterns expected for changes in food availability and reproductive activity. Our understanding about the role of genes on individual space use in wild populations is currently limited to a few species (e.g. Klemme & Hanski 2009; Stopher *et al.* 2012), therefore this thesis attempts to improve our knowledge by establishing the heritability of individual-level drivers of space use in this species, and predicting the inter-generational change in the population mean value of these traits.

The following chapters are presented in the style of journal articles:

Chapter 2: **From physiology to space use: energy reserves and androgenisation explain home range size variation in *Apodemus sylvaticus.***

This chapter examines the relationships between the size of core and periphery home range regions with i) the individual-level factors of body mass, sex, body fat and anogenital distance (as a proxy for *in utero* testosterone exposure), and ii) habitat features that reduce predation risk – *Rhododendron* and logs. This chapter has been peer-reviewed and published in the Journal of Animal Ecology as:

Godsall, B., Coulson, T. & Malo, A.F. (2014) From physiology to space use: energy reserves and androgenization explain home-range size variation in a woodland rodent. *The Journal of Animal Ecology*, **83**, 126–135.

Chapter 3: Habitat interacts with phenotypic traits to determine home range overlap.

Given the relationships between body mass, body fat and testosterone on home range size, this chapter examines their effects, in combination with habitat, population density and sex ratio, on the degree of home range overlap between same-sex and male-female overlapping dyads.

Chapter 4: Drivers of reproductive success, polygamy and the annual cycle of relatedness in the wood mouse.

A pedigree of the population is reconstructed from microsatellite data. The pedigree is used to estimate individual reproductive success, the number of reproductive mates per individual and the relatedness between individuals. An annual cycle in relatedness is revealed and analysed as a function of offspring recruitment and immigration. Individual reproductive success is analysed as a function of individual-level factors (body mass, body fat and the proxy for testosterone, anogenital distance) and both home range size and home range overlap.

Chapter 5: **Selection gradients, heritability and the response to selection of three phenotypic traits in the wood mouse, *Apodemus sylvaticus.***

Selection gradients and heritabilities are estimated for three individual-level factors: body mass, anogenital distance and foot length. Two of these individual-level factors, body mass and anogenital distance, have been shown to relate to individual variation in either home range size or home range overlap. Selection gradients are estimated for each year between 2009 and 2013 and tested for relationships with population density and sex ratio. Finally, selection gradients and heritabilities are used in the multivariate form of the Breeders equation to predict the short term (generational) response to selection.

Chapter 6: **Conclusions.**

A summary of findings is presented and the limitations and conclusions of the study are discussed.

Chapter 2

From physiology to space use: energy reserves and androgenisation explain home range size variation in *Apodemus sylvaticus*

Introduction

How an animal uses space influences individual survival and reproductive success (Gaines & McClenaghan 1980; Fisher & Lara 1999; Getz *et al.* 2005a) which in turn influences gene flow and population dynamics (Gaines & McClenaghan 1980; Booth *et al.* 2009). It is therefore important to understand what causes variation in space use by individuals. Given that few studies have characterised space use to a high level of spatiotemporal resolutions coupled with individual-, population- and environmental-level factors, we still have a relatively poor understanding of the relative contribution of these factors on space use for most species. In this study I use a wild rodent population in southern England to disentangle the relative contributions of habitat structure and individual-level variables on space use. Individuals were identified using RFID passive integrated transponder tags (PIT-tags) and measure individual space use on a study area with finely mapped microhabitat features. High spatiotemporal resolution is achieved by using a novel system of custom-designed mobile PIT-tag-recording units.

The home range concept is frequently adopted to quantify space use (Laver & Kelly 2008). A home range can be defined as the area normally used by an animal while performing essential activities to survive and reproduce (Burt 1943). Many individual–level and environmental factors have been shown to have an effect on home range size across numerous species, including season, resource availability, habitat structure, predation risk, sex, age, body size and population density (Wolton & Flowerdew 1985; Hubbs & Boonstra 1998; Jonsson *et al.* 2002; Dahle & Swenson 2003; Matthiopoulos 2003b; Kjellander *et al.* 2004; Getz *et al.* 2005b; Schradin *et al.* 2010). Two individual-level factors that have not been considered in natural populations in the wild, in terms of their relationship with home range size are body fat, relating to an individual's energy reserves (Koubi *et al.* 1991), and the degree of androgenisation resulting from an individual's exposure to testosterone during gestation (Ryan & Vandenbergh 2002).

Previous studies have not disentangled the relative contributions of body size (or age) and an individual's energy reserves (body fat) to individual variation in home range size. In this study, both body mass (as a measure of size) and a measure of an individual's body fat are included in models to assess their relationship with home range size. During periods of low food availability or high energetic demand, individuals metabolize fat reserves for energy in order to spare protein (Koubi *et al.* 1991). Energy reserves have been linked to survival (Cook *et al.* 2004) and reproductive success (Atkinson & Ramsay 1995), but little research has focused on its role in space use with wild populations.

In mammals it has been shown that anogenital distance (AGD) can be used as a proxy for individual testosterone levels (vom Saal & Bronson 1980; vom Saal & Dhar 1992; Vandenbergh & Huggett 1995; Ryan & Vandenbergh 2002). In litter-bearing mammals, individuals of the same litter can be prenatally exposed to different concentrations of testosterone depending on their position relative to male siblings (vom Saal & Dhar 1992;

Ryan & Vandenbergh 2002). An individual flanked by more males in the uterus is exposed to higher testosterone levels, resulting in a larger AGD (Ryan & Vandenbergh 2002). Subsequently, AGD has been found to correlate with androgen-dependent behaviours in adulthood (Vandenbergh & Huggett 1995; Drickamer 1996). Testosterone has been shown to influence space use behaviour in laboratory studies, with higher levels improving spatial navigation tasks for either sex (Williams, Barnett & Meck 1990; Roof & Havens 1992; Galea *et al.* 1996) and increasing exploratory behaviour and dispersal in the wild (Monclús & Blumstein 2012; Monclús *et al.* 2012). Testosterone also plays a role in aggression towards conspecifics (Drickamer *et al.* 2001) which can influence the outcome of contests therefore access to females and resources (Huang *et al.* 2011; Surbeck *et al.* 2012). However, the role of testosterone in explaining variation in home range size between individuals in the wild has received little attention (Zielinski, vom Saal & Vandenbergh 1992; Kellam, Lucas & Wingfield 2006).

In this study I test how body fat and AGD, along with other individual-level and habitat factors, explain variation in home range size between seasons for individuals in a population of the wood mouse, *Apodemus sylvaticus*. PIT tags implanted in mice were used to gather relocation data using movable recording stations. Home ranges are frequently estimated using utilization distributions derived from kernel density estimates (Worton 1989). This method is considered to be suitable for studies addressing the relationship between different factors and individual variation in the intensity of space use, providing an appropriate data-based bandwidth is selected (Laver & Kelly 2008; Kie *et al.* 2010; Fieberg & Börger 2012; Cumming & Cornélis 2012). In this study I divide each individual's home range is divided into two regions based on the intensity of use within each home range. The 'core' region represents the most frequently used areas of a home range (Samuel, Pierce & Garton 1985; Vander Wal & Rodgers 2012) where territorial behaviour is more likely to be displayed, as these areas are likely to have been selected due to the presence of resources required for an individual to survive and reproduce, such as reliable food sources and the home site (Samuel *et al.* 1985; Börger *et al.* 2006). The ‘periphery’ region in this study is defined as an area less frequently used for additional foraging and mate seeking, but still used enough to be considered part of a home range rather than exploratory behaviour (Burt 1943; Börger *et al.* 2006). The relative effects of individual-level factors and habitat factors relating to predation risk are assessed for their roles in explaining variation in region size observed between individuals.

Apodemus sylvaticus is common rodent that undergoes seasonal population cycles between the breeding and non-breeding seasons (Montgomery & Gurnell 1985; Wolton & Flowerdew 1985; Malo *et al.* 2013). During the breeding season, male and female mice attempt to establish home ranges that maximise their breeding success. Competition is subsequently high between individuals (Wolton & Flowerdew 1985; Tew & Macdonald 1994; Malo *et al.* 2013). Thus, I hypothesised that individual-level factors linked to competitive ability should be more important in explaining core region rather than outer region size variation during breeding periods. For the non-breeding season, when competition is relaxed, I hypothesised that predation risk will be more important than individual-level factors in determining core size variation. For all seasons predation risk is expected to be more important in explaining variation in outer region rather than core region size, as individuals are not expected to display territorial behaviour within this region, but rather additional food and mate-seeking behaviour.

Methods

Study site

The study area was located at Imperial College London's Silwood Park campus near Ascot in Berkshire, United Kingdom (51° 24' 50.3542"N, -0° 38' 43.4816"E). The study site is a mixed deciduous woodland most consistent with the W11 category of the National Vegetation Classification system (Rodwell 1991)(Fig. 1.1). The canopy was dominated by *Betula pubescens*, while *Corylus avellana* and the invasive species *Rhododendron ponticum* dominated the understory and shrub layer. A single patch of invasive bamboo is also present. Ground cover was dominated by bluebells (*Hyacinthoides non-scripta*) during spring and bracken (genus *Pteridium*) during summer and autumn. A 2.43ha plot was divided into a grid containing 243 10m x 10m quadrates. Data was collected between 28th March 2010 and 8th March 2012.

Trapping effort

Trapping sessions were conducted weekly between 28th March and 10th November 2010 and biweekly thereafter. During each trapping session, one Sherman trap (16cm L x 5.8cm W x 6.5cm D) was placed in each selected 10m x 10m quadrate (n=80 to 140 per session) approximately two hours before sunset, and collected the following morning approximately one hour before sunrise. In order to allow individuals to recover their natural behaviour between trapping sessions, quadrates used were alternated between trapping sessions. Each quadrate was trapped twice per month at the start of the study (28th March – 10th November 2010) and just once per month for the remainder of the study (up to 8th March 2012). All caught mice were weighed, sexed, had their anogenital distance (AGD) measured and were scored for body fat (as a measure of energy reserves). Body fat was scored from 0 to 4 by making a physical examination of the back (from the base of the tail to the mid-back between the head and tail) and dorsal pelvic area to feel for subcutaneous fat deposits. These areas were gently rubbed in order to assess how easily individual vertebrae of the spine and the pelvic bone could be identified through subcutaneous fat deposits (see justification and Table A1 in Appendix for qualitative assessment criteria). Since there is a strong correlation between body mass and anogenital distance (Gallavan *et al.* 1999), anogenital distance was normalized by using the ratio of an individual's seasonal mean anogenital distance to the cube root of seasonal mean body mass (Gallavan *et al.* 1999), and used this anogenital distance index (AGDI) in the analyses. Mice >15g were tagged using a 12mm x 2mm RFID PIT tag. Mice were released where they were caught.

Recording stations

Location fixes for each PIT tagged individual were collected using mobile recording stations. Recording stations were constructed from plastic crates (60cm L x 39cm W x 42cm H) with a 45mm diameter tube running through the inside providing two entrances on opposite sides into the crate. Inside the crate, the tube fed into in a wooden box where wood chippings were placed to help soak up urine, and a single peanut was placed as a minor reward (approximately 11% of the daily energy budget reported by Corp, Gorman & Speakman 1997). An antenna, connected to a recording unit (Francis Scientific Instruments Ltd.) on top of the wooden box, was fastened in place around the tube where it entered the wooden box. When a PIT-tagged individual entered the wooden box, the unique PIT tag number (mouse identity) and the time was recorded to under a one second resolution. Two drops of peanut oil were rubbed onto the tube entrances in order to attract in mice that were in the immediate vicinity. Five recording stations were used between 28th March 2010 and 6th June 2010 and ten were used thereafter until 8th March 2012. Within the study site each recording station was allocated to an equal sized and clearly defined 0.24ha area within which they were rotated randomly between 100m^2 quadrates each night, and placed at a random 1m^2 coordinate within that quadrate. Recording stations were moved daily (n=5/week). After all quadrates within a territory had been sampled, the list of quadrates was re-randomised and the process restarted. No two recording stations were ever less than 30m apart. A pilot study into the use of the recording stations found this a sufficient distance to negate unnatural influences on space use. The resulting data yielded a spatial location accurate to ±1m, the time of presence in the recording station and the identity of the individual. Due to the high rate at which location fixes were obtained (3/s) when a mouse was present in a recording station, the resulting data was trimmed to remove excess relocations recorded while a mouse was inside the recording station (for method see Appendix II).

Seasonal variation

Individual home ranges were generated for 3 seasons in each year (early breeding, late breeding and non-breeding) to test for seasonal differences in the determinants of home range size. These seasons were selected as they were believed to represent periods when space use behaviour would differ. The early breeding season (EBS) began when inspection of mice during trapping sessions showed an increase in testes size in over half of caught males weighing >15g, representing the increase in gonodal hormones. During this season invertebrates were the main food supply (Watts 1968; Hansson 1985). The boundary between the early and late breeding season (LBS) was marked by the onset of seed fall from trees (unpublished data), marking the availability of the main food source of the mice (Watts 1968; Hansson 1985; Gurnell 1993; Khammes & Aulagnier 2007). Precise seed fall timings were not available for the first study year (2010) but were assumed to be the same as the second year (2011). This assumption was based on observations from 2012 which showed the onset of seed fall to be less than one week different from 2011. The start of the non-breeding season (NBS) and the end of the late breeding season came when mice inspected during trapping sessions no longer showed signs of breeding condition. In total 6 seasons were used over two years. Exact dates and season lengths are shown in Table 2.1.

Table 2.1: Season dates, length and sampling effort across the study site for each season.

Study year	Year 1			Year 2		
Season	Early breeding	Late breeding	Non-breeding	Early breeding	Late breeding	Non-breeding
Start date	28th Mar 10	21st Jul 10	1st Nov 10	21st Mar 11	21st Jul 11	8th Dec 11
End date	20th Jul 10	31st Oct 10	20th Mar 11	20th Jul 11	7th Dec 11	8th Mar 12
Season length (days)	115	103	141	122	140	92
Data logger effort	558	406	567	987	1008	632
Trapping effort	1643	1041	776	973	1111	844
Unique individuals caught	43	33	30	49	135	126

Note: “Data logger effort” is the sum of the number of nights each data logger was used and in working condition within each season. “Trapping effort” is the total number of traps set within each season. “Unique individuals caught” is the number of different mice caught in each season (i.e. not including recaptures). This is considerably larger during the second study year.

Home range estimation

Home ranges were calculated from utilization distributions generated by kernel density estimation (Worton 1989). Kernel densities were estimated in *R* (version 2.13.1) using the package **ks** (Duong 2007). The direct plug-in method was used for bandwidth selection (Wand & Jones 1995) as it has been shown to outperform other methods (e.g. reference, LSCV; Gitzen, Millspaugh & Kernohan 2006; Cumming & Cornélis 2012).

Several studies have suggested a minimum sample size of 30 relocations per individual in order to reduce bias in kernel density estimation (Seaman *et al.* 1999; Girard *et al.* 2002; Börger *et al.* 2006). Individuals with fewer than 30 relocations in a single season were excluded, with the exception of four individuals in the late breeding season who had between 24 and 29 relocations. These individuals were included in order to increase sample size for this season, and because analysis before and after their inclusion showed no significant difference of the effect of the number of relocations on home range size.

For each mouse in each season, area sizes for two home range regions (HRR) were calculated. The "core" region was delineated using the time-maximizing function proposed by Vander Wal & Rodgers (2012) for each individual in each season (Fig. 2.1). The area between the core isopleth and 95% isopleth was considered as the "periphery" region (Fig. 2.1). In order to counter edge effects that can occur with grid designs, any individual with a higher number of relocations within 20m of the study site boundary versus the interior of the study site was left out of the analysis. An exception was made for the lower site boundary as this was bordered by a fast moving stream, and trappings on the non-study site side did not yield any captures.

Habitat data

All patches of *Rhododendron*, bamboo and all fallen trees (including their diameter) were mapped using ArcGIS v9.3 (ESRI 2008) to 1m accuracy. Home ranges were added to ArcGIS and the areas (m^2) of the three habitat variables contained within each individual's core and periphery HRR for each season were extracted. The map was seasonally updated. The areas for *Rhododendron* and bamboo were combined into the single variable "cover". The proportions of each HRR area occupied cover and fallen trees were calculated to be used in the analysis.

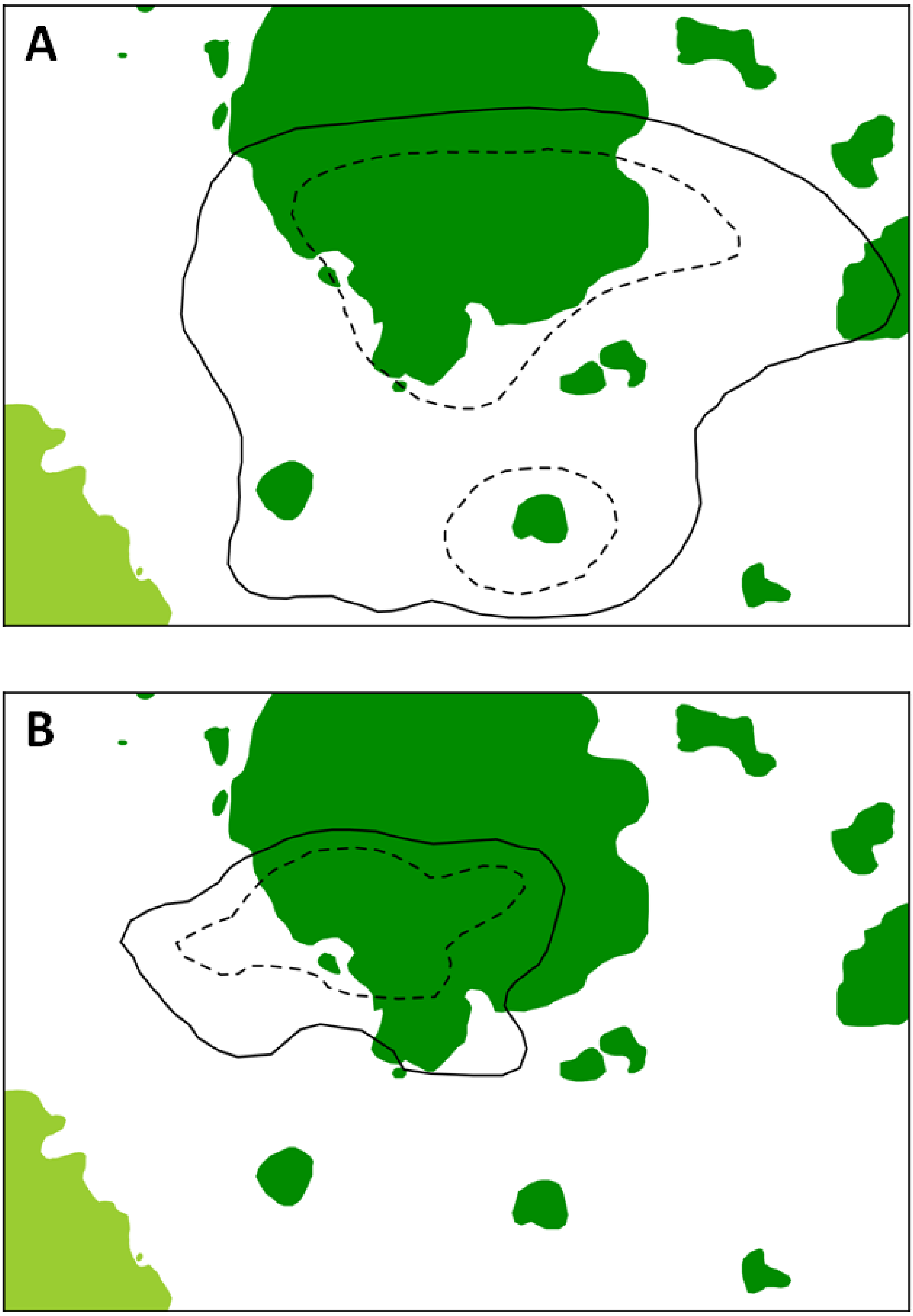


Figure. 2.1: Example of 95% isopleth home range boundaries (solid lines) and core regions (area within dashed lines) delineated by the method given by Vander Wal & Rodgers (2012). The peripheral region is the area of the home range between the 95% isopleth and the core boundary. The examples are overlaid on a map of the study site displaying patches of *Rhododendron* (dark green) and bamboo (light green), and show A) a typical, larger male home range (ID = M118), and B) a smaller, more compact female home range (ID = M222). Both examples are from the late breeding season.

Statistical analysis

All statistical analysis was performed using *R* (v. 2.13.1). Data for both study years were combined for each season. Differences in HRR size between the three seasons were tested for using ANOVA, with HRR size as the response variable (log-transformed where appropriate to better fit a normal distribution) and season as the explanatory variable.

Six generalized linear models were constructed to test how different factors were related to HRR size (2 response variables) in each season (3 seasons). A model was constructed for each HRR in each season, rather than including season as a covariate, in order to test how the relationship of variables with HRR size changed between seasons. In each case the area size of the respective HRR was used as the response variable (log- or square root-transformed where appropriate in order to fit a normal distribution). The following covariates were initially included in all models. Individual-level covariates were sex, mean seasonal body mass and mean seasonal body fat score. Habitat covariates included the proportion of HRRs occupied by fallen trees and cover.

With the PIT tag method of tracking used in this study it is not possible to set up a study design where the acquisition of location data can be standardized between individuals, as is recommended (Fieberg & Börger 2012). The PIT tag method requires an individual to be in the immediate vicinity of a recording station in order to acquire its location data. This means that neither the effort nor the number of relocations are equal between individuals, which could potentially influence the observed individual variation in home range size. Therefore three variables reflecting the variation in sampling effort between each individual were included in models. These were the number of days an individual was known to be alive during each season, the number of relocations per individual per season and the mean recording station effort per 1m^2 within each home range region.

Due to the constraints of sample size for statistical analysis (in terms of the number of home ranges estimated per season) tree analysis (Crawley 2007) was performed on the explanatory variables for each model in order to choose which interactions to test. The following two-way interactions were included in each model: sex x body mass, sex x body fat score, body mass x body fat score and cover x fallen trees. An additional two way interaction between body fat score x year was included for the EBS periphery model, and an interaction between body mass and cover was included in both HRR models for the non-breeding season. Models were simplified using a stepwise approach (Crawley 2007), starting with the interactions. Models before and after a term had been removed were compared with an F test to see if deviance was significantly increased by the removal. The minimum adequate model was selected when only significant factors, or those that caused a significant increase in deviance when removed, remained.

Due to the difference in anogenital distance between males and females, the relationship between anogenital distance and HRR size was tested separately for each sex in each HRR for each season. HRR size was the response variable and AGDI the explanatory variable.

Results

In total, 68 home ranges were calculated from 51 individual mice over 6 seasons (2 x EBS, 2 x LBS, 2 x NBS; Table 2.2). The number of relocations per individual ranged from 24 to 156 (Table 2.2). Both core and periphery regions were smaller in the late breeding season compared to the early breeding season, but although close to being, the differences were not significant (ANOVA: core, $t = -1.98$, $p = 0.0547$; periphery, $t = -2.018$, $p = 0.0504$). HRRs were significantly smaller in the non-breeding season than compared to the early breeding

(ANOVA: core, t = -3.471, p = 0.0012; periphery, t = -5.303, p = <0.0001) but not late breeding seasons (ANOVA: core, t = -1.277, p = 0.208; periphery, t = -1.683, p = 0.0993).

Table 2.2: The number of home ranges estimated for each season and the mean sizes of the three home range regions analysed during those seasons. The number of home ranges for each study year and sex are also provided.

	Early breeding season (n = 21)	Late breeding season (n = 21)	Non-breeding season (n = 26)
n Year 1	12	11	10
n Year 2	9	10	16
n females	9	7	11
n males	12	14	15
Mean core size	2733.34m^2 ± 1769.86	1880.70m^2 ± 1618.70	1481.93m^2 ± 1465.41
Mean periphery size	5643.32m^2 ± 2299.68	4027.61m^2 ± 2859.979	2656.84m^2 ± 2072.41
Mean number of relocations	75 ± 32	57 ± 36	68 ± 38
Mean effort	0.024 ± 0.003	0.023 ± 0.002	0.019 ± 0.003

Note: Mean effort relates to the mean number of recording station nights per 1m^2 within each full home range region for each season. Data for mean home range region sizes, the number of unique relocations and effort are given as the value ± 1 standard deviation.

Individual-level and habitat factors

In the EBS model for core size (log-transformed), a significant negative relationship was found for the interaction term for sex and body fat score (GLM: t = -4.067, p = 0.0012) showing males with less body fat had larger core areas than those with better fat reserves, whereas females showed the opposite relationship but with a shallower slope (Fig. 2.2A). A

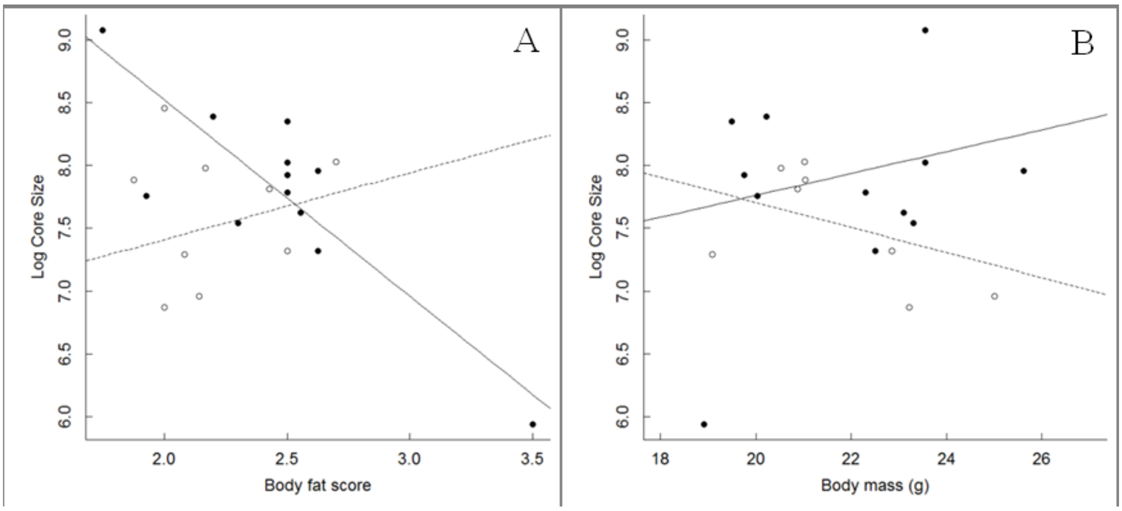


Figure 2.2: Significant interactions and their relationship with log-transformed core region size during the early breeding season. Fitted lines are given for males (dark points, solid line) and females (white points, dashed line). A) The interaction between body fat and sex. Males with greater body fat reserves have smaller core regions but females show the opposite trend with a much shallower slope. Note, the outlier (body fat score = 3.5) was retained, as removing it did not change the analysis results (GLM: $t = -2.979$, $p = 0.0107$). B) The interaction between body mass and core size. Larger females have smaller core areas, but the relationship is positive for males.

significant positive relationship was found for the interaction between sex and body mass (GLM: $t = 2.926$, $p = 0.0111$), showing that male core size increased with mass but female core size decreased (Fig. 2.2B). However, a significant negative relationship between core size and weight as a discrete covariate was also found (GLM: $t = -2.338$, $p = 0.0348$). Core regions containing a greater proportion of cover were significantly smaller (GLM: $t = -2.799$, $p = 0.0142$). The EBS model for periphery size also showed a strong negative relationship between HRR size and body fat score (GLM: $t = -4.777$, $p = 0.0002$), suggesting that in both HRR during the early breeding season fatter individuals had smaller home ranges than those with low fat reserves. Males were found to have significantly larger peripheries than females

(GLM: *t* = 2.123, *p* = 0.0487). A negative relationship with cover was found (GLM: *t* = -4.528, *p* = 0.0003) showing peripheries containing a greater proportion of cover were significantly smaller. For this season individual-level covariates explained a large proportion of deviance for both the core and periphery regions, but were more important in explaining individual variation in core size than periphery size (Table 2.3). Habitat factors explained a greater proportion of deviance for peripheries over cores. No significant relationships were found between HRR sizes and either the number of individual relocations, length of time an individual was known to be alive during the season or recording station effort.

Table 2.3: Proportion of deviance explained by individual-level and predation risk covariates for core and outer home range region size models for each season.

Season	Early breeding		Late breeding		Non-breeding	
HRR	Core	Periphery	Core	Periphery	Core	Periphery
Individual level covariates	50.9%	32.4%	15.1%	16.4%	7.9%	9.3%
Body mass	0.5%	1.7%	8.2%	0.1%	1.8%	0.4%
Body fat index	41.6%	21.4%	3.2%	1.2%	5.1%	8.2%
Sex	8.8%	9.3%	3.7%	15.1%	1.0%	0.7%
Predation risk covariates	18.4%	32.5%	70.4%	27.0%	3.9%	1.9%
Cover	12.5%	29.7%	43.6%	24.3%	1.7%	0.9%
Logs	5.9%	2.8%	26.8%	2.7%	2.2%	1.0%

Note: The proportion of deviance for each covariate was calculated by removing the covariate from the full model of the respective HRR in the relevant season, calculating the difference in residual deviance before and after removal then using this to calculate the proportion of null deviance explained by the covariate.

The LBS model for core size (log-transformed) showed a significant negative relationship between the proportion of cover and HRR size (GLM: $t = -2.328$, $p = 0.318$). The model for periphery size (square root-transformed) showed males to have significantly larger peripheries than females (GLM: $t = 2.944$, $p = 0.0091$). The proportion of cover in the periphery also had a significant negative relationship with size (GLM: $t = -3.520$, $p = 0.0026$). For both models, recording station effort had a negative relationship with size (GLM: core, $t = -3.563$, $p = 0.0022$; periphery, $t = -2.928$, $p = 0.0094$). No significant relationships were found between HRR size and either the number of individual relocations or length of time an individual was known to be alive during the season. In LBS models, individual-level covariates explained a similar proportion of deviance between the core and periphery, although body mass was more important for the core region and sex for the periphery (Table 2.3). Habitat covariates explained considerably more deviance for core size than periphery, but in both cases cover was more important than fallen trees (Table 2.3).

In both the core and periphery models for the NBS, no individual-level, habitat or effort-related covariates were found to be significant. The only significant result was for year, showing that both HRR sizes during this season were significantly smaller in the second year of the study (GLM: core, $t = -5.592$, $p = <0.0001$; periphery, $= -6.981$, $p = <0.0001$). Body fat score explained slightly more deviance in periphery size compared to core size, but all other covariates were approximately equal between the two HRR (Table 2.3).

Anogenital distance

HRR size was analysed separately for males and females in each season as a function of the anogenital distance index (AGDI). AGDI was found to have a significant positive relationship with male HRR size in the late breeding season for both the core (Fig. 2.3A; GLM: $t = 2.721$, $p = 0.0186$) and periphery (Fig. 2.3B; GLM: $t = 2.334$, $p = 0.0378$).

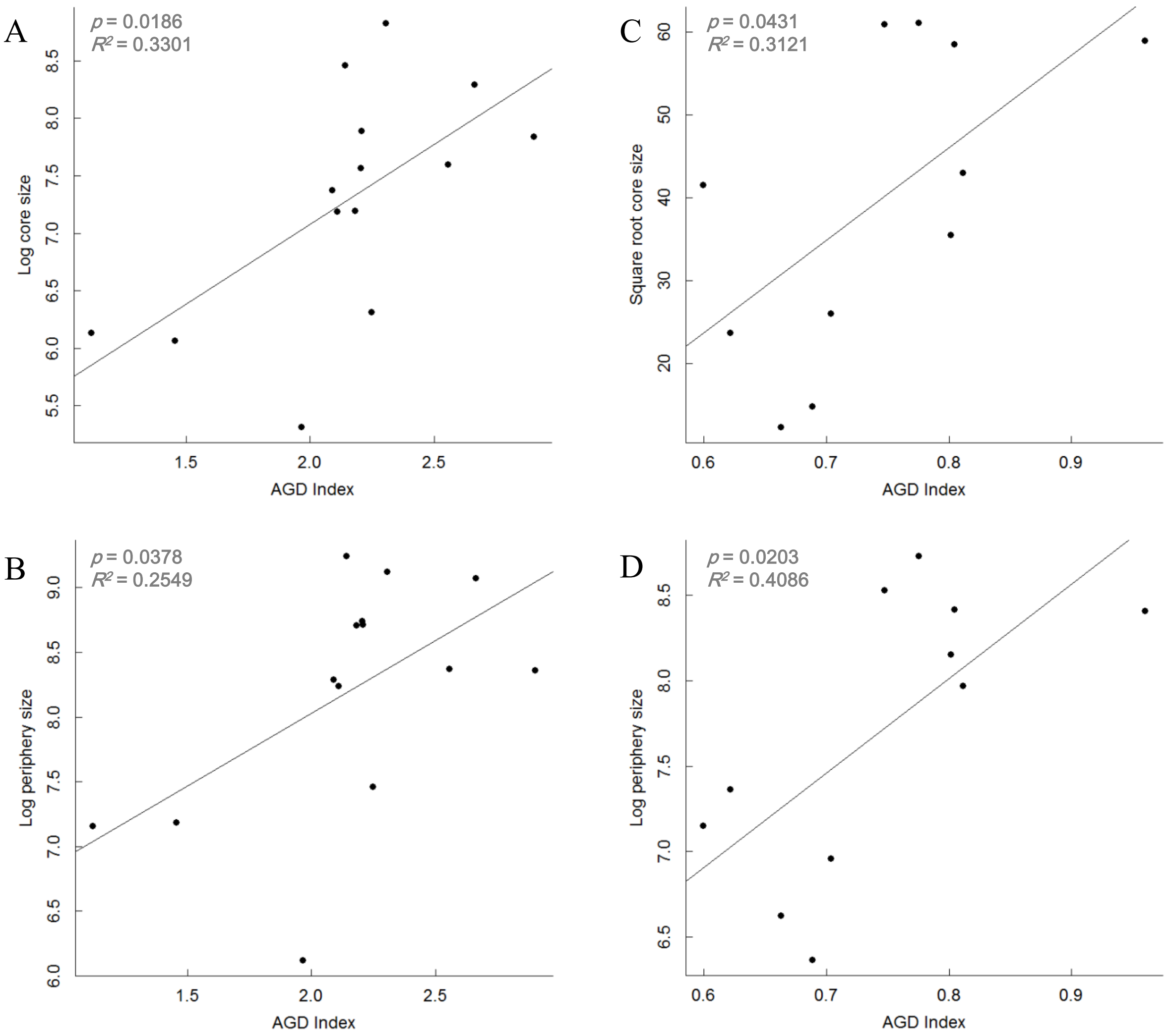


Figure 2.3: Effect of androgenisation on the size of A) male core size in the late breeding season, B) male periphery region size in the late breeding season, C) female core size in the non-breeding season, and D) female periphery size in the non-breeding season. AGD index is the ratio of an individual's anogenital distance to the cube root of their body mass. A higher index score represents a greater degree of androgenisation. Males that had been exposed to higher testosterone *in utero* had significantly larger core and periphery regions in the late breeding season than those exposed to lower levels. Females with a higher AGD index displayed more masculinised home range behaviour, with larger core and periphery regions in the non-breeding season.

A significant positive relationship was also found for females in the non-breeding season for both core (Fig. 2.3C; GLM: $t = 2.353$, $p = 0.0431$) and periphery (Fig. 2.3D; GLM: $t = 2.813$, $p = 0.0203$). No significant results were obtained for either sex in the early breeding season, females in the late breeding season or males in the non-breeding season.

Discussion

This study tested how individual-level factors and predation risk explained variation in size between core and periphery home range regions over three seasons. The results suggest that different factors are important for each HRR size at different stages of the population cycle. Individual-level factors, particularly energy reserves, are important during the transition between non-breeding and breeding seasons. Habitat factors reducing predation risk are important throughout the breeding period, having a strong relationship with peripheral region size in the early breeding season and becoming more influential on core size later in the breeding period. I have also shown how the increased androgenisation of an individual, here measured as anogenital distance scaled by body mass (Gallavan *et al.* 1999), results in larger home ranges for males in the late breeding season and for females in the non-breeding season.

The observed negative relationship between energy reserves (body fat) and both core and periphery size during the early breeding season is likely to be caused by the need for individuals to replenish their energy reserves after low food availability during winter. Koubi *et al.* (1991) demonstrated in a laboratory study that fasted rats became more active as their fat reserves decreased during the protein sparing phase of starvation, followed by a rapid increase in activity as the rats' metabolism shifted from utilizing lipids to protein. This metabolic shift, and the concomitant change in activity, was delayed in rats with greater fat reserves. It could therefore be the case that as food resources become available after a period of low availability, in this case the increase in invertebrate food sources at the beginning of spring (Hansson 1985; Rogers & Gorman 1995), individuals in the wild that have been unable to maintain energy reserves are forced to increase their foraging effort in order to regain critical energy stores. Those that have been able to maintain greater fat reserves, perhaps through more successful cache-hoarding of seeds before winter, may not need to range as far in order to meet their energetic needs. Furthermore, Gurnell (1972) found dominant wood mice become subordinate following food-deprivation. This suggests low energy reserves reduce an individual's competitive abilities (Briffa & Sneddon 2007). This could reduce access to prime food resources through competition and force individuals with low body fat to range further (and perhaps utilize areas of higher predation risk) in order to acquire sufficient resources to avoid death.

The difference in the relationship between the sexes for body mass with core size reflects the different reproductive strategies employed by males and females. The results showed a positive relationship between core size and body mass for males in the early breeding season, but a negative relationship for females. Wood mice display a polygamous mating system (Clarke 1985; Montgomery & Gurnell 1985; Booth, Montgomery & Prodöhl 2007), and during the early breeding season individuals spread out and establish home ranges that attempt to maximise their reproductive success (Montgomery & Gurnell 1985; Wolton & Flowerdew 1985; Tew & Macdonald 1994). For males reproductive success is increased by overlapping with many female home ranges and excluding other males (Wolton & Flowerdew 1985; Fisher & Lara 1999). Since size has been linked to competitive ability (Briffa & Sneddon 2007), larger males should occupy larger territories encompassing more females. A previous study on this population has shown that larger males force smaller individuals out of *Rhododendron* areas early in the breeding season (Malo *et al.* 2013) where female density is higher. Females, on the other hand, seek to control small, good quality territories which are easier to defend from potential infanticide and invading female conspecifics (Wolton & Flowerdew 1985; Maestripieri 1992; Palanza & Parmigiani 1994; Wolff & Peterson 1998; Wolff 2003). This strategy increases the probability of survival for their offspring and themselves, thereby increasing their reproductive success (Wolff & Peterson 1998; Bond & Wolff 1999; Ecuyer-dab & Robert 2004). The results have shown that not only do larger females control smaller core regions in the early breeding season, but also that females have smaller peripheral regions than males, suggesting activity was more restricted to their core regions.

Anogenital distance (AGD) has been linked with exposure to testosterone *in utero* (Ryan & Vandenbergh 2002), and increased exposure during early development has been shown to correlate with androgen-dependent behaviours later in life (Vandenbergh & Huggett 1995; Drickamer 1996). Individuals with increased testosterone levels have been shown to increase exploratory behaviour and improve spatial navigation abilities in laboratory studies (Williams *et al.* 1990; Roof & Havens 1992; Galea *et al.* 1996). Zielinski *et al.* (1992) compared home range sizes of female house mice (*Mus musculus*), finding those that had been flanked by two males *in utero* had significantly larger home ranges than individuals that were not flanked by any males. This study has shown more androgenised males and females will range further during the late and non-breeding seasons respectively. These results appear to complement those from Zielinski *et al.* (1992).

It should be noted that no research has been conducted into the direction of blood flow in the uterus in *Apodemus*, which is important for how much testosterone an individual is exposed to. However, testosterone is also able to diffuse across the amniotic fluid and foetal membranes of neighbouring foetuses, resulting in the same effect of position relative to male offspring on exposure to testosterone as with uterine blood flow (vom Saal & Dhar

1992). Furthermore, the relationship between prenatal exposure to testosterone and AGD has been found in other rodent species besides *Mus* (Cantoni, Glaizot & Brown 1999). Given these facts, I believe that it is safe to draw conclusions concerning the relationship between behaviour and AGD in this species.

The lack of effect of androgenisation during the early breeding season could be due to the reproductive state of the females. Male wood mice enter reproductive condition earlier than females (Clarke 1985; Wolton & Flowerdew 1985; pers. obs). Increases in male testosterone levels as females increase in reproductive receptiveness have been documented in several primate species (Muller & Wrangham 2004; Girard-Buttoz *et al.* 2009; Arlet *et al.* 2011). The relationship between testosterone and male ranging behaviour may therefore only be important during periods when females are more receptive to copulation during oestrus later in the breeding season.

Predation risk is a major driver of space use in prey species (Diaz *et al.* 2005; Getz *et al.* 2005b). Predation risk can be minimized by utilizing habitat patches providing dense cover, as well as microhabitat features such as fallen trees which act as physical or visual barriers to predators (Bowers & Dooley 1993; Greenberg 2002; Buesching *et al.* 2008). In this study predation risk was measured using the proportion of a home range region covered by fallen trees, *Rhododendron* and bamboo. Core and periphery HRRs containing a higher proportion of cover were found to be smaller during both the early and late breeding seasons. This could be explained by two reasons. Firstly, higher densities of individuals were found in habitat patches providing cover at this study site (Malo *et al.* 2013). During the breeding period females select patches high in *Rhododendron* or bamboo cover to establish breeding territories which reduce predation risk, maximising their reproductive success (Wolff & Peterson 1998; Bond & Wolff 1999; Ecuyer-dab & Robert 2004). Dominant males able to overlap with these females therefore maximise their own reproductive success within a smaller area (compared to individuals forced out of areas high in cover). Since population density has been shown to negatively affect home range size in a variety of species (Dahle & Swenson 2003; Wolff 2003; Kjellander *et al.* 2004; Getz *et al.* 2005b), and the density of individuals is higher within patches of *Rhododendron* (Malo *et al.* 2013), it could be the case that the negative effect of cover seen here is an effect of population density. Secondly, it has been observed at this study site that seeds, particularly the more nutritious species, are more frequently cached within patches of high *Rhododendron* cover than in areas devoid of *Rhododendron* (Malo *et al.* 2013). Due to the food stores within the *Rhododendron* an individual may be able to meet its energetic demands in a smaller area with fewer potential costs (Wolton & Flowerdew 1985; Tew & Macdonald 1994; Hubbs & Boonstra 1998; Jonsson *et al.* 2002; Dahle & Swenson 2003; Schradin *et al.* 2010). The direct and indirect effects of predation risk, population density and food abundance on the emergent home range patterns could be more easily teased apart from the data with the use of path analysis (e.g. Indermaur *et al.* 2009).

With the exception of female AGD, no significant relationships were observed in the non-breeding season for individual-level or habitat factors for either core or periphery size. This is likely to be due to a relaxation of territoriality as competition was reduced with the end of breeding (Montgomery & Gurnell 1985; Wolton & Flowerdew 1985; Malo *et al.* 2013), but such a conclusion cannot be made with certainty from the home range data presented in this study, as this data simply provides a snapshot of an emergent spatial pattern, and not the underlying behaviours that lead to it. No significant relationship was found between HRR size and the proportion of fallen trees in any season. Although microhabitat features such as these have been shown to relate to the movements of small mammals (Greenberg 2002), it is likely that their effect is relevant at smaller spatial and temporal scales than the home range. Analysis of the individual variation in behaviour underlying the emergent space use patterns of individual home ranges may be required in order to better understand the role of microhabitat features and the spatiotemporal scale at which they are ecologically relevant.

Chapter 3

Habitat interacts with phenotypic traits to determine home range overlap

Introduction

As resources are often limited, an individual's pursuit of food, shelter and breeding opportunities is likely to involve competition with conspecifics (Tilman 1994; Ryabov & Blasius 2014). Some species establish a home range that encompasses all the resources an individual needs to survive and reproduce (Burt 1943), but which may also overlap with other individuals (Ostfeld 1990). The home range overlap concept provides insights into and allows adequate quantification of the interactions between individuals, which cannot be achieved through the analysis of home ranges as discrete units. The spatial interaction of individuals is of interest in order to understand the evolutionary and ecological processes which shape and organise animal populations over time, including reproductive success (Haenel, Smith & John-Alder 2003; Say & Pontier 2004), selection (Clutton-Brock 1989; Andersson & Iwasa 1996), competition (Berger & Gese 2007), disease spread (Nunn, Thrall & Kappeler 2014) and the interaction between wildlife and humans (Boydston *et al.* 2003; Coleman *et al.* 2013).

In some cases a resident may actively defend some or all of their home range, regions referred to as 'territories', in order to protect mating opportunities, food resources, nesting sites or offspring from competitors (Maher & Lott 1995, 2000). Intraspecific variation in territoriality is not uncommon (Lott 1991; Nemtzov 1997), and has been linked with several ecological factors including resource distribution (Ostfeld 1985, 1990), population density (Vander Wal, Yip & McLoughlin 2012; Vander Wal, Laforge & McLoughlin 2014), habitat variation (Mcloughlin, Ferguson & Messier 2000; Singh *et al.* 2010) and season (Ostfeld 1990). However, our understanding of how phenotypic traits and ecological factors interact to cause individual variation in space-sharing behaviour is still lacking.

The competitive or defensive ability of an individual is often determined by particular phenotypic traits. Common examples include the size of weaponry (Sneddon *et al.* 1997), body size (Reaney, Drayton & Jennions 2010) or behavioural traits like aggressiveness (Svensson, Lehtonen & Wong 2012). Typically, the difference in these traits between two individuals reflects differences in competitive ability; the individual with the higher trait value presenting higher competitive success (Taylor & Elwood 2003). In territorial species, competitively superior individuals can exclude inferior competitors from a territory or home range (Miller *et al.* 2013). As a result, any phenotypic trait influencing competitive success would be predicted to have a negative relationship with home range overlap. Furthermore, within a population, variation in the phenotypic trait of interest would lead to population-wide changes in home range overlap behaviour.

Age, body size and body mass are positively correlated with competitive success for several species (Jacob *et al.* 2009; Arnott & Elwood 2009; Miller *et al.* 2010; Malo *et al.* 2013). Less attention has been paid to the roles of body fat and testosterone. Body fat reserves are metabolized instead of protein during periods of high energetic demand (Koubi *et al.* 1991). In mammals, fat or energy reserves have been linked to survival (in elk, *Cervus elaphus* (L.), Cook *et al.* 2004), reproductive success (general review of mammals, Gittleman & Thompson 1988) and home range size (wood mouse, *Apodemus sylvaticus* (L.), Godsall *et al.* 2014), but there is also some evidence of a relationship with competitive success in nonmammalian species (damselflies, *Calopteryx maculata* (B.), Marden & Rollins 1994; hermit crabs, *Pagurus bernhardus* (L.), Briffa & Elwood 2005). However, the relative contributions of body mass and body fat on home range overlap have yet to be disentangled.

Testosterone has been linked with aggression in mammals (Albert *et al.* 1986; Trainor & Marler 2001; Muller & Wrangham 2004; Malo *et al.* 2009; Preston *et al.* 2012). The level of aggression an individual displays can influence its competitive ability (Duckworth 2006; Arnott & Elwood 2009). Furthermore, testosterone has been correlated with space use in laboratory studies (Williams *et al.* 1990; Roof & Havens 1992; Galea *et al.* 1995), as well as home range size (Zielinski *et al.* 1992; Kellam *et al.* 2006; Godsall *et al.* 2014), exploratory behaviour and dispersal (Monclús & Blumstein 2012; Monclús *et al.* 2012), mate-seeking behaviour (Preston *et al.* 2012) and reproductive success (Miller *et al.* 2010; Malo *et al.* 2010) in wild populations. In mammals, anogenital distance (AGD) can be used as a proxy for *in utero* testosterone exposure (vom Saal & Bronson 1980; vom Saal & Dhar 1992; Vandenbergh & Huggett 1995; Cantoni *et al.* 1999; Ryan & Vandenbergh 2002), which has been found to correlate with androgen-dependent behaviours in adulthood (vom Saal & Bronson 1980; Vandenbergh & Huggett 1995; Drickamer 1996; Drickamer *et al.* 2001; Godsall *et al.* 2014).

In this study, I test how ecological and individual-level factors interact to affect home range overlap. For this I used a wild rodent population of wood mice, *Apodemus sylvaticus* (L.), using a population tracked over three years using RFID PIT-tags and mobile recording stations (Godsall *et al.* 2014). *A. sylvaticus* are a polygamous species (Booth *et al.* 2007; Bryja *et al.* 2008), and undergo seasonal changes in their social and space use behaviour in relation to their breeding condition (Wolton & Flowerdew 1985; Corp *et al.* 1997; Malo *et al.* 2013; Godsall *et al.* 2014). As predicted for polygamous species (Ostfeld 1985; Ims 1987b; Ecuyer-dab & Robert 2004), at the onset of the breeding season in early spring, as mice enter reproductive condition, females compete for high-quality (low predation-risk) habitat in which to establish small home ranges (Malo *et al.* 2013; Godsall *et al.* 2014). Males expand the size of their home ranges (in comparison to their smaller home ranges during the non-breeding season) in search of oestrus females (Wolton & Flowerdew 1985; Godsall *et al.* 2014). Aggression between individuals also increases with the onset of breeding condition (Gurnell 1978). High mortality risk for rodents comes from aerial predators (Southern & Lowe 1982). Our study site contains patches of *Rhododendron* that provide a physical and visual barrier to aerial predators. Both, mouse density and territoriality are higher in patches containing *Rhododendron* than in the open woodland (Malo *et al.* 2013).

I consider three individual-level phenotypic traits: body mass, body fat and testosterone, and three ecological factors known to drive population fluctuations: season, habitat and population density. Our first aim was to test the relationships between these factors and the degree of home range overlap between pairs of adult mice (dyads) in order to harness the complexity surrounding home range overlap and improve our understanding of how individuals within a population interact. I test the interaction between habitat and individual-level factors by dividing the analyses of individual-level factors between spatially explicit habitat types (high quality *Rhododendron* and low quality open woodland).

The second aim is to use the relationships between home range overlap, ecological and individual-level factors to determine how males compete for access to females. Although research has shown that this species is polygamous, it is not clear from the literature whether males compete for access to oestrus females by actively excluding competing males from their home ranges (female-defence hypothesis, Emlen & Oring 1977) or by scramble competition (Trivers 1972). If males compete for access to oestrus females through female-defence, then they would display territorial behaviour (Emlen & Oring 1977), resulting in males excluding other competing males from their home ranges. The emergent spatial patterns of a female-defence mating strategy would therefore be expected to have very low levels of home range overlap between males relative to home range overlap between males and females. Furthermore, male home ranges would overlap significantly less during breeding periods, when competition between males for access to females peaks and therefore territoriality is greatest, compared to non-breeding periods. Alternatively, if males compete for females through scramble competition then they would not actively exclude other males from their home ranges and a high degree of overlap between males relative to male-female overlap would be expected. Due to a lack of territoriality in breeding periods if males compete by scramble competition, there should be little difference in the degree of male-male home range overlap between breeding and non-breeding periods.

Given the effects of *Rhododendron* on mouse density, I evaluate whether there is a difference in male mating strategies between high-quality, low predation-risk *Rhododendron* patches and low-quality, high-predation-risk open woodland. Theory predicts that when females are spatially clustered they are easier to defend, and therefore the female-defence strategy should be favoured by males to enhance their reproductive success (Emlen & Oring 1977). Thus I predict that in *Rhododendron* habitat, males will compete for access to oestrus females through female-defence. In open woodland, however, where females are more scattered, I predict males will compete by scramble competition.

Methods

Data collection

Data were collected between 28th March 2010 and 12th March 2013 (Table 3.1). I provide a summary of data collection methods here. Full details of trapping effort, individual-level data collection and spatial data collection are provided in Chapter 2. Trapping sessions were conducted weekly between 28th March and 10th November 2010 and biweekly thereafter. All captured mice were sexed, weighed, measured for anogenital distance (AGD) and scored for body fat. Mice >15g were tagged using a 12mm x 2mm RFID PIT tag. Mice were released where they were caught as soon as individual data collection concluded. Use of animals and all procedures were in accordance with Imperial College London ethical committee and Home Office UK guidelines.

Table 3.1: Summary data for seasons, including data collection effort, population density, estimated home range size and the number of individuals used in home range overlap analysis. Population density was calculated as the number of unique mouse identities within each season. Individuals usable for analysis were those with > 30 relocations within a season.

Season	Breeding			Non-breeding		
Study year	Year 1	Year 2	Year 3	Year 1	Year 2	Year 3
Start date	23rd Mar 10	21st Mar 11	9th Mar 12	1st Nov 10	8th Dec 11	6th Nov 12
End date	31st Oct 10	7th Dec 11	5th Nov 12	20th Mar 11	8th Mar 12	12th Mar 13
Season length (days)	218	262	242	141	92	128
Recording station effort	964	1995	1550	567	632	490
Trapping effort	2684	2084	2402	776	844	977
Population density	60	164	158	30	132	34
Mean home range size ± S.D. (m^2)	8733.8 ± 3036.3	7402.5 ± 3217.8	5251.5 ± 2329.2	8384.6 ± 2474.0	4240.8± 731.9	11249.8 ± 3595.8
Mean relocations per individual ± S.D.	108 ± 68	89 ± 53	113 ± 72	107 ± 42	55 ± 18	123 ± 33
Individuals usable for analysis	16	20	51	10	18	7

Location fixes for each PIT tagged individual were recorded using mobile recording stations that mice can enter and leave without restrictions. Recording stations were moved to new randomly assigned grid squares (and 1m^2 positions within) each day (n=5/week). The resulting data yielded the identity of the individual, a spatial location (±1m resolution), and a time tag (1sec resolution).

Each year is divided into two seasons (Table 3.1), breeding (BS) and non-breeding (NBS). The start of the breeding season in each year occurred when >50% of all trapped male mice of reproductive age (>16g at capture) were in breeding condition, i.e. their testes had descended, marking an increase in gonodal hormone levels within males. The breeding season ended and the non-breeding season begun each year when no females inspected during trapping sessions showed signs of reproductive activity (perforate vaginas or pregnant).

For analysis, the seasonal mean of body mass (excluding weights when females were pregnant), body fat score and anogenital distance were calculated. Captured females were only found to be pregnant after they had reached a weight of 16g. Therefore for further analysis, and in order to remove any possible effects of non-competing or related juveniles, only individuals (males and females) with a mean seasonal body mass of 16g or more were used.

Home range and overlap estimation

Home range size and overlap were calculated using the **adehabitatHR** package (Calenge 2006) in the software *R* v3.1.1 (R Core Team, 2014). Home ranges for each mouse in each season over three years were estimated by kernel density estimation (Worton 1989). The direct plug-in method was used for bandwidth selection (Wand & Jones 1995) based on its performance in comparative studies (Gitzen *et al.* 2006; Cumming & Cornélis 2012).

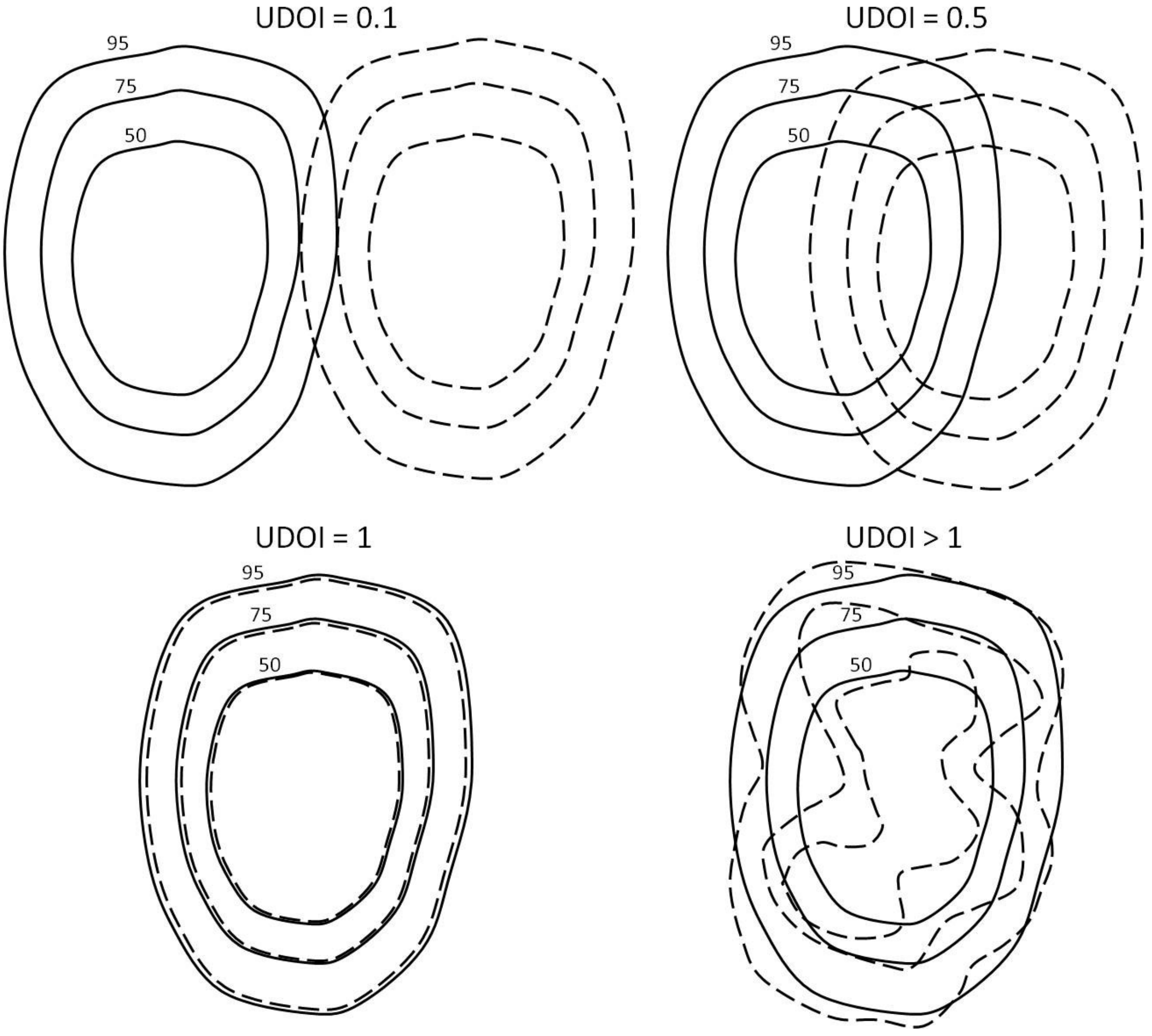


Fig. 3.1: Example of utilization distribution overlap index (UDOI) illustrated using two simplified home ranges (solid vs. dashed lines) with 95%, 75% and 50% isopleths of the utilization distribution. The UDOI score is very low when home ranges barely overlap (only outer isopleths overlap). The UDOI score increases as areas of more intense use within each home range overlap (e.g. 50% isopleths partially overlap). If home ranges overlap completely and their utilization distributions are closely aligned, the UDOI score will be close to 1. If the two home ranges have a high degree of overlap, but the utilization distributions are irregular, the UDOI score will be > 1 (Fieberg & Kochanny 2005).

Individuals with fewer than 30 relocations were excluded in order to reduce bias in home range estimation from low sample sizes (Seaman *et al.* 1999; Girard *et al.* 2002). Individuals with a higher number of relocations within 20m of the study site boundaries versus the interior of the study site were also excluded from further analysis in order to remove potential edge effects. Home range overlap for all overlapping pairs of individuals (dyads) within each season in each study year were calculated using the utilization distribution overlap index (UDOI; Fig. 3.1) (Fieberg & Kochanny 2005), using the 95% isopleth as the outer home range boundary. I elected to use UDOI as our measure of home range overlap as it has outperformed other methods in simulation studies (Fieberg & Kochanny 2005). Competition, territoriality and space-sharing do not involve independent individuals but an interaction between individuals. By analysing home range overlap in terms of dyads, rather than independent individuals, it is possible to account for the effect of both overlapping individuals' phenotypic traits on the degree of overlap.

The significance of fixed explanatory variables in models were inferred from 95% confidence intervals (CI) derived using Bayesian Markov chain Monte Carlo methods (1000 simulations) (Bolker *et al.* 2009). A fixed effect was considered significant if 95% CI did not span zero. Random effects were always retained in models due to the repeated measures of overlap for each individual used.

Statistical analysis

All statistical analyses were performed using the software *R* v3.1.1 (R Core Team, 2014) and the package **lme4** v1.1 (Bates *et al.* 2014) for constructing linear mixed-effect models (LMM). For each model described below, the degree of home range overlap between two individuals (a dyad), the utilization distribution overlap index (UDOI), was used as the response variable and was log-transformed to meet the assumption of normality. 1097 overlap dyads were categorised based on the sex-composition of dyads (hereafter 'dyad type') into male-male (MM), female-female (FF) and male-female (MF) dyads. Population density for each season in each year was taken as the total number of different *A. sylvaticus* caught during that season. The proportion of each individual's seasonal home range covered by *Rhododendron* (ranging from 0-1), was calculated from a digital map of the study site (Chapter 1, Fig 1.1) using ArcGIS v9.3 (ESRI 2008). This is used as a proxy for habitat quality (Malo *et al.* 2013). For analysis, the mean *Rhododendron* cover of both overlapping individuals was used (hereafter 'dyad cover'). Higher values of dyad cover indicated both individuals occupied high quality, low predation-risk patches of *Rhododendron*, while those with lower values occupied low quality, high predation-risk open woodland.

The significance of fixed explanatory variables in models were inferred from 95% confidence intervals (CI) derived using Bayesian Markov chain Monte Carlo methods (1000 simulations) (Bolker *et al.* 2009). A fixed effect was considered significant if 95% CI did not span zero. Random effects were always retained in models due to the repeated measures of overlap for each individual used.

Home range overlap and season, dyad type and habitat

To test for the effects of season and population density on home range overlap, the data were subdivided by dyad type, and a LMM constructed separately for FF (n = 127), MM (n = 458) and MF (n = 512). For each dyad type, log-transformed UDOI was the response variable, with season (BS/NBS) and population density as explanatory variables. Dyad cover was included as a control variable, and study year and the identity of both individuals in a dyad were included as random factors.

To test for differences in home range overlap between dyad types within each season, the full data were subdivided by season. A LMM was constructed for both breeding (n = 997) and non-breeding (n = 100) seasons with dyad type (FF, MM and MF) as the explanatory variable. Population density and dyad cover were also included as control variables. Study year and the identity of both mice in each dyad were included as separate random effects.

Given the effect of *Rhododendron* on mouse density and territoriality (Malo *et al.* 2013), differences in overlap between dyad types were reanalysed using LMMs, but separately for high and low quality habitat. Analysis was restricted to the breeding season only due to a lack of data for the non-breeding season. Data were subdivided into dyads with home ranges in high quality, low predation-risk (patches of *Rhododendron*, dyad cover > 0.5) and low quality, high predation-risk (open woodland, dyad cover < 0.5) habitat. These models included dyad type as the explanatory variable and population density as a control variable. Year and the separate identities of dyad mice were included as random effects.

Finally, to test whether home range overlap within each dyad type was significantly different between high and low quality habitat, data for the breeding season only were subdivided by dyad type. For each dyad type a LMM was constructed with log-transformed UDOI as the response variable, dyad cover as an explanatory variable and population density as a control variable. Year and both mouse identities were included as separate random effects.

Intrasexual home range overlap and individual-level factors

Here I test the relationships between individual-level factors and home range overlap for dyads of the same sex (MM, FF). Due to data limitations, analysis was restricted to the breeding season only. Three individual-level factors (ILF) relating to competitive ability were tested: body mass, body fat and testosterone, by proxy of anogenital distance (AGD). Due to a strong correlation between body mass and anogenital distance (Gallavan *et al.* 1999), AGD was normalised before analysis by using the ratio of an individual's anogenital distance to the cube root of body mass (AGDI) (Gallavan *et al.* 1999; Godsall *et al.* 2014). To account for differences in competitive ability for each ILF, the difference between seasonal mean ILF measurements for overlapping individuals were used in analysis (hereafter collectively termed "ΔILF", or individually as "ΔBM" for body mass, "ΔBF" for body fat and "ΔAGDI" for AGDI).

For both MM and FF dyads, data were subdivided by dyad cover to test for differences between high quality, low predation-risk habitat (dyads occupying *Rhododendron*: dyad cover > 0.5) and low quality, high predation-risk habitat (dyads occupying open woodland: dyad cover < 0.5). For both habitat types within both dyad types (FF high-risk: $n = 90$; FF low-risk: $n = 28$; MM high-risk: $n = 295$; MM low-risk: $n = 118$), a LMM was constructed with log-transformed UDOI as the response variable and ΔBM, ΔBF and ΔAGDI as explanatory variables. Four control variables were also included. Population density was included to control for variation in mouse density at the study site between years. A proxy for age - the mean weight of each dyad - was included to control for differences in overlap between smaller (subadult) and larger (adult) dyads, which is not controlled for by ΔBM. The mean home range size of both dyad individuals and the difference in home range size between individuals in each dyad were checked for correlation and both included in models to control for individual variation in space use. The identity of both mice in dyads and study year were included as independent random factors.

Models were constructed using every combination of the four control variables, but always retaining the individual-level factors and random effects. The model with the lowest Deviance Information Criteria (DIC) was selected for inferring the significance of individual-level factors using confidence intervals (Bolker *et al.* 2009). In every case the selected model included all four control variables.

Intersexual home range overlap and individual-level factors

Analysis focused on male-female overlap dyads and was again restricted to the breeding season with data subdivided by dyad cover as above. For both high predation-risk ($n = 339$) and low predation-risk ($n = 127$) a LMM was constructed using log-transformed UDOI as the response variable. Male BM, BF, AGDI and female BM, BF and AGDI were all included as discrete explanatory variables. Population density and the home range size of both males and females were included as control variables. Study year and both male and female identities were included as random factors. As above, models were constructed with all combinations of control variables and the model with the lowest DIC selected to infer the significance of individual-level factors. For both models all control variables were included.

Caveat for statistical analyses

The data for the degree of home range overlap between individuals initially took the form of a matrix of UDOI values for each season, with the dimensions equal to the number of individual home ranges estimated for each season. The analysis described above used a vectorised form of the overlap matrices, and this likely resulted in the use of non-independent data for constructing LMMs. This would inflate the degrees of freedom in each analysis and potentially lead to weak patterns in the data being interpreted as significant. Future researchers using similar data should consider the use of other statistical methods, such as Mantel tests (Mantel 1967; Legendre & Fortin 1989).

Results

Home range overlap and season, dyad type and habitat

Males overlapped with each other significantly less during the non-breeding season than during the breeding season, when competition for mates was highest (LMM: 95%CI = -2.378, -0.245). Neither the overlap between females nor male-female overlap differed significantly between breeding and non-breeding seasons. Across both seasons a negative relationship was found between population density and the extent of home range overlap, both within and between sexes. High population density significantly reduced FF home range overlap (LMM: 95%CI = -0.031, -0.003), MM overlap (LMM: 95%CI = -0.032, -0.012), and MF overlap (LMM: 95%CI = -0.034, -0.005).

A comparison between dyad types within seasons only revealed a significant difference during the breeding season. When the data were analysed without subdividing by habitat type, both MM overlap (LMM: 95% CI = 0.378, 1.757) and MF overlap (LMM: 95% CI = 0.041, 1.205) were significantly greater than FF overlap. Females rarely overlapped compared to the other dyad types, and when they did, it was to a significantly lesser degree than either MM or MF dyads.

The data were then subdivided by habitat type for the breeding season only (Fig. 3.2). In low quality habitat (open woodland), MM overlap was significantly greater than FF overlap (LMM: 95% CI = 0.377, 2.141). MF overlap was significantly lower than MM overlap (LMM: 95% CI = -1.175, -0.177) but not significantly different from FF overlap. In high quality habitat (high proportion of *Rhododendron* within home ranges), there were no significant differences in home range overlap between dyad types.

Across seasons, both male-male (LMM: 95% CI = 1.585, 4.460) and male-female (LMM: 95% CI = 0.255, 2.869) overlap had a significant relationship with habitat type. Individuals with a higher proportion of *Rhododendron* encompassed by their home ranges overlapped more than those occupying open woodland. No significant relationship with habitat was found for FF overlap across both seasons. When analysis was restricted to the breeding season, the same relationships were found. MM overlap (LMM: 95% CI = 0.661, 1.937) and MF overlap (LMM: 95% CI = 0.688, 2.041) both significantly increased in high quality habitat. No significant difference was found between habitat qualities for FF home range overlap (GLMM: 95% CI = -1.768, 2.978).

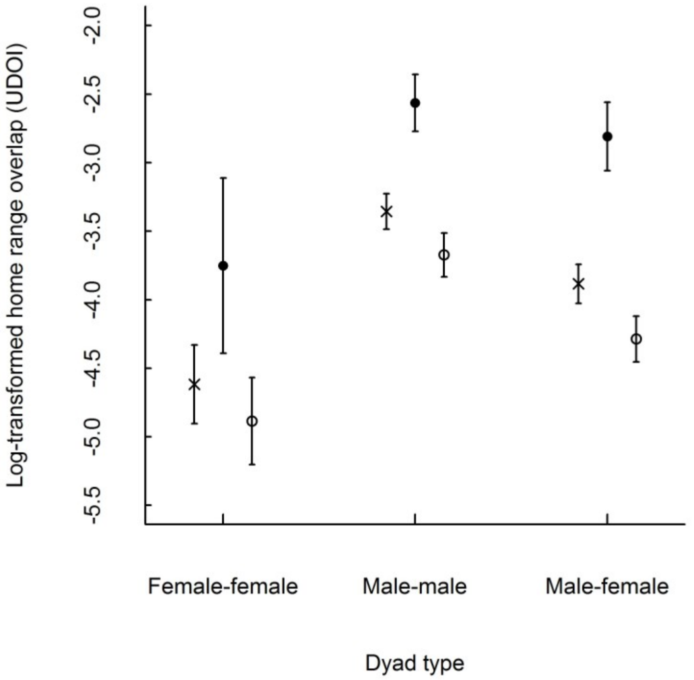


Figure 3.2: Mean log-transformed home range overlap (Log UDOI) ± 1SE during the breeding season for the three dyad types across the whole study site (x), in high quality *Rhododendron* habitat (●) and low quality open woodland (○). Across the whole study site female-female overlap was significantly less than both male-male and male-female overlap. In high quality habitat there was no significant difference in home range overlap between dyad types. In low quality habitat both female-female and male-female overlap were significantly less than male-male overlap. Male-male and male-female overlap was significantly greater in high quality habitat compared to low quality habitat.

Intrasexual home range overlap and individual-level factors

To test the relationship between same-sex home range overlap and three individual-level factors linked with competitive ability, the data were first subdivided into high and low habitat quality habitat for MM and FF dyads. For FF dyads occupying low quality habitat (open woodland), females with similar body fat reserves overlapped less than when one individual had greater fat reserves than the other (Fig. 3.3A; LMM: 95% CI = 0.761, 5.696). No significant relationships were found between FF overlap and any ILFs in high quality habitat.

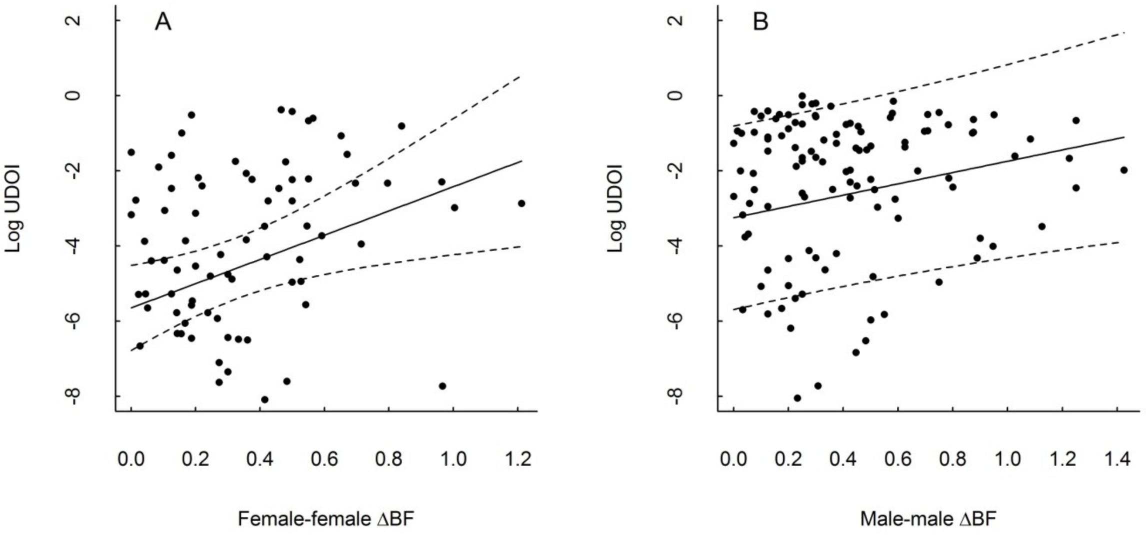


Figure 3.3: LMM-predicted relationships with 95% confidence intervals between log-transformed home range overlap (UDOI) during the breeding season and the difference in body fat (ΔBF) between A) overlapping females in low quality habitat (open woodland), and B) overlapping males in areas of high quality (*Rhododendron* cover). In both cases home range overlap increases as the difference in body fat increases.

In high quality habitat (high *Rhododendron* cover), MM overlap was greater when one individual had greater body fat reserves than the other, compared to males with similar body fat (Fig. 3.3B; LMM: 95% CI = 0.313, 2.708). Males with similar AGDI (a proxy for testosterone levels), however, overlapped more than males with a large difference in testosterone between dyad members (Fig. 3.4A; LMM: 95% CI = -4.461, -0.766). No significant relationships were found between any ILFs and MM home range overlap in low quality habitat. However, there was a positive relationship between the mean home range size of dyads and MM overlap (LMM: 95% CI = 0.0004, 0.0007).

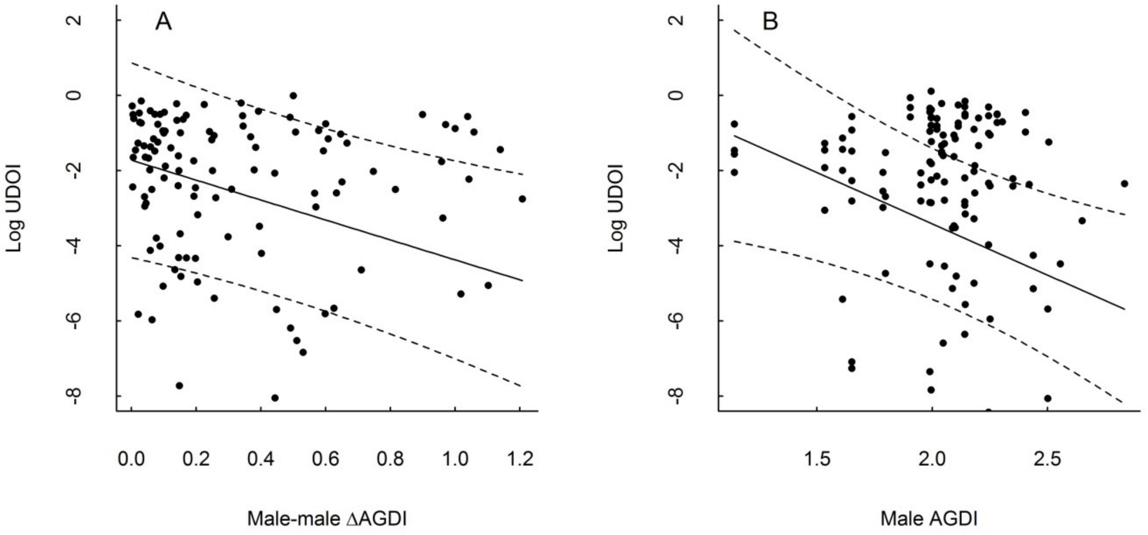


Figure 3.4: A) LMM-predicted relationship with 95% confidence intervals between log-transformed male-male overlap (UDOI) during the breeding season and the difference in normalised anogenital distance (ΔAGDI: a proxy for individual testosterone levels) in areas of low predation-risk (high shrub cover). As the difference in testosterone between overlapping males increases, home range overlap decreases. B) LMM-predicted relationship with 95% confidence intervals between log-transformed male-female overlap during the breeding season and male AGDI. Males with high testosterone levels overlap less with females than those with less testosterone.

Intersexual home range overlap and individual-level factors

To assess the relationships between ILFs and male-female overlap, the data were again subdivided and tested separately for occupants of high and low quality habitat. In high quality habitat, males with high testosterone levels overlapped with females less than those with lower testosterone (Fig. 3.4B; LMM: 95% CI = -4.725, -0.615). No significant relationships with MF overlap were found for any other male or female ILFs in high quality habitat. In low quality habitat no significant relationships were found for any male or female ILFs. However, the control variables of male home range size (LMM: 95% CI = <0.0001, 0.0003) and female home range size (LMM: 95% CI = <0.0001, 0.0006) both had significant positive relationships with MF home range overlap.

Discussion

This study, focussing on the drivers of home range overlap, has improved our knowledge about how the nature of home range overlap within a population varies between ecologically relevant habitat patches and seasons. It has also highlighted the ecological importance of individual testosterone levels and body fat in determining the spatial organisation between individuals within a population.

Habitat was a highly important ecological factor in determining the spatial overlap between individuals during periods of peak competition for mates. Not only directly, with significantly greater overlap in high quality *Rhododendron* habitat where predation risk was lower (Malo *et al.* 2013), but also as an interaction with individual-level factors. The relationships between testosterone, body fat and home range overlap differed between high and low habitat quality. Male testosterone levels had significant relationships with male-male and male-female home range overlap in high quality habitat, but not in low quality habitat. A relationship between body fat and male-male overlap was found in high quality habitat, but not in low quality habitat, while the opposite was found for female-female overlap. The relationships with home range overlap observed in this study suggest that changes in habitat, and variation in the distribution of individual-level traits across a population would result in population-level changes in the spatial organisation of individuals. For example, greater spatial overlap between individuals can result in greater population density (Chaverri, Gamba-Rios & Kunz 2007), and such changes can have population-wide effects on individual reproductive success (Andreassen & Ims 1998; Wauters *et al.* 2008), phenotypic trait selection (Reichard *et al.* 2009) as well as disease and parasite transmission (Nunn *et al.* 2014).

I tested whether the male mating strategy in this species was either female-defence or scramble competition, and whether this changed between spatially-explicit habitats. Our results suggest that scramble competition is the process by which males compete for access to oestrus females in both high and low habitat quality. A previous study on *A. sylvaticus* in an arable ecosystem also concluded scramble competition was occurring (Tew & Macdonald 1994). If males were competing through scramble competition, a high degree of overlap between males in the breeding season would be expected. Alternatively, if males were competing through female-defence, there should be little home range overlap between males during breeding seasons due to territorial behaviour and the active exclusion of competing males. These results confirmed the predictions for scramble competition. Males overlapped more during breeding seasons than non-breeding seasons. Furthermore, in low quality habitat during the breeding season, there was even greater overlap between males than between males and females. The prediction that males would compete for females through female-defence in high quality habitat where females were clustered was opposed by the fact that males overlapped with each other significantly more in high quality habitat than low quality habitat, suggesting that territoriality was not strong.

The analysis of individual-level factors within habitats of different qualities also informed our evaluation of mating strategies. If female-defence was occurring the prediction would be for a negative relationship between competition-linked phenotypic traits and male-male overlap. No such relationship was found for body mass, an individual-level factor shown to correlate with competitive dominance across a range of small mammal species (Glazier *et al.* 2002). The relationship with male body fat showed the opposite relationship than predicted in high quality habitat. The link between body fat and competitive ability is not well understood, although research on invertebrates suggests a positive relationship between body fat reserves and competitive success (Marden & Rollins 1994; Briffa & Elwood 2005). In Chapter 2 I showed that early in the breeding season, males with low body fat reserves have larger home ranges than those with larger fat reserves. The results here show a significant relationship between male-male overlap and home range size. Given the lack of evidence for territoriality in this study, the relationship with home range overlap seen here could simply result from lower-fat males spreading out more in search of nutritional resources and consequently overlapping more with the home ranges of high-fat males, which presumably contain higher quality food resources.

The only individual-level factor that did fit predictions for the female-defence hypothesis was anogenital distance, a proxy for testosterone (Ryan & Vandenbergh 2002). Low-T males overlapped with high-T males less than with similar conspecifics in high quality habitat. In high quality habitat, where female density is higher and territoriality stronger (Malo *et al.* 2013), I predicted that males would adopt a female-defence strategy. Testosterone has been linked with aggression and dominance in mammals (Trainor & Marler 2001; Clutton-Brock *et al.* 2006; Preston *et al.* 2012; Correa, Frugone & Soto-Gamboa 2013).

The observed relationship suggests low-T males are either excluded by or avoid high-T males, which represents a type of territorial behaviour and lends support to the female-defence hypothesis. However, high-T males overlapped less with females in high-quality habitat than lower-T males. If dominant males were encompassing and actively defending females within their home ranges, a positive relationship would be expected between a competition-linked trait, like testosterone, and male-female overlap.

Overlap between females was significantly less than other dyad types, which is consistent with previous results on rodents (Tew & Macdonald 1994). Female wood mice not only compete with other females for resources, but have also been shown to commit infanticide (Wilson, Elwood & Montgomery 1993). It is therefore beneficial for females in reproductive condition, and particularly those with young offspring, to actively defend their home ranges against intrusion by other females in order to increase their fitness (Wolff & Peterson 1998; Wolff 2003; Hoset *et al.* 2007).

Population density had a significant negative relationship with home range overlap across all dyad types. As population density increases, so too does intraspecific competition for food resources and mates (Jirotkul 1999). As there is little evidence for territoriality here, this relationship is most likely due to a contraction of home ranges at higher population densities (Wolton & Flowerdew 1985), rather than an increase in territoriality at high densities (Mcloughlin *et al.* 2000). Population density may therefore have direct effects on the degree of home range overlap by affecting the social behaviour of individuals towards each other (e.g. increasing territoriality at high densities)(Ostfeld 1985), but also have indirect effects on spatial overlap by affecting the size of individual home ranges (Wolton & Flowerdew 1985). In turn, there is likely to be a feedback loop between population density and home range overlap if the extent of home range overlap between individuals regulates population density.

In conclusion, the expansion of male home ranges during the breeding season (Chapter 2) seems to be an expression of their effort to find multiple mating opportunities (Lane *et al.* 2009), rather than territorial behaviour to defend multiple females from competitors. I have demonstrated that variation in individual-level factors can have significant consequences for the spatial distribution of individuals within a population. As the distribution of these factors within a population changes over time, due to either environmental change or selection, changes in space use would be expected as a result. Furthermore, including both individual body fat and testosterone levels in analyses of spatial overlap improves our understanding of space use as it allows us to disentangle their effects from body size. Habitat composition of individual home ranges has a very strong effect on the overlap behaviour of individuals, not only directly on how they use their environment, but also indirectly through its interaction with individual-level factors. This emphasizes the need for individual-based studies of wild populations involving spatially-explicit data collection matched with habitat data at an ecologically relevant resolution, in order to shed light about individual life history trajectories.

Chapter 4

Drivers of reproductive success, polygamy and the annual cycle of relatedness in the wood mouse

Introduction

In the previous chapters I have examined the drivers of space use in a wild population of wood mice (*A. sylvaticus*) and concluded that males compete for access to receptive females by scramble competition rather than by female defence. Males that increase their encounter rate with multiple receptive females should therefore have higher reproductive success (Ostfeld 1985; Ims 1987b). Females that establish smaller, easily defended and high-quality home ranges should increase their reproductive success by increasing their offspring's survival (Ostfeld 1990; Wolff & Peterson 1998). In this chapter I directly test the relationships between measures of individual space use and individual reproductive success derived from the pedigree of a wild population studied between 2008 and 2013. I also test the relationships between reproductive success and three phenotypic traits (body mass, body fat and testosterone), which I have previously shown to drive individual variation in space use.

Pedigrees describe the genealogical relationships, or family history, between individuals. Once a pedigree has been reconstructed, coefficients of relatedness can be estimated. The coefficient of relatedness is a measure of the genetic similarity between individuals (Garant & Kruuk 2005). It is calculated as the average proportion of genes shared between individuals. For example, the relatedness of parents and offspring or full siblings is 0.5, of half-siblings or grandparent-grandchildren is 0.25, and so on. This coefficient can be used to investigate a wide range of evolutionary and demographic processes, including quantitative genetic variation (Kruuk 2004; Larsen *et al.* 2014), mating systems (Liu *et al.* 2013; Clark *et al.* 2014), population structure and dispersal (Arora *et al.* 2012; Korsten *et al.* 2013; Broquet, Viard & Yearsley 2013), variance in reproductive success (Clark *et al.* 2014; Bonin *et al.* 2014), inbreeding (Pemberton *et al.* 1999; Townsend & Jamieson 2013), kin selection (Möller 2012) and cooperative behaviour (Bourke 2014).

Microsatellites are among the most commonly used markers for pedigree reconstruction (Guichoux *et al.* 2011; Liu *et al.* 2013). Microsatellites, or simple sequence repeats, are short tandem repeats of nucleotide motifs, typically 1 – 6 bases long, flanked on either side by unique sequences of nucleotide bases that can be used to develop primers that isolate the repeat region for amplification through polymerase chain reaction (Tautz & Renz 1984; Tautz 1989; Weber & May 1989; Queller, Strassmann & Hughes 1993; Jarne & Lagoda 1996; Guichoux *et al.* 2011). Microsatellite loci are a useful tool for pedigree analysis because they occur frequently in eukaryote genomes (Tautz & Renz 1984; Queller *et al.* 1993; Jarne & Lagoda 1996) and are often polymorphic (multiple alleles) due to variation in the number of repeats in the sequence (Litt & Luty 1989; Tautz 1989; Weber & May 1989). Furthermore, rapid improvement of sequencing technology has resulted in lower costs for using microsatellites allowing higher throughput (Guichoux *et al.* 2011).

COLONY is a program for reconstructing pedigrees using a full-pedigree likelihood approach (Wang 2004; Wang & Santure 2009; Jones & Wang 2010). Parent-offspring and sibling relationships are assigned via likelihood scores derived from multi-locus genotypes and missing parent genotypes can be inferred from offspring genotypes (Thomas & Hill 2000; Wang & Santure 2009). Unlike other likelihood methods which focus on inferring sibship and parentage separately (Thomas & Hill 2000, 2002; Epstein, Duren & Boehnke 2000; Sieberts, Wijsman & Thompson 2002), COLONY infers both simultaneously, partitioning individuals into family clusters (Wang & Santure 2009; Wang 2013). Furthermore, where other likelihood methods allow only a single error rate across loci to be applied (Jones & Ardren 2003), COLONY allows two error rates per individual locus, one for null alleles (Dakin & Avise 2004) and a second for other loci-specific genotyping errors or mutation rates (Wang 2004, 2013; Jones & Wang 2010).

This chapter presents the pedigree of a wood mouse population, of which the individuals were tracked and sampled between October 2008 and September 2013. COLONY was used to estimate the pedigree of 496 individuals using 10 variable microsatellite loci together with individual-level data collected during trapping sessions. The relatedness of individuals within the population is estimated from the pedigree for each month and analysed as a function of two demographic factors: monthly offspring recruitment and immigration. The recruitment of related versus non-related individuals into a population determines the variation in genetic diversity of that population over time (Lacy 1987; Born *et al.* 2008; Morandin *et al.* 2014). Genetic diversity has consequences for the occurrence or avoidance of genetic bottlenecks and inbreeding depressions (Saccheri *et al.* 1998; Lavergne & Molofsky 2007), which ultimately affect the ability of a population to adapt to changing environmental conditions (Lande & Shannon 1996; Keller & Waller 2002).

Individual reproductive success is estimated from the pedigree. Given the proposed links between space use and reproductive success (Ostfeld 1985, 1990; Ims 1987b; Wolff & Peterson 1998), in this study I test for direct relationships between three individual-level drivers of space use (body mass, body fat and testosterone) and individual reproductive success. I have shown that body mass is linked to home range size, while individual variation in body fat and testosterone explains variation in both home range size and home range overlap (Godsall, Coulson & Malo 2014; Chapter 3). Previous studies have also shown that population density (Festa-Bianchet, Gaillard & Jorgenson 1998; Zedrosser *et al.* 2007) and operational sex ratio (Emlen & Oring 1977; Klemme, Ylönen & Eccard 2007; Lodé 2009) can be important drivers of individual reproductive success in animal populations. Here I use generalised linear models to test for the associations between these individual- and population level factors and individual reproductive success. Population density and sex ratio can also drive the extent to which individuals are polygamous (Emlen & Oring 1977), therefore I test inter-annual variation in the number of reproductive partners as a response to variation in population density and sex ratio.

Finally, I test the relationships between individual reproductive success and three measures of individual space use: home range size, home range overlap with individuals of the opposite sex, and the habitat quality of the home range. 'High quality' habitat refers to dense patches of the evergreen *Rhododendron* and bamboo that occur on our study site. These two features reduce predation risk from aerial predators by providing a visual and physical barrier. Reductions in predation risk should naturally lead to a reduction in infant mortality, and therefore to an increase in female reproductive success (Roos 2002; Murphy 2003). I test the hypotheses that:1) male reproductive success is positively related to both an individual's home range size and its home range overlap with females, and 2) Female reproductive success is positively related to the quality of habitat within their home ranges.

Methods

Data collection

Trapping effort, individual-level data collection and spatial data collection methods are described in Chapters 2 & 3. A brief summary of methods is given here. Small mammal trapping was conducted between 1st May 2009 and 12th March 2013. Trapping sessions were conducted weekly between 1st May 2009 and 10th November 2010 then biweekly thereafter. All captured mice were sexed, weighed, measured for anogenital distance (AGD) and scored for body fat. Mice >15g were tagged using a 12mm x 2mm RFID PIT tag. Mice were released where they were caught as soon as individual data collection concluded. Use of animals and all procedures were in accordance with Imperial College London ethical committee and Home Office UK guidelines.

Location fixes for each PIT tagged individual were recorded using mobile recording stations that mice can enter and leave without restrictions. Between 28th March 2010 and 12th March 2013, recording stations were moved to new randomly assigned grid squares (and 1m^2 positions within) each day (n=5/week). The resulting data yielded the identity of the individual, a spatial location (±1m resolution), and a time tag (1sec resolution).

Tissue collection

Ear tissue was collected from mice at first capture using a 2mm diameter metal punch. Samples were kept in 75% ethanol and placed for long-term storage at -80˚C.

DNA extraction

DNA was extracted from ear tissue using the Quiagen DNeasy Blood & Tissue Mini Spin Kit (Quiagen, Netherlands). Extractions were performed over 25 sessions between 16th May 2012 and 18th April 2013.

Individual tissue samples were cut into small pieces (<1mm^3) and placed into a 1.8mm tube containing 180µl ATL buffer and 20µl proteinase K enzyme. Samples were incubated on a rocking plate at low speed and 56˚C for 17 hours until lysis was complete. After lysis, 200µl of AL buffer and 200µl 100% ethanol were added to each sample before vortexing. Each sample was then transferred to a mini-spin column and centrifuged at 8000rpm for 1 minute. 500µl AW1 buffer was added to each sample before centrifuging again at 8000rpm for 1 minute. 500µl AW2 buffer was then added to each sample before centrifuging at 14000rpm for 3 minutes.

DNA was eluted from the mini-spin column membrane by adding 100µl AE buffer to each sample, incubating at room temperature for 15 minutes before centrifuging at 8000µl for one minute. This procedure was repeated, rendering a final DNA elution of 200µl per sample. In the lab, samples were stored at -20˚C when not being used, and at 4˚C when in use.

Sample quality was checked using 0.8% agarose gel, and concentration quantified using a Nanodrop ND8000 spectrophotometer (Thermo Scientific, USA). For polymerase chain reactions (PCR), an aliquot of each sample was taken and diluted to between 20 – 50 ng μl^{-1}.

Genotyping

All genotyping was performed at the NERC Biomolecular Analysis Facility at the University of Sheffield. Initially, a total of 14 microsatellite loci were selected for genotyping (Table 4.1). The forward and reverse primers for eight markers were designed using Primer3 v4.0.0 (Koressaar & Remm 2007; Untergasser *et al.* 2012), specifying for GC clamp, maximum of 4 single nucleotide repeats within the primer sequence, and an ideal difference in melting temperature between forward and reverse primers of 1˚C. All primers were ordered in October 2013. Primers with NED, PET or VIC fluorescent labels were ordered from Applied Biosystems. Primers with 6FAM or HEX fluorescent labels, and all unlabelled reverse primers were ordered from Sigma-Aldrich. The primers for six other markers were provided by J. Pemberton from the Institute of Evolutionary Biology at the University of Edinburgh, and primers for the CAM-13 marker were provided by D. Dawson at the

Table 4.1: Microsatellite loci and primer sequences used in mouse genotyping and pedigree construction.

Locus	Genbank Accession no.	Repeat motif	Forward primer	Reverse primer	Cloned sequence origin	Primer source
As-7	AF246520	(GT)$_{19}$	CAGGTCTTATTCTTCCAGTTA	ACAATTGATTAAATTGGAACC	Harr *et al.* 2000	J. Pemberton
Apfl_BG9	GU481087	(CA)19	AATACTTATTTCTATAGGCAGAC	ACAAATCAATTTAGTCCTCAG	Sommer *et al.* 2010	Applied Biosystems
MSAf-8	Y09902	(CT)$_{26}$(CA)$_{12}$	CCTCCTACGTGTTGCTCC	CCTGACATCAAACTATCTAGCAC	Gockel *et al.* 1997	Sigma-Aldrich
As-12	AF246526	(TG)$_{22}$(GA)$_{24}$	TGTCAGGTCTCAACAGTAGG	CTGTTTGGAGTTGTTGTTCTG	Harr *et al.* 2000	J. Pemberton
As-20	AF246521	(GT)$_{25}$	AGCCACAGAGCCAATAAGAAG	CAGGTGAACACCCTCCCATAA	Harr *et al.* 2000	J. Pemberton
As-34	AF246524	(AC)$_{18}$	GCAAATTGTCCTTGGACCTC	TCACGGCTTAAGAATGACTAAGG	Harr *et al.* 2000	Applied Biosystems
GACAA12A	AF007205	(GA)$_{11}$(GACA)$_{6}$	GTCACTGTTGTACTGCTGCG	CTGAGGTTTACAATACCCACATGAG	Makova *et al.* 1998	Applied Biosystems
Apfl_BF6	GU481088	(TTCC)$_{2}$(TTCT)(TTCC)$_{4}$ (TTCT)(TTCC)$_{5}$(TTGC) (TTCC)(TTCT)(TTCC)$_{3}$	CACAGCTGTGCCATTCTTGC	TGCTTAGCAAGCTTGAGTCC	Sommer *et al.* 2010	J. Pemberton
CAA2A	AF007198	(CA)$_{21}$	AATTTGCCCTTAAGTGAGGAAG	GCAGTGACCCAGGAGAAATTACC	Makova *et al.* 1998	J. Pemberton
As-27	AF246522	(AG)$_{19}$	GACCCTATGAGTCAGATACCCAAC	ACCCACACCACATGCCATAC	Harr *et al.* 2000	Sigma-Aldrich
Apfl_87	GU481082	(AAC)11	GGGAAGGCTTGCAGTAATGC	TGCTCTTCCACAAGTTCCCTT	Sommer *et al.* 2010	Sigma-Aldrich
GCATD7S	AF007209	(CA)$_{6}$...(GCAT)$_{3}$(GCAC)$_{3}$	CTAAGCCATGTCTCCAGCCC	TGTAGCACTCAGATGCCCAC	Makova *et al.* 1998	Applied Biosystems
TNF-CA	AF007210	(CA)$_{17}$	AGGAAATGGGTTTCAGTTCTCAGG	GGTCCCCACCAGGATTCTGTG	Makova *et al.* 1998	J. Pemberton
CAM-13	HG518771	(CT)$_{6}$(TT)(CT)$_{11}$	TCAAATACAGCAGCAGGCAG	TTCATTACCAAACAGCATCCAG	Dawson *et al.* 2013	D. Dawson

University of Sheffield. Markers were divided into multiplexes for PCR using Multiplex Manager v.1.2 (Holleley & Geerts, 2009; Table 4.2).

Samples were prepared for PCR in a 96-well plate. Each well contained 1µl of DNA from an individual sample (dried at room temperature for 30 minutes), 1µl of Quiagen Mastermix (Quiagen, Netherlands) and 1µl of primer mix - a solution of forward and reverse primers of a specific multiplex at optimised concentrations in double deionised water (Table 4.2). Each plate included a negative control, consisting of 1µl of Quiagen Mastermix and 1µl of primer mix, and a positive control, consisting of high quality DNA from the same individual for all plates. A volume of 15µl of mineral oil was added to each well to prevent solution evaporation during PCR. Plates were covered in adhesive plastic film and placed into a DNA Engine Tetrad PCR machine (MJ Research, now Bio-Rad Ltd., USA) to denature for 15 minutes at 95˚C. The following temperature profile was then run for 45 cycles for each multiplex: 94˚C for 30 seconds; annealing temperature (Table 4.2) for 90 seconds and 72 degrees for 60 seconds. The extension time was set at 60˚C for 30 minutes.

After PCR, the product was diluted to a 1:16 PCR product to water ratio. 5µl of either Genescan LIZ or ROX 500 size standard (Applied Biosystems), depending on the multiplex (Table 2), was added to 1ml of highly deionised formamide (Applied Biosystems). 9µl of the size standard-formamide solution was added to 1µl of diluted PCR product for each sample in a sequencer plate, and heated to 95˚C for three minutes followed by rapid cooling in ice for five minutes in order to split the DNA strands apart but not allow them to recombine. DNA was then sequenced using an ABI 3730 48-well capillary sequencer (Applied Biosystems).

Table 4.2: Multiplex composition and PCR protocols for microsatellite loci.

Locus	Fluorescent label	Primer concentration (µmol)	Multiplex	Annealing temperature	Size standard
As-7	6FAM	0.2	A	50	ROX
MSAf-8	6FAM	0.2			
As-20	VIC	0.2	B	57	LIZ
As-34	PET	0.25			
Apfl_87	6FAM	0.2	C	57	LIZ
Apfl_BF6	6FAM	0.2			
GACAA12A	VIC	0.2			
TNF-CA	NED	0.3			
As-12	6FAM	0.3	D	Touchdown: 56 - 53	ROX
As-27	6FAM	0.2			
CAA2A	NED	0.2			
CAM-13	HEX	0.2			
Apfl_BG9	NED	0.3	Singleplex	50	LIZ
GCATD7S	NED	0.3	Singleplex	57	LIZ

Allele scoring was conducted using Genemapper v3.7 (Applied Biosystems). Only clearly defined peaks with a height of >1000 relative fluorescent units were accepted. All samples were re-run using fresh DNA, Mastermix and primer mix in order to test for allelic dropout. Any samples that failed to amplify, or amplified with severe stutter or mal-formed peaks for a particular locus, were rerun using 2µl of DNA, an increased primer concentration of 0.4µmol and an increased extension time of 45 minutes. If after five attempts there were no reliable results for a sample at a given locus, it was left unscored. Scoring error rate for each locus (Table 4.3) was calculated as the number of mismatches divided by the total number of samples. Mismatches were samples which, when rerun through PCR, did not match the original allele scoring from the first PCR results.

Table 4.3: Summary data for microsatellite loci, including observed (H_{Obs}) and expected (H_{Exp}) heterozygosity, deviation from the Hardy-Weinberg Equilibrium (HWE; NS = non-significant), null allele error rate and scoring error rate.

Locus	No. Alleles	Size range	No. samples successfully genotyped	H_{Obs}	H_{Exp}	HWE	Null allele	Scoring error
As7	15	92 - 132	496	0.847	0.856	NS	0.004	0.006
MSAf8	28	167 - 190	496	0.891	0.901	NS	0.004	0.009
As34	22	169 - 229	496	0.857	0.889	NS	0.017	0.000
As20	19	217 - 269	496	0.907	0.918	NS	0.006	0.000
ApflBF6	9	117 - 158	496	0.778	0.78	NS	0.003	0.013
Apfl87	12	156 - 200	496	0.365	0.763	NS	0.362	0.013
GACAA12A	9	231 - 253	496	0.685	0.699	NS	0.010	0.019
TNFCA	18	347 - 406	496	0.889	0.881	NS	0.005	0.032
As12	25	73 - 110	496	0.931	0.931	NS	0.001	0.441
CAM13	4	125 - 174	496	0.26	0.246	NS	0.030	0.053
CAA2A	12	113 - 146	495	0.818	0.826	$p < 0.01$	0.004	0.095
ApflBG9	14	173 - 227	493	0.493	0.597	$p < 0.001$	0.093	0.114
GCATD7S	13	104 - 146	493	0.793	0.807	NS	0.008	0.032
As27	24	183 - 195	457	0.403	0.902	NS	0.382	0.386

Pedigree reconstruction

Allele frequencies, identity matching, null alleles (allelic dropout), Hardy-Weinberg equilibrium (HWE) and exclusion power were all estimated from allele scoring results using Cervus v3.0.3 (Table 4.3; Kalinowski, Taper, & Marshall, 2007). Linkage disequilibrium was tested for using Genepop v4.2 (Raymond & Rousset, 1995; Rousset, 2008). Due to a high proportion of null alleles, two loci were removed (As27 & Aplf87) before continuing with pedigree construction. Two other loci were also discarded before further analysis (CAA2A and ApflBG9) as they significantly departed from HWE, voiding the assumption of pedigree reconstruction that all loci used conformed to HWE within the population (Wang 2004; Wang & Santure 2009; Jones & Wang 2010). Four individuals were found to be a different species (*Apodemus flavicollis*) and were removed from further analysis. Seven pairs of individuals were found to have had duplicated tissue samples labelled with different identities. These duplicates were removed before further analysis. The remaining 10 loci for the 496 individuals had a strong combined exclusion probability of 0.9997, meaning that the probability of falsely excluding a parent was three in ten thousand (0.0003).

The pedigree was constructed with the remaining 10 loci using COLONY v2.0.5.1 (Wang 2004, 2013; Wang & Santure 2009; Jones & Wang 2010). All 496 individuals were considered as candidate offspring. A total of 282 males and 205 females were included as candidate parents. Parental and sibship exclusion tables were constructed for all individuals based on the capture history of individuals (timings of capture, age and breeding condition).

COLONY software was prepared for the analysis using the following settings: male and female polygamy; inbreeding present; species are dioecious and diploid; allele frequencies to be updated; a "complexity" sibship prior; full-likelihood analysis with 'very high' likelihood precision; two replicate runs of medium run length. The best configuration between the two replicates (chosen by maximum likelihood) was viewed using Pedigree Viewer v6.5b (Kinghorn 2011), and all parent-offspring and full/half sibling relationships were checked against trapping data of the individuals involved to ensure the relationships proposed by COLONY were plausible. Parental and sibship exclusion databases were updated and COLONY was then re-run using the same settings as above, and the process of checking relationships and updating exclusion databases repeated until no further spurious relationships were found, at which point the pedigree was accepted.

Temporal variation in mean relatedness and the number of reproductive mates

The pairwise relatedness between all individuals was calculated from the final pedigree using the software *R* v3.1.1 (R Core Team, 2014) and the package **pedigree** (Coster

2012). Relatedness between all individuals present in the population in each month between January 2009 and March 2013 was analysed as a function of demographic factors. Population density for each month between 2009 and 2012 was calculated as the number of reproductively active individuals present in the study site. These estimates included all males in breeding condition (testes clearly descended) and females with a mean monthly body mass >16g. The 16g threshold was selected as it is the lowest weight at which captured females in our population showed signs of pregnancy, and was therefore taken as the threshold body mass for reproductive activity across all females. Offspring recruitment for each month was calculated as the number of new (not previously captured) individuals with mean body mass <19g in each month, which the pedigree confirmed to be the offspring of at least one known individual. Individuals were considered to be adults once they had reached a body mass of 19g, based on visual inspection of time series plots of each individual's body mass, showing that body mass begun to asymptote at a minimum of 19g across the population. Recruitment through immigration was calculated for each month as the number of new individuals of any body mass captured for the first time that were not confirmed by the pedigree as the offspring of at least one known individual. For analysis of monthly relatedness, both offspring and immigrant recruitment were converted into a proportion of the total population density. A binomial generalised linear model (GLM) was constructed using the pairwise relatedness between all individuals within each month as the response variable. Monthly population density, offspring recruitment and immigration for each month between January 2009 and March 2013 were included as explanatory variables.

For all further analyses of reproductive success and the number of reproductive mates per individual (NRM), data from the year 2013 was excluded as data collection ended in March 2013, and was therefore not comparable to other years. Models specified a quasipoisson error structure were necessary to account for overdispersion in the response variable of interest. NRM was estimated from the pedigree as the number of different individuals of the opposite sex that each individual was associated with as parents of offspring. NRM was compared between males and females using a quasipoisson GLM with the number of mates as the response variable and sex as the explanatory variable. NRM was compared between years separately for males and females. For each sex, a quasipoisson GLM was constructed with the number of reproductive mates as the response variable and the year their offspring were born as the explanatory variable. A post hoc Tukey multiple comparisons test was used to assess pairwise differences between years. The relationship between individual reproductive success (response variable) and NRM (explanatory variable) was tested separately for both males and females using a quasipoisson GLM

Population density and the operational sex ratio (OSR; Emlen & Oring 1977) were tested as drivers of both individual reproductive success and the degree of polygamy within each annual breeding season. Breeding season boundaries were inferred in the same manner as Chapter 3 (Table 3.1). Each annual breeding season began when >50% male mice were on breeding condition (testes descended), and ended when all females no longer showed signs of reproductive activity (perforated vaginas or pregnant). Population density was calculated from the number of reproductively active individuals within each annual breeding season using the body mass thresholds described above. OSR was calculated as the ratio of males:females within each population density estimate. For males and females separately, a quasipoisson GLM was constructed with NRM as the response variable and population density and OSR as explanatory variables.

Individual reproductive success, phenotypic traits and space use

Individual reproductive success was estimated as the number of offspring assigned to each individual by the pedigree for individuals caught between 1st May 2009 and 12th March

2013. Reproductive success was compared between males and females using a quasipoisson GLM with reproductive success as the response variable and sex as an explanatory variable. For both males and females separately, reproductive success was compared between years using a quasipoisson GLM with reproductive success as the response variable and the year offspring were born as the explanatory variable. A post hoc Tukey multiple comparisons test was then performed to evaluate which years differed significantly from each other.

Three phenotypic traits were tested for their relationship with reproductive success: body mass, body fat reserves and testosterone (using anogenital distance as a proxy). For each individual, the mean for each trait for the breeding season in which that individual was reproductively active was calculated from measurements taken during trapping sessions after the individual had reached a body mass of 16g. This threshold was applied, as above, to remove measurements taken when individuals were not in breeding condition. Analysis was conducted on a subset of individuals that had sufficient data collected for all three traits (108 males and 79 females). For each sex separately, a quasipoisson GLM was constructed with reproductive success as the response variable, and mean body mass, body fat score and anogenital distance index (AGDI, anogenital distance divided by the cube root of body mass; Gallavan *et al.* 1999; Godsall *et al.* 2014), population density and OSR as explanatory variables.

A further subset of individuals (47 males and 27 females) - those with sufficient relocation data to estimate home ranges during breeding seasons - were used to analyse the relationships between reproductive success and three measures of space use: home range size, overlap and habitat quality. Due to the reduced sample size, these factors were tested separately to avoid reducing the statistical power of the analysis of phenotypic traits. Home range size, overlap and habitat quality were estimated in the same way as Chapter 3. A brief summary of methods is given here. Home ranges were estimated for individual mice during each breeding season between 2010 and 2012. Home ranges were estimated by kernel density estimation (Worton 1989) using the **adehabitatHR** package (Calenge 2006) in the software *R* v3.1.1 (R Core Team, 2014). The direct plug-in method was used for bandwidth selection (Wand & Jones 1995; Gitzen *et al.* 2006; Cumming & Cornélis 2012) and individuals with fewer than 30 relocations were excluded to remove bias in home range size from low sample sizes (Seaman *et al.* 1999; Girard *et al.* 2002). Home range overlap for each individual was calculated as the mean utilization distribution overlap index (UDOI; Fieberg & Kochanny 2005) between that individual and all overlapping members of the opposite sex. The number of conspecifics of the opposite sex that an individual's home range overlapped with was also included. Habitat quality was measured as the proportion of each individual's home range covered by *Rhododendron* and bamboo (ranging from 0-1), calculated from a digital map of the study site with a 1m^2 resolution (Godsall *et al.* 2014) using ArcGIS v9.3 (ESRI 2008).

In order to test the relationships between individual reproductive success and space use, male and female reproductive success were analysed separately. For each sex, a quasipoisson GLM was constructed using reproductive success as the response variable. Four explanatory variables relating to an individual's space use were included in each model: home range size, home range overlap with the opposite sex, the number of individuals of the opposite sex overlapped with and habitat quality within home ranges. Population density and OSR were included in order to control for between-year differences in the size and composition of the population. 'Mouse presence' - the number of days each individual was known to be using the study site - was included to control for differences in the length of time each individual had to establish a home range and encounter conspecifics.

Model simplification and significance tests

All models were simplified using Akaike's Information Criterion (AIC). Models were simplified by removing individual variables in a stepwise manner until the lowest AIC (binomial GLM) or quasi-AIC (QAIC: quasipoisson GLMs) was reached.

Significance of variables retained in the lowest AIC or QAIC models was determined using likelihood ratio tests, by comparing model deviance before and after removal of each variable separately with Chi-squared (binomial GLM) or F-tests (quasipoisson GLMs) (Crawley 2007). If removal of a variable resulted in a significant increase in model deviance, that variable was considered to be significant.

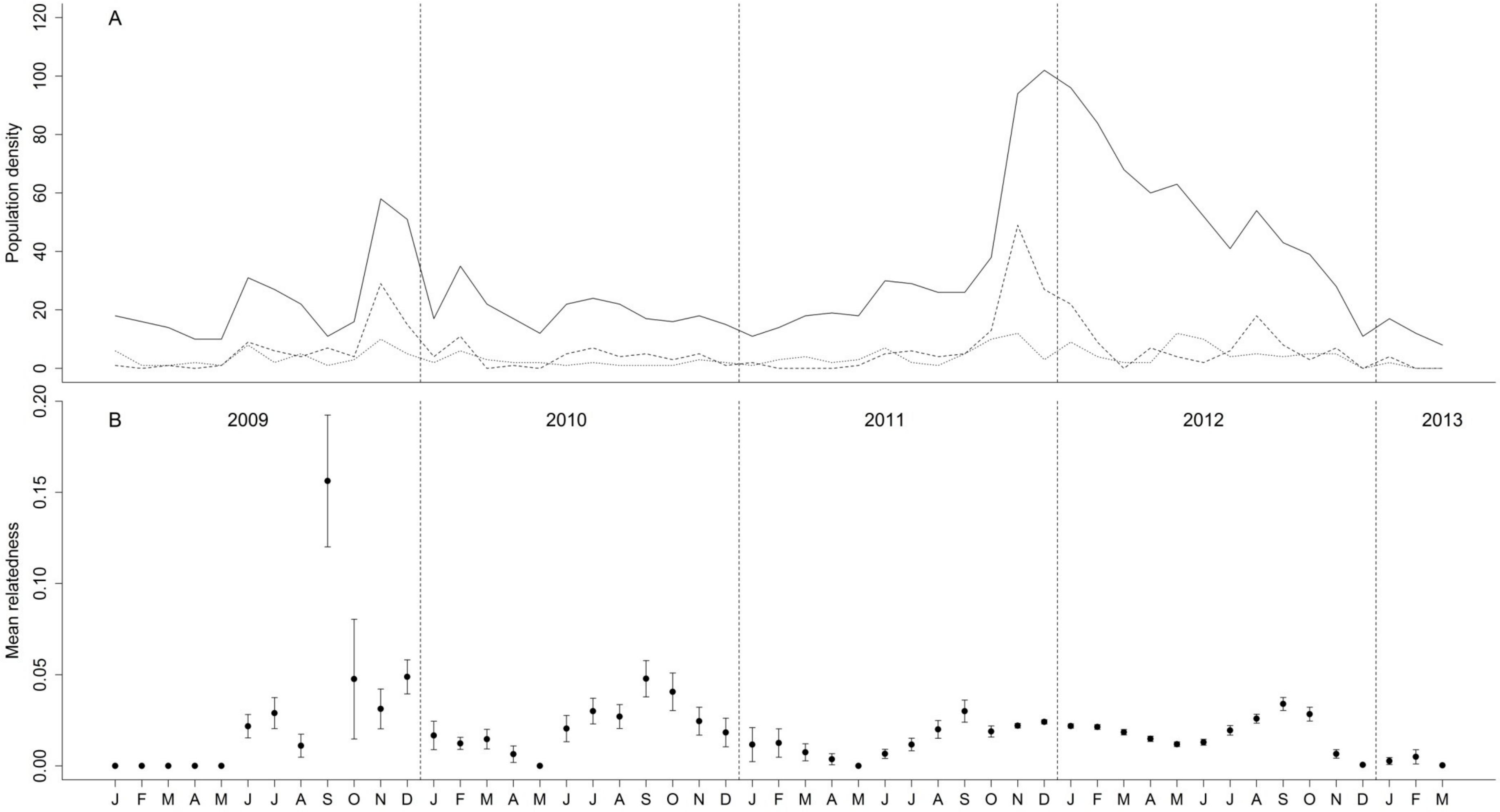


Figure 4.1: A) Monthly population density (solid line), offspring recruitment (dashed line) and recruitment of immigrants (dotted line) over time at the study site. B) Mean relatedness (±S.E.) of the individuals present in the population during each month. There is an intra-annual trend of an increase in relatedness during the breeding season from the lowest relatedness in May to peak relatedness in September, driven by the recruitment of offspring into the population. Mean relatedness then decreases through late autumn and winter as unrelated immigrants enter the population. Not all individuals captured in 2009 were genotyped.

Results

Temporal variation in mean relatedness and the number of reproductive mates

A clear annual pattern in relatedness was observed between 2009 and 2012 (Fig. 4.1). In each year (excluding 2013 due to a lack of data), the mean relatedness between individuals was highest between August and October, peaking in September. Mean relatedness then fell through the winter months until the lowest mean relatedness in May, at which point mean relatedness began to rise. Relatedness was significantly positively related to the proportion of newly recruited offspring into the population (GLM: 0.012, s.e = 0.002, $\chi^2 = 19.052$, df = 1, $p < 0.0001$), and significantly negatively related to the proportion of new immigrants in the population (GLM: -0.035, s.e. = 0.007, $\chi^2 = 14.535$, df = 1, $p = 0.0001$). Neither population density nor year were significant.

Although not significant, there is some variation between years. For example, the decline in relatedness was not as severe through the winter of 2011-12 as in other years. Consequently, the lowest relatedness observed in 2012 was higher than other years. In the winter of 2012, however, there was a considerably steeper reduction in relatedness between October and November compared to other years, resulting in all the individuals in the study site being unrelated in December 2012. The data for 2009 seemed more erratic than 2010 onwards, and this is because tissue sampling was less consistent (not all individuals were sampled) and trapping effort was lower in this year than it was in other years. The general pattern of relatedness in this population was still present in 2009, with the peak relatedness in September 2009 being the highest mean relatedness recorded. This outlier is the result of a small density of individuals in the study site at this time (n=8) which were all parent-offspring or sibling relations.

The number of reproductive mates ranged between 0 and 7 for both males and females. Males generally had more reproductive mates than females, with the exception of

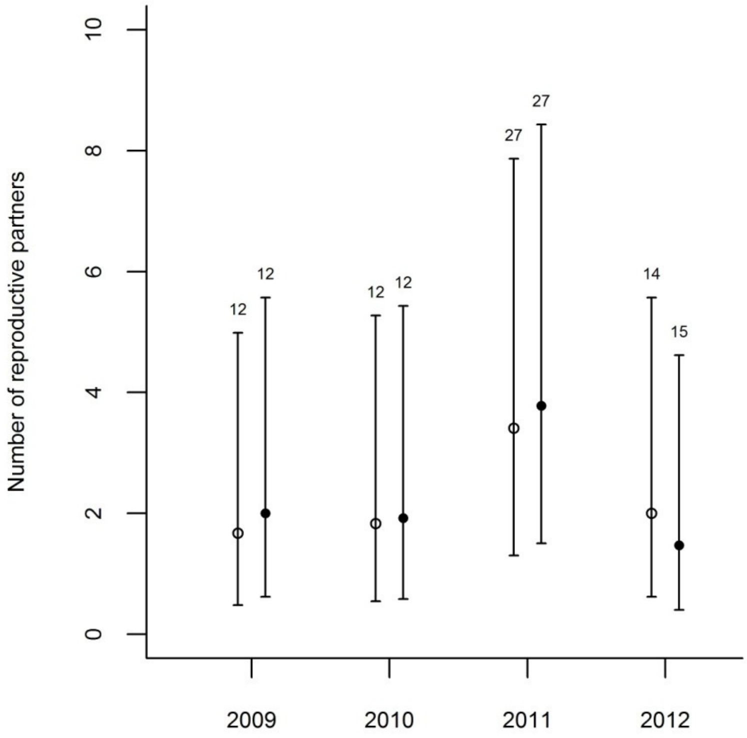


Figure 4.2: Mean (± 95% CI) number of reproductive partners between years for females (○) and males (●). Numbers above error bars give the sample size.

2012 (Fig. 4.2), although the differences between males and females were not significant (GLM: $F_{2,\ 129} = 0.125$, $p = 0.7234$). NRM differed significantly between years for both males (GLM: $F_{4,\ 62} = 8.5355$, $p < 0.0001$) and females (GLM: $F_{4,\ 61} = 5.2049$, $p = 0.0014$). Individual males sired offspring with significantly more females in 2011 than any other year (Tukey: vs. 2009, $p = 0.0099$; vs. 2010, $p = 0.0063$; vs. 2012, $p < 0.0001$). The same pattern was also seen for females (Tukey: vs. 2009, $p < 0.0001$; vs. 2010, $p = 0.0016$; vs. 2012, $p = 0.0033$). Population density and OSR both had significant relationships with the number of reproductive partners for males and females. Both males (GLM: $\beta = 0.014$, s.e. = 0.006, $F_{1,\ 65} = 6.6396$, $p = 0.0123$) and females (GLM: $\beta = 0.016$, s.e. = 0.004, $F_{1,\ 64} = 16.924$, $p = 0.0001$) had significantly more reproductive partners at high population densities. Similarly, both sexes had more reproductive partners as the male bias in OSR increased (GLM: males, $\beta =$

1.980, s.e. = 0.463, $F_{1, 65} = 19.27, p < 0.0001$; females, $\beta = 1.670$, s.e. = 0.331, $F_{1, 64} = 27.501$, $p < 0.0001$). For both males (GLM: $\beta = 0.306$, s.e. = 0.028, $F_{1, 65} = 138.59, p < 0.0001$) and females (GLM: $\beta = 0.271$, s.e. = 0.038, $F_{1, 64} = 46.597$, $p < 0.0001$) there was a strong significant positive relationship between individual reproductive success and the number of reproductive partners.

Individual reproductive success, phenotypic traits and space use

Across all study years, individual male reproductive success ranged from 0 to 15 offspring, while females ranged from 0 to 9 offspring. Males had a larger maximum of reproductive success but mean female reproductive success was higher in each study year (Fig.4.3), although the difference between males and females was not significant (GLM: $F_{2, 407} = 2.465, p = 1.117$). There was significant variation in reproductive success between years for both males (GLM: $F_{4, 234} = 19.431$, $p < 0.0001$) and females (GLM: $F_{4, 167} = 16.788$, $p < 0.0001$). In 2009 male reproductive success was significantly higher than 2012 (Tukey: $p = 0.0029$). In 2011 males sired significantly more offspring than in 2010 (Tukey: $p < 0.0001$) and 2012 (Tukey: $p < 0.0001$). Female reproductive success was significantly greater in 2011 than in 2009 (Tukey: $p = 0.0099$), 2010 (Tukey: $p = 0.0063$) and 2012 (Tukey: $p < 0.0001$).

Analysis of phenotypic traits revealed mean seasonal body mass to have a significant positive relationship with reproductive success for both males (GLM: $\beta = 0.113$, s.e. = 0.052, $F_{1, 107} = 4.749$, $p = 0.0316$) and females (GLM: $\beta = 0.134$, s.e. = 0.054, $F_{1, 77} = 5.988$, $p = 0.0167$). A significant negative relationship was also found for females between seasonal mean body fat and reproductive success (GLM: $\beta = -0.584$, s.e. = 0.291, $F_{1, 77} = 4.017$, $p = 0.0487$). No significant relationship was found between male body fat and reproductive success, nor between AGDI and reproductive success for either sex. Sex ratio had a significant positive relationship with reproductive success for both males (GLM: $\beta = 2.477$, s.e. = 0.484, $F_{1,\,107} = 32.692$, $p < 0.0001$) and females (GLM: $\beta = 1.587$, s.e. = 0.433, $F_{1,\,107} = 14.664$, $p = 0.0003$). As the proportion of males in the population increased, so did the number of offspring produced by both males and females. No significant effects were found for population density in either males or females.

No significant relationships were found between individual reproductive success and home range size, the degree of home range overlap (UDOI), the number of conspecific home ranges overlapped or habitat quality within home ranges for either males or females. The null model had the lowest QAIC.

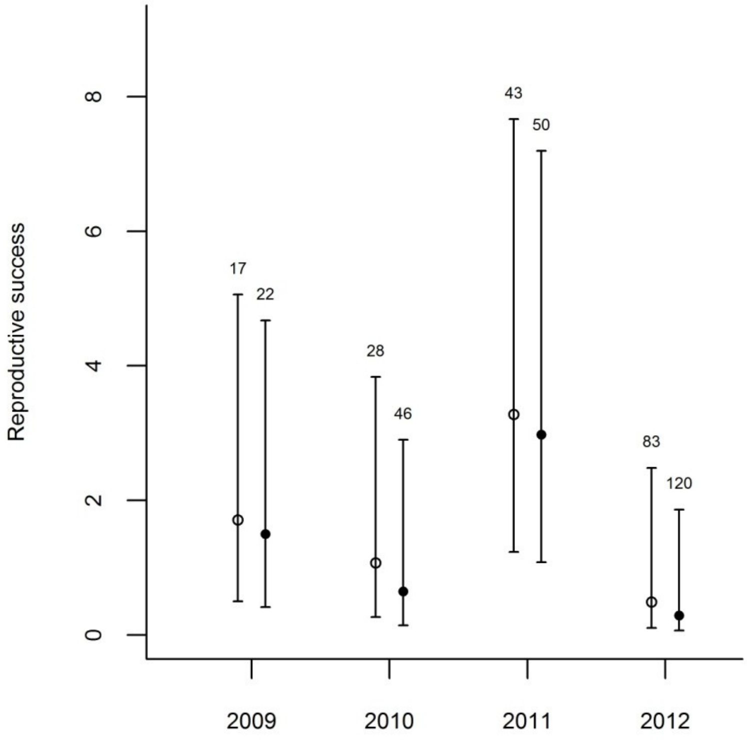


Figure 4.3: Mean (± 95% CI) of reproductive success between years for females (○) and males (●). Numbers above error bars give the sample size.

Discussion

This study has revealed that both male and female *A. sylvaticus* successfully reproduce with a greater number of mates than previously thought. Previous molecular studies of *A. sylvaticus* have confirmed female polyandry but have not highlighted polygyny (Baker, Makova & Chesser 1999; Booth *et al.* 2007; Bryja *et al.* 2008), focusing solely on females and drawing conclusions from significantly smaller sample sizes than this study. Baker *et al.* (1999) found evidence of multiple paternity in three out of six litters studied, and Booth *et al.* (2007) found a similar proportion of multiple paternity among litters, with 7 out of 13 litters studied sired by at least two different males. Bryja *et al.* (2008) found a slightly higher proportion of multiple paternity litters, with 68.2% of 22 litters being sired by two or three males. The identity of the males, and therefore the number of reproductive partners per male, were not made clear in these studies however. This study found that both males (n=282) and females (n=205) had up to seven reproductive partners within a breeding season, although it was not possible to determine the degree of multiple paternity within litters. The ability of this study to uncover the higher numbers of reproductive partners in both sexes is most likely due to the fact that the vast majority of the population at this study site was caught and genotyped. The number of reproductive partners could be even higher than the results presented here, as the genotyping of the population was restricted to individuals that had survived to an age where they became independently mobile and were caught in traps, but excluded all individuals that died before maturing to such an age.

The degree of polygamy was not constant, however, as demonstrated by the presence of significant inter-annual variation in the number of reproductive mates of both males and females. Emlen & Oring (1977) proposed that the level of polygamy within a population is determined by the degree to which males can monopolize receptive females, which is driven by the spatio-temporal distribution of females and resources. The OSR of reproductive adults within each breeding season was a strong driver of variation in both the number of reproductive partners and individual reproductive success of both males and females. Population density was also a positive driver of the number of reproductive mates for males and females. Individual reproductive success was positively related to the number of reproductive mates of each individual. As well as the direct effect of OSR on reproductive success, these results suggest that OSR and population density have indirect effects on reproductive success through their positive relationship with the number of reproductive mates. The OSR in each breeding season was male-biased, but varied in the extent of the bias. As the population density and proportion of males in the population increased, so did the reproductive success of both males and females. In a polygamous mating system where males compete for access to females by scramble competition, as observed in this population (Chapter 3), the reproductive success of females would be expected to increase as the population density and proportion of males in the population increased, due to higher encounter rates with roving males. Fertility varies amongst males (Malo *et al.* 2010), therefore females mating with multiple males increase the probability of mating with a high-fertility male and reduce the risk of failed fertilizations from copulations with low fertility males. The possible reasons for the increased reproductive success and number of mates of males at high-male OSR are less clear, however, as competition between males would be expected to increase. It is likely that other factors not analysed here, such as the spacing of females, explain variation in male reproductive success and the extent of male polygamy.

Both males and females with large body mass had higher reproductive success than smaller individuals. Reproductive success in both sexes has previously been shown to vary with body mass in mammals (Klemme *et al.* 2007; Selonen *et al.* 2013). Larger female body mass has been associated with higher female reproductive success in bighorn sheep (*Ovis canadensis*), with the proposed reason being that heavier females have higher body fat reserves, and are therefore better able to provide the energetic requirements of their offspring both *in utero* and post-parturition (Festa-Bianchet *et al.* 1998). In this study, however, I have been able to disentangle the relative contributions of both body mass and body fat to variance in reproductive success. The relationship observed here between female body fat and reproductive success was negative - females with low seasonal mean body fat had higher reproductive success. Body fat is metabolized during periods of high energetic demand (Koubi *et al.* 1991) and has been linked to reproductive success in mammals (Gittleman & Thompson 1988). The relationship seen here is most likely a response of female body fat reserves to reproduction, rather than evidence of body fat as a driver of reproductive success. Females with high reproductive success would have utilized a lot more body fat as energy reserves during energetically expensive gestation and lactation periods, resulting in a lower seasonal mean body fat score than those with low reproductive success.

Body mass is frequently associated with dominance in rodents (Gabathuler, Bennett & Jarvis 1996; Hurst *et al.* 1996; Huang *et al.* 2011), meaning larger males are more likely to gain access to mating opportunities. Female home ranges overlapped very little in this population (Chapter 3), therefore larger, dominant females may have outcompeted other females for access to nesting sites providing higher reproductive fitness benefits, such as lower offspring mortality through predation. However, the relationships between reproductive success and both male overlap with females and the habitat quality of female home ranges were tested directly in this study, but did not yield significant results (although this may be an issue with the analysis, discussed below). Nonetheless, these results highlight that body mass is an important driver of reproductive success in this species.

The annual pattern in relatedness matches the population cycle in *A. sylvaticus*. The rising relatedness seen from June to its peak in September matches the time period when the population size increases due to the birth of new offspring, which remain in the population along with their parents and siblings as they mature through the summer (Watts 1969; Montgomery 1989). Hence, the mean relatedness of the population is higher due to the increase in parent-offspring and sibling relationships present within the population at these times. The decline in relatedness results from both the death of parents and juveniles through the winter, followed by an increase in aggression between conspecifics throughout spring, resulting in the expulsion of related individuals by dominant parents or siblings (Watts 1969; Gurnell 1978; Malo *et al.* 2013). Immigration of unrelated individuals is also highest during spring (Flowerdew 1974), which contributes to the reduction in mean relatedness during these times of year. Drivers of population dynamics, i.e. reproductive success, mortality, dispersal and immigration, should therefore be expected to affect intra- and inter-annual variation in the mean relatedness of the population.

According to the predictions of scramble competition, males enhance their reproductive success by increasing their opportunities to encounter and inseminate receptive females (Ostfeld 1985; Ims 1987b). Males with large home ranges overlapping multiple females were therefore expected to have higher reproductive success than those with smaller, isolated home ranges. Females can maximise their reproductive success by inhabiting low predation-risk habitat which reduces the chances of offspring mortality through predation (Ostfeld 1990; Wolff & Peterson 1998). Females occupying patches of *Rhododendron* were therefore expected to have higher reproductive success than those in open woodland. No significant relationships were found for any space use factors for either sex, however. The lack of any relationships between reproductive success and space use factors may be in part due to the small sample sizes used, and the analysis lacked power as a result. Furthermore, the estimate of reproductive success used in this study relied on the ability to sample tissue from offspring. This measure only included offspring which had survived to the age at which they became independently mobile and could be caught in traps. Any offspring which died or were predated before this point could not incorporated into the analysis and this, combined with an already low sample size, was likely to have limited the ability of the analysis to uncover the true relationships between space use and reproductive success.

In conclusion, body mass and OSR are important drivers of individual reproductive success in both sexes of *A. sylvaticus*. OSR and population density also have indirect effects on reproductive success through their relationship with the number of reproductive mates each individual has. There is an intra-annual cycle of relatedness in this population, which is driven by the recruitment of offspring and immigration.

Chapter 5

Selection gradients, heritability and the response to selection of three phenotypic traits in the wood mouse, *Apodemus sylvaticus*

Introduction

Populations are shaped by both ecological and evolutionary processes. Ecological factors, such as resource abundance and changes in habitat or weather patterns, can drive fluctuations in population size and demography (Warren *et al.* 2001; Beaugrand *et al.* 2003; Cushman 2006). The evolutionary force of selection acts on the phenotypes of individuals, potentially resulting in changes to the distribution of character values within a population over successive generations (Kingsolver *et al.* 2001; Grant & Grant 2002; Kruuk, Slate & Wilson 2008). In order to understand the role of evolutionary processes within an ecological context, it is necessary to first quantify and understand how genetics influences variation in phenotypic traits which relate to individual fitness (Ellegren & Sheldon 2008; Kruuk *et al.* 2008).

When the variance in the value of a phenotypic trait within a population translates into variance in fitness between individuals, the trait is under selection (Kingsolver & Pfennig 2007). Viability selection acts on traits associated with the probability of an individual's survival, while sexual selection acts on traits which are linked to reproductive success. High-fitness individuals succeed in producing a large progeny and pass more copies of their genes onto the next generation, making a greater contribution to the next generation's gene pool than low-fitness individuals with smaller or no progenies. This results in a change in the frequency of genotypes that determine phenotypic trait values in the next generation (Lande 1976). A comparison of viability and sexual selection estimates suggests that the strength of selection on survival-linked traits is typically lower than on traits under sexual selection (Hoekstra *et al.* 2001). Temporal variation in the strength and direction of viability selection on traits results from temporal variation in environmental and population-level factors, or 'agents' of selection, which affect individual survival, including food availability (McAdam & Boutin 2003), predation risk (Reimchen & Nosil 2002), population density (Calsbeek & Cox 2010), and weather conditions, for example rainfall (Tarwater & Beissinger 2013) or temperature (van de Pol *et al.* 2010). The nature of sexual selection on traits is also affected by the social environment within a population. Population-level factors that affect the number of available mates and competitors, such as population density and sex ratio, can drive variation in individual reproductive success, and may consequently act as agents of sexual selection (Conner 1989; Madsen & Shine 1993; Kasumovic *et al.* 2008).

Variance in the values of phenotypic traits between individuals can arise from a combination of genetic and environmental sources (Réale, Festa-Bianchet & Jorgenson 1999; Milner *et al.* 2000; Garant *et al.* 2004). An important source of environmental variation comes from maternal effects, also referred to as the 'common environment'. Wolf & Wade (2009) define maternal effects as "the *causal* influence of the maternal genotype or phenotype on the offspring phenotype". This refers to the variance in trait values occurring between sibling groups as a result of differences in the developmental environment provided by different mothers (Fox, Waddell & Mousseau 1995; Milner *et al.* 2000; Coltman *et al.* 2001). As suggested by Wolf & Wade's (2009) definition, differences in the maternal environment can arise from both genetic and environmental sources. For example, in mammals an offspring's development is strongly related to the quantity and quality of nutrients provided by the mother through lactation (Passos, Ramos & Moura 2000). Individual variation in the quantity and nutritional quality of lactation is a function of both genetic variance between females (Chang *et al.* 2001) and their food intake, i.e. their environment (Amusquivar *et al.* 2000; Passos *et al.* 2000).

In order to understand how phenotypic traits change over time in response to either ecological or evolutionary factors, it is necessary to distinguish between different sources of variance. This can be achieved without explicit knowledge of the genetic architecture that governs a phenotypic trait by assuming a simple genetic architecture, and through examining similarities in trait values among related individuals (Hazel 1943; Henderson 1976; Lande 1979). This assumption of a simple genetic architecture states that variance in the value of a phenotypic trait is governed by the summed contribution of many genes of small effect, termed the 'breeding value'. Given this assumption, and the fact that related individuals share more genes than unrelated individuals, the additive genetic variance of a trait can be calculated using knowledge of the relatedness between individuals. The heritability of a trait can then be estimated as the proportion of the total phenotypic variance that is due to the additive genetic variance (Jacquard 1983).

The 'animal model' is frequently used to partition the variance of a phenotypic trait into environmental and additive genetic variance (Milner *et al.* 2000; Kruuk 2004; Wilson *et al.* 2010). The animal model tests the relationship between the phenotypic trait of an individual and all known relatives using breeding values, extracted from a pedigree and incorporated into a generalised linear mixed-effect model as a random effect. This method also allows the inclusion of non-genetic (environmental) variables, including maternal effects, to test or control for their effects on phenotypic size variance, allowing the total phenotypic variance to be divided into genetic and environmental variance.

The strength and direction of selection on phenotypic traits can be estimated using selection gradients (Lande 1979; Lande & Arnold 1983; Hartl & Conner 2004). The selection gradient for a trait is calculated as the regression slope between standardized measures of individual trait values and relative individual fitness (Lande 1979). In the case of a multivariate analysis of selection on multiple traits, the selection gradient of each trait is equivalent to its respective partial correlation coefficient (Lande & Arnold 1983). The proxies of fitness against which traits are typically regressed include measures of individual fecundity or reproductive success (Conner *et al.* 1996; Réale *et al.* 2003) and survival (Janzen & Stern 1998; Garant *et al.* 2004).

The response to selection ($\Delta\bar{\mathbf{z}}$) is the change in the mean of the distribution of trait values across a population over time. The change between successive generations can be calculated using the Breeders equation (Lande 1976):

$$\Delta\bar{\mathbf{z}} = h^2\beta$$

As the equation shows, the heritability (h^2) of a phenotypic trait and the selection gradient (β) imposed on the trait can be used to calculate the response to selection in the next generation.

In this chapter I estimate the response to selection of three phenotypic traits in the wood mouse, *Apodemus sylvaticus* (L.). Using lifetime reproductive success as a measure of individual fitness, I estimate the strength and direction of sexual selection on body mass, foot length and anogenital distance by calculating their selection gradients. The heritability of each trait is estimated using the animal model. I have previously shown the ecological significance of two of these traits, body mass and anogenital distance, in terms of their relationships with home range size, home range overlap and reproductive success in this species. The third trait, foot length, is used here to test for any genetic correlations with either body mass or anogenital distance. I test the relationships between annual estimates of trait selection gradients and population density and sex ratio, to assess the roles of these population-level factors as drivers of sexual selection in this population. I predict that when competition between individuals is high, as would be the case at high population densities for both sexes and increased male bias in the sex ratio for males, that selection on competition-linked traits (body mass and anogenital distance as a proxy for testosterone) will be positive and strong compared to low densities or more even sex ratios. Finally, I use the selection gradients and heritability estimates to calculate the short-term response to selection for each trait.

Methods

Data collection and preparation

Phenotypic data for individual mice were collected during trapping sessions between January 2009 and December 2012, as described in Chapter 2. In this analysis I also include foot length, measured from the ankle to the tip of the longest tarsus (excluding the nail) of the rear left foot. The pedigree of the mouse population used in this analysis is described in Chapter 4.

To estimate the selection gradients and heritability of phenotypic traits, only adult trait values were considered in order to remove individual variance in trait values associated with age. Mice with a body mass of 19g or higher were considered adults. This threshold was selected based on a visual assessment of individual time-series plots of mouse body mass, which showed that body mass generally began to asymptote across individuals at this weight or above. As it was not possible to assess a full lifetime plot of body mass for every single mouse (due to missing data), this threshold was based on a subsample of mice with sufficient data and applied across the whole population. To remove the effect of season, only measurements taken during breeding seasons were used. Additionally, male AGD increases with the onset of the breeding season due to hormonal changes causing the testes to enlarge and descend from within the abdominal cavity. Therefore, only AGD measurements taken when male mice had a body mass > 19g *and* had descended testes were used in analyses. As in previous chapters, AGD measurements were normalised to create an anogenital distance index (AGDI) by dividing AGD by the cube-root of body mass at the time of measurement (Gallavan *et al.* 1999; Godsall *et al.* 2014).

Selection

Selection on multiple phenotypic traits can be estimated from their selection gradients. These are the partial correlation coefficients obtained from multiple regression analysis of individual trait values against a measure of individual fitness (Lande 1979; Lande & Arnold 1983; Hartl & Conner 2004). Selection gradients for body mass, foot length and AGDI were estimated for males and females separately. Only individuals with measurements for all three traits were used in analyses (116 males, 89 females). The mean trait size was calculated for each individual for use in analysis. The following steps were performed separately for males and females. For each trait, trait values were log-transformed to normalise their distributions. Log-transformed distributions were then standardized to distributions with a mean of zero and variance of one (Lande & Arnold 1983). Correlations between traits were tested for, but no significant correlations were found. The measure of fitness used in this analysis was lifetime reproductive success (LRS), calculated as the number of offspring attributed to each individual by the pedigree (Chapter 4). Individual LRS for each sex was standardized to relative LRS by dividing individual LRS by the mean LRS of the relevant sex (Lande & Arnold 1983; Conner *et al.* 1996).

Standardized selection gradients were estimated for each trait in each year between 2009 and 2012 to assess any temporal changes in selection. For each year, and separately for each sex, a generalised linear model (GLM) was constructed with relative LRS as the response variable and standardized body mass, foot length and AGDI as explanatory variables. The resulting slope, β, for each trait gave the selection gradient (Lande & Arnold 1983). To test for differences in the selection gradients between years, an analysis of covariance (ANCOVA) was performed for each sex separately. Relative LRS was the response variable and three two-way interactions between year and standardized body mass, foot length and AGDI were included as explanatory variables.

Selection gradients for each trait were regressed against population density and sex ratio to test these population-level factors as drivers of selection. As with phenotypic trait measurements, population density and sex ratios were estimated only for periods of reproductive activity, when competition for mates was greatest, to remove any potential effect of season on selection gradient estimates. All males in breeding condition and all females >16g during each breeding season were included in population density estimates (as in Chapter 4). The sex ratio was estimated as the number of males:females within population density estimates. Population density and sex ratio were tested for their relationship with annual trait selection gradients separately due to low samples sizes of selection gradient estimates (n=4). For each sex, a GLM was constructed for each trait separately, with annual selection gradient estimates as the response variable and either population density or sex ratio as the explanatory variable.

Heritability

Heritability was calculated for body mass, foot length and AGDI using a repeated measures multivariate animal model (Wilson *et al.* 2010). A multivariate structure was selected in order to test for genetic correlations between traits. The repeated measures approach was used as each individual had more than one adult trait measurement.

The animal model was constructed using the *R* software (v. 3.1.0, R Core Development Team 2014) and the package **MCMCglmm** (Hadfield 2010). Trait values were first log-transformed to normalise their distributions. All three traits were simultaneously included as response variables, specifying a Gaussian error distribution for all three. The interaction between sex and study year (categorical) was included as a fixed effect to account for differences in the mean value of traits between sexes and years. The pedigree, as described in Chapter 4, was specified in the model as a random effect to provide the breeding values of individuals. Individual identity was included as a random effect in order to control for within-individual variance in repeated trait value measurements and allow for a measure of repeatability (Wilson *et al.* 2010). Maternal and paternal identities were included as separate random effects to estimate the parental effects on phenotypic variance (Wilson *et al.* 2010).

MCMCglmm requires the specification of prior distributions for model parameters (Hadfield 2010). As no suggestions or evidence for the nature of priors were found in the literature regarding the phenotypic traits tested here in this species, I follow the recommendations of Wilson *et al.* (2010) and specify 'weak' priors. The prior distribution for each model parameter was specified as a variance-covariance matrix of the three traits divided by 5 (1 + the number of random effects, including the pedigree).

The model was set to run for 200,000 iterations with a burn-in period of 50,000 iterations and a thinning interval (sampling interval) of 120 iterations. These model settings were selected by trial-and-error in order to minimise autocorrelation in the estimates of variance components between iterations (body mass = 0.039; foot length = 0.023; AGDI = 0.010).

Estimates of heritability, parental effects, repeatability and genetic correlation also followed the methods provided by Wilson *et al.* (2010). Heritability for each trait was estimated by dividing the trait's additive genetic variance by the total phenotypic variance among parents. Maternal and paternal effects on each trait were calculated in the same way by dividing variance associated with maternal or paternal identity by the total phenotypic variance among parents. Repeatability is a measure of how constant individual repeated measurements are, and represents an upper limit to the heritability estimate of a trait. The repeatability of individual trait measurements was estimated as the sum of the additive genetic variance and within-individual variance divided by total phenotypic variance among parents. Genetic correlations between traits were estimated by dividing the additive genetic covariance of two traits by the square root of the product of the additive genetic variance of both traits. 95% confidence intervals for heritabilities, parental effects and genetic correlation estimates were calculated using Bayesian MCMC methods.

Response to selection

The response to selection was predicted for body mass, foot length and AGDI as the change in mean trait values ($\Delta\bar{\boldsymbol{z}}$) in males and females using the multivariate form of the Breeders equation (Lande 1979):

$$\Delta\bar{\boldsymbol{z}} = \mathbf{G}\mathbf{P}^{-\mathbf{1}}\beta.$$

where **G** is a matrix of the additive genetic variances and covariances of the traits, **P** is a matrix of the phenotypic variances and covariances of parental traits and β is a vector of the selection gradients of traits. The dimensions of the **G** and **P** matrices are equal to the number of traits, i.e. 3 x 3. The response to selection was calculated for each trait using the selection gradients estimated for 2012, in order to predict the change in the mean sizes of traits for the next generation of mice.

Results

Selection

Selection gradients (β) for all traits showed variation between years in both sexes (Table 5.1), but no significant interactions were found for either sex between year and body mass (ANCOVA: males, $F_{3,\,91} = 0.529$, $p = 0.664$; females, $F_{3,\,68} = 1.522$, $p = 0.217$), foot length (ANCOVA: males, $F_{3,\,91} = 0.0.217$, $p = 0.884$; females, $F_{3,\,68} = 0.753$, $p = 0.524$) or AGDI (ANCOVA: males, $F_{3,\,91} = 0.683$, $p = 0.565$; females, $F_{3,\,68} = 0.647$, $p = 0.588$). These results suggest that selection gradients were not significantly different between years for any trait.

Selection gradients for body mass were positive for all years in males and females, with the exception of 2010 in females (Table 5.1). Female body mass selection gradients were significantly different from zero in 2009 and 2012, with the largest β occurring in 2012. The largest male body mass β was in 2011, but this was not significant. Foot length in both sexes had consistently negative selection gradients, and were again significant in 2009 and 2012 for females, with the largest β in 2012. All male selection gradients for foot length were weak and non-significant. There was more variation in AGDI selection gradients across years, but none were significant in either sex. Male AGDI β were negative in 2009 and 2010 and positive in 2011 and 2012, the largest being in 2011. Female AGDI β were negative in 2009 and 2012, but positive in 2010 and 2011.

Table 5.1: Temporal variation in selection gradients (β) and significance tests for body mass, foot length and AGDI in males and females. Although there is some inter-annual variation, there were no significant differences in selection gradients between years for any trait. Selection gradients for females body mass and foot length were significant in both 2009 and 2012, but for all other years gradients were not significantly different from zero. S.E. = standard error of the estimate , df = residual degrees of freedom from *F*-tests.

Trait	Year	Males					Females				
		β	S.E.	df	*F*	*p*	β	S.E.	df	*F*	*p*
Body mass	2009	0.107	0.319	13	0.113	0.742	0.256	0.118	11	4.686	0.053
	2010	0.154	0.283	16	0.295	0.595	-0.245	0.142	7	2.999	0.127
	2011	0.717	0.612	25	1.371	0.253	0.147	0.287	22	0.262	0.614
	2012	0.166	0.199	37	0.693	0.411	0.437	0.157	28	7.576	0.010
Foot length	2009	-0.157	0.272	13	0.334	0.573	-0.186	0.093	11	3.99	0.071
	2010	-0.080	0.221	16	0.13	0.723	-0.141	0.134	7	1.111	0.327
	2011	-0.043	0.518	25	0.0071	0.933	-0.303	0.342	22	0.783	0.386
	2012	-0.198	0.221	37	0.8	0.377	-0.547	0.151	28	13.084	0.001
AGDI	2009	-0.012	0.306	13	0.001	0.970	-0.101	0.084	11	1.449	0.254
	2010	-0.041	0.374	16	0.012	0.914	0.196	0.197	7	0.992	0.352
	2011	0.662	0.572	25	1.342	0.258	0.311	0.397	22	0.613	0.442
	2012	0.245	0.194	37	1.599	0.214	-0.052	0.177	28	0.085	0.773

The relationships between population density and the strength of selection on phenotypic traits calculated in each year varied between traits and sexes (Figure 5.1). The only trait with a significant relationship between inter-annual selection gradients and population density was foot length in females (GLM: -0.0058 ± 0.0004, $F_{1,3} = 151.1$, p = 0.0065). Although the relationships between body mass gradients and population density were not significantly different from zero, population density explained a greater amount of

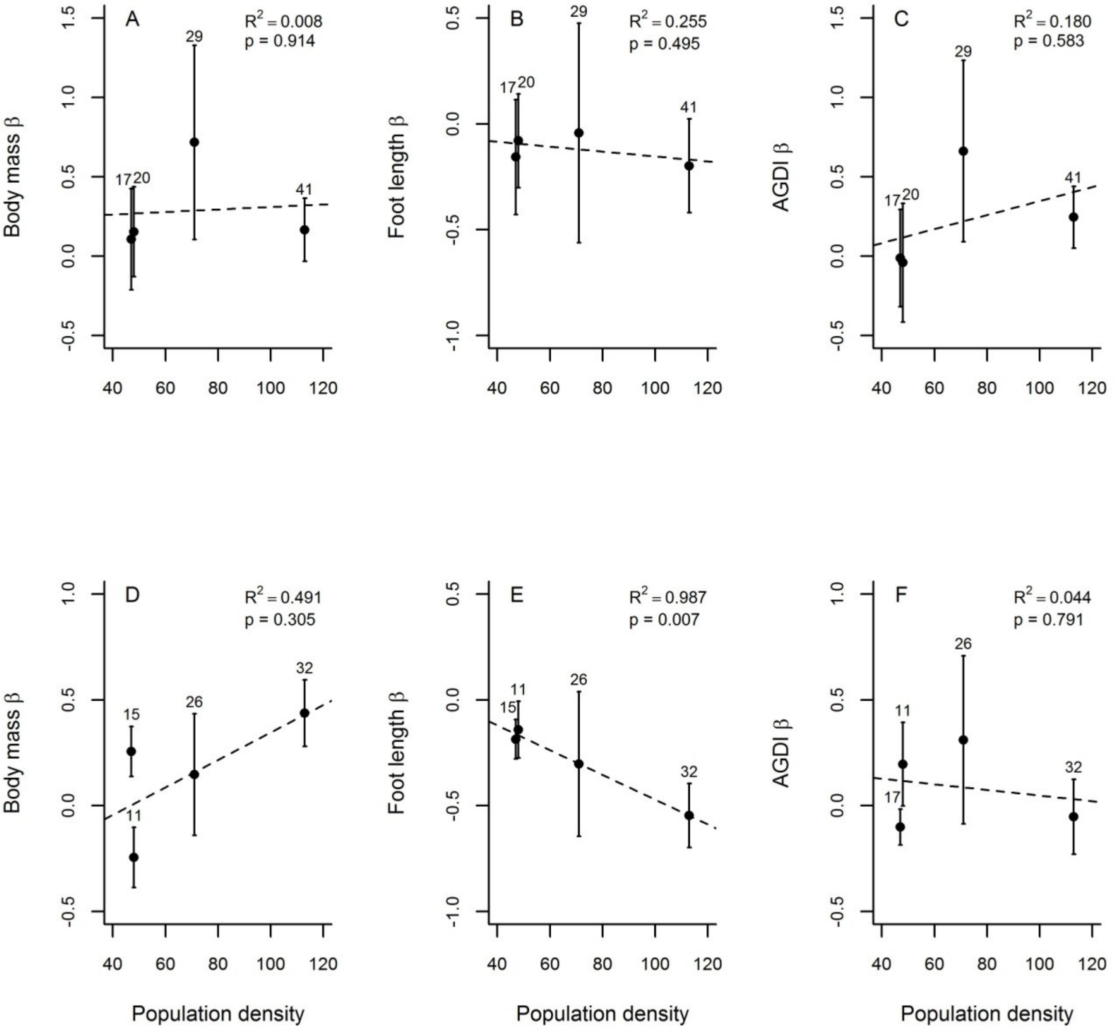


Figure 5.1: Male (A-C) and female (D-F) selection gradients (*β* ± S.E.) for body mass (A, D), foot length (B, E) and AGDI (C, F) and their relationships with population density during breeding seasons. Only selection gradients for female foot length (E) had a relationship with population density that was significantly different from zero. Numbers above error bars give the number of individuals used in the selection gradient estimate.

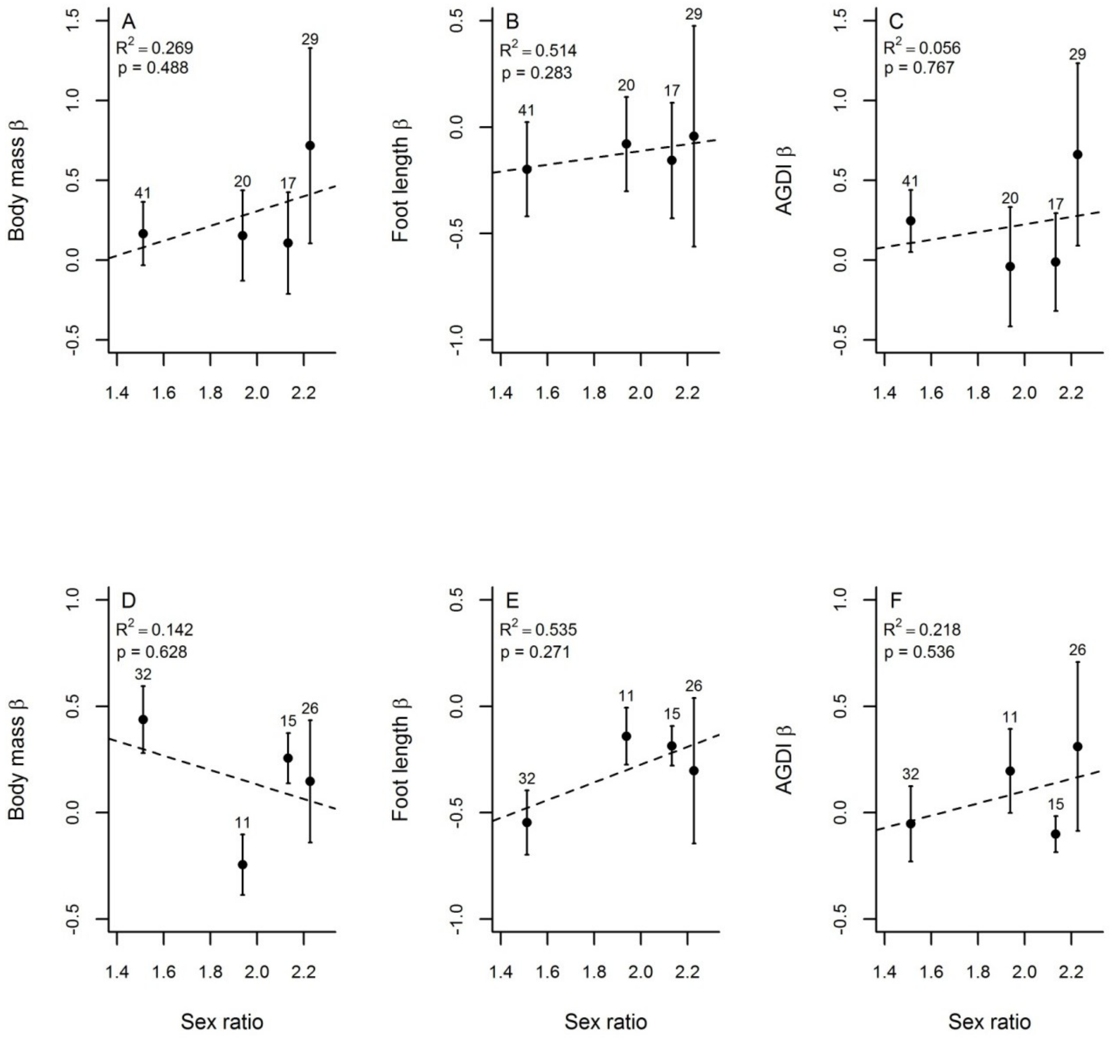


Figure 5.2: The relationships between sex ratio (male:female) and male (A-C) and female (D-F) selection gradients (*β* ± S.E.) for body mass (A, D), foot length (B, E) and AGDI (C, F). No selection gradients had a relationship with sex ratio that was significantly different from zero. Numbers above error bars give the sample size used to calculate *β*.

Sex ratio had a positive relationship with all trait selection gradients except female body mass (Figure 5.2), although none of the relationships between sex ratio and traits were found to be significant. Sex ratio explained a greater amount of variance in annual selection gradient estimates for body mass in males (R^2 = 0.269) compared to females (R^2 = 0.142). Variance explained by sex ratio for foot length gradients was similar between males (R^2 =

0.514) and females (R^2 = 0.535), but for AGDI estimates sex ratio explained more variance in females (R^2 = 0.218) versus males (R^2 = 0.056).

Heritability

The heritability estimates (h^2) for all three phenotypic traits were low but significant (Table 5.2). The heritability estimate for AGDI was twice as high as body mass. Foot length heritability was similar to body mass. Significant maternal and paternal effects were found for all three traits (Table 5.2). In each trait, estimates of maternal and paternal effects were similar in size to heritability estimates. Again, parental effects were greatest for AGDI, and similar between body mass and foot length. Repeatability of measurements, representing the upper limit possible for heritability estimates, was greatest for foot length and lowest for body mass (Table 5.2).

Table 5.2: Heritability (h^2), maternal effects and paternal effects with 95% confidence intervals of three measured phenotypic traits. Repeatability is the measure of how constant repeated adult trait measurements were, and represents the upper limit to heritability estimates.

Phenotypic trait	h^2 (95% CI)	Maternal effect (95% CI)	Paternal effect (95% CI)	Repeatability
Body mass	0.105 (0.043, 0.244)	0.11 (0.052, 0.231)	0.097 (0.044, 0.265)	0.345
Foot length	0.123 (0.057, 0.347)	0.103 (0.049, 0.241)	0.087 (0.039, 0.244)	0.499
AGDI	0.206 (0.132, 0.277)	0.185 (0.132, 0.264)	0.193 (0.126, 0.297)	0.387

By constructing multivariate animal models, testing the three traits together, it was possible to calculate the genetic correlations (cor_G) between those traits. No significant genetic correlation was found between either body mass and foot length ($cor_G = 0.198$, 95% CI = -0.431, 0.299), body mass and AGDI ($cor_G = -0. 069$, 95% CI = -0.431, 0.299), or AGDI and foot length ($cor_G = 0.181$, 95% CI = -0.212, 0.526).

Table 5.3: Variance-covariance matrices used in the multivariate Breeders equation. Above: **G** matrix - the additive genetic variance-covariance of phenotypic traits. Below: **P** matrix - total phenotypic variance-covariance of parental traits.

G	Body mass	Foot length	AGDI
Body mass	1.69×10^{-4}	2.93×10^{-5}	-8.38×10^{-5}
Foot length	2.93×10^{-5}	1.54×10^{-4}	1.68×10^{-4}
AGDI	-8.38×10^{-5}	1.68×10^{-4}	9.75×10^{-3}

P	Body mass	Foot length	AGDI
Body mass	1.89×10^{-3}	4.25×10^{-4}	6.82×10^{-3}
Foot length	4.25×10^{-4}	1.34×10^{-3}	6.20×10^{-3}
AGDI	6.82×10^{-3}	6.20×10^{-3}	0.389

Response to selection

The predicted short-term (generational) change in the mean of each phenotypic trait ($\Delta\bar{\mathbf{z}}$) was estimated for each sex using the multivariate form of the Breeders equation (Table 5.3). The largest response to selection was for female body mass (Table 5.4), which predicted a decrease in mean body mass of approximately 3.35g in the next generation, despite a positive selection gradient. This is due to the negative genetic covariance with AGDI. Mean male body mass was also predicted to decrease, but only by 0.91g. The response to selection for foot length was positive in both sexes (despite negative selection gradients) and slightly larger in females than males, resulting in a predicted increase of 1.28mm in females and 0.71mm in females. The response to selection for AGDI was small and negative in both sexes. AGDI was predicted to decrease by 0.02 (arbitrary units) in males, and 0.03 in females.

Table 5.4: The response to selection of phenotypic traits ($\Delta\bar{\mathbf{z}}$) for males and females, calculated using the multivariate form of the Breeders equation: $\Delta\bar{\mathbf{z}} = \mathbf{GP^{-1}}\boldsymbol{\beta}.$ The actual changes in mean trait values from the 2012 cohort ($\bar{\mathbf{z}}_{\mathbf{2012}}$) to the next generation ($\bar{\mathbf{z}}_{\boldsymbol{t}+\mathbf{1}}$) are predicted by: $\bar{\mathbf{z}}_{\boldsymbol{t}+\mathbf{1}} = \bar{\mathbf{z}}_{\mathbf{2012}} + \bar{\mathbf{z}}_{\mathbf{2012}}\Delta\bar{\mathbf{z}}$.

Sex	Trait	$\Delta\bar{\mathbf{z}}$	$\bar{z}_{2012}$	$\bar{z}_{t+1}$
Males	Body mass (g)	-0.049	22.09	21.00
	Foot length (mm)	0.032	22.02	22.73
	AGDI	-0.008	2.18	2.20
Females	Body mass (g)	-0.15	20.94	17.59
	Foot length (mm)	0.059	21.61	22.89
	AGDI	-0.044	0.69	0.66

Discussion

This study has shown that body mass, foot length and anogenital distance are all heritable traits in *A. sylvaticus*. The strength and direction of sexual selection on each trait varied between years, but this variation was not significant, nor was annual variation in trait selection gradients significantly related to sex ratio or population density, with the exception of female foot length. Across years, the only selection gradients to be significantly different from zero were for female body mass in 2009 and 2012, and female foot length in 2009 and 2012. Female body mass had a reasonably large response to selection, but in all other cases the responses to selection were very low, meaning changes in the population mean of trait sizes were also small.

Kingsolver *et al.* (2001) compared 993 estimates of selection presented in the literature between 1984 and 1997 for 62 species of plants, invertebrates and vertebrates. Their study concluded that the median selection gradient across a range of morphological traits was 0.16, with the vast majority of reported values being less than 0.3. A similar study reported that only 26% of directional selection gradients reported in the literature were significantly different from zero (Hoekstra *et al.* 2001). Selection gradient estimates in this study were below 0.3 in 18 out of 24 cases, and only 4 out of 24 were significantly different from zero. These results suggest that the selection gradients estimated here are in line with the pattern of estimates observed across previous studies (Hoekstra *et al.* 2001; Kingsolver *et al.* 2001).

Body mass had weak positive selection gradients for both sexes across all years with one exception, suggesting that larger body mass is generally sexually selected for in this population. In mammals, body size has been directly linked with fecundity or reproductive success (Chapter 4, Bünger *et al.* 2005) and competitive ability (Briffa & Sneddon 2007), both of which may explain the positive nature of the selection gradients estimated here. Larger, dominant females are able to outcompete smaller females for high-quality habitat, allowing higher offspring survival, while larger males can outcompete other males for access to receptive females. I predicted that selection on body mass should be positive and strongest at high population densities and sex ratios. No significant relationships were found between body mass and these population-level factors, however, suggesting that other factors, such as food abundance, may drive selection on body mass in this species. The sample size for these analyses were very low, however, and so are unlikely to represent the true dynamics of selection in this population. The response to selection for female body mass seems unrealistic. A mean body mass in females of 17.59g in the next generation suggests that the average mouse would never reach the lowest adult mass of the previous generation (~19g). Given that I have previously shown a strong relationship between female body mass and reproductive success (Chapter 4), and the selection gradients calculated here for body mass were mostly positive, including the 2012 estimate used to calculate the response to selection, this prediction must be artificially inflated.

AGDI selection gradients had the most variation between sexes and years of any trait, but none were significantly different from zero. The response to selection was small and negative for both sexes, but larger in females. AGD has been shown to correlate with individual testosterone levels (vom Saal & Bronson 1980; Vandenbergh & Huggett 1995; Ryan & Vandenbergh 2002). Testosterone can confer fitness benefits in terms of increased aggression or dominance (Preston *et al.* 2003; Muller & Wrangham 2004), sperm quality (Malo *et al.* 2009) and mate-seeking behaviour (Preston *et al.* 2012), all of which can increase a male's reproductive success. Based on these previous findings, I predicted that, similar to body mass, selection on AGDI would be strongly positive for both sexes in years with high competition. This prediction was not met, however, as no significant relationships were found for either sex between AGDI and population density or sex ratio. High testosterone levels have also been linked to immunosuppression and reduced resistance to parasites (Folstad & Karter 1992; Jacobson & Ansari 2004; Malo *et al.* 2009). Inter-annual variation in the abundance of parasites may, therefore, be a better predictor of the strength and direction of selection on anogenital distance than population density or sex ratio.

Foot length was consistently selected against in both males and females over time, but the response to selection in this trait was positive in both sexes. This is due to the genetic and phenotypic covariances with body mass and AGDI which are included in the response to selection calculation by the multivariate Breeders equation. Traits may share at least part of the same underlying genetic architecture and be affected in similar ways by environmental variation (Mackay 2001; Flint & Mackay 2009). The response to selection of each trait can therefore be indirectly influenced by the selection and heritability of other traits.

The heritability estimates for all three traits were low, but significant. There are currently no reports in the literature of heritability estimates for any of the three traits tested here for any species of the Genus *Apodemus*. Body mass is a commonly tested trait within heritability studies on laboratory mice, *Mus domesticus*, however. Reports of body mass heritability in these studies are typically around 0.5 (Beniwal *et al.* 1992; Jones, Nielsen & Britton 1992; Nielsen, Kirby & Clutter 1996), although Dohm *et al*. (1996) reported lower estimates, ranging from 0.126 to 0.386. There are few reports of body mass heritability in wild rodent populations. Sadowska *et al.* (2005) reported a heritability of 0.5 in the bank vole, *Clethrionomys glareolus*, while Nespolo *et al.* (2003) estimated a non-significant heritability close to zero for wild leaf-eared mice (*Phyllotis darwinii*). Only one study provided an estimate for the heritability of anogenital distance (Fouqueray *et al.* 2014), reporting a significant heritability of 0.14 in yellow-bellied marmots (*Marmota flaviventris*), similar to the heritability reported here. No reports of the heritability of foot length were found in rodents. The most anatomically similar measurements found in the literature were for the femur and tibia in laboratory mice, with heritability estimates of 0.32 - 0.75 and 0.13 - 0.60 respectively (Leamy 1974). Comparison of heritability estimates between studies can be misleading, due to differences in the environmental sources of phenotypic variance controlled for in different models, which ultimately affects the heritability estimate. For example, the large difference between body mass heritabilities presented here versus laboratory studies may partially result from the careful regulation of food availability and consumption between individuals in the laboratory, which cannot be controlled for in this study of a wild population. Regardless of the differences between heritability estimates here and other studies, all three traits in this study had significant estimates, showing that variation in these traits between individuals is partly driven by additive genetic effects.

Significant maternal and paternal effects were found for all three traits. These effects represent the variance in phenotypic traits resulting from the 'common environment' of siblings, or the combination of parental genetic and phenotypic effects on offspring phenotypes (Wolf & Wade 2009). Maternal effects on body mass and foot length could be attributed to variation between mothers in the energy provided for offspring growth and development during gestation and lactation (Amusquivar *et al.* 2000; Passos *et al.* 2000). Individual AGD is affected by the intra-uterine position of siblings during gestation (vom Saal & Bronson 1980; vom Saal & Dhar 1992; Vandenbergh & Huggett 1995; Ryan & Vandenbergh 2002). As a steroid, testosterone is able to permeate the fatty membranes of amniotic sacs separating foetuses and enter the amniotic fluid surrounding adjacent siblings (vom Saal & Dhar 1992). Individuals (male or female) neighbouring male siblings are exposed to a larger concentration of testosterone *in utero* than individuals surrounded by female siblings (vom Saal & Bronson 1980; vom Saal & Dhar 1992). Higher testosterone exposure during embryonic development results in a larger AGD of the individual (Vandenbergh & Huggett 1995), and in this way differences in the maternal environment of the uterus between different litters of siblings can result in variation in AGD, and therefore the maternal effect observed here.

I have previously shown body mass and anogenital distance to relate to home range size and home range overlap in this species. Excluding the seemingly inflated response to selection for female body mass, the small responses to selection of these traits suggest that neither home range size nor the degree of home range overlap between individuals will change significantly in the next generation in response to the minor shifts in the means of these two traits. Variation in ecological factors between generations, such as food abundance, are more likely to drive inter-generational changes to patterns of space use than minor changes in the distribution of phenotypic traits. Further research could use the results from this and previous chapters to construct a path analysis that would disentangle the direct and indirect links between individual genetic variation, phenotypic variation, habitat, population-level factors and the emergent spatial patterns that result from individual space use.

Chapter 6

Conclusions

Summary of findings

Space use differed between seasons, habitats, sexes and in relation to body mass, body fat and testosterone (by proxy of anogenital distance, AGD). Individual home ranges during non-breeding periods were approximately half the size, on average, of home ranges during the early breeding season, a time when males began to enter breeding condition and both sexes spread out after winter in an attempt to establish home ranges that would maximise their reproductive success. There was also an effect of season on the degree of home range overlap between males, whereby males overlapped with each other significantly more during the breeding season than the non-breeding season.

Seasonal variation influenced space use patters differently in males and females. During breeding periods, the periphery regions of home ranges - the area of a home range surrounding the core - were 20-50% larger (early-late breeding seasons respectively) for males than for females, an effect that was not observed during non-breeding seasons. There were also differences between the sexes in home range overlap during breeding seasons, with the degree of home range overlap between females being approximately 40% less than male-male and approximately 25% less than male-female overlap on average.

Season also interacted with habitat type to influence the size of the home ranges. In breeding seasons, core regions of home ranges in both males and females decreased as home ranges encompassed a larger area of high-quality, low-predation risk *Rhododendron*, compared to those occupying open woodland. In non-breeding seasons, however, home range size was not related to habitat quality. Between-season differences in space use were also explained by an interaction between sex and habitat. Across both breeding and non-breeding seasons together, home range overlap in high-quality habitat did not differ between sexes. In low-quality, high predation-risk habitat (open woodland), however, males overlapped with other males approximately 20% more than they did with females, and 40% more than females overlapped with other females. However, when breeding seasons were considered independently of non-breeding seasons, differences in overlap behaviour between sexes was observed within high-quality *Rhododendron* habitat, with male-male and male-female overlap being 40% and 30% greater, respectively, than female-female overlap.

The relationships between individual space use and body mass, body fat and testosterone differed between sexes and habitat types. In the early breeding season, core regions of home ranges increased in relation to body mass in males, but decreased in females. During the same season male core regions increased as male body fat reserves decreased, but this relationship was not found for females. Home range peripheries were smaller for both males and females with higher body fat reserves than those with lower reserves. Variation in both sex and habitat caused variation in the relationship between body fat and home range overlap. In the open woodland, female-female overlap was greater between individuals that differed in their body fat reserves (i.e. one individual with high body fat, the other low) compared to females with similar body fat reserves. Overlap between females occupying patches of *Rhododendron*, however, was not driven by differences in body fat reserves. Males showed the opposite pattern: inside *Rhododendron* there was significantly less overlap between males with similar body fat reserves than those with dissimilar fat reserves, but in the open woodland there was no effect of body fat on home range overlap. Sex-related differences in the role of testosterone as a driver of space use were found for both home range size and overlap. Male core and periphery size increased with individual testosterone levels in the late breeding season, but in females this trend was found for the non-breeding season. Habitat interacted with testosterone in males, resulting in greater overlap between males with similar testosterone levels than dissimilar males inside patches of *Rhododendron*, but no effect of testosterone on male-male overlap was observed in open woodland. Similarly, high-testosterone males were found to overlap with females less than low-testosterone males inside *Rhododendron*, but no such relationship was found in open woodland.

Home range overlap, reproductive success and the number of reproductive partners for both sexes were all found to be density-dependent. Home range overlap between males, between females and between males and females all decreased as population density increased. The number of reproductive partners for both sexes increased with both population density and the male-bias in the sex ratio. Male and female reproductive success also increased as the male-bias in the sex ratio increased. Population density and sex ratio also indirectly affected individual reproductive success, as the number of offspring produced by both males and females increased with the number of reproductive partners. Seasonal body mass - the mean body mass for the breeding season in which individuals were reproductively active (excluding pregnant females) - was found to have a positive relationship with reproductive success in both males and females. Body fat had a significant negative relationship with female reproductive success, but this is likely to be evidence of a response to the energetic costs of reproduction on females. Regarding the effects of demographic parameters, results revealed that offspring recruitment and immigration were strong drivers of the relatedness, or genetic diversity, of the population.

Body mass, anogenital distance and foot length were all found to have a low but significant heritability in this species, with additive genetic variance explaining the greatest proportion of total phenotypic variance in anogenital distance. Furthermore, significant parental, or 'common environment' effects were found to explain a similar proportion of total phenotypic variation as additive genetic variation in all traits. Selection gradients for traits showed some variance between years, but annual differences were not significant. Selection gradients for foot length had a significant negative relationship with population density, but no other significant relationships were found between population density or sex ratio and male or female traits. The responses to selection for male and female traits were low, and the predicted short-term changes in the population mean of traits were unlikely to have any concomitant effect on space use. The exception to this was the response to selection of female body mass which predicted an unrealistic, single-generation shift in the population mean of female body mass of 3.35g.

Limitations of the study

"Predation-risk" in this thesis was measured by proxy of dense shrub cover (*Rhododendron* and bamboo) that provide a physical and visual barrier to aerial predators. I believe the assumption that dense shrub cover resulted in lower rates of predation was fair, given similar findings of previous studies assessing predation in small mammals (Kotler *et al.* 1991; Longland & Price 1991; Bowers & Dooley 1993) and the considerable increase in mouse density and trapability under patches of *Rhododendron* and bamboo versus the open woodland (Malo *et al.* 2013). An estimate of predator density was attempted using camera traps, but in the few months they were in operation at the study site, before they all broke at the first sign of rain, I was only able to identify a fox, a badger, some dogs and our Masters students.

This study also lacked estimates of food availability for the mice. Starting in 2011, seed traps were distributed around the study site in an attempt to quantify the abundance of their main food sources, tree seeds. The design only yielded a quality of data that allowed me to infer the timings of seed fall, but not the spatial distribution. In 2012 the design was improved, but no seeds fell that year. As the spatial data for estimating home ranges was collected between March 2010 and 2013, there was insufficient data to perform an analysis relating food availability to space use.

Conclusions

Taken together, the results of this thesis suggest that the mechanism behind space use in this population of *A. sylvaticus* involves interactions between season, habitat, sex and the three individual-level factors tested. Seasonal effects relate to the shift in behaviour from non-breeding to breeding periods, which occurs as a result of physiological changes driven by changes in photoperiod and food availability (Pinter & Negus 1965; Demas & Nelson 1998). *Rhododendron*, the habitat type that reduces predation risk, is highly important for a prey species such as the wood mouse (*A. sylvaticus*), and is, as a result, a sought-after resource, which drives competition between individuals and the roles of individual-level factors relating to competitive ability. The effects of sex on space use result from the polygamous mating system, confirmed in this population, which leads to differential space use patterns between sexes, as each sex has differing requirements for maximising their reproductive success. Population density and sex ratio, both shown to be direct drivers of space use and reproduction in this species, also relate to the degree of polygamy expressed in both males and females (Emlen & Oring 1977). Body fat and testosterone, two physiological traits which have received little attention in the literature in relation to space use, have been shown to be just as, if not more important as drivers of space use than the more commonly tested body mass. As physiology inherently drives an individual's state, space use is inevitably affected as well.

Body mass and anogenital distance were both found to be heritable traits. Given their importance in driving variation in space use, these results provide evidence of a genetic component to space use in this species. However, at this stage it is only possible to conclude that the actions of genes on space use are indirect, by generating variation in phenotypic traits that drive space use. The small responses to selection observed for each trait also suggest that, under similar selective pressures as the ones quantified here, gene-driven changes to space use patterns will happen very slowly, and will most likely be indistinguishable between generations. As traits were also subject to variance as a result of maternal and paternal 'common environment' effects, disentangling the long-term effects of genes on space use from the effects of a changing environment (which governs the nature of selection on traits) will be very challenging. To do so will require methods that isolate the specific genetic architecture responsible for modular behaviours, which combine to form the complex behavioural patterns we broadly define as 'space use'.

This thesis has highlighted the direct relationships between both individual phenotypic variation, habitat and population-level factors with individual variation in home range size and the degree of home range overlap between individuals. Indirect relationships with space use patterns were also suggested by the heritability of phenotypic traits relating to variation in home range size and overlap. Further work could use these results to construct a path analysis that better disentangles the direct and indirect relationships between genetic variation, individual-level factors, habitat and population-level factors as well as their relationships with space use patterns.

References

Alatalo, R. V, Eriksson, D., Gustafsson, L., Larsson, K., Alatalo, R. V, Eriksson, D.A.G., Gustafsson, L. & Larsson, K. (1987) Exploitation competition influences the use of foraging sites by tits: experimental evidence. *Ecology*, **68**, 284–290.

Alberini, C.M. (1999) Genes to remember. *Journal of Experimental Biology*, **202**, 2887–2891.

Albert, D.J., Walsh, M.L., Gorzalka, B.B., Siemens, Y. & Louie, H. (1986) Testosterone removal in rats results in a decrease in social aggression and a loss of social dominance. *Physiology & Behavior*, **36**, 401–407.

Albon, S.D., Staines, H.J., Guinness, F.E. & Cluttonbrock, T.H. (1992) Density-dependent changes in the spacing behavior of female kin in red deer. *Journal of Animal Ecology*, **61**, 131–137.

Amusquivar, E., Rupérez, F.J., Barbas, C. & Herrera, E. (2000) Low arachidonic acid rather than alpha-tocopherol is responsible for the delayed postnatal development in offspring of rats fed fish oil instead of olive oil during pregnancy and lactation. *The Journal of Nutrition*, **130**, 2855–2865.

Andersson, M. & Iwasa, Y. (1996) Sexual selection. *Trends in Ecology & Evolution*, **11**, 53–58.

Andreassen, H.P. & Ims, R. A. (1998) The effects of experimental habitat destruction and patch isolation on space use and fitness parameters in female root vole Microtus oeconomus. *Journal of Animal Ecology*, **67**, 941–952.

Andreassen, H.P. & Ims, R.A. (2001) Dispersal in patchy vole populations: Role of patch configuration, density dependence, and demography. *Ecology*, **82**, 2911–2926.

Arditi, R. & Dacorogna, B. (1988) Optimal foraging on arbitrary food distributions and the definition of habitat patches. *The American Naturalist*, **131**, 837–846.

Arlet, M.E., Kaasik, A., Molleman, F., Isbell, L., Carey, J.R. & Mänd, R. (2011) Social factors increase fecal testosterone levels in wild male gray-cheeked mangabeys (Lophocebus albigena). *Hormones and Behavior*, **59**, 605–611.

Arnott, G. & Elwood, R.W. (2009) Assessment of fighting ability in animal contests. *Animal Behaviour*, **77**, 991–1004.

Arora, N., Van Noordwijk, M.A., Ackermann, C., Willems, E.P., Nater, A., Greminger, M., Nietlisbach, P., Dunkel, L.P., Utami Atmoko, S.S., Pamungkas, J., Perwitasari-Farajallah, D., Van Schaik, C.P. & Krützen, M. (2012) Parentage-based pedigree reconstruction reveals female matrilineal clusters and male-biased dispersal in nongregarious Asian great apes, the Bornean orang-utans (Pongo pygmaeus). *Molecular Ecology*, **21**, 3352–3362.

Arsenault, R. & Owen-Smith, N. (2002) Facilitation versus competition in grazing herbivore assemblages. *Oikos*, **3**, 313–318.

Atkinson, S.N. & Ramsay, M.A. (1995) The effects of prolonged fasting of the body composition and reproductive success of female Polar Bears (Ursus maritimus). *Functional Ecology*, **9**, 559–567.

Ayres, H., Ferreira, R.M., Torres-Júnior, J.R. de S., Demétrio, C.G.B., de Lima, C.G. & Baruselli, P.S. (2009) Validation of body condition score as a predictor of subcutaneous fat in Nelore (Bos indicus) cows. *Livestock Science*, **123**, 175–179.

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M. & Sims, P.L. (1996) Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, **49**, 386–400.

Baker, R.J., Makova, K.D. & Chesser, R.K. (1999) Microsatellites indicate a high frequency of multiple paternity in Apodemus (Rodentia). *Molecular Ecology*, **8**, 107–111.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) Linear mixed-effects models using Eigen and S4. http://CRAN.R-project.org/package=lme4

Barnett, S.A. & Bathard, A.H. (1953) Population dynamics of sewer rats. *The Journal of Hygiene*, **51**, 483–491.

Bartness, T.J., Demas, G.E. & Song, C.K. (2002) Seasonal changes in adiposity: the roles of the photoperiod, melatonin and other hormones, and sympathetic nervous system. *Experimental Biology and Medicine*, **227**, 363–376.

Beaugrand, G., Brander, K.M., Alistair Lindley, J., Souissi, S. & Reid, P.C. (2003) Plankton effect on cod recruitment in the North Sea. *Nature*, **426**, 661–664.

Benhamou, S. & Bovet, P. (1989) How animals use their environment: a new look at kinesis. *Animal Behaviour*, **38**, 375–383.

Beniwal, B.K., Hastings, I.M., Thompson, R. & Hill, W.G. (1992) Estimation of changes in genetic parameters in selected lines of mice using REML with an animal model. 2. Body weight, body composition and litter size. *Heredity*, **69**, 361–371.

Ben-Shahar, Y., Robichon, A., Sokolowski, M.B. & Robinson, G.E. (2002) Influence of gene action across different time scales on behavior. *Science*, **296**, 741–4.

Berger, K.M. & Gese, E.M. (2007) Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology*, **76**, 1075–1085.

Beyer, H.L., Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M. & Matthiopoulos, J. (2010) The interpretation of habitat preference metrics under use–availability designs. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2245–2254.

Bjørneraas, K., Herfindal, I., Solberg, E.J., Sæther, B.E., van Moorter, B. & Rolandsen, C.M. (2012) Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. *Oecologia*, **168**, 231–243.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–35.

Bond, M.L. & Wolff, J.O. (1999) Does access to females or competition among males limit male home-range size in a promiscuous rodent? *Journal of Mammalogy*, **80**, 1243–1250.

Bonin, C.A., Goebel, M.E., Hoffman, J.I. & Burton, R.S. (2014) High male reproductive success in a low-density Antarctic fur seal (Arctocephalus gazella) breeding colony. *Behavioral Ecology and Sociobiology*, **68**, 597–604.

Boon, A.K., Reale, D. & Boutin, S. (2008) Personality , habitat use , and their consequences for survival in North American red squirrels Tamiasciurus hudsonicus. *Oikos*, **117**, 1321–1328.

Booth, W., Montgomery, W.I. & Prodöhl, P.A. (2007) Polyandry by wood mice in natural populations. *Journal of Zoology*, **273**, 176–182.

Booth, W., Montgomery, W.I. & Prodöhl, P.A. (2009) Spatial genetic structuring in a vagile species, the European wood mouse. *Journal of Zoology*, **279**, 219–228.

Börger, L., Dalziel, B.D. & Fryxell, J.M. (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, **11**, 637–50.

Börger, L., Franconi, N., Ferretti, F., Meschi, F., de Michele, G., Gantz, A. & Coulson, T. (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *The American Naturalist*, **168**, 471–485.

Born, C., Kjellberg, F., Chevallier, M.-H., Vignes, H., Dikangadissi, J.-T., Sanguié, J., Wickings, E.J. & Hossaert-McKey, M. (2008) Colonization processes and the maintenance of genetic diversity: insights from a pioneer rainforest tree, Aucoumea klaineana. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2171–2179.

Bourke, A.F.G. (2014) Hamilton's rule and the causes of social evolution. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, **369**, 20130362.

Bowers, M.A. & Dooley, J.L. (1993) Predation hazard and seed removal by small mammals : microhabitat versus patch scale effects. *Oecologia*, **94**, 247–254.

Bowler, D.E. & Benton, T.G. (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, **80**, 205–225.

Boydston, E.E., Kapheim, K.M., Watts, H.E., Szykman, M. & Holekamp, K.E. (2003) Altered behaviour in spotted hyenas associated with increased human activity. *Animal Conservation*, **6**, 207–219.

Boyer, N., Réale, D., Marmet, J., Pisanu, B. & Chapuis, J.L. (2010) Personality, space use and tick load in an introduced population of Siberian chipmunks Tamias sibiricus. *Journal of Animal Ecology*, **79**, 538–547.

Briffa, M. & Elwood, R.W. (2005) Rapid change in energy status in fighting animals: causes and effects of strategic decisions. *Animal Behaviour*, **70**, 119–124.

Briffa, M. & Sneddon, L.U. (2007) Physiological constraints on contest behaviour. *Functional Ecology*, **21**, 627–637.

Broquet, T., Viard, F. & Yearsley, J.M. (2013) Genetic drift and collective dispersal can result in chaotic genetic patchiness. *Evolution*, **67**, 1660–1675.

Brown, P.R. & Lundie-Jenkins, G. (1999) Non-target mortalities during aerial strychnine baiting of house mice. *Wildlife Research*, **26**, 117–128.

Brown, J.L. & Orians, G.H. (1970) Spacing patterns in mobile animals. *Annual Review of Ecology and Systematics*, **1**, 239–262.

Brown, P.R., Tuan, N.P., Singleton, G.R., Ha, P.T.T., Hoa, P.T., Hue, D.T., Tan, T.Q., Tuat, N. Van, Jacob, J. & Müller, W.J. (2006) Ecologically based management of rodents in the real world: applied to a mixed agroecosystem in Vietnam. *Ecological Applications*, **16**, 2000–2010.

Bryja, J., Patzenhauerová, H., Albrecht, T., Mošanský, L., Stanko, M. & Stopka, P. (2008) Varying levels of female promiscuity in four Apodemus mice species. *Behavioral Ecology and Sociobiology*, **63**, 251–260.

Bshary, R. & Noe, R. (1997) Red colobus and Diana monkeys provide mutual protection against predators. *Animal Behaviour*, **54**, 1461–1474.

Buesching, C.D., Newman, C., Twell, R. & Macdonald, D.W. (2008) Reasons for arboreality in wood mice Apodemus sylvaticus and Bank voles Myodes glareolus. *Mammalian Biology*, **73**, 318–324.

Bünger, L., Lewis, R.M., Rothschild, M.F., Blasco, A., Renne, U. & Simm, G. (2005) Relationships between quantitative and reproductive fitness traits in animals. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **360**, 1489–1502.

Burt, W.H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, **24**, 346–352.

Byrom, A. (2003) Predation risk and behaviour during dispersal: implications for population dynamics of rodents. *ACIAR Monograph*, **96**, 165–168.

Calenge, C. (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.

Calsbeek, R. & Cox, R.M. (2010) Experimentally assessing the relative importance of predation and competition as agents of selection. *Nature*, **465**, 613–616.

Campioni, L., Delgado, M.D.M., Lourenço, R., Bastianelli, G., Fernández, N. & Penteriani, V. (2013) Individual and spatio-temporal variations in the home range behaviour of a long-lived, territorial species. *Oecologia*, **172**, 371–385.

Cantoni, D., Glaizot, O. & Brown, R.E. (1999) Effects of sex composition of the litter on anogenital distance in California mice (Peromyscus californicus). *Canadian Journal of Zoology*, **77**, 124–131.

Carfagno, G.L.F. & Weatherhead, P.J. (2008) Energetics and space use: intraspecific and interspecific comparison of movements and home ranges of two Colubrid snakes. *Journal of Animal Ecology*, **77**, 416–424.

Carrière, M.-A., Bulté, G. & Blouin-Demers, G. (2009) Spatial ecology of Northern Map Turtles (Graptemys geographica) in a lotic and a lentic habitat. *Journal of Herpetology*, **43**, 597–604.

Chang, Y.M., Rekaya, R., Gianola, D. & Thomas, D.L. (2001) Genetic variation of lactation curves in dairy sheep: A Bayesian analysis of Wood’s function. *Livestock Production Science*, **71**, 241–251.

Charnov, E.L. (1976a) Optimal foraging: attack strategy of a mantid. *The American Naturalist*, **110**, 141–151.

Charnov, E.L. (1976b) Optimal foraging, marginal value theorem. *Theoretical Population Biology*, **9**, 129–136.

Chaverri, G., Gamba-Rios, M. & Kunz, T.H. (2007) Range overlap and association patterns in the tent-making bat Artibeus watsoni. *Animal Behaviour*, **73**, 157–164.

Clark, R.W., Schuett, G.W., Repp, R.A., Amarello, M., Smith, C.F. & Herrmann, H.-W. (2014) Mating systems, reproductive success, and sexual selection in secretive species: a case study of the western diamond-backed rattlesnake, Crotalus atrox. *PloS One*, **9**, e90616.

Clarke, J.R. (1985) The reproductive biology of the bank vole (Clethrionomys glareolus) and the wood mouse (Apodemus sylvaticus). *Symposium of the Zoological Society of London*.

Clutton-Brock, T.H. (1989) Mammalian mating systems. *Proceedings of the Royal Society B: Biological Sciences*, **236**, 339–72.

Clutton-Brock, T.H., Hodge, S.J., Spong, G., Russell, A.F., Jordan, N.R., Bennett, N.C., Sharpe, L.L. & Manser, M.B. (2006) Intrasexual competition and sexual selection in cooperative mammals. *Nature*, **444**, 1065–1068.

Clutton-Brock, T.H., Rose, K.E. & Guinness, F.E. (1997) Density-related changes in sexual selection in red deer. *Proceedings of the Royal Society B: Biological Sciences*, **264**, 1509–1516.

Clutton-Brock, T.H. & Vincent, A.C.J. (1991) Sexual selection and the potential reproductive rates of males and females. *Nature*, **351**, 58–60.

Coleman, T.H., Schwartz, C.C., Gunther, K.A. & Creel, S. (2013) Grizzly bear and human interaction in Yellowstone National Park: An evaluation of bear management areas. *The Journal of Wildlife Management*, **77**, 1311–1320.

Coltman, D.W., Pilkington, J., Kruuk, L.E., Wilson, K. & Pemberton, J.M. (2001) Positive genetic correlation between parasite resistance and body size in a free-living ungulate population. *Evolution*, **55**, 2116–2125.

Conner, J. (1989) Density-dependent sexual selection in the fungus beetle, Bolitotherus cornutus. *Evolution*, **43**, 1378–1386.

Conner, J., Rush, S., Kercher, S. & Jennetten, P. (1996) Measurements of natural selection on floral traits in wild radish (Raphanus raphanistrum). II. Selection through lifetime male and total fitness. *Evolution*, **50**, 1137–1146.

Cook, J.G., Grande, L.A., Johnson, B.K., Cook, R.C., Riggs, R.A., Bryant, L.D. & Irwin, L.L. (2004) Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs*, **155**, 1–61.

Corp, N., Gorman, M.L. & Speakman, J.R. (1997) Ranging behaviour and time budgets of male wood mice Apodemus sylvaticus in different habitats and seasons. *Oecologia*, **109**, 242–250.

Correa, L.A, Frugone, M.J. & Soto-Gamboa, M. (2013) Social dominance and behavioral consequences of intrauterine position in female groups of the social rodent Octodon degus. *Physiology & behavior*, **119**, 161–7.

Coster, A. (2012) pedigree: Pedigree functions. http://CRAN.R-project.org/package=pedigree

Crawley, M.J. (2007) *The R Book*, 1st ed. Wiley Publishing.

Cumming, G.S. & Cornélis, D. (2012) Quantitative comparison and selection of home range metrics for telemetry data. *Diversity and Distributions*, **18**, 1057–1065.

Cushman, S.A. (2006) Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation*, **128**, 231–240.

Cuyler, C. & Oritsland, N.A. (2004) Rain more important than windchill for insulation loss in Svalbard reindeer fur. *Rangifer*, **24**, 7–14.

Dahle, B. & Swenson, J.E. (2003) Home ranges in adult Scandinavian brown bears (Ursus arctos): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology*, **260**, 329–335.

Dakin, E.E. & Avise, J.C. (2004) Microsatellite null alleles in parentage analysis. *Heredity*, **93**, 504–509.

Danielson, B.J. (1991) Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. *The American Naturalist*, **138**, 1105–1120.

Dawson, D.A., Ball, A.D., Spurgin, L.G., Martín-Gálvez, D., Stewart, I.R.K., Horsburgh, G.J., Potter, J., Molina-Morales, M., Bicknell, A.W.J., Preston, S.A.J., Ekblom, R., Slate, J. & Burke, T. (2013) High-utility conserved avian microsatellite markers enable parentage and population studies across a wide range of species. *BMC Genomics*, **14**, 176.

Demas, G.E. & Nelson, R.J. (1998) Photoperiod, ambient temperature, and food availability interact to affect reproductive and immune function in adult male deer mice (Peromyscus maniculatus). *Journal of Biological Rhythms*, **13**, 253–262.

Diaz, M., Torre, I., Peris, A. & Tena, L. (2005) Foraging behavior of wood mice as related to presence and activity of genets. *Journal of Mammalogy*, **86**, 1178–1185.

Dingemanse, N.J., Both, C., van Noordwijk, A.J., Rutten, A.L. & Drent, P.J. (2003) Natal dispersal and personalities in great tits (Parus major). *Proceedings of the Royal Society B: Biological Sciences*, **270**, 741–747.

Dohm, M.R., Hayes, J.P. & Garland, T. (1996) Quantitative genetics of sprint running speed and swimming endurance in laboratory house mice (Mus domesticus). *Evolution*, **50**, 1688–1701.

Domecq, J.J., Skidmore, A.L., Lloyd, J.W. & Kaneene, J.B. (1995) Validation of body condition scores with ultrasound measurements of subcutaneous fat of dairy cows. *Journal of Dairy Science*, **78**, 2308–2313.

Donnelly, M.A. (1989) Effects of reproductive resource supplementaiton on space-use patters in Dendrobates pumilio. *Oecologia*, **81**, 212–218.

Donovan, T.M., Freeman, M., Abouelezz, H., Royar, K., Howard, A. & Mickey, R. (2011) Quantifying home range habitat requirements for bobcats (Lynx rufus) in Vermont, USA. *Biological Conservation*, **144**, 2799–2809.

Drickamer, L.C. (1996) Intra-uterine position and anogenital distance in house mice: consequences under field conditions. *Animal Behaviour*, **51**, 925–934.

Drickamer, L.C., Robinson, A.S. & Mossman, C.A. (2001) Differential responses to same and opposite sex odors by adult house mice are associated with anogenital distance. *Ethology*, **107**, 509–519.

Duckworth, R.A. (2006) Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology*, **17**, 1011–1019.

Duong, T. (2007) ks: Kernel density estimation and kernel discriminant analysis for multivariate data in R. *Journal Of Statistical Software*, **21**, 1–16.

Ecuyer-dab, I. & Robert, M. (2004) Have sex differences in spatial ability evolved from male competition for mating and female concern for survival? *Cognition*, **91**, 221–257.

Edmonson, A.J., Lean, I.J., Weaver, L.D., Farver, T. & Webster, G. (1989) A body condition scoring chart for Holstein dairy cows. *Journal of Dairy Science*, **72**, 68–78.

Ekdahl, S., Malmgren, J. & Andersson, P.-Å. (2007) Modelling terrestrial interactions and shelter use in great crested newts (Triturus cristatus). *Amphibia-Reptilia*, **28**, 205–215.

Ellegren, H. & Sheldon, B.C. (2008) Genetic basis of fitness differences in natural populations. *Nature*, **452**, 169–175.

Emlen, S. & Oring, L. (1977) Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.

Epstein, M.P., Duren, W.L. & Boehnke, M. (2000) Improved inference of relationship for pairs of individuals. *American Journal of Human Genetics*, **67**, 1219–1231.

Fagan, W.F., Lutscher, F. & Schneider, K. (2007) Population and community consequences of spatial subsidies derived from central-place foraging. *The American Naturalist*, **170**, 902–15.

Fahrig, L. (1988) A general model of populations in patchy habitats. *Applied Mathematics and Computation*, **27**, 53–66.

Falconer, D.S. & Mackay, T.F.C. (1996) *Introduction to Quantitative Genetics*, 4th ed. Longman Group Ltd., Essex, UK.

Fernández, G. & Lank, D.B. (2012) Territorial behavior of western sandpipers on their nonbreeding grounds: effect of sex and foraging interference. *Journal of Field Ornithology*, **83**, 272–281.

Fernández, M.H. & Vrba, E.S. (2005) Body size, biomic specialization and range size of African large mammals. *Journal of Biogeography*, **32**, 1243–1256.

Festa-Bianchet, M., Gaillard, J.-M. & Jorgenson, J.T. (1998) Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *The American Naturalist*, **152**, 367–379.

Fieberg, J. (2007) Utilization distribution estimation using weighted kernel density estimators. *Journal of Wildlife Management*, **71**, 1669–1675.

Fieberg, J. & Börger, L. (2012) Could you please phrase "home range" as a question? *Journal of Mammalogy*, **93**, 890–902.

Fieberg, J. & Kochanny, C.O. (2005) Quantifying home-range overlap: the importance of the utilization distribution. *Journal of Wildlife Management*, **69**, 1346–1359.

Fink, S., Excoffier, L. & Heckel, G. (2007) High variability and non-neutral evolution of the mammalian avpr1a gene. *BMC Evolutionary Biology*, **7**, 176–190.

Fisher, D.O. & Lara, M.C. (1999) Effects of body size and home range on access to mates and paternity in male bridled nailtail wallabies. *Animal Behaviour*, **58**, 121–130.

Fitzpatrick, M.J., Ben-Shahar, Y., Smid, H.M., Vet, L.E.M., Robinson, G.E. & Sokolowski, M.B. (2005) Candidate genes for behavioural ecology. *Trends in Ecology & Evolution*, **20**, 96–104.

Flint, J. & Mackay, T.F.C. (2009) Genetic architecture of quantitative traits in mice, flies, and humans. *Genome Research*, **19**, 723–733.

Flowerdew, J.R. (1974) Field and laboratory experiments on the social behaviour and population dynamics of the wood mouse (Apodemus sylvaticus). *Journal of Animal Ecology*, **43**, 499–511.

Flowerdew, J.R. (1985) The population dynamics of wood mice and yellow-necked mice. *Symposium of the Zoological Society of London*.

Fokidis, H.B., Risch, T.S. & Glenn, T.C. (2007) Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism. *Animal Behaviour*, **73**, 479–488.

Folstad, I. & Karter, A.J. (1992) Parasites, bright males, and the immunocompetence handicap. *The American Naturalist*, **139**, 603.

Fouqueray, T.D., Blumstein, D.T., Monclús, R. & Martin, J.G.A. (2014) Maternal effects on anogenital distance in a wild marmot population. *PloS one*, **9**, e92718.

Fox, C.W., Waddell, K.J. & Mousseau, T.A. (1995) Parental host plant affects offspring life histories in a seed beetle. *Ecology*, **76**, 402–411.

Gabathuler, U., Bennett, N.C. & Jarvis, J.U.M. (1996) The social structure and dominance hierarchy of the Mashona mole-rat, Cryptomys darlingi (Rodentia: Bathyergidae) for Zimbabwe. *Journal of Zoology*, **240**, 221–231.

Gaines, M.S. & McClenaghan, L.R. (1980) Dispersal in small mammals. *Annual Review of Ecology and Systematics*, **11**, 163–196.

Galea, L.A.M., Kavaliers, M. & Ossenkopp, K. (1996) Sexually dimorphic spatial learning in meadow voles Microtus pennsylvanicus and deer mice Peromyscus maniculatus. *Journal of Experimental Biology*, **199**, 195–200.

Galea, L.A., Kavaliers, M., Ossenkopp, K.P. & Hampson, E. (1995) Gonadal hormone levels and spatial learning performance in the Morris water maze in male and female meadow voles, Microtus pennsylvanicus. *Hormones and Behavior*, **29**, 106–25.

Gallavan, R.H., Holson, J.F., Stump, D.G., Knapp, J.F. & Reynolds, V.L. (1999) Interpreting the toxicologic significance of alterations in anogenital distance: potential for confounding effects of progeny body weights. *Reproductive Toxicology*, **13**, 383–390.

Garant, D. & Kruuk, L.E.B. (2005) How to use molecular marker data to measure evolutionary parameters in wild populations. *Molecular Ecology*, **14**, 1843–1859.

Garant, D., Kruuk, L.E.B., McCleery, R.H. & Sheldon, B.C. (2004) Evolution in a changing environment: a case study with great tit fledging mass. *The American Naturalist*, **164**, 115–129.

Gaulin, S.J.C. & FitzGerald, R.W. (1986) Sex differences in spatial ability: an evolutionary hypothesis and test. *The American Naturalist*, **127**, 74–88.

Gaulin, S.J.C. & FitzGerald, R.W. (1989) Sexual selection for spatial-learning ability. *Animal Behaviour*, **37**, 322–331.

Gautestad, A.O. & Mysterud, I. (2010a) Spatial memory, habitat auto-facilitation and the emergence of fractal home range patterns. *Ecological Modelling*, **221**, 2741–2750.

Gautestad, A.O. & Mysterud, I. (2010b) The home range fractal: from random walk to memory-dependent space use. *Ecological Complexity*, **7**, 458–470.

Getz, L.L., Oli, M.K., Hofmann, J.E. & McGuire, B. (2005a) Habitat-specific demography of sympatric vole populations over 25 years. *Journal of Mammalogy*, **86**, 561–568.

Getz, L.L., Oli, M.K., Hofmann, J.E., McGuire, B. & Ozgul, A. (2005b) Factors influencing movement distances of two species of sympatric voles. *Journal of Mammalogy*, **86**, 647–654.

Girard, I., Ouellet, J.-P., Courtois, R., Dussault, C. & Breton, L. (2002) Effects of sampling effort based on GPS telemetry on home-range size estimations. *The Journal of Wildlife Management*, **66**, 1290–1300.

Girard-Buttoz, C., Heistermann, M., Krummel, S. & Engelhardt, A. (2009) Seasonal and social influences on fecal androgen and glucocorticoid excretion in wild male long-tailed macaques (Macaca fascicularis). *Physiology and Behavior*, **98**, 168–175.

Gittleman, J.L. & Thompson, S.D. (1988) Energy allocation in mammalian reproduction. *Integrative and Comparative Biology*, **28**, 863–875.

Gitzen, R.A., Millspaugh, J.J. & Kernohan, B.J. (2006) Bandwidth selection for fixed-kernel analysis of animal utilization distributions bandwidth selection for fixed-kernel analysis of animal utilization distributions. *Journal of Wildlife Management*, **70**, 1334–1344.

Glazier, D.S., Glazier, D.S., Eckert, S.E. & Eckert, S.E. (2002) Competitive ability, body size and geographical range size in small mammals. *Journal of Biogeography*, **29**, 81–92.

Gockel, J., Harr, B., Schlötterer, C., Arnold, W., Gerlach, G. & Tautz, D. (1997) Isolation and characterization of microsatellite loci from Apodemus flavicollis (rodentia, muridae) and Clethrionomys glareolus (rodentia, cricetidae). *Molecular Ecology*, **6**, 597–599.

Godsall, B., Coulson, T. & Malo, A.F. (2014) From physiology to space use: energy reserves and androgenization explain home-range size variation in a woodland rodent. *The Journal of Animal Ecology*, **83**, 126–135.

Godvik, I.M.R., Loe, L.E., Vik, J.O., Veiberg, V., Langvatn, R. & Mysterud, A. (2009) Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology*, **90**, 699–710.

Grant, P.R. & Grant, B.R. (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science*, **296**, 707–711.

Gray, T.N.E., Chamnan, H., Collar, N.J. & Dolman, P.M. (2009) Sex-specific habitat use by a lekking bustard: conservation implication for the critically endangered Bengal florican (Houbaropsis bengalensis) in an Intensifying Agroecosystem. *The Auk*, **126**, 112–122.

Greenberg, C.H. (2002) Response of white-footed mice (Peromyscus leucopus) to coarse woody debris and microsite use in southern Appalachian treefall gaps. , **164**, 57–66.

Greenwood, P.J. (1978) Timing of activity of the bank vole Clethrionomys glareolus and the wood mouse Apodemus sylvaticus in a deciduous woodland. *Oikos*, **31**, 123–127.

Guichoux, E., Lagache, L., Wagner, S., Chaumeil, P., Léger, P., Lepais, O., Lepoittevin, C., Malausa, T., Revardel, E., Salin, F. & Petit, R.J. (2011) Current trends in microsatellite genotyping. *Molecular Ecology Resources*, **11**, 591–611.

Gurnell, J. (1972) *Studies on the Behaviour of Wild Wood Mice, Apodemus Sylvaticus*. University of Exeter.

Gurnell, J. (1978) Seasonal changes in numbers and male behavioural interaction in a population of wood mice Apodemus sylvaticus. *Journal of Animal Ecology*, **47**, 741–755.

Gurnell, J. (1993) Tree seed production and food conditions for rodents in an aak wood in southern England. *Forestry*, **66**, 291–315.

Hadfield, J.D. (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, **33**, 1–22.

Haenel, G.J., Smith, L.C. & John-Alder, H.B. (2003) Home-Range Analysis in Sceloporus undulatus (Eastern Fence Lizard). I. Spacing Patterns and the Context of Territorial Behavior. *Copeia*, **2003**, 99–112.

Hansson, L. (1985) The food of bank voles, wood mice and yellow-necked mice. *Symposium of the Zoological Society of London*.

Harr, B., Musolf, K. & Gerlach, G. (2000) Characterization and isolation of DNA microsatellite primers in wood mice (Apodemus sylvaticus, Rodentia). *Molecular Ecology*, **9**, 1664–1665.

Hartl, D.L. & Conner, J.K. (2004) *A Primer of Ecological Genetics*, 1st ed. Sinauer Associates, Inc.

Hazel, L.N. (1943) The genetic basis for constructing selection indexes. *Genetics*, **28**, 476–490.

Heisenberg, M. (1997) Genetic approach to neuroethology. *BioEssays*, **19**, 1065–1073.

Henderson, C.R. (1976) A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. *Biometrics*, **32**, 69–83.

Hobbs, N.T. (1996) Modification of ecosystems by ungulates. *The Journal of Wildlife Management*, **60**, 695–713.

Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hoang, A., Hill, C.E., Beerli, P. & Kingsolver, J.G. (2001) Strength and tempo of directional selection in the wild. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 9157–9160.

Holleley, C.E. & Geerts, P.G. (2009) Multiplex Manager 1.0: a cross-platform computer program that plans and optimizes multiplex PCR. *BioTechniques*, **46**, 511–517.

Horne, J.S. & Garton, E.O. (2006) Selecting the best home range model: an information-theoretic approach. *Ecology*, **87**, 1146–1152.

Hoset, K.S., Galliard, J.-F.L., Gundersen, G. & Steen, H. (2007) Home range size and overlap in female root voles: effects of season and density. *Behavioral Ecology*, **19**, 139–145.

Huang, B., Wey, T.W. & Blumstein, D.T. (2011) Correlates and consequences of dominance in a social rodent. *Ethology*, **117**, 573–585.

Hubbs, A.H. & Boonstra, R. (1998) Effects of food and predators on the home-range sizes of Arctic ground squirrels (Spermophilus parryii). *Canadian Journal of Zoology*, **76**, 592–596.

Hurst, J.L., Hall, S., Roberts, R. & Christian, C. (1996) Social organization in the aboriginal house mouse, Mus spretus Lataste: Behavioural mechanisms underlying the spatial dispersion of competitors. *Animal Behaviour*, **51**, 327–344.

Hygnstrom, S.E., VerCauteren, K.C., Hines, R.A. & Mansfield, C.W. (2000) Efficacy of in-furrow zinc phosphide pellets for controlling rodent damage in no-till corn. *International Biodeterioration and Biodegradation*, **45**, 215–222.

Ims, R.A. (1987a) Responses in spatial organization and behaviour to manipulations of the food resource in the vole Clethrionomys rufocanus. *Journal of Animal Ecology*, **56**, 585–596.

Ims, R.A. (1987b) Male spacing systems in Microtine rodents. *The American Naturalist*, **130**, 475–484.

Ims, R.A. (1989) Kinship and origin effects on dispersal and space sharing in Clethrionomys rufocanus. *Ecology*, **70**, 607–616.

Indermaur, L., Gehring, M., Wehrle, W., Tockner, K. & Naef-Daenzer, B. (2009) Behavior-based scale definitions for determining individual space use: requirements of two amphibians. *The American Naturalist*, **173**, 60–71.

Insel, T.R. & Young, L.J. (2000) Neuropeptides and the evolution of social behavior. *Current Opinion in Neurobiology*, **10**, 784–789.

Jacob, A., Evanno, G., Renai, E., Sermier, R. & Wedekind, C. (2009) Male body size and breeding tubercles are both linked to intrasexual dominance and reproductive success in the minnow. *Animal Behaviour*, **77**, 823–829.

Jacobson, J.D. & Ansari, M.A. (2004) Immunomodulatory actions of gonadal steroids may be mediated by gonadotropin-releasing hormone. *Endocrinology*, **145**, 330–6.

Jacquard, A. (1983) Heritability: one word, three concepts. *Biometrics*, **39**, 465–477.

Janzen, F.J. & Stern, H.S. (1998) Logistic regression for empirical studies of multivariate selection. *Evolution*, **52**, 1564–1571.

Jarne, P. & Lagoda, P.J. (1996) Microsatellites, from molecules to populations and back. *Trends in Ecology & Evolution*, **11**, 424–429.

Jenkins, A.R. (2000) Hunting mode and success of African Peregrines Falco peregrinus minor: does nesting habitat quality affect foraging efficiency? *Ibis*, **142**, 235–246.

Jennings, D.J., Carlin, C.M., Hayden, T.J. & Gammell, M.P. (2010) Investment in fighting in relation to body condition, age and dominance rank in the male fallow deer, Dama dama. *Animal Behaviour*, **79**, 1293–1300.

Jensen, S.P. (1993) Temporal changes in food preferences of wood mice (Apodemus sylvaticus L.). *Oecologia*, **94**, 76–82.

Jensen, T.S. & Nielsen, O.F. (1986) Rodents as seed dispersers in a heath-oak wood succession. *Oecologia*, **70**, 214–221.

Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. (2004) The scaling of animal space use. *Science*, **306**, 266–8.

Jirotkul, M. (1999) Population density influences male-male competition in guppies. *Animal Behaviour*, **58**, 1169–1175.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.

Johnson, M.L. & Gaines, M.S. (1990) Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics*, **21**, 449–480.

Jones, A.G. & Ardren, W.R. (2003) Methods of parentage analysis in natural populations. *Molecular Ecology*, **12**, 2511–2523.

Jones, L.D., Nielsen, M.K. & Britton, R.A. (1992) Genetic variation in liver mass, body mass, and liver:body mass in mice. *Journal of Animal Science*, **70**, 2999–3006.

Jones, O.R. & Wang, J. (2010) COLONY: a program for parentage and sibship inference from multilocus genotype data. *Molecular Ecology Resources*, **10**, 551–555.

Jonsson, P., Hartikainen, T., Koskela, E. & Mappes, T. (2002) Determinants of reproductive success in voles: space use in relation to food and litter size manipulation. *Evolutionary Ecology*, **16**, 455–467.

Kaczmarek, L. & Chaudhuri, A. (1997) Sensory regulation of immediate-early gene expression in mammalian visual cortex: implications for functional mapping and neural plasticity. *Brain Research Reviews*, **23**, 237–56.

Kalinowski, S.T., Taper, M.L. & Marshall, T.C. (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, **16**, 1099–1106.

Kasumovic, M.M., Bruce, M.J., Andrade, M.C.B. & Herberstein, M.E. (2008) Spatial and temporal demographic variation drives within-season fluctuations in sexual selection. *Evolution*, **62**, 2316–2325.

Kellam, J.S., Lucas, J.R. & Wingfield, J.C. (2006) The role of testosterone in male downy woodpeckers in winter home range use, mate interactions and female foraging behaviour. *Animal Behaviour*, **71**, 695–707.

Keller, L.F. & Waller, D.M. (2002) Inbreeding effects in wild populations. *Trends in Ecology and Evolution*, **17**, 230–241.

Kelt, D.A. & Van Vuren, D.H. (2001) The ecology and macroecology of mammalian home range area. *The American Naturalist*, **157**, 637–645.

Kenkre, V.M., Giuggioli, L., Abramson, G. & Camelo-Neto, G. (2007) Theory of hantavirus infection spread incorporating localized adult and itinerant juvenile mice. *The European Physical Journal B*, **55**, 461–470.

Kernohan, B.J., Gitzen, R.A. & Millspaugh, J.J. (2001) Analysis of animal space use and movements. *Radio tracking and animal populations* (eds J.J. Millspaugh & J.M. Marzluff), pp. 125–166. Academic Press, New York, New York, USA.

Khammes, N. & Aulagnier, S. (2007) Diet of the wood mouse, Apodemus sylvaticus in three biotopes of Kabylie of Djurdjura (Algeria). *Folia Zoologica*, **56**, 243–252.

Kie, J.G. & Bowyer, R.T. (1999) Sexual segregation in white-tailed deer: Density-dependent changes in use of space, habitat selection, and dietary niche. *Journal of Mammalogy*, **80**, 1004–1020.

Kie, J.G., Matthiopoulos, J., Fieberg, J., Powell, R.A., Cagnacci, F., Mitchell, M.S., Gaillard, J. & Moorcroft, P.R. (2010) The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2221–2231.

Kikkawa, J. (1964) Movement, activity and distribution of the small rodents Clethrionomys glareolus and Apodemus sylvaticus in woodland. *Journal of Animal Ecology*, **33**, 259–299.

Kinghorn, B.P. (2011) An algorithm for efficient constrained mate selection. *Genetics, Selection, Evolution : GSE*, **43**, 4.

Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E., Hoang, A., Gibert, P. & Beerli, P. (2001) The strength of phenotypic selection in natural populations. *The American Naturalist*, **157**, 245–261.

Kingsolver, J.G. & Pfennig, D.W. (2007) Patterns and power of phenotypic selection in nature. *BioScience*, **57**, 561.

Kjellander, P., Hewison, A.J.M., Liberg, O., Angibault, J.-M., Bideau, E. & Cargnelutti, B. (2004) Experimental evidence for density-dependence of home-range size in roe deer (Capreolus capreolus L.): a comparison of two long-term studies. *Oecologia*, **139**, 478–485.

Klemme, I. & Hanski, I. (2009) Heritability of and strong single gene (Pgi) effects on life-history traits in the Glanville fritillary butterfly. *Journal of Evolutionary Biology*, **22**, 1944–1953.

Klemme, I., Ylönen, H. & Eccard, J.A. (2007) Reproductive success of male bank voles (Clethrionomys glareolus): The effect of operational sex ratio and body size. *Behavioral Ecology and Sociobiology*, **61**, 1911–1918.

Konopka, R.J. & Benzer, S. (1971) Clock mutants of Drosophila melanogaster. *Proceedings of the National Academy of Sciences of the United States of America*, **68**, 2112–6.

Koressaar, T. & Remm, M. (2007) Enhancements and modifications of primer design program Primer3. *Bioinformatics*, **23**, 1289–1291.

Korsten, P., van Overveld, T., Adriaensen, F. & Matthysen, E. (2013) Genetic integration of local dispersal and exploratory behaviour in a wild bird. *Nature Communications*, **4**, 2362.

Kotler, B.P., Brown, J.S. & Hasson, O. (1991) Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology*, **72**, 2249–2260.

Koubi, H.E., Robin, J.P., Dewasmes, G., Le Maho, Y., Frutoso, J. & Minaire, Y. (1991) Fasting-induced rise in locomotor activity in rats coincides with increased protein utilization. *Physiology & Behavior*, **50**, 337–343.

Krivan, V. (1997) Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. *The American Naturalist*, **149**, 164–178.

Kruuk, L.E.B. (2004) Estimating genetic parameters in natural populations using the “animal model”. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **359**, 873–890.

Kruuk, L.E.B., Slate, J. & Wilson, A.J. (2008) New answers for old questions: the evolutionary quantitative genetics of wild animal populations. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 525–548.

Kvarnemo, C. & Ahnesjö, I. (1996) The dynamics of operational sex ratios and competition for mates. *Trends in Ecology and Evolution*, **11**, 404–408.

Lacy, R.C. (1987) Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection, and population subdivision. *Conservation Biology*, **1**, 143–158.

Lair, H. (1987) Estimating the location of the focal center in red squirrel home ranges. *Ecology*, **68**, 1092–1101.

Lande, R. (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution*, **30**, 314–334.

Lande, R. (1979) Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution*, **33**, 402–416.

Lande, R. & Arnold, S.J. (1983) The measurement of selection on correlated characters. *Evolution*, **37**, 1210–1226.

Lande, R. & Shannon, S. (1996) The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution*, **50**, 434–437.

Landgraf, R., Kessler, M.S., Bunck, M., Murgatroyd, C., Spengler, D., Zimbelmann, M., Nussbaumer, M., Czibere, L., Turck, C.W., Singewald, N., Rujescu, D. & Frank, E. (2007) Candidate genes of anxiety-related behavior in HAB/LAB rats and mice: focus on vasopressin and glyoxalase-I. *Neuroscience and Biobehavioral Reviews*, **31**, 89–102.

Landman, M., Schoeman, D.S. & Kerley, G.I.H. (2013) Shift in black rhinoceros diet in the presence of elephant: evidence for competition? *PloS One*, **8**, e69771.

Lane, J.E., Boutin, S., Gunn, M.R. & Coltman, D.W. (2009) Sexually selected behaviour: red squirrel males search for reproductive success. *The Journal of Animal Ecology*, **78**, 296–304.

Larsen, C.T., Holand, A.M., Jensen, H., Steinsland, I. & Roulin, A. (2014) On estimation and identifiability issues of sex-linked inheritance with a case study of pigmentation in Swiss barn owl (Tyto alba). *Ecology and Evolution*, **4**, 1555–1566.

Laver, P.N. & Kelly, M.J. (2008) A critical review of home range studies. *Journal of Wildlife Management*, **72**, 290–298.

Lavergne, S. & Molofsky, J. (2007) Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3883–3888.

Leamy, L. (1974) Heritability of osteometric traits in a randombred population of mice. *The Journal of Heredity*, **65**, 109–120.

Legendre, P. & Fortin, M.J. (1989) Spatial pattern and ecological analysis. *Vegetatio*, **80**, 107–138.

Lenormand, T. (2002) Gene flow and the limits to natural selection. *Trends in Ecology & Evolution*, **17**, 183–189.

Lima, S.L. & Zollner, P.A. (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution*, **11**, 131–135.

Litt, M. & Luty, J.A. (1989) A hypervariable microsatellite revealed by in vitro amplification of a dinucleotide repeat within the cardiac muscle actin gene. *American Journal of Human Genetics*, **44**, 397–401.

Liu, X.H., Yue, L.F., Wang, D.W., Li, N. & Cong, L. (2013) Inbreeding avoidance drives consistent variation of fine-scale genetic structure caused by dispersal in the seasonal mating system of Brandt’s voles. *PloS One*, **8**, e58101.

Lodé, T. (2009) For a few males more: Do changes in sex ratio predict reproductive success and offspring survival? *Evolutionary Ecology Research*, **11**, 95–107.

Longland, W.S. & Price, M. V. (1991) Direct observations of owls and Heteromyid rodents: can predation risk explain microhabitat use? *Ecology*, **72**, 2261.

Lott, D.F. (1991) *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge University Press, Cambridge.

Lurz, P.W.W., Garson, P.J. & Wauters, L.A. (2000) Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (Sciurus vulgaris L.). *Journal of Zoology*, **251**, 167–178.

Macdonald, D.W., Hart, B.J., Manley, W.J. & Feber, R.E. (2001) Habitat use by wood mice (Apodemus sylvaticus) in a changeable arable landscape. *Journal of Zoology*.

Mackay, T.F.C. (2001) The genetic architecture of quantitative traits. *Annual Review of Genetics*, **35**, 303–339.

Madsen, T. & Shine, R. (1993) Temporal variability in sexual selection acting on reproductive tactics and body size in male snakes. *The American Naturalist*, **141**, 167–171.

Maestripieri, D. (1992) Functional aspects of maternal aggression in mammals. *Canadian Journal of Zoology*, **70**, 1069–1077.

Maher, C.R. & Lott, D.F. (1995) Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour*, **49**, 1581–1597.

Maher, C.R. & Lott, D.F. (2000) A review of ecological determinants of territoriality within vertebrate species. *The American Midland Naturalist*, **143**, 1–29.

Majolo, B. & Ventura, R. (2004) Apparent feeding association between Japanese macaques (Macaca fuscata yakui) and sika deer (Cervus nippon) living on Yakushima Island , Japan. *Ethology Ecology & Evolution*, **16**, 33–40.

Makova, K.D., Patton, J.C., Krysanov E.Yu., Chesser, R.K. & Baker, R.J. (1998) Microsatellite markers in wood mouse and striped field mouse (genus Apodemus). *Molecular Ecology*, **7**, 247–249.

Malo, A.F., Godsall, B., Prebble, C., Grange, Z., McCandless, S., Taylor, A. & Coulson, T. (2013) Positive effects of an invasive shrub on aggregation and abundance of a native small rodent. *Behavioral Ecology*, **24**, 759–767.

Malo, A.F., Martinez-Pastor, F., Alaks, G., Dubach, J. & Lacy, R.C. (2010) Effects of genetic captive-breeding protocols on sperm quality and fertility in the white-footed mouse. *Biology of Reproduction*, **83**, 540–8.

Malo, A.F., Roldan, E.R.S., Garde, J.J., Soler, A.J., Vicente, J., Gortazar, C. & Gomendio, M. (2009) What does testosterone do for red deer males? *Proceedings of the Royal Society B: Biological Sciences*, **276**, 971–80.

Mantel, N. (1967) The detection of disease clustering and a generalized regresion approach. *Cancer Research*, **27**, 209–220.

Marden, J.H. & Rollins, R.A. (1994) Assessment of energy reserves by damselflies engaged in aerial contests for mating territories. *Animal Behaviour*, **48**, 1023–1030.

Marmet, J., Pisanu, B., Chapuis, J.-L., Jacob, G. & Baudry, E. (2012) Factors affecting male and female reproductive success in a chipmunk (Tamias sibiricus) with a scramble competition mating system. *Behavioral Ecology and Sociobiology*, **66**, 1449–1457.

Matthiopoulos, J. (2003a) Model-supervised kernel smoothing for the estimation of spatial usage. *Oikos*, **102**, 367–377.

Matthiopoulos, J. (2003b) The use of space by animals as a function of accessibility and preference. *Ecological Modelling*, **159**, 239–268.

Mauritzen, M., Belikov, S.E., Boltunov, A.N., Derocher, A.E., Hansen, E., Ims, R.A., Wiig, Ø. & Yoccoz, N. (2003) Functional responses in polar bear habitat selection. *Oikos*, **100**, 112–124.

McAdam, A.G. & Boutin, S. (2003) Variation in viability selection among cohorts of juvenile red squirrels (Tamiasciurus hudsonicus). *Evolution*, **57**, 1689–1697.

Mcloughlin, P.D., Ferguson, S.H. & Messier, F. (2000) Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology*, **14**, 39–60.

Meerburg, B.G., Singleton, G.R. & Kijlstra, A. (2009) Rodent-borne diseases and their risks for public health. *Critical Reviews in Microbiology*, **35**, 221–270.

Miller, E.J., Eldridge, M.D.B., Cooper, D.W. & Herbert, C.A. (2010) Dominance, body size and internal relatedness influence male reproductive success in eastern grey kangaroos (Macropus giganteus). *Reproduction, Fertility, and Development*, **22**, 539–49.

Miller, J.A., Pusey, A.E., Gilby, I.C., Schroepfer-Walker, K., Catherine Markham, A. & Murray, C.M. (2013) Competing for space: female chimpanzees are more aggressive inside than outside their core areas. *Animal Behaviour*, **87**, 147–152.

Milner, J.M., Pemberton, J.M., Brotherstone, S. & Albon, S.D. (2000) Estimating variance components and heritabilities in the wild: a case study using the “animal model” approach. *Journal of Evolutionary Biology*, **13**, 804–813.

Mitchell, M.S. & Powell, R.A. (2004) A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling*, **177**, 209–232.

Möller, L.M. (2012) Sociogenetic structure, kin associations and bonding in delphinids. *Molecular Ecology*, **21**, 745–764.

Monclús, R. & Blumstein, D.T. (2012) Litter sex composition affects life-history traits in yellow-bellied marmots. *Journal of Animal Ecology*, **81**, 80–86.

Monclús, R., Cook, T. & Blumstein, D.T. (2012) Masculinized female yellow-bellied marmots initiate more social interactions. *Biology Letters*, **8**, 208–210.

Montgomery, W.I. (1989) Population regulation in the wood mouse Apodemus sylvaticus. I. Density dependence in the annual cycle of abundance. *Journal of Animal Ecology*, **58**, 465–475.

Montgomery, W.I. & Gurnell, J. (1985) The behaviour of Apodemus. *Symposium of the Zoological Society of London*.

Morales, J.M. & Ellner, S.P. (2002) Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology*, **83**, 2240–2247.

Morandin, C., Loveridge, A.J., Segelbacher, G., Elliot, N., Madzikanda, H., Macdonald, D.W. & Höglund, J. (2014) Gene flow and immigration: genetic diversity and population structure of lions (Panthera leo) in Hwange National Park, Zimbabwe. *Conservation Genetics*, **15**, 697–706.

Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**, 1–13.

Mowles, S.L. & Briffa, M. (2012) Forewarned is forearmed: early signals of RHP predict opponent fatigue in hermit crab shell fights. *Behavioral Ecology*, **23**, 1324–1329.

Mueller, T. & Fagan, W.F. (2008) Search and navigation in dynamic environments - From individual behaviors to population distributions. *Oikos*, **117**, 654–664.

Muller, K.L., Stamps, J.A., Krishnan, V. V & Willits, N.H. (1997) The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (Troglodytes aedon). *The American Naturalist*, **150**, 650–661.

Muller, M.N. & Wrangham, R.W. (2004) Dominance, aggression and testosterone in wild chimpanzees: a test of the “challenge hypothesis.” *Animal Behaviour*, **67**, 113–123.

Murphy, P.J. (2003) Does reproductive site choice in a neotropical frog mirror variable risks facing offspring? *Ecological Monographs*, **73**, 45–67.

Nakano, S. (1995) Individual differences in resource use , growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. *Journal of Animal Ecology*, **64**, 75–84.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19052–19059.

Nemtzov, S.C. (1997) Intraspecific variation in home range exclusivity by female green razorfish, Xyrichtys splendens (family Labridae), in different habitats. *Environmental Biology of Fishes*, **50**, 371–381.

Nespolo, R.F., Bacigalupe, L.D. & Bozinovic, F. (2003) Heritability of energetics in a wild mammal, the leaf-eared mouse (Phyllotis darwini). *Evolution*, **57**, 1679–1688.

Nielsen, M.K., Kirby, Y.L.K. & Clutter, A.C. (1996) Estimates of heritabilities and genetic and environmental correlations for left- and right-side uterine capacity and ovulation rate in mice. *Journal of Animal Science*, **74**, 529–534.

Niitepõld, K., Smith, A.D., Osborne, J.L., Reynolds, D.R., Carreck, N.L., Martin, A.P., Marden, J.H., Ovaskainen, O. & Hanski, I. (2009) Flight metabolic rate and Pgi genotype influence butterfly dispersal rate in the field. *Ecology*, **90**, 2223–2232.

Nonacs, P. (2001) State dependent behavior and the Marginal Value Theorem. *Behavioral Ecology*, **12**, 71–83.

Nunn, C.L., Thrall, P.H. & Kappeler, P.M. (2014) Shared resources and disease dynamics in spatially structured populations. *Ecological Modelling*, **272**, 198–207.

Olsson, M., Wapstra, E., Healey, M., Schwartz, T. & Uller, T. (2008) Selection on space use in a polymorphic lizard. *Evolutionary Ecology Research*, **10**, 621–627.

Ostfeld, R.S. (1985) Limiting resources and territoriality in Microtine rodents. *The American Naturalist*, **126**, 1–15.

Ostfeld, R.S. (1990) The ecology of territoriality in small mammals. *Trends in Ecology & Evolution*, **5**, 411–415.

Palanza, P. & Parmigiani, S. (1994) Functional analysis of maternal aggression in the house mouse (Mus musculus domesticus). *Behavioural Processes*, **32**, 1–16.

Passos, M.C.F., Ramos, C.F. & Moura, E.G. (2000) Short and long term effects of malnutrition in rats during lactation on the body weight of offspring. *Nutrition Research*, **20**, 1603–1612.

Pavey, C.R., Eldridge, S.R. & Heywood, M. (2008) Population dynamics and prey selection of native and introduced predators during a rodent outbreak in arid Australia. *Journal of Mammalogy*, **89**, 674–683.

Pemberton, J., Coltman, D., Coulson, T. & Slate, J. (1999) Using microsatellites to measure the fitness consequences of inbreeding and outbreeding. *Microsatellites: evolution and applications* (eds D. Goldstein & C. Schlötterer), pp. 151–164. Oxford University Press, Oxford.

Perret, M. & Aujard, F. (2001) Regulation by photoperiod of seasonal changes in body mass and reproductive function in gray mouse lemurs (Microcebus murinus): differential responses by sex. *International Journal of Primatology*, **22**, 5–24.

Pinter, A.J. & Negus, N.C. (1965) Effects of nutrition and photoperiod on reproductive physiology of Microtus montanus. *The American Journal of Physiology*, **208**, 633–638.

Pitkow, L.J., Sharer, C.A., Ren, X., Insel, T.R., Terwilliger, E.F. & Young, L.J. (2001) Facilitation of affiliation and pair-bond formation by vasopressin receptor gene transfer into the ventral forebrain of a monogamous vole. *Journal of Neuroscience*, **21**, 7392–7396.

Poole, J.H. (1989) Announcing intent: the aggressive state of musth in African elephants. *Animal Behaviour*, **37**, 140–152.

Pounds, J.A. (1988) Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland Anolis community. *Ecological Monographs*, **58**, 299–320.

Preston, B.T., Stevenson, I.R., Lincoln, G.A., Monfort, S.L., Pilkington, J.G. & Wilson, K. (2012) Testes size, testosterone production and reproductive behaviour in a natural mammalian mating system. *The Journal of Animal Ecology*, **81**, 296–305.

Preston, B.T., Stevenson, I.R., Pemberton, J.M., Coltman, D.W. & Wilson, K. (2003) Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 633–640.

Pröhl, H. & Berke, O. (2001) Spatial distributions of male and female strawberry poison frogs and their relation to female reproductive resources. *Oecologia*, **129**, 534–42.

Pulliam, H.R. (1988) Sources, sinks and population regulation. *The American Naturalist*, **132**, 652–661.

Pulliam, H.R., Dunning, J.B. & Liu, J. (1992) Population dynamics in complex landscapes: a case study. *Ecological Applications*, **2**, 165–177.

Pyke, G.H. (1984) Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics*, **15**, 523–575.

Queller, D.C., Strassmann, J.E. & Hughes, C.R. (1993) Microsatellites and kinship. *Trends in Ecology & Evolution*, **8**, 285–288.

R Development Core Team. (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Réale, D., Festa-Bianchet, M. & Jorgenson, J.T. (1999) Heritability of body mass varies with age and season in wild bighorn sheep. *Heredity*, **83**, 526–532.

Réale, D., McAdam, A.G., Boutin, S. & Berteaux, D. (2003) Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 591–596.

Réale, D., Reader, S.M., Sol, D., McDougall, P.T. & Dingemanse, N.J. (2007) Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**, 291–318.

Reaney, L.T., Drayton, J.M. & Jennions, M.D. (2010) The role of body size and fighting experience in predicting contest behaviour in the black field cricket, Teleogryllus commodus. *Behavioral Ecology and Sociobiology*, **65**, 217–225.

Reichard, M., Jurajda, P. & Smith, C. (2004) Male-male interference competition decreases spawning rate in the European bitterling (Rhodeus sericeus). *Behavioral Ecology and Sociobiology*, **56**, 34–41.

Reichard, M., Ondračková, M., Bryjová, A., Smith, C. & Bryja, J. (2009) Breeding resource distribution affects selection gradients on male phenotypic traits: Experimental study on lifetime reproductive success in the bitterling fish (Rhodeus amarus). *Evolution*, **63**, 377–390.

Reimchen, T.E. & Nosil, P. (2002) Temporal variation in divergent selection on spine number in threespine stickleback. *Evolution*, **56**, 2472–2483.

Rhodes, J.R., McAlpine, C.A., Lunney, D. & Possingham, H.P. (2005) A spatially explicit habitat selection model incorporating home range behavior. *Ecology*, **86**, 1199–1205.

Rodwell, J.S. (ed). (1991) *British Plant Communities. Volume 1. Woodlands and Scrub.* Cambridge University Press, Cambridge, UK.

Rogers, L.M. & Gorman, M.L. (1995) The diet of the wood mouse Apodemus sylvaticus on set-aside land. *Journal of Zoology*, **235**, 77–83.

Roof, R.L. & Havens, M.D. (1992) Testosterone improves maze performance and induces development of a male hippocampus in females. *Brain Research*, **572**, 310–313.

Roos, S. (2002) Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia*, **133**, 608–615.

Rosalino, L.M., Ferreira, D., Leitão, I. & Santos-Reis, M. (2011a) Selection of nest sites by wood mice Apodemus sylvaticus in a Mediterranean agro-forest landscape. *Ecological Research*, **26**, 445–452.

Rosalino, L.M., Ferreira, D., Leitão, I. & Santos-Reis, M. (2011b) Usage patterns of Mediterranean agro-forest habitat components by wood mice Apodemus sylvaticus. *Mammalian Biology*, **76**, 268–273.

Russell, C.A., Smith, D.L., Waller, L.A., Childs, J.E. & Real, L.A. (2004) A priori prediction of disease invasion dynamics in a novel environment. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 21–5.

Ryabov, A.B. & Blasius, B. (2014) Depth of the biomass maximum affects the rules of resource competition in a water column. *The American Naturalist*, **184**, E132–46.

Ryan, B.C. & Vandenbergh, J.G. (2002) Intrauterine position effects. *Neuroscience & Biobehavioral Reviews*, **26**, 665–678.

Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W. & Hanski, I. (1998) Inbreeding and exctinction in a butterfly metapopulation. *Nature*, **392**, 491–494.

Sadowska, E.T., Labocha, M.K., Baliga, K., Stanisz, A., Wróblewska, A.K., Jagusiak, W. & Koteja, P. (2005) Genetic correlations between basal and maximum metabolic rates in a wild rodent: consequences for evolution of endothermy. *Evolution*, **59**, 672–681.

Samuel, M.D., Pierce, D.J. & Garton, E.O. (1985) Identifying areas of concentrated use within the home range. *Journal of Animal Ecology*, **54**, 711–719.

Say, L. & Pontier, D. (2004) Spacing pattern in a social group of stray cats: Effects on male reproductive success. *Animal Behaviour*, **68**, 175–180.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, **185**, 27–39.

Schoener, T.W. & Schoener, A. (1982) Intraspecific variation in home-range size in some Anolis lizards. *Ecology*, **63**, 809–823.

Schradin, C., Schmohl, G., Rödel, H.G., Schoepf, I., Treffler, S.M., Brenner, J., Bleeker, M., Schubert, M., König, B. & Pillay, N. (2010) Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. *Animal Behaviour*, **79**, 195–203.

Schröder, U.J. & Staufenbiel, R. (2006) Methods to determine body fat reserves in the dairy cow with special regard to ultrasonographic measurement of backfat thickness. *Journal of Dairy Science*, **89**, 1–14.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A. (1999) Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management*, **63**, 739–747.

Selonen, V., Painter, J.N., Rantala, S. & Hanski, I.K. (2013) Mating system and reproductive success in the Siberian flying squirrel. *Journal of Mammalogy*, **94**, 1266–1273.

Sieberts, S.K., Wijsman, E.M. & Thompson, E.A. (2002) Relationship inference from trios of individuals, in the presence of typing error. *American Journal of Human Genetics*, **70**, 170–180.

Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004) Behavioural syndromes: an integrative overview. *The Quarterly Review of Biology*, **79**, 241–277.

Silva, A.J., Kogan, J.H., Frankland, P.W. & Kida, S. (1998) CREB and memory. *Annual Review of Neuroscience*, **21**, 127–48.

Singh, N.J., Bonenfant, C., Yoccoz, N.G. & Côté, S.D. (2010) Sexual segregation in Eurasian wild sheep. *Behavioral Ecology*, **21**, 410–418.

Singleton, G. (2003) Impacts of rodents on rice production in Asia. *IRRI Discussion Paper Series*, **45**, 1–30.

Singleton, G.R., Brown, P.R., Jacob, J. & Aplin, K.P. (2007) Unwanted and unintended effects of culling: a case for ecologically-based rodent management. *Integrative Zoology*, **2**, 247–259.

Singleton, G.R., Leirs, H., Hinds, L.A. & Zhang, Z.B. (1999) *Ecologically-Based Rodent Management* (eds GR Singleton, H Leirs, LA Hinds, and ZB Zhang). ACIAR, Canberra, Australia.

Singleton, G.R., Sudarmaji, Jacob, J. & Krebs, C.J. (2005) Integrated management to reduce rodent damage to lowland rice crops in Indonesia. *Agriculture, Ecosystems and Environment*, **107**, 75–82.

Singleton, G.R., Sudarmaji Tuan, N.P., Sang, P.M., Huan, N.H., Brown, P.R., Jacob, J., Heong, K.L. & Escalada, M.M. (2003) Reduction in chemical use following integrated ecologically based rodent management. *International Rice Research Notes*, **28**, 33–35.

Sinsch, U. (1990) Migration and orientation in anuran amphibians. *Ethology Ecology & Evolution*, **2**, 65–79.

Sneddon, L.U., Huntingford, F.A. & Taylor, A.C. (1997) Weapon size versus body size as a predictor of winning in fights between shore crabs, Carcinus maenas (L .). *Behavioral Ecology and Sociobiology*, **41**, 237–242.

Sokolowski, M.B. (1980) Foraging strategies of Drosophila melanogaster: a chromosomal analysis. *Behavior Genetics*, **10**, 291–302.

Sokolowski, M.B. (2001) Drosophila: genetics meets behaviour. *Nature Reviews Genetics*, **2**, 879–890.

Sommer, S., Taubert, R. & Schmidt, A. (2010) Isolation of new microsatellite markers using genome screening and restriction-ligation for Apodemus flavicollis. Added to Permanent Genetic Resources Database (1 February 2010–31 March 2010). *Molecular Ecology Resources*, **10**, 751–754.

Southern, H.N. & Lowe, V.P.W. (1982) Predation by Tawny owls (Strix aluco) on Bank voles (Clethrionomys glareolus) and Wood mice (apondemus sylvaticus). *Journal of Zoology*, **198**, 83–102.

Spreng, M., Cotecchia, S. & Schenk, F. (2001) A behavioral study of alpha-1b adrenergic receptor knockout mice: increased reaction to novelty and selectively reduced learning capacities. *Neurobiology of Learning and Memory*, **75**, 214–29.

Stamps, J. (1995) Motor learning and the value of familiar space. *The American Naturalist*, **146**, 41–58.

Stenseth, N.C., Leirs, H., Skonhoft, A., Davis, S.A., Pech, R.P., Andreassen, H.P., Singleton, G.R., Lima, M., Machang'u, R.S., Makundi, R.H., Zhang, Z., Brown, P.R., Shi, D. & Wan, X. (2003) Mice, rats, and people: the bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment*, **1**, 367–375.

Stephens, D.W. & Charnov, E.L. (1982) Optimal foraging : some simple stochastic models. *Behavioral Ecology and Sociobiology*, **10**, 251–263.

Stokes, M.K., Slade, N.A. & Blair, S.M. (2001) Influences of weather and moonlight on activity patterns of small mammals: a biogeographical perspective. *Canadian Journal of Zoology*, **79**, 966–972.

Stopher, K. V, Walling, C.A., Morris, A., Guinness, F.E., Clutton-Brock, T.H., Pemberton, J.M. & Nussey, D.H. (2012) Shared spatial effects on quantitative genetic parameters: Accounting for spatial autocorrelation and home range overlap reduces estimates of heritability in wild red deer. *Evolution*, **66**, 2411–2426.

Stuart, A.M., Prescott, C.V., Singleton, G.R., Joshi, R.C. & Sebastian, L.S. (2007) The rodent species of the Ifugao Rice Terraces, Philippines - target or non-target species for management? *International Journal of Pest Management*, 37–41.

Stuart-Fox, D.M. & Johnston, G.R. (2005) Experience overrides colour in lizard contests. *Behaviour*, **142**, 329–350.

Sugg, D.W., Chesser, R.K., Dobson, F.S. & Hoogland, J.L. (1996) Population genetics meets behavioral ecology. *Trends in Ecology & Evolution*, **11**, 338–342.

Surbeck, M., Deschner, T., Schubert, G., Weltring, A. & Hohmann, G. (2012) Mate competition, testosterone and intersexual relationships in bonobos, Pan paniscus. *Animal Behaviour*, **83**, 659–669.

Svensson, P.A., Lehtonen, T.K. & Wong, B.B.M. (2012) A high aggression strategy for smaller males. *PloS One*, **7**, e43121.

Swihart, R.K. & Slade, N.A. (1989) Differences in home-range size between sexes of Microtus ochrogaster. *Journal of Mammalogy*, **70**, 816–820.

Swihart, R.K., Slade, N.A. & Bergstrom, B.J. (1988) Relating body size to the rate of home range use in mammals. *Ecology*, **69**, 393–399.

Tarwater, C.E. & Beissinger, S.R. (2013) Opposing selection and environmental variation modify optimal timing of breeding. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 15365–15370.

Tautz, D. (1989) Hypervariabflity of simple sequences as a general source for polymorphic DNA markers. *Nucleic Acids Research*, **17**, 6463–6471.

Tautz, D. & Renz, M. (1984) Simple sequences are ubiquitous repetitive components of eukaryotic genomes. *Nucleic Acids Research*, **12**, 4127–4138.

Taylor, P. & Elwood, R. (2003) The mismeasure of animal contests. *Animal Behaviour*, **65**, 1195–1202.

Tew, T.E. & Macdonald, D.W. (1994) Dynamics of space use and male vigour amongst wood mice, Apodemus sylvaticus, in the cereal ecosystem. *Behavioral Ecology and Sociobiology*, **34**, 337–345.

Thomas, S.C. & Hill, W.G. (2000) Estimating quantitative genetic parameters using sibships reconstructed from marker data. *Genetics*, **155**, 1961–1972.

Thomas, S.C. & Hill, W.G. (2002) Sibship reconstruction in hierarchical population structures using Markov chain Monte Carlo techniques. *Genetical Research*, **79**, 227–234.

Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.

Timoney, K. (1999) The habitat of nesting whooping cranes. *Biological Conservation*, **89**, 189–197.

Townsend, S.M. & Jamieson, I.G. (2013) Molecular and pedigree measures of relatedness provide similar estimates of inbreeding depression in a bottlenecked population. *Journal of Evolutionary Biology*, **26**, 889–899.

Trainor, B.C. & Marler, C. A. (2001) Testosterone, paternal behavior, and aggression in the monogamous California mouse (Peromyscus californicus). *Hormones and behavior*, **40**, 32–42.

Trivers, R.L. (1972) Parental investment and sexual selection. *Sexual Selection and the Descent of Man, 1871-1971* (ed B. Campbell),.

Trumpp, A., Refaeli, Y., Oskarsson, T., Gasser, S., Murphy, M., Martin, G.R. & Bishop, J.M. (2001) c-Myc regulates mammalian body size by controlling cell number but not cell size. *Nature*, **414**, 768–773.

Unnsteinsdottir, E.R. & Hersteinsson, P. (2011) Effects of contrasting habitats on population parameters and diet of Apodemus sylvaticus (Rodentia) in south-western Iceland. *Mammalia*, **75**, 13–21.

Untergasser, A., Cutcutache, I., Koressaar, T., Ye, J., Faircloth, B.C., Remm, M. & Rozen, S.G. (2012) Primer3 - new capabilities and interfaces. *Nucleic Acids Research*, **40**, e115.

Vandenbergh, J.G. & Huggett, C.L. (1995) The anogenital distance index, a predictor of the intrauterine position effects on reproduction in female house mice. *Laboratory Animal Science*, **45**, 567–573.

Van de Pol, M., Brouwer, L., Ens, B.J., Oosterbeek, K. & Tinbergen, J.M. (2010) Fluctuating selection and the maintenance of individual and sex-specific diet specialization in free-living oystercatchers. *Evolution*, **64**, 836–851.

Vander Wal, E., Laforge, M.P. & McLoughlin, P.D. (2014) Density dependence in social behaviour: home range overlap and density interacts to affect conspecific encounter rates in a gregarious ungulate. *Behavioral Ecology and Sociobiology*, **68**, 383–390.

Vander Wal, E. & Rodgers, A.R. (2012) An individual-based quantitative approach for delineating core areas of animal space use. *Ecological Modelling*, **224**, 48–53.

Vander Wal, E., Yip, H. & McLoughlin, P.D. (2012) Sex-based differences in density-dependent sociality: an experiment with a gregarious ungulate. *Ecology*, **93**, 206–12.

VanderWaal, K.L., Wang, H., McCowan, B., Fushing, H. & Isbell, L.A. (2014) Multilevel social organization and space use in reticulated giraffe (Giraffa camelopardalis). *Behavioral Ecology*, **25**, 17–26.

Van Overveld, T. & Matthysen, E. (2010) Personality predicts spatial responses to food manipulations in free-ranging great tits (Parus major). *Biology letters*, **6**, 187–190.

Vickery, W.L. & Bider, J.R. (1981) The influence of weather on rodent activity. *Journal of Mammalogy*, **62**, 140–145.

Vitaterna, M.H., King, D.P., Chang, A.-M., Kornhauser, J.M., Lowrey, P.L., McDonald, J.D., Dove, W.F., Pinto, L.H., Turek, F.W. & Takahashi, J.S. (1994) Mutagenesis and mapping of a mouse genome, Clock, essential for circadian behaviour. *Science*, **264**, 719–725.

Volampeno, M.S.N., Masters, J.C. & Downs, C.T. (2011) Home range size in the blue-eyed black lemur (Eulemur flavifrons): A comparison between dry and wet seasons. *Mammalian Biology*, **76**, 157–164.

Vom Saal, F. & Bronson, F. (1980) Sexual characteristics of adult female mice are correlated with their blood testosterone levels during prenatal development. *Science*, **208**, 597–599.

Vom Saal, F.S. & Dhar, M.G. (1992) Blood flow in the uterine loop artery and loop vein is bidirectional in the mouse: implications for transport of steroids between fetuses. *Physiology & Behavior*, **52**, 163–171.

Wakefield, E.D., Bodey, T.W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R.G., Green, J.A., Grémillet, D., Jackson, A.L., Jessopp, M.J., Kane, A., Langston, R.H.W., Lescroël, A., Murray, S., Le Nuz, M., Patrick, S.C., Péron, C., Soanes, L.M., Wanless, S., Votier, S.C. & Hamer, K.C. (2013) Space partitioning without territoriality in gannets. *Science*, **341**, 68–70.

Wand, M.P. & Jones, M.C. (1995) *Kernel Smoothing*. Chapman and Hall, London, United Kingdom.

Wang, J. (2004) Sibship reconstruction from genetic data with typing errors. *Genetics*, **166**, 1963–1979.

Wang, J. (2013) An improvement on the maximum likelihood reconstruction of pedigrees from marker data. *Heredity*, **111**, 165–174.

Wang, M. & Grimm, V. (2007) Home range dynamics and population regulation: an individual-based model of the common shrew Sorex araneus. *Ecological Modelling*, **205**, 397–409.

Wang, J. & Santure, A.W. (2009) Parentage and sibship inference from multilocus genotype data under polygamy. *Genetics*, **181**, 1579–1594.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

Watts, C.H.S. (1968) The foods eaten by wood mice (Apodemus sylvaticus) and bank voles (Clethrionomys glareolus) in Wytham Woods, Berkshire. *The Journal of Animal Ecology*, **37**, 25–41.

Watts, C.H.S. (1969) The regulation of wood mouse (Apodemus sylvaticus) numbers in Whytham Woods, Berkshire. *Journal of Animal Ecology*, **38**, 285–304.

Wauters, L. A., Gurnell, J., Preatoni, D. & Tosi, G. (2008) Effects of spatial variation in food availability on spacing behaviour and demography of Eurasian red squirrels. *Ecography*, **24**, 525–538.

Weber, J.L. & May, P.E. (1989) Abundant class of human DNA polymorphisms which can be typed using the polymerase chain reaction. *American Journal of Human Genetics*, **44**, 388–396.

Weber, J.N., Peterson, B.K. & Hoekstra, H.E. (2013) Discrete genetic modules are responsible for complex burrow evolution in Peromyscus mice. *Nature*, **493**, 402–5.

White, G.C. & Garrott, R.A. (1990) *Analysis of Wildlife Radio-Tracking Data*. Academic Press, San Diego, California, USA.

Williams, C.L., Barnett, A.M. & Meck, W.H. (1990) Organizational effects of early gonadal secretions on sexual differentiation in spatial memory. *Behavioral Neuroscience*, **104**, 84–97.

Wilson, W.L., Elwood, R.W. & Montgomery, W.I. (1993) Infanticide and maternal defence in the wood mouse Apodemus sylvaticus. *Ethology Ecology & Evolution*, **5**, 365–370.

Wilson, A.J., Réale, D., Clements, M.N., Morrissey, M.M., Postma, E., Walling, C.A., Kruuk, L.E.B. & Nussey, D.H. (2010) An ecologist's guide to the animal model. *The Journal of Animal Ecology*, **79**, 13–26.

Wolf, J.B. & Wade, M.J. (2009) What are maternal effects (and what are they not)? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **364**, 1107–1115.

Wolff, J.O. (2003) Density-dependence and the socioecology of space use in rodents. *ACIAR Monograph*, **96**, 124–130.

Wolff, J.O. & Peterson, J.A. (1998) An offspring-defense hypothesis for territoriality in female mammals. *Ethology Ecology & Evolution*, **10**, 227–239.

Wolton, R.J. (1983) The activity of free-ranging wood mice Apodemus sylvaticus. *Journal of Animal Ecology*, **52**, 781–794.

Wolton, R.J. (1985) The ranging and nesting behaviour of wood mice, Apodemus sylvaticus (Rodentia; Muridae), as revealed by radio-tracking. *Journal of Zoology*, **206**, 203–224.

Wolton, R.J. & Flowerdew, J.R. (1985) Spatial distribution and movements of wood mice, yellow-necked mice and bank voles. *Symposium of the Zoological Society of London*, **55**, 249–275.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. & Warren, P.H. (2005) Body size in ecological networks. *Trends in Ecology & Evolution*, **20**, 402–9.

Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164–168.

Young, L.J., Nilsen, R., Waymire, K.G., Macgregor, G.R. & Insel, T.R. (1999) Increased affiliative response to vasopressin in mice expressing the V1a receptor from a monogamous vole. *Nature*, **400**, 766–768.

Zamudio, K.R., Huey, R.B. & Crill, W.D. (1995) Bigger isn't always better: body -size, developmental and parental temperature and male territorial success in Drosophila melanogaster. *Animal Behaviour*, **49**, 671–677.

Zedrosser, A., Bellemain, E., Taberlet, P. & Swenson, J.E. (2007) Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age, internal relatedness and population density. *Journal of Animal Ecology*, **76**, 368–375.

Zhang, X. & Firestein, S. (2002) The olfactory receptor gene superfamily of the mouse. *Nature Neuroscience*, **5**, 124–33.

Zhang, Y., Proenca, R., Maffei, M., Barone, M., Leopold, L. & Friedman, J.M. (1994) Positional cloning of the mouse obese gene and its human homologue. *Nature*, **372**, 425–432.

Zheng, C., Ovaskainen, O. & Hanski, I. (2009) Modelling single nucleotide effects in phosphoglucose isomerase on dispersal in the Glanville fritillary butterfly: coupling of ecological and evolutionary dynamics. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, **364**, 1519–1532.

Zielinski, W.J., vom Saal, F.S. & Vandenbergh, J.G. (1992) The effect of intrauterine position on the survival , reproduction and home range size of female house mice (Mus musculus). *Behavioral Ecology and Sociobiology*, **30**, 185–191.

Ziv, Y., Kotler, B.P., Abramsky, Z. & Rosenzweig, M.L. (1995) Foraging efficiencies of competing rodents: why do gerbils exhibit shared-preference of habitat selection. *Oikos*, **73**, 260–268.

Appendix

Appendix 1: Justification of body fat scoring method

Measures of body fat are commonly used in the livestock industry to assess the energy reserves of dairy cows (Schröder & Staufenbiel 2006). The traditional method of assessing body fat has been through visual and tactile evaluation using a point scale, referred to in the industry as “Body Condition Scoring” (BCS). In the United States and Ireland the most common scoring system is between 1 (severe lack of body fat) and 5 (obese) using 0.25 increments. Scores are derived from visual and tactile inspection of multiple body regions. Research conducted into the variance and repeatability of BCS between different observers using this technique has shown that the score given does not significantly differ between or within observers (Edmonson *et al.* 1989). More recently, modern methods of subcutaneous fat detection have been adapted for field measurements, most notably the use of ultrasound. Research conducted into the relationship between the visual/tactile BCS and ultrasound approaches has shown a significant association (Domecq *et al.* 1995), leading the authors to conclude that the visual/tactile BCS method was a valid way to quantify subcutaneous body fat in cows. Other studies have revealed significant relationships between ultrasonic measurements of rump fat and overall BCS (Ayres *et al.* 2009). We believe, given the tested validity of similar methods in other fields, that our method is sufficient to allow variation in energy reserves between individuals of a population to be detected.

Table A1: Inspection criteria for scoring body fat.

Body fat score	Qualitative criteria
0	Individual vertebrae and pelvic bone can be visibly defined without parting fur. Absolutely no subcutaneous fat deposits detected by physical examination.
0.5	Individual vertebrae and pelvic bone can be visibly defined without parting fur. Minor fat deposits can be detected by physical examination but each individual vertebrae and pelvic bone can be clearly felt.
1	Spine and pelvic bone can be visibly defined only after parting fur. Individual vertebrae and pelvis can be detected by physical examination.
1.5	Only spine visible after parting fur. Individual vertebrae and pelvis can be detected by physical examination.
2	Neither spine nor pelvis visible after parting fur. Spine (but not individual vertebrae) and pelvic bone can be detected by physical examination.
2.5	Neither spine nor pelvis visible after parting fur. Spine (but not individual vertebrae nor pelvic bone) can be detected by physical examination.
3	Clear fat deposits through physical examination. Spine and pelvic bone only just detectable.
3.5	Clear fat deposits through physical examination. Pelvic bone cannot be felt.
4	Visibly fat. Cannot feel spine or pelvic bone during physical examination

Appendix II: Accounting for behaviour within recording stations

Location fixes were obtained at a rate of 3 s^{-1} when a mouse was present in a recording station. The rate was set this high to avoid missing location fixes of individuals that ran through without stopping. The data therefore needed to be sub-sampled in order to account for very high numbers of relocations if individuals paused in the recording stations (e.g. to eat the peanut), which would bias the resulting kernel density estimates. Here we use an adapted method of the biological independence approach (Lair 1987) of taking a biologically meaningful minimum time interval between location fixes. When the same individual had moved between two different recording stations on the same night, the distance between those stations and the time it took the individual to move from one to the other were used to calculate a movement rate (m s^{-1}). The movement rate was then taken for a sample of mice (n=249) and the mean calculated as 0.0459m s^{-1}. It was assumed that movement within a quadrate was not independent as recording stations could have influenced space use behaviour at this scale, e.g. individuals exploring around the recording stations. Movement between quadrates was considered independent. The mean movement rate was therefore used to calculate the time it would take for an average mouse to move from the centre of one quadrate to the centre of an adjacent quadrate and back again (distance=20m). The resulting time for independence was 436 seconds. Thus, any location fixes of the same individual in the same recording station on the same night that were within 436s of each other were discarded.