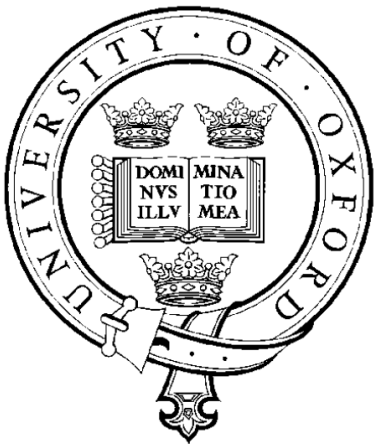
Space use patterns and population dynamics in two common European rodents, *Apodemus sylvaticus* and *Myodes glareolus*

A thesis submitted for the degree of Doctor of Philosophy

by

Severin F. Dreßen



University of Oxford

Jesus College

Michaelmas Term 2016

Supervisors: Prof. Tim Coulson, Dr. Aurelio F. Malo

Abstract

Space use patterns and population dynamics in two common European rodents, *Apodemus sylvaticus* and *Myodes glareolus*

A DPhil thesis by Severin F. Dreßen

Jesus College, University of Oxford, Michaelmas Term 2016

Space use patterns are driven by the individual's need to acquire enough resources to survive and reproduce. Population dynamics, in turn, are determined by individual survival and reproduction. In rodents, these two key elements to a species' ecology have been investigated for decades, but often data quality is insufficient to address important questions. This thesis aims to improve our understanding of space use patterns and population dynamics in the bank vole (*Myodes glareolus*) and the wood mouse (*Apodemus sylvaticus*). I also try to overcome current methodological limitations by using a new method for field data collection and exploring the use of in-silico methods. In chapters 2 and 3, I analyse space use patterns of both species. My results highlight the importance of predation risk and food availability for space use patterns. Chapter 3 also reveals the advantage of using an individual based model to address space use related questions. In chapter 4, I analyse the density dependence of body weight and life history parameters in our wood mice population by constructing an integral projection model. I found mixed results for the density dependence of body weight but proof for changes of generation time and reproductive success at higher densities. Using an individual based model, I show in chapter 5 that sensitivity of space use estimates to low temporal resolution of location fixes varies between different movement types. This thesis shows that space use patterns are driven by interactions of many drivers, including sex, season, food availability and body weight, but are dominated by predation risk. It also supports the importance of population density for space use patterns and population dynamics. Finally, I highlight the potential of using in-silico methods to investigate the ecology of rodents and the current vulnerability of space use estimates to bias.

Acknowledgements

First and foremost I want to especially thank my supervisors Prof. Timothy Coulson and Dr. Aurelio F. Malo. It was an honour to work and learn under their supervision and to be mentored by two great scientists. I am deeply grateful for their continuous support, for motivating discussions and also for their relaxed British/ Spanish attitude when once again I was turning ‘too German’.

This thesis would not have been possible if not for the scholarship awarded by the Cusanuswerk foundation. I also want to thank my fellow PhD student, Benedict Godsall. He introduced me to our study site and taught me how to handle rodents, find my way through dense and spiky shrub patches and withstand the pervasive British rain. With him many long days in the field and even longer nights at DTT were much easier to enjoy.

A big thanks also belongs to all former and current members of Timothy’s lab group E2D for creating an atmosphere of great spirit, constant support and distraction when needed: Jack Massey, Jeremy Cusack, Rocio Pozo, Marc Brouard, Jacques Deere, Julia Barthold, Sarah Cubaynes, Sonya Clegg, Alex Lee, Susanne Schindler, Erik Sandvig, Philip Riodan, Emily Simmonds and Ron Bassar. I am also thankful for inspiring and motivating discussions with my fellow researchers David Labonte and Thomas Creedy.

I want to thank all master students and volunteers for their tremendous support and hard of work during field data collection: R. Barker, O. Hicks, G. Kingcome, M. Massam, S. McCandless, S. McLoughlin, R. Moorhouse-Gann, T. Powell, L. Sandbach and C. Weevil.

Many thanks for the guidance and help provided by of the staff of the Department of Zoology and Jesus College, especially by Esme Taylor, Heather Green, Alexandra Lumbers and Carole Thomas.

My family also deserves a very special thank for always supporting me in pursuing my goal to become a biologist, for helping me in great need and for always believing in me.

The final and most deserved thanks goes to my wife Dhruvi Dressen. Our lives will always be interwoven with our time at Oxford and with Tim our match maker. Without her continuous love, care, support, and motivation - especially during the very last long stretch - this thesis would not have been finished.

Author Contributions

Chapter 1

Author: Severin F. Dreßen

Chapter 2

Authors: Severin F. Dreßen (SD), Ben Godsall (BG), Aurelio F. Malo (AM), Tim Coulson (TC)

SD, AM and TC conceived the research question. SD and BG carried out field data collection. SD conducted the analysis and wrote the manuscript. All co-authors contributed to the interpretation of results and commented on the manuscript.

Chapter 3

Authors: Severin F. Dreßen (SD), Ben Godsall (BG), Aurelio F. Malo (AM), Tim Coulson (TC)

SD, AM and TC conceived the research question. SD and BG carried out field data collection. SD constructed the model. SD conducted the analysis and wrote the manuscript. All co-authors contributed to the interpretation of results and commented on the manuscript

Chapter 4

Authors: Severin F. Dreßen (SD), Marc Brouard (MB), Aurelio F. Malo (AM), Tim Coulson (TC)

SD and TC conceived the research question. SD carried out field data collection. MB calculated recapture rate for the survival analysis. SD constructed the model. SD conducted the analysis and wrote the manuscript. All co-authors contributed to the interpretation of results and commented on the manuscript.

Chapter 5

Authors: Severin F. Dreßen (SD), Aurelio F. Malo (AM), Tim Coulson (TC)

SD conceived the research question, constructed the model, conducted the analysis and wrote the manuscript. All co-authors contributed to the interpretation of results and commented on the manuscript.

Chapter 6

Author: Severin F. Dreßen

Contents

Chapter 1

An introduction to animal space use and population dynamics

1.1 General introduction

Motion requires energy. If energy-providing resources, e.g. food, are limited, animals should only move and hence spend energy for activities essential for survival or reproduction such as foraging, finding mates and - if applicable - to avoid predation. Animals, therefore, should try to minimise the space they require to acquire all essential resources in order to minimise energetic costs. In many habitats, however, resources are distributed heterogeneously, creating areas that differ qualitatively. In addition, the distribution of one type of resource is not necessarily concurrent with another resource's distribution (Holbrook and Schmitt 1988). An area of high food density, for instance, might also be an area of high predation risk. Patches of high quality habitat containing valuable resources, are also likely to be subject to more intense competition than low quality patches, increasing the cost-benefit ratio of inhabiting (or defending) a high quality patch (Riechert 1979; Frost and Frost 1980). In seasonal environments, temporal variation in the distribution of quantity and quality of resources adds an extra layer of complexity. For instance, males only need to defend courtship arenas during breeding season; foraging patterns can change as a species' diet varies between seasons; and an area that provides excellent shelter in one season, can be risky to live in during another (Hardenberg, Bassano et al. 2000; Stokes, Slade et al. 2001; Volampeno, Masters et al.

2011). In many habitats, the non-concurrent, seasonally fluctuating distribution of resources creates a highly complex landscape of interacting factors. Here, animal space use is likely to be affected by many ecological factors, which then has implication for animal survival, reproduction and dispersal immigration and emigration. These, however, are also the drivers of dynamics in a population. Therefore, many ecological processes at individual and population level cannot be understood without considering the underlying drivers of space use (Levin 1992; Coulson, Albon et al. 1999; Cowen, Paris et al. 2006). This thesis aims to improve our understanding of drivers of space use and population dynamics in rodents. This taxon has been intensively studied, providing a large body of knowledge on space use and population dynamics. However, technological and methodological constraints of data collection and analysis have made it challenging so far to address important aspects of rodent space use and population dynamics. This thesis, therefore, tries to overcome some of the current constraints by using recently developed technological and methodological approaches.

The following introduction starts with a summary on population dynamic (1.2) and space use drivers (1.3.). It continues with sections on space use estimations (1.4) and methodological approaches to address questions on space use and population dynamics (1.5), followed by review on the study species (1.6) and the study site (1.7). The introduction concludes with the aims of the thesis and an outline of the data chapters (1.8).

1.2 Population dynamics

The dynamics of a population describes changes in population composition and size. These changes are driven by survival, reproduction and dispersal immigration and emigration of individuals in a population. Survival, reproduction anddispersal immigration and emigration, however, are often affected by abiotic and biotic factors, or a combination of both (Elton 1924; Blair 1948; Gaines and McClenaghan Jr 1980; Ostfeld, Jones et al. 1996; Hubbs and Boonstra 1997; Getz, Oli et al. 2005; Booth, Montgomery et al. 2009).

Abiotic drivers of population dynamic

Abiotic factors, such as weather conditions, can directly or indirectly affect survival, reproduction and dispersal immigration and emigration (Elton 1924; Gilbert and Krebs 1991; Madsen and Shine 1999; Aars and Ims 2002; Previtali, Lima et al. 2009). Deviations from the optimal range of ambient temperatures can, for instance, negatively impact survival rates (Aars and Ims 2002). Other weather factors can also affect survival (Elton 1924). Rainfall, for example, can reduce insulation and increase the resources required to maintain metabolism and constant body temperature (Cuyler and Øritsland 2004). In seasonal ecosystems, rainfall, temperature and other climatic factors, including day length and humidity, vary between seasons. Population dynamics affected by abiotic factors consequently can also differ between seasons (Elton 1924; Bronson and Pryor 1983; Aars and Ims 2002). In many rodent species, for example, survival and reproduction rates tend to be lower during the climatically less favourable season (Watts 1969; Flowerdew, Gurnell et al. 1985; Gilbert and Krebs 1991).

Biotic drivers of population dynamic

Biotic factors also affect population dynamics. Quality and quantity of resource providing habitat features directly affect survival, reproduction and dispersal immigration and emigration (Watts 1969; Ford and Pitelka 1984; Desy and Batzli 1989 ; Malo, Godsall et al. 2013). Insufficient quality and quantity of food directly reduces an individual's ability to maintain its metabolism, hence decreasing its survival rate (Cole and Batzli 1978), its reproductive success (Desy and Batzli 1989) or its offspring's fitness (Rhees and Fleming 1981). Insufficient food supplies can also trigger dispersal immigration and emigration (Hubbs and Boonstra 1997) or affect individuals indirectly by weakening the immune system and the ability to escape predation (Gese and Grothe 1995; Ritz and Gardner 2006). Similarly, insufficient shelter can reduce survival rates and reproductive success, exposing an individual to a higher risk of predation and to potentially adverse meteorological conditions (Desy and Batzli 1989; Tallmon and Mills 1994; Malo, Godsall et al. 2013).

Additional biotic factors that can affect population dynamics are intraspecific and interspecific competition as well as individual level factors. The latter, including genetic variation, body size and behaviour, can affect rates of survival, reproduction and dispersal immigration and emigration both directly and indirectly. Individual genetic variation, for instance, is related to reproductive success, either directly by affecting sperm and egg quality or indirectly by influencing the development of species-specific secondary sexual traits (Hedrick 1988; Karino and Haijima 2001; Kruuk, Slate et al. 2002; Schulte-Hostedde and

Millar 2004; Seddon, Amos et al. 2004; Malo, Martinez-Pastor et al. 2010). Difference in genotype also contributes to variation in body size, which in turn is often positively correlated with success in intra- and interspecific direct competition, resulting in higher survival and reproduction rates (Brackin 1978; Garnett 1981; Huang, Wey et al. 2011). Individual differences in behaviour, both inherited (Brown, Burgess et al. 2007) and non-inherited behaviour traits (Freund, Brandmaier et al. 2013), can also affect survival and reproduction (Spritzer, Meikle et al. 2005; Boon, Réale et al. 2008). Bolder individuals, for example, might be more likely to explore more areas than their shy conspecifics (Freund, Brandmaier et al. 2013). The first group, therefore, increase their long-term survival probability by exploiting additional food sources or increasing their reproductive success but also decrease their short-term survival probability by increasing the risk of predation (Spritzer, Meikle et al. 2005; Boon, Réale et al. 2008).

Intraspecific competition, through direct competition or resource depletion, can also affect survival, reproduction and dispersal immigration and emigration (Gliwicz 1981; Hanski, Peltonen et al. 1991; Nakano 1995; Eccard and Ylönen 2007). One special case, competition for mating partners, directly affects survival, reproduction and dispersal immigration and emigration in many species (Clutton-Brock 1989; Huang, Wey et al. 2011). Intraspecific competition can also be density dependent. High population density can decrease survival and reproduction rates through direct competition (Brown and Orians 1970; Krebs 1970; Rose and Gaines 1976; Kie and Bowyer 1999; Wakefield, Bodey et al. 2013), resource depletion (Watts 1969; Alatalo, Eriksson et al. 1987) and by facilitating the spread of diseases through the population (Hammer 1906;

Kermack and McKendrick 1927). In some rodents, for example, reproduction is suppressed at high densities (Boonstra 1989; Gilbert and Krebs 1991). High population density, however, can also increase survival rates, reducing individual predation risk and increasing the group's ability to defend itself (Lima and Zollner 1996; Bowler and Benton 2005). Additionally, high population density can also trigger dispersal immigration and emigration, often of sub-dominant-individuals in the population (Gaines and McClenaghan Jr 1980; Hanski, Peltonen et al. 1991). In the *Apodemus* genus, for instance, sub-dominant males disperse when population density increases (Gliwicz 1988).

Interspecific competition also drives population dynamics. Similar to intraspecific competition, interspecific competition can affect survival, reproduction and dispersal immigration and emigration rates by direct competition and resource depletion (Gliwicz 1981; Hanski, Peltonen et al. 1991; Brown, Laundré et al. 1999; Eccard and Ylönen 2002; Berger and Gese 2007). Often, these effects are density dependent. In rodents, levels of direct competition and resource depletion increase with density of one or both interacting species (Eccard and Ylönen 2002). An important case of direct competition is predator-prey interaction, as survival and reproduction of predators and prey ultimately depend on their encounter probabilities. This is particularly important for many rodent species, which are often prey to many carnivorous species (Southern and Lowe 1968; King 1980; Southern and Lowe 1982; King 1985).

Seasonal population fluctuation

If biotic and abiotic factors undergo seasonal variation, subsequent changes in survival, reproduction and dispersal immigration and emigration can generate regular patterns in populations (Boonstra, Krebs et al. 1998). An example of pronounced population fluctuations over short time periods are population dynamics in r-selected species - such as many rodents - with high growth rate, high fecundity, early maturity and short generation time (Krebs and Myers 1974). These fluctuations not only cause changes in population size and composition but can also drive changes of other population aspects, including behavioural and physiological changes (Krebs and Myers 1974; Boonstra 1989; Boonstra, Krebs et al. 1998; Eccard and Ylönen 2002; Eccard, Jokinen et al. 2011). In chapter 4, I assess how changes in population density affect behavioural and physiological processes within a population.

1.3 Space use

Defining space use

To compare space use across individuals, population or species, a general definition of how to quantify animal space use is needed. Burt (1943) defined the term 'home range' as the space that an animal requires to survive and reproduce. Since then the home range concept has been widely used as an approximate estimation for animal space use (Kie, Jason et al. 2010). A home range, however, is not equivalent to the total space used by an animal, as an individual can move outside its normal home range to explore their surroundings (Burt 1943). Furthermore, home ranges should not be confounded with territories. Home ranges of different individuals can overlap extensively,

while territories – “an area defended by one individual against conspecifics” (Maher and Lott 1995) – cannot. More recently, it has been acknowledged that the utilization of space within a home range is likely to be hetero- rather than homogeneous (Samuel, Pierce et al. 1985; Vander Wal and Rodgers 2012; Godsall, Coulson et al. 2014). More time is usually spent within one or several core parts of the home range, which are often characterized by high quality patches (Samuel, Pierce et al. 1985; Vander Wal and Rodgers 2012; Godsall, Coulson et al. 2014) and can be concurrent with an animal’s territory (Samuel, Pierce et al. 1985; Eccard, Jokinen et al. 2011). The periphery of the home range is used less frequently, but is still important as a foraging and courtship area (Burt 1943). Space use of both high quality core areas and the home range periphery can be affected by many different factors, though the main drivers relate to foraging, reproduction and shelter seeking. These space use drivers can be categorized into abiotic or biotic factors.

Abiotic drivers of space use

Abiotic drivers such as weather variation can affect animal space use directly and indirectly (Vickery and Bider 1981; Kotler, Brown et al. 1991; Lima, Keymer et al. 1999; Stokes, Slade et al. 2001; LaFleur and Gould 2009; Volampeno, Masters et al. 2011; Udyawer, Chin et al. 2013). Weather variation in cloud cover, humidity, rainfall, temperature and wind speed, can occur at different spatial (local, regional) and temporal (short-term, long-term) scales and the effect of the same driver on animal space use can differ depending of the scale. These spatial and temporal scales are often related to climatic changes on a local scale triggering more short-term changes of space use, while regional and global changes in climatic variables induce long-term changes on animal space

use (Vickery and Bider 1981; Kotler, Brown et al. 1991; Lima, Keymer et al. 1999; Stokes, Slade et al. 2001; LaFleur and Gould 2009; Volampeno, Masters et al. 2011; Udyawer, Chin et al. 2013). In rodents, local, short-term factors include changes in temperature (Vickery and Bider 1981), rainfall (Vickery and Bider 1981) and cloud cover or moonlight level (Kaufman and Kaufman 1982; Kotler, Brown et al. 1991). These factors can directly affect space use patterns, for instance, by reducing activity levels as energetic requirements for metabolism and insulation are higher during adverse climatic conditions (Webb and King 1984; Webb, Porter et al. 1990; Cuyler and Øritsland 2004). Local, short-term factors can also affect rodent space use indirectly by driving space use activities of heterospecifics with cascading effects on rodents. Light cloud cover, for example, can restrict space use of nocturnal rodents with aerial predators using visual cues to locate prey, because hunting success is dependent on nocturnal light levels (Kotler, Brown et al. 1991; Bowers and Dooley Jr 1993; Díaz, Torre et al. 2005). Similarly, some rodents species that are vulnerable to predators using audio cues show increased space use activities during rain fall (Vickery and Bider 1981), i.e. when locating prey by auditory cues is much harder for predators.

On a regional scale, abiotic factors can fluctuate periodically (e.g. seasonal climate) or non-periodically (e.g. cyclones, droughts, fire, Northern/Southern Atlantic Oscillation), and both categories can induce long-term changes in space use patterns (Haugen 1942; Cook 1959; Lima, Keymer et al. 1999; LaFleur and Gould 2009; Udyawer, Chin et al. 2013). Similar to local short-term effects of climatic factors, regional long-term factors can affect animal space use directly and indirectly. Seasonal variation in abiotic factors, for example,

can directly affect animal space use activity (Grodzinski 1963; Godsall, Coulson et al. 2014). In nocturnal rodents from temperate regions, temporal space use pattern varies between seasons because of variation in day length (Grodzinski 1963). Indirect effects of abiotic drivers on animal space use occur if they affect the ecological environment (e.g. food, conspecifics, heterospecifics etc.) of an individual. For example, if migratory prey is only seasonally present, predator space use is likely to vary between seasons (Hofer and East 1993). Similarly, diet composition often varies between seasons, causing changes in space use patterns to adapt to differences in foraging requirements (Robinson 1986). During winter, some species alter space use patterns by aggregating into groups, for example to improve heat retention (Stapp, Pekins et al. 1991; Furukawa, Suzuki et al. 2015).Seasonal variation in resource abundance can also cause energetically demanding life history events (such as breeding and dispersal) to be timed to fit with the peak of resource availability, which also affects animal space use. In many rodent species from temperate regions, for example, reproduction occurs only between late spring and early autumn, when food availability is high and more favourable climatic conditions reduce energetic requirements for metabolism and insulation (Christian 1980; Bronson and Pryor 1983; Bronson and Perrigo 1987). Non-periodic climatic events, including cyclones, droughts and fire, can affect space use by rapidly altering existing habitat, forcing species either to alter space use patterns or to migrate (Lima, Keymer et al. 1999; Waterman and Fenton 2000). Prolonged droughts, for example, alter rodent habitat structure and reduce resource availability, increasing predation risk and the home range size required to secure sufficient resources to survive and reproduce (Waterman and Fenton 2000).

Biotic drivers of space use

Habitat, interspecific and intraspecific effects and individual-level factors are important biotic drivers of animal space use. Habitat features providing food, shelter and the environmental conditions for reproduction are distributed heterogeneously across a landscape, creating local patches of higher quality, surrounded by patches of lower quality (Charnov 1976; Benhamou 1991; Bailey, Gross et al. 1996; Mueller and Fagan 2008). Animals, consequently, should aim to inhabit an optimal amount of high quality patches covering the animal's needs for food, shelter and reproduction. In many rodents, habitat features providing cover against predators (e.g. vegetation, rocks) are particularly important drivers of space use due to the abundance of aerial and terrestrial predators (Tallmon and Mills 1994; Lagos, Contreras et al. 1995; Mandelik, Jones et al. 2003; Trebatická, Sundell et al. 2008; Thompson, Chambers et al. 2009).

Interspecific interactions are a key factor in animal space use, as all predator-prey relationships are based on a predator trying to find prey, with the latter trying to avoid being found (Kotler, Brown et al. 1991; Longland and Price 1991). Rodents, therefore, often present spatial and temporal space use patterns that reduce predation risk (Kotler 1984; Kotler, Brown et al. 1991; Tallmon and Mills 1994; Lagos, Contreras et al. 1995; Mandelik, Jones et al. 2003; Trebatická, Sundell et al. 2008; Thompson, Chambers et al. 2009). The effect of interspecific interactions on animal space use is not restricted to predator-prey relations but also include competition between species for food and shelter (Connell 1961; Grant 1972; Berger and Gese 2007). In temperate woodlands, for example, the wood mouse (*Apodemus sylvaticus*) has been found to be

more arboreal, possibly in order to avoid resource competition with the bank vole (*Myodes glareolus)* (Buesching, Newman et al. 2008).

Intraspecific competition, both density dependent and independent, can affect animal space use. Space use patterns of a given species can change when density exceeds or drops below a threshold (Brown and Orians 1970; Kie and Bowyer 1999; Wakefield, Bodey et al. 2013). High density of conspecifics increases aggressive spacing behaviour in microtine rodents (Krebs 1970; Rose and Gaines 1976). Increasing population size can also force rodent conspecifics to alter space use patterns in order to gather enough resources (Watts 1969; Alatalo, Eriksson et al. 1987) or by suppressing reproductive behaviour (Boonstra 1989; Gilbert and Krebs 1991). In some species, high density can also be beneficial by decreasing individual predation risk and increasing predator detection rate and group defence ability (Lima and Zollner 1996; Ebensperger and Wallem 2002; Bowler and Benton 2005). Density independent competition for high quality patches also shapes animal space use (Börger, Franconi et al. 2006). In rodents, for instance, females maintain a same size core home range with high quality breeding and foraging patches independently of population density (Crawley 1969; Wolton and Flowerdew 1985; Attuquayefio, Gorman et al. 1986; Korn 1986; Hoset, Galliard et al. 2008). Males of many species, including rodents, compete with other male for reproductively active females. Often the defeated competitor is forced to migrate to avoid continuous competition (Hanski, Peltonen et al. 1991; Nakano 1995; Bowler and Benton 2005).

Differences in competitive ability are often related to variation in individual level factors, which also affect space use patterns: individual genotype (Smith,

Garten Jr et al. 1975; Garten Jr 1976; Seddon, Amos et al. 2004), body mass (Litvaitis, Sherburne et al. 1986; Kelt and Van Vuren 2001; Schradin, Schmohl et al. 2010) and body condition (Godsall, Coulson et al. 2014) can all drive space use. Body mass can positively correlate with the individual hierarchical position in a population (Brackin 1978; Nakano 1995; Huang, Wey et al. 2011). In many rodents, therefore, body mass influences individual space use, as higher-ranking individuals are found to inhabit higher quality patches (Bowers and Brown 1992; Huang, Wey et al. 2011). Males and females also often differ in their space use preferences (Haugen 1942; Gaulin and FitzGerald 1986; Clutton-Brock 1989; Ecuyer-Dab and Robert 2004). Females often aim to guarantee access to food and shelter to increase reproductive success (Ostfeld 1990; Clutton-Brock and Vincent 1991; Hoset, Galliard et al. 2008). Males, in contrast, have to secure access to females to increase their reproductive success (Crawley 1969; Korn 1986; Ostfeld 1990; Clutton-Brock and Vincent 1991; Hoset, Galliard et al. 2008). In some species, communal nesting/breeding can drive space use patterns of both sexes, depending on the species specific reproductive behaviour (Hayes 2000; Mateo and Cuadrado 2012; Furukawa, Suzuki et al. 2015). Individual variation in behaviour can also alter space use patterns (Bailey, Gross et al. 1996; Morales and Ellner 2002 ; Mueller and Fagan 2008). Behavioural differences in food preferences, for example, lead to individual variation in space use (Estes, Riedman et al. 2003). In rodents, exploratory behaviour (Freund, Brandmaier et al. 2013) and levels of aggressiveness (Godsall, Coulson et al. 2014) might vary between individuals leading to differences in space use.

1.4 Space use estimation

Challenges of space use data collection

Home range size and shape can be estimated, using spatial data that is sampled from individuals, population or species. Only in very few, exceptional cases is continuous monitoring possible, providing the complete utilization distribution of space. Normally, researchers rely on a subset of spatial location data of an unknown, heterogeneous utilization distribution of space (Calhoun and Casby 1958). However, using a subset of spatial data to calculate home range size or shape creates two problems: First, a home range is not equivalent to the total space used by an individual. For example, explorative behaviour or escaping predators can lead an individual to leave its home range (Burt 1943). A complete utilization distribution would allow an easy identification of such occasional trips, but a subset of spatial data might not. Therefore, the outmost 5% of the spatial data are usually disregarded (White and Garrott 1990). More recently, it has been suggested to only include the innermost 50 - 90 % of the data to further reduce the risk of including non-home range data (Borger, Franconi et al. 2006). Second, a non-real-time resolution means an arbitrary reduction in the number of spatial points, and may not accurately represent true utilization distribution, resulting in an increased risk of biased home range estimation (Börger, Franconi et al. 2006). Several approaches have been proposed to minimise the risk of biased data, either during data collection or at the stage of statistical analysis.

During data collection, many studies are designed to record locations at regular time intervals. If the sampling rate is higher than a species-specific minimum,

bias of home range estimation can be reduced (Seaman, Millspaugh et al. 1999; Fieberg 2007). In practice, however, many approaches cannot guarantee systematic sampling, but collect temporally clumped spatial data (Swihart and Slade 1985; Rooney, Wolfe et al. 1998; Solla, Shane et al. 1999). Remote sensing monitoring techniques, such as telemetry, still rely in many cases on researchers in the field actively recording the animal's location. Studies are likely to neglect sampling times that are inconvenient for the researcher (e.g. early hours in the morning) or locations (e.g. difficult-to-access parts of an animal's home range). Other remote approaches, for instance GPS systems, have advantages such as not relying on researcher's sampling effort. However, they are even more sensitive than telemetry to vegetation or topography (Ganskopp and Johnson 2007). For example, if an animal moves regularly between patches of dense vegetation (e.g. to rest) and open patches (e.g. to forage) accurate GPS data will be skewed towards periods in open patches. In contrast, non-remote sensing monitoring techniques, for example live trapping, rely on the animal actively accessing the device and its temporal resolution depends on sampling effort and the density of the device. Effort, however, can only be increased to a certain level, limited by economical and practical reasons. For instance, if data is collected by trapping animals, daily trapping would increase the temporal resolution but would also alter the behaviour of the focal species (Korn 1987; Rowley and Alford 2007; Tarlow and Blumstein 2007). In chapter 5, I assess how space use estimates are affected by different sampling intervals, commonly used in monitoring approaches.

If data has not been sampled in regular intervals, two approaches exist to reduce bias of home range estimation at the analytical stage. One approach is

to allow for sufficient time between two sampling events so that, theoretically, the individual can move to any other point in its home range and to discard all other spatial points (Swihart and Slade 1985; McNay, Morgan et al. 1994; Kernohan, Gitzen et al. 2001). However, increasing the sampling interval might then further reduce the sample size and exclude a large amount of useful information from the analysis (Otis and White 1999; Seaman, Millspaugh et al. 1999; Solla, Shane et al. 1999; Blundell, Maier et al. 2001; Börger, Franconi et al. 2006; Fieberg 2007). The risk of small sample sizes is of particular concern for studies focussing on changes in space use over short periods of time, for example space use differences between breeding and non-breeding seasons. More recently, methods have been developed to avoid such loss of data by weighting spatial data according to the degree of spatial and temporal autocorrelation (Matthiopoulos 2003; Katajisto and Moilanen 2006; Fieberg 2007; Keating and Cherry 2009).

Home range estimations

Many different home range estimation methods exist (Worton 1987; Kernohan, Gitzen et al. 2001; Gula and Theuerkauf 2013), but the two most commonly used are minimum-convex polygon (MCP) (Harris, Cresswell et al. 1990) and kernel density estimator (KDE) (Worton 1989).

The KDE estimates a utilization distribution, adding a third dimension, the frequency of use to the two-dimensional spatial information (Van Winkle 1975). The frequency of use of each home range part can reveal valuable insights about animal space use (Samuel, Pierce et al. 1985; Vander Wal and Rodgers

2012; Godsall, Coulson et al. 2014). Here, only the general approach of KDE estimation with respect to ecological applications is illustrated.

Let $x_1, \ldots, x_n$ be a set of independent observations from a random variable X. The independent observations are the spatial data points that are obtained from X, the unknown utilization distribution of the focal individual, population, or species. The aim of the KDE is to approximate the probability density function f of X. The density function f(x) at point x can be estimated by a kernel density estimator $\widehat{f_h}(x)$:

$$\widehat{\mathrm{f_h}}(\mathrm{x}) = \frac{1}{\mathrm{nh}} \sum_{\mathrm{i}=1}^{\mathrm{n}} \mathrm{K}\left(\frac{\mathrm{x}-\mathrm{x_i}}{\mathrm{h}}\right) \qquad (1.1)$$

where K is the kernel function and h the bandwidth. The kernel function K estimates the density function at point x as the relative frequency of all x_i that are within an interval of the bandwidth h around x. In unweighted, or fixed, kernels, all x_i have the same weight regardless of its distance to x. A common example for unweighted kernel is the uniform kernel. Sometimes, however, it is more feasible to assume that more weight should be given to a x_i that is closer to x than a x_i that is further away. Several such weighted, or adaptive, kernel functions exist, for instance the Gaussian, Epanechnikov or biweight kernel. The selection of the bandwidth h, the length of the interval around x, is performed by minimizing the mean integrated square error (MISE):

$$\mathrm{MISE}\left(\widehat{\mathrm{f_h}}(\mathrm{x})\right) = \int_{-\infty}^{+\infty} \mathrm{MSE}\left\{\widehat{\mathrm{f_h}}(\mathrm{x})\right\} \mathrm{dx} \qquad (1.2)$$

where MSE is the sum of the variance V and the squared bias B of $\widehat{f_h}(x)$:

$$\mathrm{MSE}\left(\widehat{f_h}(x)\right) = V\left(\widehat{f_h}(x)\right) + \left[B\left(\widehat{f_h}(x)\right)\right]^2 \quad (1.3)$$

The selection of the appropriate bandwidth is critical to increase accuracy of home range size estimation (Silverman 1986; Wand and Jones 1995; Bowman and Azzalini 1997). Several methods exists to estimate MISE, including least-square cross validation (LCSV) (Worton 1995), reference (Seaman and Powell 1996) and plug-in (Wand and Jones 1995) and there has been an ongoing debate which bandwidth estimator can provide the most reliable estimates (Worton 1995; Seaman, Millspaugh et al. 1999; Blundell, Maier et al. 2001; Hemson, Johnson et al. 2005; Borger, Franconi et al. 2006). More recently, studies showed that the plug-in method outperforms both LCSV and reference (Millspaugh, Nielson et al. 2006; Cumming and Cornélis 2012). In this thesis, therefore, I used the plug-in method for bandwidth selection.

In addition to the KDE, MCP is the other commonly used home range estimation method. An MCP is the smallest polygon that encircles all data points and all the line segments connecting any pair of points in the data set. The area A of an MCP can be calculated:

$$A = \frac{x_1(y_n - y_2) + \sum_{i=2}^{n-1} x_i(y_{i-1} - y_{i+1}) + x_n(y_{n-1} - y_1)}{2} \quad (1.4)$$

At first, the benefits of MCP seem obvious: It is easy to calculate and does not require choosing the appropriate kernel or bandwidth. It is, therefore, still widely used in both comparative (Kelt and Van Vuren 2001; Perry and Garland Jr 2002; Kjellander, Hewison et al. 2004; Herfindal, Linnell et al. 2005) and single population studies (Creel and Creel 2002; List and Macdonald 2003; Briner, Nentwig et al. 2005; McCarthy, Fuller et al. 2005; Spritzer, Meikle et al. 2005;

Howze and Smith 2015; Ramesh, Kalle et al. 2015). It is used, however, despite pressing evidence that KDE outperforms any other home range estimator, including MCP (Worton 1995, Naef-Daenzer, 1993; Seaman and Powell 1996; Matthiopoulos 2003; Barg, Jones et al. 2005; Borger, Franconi et al. 2006; Katajisto and Moilanen 2006; Millspaugh, Nielson et al. 2006) but see (Lawson and Rodgers 1997; Casaer, Hermy et al. 1999; Ostro, Young et al. 1999; Getz and Wilmers 2004)). Only KDEs can account for heterogeneity in space use, such as multiple core areas within the home range (Seaman, Millspaugh et al. 1999; Kernohan, Gitzen et al. 2001). In addition, MCP home range size estimates only reach asymptotic levels with 100-300 locations (Harris, Cresswell et al. 1990), while KDE require 30 locations (Seaman, Millspaugh et al. 1999) or even only 10 locations (Borger, Franconi et al. 2006), providing that the locations are sampled over a standardized number of days. MCP are also more sensitive to outliers than KDE (Hansteen, Andreassen et al. 1997). In this thesis, therefore, I only use KDE for home range size estimations.

1.5 Methodological approaches to address questions on space use and population dynamics

Analyses of animal space use and population dynamics are based on data from experimental, correlational or simulation approaches. Experiments investigate the effect of one or more factors on a response variable by manipulating the factor and comparing the observed change with a control. Ex-situ experiments create a simplified version of reality to control for all factors, so that any changes observed can be related to the manipulated factor. Some ex-situ experimental studies provided valuable insights by identifying causal factors of rodent space use (Mihok 1981; Freund, Brandmaier et al. 2013). Often,

however, results from simplified and artificial laboratory conditions are not applicable to in-situ processes that are driven by a complex network of factors. In-situ experiments aim to overcome these limitations by manipulating a factor in otherwise natural conditions. Results based on in-situ experiments can provide useful insights and have improved our understanding of how predation risk (Lagos, Contreras et al. 1995) or intraspecific density (Eccard, Jokinen et al. 2011) affect space use. In-situ supplementary feeding experiments in temperate rodent species, for example, revealed a positive relationship between winter survival and food availability (Cole and Batzli 1978). In theory, in-situ experiments are an ideal approach to extend our knowledge on animal space use and population dynamics. However, most experiments are also logistically demanding, uneconomical and, particularly in studies on population dynamics, require years of data collection. These reasons make it challenging for researchers to pursue such experiments in the modern research environment.

Observational approaches are an alternative to experiments, providing data from complex systems with many, often interacting drivers (Clutton-Brock and Sheldon 2010). This is particularly useful when the potential effects of manipulating a factor are not fully understood. However, and contrary to experimental approaches, observational research does not allow causality inference. Similar to in-situ experiments, they also hold several practical challenges for space use analyses in rodents. Most rodent species are small, crepuscular or nocturnal, and spend at least parts of their lives underground (Walker 1975). These factors make any direct observational research almost impossible and remote monitoring devices (e.g. GPS, telemetry) are too large, too heavy or not accurate enough to be used for monitoring space use in most

rodent species (Wikelski, Kays et al. 2007). Unfortunately the use of the new monitoring technologies was beyond the scope of this thesis. A summary of the current state of monitoring technologies, with a focus on small mammal tracking, can be found in the appendix. For now researchers rely on indirect observation methods. The most common approach for data collection in rodent studies is currently live trapping, usually combined with a mark-recapture approach (Hoffmann, Decher et al. (2010) and Barnett and Dutton (1995) provide a summary on small mammals monitoring techniques). Trapping alone, however, cannot provide a temporal and spatial resolution that is required to answer most space use questions, although it is considered an adequate method to assess population dynamics (e.g. Burthe, Lambin et al. (2010)). Recently, a new indirect observational approach has been developed. Malo, Godsall et al. (2013) track rodents with implanted RFID tags via RFID logging devices that change locations across the study area. The tags are small and light enough to be used in most rodents but cannot actively transmit location information (unlike GPS or VHF tags). Tagged individuals, therefore, are only recorded at close proximity of one of the mobile RFID readers. This approach increases temporal resolution of space use data collection from once a fortnight (a common interval of live trapping) to approximately once a day. To our knowledge, it is currently the only method capable of collecting such high spatio-temporal resolution data for rodents.

In addition to empirical and experimental methods, in-silico simulations have become a common third methodological approach, assisted by the rapid increase in computational power over the last two decades. As in-situ approaches are often restricted by technological, financial and logistic

constraints, in-silico simulations can be an adequate support for in-situ approaches or, in some cases, even a replacement. In-silico approaches simulating space use and population dynamics can be broadly categorized into individual and population level simulations. Individual level simulations, for example the individual based model, can track both individuals and a population through space and time (Letcher, Rice et al. 1996; Grimm, Revilla et al. 2005; Liu, Sibly et al. 2013). They can be spatially explicit and are capable of creating complex patterns based on simple rules by assigning variable characteristics to individuals (Grimm, Berger et al. 2006). Originating in game theory and used in economic and sociological research (Epstein 1999; Tesfatsion 2003), individual based models are now also used to address ecological and evolutionary questions (e.g. (DeAngelis and Gross 1992; Grimm 1999; DeAngelis and Mooij 2005; Grimm, Revilla et al. 2005; Liu, Sibly et al. 2013)). In chapter 3, I use this model to investigate the effect of food availability and predation risk on home range size in wood mice.

In population biology, however, many questions are not spatially explicit and do not require information about an individual's location. Population level models, therefore, can simulate the change of a character distribution (rather than individuals with different characters) in a population over time. Matrices track and store character distributions within a population or of a population over time (Leslie 1945; Lefkovitch 1965; Tuljapurkar). If the character is discrete (e.g. age class or sex) a matrix population model can be used (Caswell 2001). In some cases, discretizing a character (e.g. different age classes based on arbitrary body weights) can decrease the biological realism. Easterling, Ellner et al. (2000), therefore, developed the integral projection model that can track the

distribution of a continuous character (e.g. body weight, size, height etc.) in a population over time. These types of models are being increasingly used to link environmental variables to population growth (Dahlgren and Ehrlén 2009; Ozgul, Childs et al. 2010; Simmonds and Coulson 2015), evaluate viability of harvested wild populations (Wallace, Leslie et al. 2013) and investigate life history evolution (Childs, Rees et al. 2004; Metcalf, Rose et al. 2008; Miller, Louda et al. 2009). In chapter 4, I use an integral projection model to test the effect of population density on body weight and life history parameters.

1.6. Study species

The relevance of rodents

Rodents are the most numerous order of mammals, accounting for around 40% of all known mammalian species (Nowak 1936). Many species are fundamental for a functioning ecosystem, representing an important trophic level where they are a food source for many predators (e.g. for mammals (King 1980), birds (Southern and Lowe 1982) and reptiles (Hisaw and Gloyd 1926)). Rodents also contribute to maintaining ecosystems by foraging on shrub and tree seeds and seedlings (Batzli and Pitelka 1970; Davidson, Detling et al. 2012; Lyly, Klemola et al. 2014) and dispersing seeds (Jensen and Nielsen 1986; Hulme 1994; Santos and Tellería 1997), which can contribute to a heterogeneous, more stable plant community (Cottingham, Brown et al. 2001; Tilman, Reich et al. 2006). In the last few decades, animal research on several rodent species has contributed to large increase of knowledge on many human disorders and diseases, including diabetes, obesity, Alzheimer's disease, cancer, HIV and heart disease (Doggrell and Brown 1998; Chen and Wang 2005; Van Dam and

De Deyn 2006; Denton and Garcia 2011; Seigers and Fardell 2011). For much longer, however, this mammalian taxon has already been linked to human culture as a protein source (Murdock 1967; Fa, Ryan et al. 2005), as disease vectors (McCormick 2003) and as pests (O'Connor 1992).

Rodents are a global agricultural pest (e.g. in Africa (Leirs 2003), America (Marsh 1988; Rodriguez 1993), Asia (Singleton 2003), Australia (Caughley, Bomford et al. 1998) and Europe (Jacob and Tkadlec 2010)), leading to losses of up 77 million tonnes of pre-harvest crops (Stenseth, Leirs et al. 2003; John 2014). They are also vectors for around 60 human diseases, transmitting them either directly (e.g. hanta virus, lassa fever, plaque, meningitis and salmonellosis) or indirectly by hosting disease carrying parasites (e.g. leishmaniosis, encephalitis, Lyme disease, typhus and west Nile virus) (MClEan 2007; CDC 2011). Lassa fever alone transmitted primarily by the Natal multimammate mouse (*Mastomys natalensis)*, is estimated to infect up to 500 000 people in West Africa annually (Ogbu, Ajuluchukwu et al. 2007). Rodents not only affect human food security and health, but as invasive species they can also threaten native fauna and flora. Hitch-hiking with humans on expeditions and global ship trades, rodents have reached many remote places, particularly islands. They encountered ecosystems vulnerable to invasion by rodents, with devastating effect on plants (Athens 2009), mammals (Harris 2009), invertebrates (St Clair 2011) and especially birds, where rodents account for more recent extinctions than any other single factor (Blackburn, Cassey et al. 2004). Rodents are not only a threat to others. Habitat alteration and destruction as well as illegal hunting and poisoning contributes to rodents being under

threat, with 352 species currently listed as critically endangered, endangered or vulnerable and 37 species listed as recently extinct by the IUCN (IUCN 2015).

As rodents contribute to such a variety of fields, understanding space use patterns and population dynamics is essential in order to address many questions related to rodent ecology. Improving our understanding of ecosystem functioning (Dickman 1999) can contribute to the success of conservation effort for both endangered rodent species as well as for threatened habitats (Davidson and Lightfoot 2006; Santos, Simões et al. 2006; Letnic, Crowther et al. 2009; Davidson, Ponce et al. 2010; Bean, Prugh et al. 2014) and improving our success rate of eradicating pests, disease vectors and invasive species (Stenseth, Leirs et al. 2003; Capizzi 2014; Holmes, Griffiths et al. 2015). Due to their importance in many different fields, numerous rodent species have been studied intensively for decades (e.g. (Steen, Yoccoz et al. 1990; Boonstra, Krebs et al. 1998; Wolff and Sherman 2008)). Yet, even for well-studied species many questions are only partly answered or remain still unsolved (Boonstra, Krebs et al. 1998). The two main reasons for this are a) the complexity and multifactorial of most ecological questions on space use and population dynamics, and b) the challenges in data collection from a taxon that consists of many small, nocturnal, short-lived, and cryptic species. Although not all rodent species can be described using the mentioned criteria many fit under this umbrella. Therefore, in this thesis I use the term rodents synonymously for the group of rodents species that meet the mentioned criteria. The wood mouse (*Apodemus sylvaticus)* and the bank vole (*Myodes glareolus)* are two examples of this. They are relevant for ecosystem functioning due to their roles as seed dispersers (Hansson 1985; Jensen and Nielsen 1986) and prey to many

carnivorous species (Southern and Lowe 1968; King 1980; Southern and Lowe 1982; King 1985). They have been intensively studied for more than a century (e.g (Harting and West 1887; De Larramendi 1900; Hacker and Pearson 1944; Miller and Elton 1955; Andrzejewski and Olszewski 1963; Kikkawa 1964; Crawley 1969; Watts 1969; Randolph 1977; Wolton 1983; Alibhai and Gipps 1985; Clarke 1985; Benhamou 1991; Canova 1993; Tew and Macdonald 1994; Montgomery, Wilson et al. 1997; Eccard and Ylönen 2007; Buesching, Newman et al. 2008; Trebatická, Sundell et al. 2008; Malo, Godsall et al. 2013; Godsall 2015) . Thanks to their research we now have a foundation to study their space use patterns and population dynamics.

Bank vole and wood mouse

The two study species, the wood mouse and the bank vole, are both common rodents across Europe (Nowak 1936; Tew and Macdonald 1994). Due to the large latitudinal range, their biology varies considerably between the Mediterranean region and Northern Scandinavia. The following summary of the species' biology is mainly based on findings from Central Europe because of their relevance for our study system in the United Kingdom. Both species inhabit woodlands, grasslands and hedgerows (Nowak 1936). Wood mice are nocturnal, with two activity peaks two to four hours after sunset and before sunrise during winter and a single activity peak during summer nights (Montgomery and Gurnell 1985). Bank voles are less strictly nocturnal and can be active through the day with activity peaks at dusk and dawn (Grodzinski 1963; Kikkawa 1964; Gipps 1985). The diet of wood mice varies between seasons and includes roots, seeds, berries, nuts and invertebrates (Flowerdew, Gurnell et al. 1985; Jensen 1993; Kai and Walter 1998). During the summer

reproductive season, protein rich invertebrates are preferred, while cached seeds and nuts are the main energy source over the winter (Hansson 1985). Voles have a more folivorous diet, but show otherwise similar food preferences, except of a lower percentage of invertebrate during breeding season (Hansson 1985). Both species are prey for several terrestrial and aerial hunting predators, including *Mustela erminea, M. nivalis, Vulpes vulpes* and *Strix aluco* (King 1980; Southern and Lowe 1982; King 1985). Wood mice reproduce between March and September, although breeding can continue throughout the year in Mediterranean regions and in Northern regions during mild winter (Larsson, Hansson et al. 1973; Clarke 1985)(pers. obs.). They can produce up to six litters per year (average 2) with 4-7 young each (Clarke 1985). The breeding season in bank voles is less temporally fixed, but usually starts in April and last until September (Alibhai and Gipps 1985), although occasional winter breeding has also been reported (Smyth 1966). Litter size in voles (n = 1-13) shows more variance than in wood mice (n = 4-7) and higher numbers of litters (n = 4), while mean litter size (n = 5.5) is similar (Nyholm and Meurling 1979; Gustafsson, Andersson et al. 1983).

Space use behaviour in both species varies between breeding and non-breeding season (Randolph 1977; Wolton and Flowerdew 1985). With the onset of the breeding season, males extend their home range in order to maximize access to females (Crawley 1969; Wolton and Flowerdew 1985; Attuquayefio, Gorman et al. 1986; Korn 1986). During the non-breeding season, when foraging and predation risk are expected to be the main drivers of space use, the size of the male home range decreases (Crawley 1969; Wolton and Flowerdew 1985; Attuquayefio, Gorman et al. 1986; Korn 1986). Females, in

contrast, seem to inhabit high quality patches to maximize food access and reduce predation risk all year around, resulting in a relatively consistent home range size across seasons (Crawley 1969; Wolton and Flowerdew 1985; Attuquayefio, Gorman et al. 1986; Korn 1986; Hoset, Galliard et al. 2008). Direct interspecific competition seems to exist, but the extent to which direct competition affects space use and population dynamic remains unclear. Laboratory experiments revealed either dominance of *Apodemus* spp over bank voles or avoidance/ignorance between the two species (Andrzejewski and Olszewski 1963; Gurnell 1985). Gliwicz (1981) found lower mortality and higher survival rates of offspring in *Apodemus agrarius* when bank voles were removed. During the breeding season, vole home range size decreases with increasing wood mouse densities, probably due to direct interference (Eccard and Ylönen 2002; Eccard and Ylönen 2007; Eccard, Fey et al. 2011). During the non-breeding season, higher density of *Apodemus spp*. increases home range size in voles, suggesting that indirect resource exploitation is affecting space use (Eccard, Fey et al. 2011).

Although drivers of space use in mice and voles have been previously studied, the relative relevance of individual drivers and the different effect of one driver on core and peripheral home range has not been fully understood. In chapters 2 and 3, we try to improve our knowledge by investigating the relative contribution of individual drivers on vole home range size (Chapter 2) and the effect of annual fluctuations in food availability on wood mouse home range size (Chapter 3).

Both species also undergo super annual and annual population cycles. Their annual cycles are mainly driven by an increase in population size during the

summer breeding season. The dispersal of sub-adult (males) at the end of the breeding season and a population decrease is the result of lower survival rates due to harsher climatic conditions and food shortage during winter (Alibhai and Gipps 1985; Flowerdew 1985). The super annual cycles, however, are likely to be driven by different mechanisms. Super annual population peaks in wood mouse could be correlated with years of mast crops in acorn, one of their main winter food sources (Flowerdew 1985). The drivers for super annual cycles across different vole species are still debated, as they appear to be unrelated to food availability (Ford and Pitelka 1984; Desy and Batzli 1989; Schweiger and Boutin 1995). A large body of literature proposing different hypotheses tries to explain super–annual population cycles in rodents (e.g. (Chitty 1967; Krebs 1978; Boonstra, Krebs et al. 1998; Oli 1999).

1.7. Study site

The study site was located in a mixed deciduous woodland (National Vegetation Classification: W10a Typical sub-community) at Silwood Park, Imperial College London (OS grid ref.: SU 9430 6920). The dominant tree species are *Betula pendula* and *Betula pubescens*, with some ancient *Fagus sylvatica.* Additional tree species are *Acer pseudoplanatus, Quercus petraea, Fraxinus excelsior* and *Alnus glutinosa*. The shrub layer is dominated by *Rhododendron ponticum* and *Corylus avellana*. In the Northeast corner of the study site *Sasa palmate* forms a dense patch of approximately 700m^2. The most prominent ground layer species are *Hyacinthoides non-scripta*, *Pteridium aquilinum, Oxalis acetosella* and, although not as common as the previous species, *Urtica dioica, Lysimachia nemorum* and *Anemone nemorosa.* The study site is 2.47 ha, and is subdivided into 10 x 10 m grid squares (Figure 1.1).

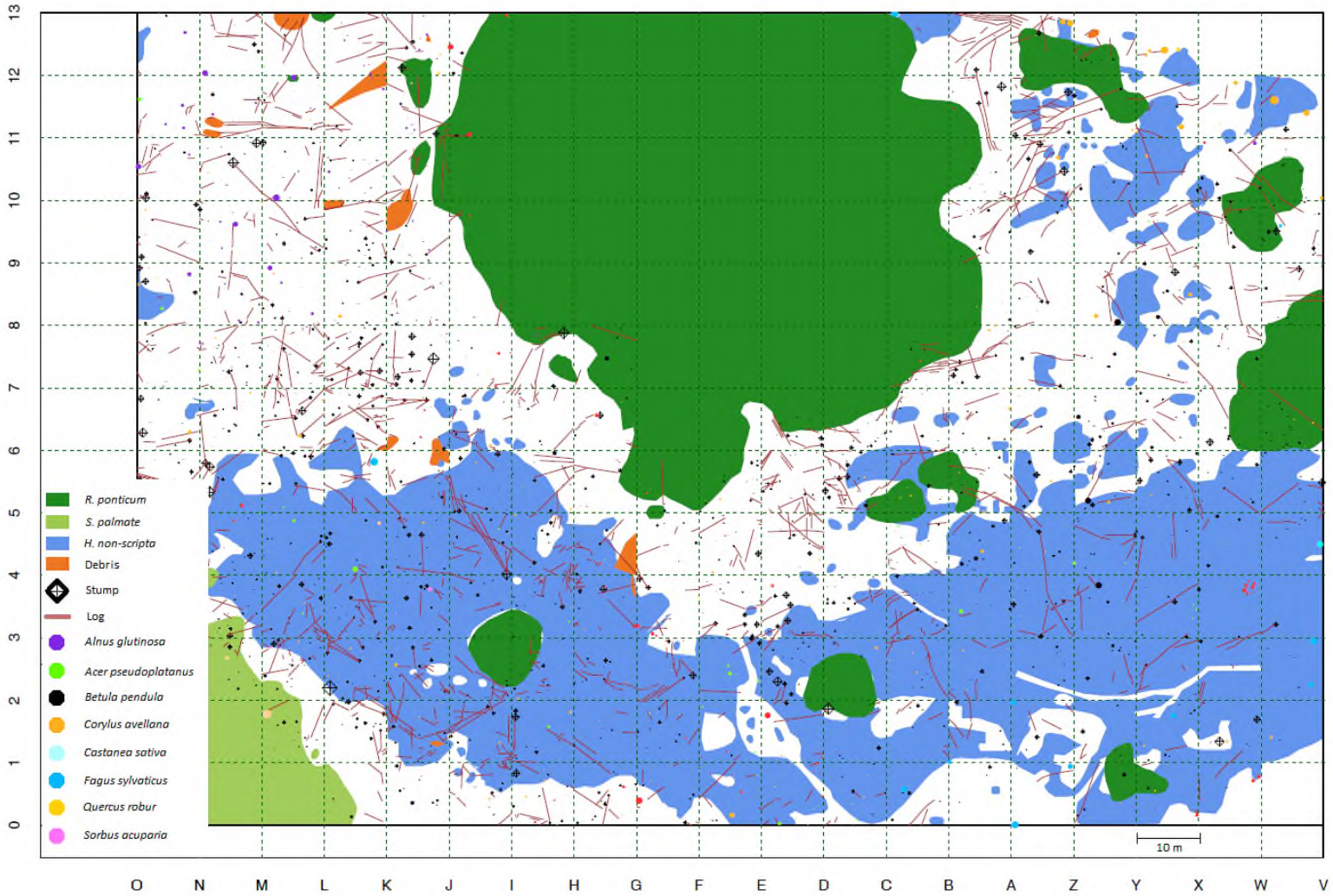


Figure 1.1: Map of the study site showing Rhododendron (dark green), bamboo (light green), bluebells (blue), debris (orange), stumps (square), logs (red lines) and trees (dots). Trees inside of Rhododendron and bamboo are not shown. Dotted lines represent 10 x 10 m squares used for placement of traps and mobile recording stations. Map was created in GIS (ArcGIS, v9.3).

1.8. Aims and outline of thesis

This thesis aims to investigate space use drivers, space use patterns and drivers of population dynamics in two common European rodents, *Apodemus sylvaticus* and *Myodes glareolus,* and to contribute to our understanding of bias in space use estimates.

The following chapters 2 – 5 are presented in the style of journal articles.

Chapter 2

This chapter aims to improve our understanding of the relationship of core and periphery home range size in voles with space use drivers, including habitat features that reduce predation risk (i.e. patches of Rhododendron and logs), sex, season, inter- and intra-specific density.

Chapter 3

This chapter examines the relationship of home range size in wood mice with annual fluctuations in food availability. In-situ home range size estimations are compared with home range size estimations from in-silico estimations. Three sets of simple movement rules are constructed, modelling different types of space use patterns.

Chapter 4

This chapter assesses if the Chitty effect - heavier individuals at high population densities – can be found in our wood mouse population. A stochastic, density dependent integral projection model is constructed to analyse how body weight and life history parameters change as a function of population density.

Chapter 5

This chapter investigates the relationship of bias in core, peripheral and full home range size estimation with different space use pattern. Six different types of movement patterns are simulated providing a total utilization distribution of space. Home ranges are then estimated based on subsets of spatial data of different temporal resolutions. This allows a comparison of sensitivity in bias home range size estimation due to differences in space use patterns.

Chapter 2

Undercover: Predation risk-reducing habitat features drive home range size variation in a woodland rodent

Abstract:

Intra-specific home range size variation can be influenced by many factors. For small mammal species, the drivers of home range size are known but their relative importance often remains unexplored. In this study we tested the influence of population-level drivers (both abiotic and biotic) and individual-level drivers on the home range size. We used a novel method of mobile recording stations to obtain space use information at high spatio-temporal resolution from a field population of bank voles (*Myodes glareolus*) in which individuals have PIT tags implanted. Relevant ecological habitat features were mapped at high spatial resolution. A total of 117 home ranges were estimated for 35 individuals covering six seasons using kernel density estimation. Full home ranges were split into the core home range, representing the most intensively used area, and the periphery home range. Abiotic (season, year), individual-level (body mass, sex) and biotic factors (population densities of voles and wood mice, proportion of the home range covered by different habitat features) were tested for their relationship with core, periphery and full home ranges. Full home ranges and periphery home ranges are smaller during the breeding season than during the non-breeding season, and are smaller for females than males. Full home range size has a negative relationship with population density of wood mice. Biotic factors explain a greater proportion of deviance in all three home range parts during breeding and non-breeding season than abiotic and individual-level factors. This study stresses the importance of analysing different abiotic, biotic and individual-level factors to gain insight into animal space use behaviour and to assess the relative importance of different drivers on space use variation. Our

findings highlight the general importance of habitat features that reduce predation risk for space use in small mammals. It is suggested that preferences for habitat features could lead to interspecific competition.

Keywords: bank vole*,* habitat selection, inter-specific competition, *Myodes glareolus,* space use, spatially-explicit

Introduction

Animal space use has been linked to key life history traits including survival and reproductive success (Gaines and McClenaghan Jr 1980; Hubbs and Boonstra 1997; Getz, Oli et al. 2005) and can consequently influence population dynamics and gene flow (Gaines and McClenaghan Jr 1980; Booth, Montgomery et al. 2009). It is therefore important to understand the population-level and individual-level drivers of space use and to disentangle the relative importance of drivers for variation in space use.

Many questions regarding space use have focussed on understanding home ranges, which has been defined as the space an animal needs to survive and reproduce (Burt 1943). Numerous factors can influence home range variation in natural populations. These factors can be categorised into (1) population-level abiotic factors (seasonal variation (Haugen 1942), weather (Morellet, Bonenfant et al. 2013)), (2) population-level biotic factors (e.g. resource availability (Litvaitis, Sherburne et al. 1986; Hubbs and Boonstra 1997), intra- and interspecific population density (Kleeberger 1985; Trombulak 1985), predation risk (Hayes, Chesh et al. 2007)) and (3) individual – level factors (e.g. age

(Ingles 1961), body condition (Godsall, Coulson et al. 2014), body mass (Litvaitis, Sherburne et al. 1986), genetics (Seddon, Amos et al. 2004) and sex (Haugen 1942)). The importance of a factor can vary between the core of a home range and its periphery (Samuel, Pierce et al. 1985; Vander Wal and Rodgers 2012; Godsall, Coulson et al. 2014). The core covers the area with greatest activity and is thought to be subject to more intense territorial behaviour, as it usually includes the highest foraging and nesting quality patches within a home range (Samuel, Pierce et al. 1985; Vander Wal and Rodgers 2012). The periphery of the home range is used less frequently, but it is considered still important as a foraging and courtship area (Burt 1943).

In bank voles (*Myodes glareolus)*, a common rodent in Central and Northern Europe, several factors are known to drive space use patterns (Crawley 1969; Flowerdew, Gurnell et al. 1985; Wolton and Flowerdew 1985; Löfgren 1995; Trebatická, Sundell et al. 2008; Eccard, Fey et al. 2011). The size of its home range varies with body mass (as a proxy for age) and sex, with heavier adults having larger home ranges than lighter sub-adults, and males having larger home ranges than females (Andrzejewski and Mazurkiewicz 1976; Flowerdew, Gurnell et al. 1985). Like many mammals living in temperate regions, the vole's year cycle can be divided into a breeding season (from late spring to early autumn), and a non-breeding season (from late autumn to early spring) (Flowerdew, Gurnell et al. 1985). With the onset of the breeding season, males extend their home range in order to maximize access to females (Crawley 1969; Flowerdew, Gurnell et al. 1985; Korn 1986; Ims 1987; Ims 1988). During the non-breeding season, when foraging and predation risk are expected to be the main drivers of space use, the size of the male home range decreases

(Flowerdew, Gurnell et al. 1985). If core home ranges are established to guarantee access to high quality food patches and nesting sites (Samuel, Pierce et al. 1985; Vander Wal and Rodgers 2012), we would expect that changes in male home range sizes due to reproductive behaviour is restricted to the periphery home range size and that core home ranges do not change in size between seasons.

Females, in contrast, seem to inhabit high quality patches to optimize food access and reduce predation risk all year around, resulting in a relatively consistent home range size across seasons (Flowerdew, Gurnell et al. 1985; Hoset, Galliard et al. 2008). Both sexes can reduce predation risk by using patches with a high density of cover-providing habitat features such as logs, shrubs and trees (Kotler 1984; Trebatická, Sundell et al. 2008).Therefore, we would expect parts of home range size variation to be explained by the availability and distribution of these habitat features, independent of season and part of the home range (core and periphery). In addition to individual-level and habitat factors, intraspecific and interspecific competition can also affect home range size (Kleeberger 1985).

During the breeding season, the increase in both bank vole and wood mouse densities results in a decrease of bank vole home range size for both sexes due to direct interference (Eccard and Ylönen 2002; Eccard and Ylönen 2007; Eccard, Fey et al. 2011). During the non-breeding season, increased density of conspecifics and rodent heterospecifics results in larger home ranges, suggesting that indirect resource exploitation is affecting space use (Eccard, Fey et al. 2011). The findings of density dependent home range size variation in both seasons are based on full home range analysis. It has been shown,

however, that even under high density vole maintain a minimum territory size (Eccard, Jokinen et al. 2011). Therefore, it is likely that density as a driver of home range size variation applies only to the periphery home range size and the core home range remains unaffected.

Although previous research has identified several potential drivers of space use in voles, to our knowledge no one has investigated their combined effects nor disentangled the relative importance of individual-level and population-level drivers on space use. In addition, no study on voles has investigated how the importance of space use drivers varies between different parts of a home range. In this study, we test the importance of space use drivers on different parts of a home range in a population of bank voles by using a spatially-explicit approach to collect high resolution individual-level data of space use matched with high resolution habitat data. We collected relocation fixes per individual with high spatiotemporal resolution by combining live trapping with a novel monitoring technology using mobile data loggers that allow data collection without interfering with rodent natural behaviour. We used kernel density estimates (Worton 1989) to estimate three measures of the home range: the core range, the periphery and the full home range (the core and periphery combined). Habitat features predicted relevant for voles, either for providing food resources or protection from predators, were mapped to a one meter resolution level, allowing us to capture and incorporate in our models different axes of habitat quality as predictors of space use.

In this study we test four hypotheses: (1) Full home ranges and periphery home ranges, but not core home ranges, are larger during breeding season than during non-breeding season. (2) Variation in core range size in both seasons is

mainly driven by population-level biotic factors. (3) During the breeding season, variation in full home ranges size and periphery home range size is mainly driven by the population-level biotic factors habitat features, inter- and intra-specific density and the individual-level factor sex. (4) During the non-breeding season, variation in full home range size and periphery home range size is only driven by population-level biotic factors.

Material and Methods

Study site

The study site was located in a mixed deciduous woodland (National Vegetation Classification: W10a Typical sub-community) at Silwood Park, Imperial College London (OS grid ref.: SU 9430 6920). The dominant tree species are *Betula pendula* and B*etula pubescens*, with some ancient *Fagus sylvatica.* Additional tree species are *Acer pseudoplanatus, Quercus petraea, Fraxinus excelsior* and *Alnus glutinosa*. The shrub layer is dominated by *Rhododendron ponticum* and *Corylus avellana*. In the Northeast corner of the study site *Sasa palmate* forms a dense patch of approximately 700m^2. The most prominent ground layer species are *Hyacinthoides non-scripta*, *Pteridium aquilinum, Oxalis acetosella* and, although not as common as the previous species, *Urtica dioica, Lysimachia nemorum* and *Anemone nemorosa.* The study site is 2.47 ha, and is subdivided into 10 x 10 m grid squares.

Trapping sessions

Weekly trappings were conducted from March to November 2010, and biweekly from November 2010 to March 2013. During each trapping session, one

Sherman trap (16 cm L x 5.8 cm W x 6.5 cm D) was placed in one 10m x 10m grid square ($n_{traps/session}$ = 80-140). Each grid square was only used once per two trapping sessions. Thus each grid square was used twice a month during the period of weekly trapping sessions and once a month otherwise. All captured voles were weighted, sexed, and their reproductive status assessed. For more information about the assessment of the reproductive status see Godsall et al. (2014). All individuals were released immediately after data collection in the same location where they were caught. To assess how home range size was affected by intraspecific and interspecific density, population sizes for voles and two wild mouse species, *Apodemus sylvaticus* and *A. flavicollis*, were estimated for each season by counting all individuals that were monitored during a season (Table 2.1).

Recording stations

Location fixes of voles were collected using mobile recording stations with radio frequency identification (RFID). RFID technology has two components, the passive integrated transponder tag (PIT tag), which has a unique character string that identifies the animal to which it is fixed, and the recoding station, which recognizes the tag (Howerton, Garner et al. 2012). When a vole over 15g of weight was caught for the first time during trapping sessions, a 12mm x 2mm PIT-tag was inserted. Studies have shown that in species with lower body mass than voles behaviour and survival is not affected by PIT tags (Nicolaus, Bouwman et al. 2008; Cousin, Daouk et al. 2012).

Recording stations were constructed from plastic crates (60 cm L x 39 cm W x 42 cm H) with a plastic tube (45 mm diameter) running through the crate to

provide two entrances on opposite sites. Inside the crate, the tube was connected to a wooden box filled with wood chippings to soak up urine, hence facilitating cleaning and reducing a potential effect of scent marking. Also, a single peanut was placed in the wooden box as a minor reward (approx. 11 % of the daily budget; estimated from data in Corp, Gorman et al. (1999)). An antenna, fastened around the tube where it fed into the wooden box, recorded the unique PIT tag number (mouse identity) and time, when the animal entered the tube. Data was stored at an under one-second resolution at a recording unit connected to the antenna (Francis Scientific Instruments Ltd., Huntingdon, UK). Two drops of peanut oil were applied on the tube entrances to attract mice in the immediate vicinity. Five mobile recording stations were used between March 2010 and June 2010 and 10 were used from June 2010 until the end of the study. Each recording station was only used in a clearly defined 0.24 ha woodland area. Within each area, stations where rotated randomly between 100 m^2 quadrates every night with at least 30m distance between quadrates used in consecutive nights (see Godsall et al. (2014) for further information). Within a quadrate, the station was placed at a random 1 m^2 coordinate. Recording stations where moved daily (n = 5 per week). Once all quadrates within a given area had been sampled, the list of quadrates was re-randomized and the process started again. The resulting data had a spatial location resolution of ± 1m, the individual time of presence in the recording station and the vole identity. Location rates were obtained at high temporal resolution (3 fixes per second) and, consequently, were trimmed to remove excess relocation data of individuals remaining inside of the recording station (see Godsall et al. (2014) for further information).

Seasonal variation

Vole space use behaviour varies between the breeding and non-breeding season (Flowerdew, Gurnell et al. 1985). We consequently estimated individual home ranges for each season. The onset of the breeding season was defined as the date of the trapping session when over half of the males caught were in breeding condition (see Godsall et al. (2014) for methods of assessing breeding condition). The non-breeding season was considered to have started when no males in breeding condition were caught. The onset and duration of the seasons varied over the three years (Table 2.1).

Home range estimation

Kernel density estimation calculates home ranges based on an individual's spatial utilization distribution (Worton 1989) and was calculated in R (version 3.0.2, Core Development Team, Vienna, Austria), using the package '*ks*' with a Gaussian kernel and the direct plug-in method for bandwidth selection (Wand and Jones 1994). Direct plug-in method is the recommended over other bandwidth selections, including least square cross validation and reference methods (Millspaugh, Nielson et al. 2006; Cumming and Cornélis 2012). If a minimum sample size of relocations per individual is provided, kernel density estimations can reliably quantify individual variation of space use and can be used to test the association with explanatory factors (Laver and Kelly 2008; Kie, Jason et al. 2010; Cumming and Cornélis 2012; Fieberg and Börger 2012). For the breeding season, we used a minimum sample size of 30 location fixes per individual (Seaman, Millspaugh et al. 1999; Girard, Ouellet et al. 2002).

Table 2.1: Season dates, monitoring effort and capture success across the study site.

Study year	2010		2011		2012	
Season	Breeding	Non-breeding	Breeding	Non-breeding	Breeding	Non-breeding
Start date	8th Apr 10	7th Oct 10	24th Mar 11	27th Oct 11	29th Mar 12	25th Oct 12
End date	6th Oct 10	23rd Mar 11	26th Oct 11	28th Mar 12	24th Oct 12	12th Mar 13
Season length (days)	181	167	216	152	209	138
Data logger effort	920	723	1595	1289	1377	518
Trapping effort (traps)	2615	1037	1665	1568	2096	1097
Unique **voles** caught	38	14	57	43	212	23
Unique *A. flavicollis* caught	10	5	15	15	49	6
Unique *A. sylvaticus* caught	67	38	166	146	163	34

'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 per season. 'Unique individuals caught' is the number of different animals caught per season.

For the non-breeding season, and due to a smaller sample size, we were forced to reduce the minimum sample size per individual to 20 location fixes, which increased the total number of individuals in the statistical analysis. However, the new minimum number of location fixes (n=20) did not increase significantly the effect of number of fixes on home range size. In order to assess the relative importance of space use drivers for different parts of the home range, the full home range estimated for each vole-season combination is divided into two areas, the core home range and the periphery. The core home range size of an individual was estimated using the time-maximizing function developed by Vander Wal & Rodgers (2012). The area between the full home range isopleth (95% isopleth) and the core home range isopleth was defined as periphery home range. In order to avoid an edge effect that can occur in study sites with grid design, only individuals with a lower number of relocations within 10m of the study site boundary versus the study site interior were used for analysis. An exception was made for the bottom boundary and the bottom left corner as they are bordered by a fast-moving stream and trappings on the other side of the stream did not find any tagged rodents (Godsall et al. 2014).

Habitat data

We mapped all habitat features in our study site at a $1m^2$ resolution and updated the map every six months. Individual trees were identified, tagged, their locations mapped and their diameter at breast height (1.5m) recorded. The circumference and length of all fallen trees (termed logs) was recorded. If the circumference of a log changed from one end to the other, multiple measurements were taken and their mean value was used for further analysis.

In addition, stump circumference and height were measured. We then calculated the total volume of wood for logs, stumps and trees up to a height of 1.5m, using the equation for cylindrical bodies. The area covered by the patch-forming shrubs rhododendron (*R. ponticum)* and bamboo (*S. palmate)* was measured by mapping the outline of the patches. In contrast, the other dominant shrub species, *C. avellana,* was treated as a tree and measured accordingly. Maps were created with GIS (ArcGIS, v9.3) including absolute and relative coverage of *R. ponticum, S. palmate,* log volume, stump volume and tree volume ("tree") for each square meter. For further analyses, coverage of *R. ponticum* and *S. palmate* were merged into one variable called *cover*. Similarly, log volume and stump volume was merged into a single variable called *logs*.

Statistical analysis

All statistical analyses were conducted using R (3.0.2). Nine generalized linear models (GLM) were constructed to test whether and how variation in home range size is affected by ecological drivers. One set of GLMs including season as a factor (n = 3; "Yearly model") was fitted to the three parts of the home range (HR). HR size was the response variable (log- transformed if necessary to ensure residuals conformed to a normal distribution). For every model, two individual-level covariates (sex and mean body weight) and two abiotic covariates (season and year) were initially included. An interaction between sex and body weight was also included to account for male voles generally being heavier. Five biotic covariates were also included in every initial model, namely vole density, a combined density measure of both *Apodemus* species, and the

proportions of cover, logs and trees. A quadratic term for logs and trees was also included. To test for variation in home range size within a season, additional models were constructed for each season. For the breeding season, a GLM was constructed for the three HRs with the same covariates as before (n = 3). For the core home range analysis of the breeding season, one individual (BDAF35) was excluded as it included a large outlier in proportion of logs. For the non-breeding season, a GLM was constructed for the three HRs with the same covariates as before (n = 3). However, due to the small number of individuals for the non-breeding season (n = 13), combinations of the four covariates were tested separately. Individual home ranges in all models were weighted according to their number of location fixes. Model simplification was conducted using a step wise approach (Crawley 2012). Models, before and after removing a covariate, were compared with an F-statistic to test for a significant increase in deviance after term removal. The minimum adequate model was obtained when only significant covariates remained or when the removal of a non-significant term resulted in a significant increase of the deviance.

The proportion of explained deviance for each covariate was calculated using the equation

$$P = ((N - R)/N) - ((N - C)/N) \quad (2.1)$$

where P is the proportion of the deviance explained by the covariate, N is the null model deviance, R is the residual deviance and C is the covariate deviance.

Results

In total, 117 home ranges (39 core home ranges, 39 periphery home ranges and 39 full home ranges) from 35 individuals were computed covering six seasons (3 breeding season, 3 non-breeding season) over three years (Table 2.3). For the breeding season, 78 home ranges from 26 individuals were created (e.g. Figures 2.1 – 2.3). For the non-breeding season, 39 home ranges from 13 individuals were calculated.

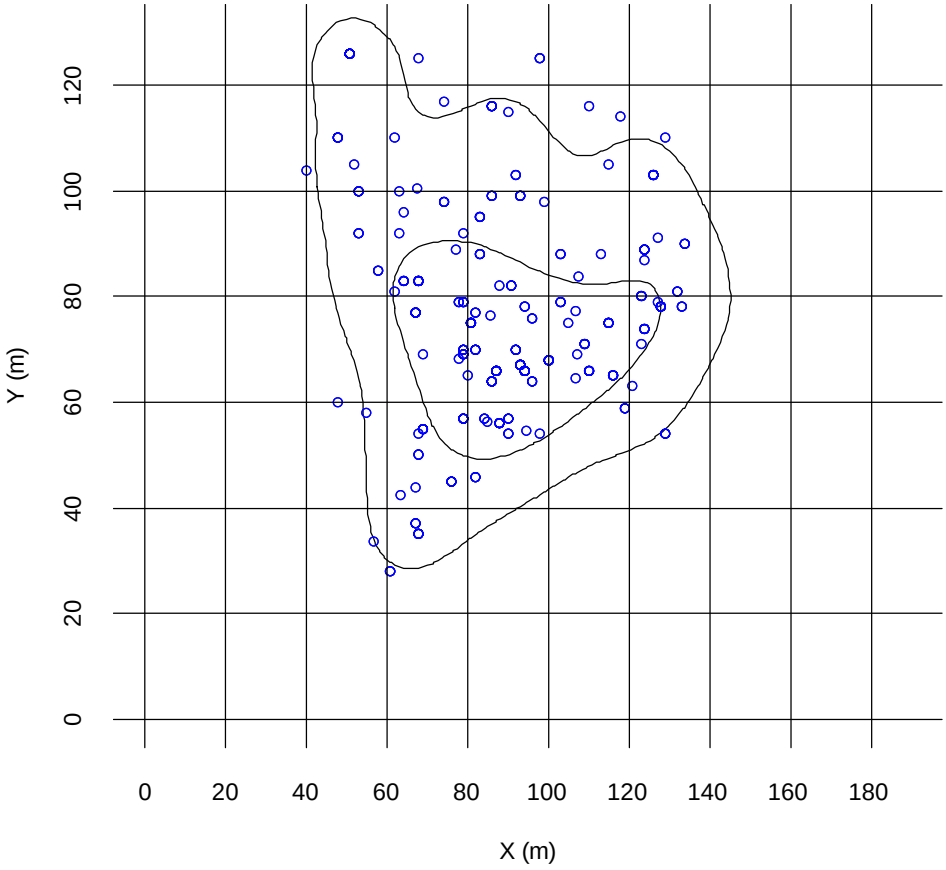


Figure 2.1.: Home range of a male vole during breeding season in 2012. 'Blue points' (n = 260) are individual location fixes of traps and mobile recording stations. Outer solid line illustrates the full home range (6829.11 m²) and encircles 95% of location fixes. Inner solid line respresents the core home range (947.31 m²) that covers 39.6% of the full home range.

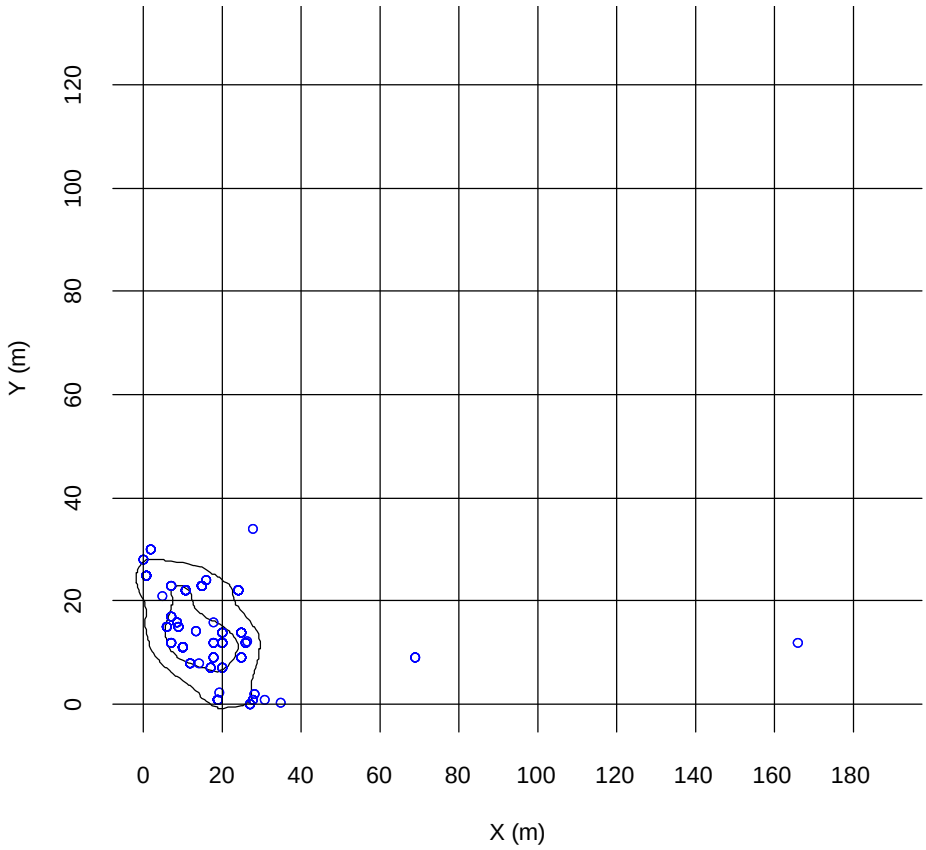


Figure 2.2.: Home range of a female vole during breeding season in 2012. 'Blue points' (n = 140) are individual location fixes from traps and mobile recording stations. Outer solid line illustrates the full home range (782.27 m²) and encircles 95% of location fixes. Inner solid line represents the core home range (167.44 m²) that covers 38.2% of the full home range.

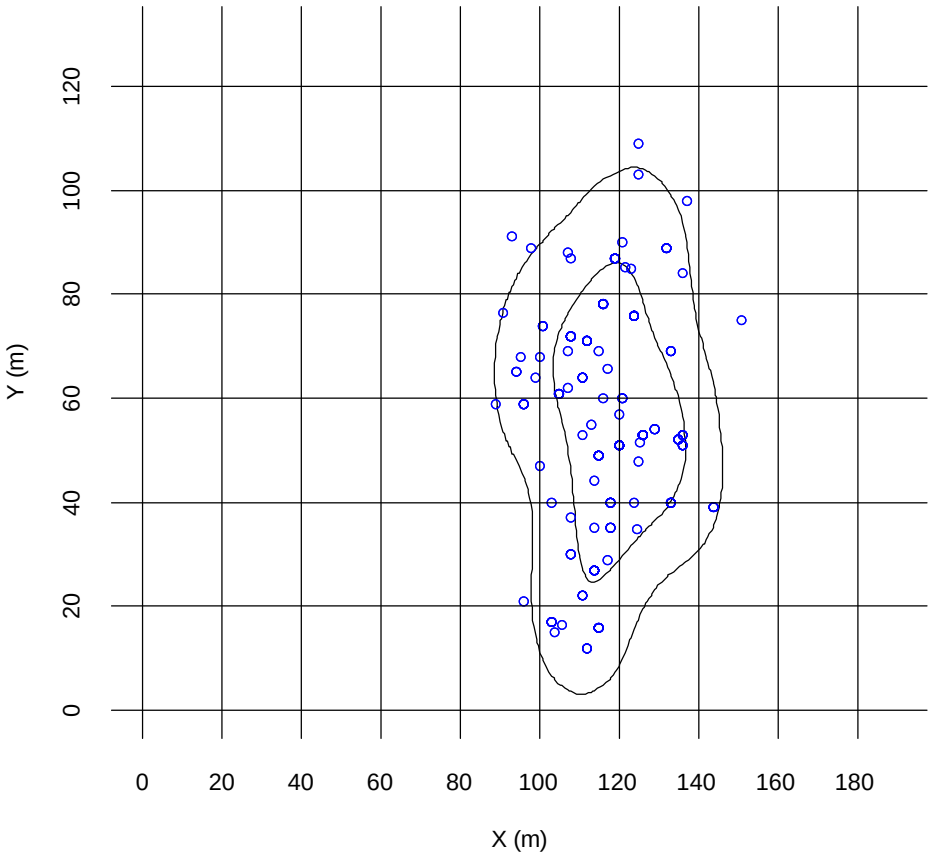


Figure 2.3.: Home range of a female vole during breeding season in 2012. 'Blue points' (n = 165) are individual location fixes from traps and mobile recording stations. Outer solid line illustrates the full home range (3729.7 m²) and encircles 95% of location fixes. Inner solid line represents the core home range (910.29 m²) that covers 39.9% of the full home range.

The percentage of the full home range that is covered by the core home range varied between 28.39 – 62.84% (Figure 2.4).

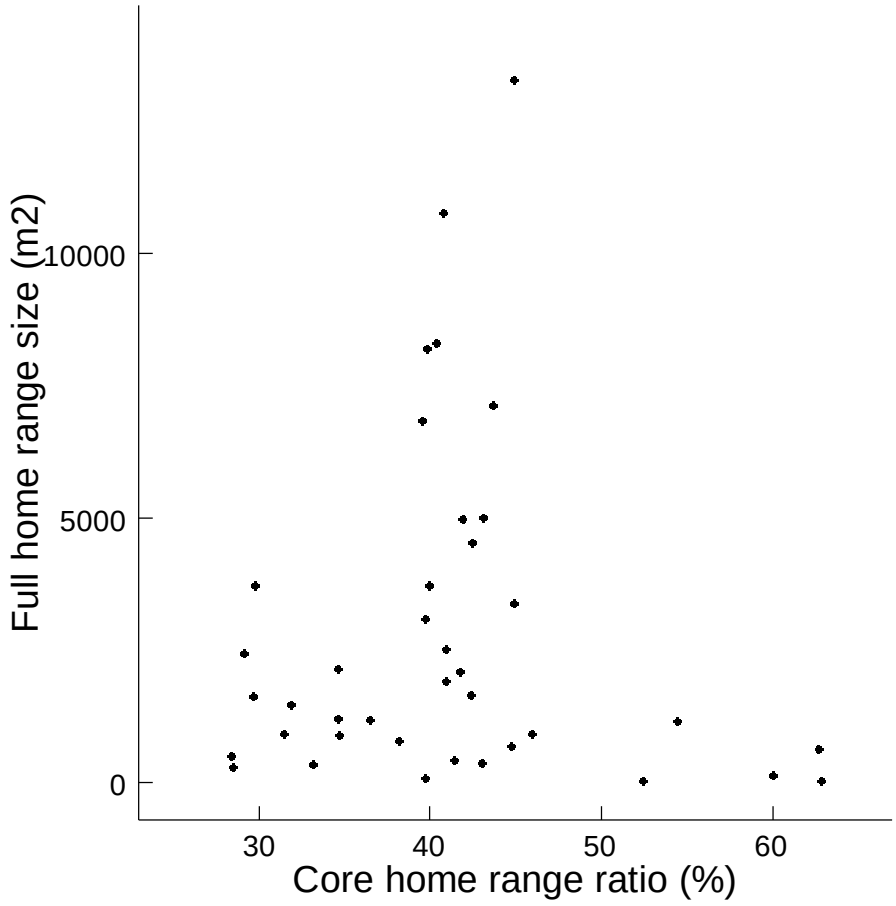


Figure 2.4. Individual proportion of the full home range that is covered by the core home range ('Core home range ratio') in relation to the corresponding full home range size (m2).

The model fit for the nine GLMs that were constructed to test whether and how variation in home range size is affected by ecological drivers is summarized in table 2.2. Additional data for each GLM is provided in the supporting information (table S2.1).

Table 2.2: Model fit for nine generalized linear models (GLM). Year: yearly model including breeding season (BS) and non-breeding season (NBS). HR: home range. df: degrees of freedom. In all models but the 'NBS – periphery HR model', the response variable was log-transformed to ensure residuals conformed to a normal distribution.

GLM	Null deviance (df)	Residual deviance (df)	Proportion of deviance explained by covariates (%)
Year - full HR	3041.13 (34)	829.63 (28)	72.72
Year - periphery HR	3110.8 (34)	1071.7 (30)	65.55
Year - core HR	3454.9 (32)	1555.9 (29)	54.97
BS - full HR	1819.69 (23)	841.05 (20)	54.78
BS - periphery HR	1776.84 (23)	840.09 (20)	52.72
BS - core HR	4731.5 (22)	3046.8 (20)	35.61
NBS - full HR	1246.89 (12)	125.41 (9)	89.94
NBS - periphery HR	219508589 (12)	32584758 (9)	85.16
NBS - core HR	1957.57 (12)	412.47 (9)	78.93

Seasonal variation in home range size

Full home ranges and periphery home ranges were larger during breeding season than during non-breeding season (Table 2.3). Core home range size did not vary significantly between seasons (Table 2.3).

Table 2.3: Number of voles used for home range analysis, mean sizes of different home range parts (± 1SD) and mean number of location fixes per individual (± 1SD).

	Yearly	Breeding season	Non-breeding season
n voles	39	26	13
n females	19	12	7
n males	16	13	3
Mean core size	563·47m² ± 597·42	624·15 m² ± 585·45	361·12 m² ± 605·12
Mean periphery size	2263·38 m² ± 2690·55	3114·07 m² ± 2924·62	562 m² ± 632·57
Mean full home range	2799·85 m² ± 3162·9	3738·23m² ± 3425·84	923·11 m² ± 1226·77
Mean number of location fixes	77 ± 51	75 ± 54	38 ± 12
Range of location fixes per individual (min – max)	22 - 260	30 - 260	22 - 59
Range of location fixes per individual per night (min – max)	0.33 – 1.89	0.33 – 1.89	0.23 – 1.40

Core home range drivers

During the breeding season, the proportion of trees remained the only significant term (quadratic) explaining variation in HR size. Medium-sized core home ranges during breeding season were found to have a higher proportion of trees than small or large core home ranges (Table 2.4). During the non-breeding season, larger core home ranges had a higher proportion of trees and a lower proportion of cover than smaller core home ranges (Table 2.4). Additionally, heavier animals were found to have larger core home ranges

during non-breeding season than lighter individuals (Table 2.4). Body weight (12.9%) explained a smaller proportion of deviance in the non-breeding season than proportion of cover (20.3%) and proportion of trees (26.6%)

Table 2.4: Results of the statistical analysis. Terms of the minimal adequate model are shown for the core home range in the yearly model, the breeding season model (BS) and the non-breeding season model (NBS). p-values (.<0.1,*p<0.05, **p<0.01, ***p<0.001) correspond to F-statistics and corresponding sample size can be found in table 2.2. 'Dev' is the proportion of deviance explained by each covariate. 'Total' is the total deviance.

	Yearly			BS			NBS		
	p	Dev	t	p	Dev	t	p	Dev	t
Weight							.	12·9	1·9
Cover	**	12·2	-2·5				*	20·3	-2·8
Trees	***	38·1	4·3	***	29·6	3·8	**	26·6	3·2
Trees^2	***	21·2	-3·0	**	20	-3·2			
Total		**71·5**			**49·6**			**59·8**	

The proportion of deviance for each term was calculated

as shown in equation 2.1 in the methods section.

Full and periphery home range drivers

During the breeding season, male voles had larger full home ranges and larger periphery home ranges than females (Tables 2.5 – 2.6). Larger full home ranges and larger periphery home ranges tended to have higher proportion of trees and a lower proportion of cover (Figure 2.5) than smaller home ranges (Tables 2.5 – 2.6). Inter- and intra-specific density was not significant in the breeding season model. In the yearly model, however, density dependence effects on the home range were apparent; full home ranges were larger when the density of *Apodemus* mice was lower (Figure 2.7, Table 2.6). Biotic factors

explained a larger fraction of deviance in full home ranges (55.8 %) and periphery home ranges (55.2 %) than individual-level factors (15.2 % and 20.2 % respectively) (Tables 2.5 – 2.6).

Table 2.5: Results of the statistical analysis. Terms of the minimal adequate model are shown for the periphery home range in the yearly model, the breeding season model (BS) and the non-breeding season model (NBS). p-values (.<0.1,*p<0.05, **p<0.01, ***p<0.001) correspond to F-statistics and corresponding sample size can be found in table 2.2. 'Dev' is the proportion of deviance explained by each covariate. 'Season' was only fitted in the yearly model. 'Total' is the total deviance.

	Yearly			BS			NBS		
	p	Dev	t	p	Dev	t	p	Dev	t
Season	*	8	-2·6						
Weight							***	36·3	6·3
Sex	**	12·4	3·3	**	20·2	2·9			
Cover	***	20·5	-4·2	**	22·1	-3·1	**	21·9	-6·4
Trees	***	24·8	4·7	***	32	3·7	*	14·3	3·9
Total		**65·7**			**74**·3			**72·5**	

The proportion of deviance for each term was calculated as shown in equation 2.1 in the methods section.

Table 2.6: Results of the statistical analysis. Terms of the minimal adequate model are shown for the full home range in the yearly model, the breeding season model (BS) and the non-breeding season model (NBS). p-values (.<0.1,*p<0.05, **p<0.01, ***p<0.001) correspond to F-statistics and corresponding sample size can be found in table 2.2. 'Dev' is the proportion of deviance explained by each covariate. 'Season' was only fitted in the yearly model. '*A.* den' is the density of the *Apodemus sylvaticus* population. 'Total' is the total deviance.

	Yearly			BS			NBS		
	p	Dev	t	p	Dev	t	p	Dev	t
Season	*	10·6	-3·3						
Weight							***	25·8	4·8
Sex	*	4·7	2·2	*	15·2	2·6			
Cover	***	15·3	-4·0	**	21·2	-3·0	**	18·7	-4·1
Logs	*	4·4	-2·1						
Trees	***	29·3	5·5	***	34·3	3·9	***	41·1	6·1
A. den	*	6·1	-2·5						
Total		**70·4**			**70·7**			**85·6**	

The proportion of deviance for each term was calculated as

shown in equation 2.1 in the methods section.

During the non-breeding season, models for full home range and periphery home range revealed similar patterns (Tables 2.5 – 2.6). Larger home ranges had a higher proportion of trees and a lower proportion of cover than smaller home ranges (Tables 2.5 – 2.6). Additionally, heavier animals were found to have larger home ranges than lighter individuals (Figure 2.6, Tables 2.5 – 2.6). Habitat data (59.8 %) explained more deviance than weight (25.8 %) in full home ranges, but not in periphery home ranges where habitat and weight explained roughly the same deviance (36.2 % and 36.6 % respectively) (Tables

2.5 – 2.6). Regarding the habitat drivers, the proportion of cover (21.6 %) explained more deviance than the proportion of trees (14.3 %) for periphery home ranges (Table 2.5). However, in full home ranges, the proportion of trees (41.1 %) explained a greater proportion of deviance than the proportion of cover (18.7 %) (Table 2.6).

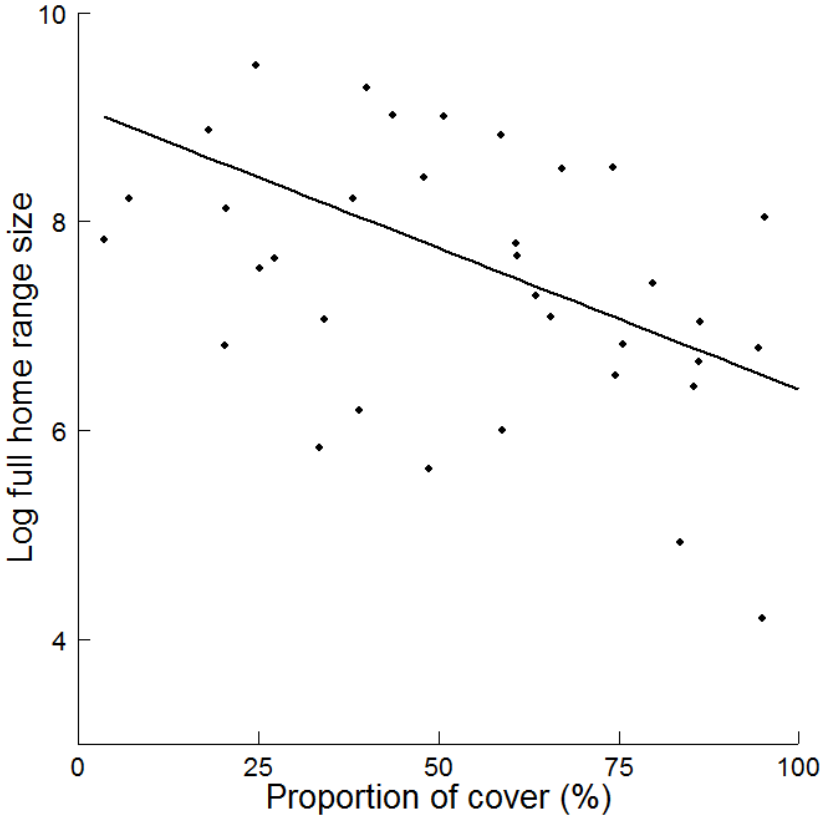


Figure 2.5. Interaction between proportion of cover (%) and full home range size (log-transformed). Fitted line for estimated values. Larger full home ranges have lower proportion of cover as compared to smaller full home ranges.

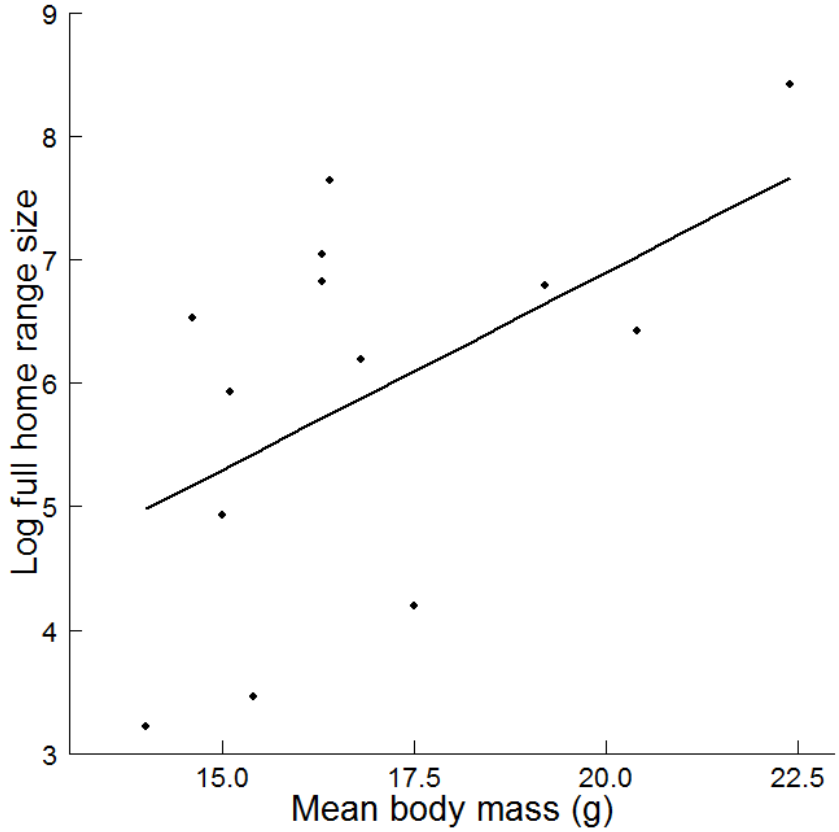


Figure 2.6. Interaction between body weight and full home range size (log-transformed) in the non-breeding season. Fitted line for estimated values. Heavier voles have larger full home ranges as compared to lighter voles.

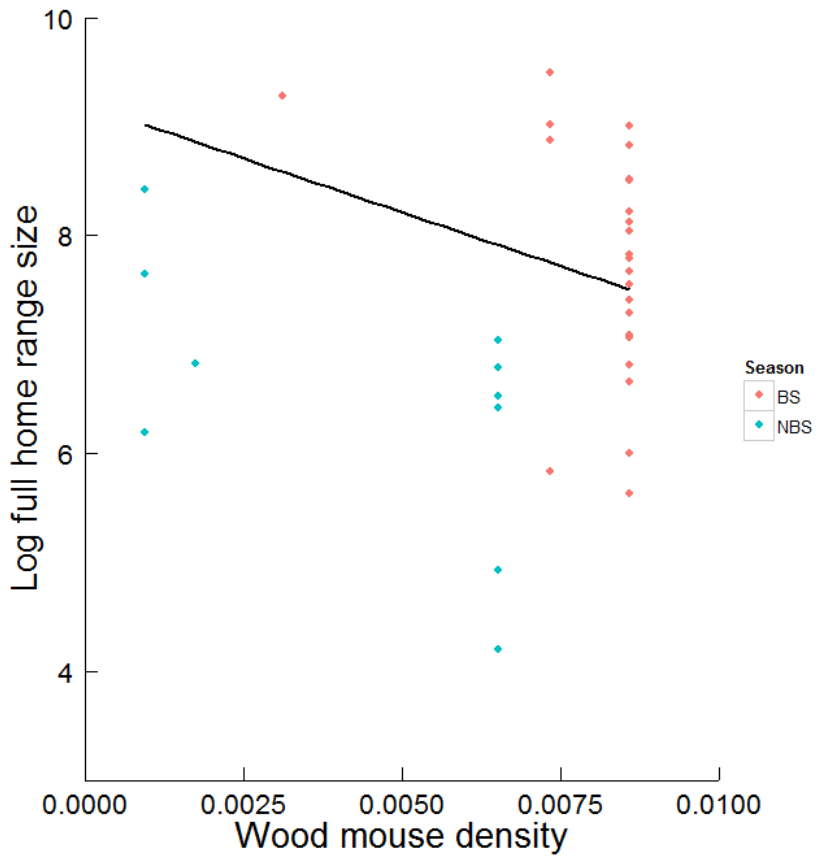


Figure 2.7. Interaction between wood mouse density (mice/sqm) and full home range size (log-transformed). Blue: non-breeding season (NBS). Red: breeding season (BS). Fitted line for estimated values. Voles at higher wood mouse density have smaller full home ranges than voles at lower wood mouse density.

Discussion

In this study, we found that the relative importance of individual-level and biotic factors differed between seasons and for different parts of the home range. During the breeding season, variation in full home range size and periphery home range size is driven, as we predicted, by a combination of sex and biotic drivers, while variation in core range size is only driven by biotic factors. During the non-breeding season, we hypothesized that variation of all home range parts is driven by biotic factors. Indeed biotic drivers are important for home

range size variation in the non-breeding season. Interestingly, we also found one individual-level driver, body weight, predicted home range size variation, with heavier individuals showing larger home ranges.

The effect of body weight on home range size can be partly explained by the greater number of sub-adults at the beginning of the non-breeding season, which are lighter than adult voles and have been shown to have smaller home ranges (Andrzejewski and Mazurkiewicz 1976). Sex was an important explanatory factor of full home range and periphery home range variation in the breeding season (Ims 1987; Ims 1988). As hypothesized, breeding males tend to have a larger periphery and full home range than breeding females but the two sexes do not differ in their core home range sizes. This supports the idea that breeding males expand the periphery of their home ranges in order to maximise access to females (Ims 1987; Ims 1988), but that the core home range appears to be unaffected by reproductive behaviour, and to be established to minimize predation risk and maximize food accessibility all year round. Our results indicate that the home range size variation during both seasons is affected by different individual-level factors, sex in the breeding season and weight in the non-breeding season, and that these factors have a varying impact on the different parts of the home range.

Compared to individual-level factors, biotic factors explain more deviance and most of it is explained by habitat features that are thought to reduce predation risk. We found that proportion of cover and trees explain size variation in all parts of the home range across seasons and for both sexes. Bank voles in our study population tend to maximise the proportion of cover in their home ranges by establishing small home ranges with high proportion of cover. For this study,

we lacked data on actual predator presence in our study site. Instead we use cover seeking behaviour as a proxy for predator avoidance, as it is thought that cover seeking behaviour is an indicator for the presence of aerial predators (Southern and Lowe 1982; Korpimaki, Koivunen et al. 1996), that rarely catch rodents in covered areas. It is also known that if both aerial and ground-based predators are present, the first group drives microhabitat selection in voles (Korpimaki, Koivunen et al. 1996). Therefore, cover seeking could be seen as a more generalist behavioural response to predation risk. Conseuqently, habitat features that reduce predation risk could be a general driver of home range size variation, explaining a majority of deviance of individual home range size variation in voles as compared to other well-known drivers. Studies including predation risk in spatial analysis of small mammals often focus on space use changes at a micro habitat scale (Dickman 1992; Trebatická, Sundell et al. 2008) or on the effect of predation risk on behavioural patterns (Kotler 1984; Perea, González et al. 2011). To our knowledge, only one different study system on small mammal home ranges included predation risk as a potential home range driver, analysing home range size variation of two distinct populations of desert rodents (Lagos, Contreras et al. 1995; Hayes, Chesh et al. 2007). Our findings support a previous study on a different rodent, *Apodemus sylvaticus*,

in our study site that found the same cover providing habitat features to be important in explaining home range size variation (Godsall, Coulson et al. 2014). Both species share the same habitat but it has been suggested that direct competition is reduced by niche partitioning involving first, a partly different diet (Flowerdew, Gurnell et al. 1985; Butet and Delettre 2011) and

second, a non-overlapping (yet not completely opposite) activity pattern (Greenwood 1978). The results from our studies stress the importance of the presence of cover (and very likely, predation risk reduction) for rodent home range size. If variation in space use is mainly driven by habitat features reducing predation risk, different species will try to use, and to establish their home ranges in, the same microhabitat regardless of other differences. This could potentially lead to higher inter-specific interactions and to an increase in inter-specific disease transmission rates (Malo, Godsall et al. 2013). The similarity in space use preferences is likely to cause competition, reducing the overall space available for each competing species (Gliwicz 1981; Eccard and Ylönen 2007; Eccard, Fey et al. 2011). The negative correlation of full home range size in our vole population and density of the *Apodemus* population indicates direct inter-specific competition (Haapakoski, Sundell et al. 2015). Our findings show that species, despite partial niche separation, can still be exposed to direct competition if they share a common space use driver. Furthermore, the results from our studies suggest that competition can also be caused by habitat features that reduce predation risk.

As rodent space use patterns in our study site cannot be linked directly to presence of predators, future research should aim to identify predator species in the study site and quantify their population density. This would lend additional support to the use of cover as a proxy for predation risk as a space use driver. However, it is also possible that cover seeking behaviour is driven by additional factors which so far have not been investigated. For example, the vegetation cover provided by evergreen plant species (e.g. Rhododendron and Bamboo) could be preferred by rodents as it reduces the need to adjust space use

patterns to seasonal changes in understorey vegetation. Additionally, patches covered by evergreen plants could also provide a more stable climatic environment reducing rodent exposure to wind, rain and low temperatures. A microhabitat with a more stable plant community and a more stable climatic environment could then be preferred as breeding and nesting sites. To test whether these factors actually drive space use patterns, future research would benefit from three different approaches. First, our understanding of climatic variation at the micro habitat level and its effect on rodent energy requirements needs to be improved. Therefore, fine scale assessments of climatic variation across the study site and ex-situ experiments that expose rodents to the different climatic conditions are required. Second, further research could use experimental predator exclusion to test for habitat preferences between evergreen and seasonal understorey vegetation, providing that voles adjust their space use patterns to direct and not to perceived predation risk. Third, identifying individual nests and burrows and increasing the spatio-temporal resolution of location fixes would allow a more accurate assessment to which extent covered habitats are preferred as nesting sites.

Due to the suggested importance of predation risk for home range size variation of small mammal species, we recommend that future studies analysing drivers of home range size variation should include factors that are associated with predation risk. Highlighting the general importance of predation risk for small mammals and its potential effect on inter-specific competition, we also recommend including space use data of potentially competing species into home range analysis to deepen our understanding of drivers of space use.

Acknowledgement

The authors wish to thank M. Brouard, O. Hicks, G. Kingcombe, M. Massam, S. McLoughlin, R. Moorhouse-Gann, T. Powell and C. Weevil for assistance with field data collection. S. Dreßen would like to thank D. Labonte for helpful comments. This work was funded by an Advanced ERC grant (LEED: number 249872) awarded to T. Coulson, Marie Curie (PIEF-GA-2008-220322) awarded to A. Malo and a Cusanuswerk scholarship awarded to S. Dreßen. The manuscript was enhanced by comments from two anonymous reviewers on a previous version of this article. The authors declare that they have no conflict of interest.

Supporting Information

Table S2.1: Output of the corresponding minimal adequate model of nine GLMs is shown. The model 'Year' includes breeding season (BS) and non-breeding season (NBS). 'HR' is the home range. In all models but the 'NBS – periphery HR' model, the response variable was log-transformed to ensure residuals conformed to a normal distribution. p-values correspond to F-statistics and corresponding sample size can be found in table 2.3. '*A.* den' is the density of the *Apodemus sylvaticus* population. 'M' is the male sex. 'SE' is the standard error of the estimate.

Model	Covariate	Estimate	SE	p-value
Year - full HR	Intercept	10.25	0.8055	3.70E-13
Year - full HR	A. *den*	-197.60	78.9500	0.018422
Year - full HR	Cover	-0.03	0.0067	0.000471
Year - full HR	Season (NBS)	-1.57	0.4762	0.002657
Year - full HR	Sex (M)	0.49	0.2216	0.035378
Year - full HR	Logs	-0.22	0.1019	0.042396
Year - full HR	Trees	0.88	0.1606	7.40E-06
Year - periphery HR	Intercept	7.64	0.3152	< 2e-16
Year - periphery HR	Cover	-0.02	0.0058	0.000207
Year - periphery HR	Season (NBS)	-0.94	0.3574	0.013188
Year - periphery HR	Sex (M)	0.77	0.2347	0.002597
Year - periphery HR	Trees	0.82	0.1756	6.23E-05
Year - core HR	Intercept	5.65	0.3625	1.26E-15
Year - core HR	Cover	-0.01	0.0047	0.008836
Year - core HR	Trees^2	-0.57	0.1554	0.000916
Year - core HR	Trees	2.32	0.4695	2.91E-05
BS - full HR	Intercept	7.64	0.3491	1.94E-15
BS - full HR	Cover	-0.02	0.0065	0.006581
BS - full HR	Sex (M)	0.70	0.2742	0.018572
BS - full HR	Trees	0.84	0.2189	9.99E-04
BS - periphery HR	Intercept	7.49	0.3639	6.31E-15
BS - periphery HR	Cover	-0.02	0.0071	0.00622
BS - periphery HR	Sex (M)	0.80	0.2736	0.00845
BS - periphery HR	Trees	0.80	0.2170	1.49E-03
BS - core HR	Intercept	4.73	0.4939	6.50E-09
BS - core HR	Trees^2	-0.86	0.3444	0.0217
BS - core HR	Trees	2.89	0.9527	0.00661
NBS - full HR	Intercept	1.90	1.4217	2.14E-01
NBS - full HR	Cover	-0.03	0.0083	0.002707
NBS - full HR	Trees	1.07	0.1771	1.87E-04
NBS - full HR	Weight	0.32	0.0666	0.00097
NBS - periphery HR	Intercept	-1285.82	725.3300	1.10E-01

NBS - periphery HR	Cover	-15.63	4.2900	0.00537
NBS - periphery HR	Trees	263.83	89.4500	1.62E-02
NBS - periphery HR	Weight	159.80	34.0600	0.00113
NBS - core HR	Intercept	2.39	2.7577	4.08E-01
NBS - core HR	Cover	-0.04	0.0142	0.01639
NBS - core HR	Trees	0.83	0.2459	8.22E-03
NBS - core HR	Weight	0.29	0.1248	0.04376

Chapter 3

How does food availability influence home range size? Using a combined in-situ and in-silico approach to investigate a small mammal's space use.

Abstract

Animal space use is species-specific. Foraging is one important type of behaviour, making resource distribution and temporal availability a key driver of animal space use. We used data from an in-situ and in-silico rodent population to study the effect of foraging behaviour and food availability on home range size. We used a high spatio-temporal resolution data set to obtain space use information from an in-situ population of wood mice, *Apodemus sylvaticu*s and compared it to a spatially explicit, individual based model constructed to mirror the study site. We created three different sets of simple behavioural rules and simulated three different food scenarios, parameterized with data from our study site. Simulations based on pure food-seeking behaviour rules produced smaller home ranges than simulations that also included behavioural rules accounting for predation risk. In-situ and in-silico individuals had larger home ranges in years of lower food abundance. We also found support for food availability being an important driver of inter-annual home range size variation. Our results highlight the potential of a modelling approach with simple sets of movement rules combined with field data to help us understand home range dynamics in the wild.

Key-words: *Apodemus sylvaticus*, individual based model (IBM), PIT tag, predation risk, wood mouse

Introduction

Animal space use can affect individual life history, reproductive success and survival, ultimately impacting population dynamics and gene flow (Gaines and McClenaghan Jr 1980; Ostfeld, Jones et al. 1996; Hubbs and Boonstra 1997; Getz, Oli et al. 2005; Booth, Montgomery et al. 2009). It is therefore important to understand which factors generate variation in space use. In statistical models applied to data collected from wild populations, many factors explain space use variation including food availability, water access, shelter and cover (Bowers 1995; Malo, Godsall et al. 2013; Newsome, Ballard et al. 2013; Godsall, Coulson et al. 2014). However, current technological constraints in field data collection mean it is nearly impossible to continuously monitor individual movement trajectories. Therefore, we have a limited understanding about the processes and drivers that generate the movement rules that lead to patterns of animal space use. One approach to understand the effects of different drivers of animal space use is to compare the patterns observed in the field with the patterns generated by in-silico populations where individuals move using different behaviour rules (Grimm, Frank et al. 1996). In this study, we use that combination of in-situ and in-silico population data sets to reveal how different movement behaviours in combination with different food availability scenarios affect space use.

A common method to analyse space use variation is to define the space that an animal uses regularly as its home range (Burt 1943). Many factors have been found to explain variation in home range size, including abiotic factors (seasonal variation (Haugen 1942), weather (Morellet, Bonenfant et al. 2013), biotic factors (e.g. resource availability (Litvaitis, Sherburne et al. 1986; Hubbs and

Boonstra 1997), intra- and interspecific population density (Kleeberger 1985; Trombulak 1985), predation risk (Hayes, Chesh et al. 2007) and individual – level factors (e.g. age (Ingles 1961), body condition (Godsall, Coulson et al. 2014), body mass (Litvaitis, Sherburne et al. 1986), genetics (Seddon, Amos et al. 2004), sex (Haugen 1942). Studies often investigate drivers of home range size variation by comparing home ranges of (1) different individuals during one time period (for example for age dependent variation (Ingles 1961; Cederlund and Sand 1994)), (2) the same individuals during two adjacent time periods (for example variation during breeding and non-breeding season (Haugen 1942; Godsall, Coulson et al. 2014)) or (3) two different populations (for example habitat structure dependent variation (Schoepf, Schmohl et al. 2015)). So far, drivers of inter-annual home range variation have received less attention, and most research has focused on a few larger herbivores (Tufto, Andersen et al. 1996; Van Beest, Rivrud et al. 2011). This is primarily due to practical and technological limitations of observational and experimental studies that are often used to investigate drivers of home range size variation. Inter-annual studies require long-term data collection of animal movement and of space use drivers at a fine spatial and temporal resolution. Unfortunately, both habitat data collection and movement monitoring at fine resolutions are often uneconomical, labour intensive or plainly infeasible.

Numerous factors are known to affect home range size, but only some are likely to affect inter-annual home range size variation. For example, a sex-based home range size difference is unlikely to vary between years, unless the population's sex ratio changes dramatically. Food availability, in contrast, is not only an important home range driver (Lagos, Contreras et al. 1995; Tufto,

Andersen et al. 1996; Hayes, Chesh et al. 2007; Corriale, Muschetto et al. 2013; Emsens, Suselbeek et al. 2013), but also regularly fluctuates over space and time (Rey 1995; Lurz, Garson et al. 2000). So far, however, few studies have investigated the effect of food availability on inter-annual variation in home range size (Tufto, Andersen et al. 1996; Van Beest, Rivrud et al. 2011). According to optimal foraging theory, individuals should try to maximise their net energetic gain by increasing their energy intake rate and reducing searching or handling costs (Emlen 1966; Charnov 1976; Brown 1988; Kerley and Erasmus 1991; Kotler, Brown et al. 1991). All else being equal, patches with high food availability (low search time, high intake) should preferentially be selected (Brown 1988).

In addition to food availability, predator presence should substantially influence animal space use (Lagos, Contreras et al. 1995; Trebatická, Sundell et al. 2008). Prey species can not only adjust their space use to reduce direct exposure to predators (Lagos, Contreras et al. 1995; Trebatická, Sundell et al. 2008), but can also use indirect cues to assess and reduce predation risk (Orrock, Danielson et al. 2004). Adjusting foraging behaviour to minimise exposure to predators can be achieved by using patches with habitat features that exclude or obstruct predators (Tallmon and Mills 1994; Trebatická, Sundell et al. 2008). However, patches of low predation risk are not necessarily patches of high food availability, so individuals may face constant decisions about where to forage (Lima, Valone et al. 1985; Holbrook and Schmitt 1988).

This study investigates the effect of food availability and predation risk on home range size. We do this by modelling individual behaviour according to sets of different movement rules that focus either only on food acquisition or on both,

food acquisition and predator avoidance. In a second step, the different sets of movement rules are then applied to different food abundance scenarios to compare the results of the simulations with the real movement patterns observed in the wood mouse wild population. We use individual based models (IBM) to do this, as they are a useful modelling tool to address questions about population dynamics and animal space use (Letcher, Rice et al. 1996; Wang and Grimm 2007). IBMs provide a framework for individuals created in-silico to be autonomous and - by following potentially simple rules – to create complex behaviours. Additionally, IBMs include factors like individual variability and local animal-environment interactions in spatially complex habitats, which are sometimes neglected in analytical models (Grimm, Berger et al. 2006).

We use a 2-dimensional, spatially-explicit individual based model to investigate the effect of differing movement rules and food availability on home range size and to compare our results with observational data from a free-ranging population of wood mice. In particular, we test three hypotheses:

(1) Variation in movement rules followed by individuals lead to variation in in-silico home range sizes.

(2) Individuals behaving only according to foraging rules have larger in-silico home ranges than those also incorporating cover-seeking movement rules.

(3) Food availability affects home range size, with home ranges being smaller when food availability is high.

Material and Methods

This section is divided into three parts. First, “Field data collection”, describes field data collection of habitat data and food availability data that is later used to

create the in-silico arena for our simulations. It also explains the space use data collection from our rodent study population. Second, “Model simulations”, describes the spatial and temporal structure of the model, the different movement rules and how simulations were set up. Finally, "Home range estimation and statistical analysis", describes the estimation and statistical analysis of in-situ and in-silico individual home ranges.

Field data collection

Study site

The study site is located in a mixed deciduous woodland (National Vegetation Classification: W10a Typical sub-community) at Silwood Park, Imperial College London (OS grid ref.: SU 9430 6920) and spans an area of 2.47 ha, subdivided into 10 x 10 m grid squares. The dominant tree species are *Betula pendula* and B*etula pubescens*, with some ancient *Fagus sylvatica.* Additional tree species are *Acer pseudoplanatus, Quercus petraea, Fraxinus excelsior* and *Alnus glutinosa*. The shrub layer is dominated by *Rhododendron ponticum* and *Corylus avellana*. In the Northeast corner of the study site *Sasa palmate* forms a dense patch of approximately 700m^2.

Trapping effort and mobile recording stations

Here we provide a summary of data collection methods. Full details can be found in Malo et al. (2013) and Godsall et al. (2014). Trapping was conducted weekly from March to November 2010, and biweekly from November 2010 to March 2014. During each trapping session, one Sherman trap (16 cm L x 5.8 cm W x 6.5 cm D) was placed in one 10m x 10m grid square (n = 80-140). Each grid square was only used once per two trapping sessions to allow individuals to

recover their natural behaviour. Mice > 14g were tagged with a 12mm x 2mm RFID PIT-tag providing them with a unique ID. All individuals were released where caught.

Location fixes for tagged individuals were collected using mobile recording stations. In order to maintain data logger monitoring effort constant, the study site was split into ten 60x40m areas (0.24 ha each) and one mobile recording station was assigned to each unique section of the study site. Within each section, the mobile recording station was moved daily between different $100m^2$ squares, following a randomised list of squares in the section. Within the $100m^2$ square, the mobile recording stations were placed at a randomly chosen 1m coordinate, providing a $1m^2$ resolution of location fixes. Once the 24 squares (each $100m^2$) of one section had been used, the list was re-randomized and started again. Mobile recording stations were moved daily (n = 5-7 per week) around midday, when the risk of disturbing the nocturnal rodent was very low (see Figure S3.1). The mobile recording stations were at least 30m apart. Five mobile recording stations were used between March 2010 and June 2010 and 10 were used between June 2010 and March 2014.

Habitat data collection

We mapped all habitat features in our study site at a $1m^2$ resolution and updated the map every six months. Individual trees were identified, tagged, their locations mapped and their diameter at breast height (1.5m) recorded. For three species in the study site – Beech (*Fagus sylvatica)*, Oak *(Quercus petraea)* and Hazel *(Corylus avellana)* - the radius of the tree crowns were taken to estimate the seed fall area. To characterize the crown dimensions, four measurements

per tree were taken, from the stem to the end of the longest branch with a 90-degree angle between each measurement. The mean of the four measurements was used to estimate the circular tree crown radius. The mean circumference and length of all branches (diameter > 5cm) and fallen trees (termed logs) was recorded. In addition, stump circumference and height were measured. We then calculated the total volume of wood for logs, stumps and trees up to a height of 1.5m, using the equation for cylindrical bodies. The area covered by the patch forming shrubs Rhododendron (*Rhododendron ponticum)* and bamboo (*S. palmate)* was measured by mapping the outline of the individual patches. In contrast, the other dominant shrub species, *C. avellana,* was treated as a tree and measured accordingly. Maps were created with GIS (ArcGIS, v9.3) including absolute and relative coverage of *R. ponticum, S. palmate,* log volume, stump volume and tree volume ("tree") for each square meter.

Seed fall data collection

Seeds were collected on a weekly basis from two different types of seed trap, dried for seven days and then weighed . Trap type A collected the seeds from a $1m^2$ area and was elevated by approximately 1m from the ground to prevent seed depletion by ground based seed predators. Thirty-four type A traps were set up across the study site with 20 m spacing between traps. Type B traps collected seeds from an area of 0.07 m^2 and were covered with a mesh to prevent seed removal from seed predators. Seventy-five traps in groups of three were placed across the study site under trees of animal-dispersed seed producers, including beech, hazel and oak, at distances of 1m, 2m and 5m (and

10m where applicable) from each tree, respectively. More details on seeds are summarized in Table S3.1.

Simulations

Overview of the modelling approach

We used an IBM to simulate the movement trajectories of individuals of wood mice to analyse how different sets of movement rules and variation in food availability affect home range size. The general concept is illustrated in Figure 3.1. The model used a high-resolution in-silico replicate of our study site as its 2-dimensional arena. We modelled individual wood mouse energy level, location and survival per time step over a total model period of three months. Three sets of movement rules were created and different food availabilities were modelled by using seed data from three different years. All models were run using NetLogo (Wilensky 1999) and R (R Core Development Team 2005). The two software packages were linked with the Rserve package (Urbanek 2013). In this section the term “home range size” is defined as the area covered by the 95% isopleth, which includes 95% of the individual locations where the individual was observed and is commonly used as the equivalent of a home range (Harris, Cresswell et al. 1990).

Model arena and in-silico habitat features

The arena, designed as a high-resolution replicate of our study site, measured 190m x 130m. Each grid cell had a side length of 1m, resulting in 24700 cells. The grid origin (cell 1, 1) was located in the bottom left corner and orientation of the grid had North at the top and West to the left.

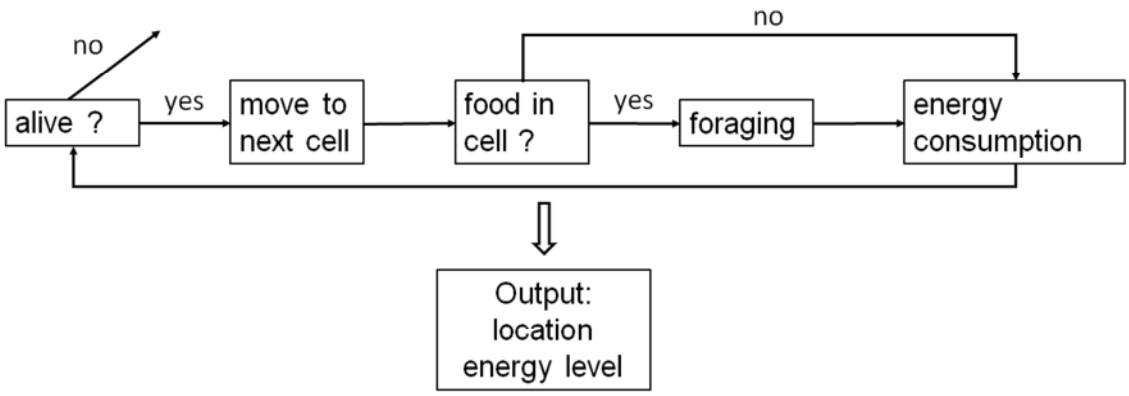


Figure 3.1. Structure of the animal protocol A during a single time step. Every time step includes at least three different protocols that may vary between different sets of movement rules: If an individual is alive at the beginning of a time step it moves to a neighbouring cell. If it moves to a cell with food it forages and pauses foraging to handle the seed it is consuming. Finally, it reduces its own energy resource to account for its metabolism. The model is simulated on a six second time step and individual location and energy level are recorded every time step.

The grid was divided into discrete rows (y-axis) and columns (x-axis) that allowed us to keep track of all individuals' locations relative to the origin. The arena was surrounded by reflecting boundaries, preventing animals from leaving. Reflecting boundaries seemed appropriate to meet our simulation assumptions of low dispersal levels due to reduced intra-specific aggression during the model period of winter (Wolton and Flowerdew 1985; Tew and Macdonald 1994; Malo, Godsall et al. 2013) and have been used in spatially-explicit models to simulate resource based interaction of species (Keitt 1997). The GIS map of the study site (see "habitat data collection") — where high-level resolution information on habitat features is contained — was used to assign a level of cover for each cell. The habitat features considered to be relevant for cover in the model are trees, logs, stumps, bamboo, and Rhododendron. Cover per feature and grid cell could vary between 0 (no cover) and 1 (completely

covered) and a grid cell could be covered by multiple features. However, cover of one cell by multiple habitat features, e.g. by a log and a shrub, still summed up to 1.

In-silico model period and time steps

The model was developed for the non-breeding season of wood mice. The non-breeding season was chosen as it coincides with the winter season when the diet is restricted primarily to tree seeds (Watts 1969; Flowerdew, Gurnell et al. 1985). A period where a single food resource is used by the real population is easier to replicate in-silico than a period with a more variable diet and therefore will allow more robust inferences after comparison with in-situ data. Additionally, during non-breeding seasons social interactions between conspecifics are reduced (Montgomery and Gurnell 1985; Wolton and Flowerdew 1985) and were not included in our models. Each model covered a time span of three months ($n_{timesteps}$ = 756 000), which was similar to the average duration of the non-breeding season of wood mice (Montgomery and Gurnell 1985; Godsall, Coulson et al. 2014). Between time steps, individuals could only move a maximum distance of one grid cell. A constant speed *S* of 0.167 $\frac{m}{sec}$ was found to fit best the average foraging movement speed, based on literature (Benhamou 1991). Mice are crepuscular or nocturnal and do not leave their burrow during the day (Wolton 1983) (Figure S3.1). Therefore, each 24hr-day was reduced to an activity period of 14 hours.

In-silico food availability

In our model, seeds from three species *Fagus sylvaticus*, *Coryllus avellana* and *Quercus robur*, were considered to be the main sources of food for wood mice (Watts 1969; Flowerdew, Gurnell et al. 1985; Gurnell 1993). Tree crown radius data from our study site (see habitat data) were used to assign a proportion of cver by tree species to each cell. We used seed fall data from our study site for the years 2011, 2012 and 2013 to estimate seed production per tree and seed weight (Table S3.1). Using data from the literature and the British Forestry Commission we estimated energy per seed (kJ/gram) (Grodziński and Sawicka-Kapusta 1970; Wästljung 1989; Gordon 1992; Gurnell 1993) (Table S3.1). Total food availability *TF* (in kJ) for each species and cell was calculated with

$$TF = P \cdot T \cdot W \cdot E \tag{3.1}$$

where *P* was the proportion of tree cover of the cell, *T* was the total number of seeds per square meter and year, *W* was the average seed weight (g) per square meter and *E* was the energy (kJ) per seed. *T* and *W* were obtained from a probability distribution of the data collected during the corresponding year in our field site. For years with insufficient data to create a probability distribution, *T* and *W* were random numbers between the minimum and maximum seed number and weight, respectively, collected during the corresponding year.

Each day ($\mathrm{n}_{\mathrm{time\ steps}} = 8400$) on each cell, food availability *F* (in kJ) for each species was updated with the logistic equation:

$$\mathrm{F}_{(\mathrm{t}+1)} = \mathrm{F}_{(\mathrm{t})} + \frac{\mathrm{TF}}{\mathrm{n}} \tag{3.2}$$

where *TF* was the total food availability (in KJ) per cell and *n* was the number of days in the simulation

Energy budget

The energy budget (E) per mouse was calculated each time step with

$$E_{t+1} = E_t + C_S - \text{DE} \quad (3.3)$$

where *C* was the energy of a seed of species *S* (kJ) consumed during the time step and *DE* the metabolic rate (kJ/6 sec) spent by an individual. Mouse daily metabolic rate (DMR) was obtained from the literature (Flowerdew, Gurnell et al. 1985; Koteja and Weiner 1993). *DE* was calculated by including the metabolic costs of the 10h not included in the model (see "Model period and time steps") with the equation:

$$\text{DE} = \frac{DMR}{(14h \cdot 60min \cdot 10sec)} \quad (3.4)$$

The maximum daily intake of energy was twice the DMR (Tamburino and Bravo 2013). If E_{t+1} = 0, the individual died.

Model structure

The model was partitioned into two main protocols that operated at two different temporal scales: (A) the animal protocol ran every time step (Figure 1) and (B) the food availability protocol ran once every 8400 time steps (equivalent to one day). (A) The animal movement protocol was divided into four steps and total population size, individual location and energy level of every individual was

calculated after step four. (1) If an individual was alive at the beginning of a time step, it moved to a neighbouring grid cell, based on model specific movement rules. (2) If the new cell contained food, the individual foraged by reducing the cell's food count by one seed and added the equivalent amount of energy to its energy budget. In case the cell did not contain food, the individual returned to step 1. (3) If the individual foraged during step 2, it continued to step 3, the handling time step, based on model-specific handling time rules. (4) As the last step, the individual reduced its energy budget to account for its own metabolism. (B) The food availability protocol added new food in the form of seeds to grid cells (see section "Food availability").

Movement rules

Three different movement models were considered: food-seeking, cover-seeking and central place forager models. The sets of movement rules for the three models included a random component. The specific movement rule only applies if $p =< q$, where p is a randomly chosen number between 0 and 1 and q the threshold value over which the specific movement rule applied. If p > q the individual moved to a randomly chosen neighbouring cell.

Food-seeking model

In this model, individuals move to maximize daily food intake. Individuals had perfect knowledge about the food content of all eight cells neighbouring its current location and moved to the cell with the largest amount of food, if $p =< q$. If an individual moved to a cell with seeds, it removed one seed from the seed count of the cell and added the seed energy to its individual energy budget (E).

To simulate handling time and cost, the individual stopped foraging after every seed consumed and remained at the cell for the number of time steps that constituted the handling time *H*. Once the maximum daily intake rate (2 x daily metabolic rate) was reached the individual kept moving according to the rules for $p > q$ for the rest of the day.

Cover-seeking model

To simulate a set of movement rules that combine foraging and minimise predation risk we included knowledge about the presence of habitat features that reduce predation risk (Cross 1973; Tallmon and Mills 1994; Thompson, Chambers et al. 2009; Hinkelman, Orrock et al. 2012; Malo, Godsall et al. 2013). In addition to the assessment of the food content of the eight neighbouring cells, individuals also had perfect knowledge about the habitat features of the 24 cells surrounding its current location. We assumed that individuals can assess the presence of large habitat features over a longer distance (24 cells) than small food items on the forest floor (8 cells). The individual moved to the closest cell with the largest amount of food that had at least 1/4 of the neighbouring cells (including its own cell) covered with habitat features, if $p =< q$. If an individual moved to a cell with seeds, it removed one seed from the seed count of the cell and added the seed energy to its individual energy budget (E). To simulate seed handling time and cost, the individual stopped foraging after every seed consumed and remained at the cell for the number of time steps that constituted the handling time *H*. If the maximum daily intake rate was reached, the individual moved to the neighbouring cell with the highest amount of cover.

Central place forager model

This model extended the “cover-seeking” model but assumes that an individual within a defined distance to its nest will return to it for feeding, as seeds coats can be found within nests of wood mice (Jennings 1975). At the beginning of the simulation, each individual was placed at a randomly assigned nest, a cell that was covered with habitat features and also had a minimum of 8 out of 12 neighbouring cells covered. Movement rules were equal to the “cover-seeking” model. If the individual moved to a cell with seeds, it removed one seed from the cell’s seed count and moved back to its nest if the distance between the individual and its nest was less than 10 cells (10-14 m). For distances larger than 10 cells the individual moved to the closest cell with cover. Either there, or at the nest, the individual added the seed energy to its individual energy budget and remained at the cell for the time steps of the handling time *H*. In case the maximum daily intake rate was reached, the same rule as in the cover-seeking model applied.

Model simulations

To test for sensitivity of simulations to changes in parameters, namely the threshold of random movement *q,* the handling time *H* and the movement speed *S,* we ran for each parameter combination a full simulation ($n_{timesteps}$ = 756 000; 50 repetitions) for a 1% increase/decrease of *q* and *S* and an increase/decrease by one time step for *H* and calculated the home range size for all individuals. Sensitivity analyses assume linearity, so a small change to parameter values is chosen deliberately. If larger values are used and if some values have a significant curvilinear association with the model prediction, the

reason for the sensitivities cannot be derived. Therefore, by assuming linearity and choosing small changes, sensitivity across parameters can be compared. For each set of movement rules (n = 3) and year of seed fall data (n = 3) we simulated individual movement and calculated the home range size. We ran each combination (n = 9) with 10 repetitions, producing a total of 90 simulations.

Home range estimation and statistical analysis

To obtain home range sizes, kernel density estimations were used to create utilization distributions of space use (Worton 1989). Kernel densities were estimated using the R package '*ks*' with a Gaussian kernel and the direct plug-in method for bandwidth selection (Wand and Jones 1994). For more detailed information see Godsall et al. (2014). Home range size is known to vary with sample size (Seaman, Millspaugh et al. 1999; Borger, Franconi et al. 2006). Therefore, the mean annual number of locations for in-situ home range size estimation ($n_{2011} = 45, n_{2012} = 79, n_{2013} = 7$) was used to calculate 10 homes ranges per number of locations and in-silico individual. Using the mean of the 10 home range calculations per individual, the mean home range size of the population ($n_{individual} = 45$) from each repetition ($n = 10$) was calculated, producing 10 mean home range sizes per set of movement rules and year. ANOVA and student's t-test were used to test for the between-year differences in home range size, the home range size differences in different simulations and the home range size differences with different number of locations for home range size estimation. Despite some limitations of using p-values for simulated data when sample sizes tend to be large and differences between simulations can be small (Dick and Tevaearai 2015), p-values are provided in this study due

to the small sample size of mean home ranges (n = 10 mean home range sizes per set of movement rules and year) and the difference of simulations (e.g. different movement rules) that was used for comparison. All statistical analyses were performed using R (3.0.2, Core Development Team, Vienna, Austria).

Results

From field data, 147 home ranges were calculated (Table 3.1). Home ranges in 2012 were significantly larger compared to 2011 (Figure 3.2, Table 3.2). Home range sizes in 2013 ranged between home ranges in 2011 and 2012, but home range size differences were not significant (Table 3.2).

Table 3.1. In-silico and in-situ home range sizes. Mean home range size in m^2 (± 1SD) per year (2011, 2012, 2013) and set of movement rules or field data ('Real wood mice'). Different movement rules are 'In-silico food-seeking', 'In-silico cover-seeking' and 'In-silico Central place forager'. 'n' is the number of location fixes used for in-silico home range size estimation.

Simulation/Field data	n	2011	2012	2013
In-silico food-seeking	79	1633.7 m^2 ± 115.1	1758.0 m^2 ± 221.3	1598.6 m^2 ± 169.8
	45	1822.9 m^2 ± 180.6	1977.4 m^2 ± 194.3	1818.9 m^2 ± 204.7
	7	2808.6 m^2 ± 204.2	2896.1 m^2 ± 360.1	2800.9 m^2 ± 336.6
In-silico cover-seeking	79	1829.5 m^2 ± 168.6	2103.2 m^2 ± 132.8	1790.1 m^2 ± 175.7
	45	1974.0 m^2 ± 195.3	2205.2 m^2 ± 186.7	1887.1 m^2 ± 191.6
	7	2466.6 m^2 ± 204.7	2695.5 m^2 ± 204.3	2572.4 m^2 ± 257.7
In-silico Central place forager	79	1931.1 m^2 ± 192.0	2196.7 m^2 ± 420.6	1760.1 m^2 ± 227.1
	45	1990.7 m^2 ± 236.7	2284.2 m^2 ± 390.1	1882.3 m^2 ± 226.8
	7	2424.2 m^2 ± 319.4	2529.8 m^2 ± 310.8	2566.0 m^2 ± 423.6
Real wood mice	-	2117.3 m^2 ± 2389.68	5333.1 m^2 ± 3954.72	4064 m^2 ± 3095.10

n: number of locations used for individual home range size estimation.

Table 3.2. Inter-annual home range size difference for in-silico and observed wood mouse population.

Simulation/Species	2011 - 2012		2011 - 2013		2012 - 2013	
	F (df)	p	F (df)	p	F (df)	p
In-silico food-seeking	$F_{(1,18)} = 2.5$	0.13	$F_{(1,18)} = 0.3$	0.59	$F_{(1,18)} = 3.27$	0.09
In-silico cover-seeking	$F_{(1,18)} = 16.25$	< 0.001	$F_{(1,18)} = 0.3$	0.61	$F_{(1,18)} = 20.2$	< 0.001
In-silico central place forager	$F_{(1,18)} = 3.3$	0.09	$F_{(1,18)} = 3.3$	0.09	$F_{(1,18)} = 8.3$	0.01
Real wood mouse	$F_{(1,139)} = 33.46$	< 0.001	$F_{(1,108)} = 3.57$	0.062	$F_{(1,41)} = 0.54$	0.47

Home range sizes in the years 2011, 2012 and 2013 were estimated using three different sets of movement rules, and for an in-situ wood mouse population. Individual home range size estimation for in-silico individuals was based on 79 relocations. ANOVA was used to test for significant inter-annual home range size difference.

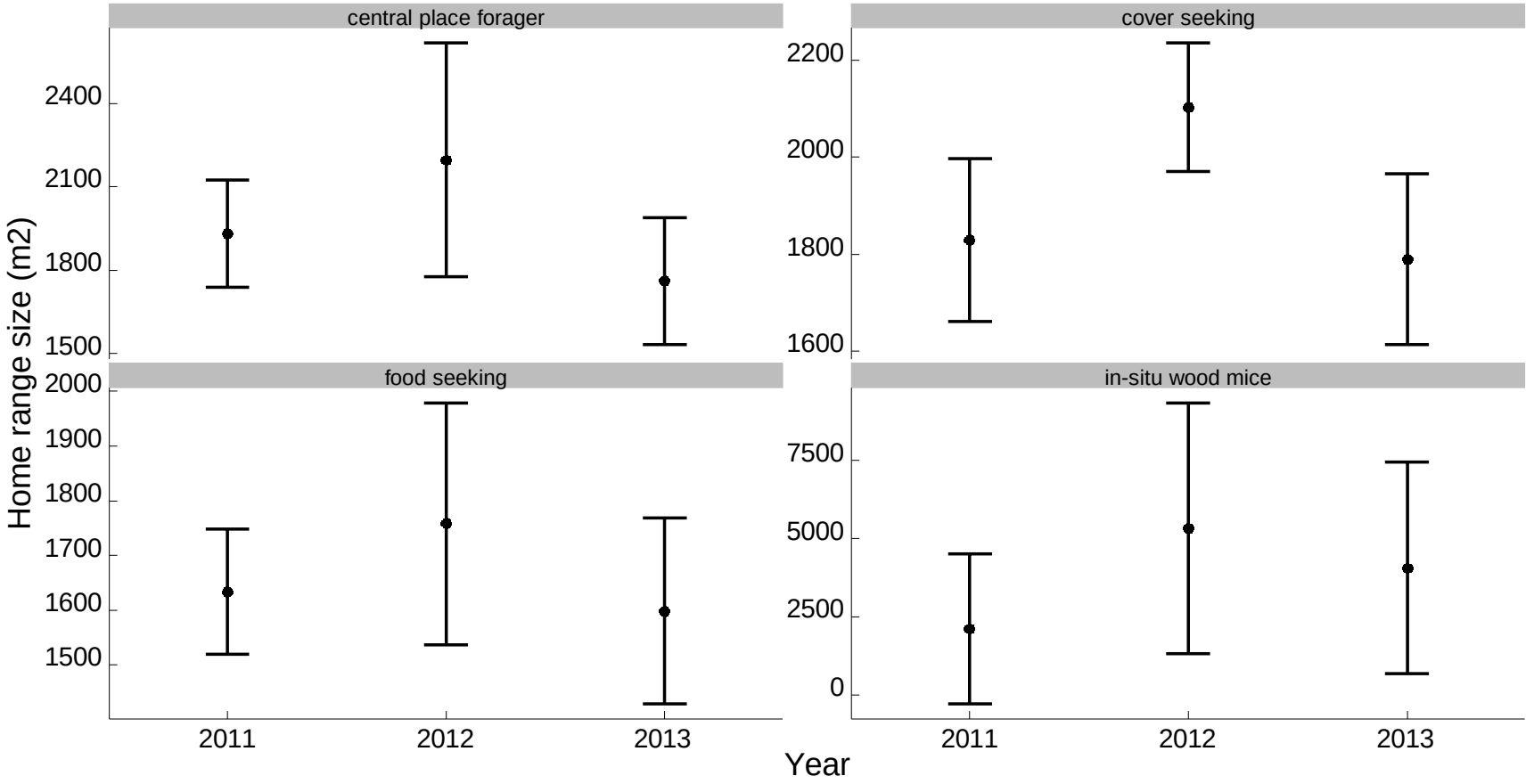


Figure 3.2. Effect of food availability in different years on home range size (m^2) (± 1SD). Home range size was estimated for in-silico populations of wood mice generated under three different sets of movement rules (central place forager, cover seeking, food seeking) and for an in-situ population of wood mice. Simulations for the central place forager and the cover seeking model movement are based on foraging behaviour and behaviour to minimise predation risk, while food seeking model movement is based on foraging behaviour only.

In total, 121 500 home ranges were calculated from simulations. Home ranges were largest in 2012 and smaller in 2011 and 2013 (Figure 3.2, Table 3.1). In 2011 and 2013, mean home range sizes estimated from all three simulations was not significantly different from the mean home range size from field data (Table 3.2; results only shown for the comparison of field data and central place forager). In the food-seeking simulation, home range size did not vary significantly between years (Figure 3.2, Table 3.2). Both cover-seeking simulations created home ranges with sizes that varied significantly between 2012 and the two other years (Figure 3.2, Table 3.2). For the central place forager simulations of 2011 and 2012, the difference in home range size was only close to significant ($F_{(1,18)} = 3.3, p = 0.09$). Home ranges in the food-seeking simulation were significantly smaller than home ranges in both cover-seeking simulations (Table 3.3). Home range sizes of the cover-seeking simulation and the central place forager simulation did not vary significantly (Table 3.3). Home range size across simulations and years increased as sample size decreased (Table S3.3). The model's sensitivity to changes in the threshold of random movement *q,* the handling time *H* and the movement speed *S* was tested by running a full simulation ($n_{timesteps}$ = 756 000; 50 repetitions) of the central place forager model per parameter, keeping the other two parameters fixed. A decrease of *q* from 0.8 to 0.79 caused a mean home range size increase of 0.36 %. A reduction of the handling time *H* by one time step from 20 to 19 caused a mean home range size increase of 0.08 %. Slowing down movement speed *S* by 1% caused a mean home range size decrease of 0.67%.

Table 3.3. Comparison of mean annual home range sizes from in-silico simulations and field data. The annual range and mean of number of locations for in-situ home range size estimation was $n_{2011} = 10 - 181\ (\text{mean} = 45), n_{2012} = 10 - 410\ \ (\text{mean} = 79), n_{2013} = 6 - 8\ (\text{mean}\ = 7)$.

In-silico simulations	Year	F (df)	p
food-seeking vs cover-seeking	2011	$F_{(1,18)} = 9.20$	0.007
	2012	$F_{(1,18)} = 17.89$	<0.001
	2013	$F_{(1,18)} = 6.14$	0.02
food-seeking vs central place forager	2011	$F_{(1,18)} = 17.65$	<0.001
	2012	$F_{(1,18)} = 8.52$	0.009
	2013	$F_{(1,18)} = 3.25$	0.09
cover-seeking vs food seeking	2011	$F_{(1,18)} = 1.58$	0.22
	2012	$F_{(1,18)} = 0.45$	0.51
	2013	$F_{(1,18)} = 0.11$	0.75
central place forager vs in-situ	2011	$F_{(1,112)} = 0.6$	0.81
	2012	$F_{(1,45)} = 5.84$	0.02
	2013	$F_{(1,14)} = 1.7$	0.21

Individual home range size estimation for in-silico individuals was based on 79 relocations. ANOVA was used to test for significant home range size difference between simulations.

Discussion

In this study we simulated individual mouse movement behaviour according to different sets of rules for different scenarios of food availability, and compared the resulting space use patterns to those observed in a an intensively monitored

wild wood mouse population. We hypothesized that (1) variation in movement rules followed by individuals lead to variation in in-silico home range sizes, (2) individuals behaving only according to foraging rules have larger in-silico home ranges than those also incorporating cover-seeking movement rules and that (3) food availability affects home range size, with home ranges being smaller when food availability is high.

As predicted, mean home range size varied between simulations of different movement rules. Contrary to our predictions, however, home range size decreased when we modelled movement as a function of foraging rules, as compared to modelling movement as a function of both foraging and cover-seeking. Although desirable, we cannot compare our in-silico results to in-situ predator exclusion treatment in our study site due to practical and logistical constraints of such treatment over a wide area. Some studies excluding the effects of predation from their study site, however, found a decrease in home range size (Lagos, Contreras et al. 1995). This supports the idea that individuals freed from predation risk have lower opportunity costs (Winterhalder 1983) and can focus on depleting smaller food-rich patches more thoroughly (Lagos, Contreras et al. 1995). Other studies observed an increase in home range size after predators were excluded from the study site, indicating that predation risk prevented animals from accessing additional food-rich but unprotected patches (Orrock, Danielson et al. 2004; Hayes, Chesh et al. 2007; Hinkelman, Orrock et al. 2012). The latter findings are somehow corroborated with anecdotal data from our study site, where some patches provide high resource density but are hardly visited by rodents due to a lack of cover providing understorey habitat features (Malo, Godsall et al. 2013) that increases

the predation risk by the mice's main predator, the tawny owl (Southern and Lowe 1968). The result from our simulations, in turn, support the first argument, suggesting that without a perceived predation risk and the resulting cover-seeking behaviour, individuals in our simulations are able to explore food-rich patches more thoroughly. However, this remains speculative due to the lack of comparable predation exclusion data from our study site. In contrast to our cover-seeking simulations, individuals in the food-seeking simulation were able to access neighbouring cells with food irrespectively of cover, allowing them to minimise the total space required to forage. If a food patch, e.g. the area under a seed producing tree, is larger than the area under the tree that is covered with cover providing features, an individual that only focuses on foraging can explore the entire food patch instead of only the safe parts of it. It is therefore possible that such marginal increase in space use would be less than the increase in space to explore completely new, safe food patches.

All simulations displayed the same temporal pattern of home range size variation as observed in our field data. Simulated home ranges and home ranges based on field data varied in size depending on food availability, with larger home ranges in the year of lower food availability. Previous studies have highlighted the importance of food abundance as a driver of home range size between different patches, habitat types or intra-annual trends (Mares, Watson et al. 1976; Emsens, Suselbeek et al. 2013; Schoepf, Schmohl et al. 2015). Here, however, we found that food abundance is an important driver of inter-annual variation in home range size within the same habitat. With a set of simple movement rules we managed to simulate the same home range size variation pattern as observed in the field (by only including food-seeking and

cover-seeking behaviour). Studies analysing the relative contribution of different factors on home range size variation often found many factors determining home range size variation (Haugen 1942; Ingles 1961; Trombulak 1985; Litvaitis, Sherburne et al. 1986; Bowers 1995; Godsall, Coulson et al. 2014). Our findings show that food availability and predation risk alone can replicate natural home range size variation in the wood mice.

Several modelling approaches have investigated parts of wood mouse biology that are difficult to answer through empirical or experimental approaches (e.g. the effect of mast seeding (Tamburino and Bravo 2013) or pesticide exposure (Liu, Sibly et al. 2013) on population dynamics and space use). Despite their valuable insights, these studies cannot be directly linked to an in-situ study. A combined approach using field data and modelling allows us to compare in-silico patterns to real wild population patterns observed. Consequently, we demonstrate that a set of simple rules create not only a biologically meaningful pattern, but that the same patterns produced by a simple model can be found in a real system. Without a comparison to field data, the explanatory power of our simple set of behavioural rules could not have been validated. In turn, without our modelling approach we would not have seen able to highlight the general importance of the two drivers of home range size variation in our study population. However, caution must be taken when using in-silico data to make inferences on in-situ conditions. Even if in-silicio and in-situ data show the same patterns, causality is not provided and the explanatory power remains at the comparison level as many potential space use drivers that affect the in-situ population were not included in the analysis. For example, it is possible that the driver of in-situ home range size variation is in fact variation in predator

population density that coincides with the annual variation in food availability. Nevertheless, comparing in-silico and in-situ patterns can provide valuable insights and IBMs are a useful approach to analyse animal space use (for reviews see (Grimm 1999) and (DeAngelis and Mooij 2005)). For a realistic simulation of the effect of food availability on space use dynamics in our study site, we had to model the individual's exact location at high temporal resolution. This allowed us to analyse the spatial dynamics of mice, being exposed to fluctuating food abundance. Additionally, using the IBM allowed us to follow individual movement patterns and therefore analyse our simulated data at both the individual level and population level.

Despite similarity of the pattern generated by the simulated data and the field data, simulations in 2012 failed to replicate the mean home range size observed in the field. Potential reasons for discrepancies in home range size between the model (smaller) and the field data (larger) could be attributed to both model assumptions and estimation techniques. First, home range sizes can vary considerably between individuals within a population (Emsens, Suselbeek et al. 2013). The in-situ and in-silico home range size estimates varied across two orders of magnitudes. In fact, several mean home range sizes of in-silico individuals in the 2012 central place forager simulation had the same mean size as the in-situ home range estimation in the same year. They do, however, disappear in the mean home range size per year and model, due to the need of re-sampling over many individuals and repetitions in order to avoid estimating random home range sizes. The validity of a comparison of pattern of home range size variation, consequently, is much higher than of a numerical comparison of mean home range sizes. Second, a model, by definition a

simplified version of the reality, includes fewer factors than the field system. A higher number of factors impacting on a system will naturally increase its variance and could, therefore, explain the estimation differences between in-situ and in-silico home ranges. For parsimonious reasons, for example, we restricted food acquisition to the three seed producing tree species in our simulations. These do constitute most of the diet of mice during the non-breeding season, the period that we modelled (Watts 1969; Flowerdew, Gurnell et al. 1985; Gurnell 1993). There are, however, other plants, seeds and invertebrates that could contribute to the rodent diet during this period (Watts 1969). Additional food sources such as these, not accounted for by our models, could contribute to variation in home range size.

In-silico home range size estimates based on three different sample sizes revealed a significant increase in mean home range size and variance as sample size decreases. KDE based home range size estimation requires between 10 (Borger, Franconi et al. 2006) and 30 locations (Seaman, Millspaugh et al. 1999), but our mean sample size from 2013 is only 7 locations per individual. The conclusions of this study are not affected if the 2013 results are excluded, but it clearly highlights the need to improve current monitoring technique to increase sample size. Especially as the monitoring technique used in this study already provides larger sample sizes of locations than studies only relying on conventional trapping data. This should make the need of new monitoring techniques – especially for small sized animals – even more notable (Wikelski, Kays et al. 2007; Wikelski, Moxley et al. 2010; Kays, Tilak et al. 2011).

Based on our initial findings, we can now use our model structure to extend our investigation to the effect of additional scenarios of food availability, predation risk, sex ratio, rodent density on space use, and ultimately on population dynamics. By linking our model to our in-situ population we will be able to directly infer how the field population will be affected. For instance, as seed crop of many tree species in temperate regions is influenced by climatic cues, climate change is expected to cause changes in pattern of food availability (Smaill, Clinton et al. 2011; Kelly, Geldenhuis et al. 2013; Roland, Schmidt et al. 2014). With our model as a starting point, we will be able to predict to what extent a shift in food production and composition would affect home ranges. In addition, based on our models investigating basic effects of mice movement and foraging behaviour we can now extend our simulations to investigate both resource-dependent dispersal and variation in fecundity.

Acknowledgement

The authors wish to thank M. Brouard, O. Hicks, G. Kingcombe, M. Massam, S. McLoughlin, R. Moorhouse-Gann, T. Powell and C. Weevil for assistance with field data collection and J. Massey for helpful comments.

Supporting Information

Table S3.1. Real seed fall data from the study site. Minimum and maximum number of seeds collected per square meter (m²) and year. Seed trap type B covers 1/14 square meter (more details on seed trap types used in this study can be found in the method section 'seed fall data collection'). Seed fall data from trap type B was multiplied by 14 to scale to one square meter. Minimum and maximum seed weight per year. Minimum and maximum energy (in kJ) per square meter (m²). Energy value (kJ/gr): Beech 25.05 kJ/gr; Hazel 24.94 kJ/gr, Oak 18.49 kJ/gr (Grodziński and Sawicka-Kapusta 1970; Wästljung 1989; Gordon 1992; Gurnell 1993)

Species	Year	Seeds per sqm	Weight per seed (g)	Energy per sqm (kJ)
Beech	2011	14 - 6230	0.0346 – 0.22	12.13 – 34333.53
	2012	0 - 28	0 - 0.09	0 - 60.74
	2013	14 – 160	0.06 - 0.15	22.09 – 589.18
Hazel	2011	14 - 42	0.16 – 1.6	54.12 – 1678.06
	2012	4 - 28	0.12 – 1.34	11.47 – 935.75
	2013	14 - 28	0.75 - 2.66	261.87 - 1857.53
Oak	2011	14- 168	0.13 – 2.96	34.69 – 9197.81
	2012	0 - 28	0 - 0.07	0 - 36.03
	2013	16 - 84	0.27 - 1.91	78.4 – 2963.43

Table S3.2. Additional data for home range size calculation. Mean number of fixes (hits) (± 1 SD) and population size (n) per year.

	2011		2012		2013	
	n	hits (± 1SD)	n	hits (± 1SD)	n	hits (± 1SD)
In-situ wood mice	104	44.55 (±36.06)	37	78.6 (± 85.85)	6	6.8 (± 0.9)
In-silico simulations	1350	7/45/79	1350	7/45/79	1350	7/45/79

Table S3.3. Mean annual home range size as a function of sample size used to calculate individual home range size (n = 7; 45; 79). Mean home range sizes can be found in table 1. ANOVA was used to test for significant home range size difference.

In-silico simulation	Year	F (df)	p
food-seeking	2011	$F_{(1,28)} = 118$	<0.001
	2012	$F_{(1,28)} = 70.7$	<0.001
	2013	$F_{(1,28)} = 79.6$	<0.001
cover-seeking	2011	$F_{(1,28)} = 50.9$	<0.001
	2012	$F_{(1,28)} = 47.5$	<0.001
	2013	$F_{(1,28)} = 51.8$	<0.001
central place forager	2011	$F_{(1,28)} = 17.9$	<0.001
	2012	$F_{(1,28)} = 4.1$	0.05
	2013	$F_{(1,28)} = 31.2$	<0.001

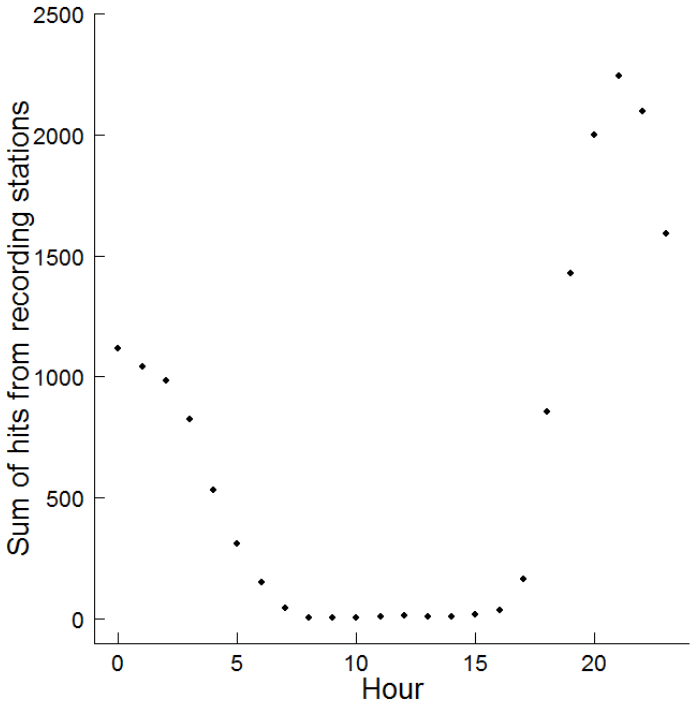


Figure S3.1. Activity pattern of the wood mouse population. A hit is recorded when a tagged wood mouse enters a mobile recording station (see methods ‘Trapping effort and mobile recording stations’).

Chapter 4

Chitty's effect in mice? Using an integral projection model to analyse density driven dynamics in a European rodent population, *Apodemus sylvaticus.*

Abstract:

Population dynamics are determined by survival, reproduction and dispersal and in seasonal ecosystems often exhibit regular patterns of changes in population size and composition. In contrast to many species, some rodents are found to have a positive density dependence of body weight with heavier individuals at high population densities. This is known as the Chitty effect which can be explained by the dynamic energy allocation hypothesis. In this study, we looked for evidence of the Chitty effect in a population of the wood mouse', *Apodemus sylvaticu*s by testing the effect of population density on body weight and on the life history parameters generation time and lifetime reproductive success. We used a high spatio-temporal resolution data set to obtain space use information from an in-situ population and used these data for parametrisation of a density dependent, stochastic IPM for the female part of the wood mice population. We found a small but significant positive density dependence of body weight in in-situ and in-silico juvenile and sub-adults and a negative density dependence of asymptotic growth for in-silico individuals. We also found a positive density dependence on generation time and a negative density dependence of lifetime reproductive success. Our results support the dynamic energy allocation hypothesis due to evidence of positive density dependence growth rates in sub-adults and juveniles as well as clear signs of suppression of reproduction at high population densities. Our findings also highlight that patterns explained by this hypothesis are not restricted to species with multi annual population dynamics but can also be used to explain annual population cycles.

Keywords: *Apodemus sylvaticus,* body weight, Chitty effect, density dependence, dynamic energy allocation, population dynamics, wood mouse

Introduction

Population composition and dynamics are determined by survival, reproduction and dispersal. All three components can be affected by biotic factors, such as competition (Boonstra 1989), resource availability (Dobson 1995), predation (Jędrzejewski, Jędrzejewska et al. 1995) and abiotic factors, including climate (Elton 1924; Gilbert and Krebs 1991), and interactions between them (Hörnfeldt 1994). In ecosystems with seasonal variation in abiotic and biotic factors, subsequent changes in survival, reproduction and dispersal can generate regular patterns in population size and composition (Boonstra, Krebs et al. 1998; Aars and Ims 2002). Reproduction rates, for example, tend to be lower during the climatically less favourable season (Watts 1969; Flowerdew, Gurnell et al. 1985; Gilbert and Krebs 1991), causing population size and composition to change between seasons. The population dynamic of a species is also affected by the species' life-history, often classified as falling on a continuum from K-selected to r-selected species (MacArthur and Wilson 1967). Species with r-selected life histories have high growth rates, high fecundity, early maturity and short generation times (MacArthur and Wilson 1967) and often exhibit pronounced population fluctuations over short time periods (Krebs and Myers 1974). A taxon containing many r-selected species is rodents (Macdonald 2009). Understanding the mechanisms of their population dynamics would allow improvement to pest management (Stenseth, Leirs et al. 2003), prevent spread of diseases (MClEan 2007) and optimise conservation

strategies for ecosystems where rodents are an integral part (Hulme 1994; Santos and Tellería 1997).

One important individual-level factor that correlates with survival and reproductive success is body weight (Festa-Bianchet, Jorgenson et al. 1997; Festa-Bianchet, Gaillard et al. 1998; Aars and Ims 2002). In many species, heavier individuals survive longer and have a higher reproductive output (Cuthill and Houston 1997; Blanckenhorn 2000). Body weight is heritable (Boonstra and Boag 1987; Hansson 1988; Williams, Krueger et al. 1994; Réale, Festa-Bianchet et al. 1999) and driven by (interacting) abiotic and biotic factors (Simons and Roff 1994; Aars and Ims 2002). Favourable climatic conditions, for example, can increase food availability which in turn allows individuals to increase body weight, improving their probability of survival and reproduction (Flowerdew 1972; Wolff 1996). Especially under favourable conditions, mechanisms are required to prevent populations with a positive growth rate from uncontrolled increase. In density-dependent species, population growth at high densities is regulated through suppression of reproduction (Boonstra 1989; Gilbert and Krebs 1991) and a decrease in survival rates, for example, through increased levels of aggression (Krebs 1970; Rose and Gaines 1976) or depletion of resources (Watts 1969). At high densities, a population often consists of smaller individuals (as in some mammals (Zedrosser, Dahle et al. 2006), birds (Larsson, Jeugd et al. 1998), amphibians (Wilbur 1977) and fish (Holm, Refstie et al. 1990)). In some rodent species, however, the opposite is observed: individuals are heavier during periods of high density, which is known as the 'Chitty effect' (Krebs and Myers 1974; Boonstra 1989; Norrdahl 1995; Norrdahl and Korpimäki 2002). According to Chitty’s polymorphic behaviour

hypothesis, two different types of behaviour exist: a docile and an aggressive type (Chitty 1967; Krebs 1978). In a growing population, selection favours the aggressive type that is a better competitor for resources in a crowded environment. The aggressive type, however, is also a bad reproducer. At the population peak, aggressive individuals mostly remain in the population, which then declines and remains at low density levels until selection favours the docile type (bad competitor, good reproducer). Initially, Chitty's hypothesis received empirical support by findings of a positive correlation between heterozygosity and aggressiveness in oldfield mice (Smith, Garten Jr et al. 1975; Garten Jr 1976), differences in spacing behaviour dependent on aggressiveness in voles (Krebs 1970), paternal heritability of body weight (as a proxy for dominance) in voles (Hansson 1988) and environment-dependent reproductive strategies in lizards (Sinervo, Svensson et al. 2000; Bjørnstad 2001). However, there was also increasing evidence against Chitty's hypothesis due to no fitness advantages of larger individuals at high densities in voles (Lidicker Jr and Ostfeld 1991), no observed heritability of behavioural traits like aggression, activity or dispersal in lemmings (Boonstra and Hochachka 1997) and only maternal but no paternal heritability of body weight in Californian voles (Boonstra and Boag 1987). The polymorphic behaviour hypothesis was then thought to be finally refuted by a large scale translocation experiment that highlighted the over-riding role of the immediate environment, rather than of any intrinsic driver, in shaping life-history traits of voles (Ergon, Lambin et al. 2001).

An alternative explanation for the Chitty effect is known as the dynamic energy allocation hypothesis (Oli 1999). Individuals in a high density–high competition environment are known to suppress reproduction (Boonstra 1989; Gilbert and

Krebs 1991; Montgomery, Wilson et al. 1997) leading to surplus energy (total energy intake minus metabolic costs) that can then be allocated to somatic rather than reproductive growth. Individuals in a low density environment, in turn, may allocate more surplus energy to reproductive investment to increase reproductive success. Indeed, the idea of dynamic energy allocation has received some initial, empirical support (Lidicker Jr and Ostfeld 1991; Wolff 1993; Burthe, Lambin et al. 2010).

A test of the dynamic energy allocation hypothesis explaining the Chitty effect requires continuous data about population size, composition and kin relations (Krebs 1978; Oli 1999). Two factors have made the possibility of adequately testing the hypothesis in a rodent population challenging thus far: First, most rodent species are small, crepuscular or nocturnal and live in habitats with dense vegetation. This makes a continuous monitoring of individuals to infer population parameters challenging, if not impossible. Second, the potentially complex interactions of parameters causing the Chitty effect make it necessary to acquire (at least most of) the data from the same field population. For example, investigating the critical question of weight heritability in a lab population or with predetermined mating partners (preventing mate choice based on competitive behaviour) substantially reduces the explanatory power of the results (Riska, Prout et al. 1989; Simons and Roff 1994). One approach to overcome current limitations is to use an integral-projection-model (IPM), parameterized with data from a wild rodent population. An IPM tracks a population over time, if individuals are measured on a continuous character (Easterling, Ellner et al. 2000; Ellner and Rees 2006; Rees and Ellner 2009). Coulson and Tuljapurkar (2008) separated the fitness component of the IPM

into a survival and a fertility component, allowing to assess their relative contribution to the dynamic of a population. To our knowledge, no IPM has been used to investigate r-selected rodent population dynamics. The only available rodent IPM, an analysis of a marmot population dynamic (Ozgul, Childs et al. 2010), investigates a long-lived, large rodent species without pronounced population cycles (Walker 1975), a life-history that is atypical of most rodent species.

The wood mouse (*Apodemus sylvaticus)* is a small and short lived rodent species that shows both super annual and annual population density cycles. Super annual cycles appear to be mainly driven by resources, with population peak coinciding with mast crops in the previous autumn (Flowerdew, Gurnell et al. 1985) (but see Watts (1969)). The second set of cycles occurs on an annual time scale, with a population increase over the late breeding season (late summer/autumn), followed by a peak at the beginning of the non-breeding season (late autumn/ early winter) and a subsequent population decrease until summer (Flowerdew, Gurnell et al. 1985; Malo, Godsall et al. 2013). Although the *Apodemus* population have been studied intensively for decades, it remains unknown whether they show the Chitty effect. They therefore constitute an ideal model species to investigate density dependent changes in body weight distribution and the contribution of survival, growth and reproduction to density dependent cycles. In this study, we construct a density dependent, stochastic *Apodemus* IPM, parametrised with data from our field study system and the literature, to assess two hypotheses:

First, if the Chitty effect can be found in *Apodemus*, we expect individuals to be larger at higher densities as compared to individuals at lower densities. Second,

if Oli's interpretation of the Chitty effect is correct, we expect a high sensitivity of body growth dynamics on population size and we expect generation time and lifetime reproductive success to be affected by population size.

Material and methods

Study site

The study site covered 2.47 ha, subdivided into 10 x 10 m grid squares, in a mixed deciduous woodland (National Vegetation Classification: W10a Typical sub-community) at Silwood Park, Imperial College London (OS grid ref.: SU 9430 6920). The dominant tree species are *Betula pendula* and B*etula pubescens*, and *Fagus sylvatica.* Additional tree species were *Acer pseudoplanatus, Quercus petraea, Fraxinus excelsior* and *Alnus glutinosa*. The shrub layer was dominated by *Rhododendron ponticum* and *Corylus avellana*. In the Northeast corner of the study site *Sasa palmate* formed a dense patch of approximately 700m^2. The most prominent ground layer species were *Hyacinthoides nonscripta*, *Pteridium aquilinum, Oxalis acetosella* and, although not as common as the previous species, *Urtica dioica, Lysimachia nemorum* and *Anemone nemorosa.*

Data collection

Trapping was conducted weekly from October 2008 to November 2010, and biweekly from November 2010 to November 2014. During each trapping session, one Sherman trap (16 cm L x 5.8 cm W x 6.5 cm D) was placed into a 10m x 10m grid square ($n_{traps/session}$ = 80-140). Each grid square was only used once per two trapping sessions. Thus, each grid square was used twice a month during the period of weekly trapping sessions and once a month

otherwise. All captured mice were weighed, sexed and their reproductive status assessed (for more information about the assessment of the reproductive status see Godsall et al. (2014)). The start of the early breeding season (EBS) was defined as the trapping session at which more than half of all males heavier than 15gr showed an increase in testes size. As the onset of the late breeding season (LBS), we chose the trapping session when seed fall started, marking the change in diet from invertebrates to seeds (Watts 1969; Hansson 1985; Gurnell 1993). The trapping session at which mice no longer showed signs of breeding conditions marked the onset of the non-breeding season (NBS). This novel and more adequate split of seasons in EBS, LBS and NBS was used in our field study as it depicts better seasonal changes in space use behaviour (Godsall, Coulson et al. 2014) . Its validity was also confirmed by physiological changes in wood mice due to the change of diet between EBS and LBS (Maurice, Cl Knowles et al. 2015).

Integral Projection Model (IPM)

Every individual has genotypic and phenotypic characteristics that can be measured on a continuous scale. At any point in time, the distribution of a trait *z* within a population can be estimated. Often researchers are interested how *z* changes over time and how it relates to other population parameters. For many study systems, collecting this data is at best logistically and practically challenging or even impossible. An IPM parameterized with data from a real population, provides an efficient solution to model population dynamics and explore its drivers. The model allows us to track a population over time, to obtain at every time step not only a trait distribution of *z* within the population but also to calculate the population parameters wanted. This is achieved by

splitting the complex dynamics of a population into four demographic functions, each as a function of z:

1) The survival function *S(z,t)*
2) The growth function *G(z'|z,t)*
3) The inheritance function *D(z'|z,t)*
4) The recruitment function *R(z,t)*

All four functions together predict the distribution of *z* at time *t+1 , n(z',t+1),* as a function of *z* at time *t, n(z,t)*:

$$n(z', t+1) = \int [G(z'|z,t)S(z,t) + D(z'|z,t)R(z,t)]n(z,t)dz \qquad (4.1)$$

An IPM for the Chitty effect

The Chitty effect links body weight to population density. To track changes of body weight in relation to population density dynamics, we constructed a density-dependent, stochastic IPM of body weight (z). The IPM was parameterised with data from the literature and from the female individuals of our wood mouse population (Briffa 2007). According to the dynamic energy allocation hypothesis, surplus energy is either allocated to somatic growth or reproductive effort, depending on population densities (Oli 1999). Higher investment in somatic growth can be approximated by higher body weights. Suppression of reproduction and lower investment in reproductive effort at high population density increase generation time and decrease LRS. Both parameters are outputs from an IPM and they can be calculated for cohorts born at different population densities.

IPM Construction

Each function consisted of a slope and multiple intercepts. Parameters for each function were estimated by constructing a linear or generalized mixed effect model, using the R-package lme4 (Bates, Mächler et al. 2015). Explanatory variables in each function were body weight *z* at time *t,* population size *n* of female mice at time *t*, the interaction between *z* and *n*, season *S* and year *y* as well as trapping session *T* as a random effect. The following parameters were estimated by the model: intercept *a,* body weight slope *b*, population size slope *p*, slope of the *z-n* interaction *I,* the mean of all year effects *y* and season *S*. The random effect of trapping session *T* was obtained from a normal distribution with mean and variance estimated for each function. Variables and parameters were combined in a general basis function X:

$$X(z') = a + b * z + p * n + I * z * n + y + S + T(0, \boldsymbol{\sigma}) \qquad (4.2)$$

The IPM was constructed on a two-week time interval, equivalent to the time frame of the trapping sessions from 2011 to 2014. For the years 2008 – 2010, we created two week intervals by merging two consecutive weekly trapping sessions (see “Data collection”). A bi-weekly time interval divides a year into 26 time steps, which in turn are split between the three seasons. The length of each season was derived from the mean season lengths in the study years 2008 – 2014: EBS 11 trapping sessions, LBS 8 trapping sessions, NBS 7 trapping sessions. As reproduction very rarely occurs in the NBS, the inheritance and recruitment functions were not included in the last seven time steps of each year.

Survival function: *S(z,t)* describes the probability of an individual surviving from time *t* to *t+1* as a function of body weight *z.* Not all individuals were caught every trapping session, making it necessary to calculate the recapture rate for each season using E-SURGE (Choquet, Rouan et al. 2009). The absence of body weight data for non-caught individuals, made a mark-recapture model challenging, as it would require weights to be inputed for those individuals that survived but were not captured. Instead, the recapture rate was used as an offset in the generalized mixed effect model (binomial distribution, logit link function) (Catchpole, Morgan et al. 2000). The binomial response variable was individual survival at time *t + 1.* The parameters (e.g for EBS: $z'_{t+1} = 0.83 + 0.025 * z + 0.023 * n - 0.0013 * z * n - 0.024 + T_s$) were combined into a single survival function *S*:

$$S(z,t) = \frac{1}{1+e^{-(a_S+b_S*z+p_S*n+I_S*z*n+y_S+T_S)}} \quad (4.3)$$

T_s was obtained from the normal distribution N (0, 0.5568). Additional data of parameter estimates can be found in table S4.1.

Growth function: The growth function describes the probability for an individual of body weight *z* at time *t* to grow to the body weight *z'* at time *t+1*. For growth estimation, two sets of parameters were estimated: The probability of a mean body weight at time *t+1,* given a body weight at time *t* and the variance around each mean body weight transition. The data were restricted to individuals that were caught in two consecutive trapping sessions. The first linear mixed effect model used body weight at *t+1* as response variable, providing the parameters (e.g for EBS: $z'_{t+1} = 5.25 + 0.718 * z - 0.084 * n + 0.003 * z * n + 1.366 + T_g$) for the mean growth function E:

$$E(z') = a_g + b_g * z + p_g * n + I_g * z * n + y_g + T_g \quad (4.4)$$

T_g was obtained from the normal distribution N (0, 0.921). Additional data of parameter estimates can be found in table S4.1.

The squared residuals of the first model were used as response variable in a second linear mixed effect model. Using the obtained parameters (e.g for EBS: $z'_{t+1} = -2.975 + 0.328 * z - 0.097 * n + 0.003 * z * n + 1.026 + T_{gv}$) the model of growth variance σ^2 was constructed (Easterling, Ellner et al. 2000):

$$\sigma^2(z') = a_{gv} + b_{gv} * z + p_{gv} * n + I_{gv} * z * n + y_{gv} + T_{gv} \quad (4.5)$$

T_{gv} was obtained from the normal distribution N (0, 1.952). Additional data of parameter estimates can be found in table S4.1.

The combination of equation 3 and 4 is the growth function *G*:

$$G(z'|z,t) = \frac{1}{\sqrt{2\pi\sigma^2(z)}} e^{\frac{-\left(z' - E(z)\right)^2}{2\sigma^2(z)}} \quad (4.6)$$

A negative $\sigma^2(z)$ term would lead to a negative value in the denominator's square root term. Due to a negative intercept a_{gv} in the model of growth variance σ^2 it was necessary to scale up a_{gv} by 81% to avoid a negative $\sigma^2(z)$.

Inheritance function: *D(z'|z,t)* describes the probability for an individual of body weight *z* at time *t* to give birth to an individual of body weight *z'* at time *t+1*. The inheritance function requires the same structure as the growth function, but here the offspring weight at time *t+1* is regressed against the body weight of the

mother at time *t*. Pedigree data from the study population were obtained from (Godsall 2015). The data set was reduced to mother-offspring data where birth was assignable to a two week period (see “Data collection” for additional information). At time *t+1*, the offspring are about to leave the nest (Harris and Yalden 2008) and were not heavy enough to set off the trigger of our traps. Therefore, individual offspring body weight *W* at *t+1* was extrapolated from its body weight at first capture using the von-Bertalanffy growth equation (R-package FSA (Ogle 2012)):

$$W(t) = W_{max} * (1 - e^{(-K(t-t_0))}) \quad (4.7)$$

with W_{max} being the maximum body weight of female mice before pregnancy, *K* the increase of body weight over time (*K* = 0.91), *t* the age and t_0 the (hypothetical) age at a body weight of 0 grams ($t_0 = -0.677$). To obtain reliable estimates, the data set was reduced even further and only mother-offspring data was used if the offspring was caught within two months after birth. An average birth weight of 1.5 grams (Harris and Yalden 2008) was added to the data set when calculating *W (t+1)*. Using the estimated body weights, two linear mixed effect models were constructed to estimate the association between mother weight at time *t* and offspring weight at time *t+1* (E (z’)) (e.g for EBS: $z'_{t+1} = 7.588 + 0.185 * z - 0.067 * n + 0.003 * z * n - 2.657 + T_d)$ and the variance of this association (σ² (z’)) (e.g for EBS: $z'_{t+1} = -3.207 + 0.116 * z - 0.042 * n + 0.002 * z * n + 0.497)$. T_d was obtained from the normal distribution N (0, 0.957). Additional data of parameter estimates can be found in table S4.1. Using both models, we constructed the inheritance function *D*:

$$D(z'|z,t) = \frac{1}{\sqrt{2\pi\sigma^2(z)}} e^{\frac{-\left(z'-E(z)\right)^2}{2\sigma^2(z)}} \quad (4.8)$$

Similar to the growth function, a negative $\sigma^2(z)$ term would lead to a negative value in the denominator's square root term. Due to a negative intercept a_{gv} in the model of inheritance variance σ^2 it was necessary to scale up a_{gv} by 87% to avoid a negative $\sigma^2(z)$.

Recruitment function: *R(z,t)* describes the number of offspring of an individual of body weight *z* at time *t* that enter the population at time *t+1*. There was a high probability of not catching all offspring produced by a female in one litter. To avoid underestimating the number of offspring produced, the generalized linear mixed effect model was constructed for successful or unsuccessful reproduction for one offspring, converting the recruitment function into a function with binomial distribution (recruitment or no recruitment). Consequently, the function follows the same structure as the survival function. Data for two years (2008 and 2014) were excluded, because no reproduction was recorded. This was most likely due to our inability to catch reproducing females (or to assign their birth to a given trapping session) and, therefore, both years artificially decreased the intercept of the recruitment function. The generalized linear mixed effect model was offset by the recapture rate, providing the parameters for R(z,t) (e.g for EBS: $z'_{t+1} = -6.051 + 0.269 * z - 0.091 * n + 0.004 * z * n - 0.318 + T_r$). Additional information on parameter estimates can be found in table S4.1. It was necessary to scale up the intercept to prevent the population from going extinct. The intercept of the EBS recruitment function had to be increased by a minimum of 20% and the intercept of the LBS recruitment

function by 35% to acquire a non-crashing population. For the reproducing females, we sampled the litter size from a normal distribution N_{litter} with mean 2.75 and standard deviation of 1.006, equivalent to half of the mean litter size of wood mice, assuming a 1:1 sex ratio (Clarke 1985). The resulting recruitment function *R* was:

$$R(z,t) = \left(\frac{1}{1+e^{-(a+b*z+p*n+I*z*n+y+T)}}\right) * N_{litter} \quad (4.9)$$

T_r was obtained from the normal distribution N (0, 0.112).*Numerical implementation and sensitivities*

We approximated the IPM as a high dimensional matrix and tested for sensitivity of population growth rate (λ) to number of mesh points (the number of size classes) in our matrix model. With a minimum of 200 mesh points, λ is unaffected to the sixth decimal point. To avoid unintentional eviction due to mis-specified boundaries of size ranges (Williams, Miller et al. 2012), we created weight classes ranging from 5 – 75 grams, considerably larger than the maximum weight of a female wood mouse from our field population (33grams). We simulated population dynamics for 1 300 time steps (26 time steps = 1 year) and excluded the first 100 time steps from analysis to avoid bias from random initial conditions. From this simulation, we calculated the following parameters by using methods from (Easterling, Ellner et al. 2000; Rees and Ellner 2009; Coulson 2012):

Lambda (λ) - population growth rate at equilibrium.

Mean body weight – the mean body weight of all individuals alive at a time step.

Population size – number of individuals at each time step.

Life time reproductive success (LRS) – the mean number of female offspring produced by a female.

Generation time - sum of offspring produced per original individual at each time step divided by total number of offspring produced.

In order to assess the effect of each function and its containing variables on the and specifically whether body weight and population density changed together as Chitty predicted, we conducted sensitivity analyses. The slopes and intercepts of each function, and the mean and variance of the litter size distribution in the recruitment function were perturbed independently by 1%. All parameters were perturbed upwards, hence multiplying a positive parameter by 1.01 and a negative parameter by 0.99. Every perturbed IPM (n = 38) was compared with a baseline IPM (no perturbation) and the differences on population size, mean body weight and its variance were calculated.

Data analysis

Based on equation 4, asymptotic growth - the growth where body weight at t equals body weight at t+1 - was calculated with equation z* at different population sizes:

$$z^* = (a_g + y_g + T_g + p_g * n) \,/\, (1 - b_g - I_g * n) \qquad (4.10)$$

Linear and generalized linear models (log or square-root transformed to fit normal distribution) were constructed to analyse the relationship between the population parameters: Mean body weight as a function of population size and season; Lifetime reproductive success (LRS) as a function of population size at

birth and season; and generation time as a function of trapping session, season, population size and LRS. Additional linear models were constructed using data from the field population to analyse the density dependence of body growth during the breeding season: Separate models were constructed for juvenile/sub-adults mice (< 18gr) and adults (≥ 18 – 25 gr), using the same weight threshold as in our study site to distinguish adults from sub-adults. All caught female mice heavier than 25 grams gave birth subsequently (defined by sharp weight loss between two consecutive trapping sessions and examination of sex characteristics, including perforated vagina and lactating nipples). Therefore, adult individuals above 25 grams were excluded from analysis to avoid the biasing effect of pregnancies on body weight. Field data analysis during the EBS revealed a clear three level population structure of high density level (n > 35), intermediate density level (n = 23 - 28) and low density levels (n < 10),. Intermediate population sizes were omitted to compare most contrasting population sizes (‘high’ and ‘low’), which were analysed separately. To allow for analysis comparison between seasons, the same thresholds were used for the LBS despite a less clear population size structure. For each age class and density level, a linear model for body weight as a function of population density was created.

Results

Sensitivity analysis

Sensitivity analyses were conducted to assess the effect of each function and its containing variables on the output of the IPM. As population size increases, the relative size of sensitivities of reproductive success (R0), bodyweight (z) and population growth rate (λ) to model parameters changed (Figure 4.1 – 4.3 for sensitivities of R0, z and λ during EBS). At higher densities, the sensitivities of R0 to parameters in the survival and growth functions increased, and decreased to parameters in the recruitment and inheritance functions (Figure 4.1). The sensitivities of λ to parameters in all four functions increased with higher population densities. The sensitivities of z to parameters in the growth function increased with higher population densities and decreased to parameters in the recruitment and inheritance functions (Figure 4.2). In the survival function, sensitivities of z to the intercept and the body mass slope decreased at higher population densities but increased to the density slope and the body mass – density interaction slope (Figure 4.3).

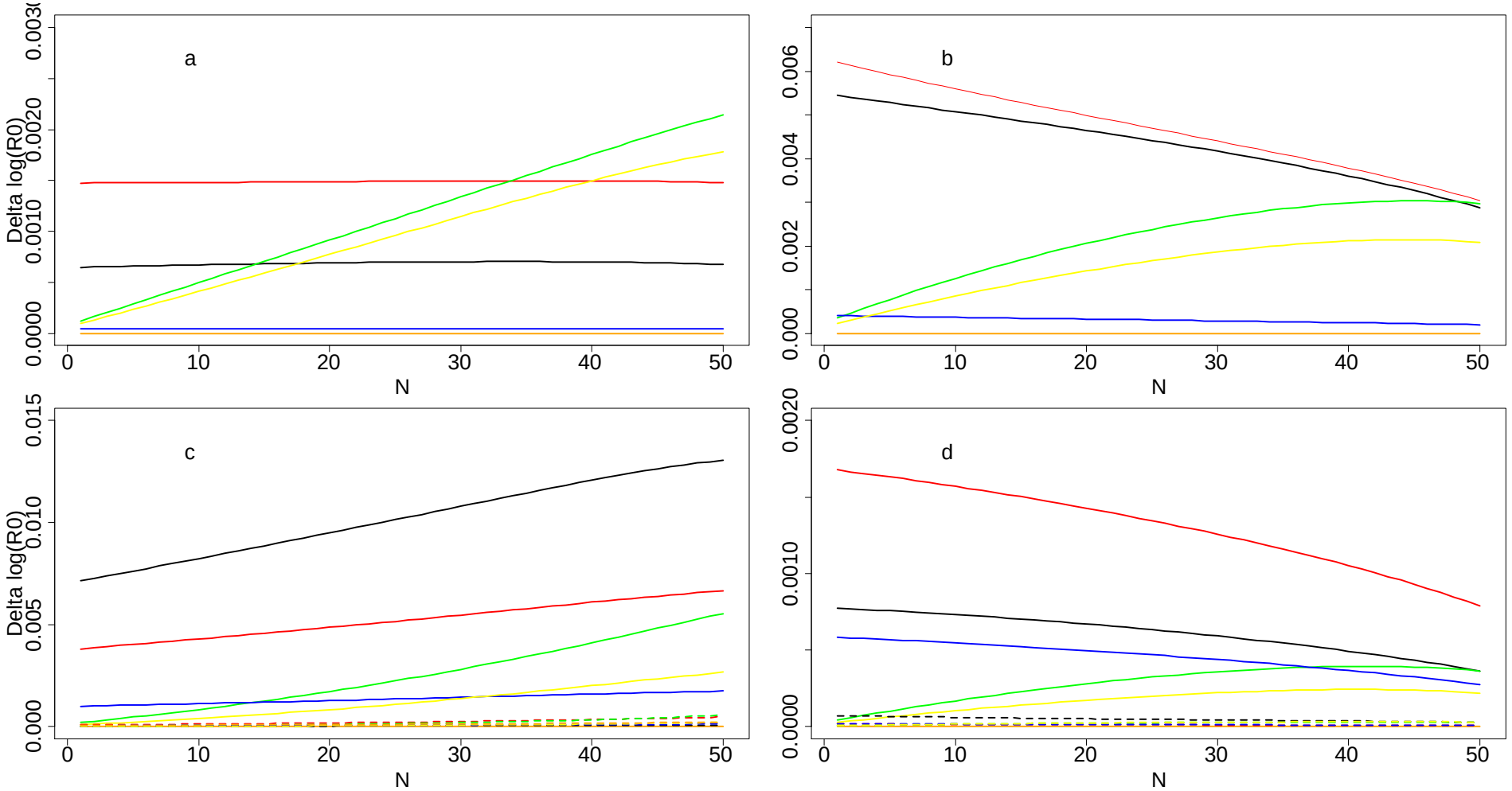


Figure 4.1. Relative size of sensitives of R0 (“Delta log(R0)”) during the early breeding season to model parameters in the four functions (a) survival, (b) recruitment, (c) growth, and (d) inheritance evaluated at a range of population densities (“N”). Black, red, green, blue, yellow and orange lines represent sensitives to the intercept, body mass slope, density slope, year, body mass - density interaction slope and trapping session respectively. Solid lines represent perturbations to parameters in the mean functions and dashed lines represent perturbations to parameters in the variance functions.

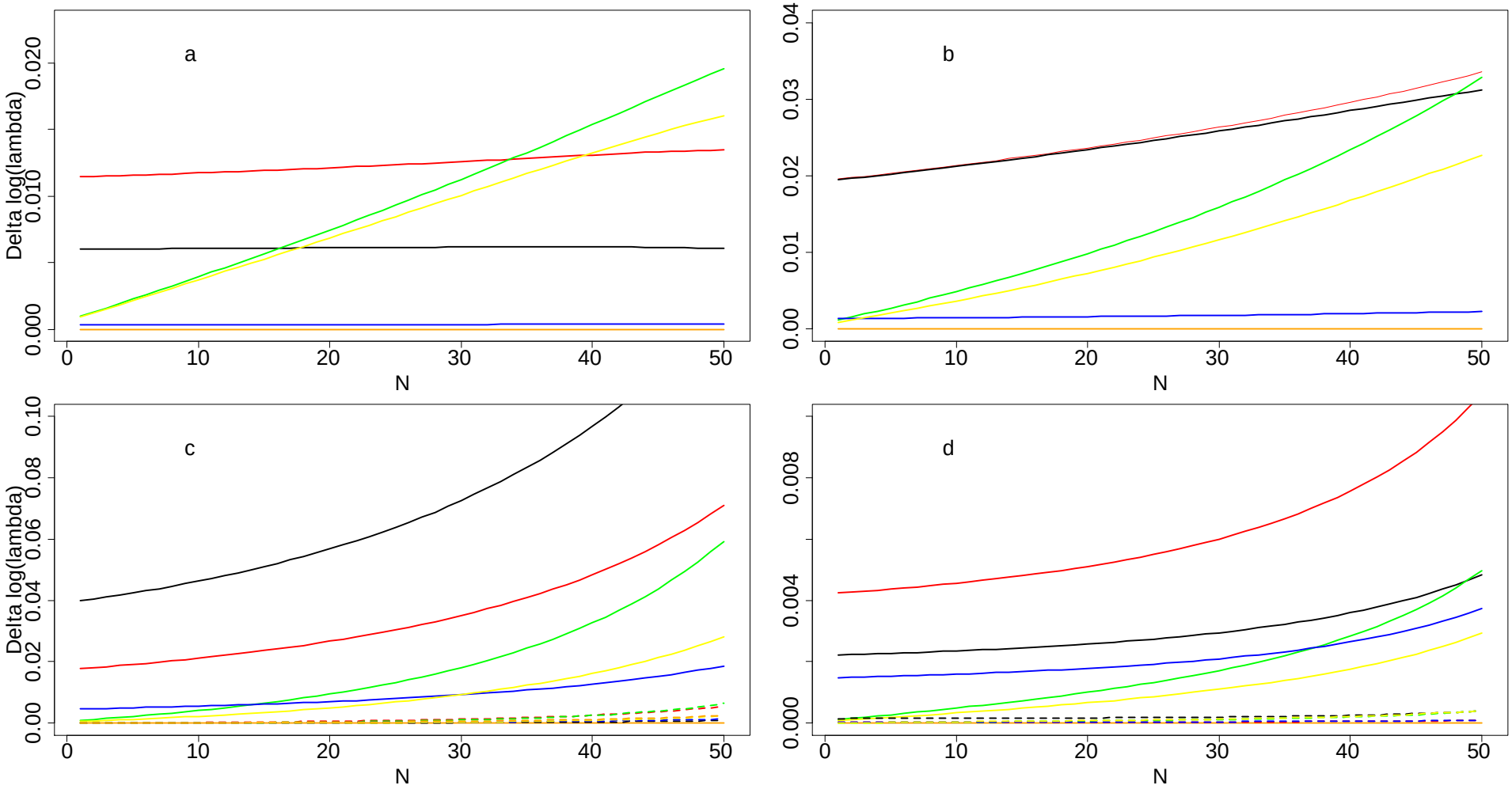


Figure 4.2. Relative size of sensitives of population growth rate (“Delta log(lambda)”) during the early breeding season to model parameters in the four functions (a) survival, (b) recruitment, (c) growth, and (d) inheritance evaluated at a range of population densities (“N”). Black, red, green, blue, yellow and orange lines represent sensitives to the intercept, body mass slope, density slope, year, body mass - density interaction slope and trapping session respectively. Solid lines represent perturbations to parameters in the mean functions and dashed lines represent perturbations to parameters in the variance functions.

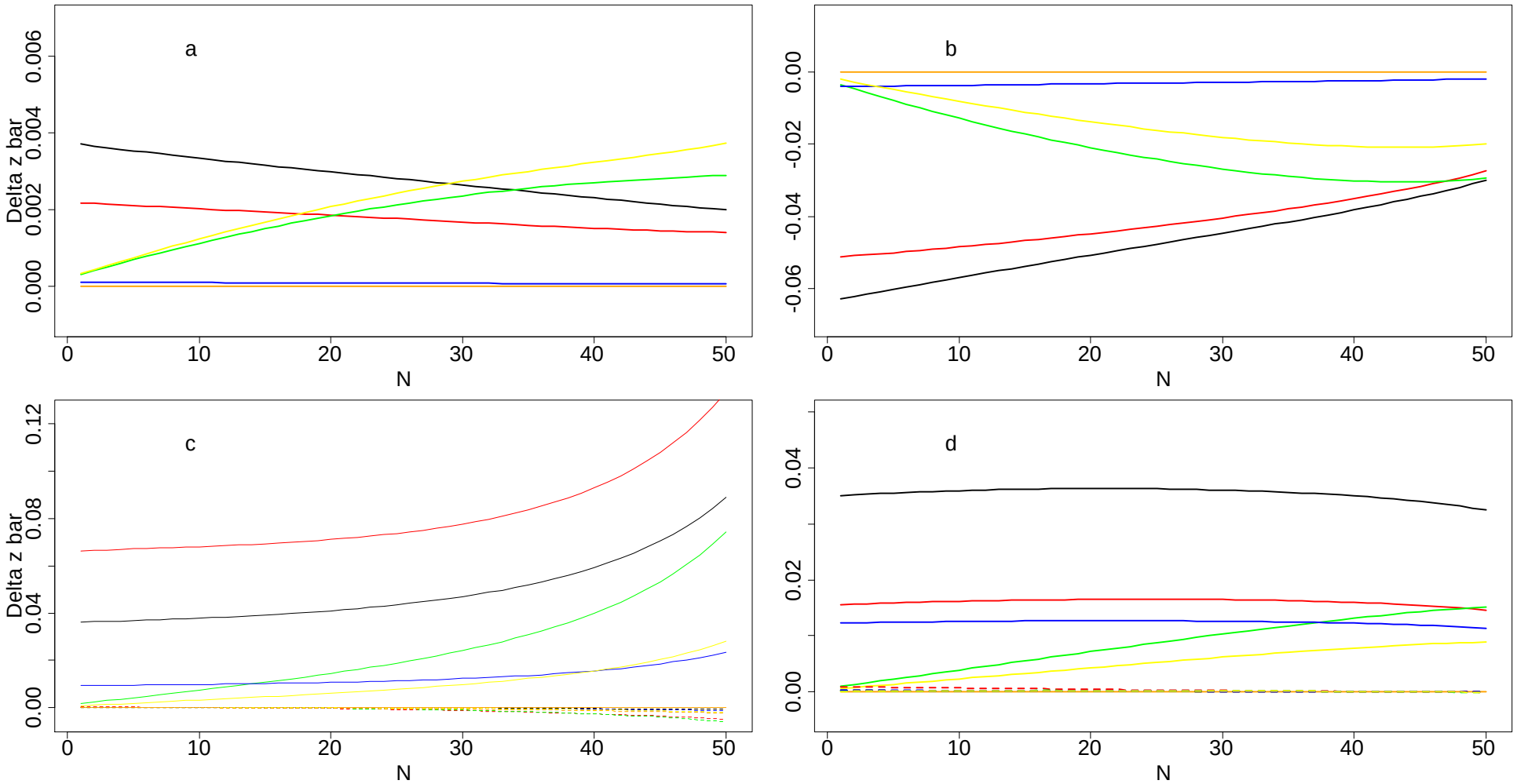


Figure 4.3. Relative size of sensitives of body weight (z) during the early breeding season to model parameters in the four functions (a) survival, (b) recruitment, (c) growth, and (d) inheritance evaluated at a range of population densities ("N"). Black, red, green, blue, yellow and orange lines represent sensitives to the intercept, body mass slope, density slope, year, body mass - density interaction slope and trapping session respectively. Solid lines represent perturbations to parameters in the mean functions and dashed lines represent perturbations to parameters in the variance functions.

Population parameters for model validation

In order to validate the model and to assess the realism of the modelled population dynamic, annual and seasonal values of the model parameters body weight, population size, LRS and generation time were calculated and, if available, compared to data from our field site and from the literature. We simulated 1300 time steps, equivalent to 50 years (26 time steps per year). In the IPM, predicted mean body weight varied between seasons (Figure 4.4). During the NBS, mean body weight was highest (mean 15.47 gr ± 2.54 SD, t = 40.1, p <0.0001), followed by mean body weight during the EBS (mean 12.52 g ± 0.86 SD, t (intercept) = 195.5, $F_{2,1096}$= 779.1, p <0.0001). During the LBS, mean body weight was lowest (mean 11.79 gr ± 0.82 SD, t = -7.9, p <0.0001). Population size varied between trapping sessions (Figure 4.5), with a higher mean population size during the LBS (22.4 ± 12.9 SD) as compared to the EBS (6.5 ± 7.2 SD) or the NBS (6.0 ± 7.2 SD) (t = 23.8, $F_{2,1096}$= 394.2, p <0.0001). Mean population size was higher in the field (13.6 individuals ± 11.53 SD) as compared to the IPM data (11.6 individuals ± 11.46 SD). Mean LRS was 1.22 (± 1.21 SD). LRS varied according to the trapping session, when the cohort was born (Figure 4.6). In the LBS, LRS is lower (mean 0.76 ± 0.57 SD) as compared to the EBS (mean 2.41 ± 1.04 SD) (t-test= -28.8, df =791.8, p < 0.0001). Mean generation time was 83.8 days (± 27.8 SD) and did not differ between early and late breeding season (Figure 4.7). The generation time, however, varied depending on the time of year, i.e. the trapping session when the cohort was born (Figure 4.7). Mean number of days of 360 female wood mice detectable in the field study site was 77.1 days (SD 77.37 days). The 77.1 days do not reflect

the fact that mice live a few weeks before they are heavy enough to set off the trigger and be caught in the traps.

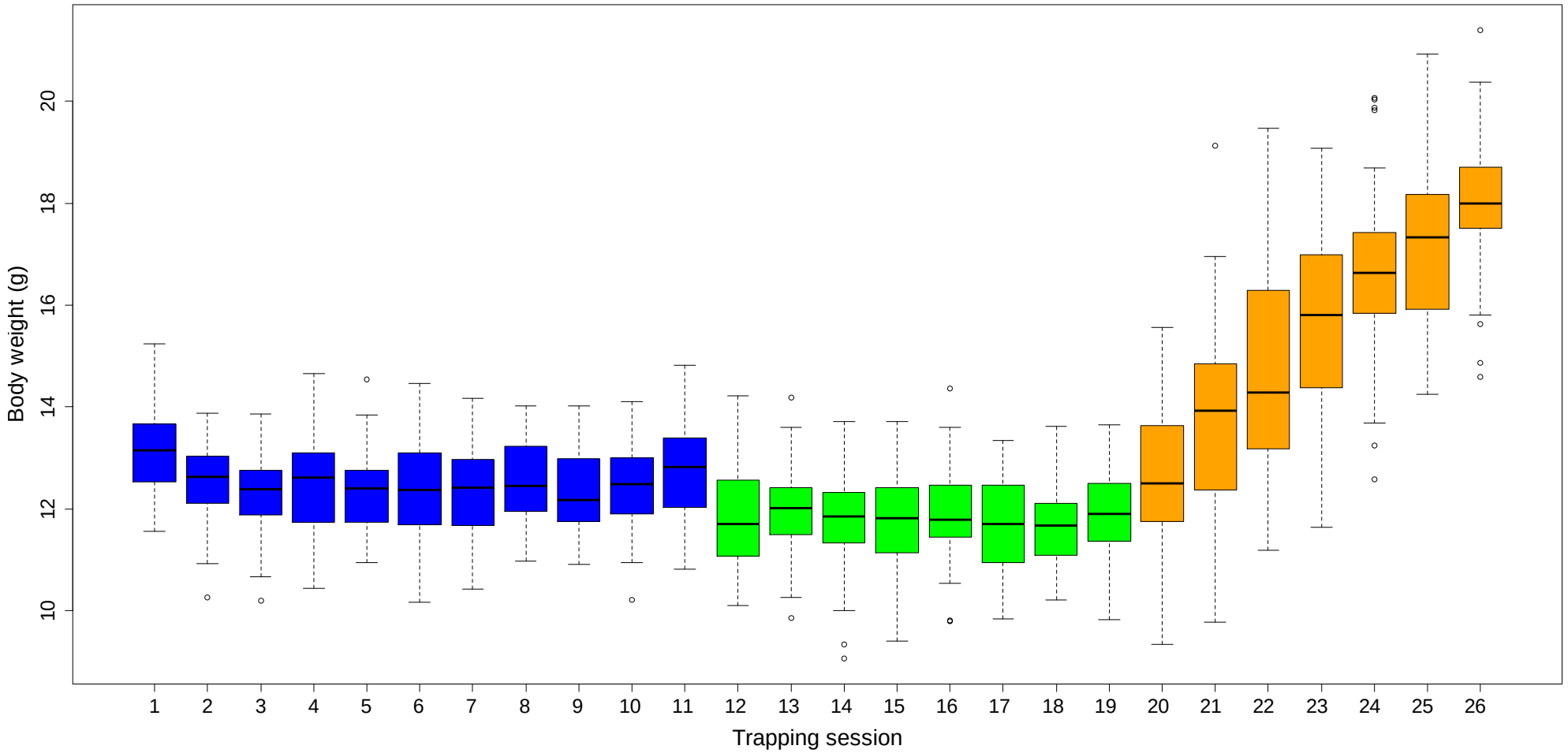


Figure 4.4. Summary of mean body weight (g) over 50 years. 26 bi-weekly trapping sessions equal to one year. Blue: early breeding season. Green: Late breeding season. Orange: Non-breeding season. The lower limit of each box represents the lower quartile, the heavy line inside each box represents the median and the upper limit of each box represents the upper quartile. The upper and lower whiskers represent the limits of the nominal range of the data inferred from the upper and lower quartiles. Outliers are shown as white dots.

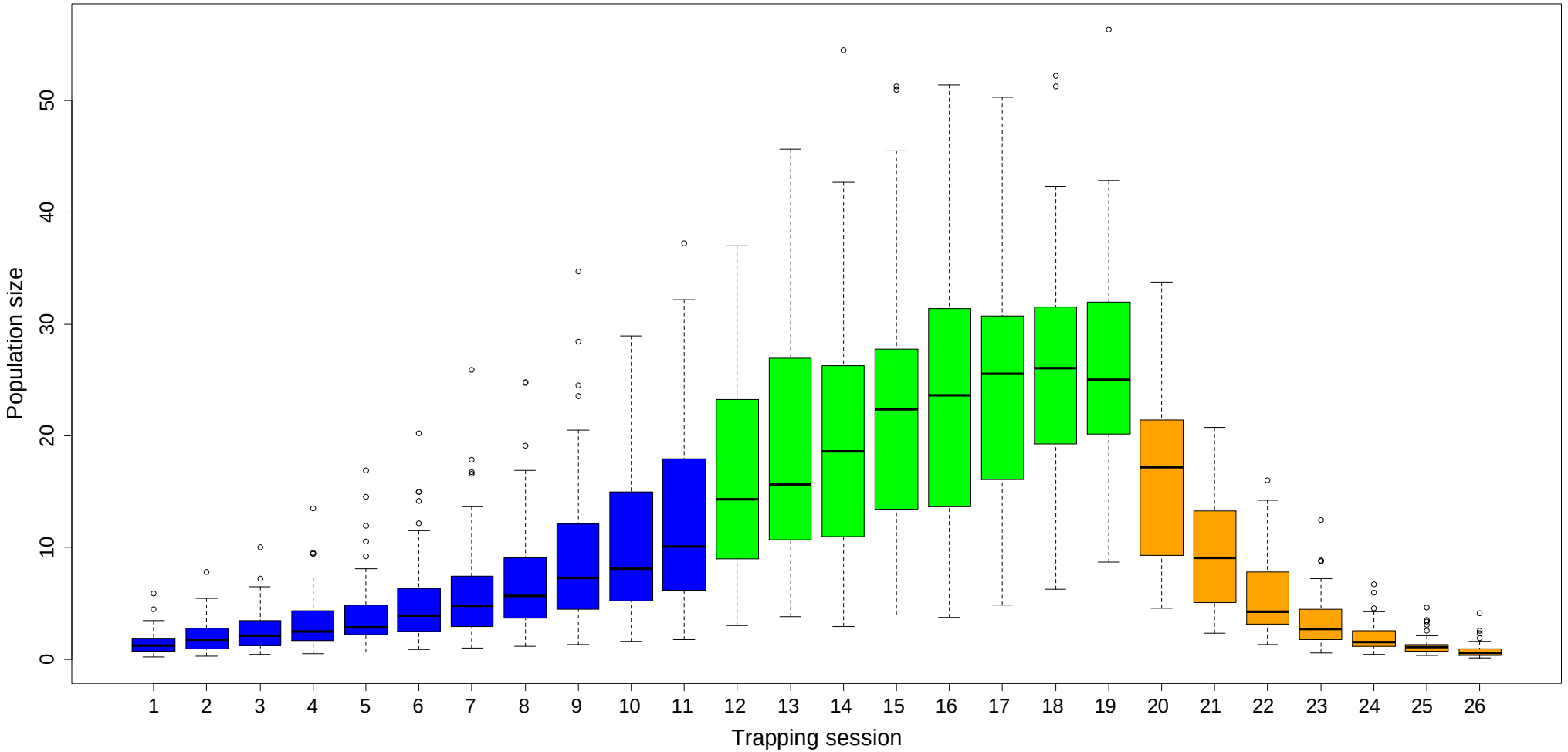


Figure 4.5. Summary of population size per trapping session over 50 years. 26 bi-weekly trapping sessions equal to one year. Blue: early breeding season. Green: Late breeding season. Orange: Non-breeding season. The lower limit of each box represents the lower quartile, the heavy line inside each box represents the median and the upper limit of each box represents the upper quartile. The upper and lower whiskers represent the limits of the nominal range of the data inferred from the upper and lower quartiles. Outliers are shown as white dots.

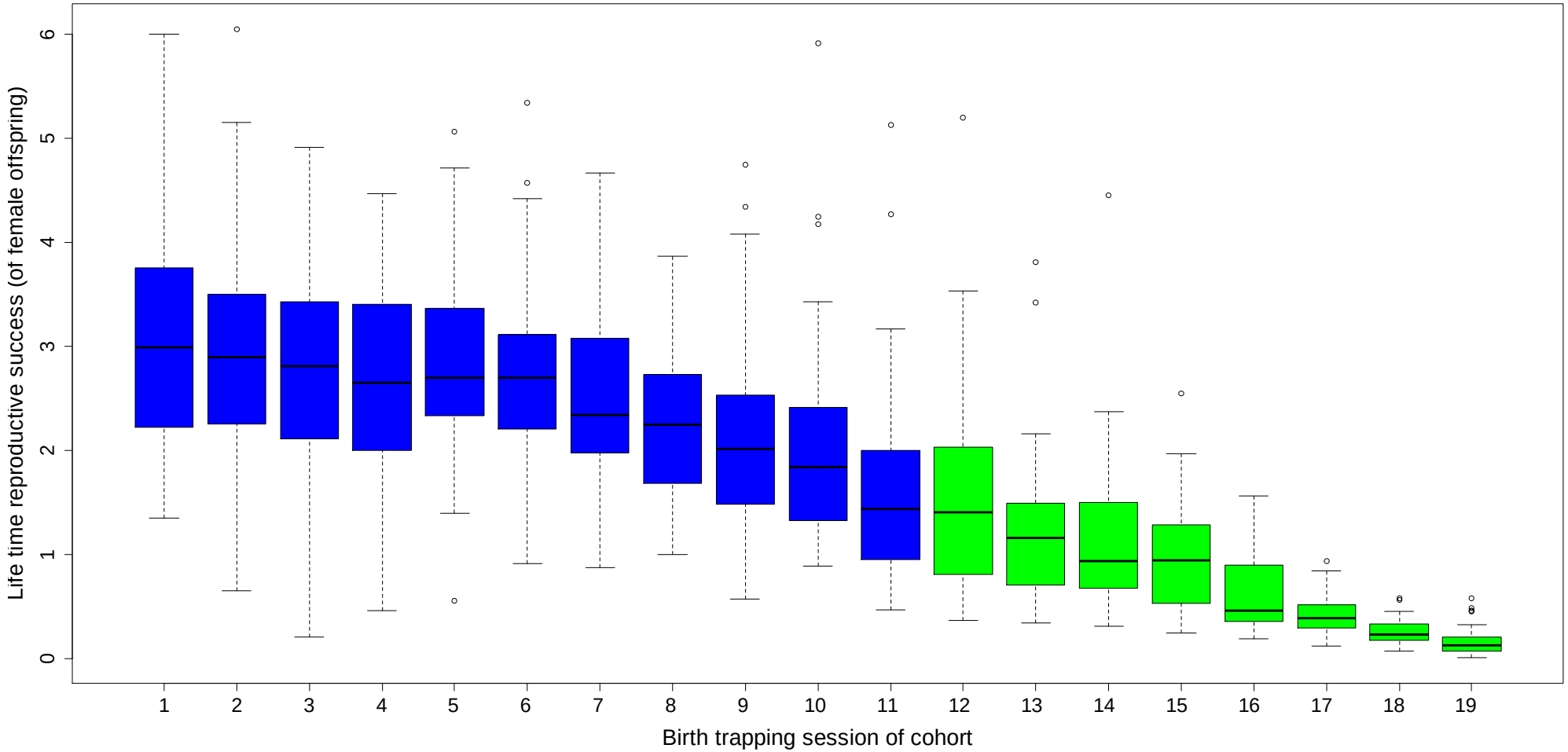


Figure 4.6. Yearly variation in life time reproductive success of individuals born in different trapping sessions (mean derived from 46 cohorts per trapping session). 26 bi-weekly trapping sessions equal to one year. Blue: early breeding season. Green: Late breeding season. The lower limit of each box represents the lower quartile, the heavy line inside each box represents the median and the upper limit of each box represents the upper quartile. The upper and lower whiskers represent the limits of the nominal range of the data inferred from the upper and lower quartiles. Outliers are shown as white dots.

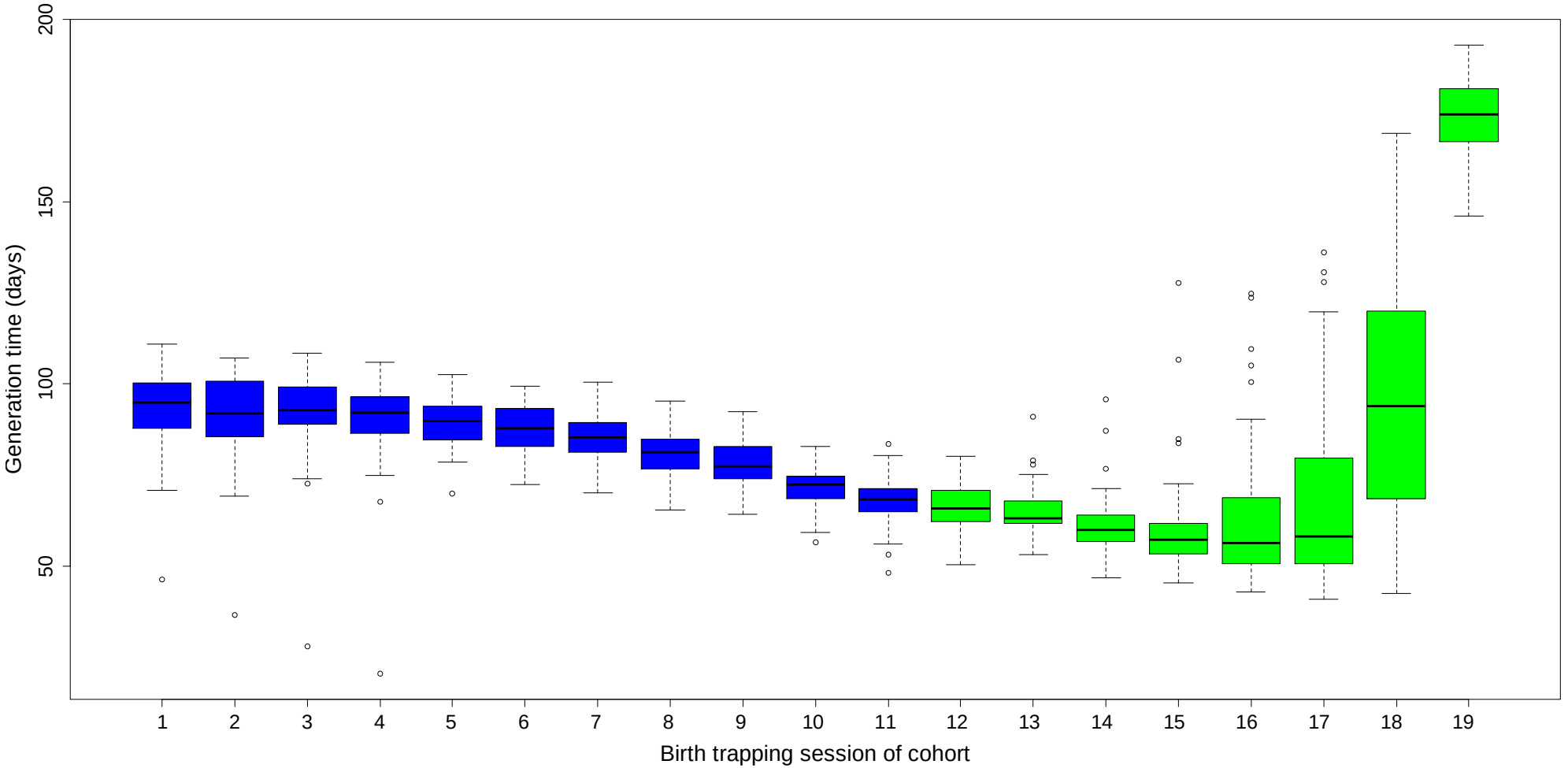


Figure 4.7. Yearly variation of cohort generation time (mean derived from 46 cohorts per trapping session). 26 bi-weekly trapping sessions equal to one year. Blue: early breeding season. Green: Late breeding season. No reproduction occurred in the non-breeding season. The lower limit of each box represents the lower quartile, the heavy line inside each box represents the median and the upper limit of each box represents the upper quartile. The upper and lower whiskers represent the limits of the nominal range of the data inferred from the upper and lower quartiles. Outliers are shown as white dots.

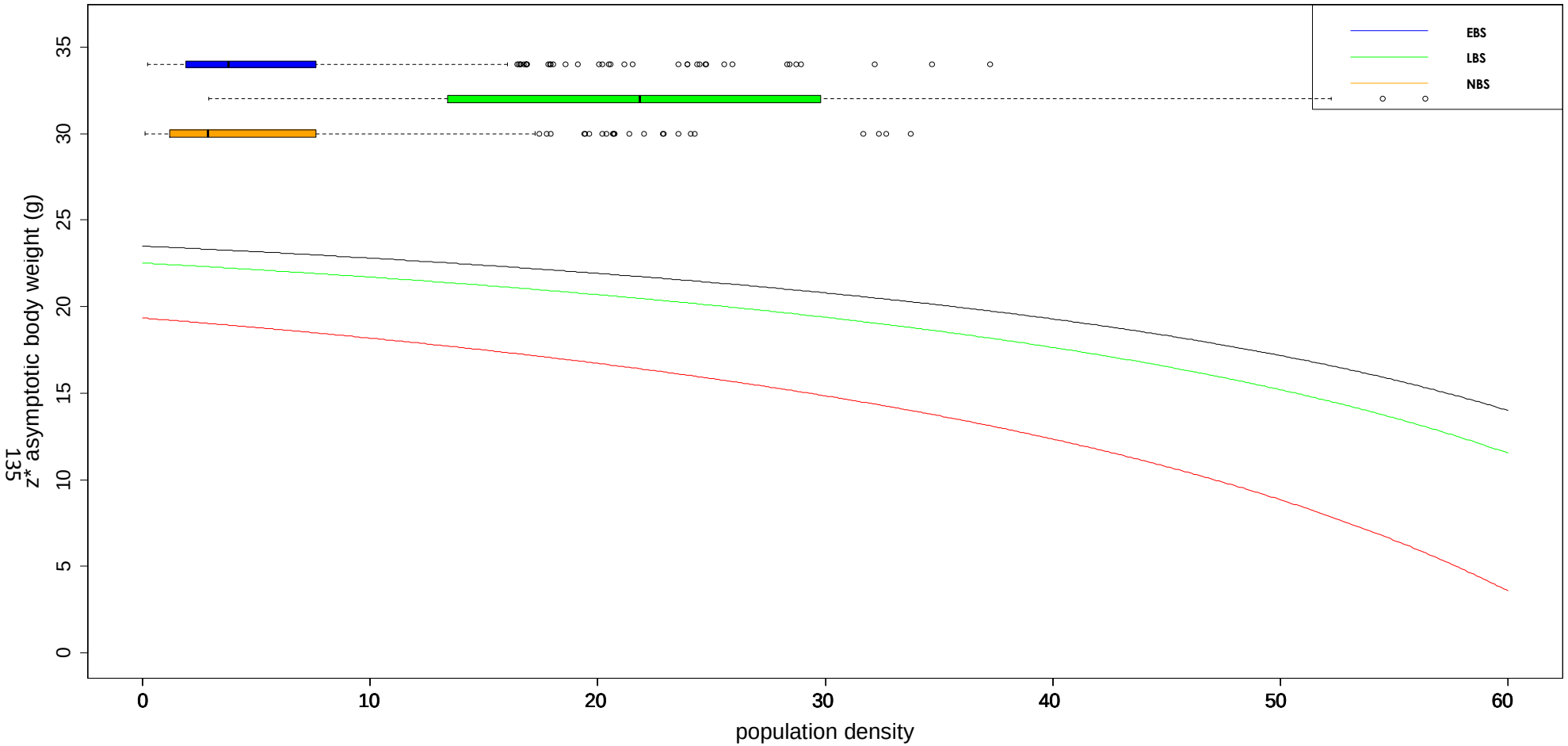


Figure 4.8. Asymptotic body weight (g) at different population densities and for the three different seasons. Horizontal box plots show range of population densities for each season. Blue: early breeding season (EBS). Green: late breeding season (LBS). Orange: non-breeding season (NBS).

The Chitty effect

We tested if the modelled population showed the pattern predicted by the Chitty effect, a positive correlation of body weight and population density (hypothesis 1). In the IPM, predicted mean body weight varied as a function of population size (Figure 4.4). During the EBS and LBS, mean body weight increased with population size (t = 2.65, $F_{2,798}$= 20.26, p = 0.008, R^2: 0.02 (EBS) & 0.06 (LBS)). During the NBS, mean body weight decreased with population size (t = -21.04, $F_{2,295}$= 193, p < 0.0001, R^2: 0.57). For all three seasons, asymptotic growth decreased with increasing population density (Figure 4.8). Perturbing the interaction term in the growth function from 0.0028 to 0.004 (EBS), 0.0038 (LBS) and 0.0044 (NBS) results in an increase of asymptotic growth with increasing population density (Figure S4.1). In the field population, at high densities (n > 35) juveniles and sub-adults grow quicker (growth slope: 0.84 gram per two weeks; SE 0.04) compared to low densities (n < 10) (growth slope: 0.82 gram per two weeks; SE 0.09). For adult wood mice, the growth slope is shallower (0.39 gram per two weeks; SE 0.15) at high densities (n > 35) compared to low densities (n < 10) (growth slope: 0.57 gram per two weeks; SE: 0.25). For analysis on adult wood mice, individuals > 25 grams were excluded to avoid effect of pregnancies.

The dynamic energy allocation hypothesis infers that with increasing population size LRS decreases and generation time increases (hypothesis 2). Therefore, we tested the correlation of population size with LRS and generation time. In the IPM, during the EBS and LBS, LRS (square-root transformed) is negatively correlated with population size at birth (EBS: t = -14.7, LBS: t = -9.1, $F_{5,796}$=

461.7, p < 0.0001). Generation time (log transformed) increased with population size at birth (t = 4.8, $F_{6,795}$= 59.48, p < 0.0001). A significant quadratic interaction was found between generation time and LRS. Generation time decreases with increasing LRS (t = -3.5, p = 0.0003) until a LRS of 1 and then increased with increasing LRS (t = 5.5, p < 0.0001). This pattern was significantly stronger in the LBS as compared to the EBS (decrease: t = 14.2, p < 0.0001; increase: t = 10.9, p < 0.0001).

Discussion

Every population consists of individuals, which can be described by measuring continuous and categorical characters. At any point in time a character can be measured for any individual, showing the character distribution for the population. Driven by both internal and external factors a character distribution can change over time. An integral projection model (IPM) allows one to track the change of a continuous character in a population over time and to calculate several important population level parameters. For small species, few IPMs have been constructed, largely due to difficulties in obtaining the data required to parameterise the model and to our knowledge no IPM has been used to analyse an r-selected rodent species. In this study, we constructed an IPM to investigate the population dynamics of wood mice with a particular interest in the effect of population size on individual body weight, cohort generation time and cohort lifetime reproductive success (LRS).

Population dynamics in wood mice

The modelled population revealed dynamics similar to our field population as well as other wood mice populations (Flowerdew 1985; Montgomery 1989;

Montgomery, Wilson et al. 1997). Following a non-breeding season with low survival rate, population size increases during the breeding season (Flowerdew 1985; Montgomery 1989; Montgomery, Wilson et al. 1997). The variance in population size in the IPM also increases as the breeding season proceeds with 10-fold inter-annual differences during the late breeding season, similar to those observed in our field population and in other studies (Montgomery and Gurnell 1985; Montgomery 1989).

For mean body weight, no comparable field data was found, as field studies struggle to record weights from new born and juvenile mice. However, through our model we were able to observe increases of mean body weight during non-breeding season, in addition to intermediate values during the early breeding season and lower values during late breeding season. This pattern can be explained through the lack of new born and juvenile mice in our population during the non-breeding season, which increases mean body weight. In contrast, during the breeding season a large number of offspring reduces the mean body weight.

The mean generation time in our IPM (83.8 days (± 27.8 SD)) is higher than findings from other studies (35 – 50 days (Bartmann and Gerlach 2001) and “longer than 6 weeks” (Clarke 1985)). Difficulties lie, however, with directly comparing the different generation times as the named studies do not specify additional information regarding how the generation times were obtained (e.g. sample size or formula to calculate generation time). Our research shows that mean generation time decreases until the middle of the late breeding season followed by an increase until the end of the late breeding season. The decrease of mean generation time until the middle of the late breeding season is possibly

due to low survival rates of wood mice during the non-breeding season (Flowerdew 1972; Flowerdew, Gurnell et al. 1985). Therefore, to maximise reproductive success, wood mice should reproduce in the same breeding season they were born in (Bergstedt 1965; Flowerdew, Gurnell et al. 1985), resulting in shorter generation times for cohorts born later in the breeding season. Our data adds to existing research by showing that wood mice born during the late breeding season are faced with the choice between two different strategies. Firstly, wood mice can reproduce in the same breeding season they were born in (Zizkova and Frytna 1996) and generation time is likely to be shortened the later they are born. Therefore, quick maturation at the end of the breeding season could be possible through compensatory growth. In other taxa, it has been shown that season related climate cues or being born late in the breeding season can lead to compensatory growth (Nicieza and Metcalfe 1997; Nylin and Gotthard 1998). In rodents, the effect of external factors on compensatory growth is less well studied and requires further research. It has been shown, however, that maternal differences can induce compensatory growth resulting in different maturation rates (Monteiro and Falconer 2010). Secondly, wood mice can postpone reproduction until the next breeding season, which is already known from other rodents from seasonal environments (Eccard and Herde 2013). Postponing reproduction frees female wood mice from investing energy in costly reproduction shortly before the start of non-breeding season with low food availability and high energy demand due to adverse climatic conditions. However, it also decreases the likelihood of reproductive success, if the individual does not survive the non-breeding season.

In our IPM, lifetime reproductive success (LRS) is highest in cohorts born early in the breeding season and decreases during the breeding season. Female wood mice can conceive soon after parturition (Clarke 1985) and have up to six litters per season (Flowerdew, Gurnell et al. 1985). However, many external factors, including food availability and competition related stress, can reduce the number of litters per season and increase the time between two successful pregnancies (Saitoh 1990). Therefore, the majority of females have only one or two successful litter per breeding season (Flowerdew, Gurnell et al. 1985). In our IPM, female wood mice born early in the breeding season, have more time to successfully reproduce and increase their LRS.

Chitty effect in wood mice?

To better understand the population dynamics of wood mice we investigated body weight as a driver. More specifically, we explored if the Chitty effect - heavier individuals at higher densities - can be found in the *Apodemus* population, due to dynamic energy allocation (Oli 1999). We hypothesized that a) individuals will be heavier at higher densities in comparison to individuals at lower densities, and b) a high sensitivity of body growth dynamics on population size and an effect of population size on generation time and LRS (Oli's interpretation of the Chitty effect).

We found mixed evidence for the Chitty effect in wood mice. A positive density dependence of mean body weight as well as a negative density dependence of asymptotic body weight was found. So far, density dependence of body weight in *Apodemus* has not been investigated and, to our knowledge, this is the first study reporting a positive density dependence of body weight in *A. sylvaticus.*

However, due to the small effect size of the positive density dependence of mean body weight, further research should be conducted to verify our findings. In general, a positive density dependence of mean body weight and a negative density dependence of asymptotic body weight are not necessarily contradicting results. The latter shows that adult wood mice reach lower asymptotic body weights when population density is high, contrary to the prediction of the Chitty effect (Chitty 1967; Krebs 1970; Krebs 1978). The positive density dependence of mean body weight in our IPM, however, reveals that if adults are not heavier at higher densities, sub-adults must be heavier during periods of high population density.

Our data reinforce Oli's theory of dynamic energy allocation. Both assumptions, ample food supply and suppression of reproduction, are likely to be fulfilled in our field population. While food is known to be a limiting factor during the non-breeding season (Watts 1969; Flowerdew 1972), it is thought to be abundant during the breeding season. Density dependent suppression of reproduction is also known from several *Apodemus* species (Montgomery, Wilson et al. 1997; Nakata 1998), although the exact mechanisms are not fully understood. However, studies on other rodent species found several mechanisms of social suppression of reproduction (for a detailed review see Oli (1999)), which are likely to be also applicable to *Apodemus*. Suppressed reproduction can negatively affect lifetime reproductive success and can increase generation time, a proxy for maturation age. In our population, at high densities female cohorts had prolonged generation time, possibly driven by longer maturation rates, and reduced lifetime reproductive success as compared to low densities. If individuals at high density delay maturation, all energy can be allocated to

growth. Results from our model only found support for higher growth rates in juvenile and sub-adult wood mice but not in adults. This is supported by field data indicating that at high densities juveniles and sub-adults but not adult wood mice grow quicker. The idea of dynamic energy allocation has already received some empirical support, but so far only external factors (e.g. temperature) were identified as drivers (Ross and Nisbet 1990; McManus and Travis 1998). In rodents, the existence of dynamic energy allocation has been suggested by several authors (e.g.(Lidicker Jr and Ostfeld 1991; Boonstra, Krebs et al. 1998). Recently, empirical support for dynamic energy allocation revealed that voles at high densities grow for longer and reach higher asymptotic body weights (Burthe, Lambin et al. 2010). Interestingly, our results indicate, that in wood mice dynamic energy allocation is restricted to the non-adult age classes. Our data therefore, does not reveal any signs of heavier individuals at higher densities, one key aspect of the original chitty effect. Our results, however, support Oli's interpretation of dynamic energy allocation and the idea that the Chitty effect arises as a consequence of population dynamics and is not its driving cause (Burthe, Lambin et al. 2010). Density affects life history (e.g. generation time, LRS) which in turn allows individuals to allocate their energy differently, resulting in heavier sub-adult individuals. To our knowledge, this is the first study on non-microtine rodents providing initial evidence for density dependent energy allocation and growth rates. Our findings also highlight that Oli's re-definition of the Chitty effect is not restricted to taxa with super annual fluctuations in population size, which are mainly driven by internal factors. Instead the effect can also be found in a taxon were super annual cycles, if they occur at all, are less pronounced and predominately driven by external factors

(e.g. food). In fact, as the dynamic energy allocation hypothesis does not specifically include a multi annual time scale, it has also been used to explain year to year body weight fluctuations in microtine rodents (Burthe, Lambin et al. 2010).

We used the dynamic energy allocation hypothesis in order to assess the annual dynamic of a population with food driven super annual cycles. We argue, that the parameters used in this study are sufficient to test the dynamic energy allocation because the effect of mast seeding is largely irrelevant to the dynamic energy allocation in wood mice. Allocation of surplus energy due to delay of maturation occurs during the early and late breeding season. The density dependence of growth rates and life history parameters is relatively constant across both breeding seasons. If mast crops would be the driver of growth rates during the late breeding season, we would expect parameters to differ between early and late breeding seasons. In particular, because differences of food availability in normal and mast years are likely to be irrelevant for wood mice until the non-breeding season, when in normal years food becomes scarce.

Further research is now required on rodents and other r-selected species, in order to test if dynamic energy allocation and the positive density dependence of body weight (of some age classes) is more common than currently thought. Additional research, particularly for the *Apodemus* genus, is required to improve our understanding of growth rates in rodents. Currently, all studies rely on data with low sample size and large temporal gaps between two data points. A better understanding of growth rates, however, is crucial to understand how dynamic energy allocation affects population dynamics in rodents.

Acknowledgements

The authors wish to thank O. Hicks, G. Kingcombe, M. Massam, S. McLoughlin, R. Moorhouse-Gann, T. Powell and C. Weevil for assistance with field data collection that was used to parametrize the IPM. This work was funded by an Advanced ERC grant (LEED: number 249872) awarded to T. Coulson, Marie Curie (PIEF-GA-2008-220322) awarded to A.F. Malo and a Cusanuswerk scholarship awarded to S. Dreßen. The authors declare that they have no conflict of interest.

Supporting information

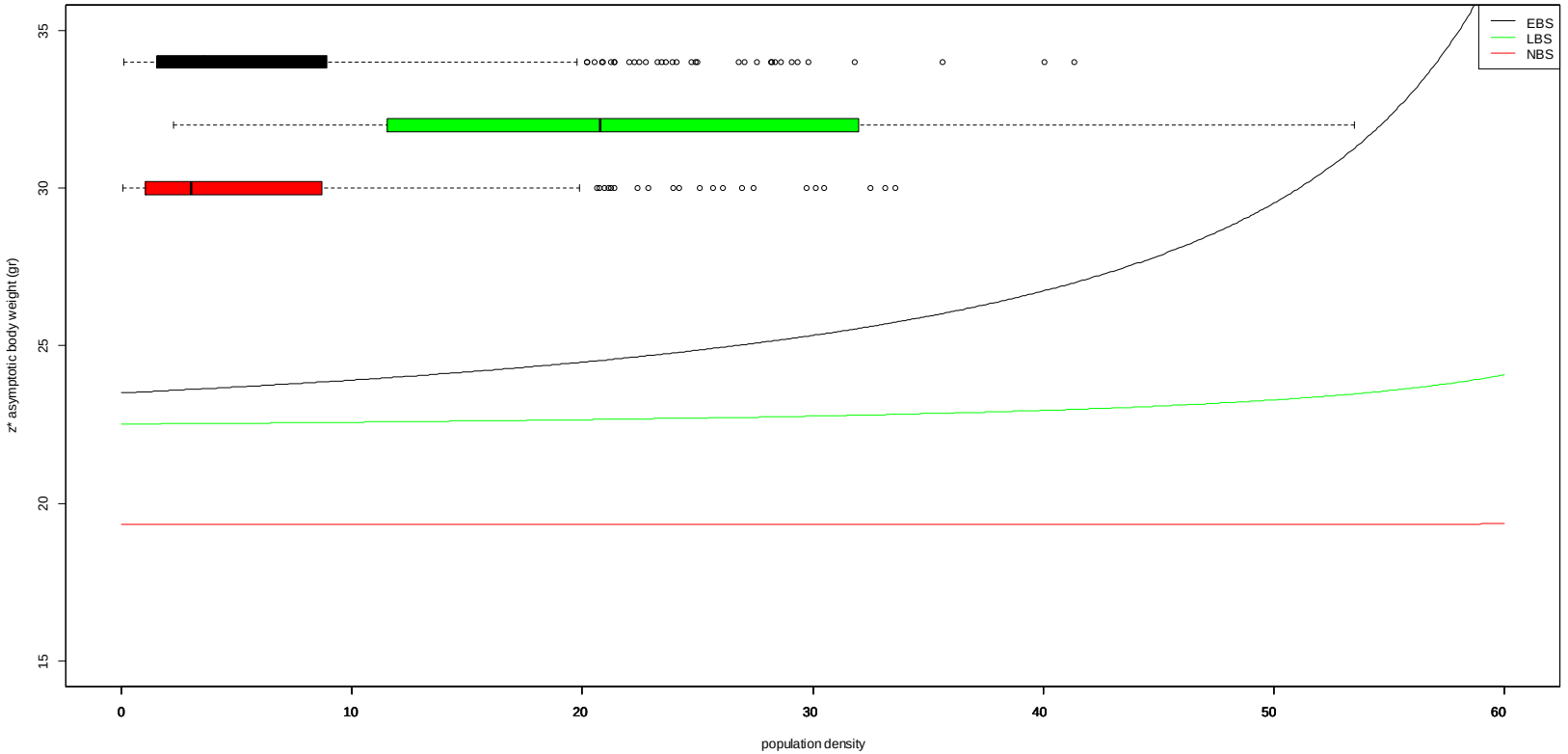


Figure S.4.1. Perturbed asymptotic body weight (gr) at different population densities and for the three different seasons. Horizontal box plots show range of population densities for each season.

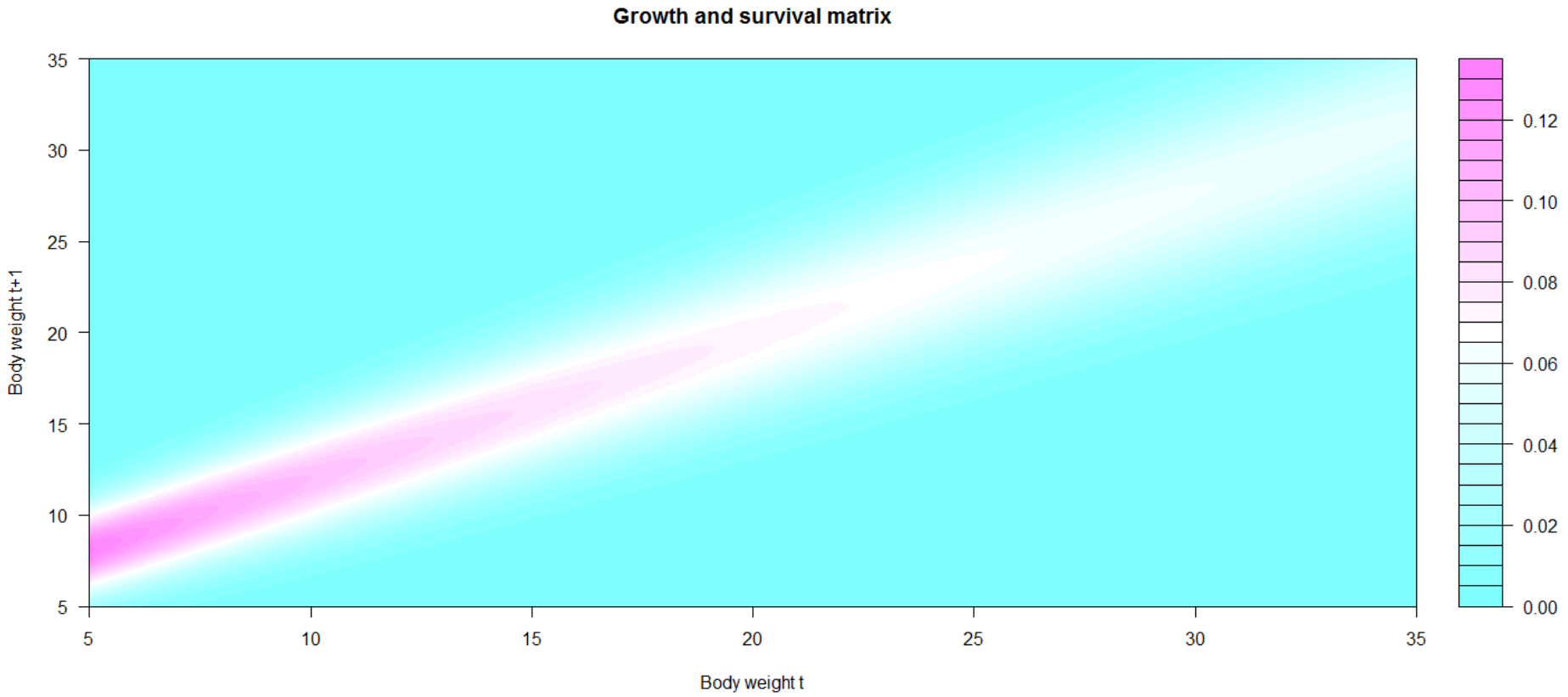


Figure S4.2. Transition surface of the growth and survival functions at a population size of 23 individuals. The axes represent body weight within a range from 5-35 grams at time t and t+1. The colour code is the transition rate between size classes.

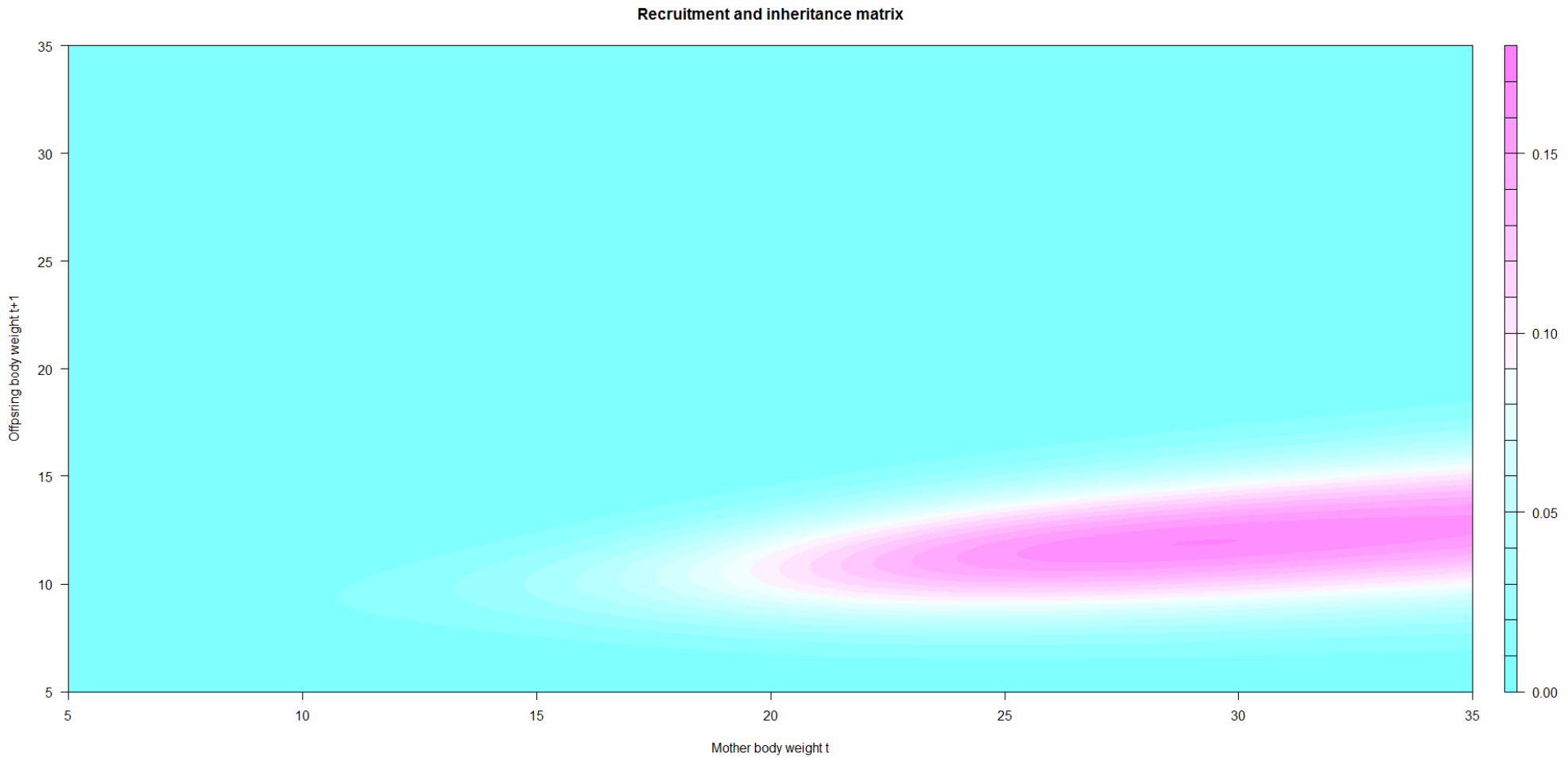


Figure S4.3: Transition surface of the recruitment and inheritance functions at a population size of 23 individuals. The axes represent body weight within a range from 5-35 grams at time t and t+1. The colour code is the transition rate between size classes.

Table S4.1.: Model output used to parameterise the four IPM functions survival, growth, inheritance and recruitment. 'n' is the number of data points used for the model. 'LBS' is the late breeding season. 'NBS' is the non-breeding season. ′²′ is highlighting the intercepts which had to be scaled up to prevent population from going extinct.

Survival (n = 1537)			
Covariate	Estimate	Std. Error	z value
Intercept	0.830036	0.745624	1.113
Body weight	0.02545	0.028433	0.895
Population	0.023192	0.023408	0.991
Year	-0.024	0.6011747	-0.03083
Season LBS	-0.47107	0.187004	-2.519
Season NBS	-0.72955	0.21605	-3.377
Body weight : Population	-0.0013	0.00118	-1.099

Growth (n = 939)			
Covariate	Estimate	Std. Error	t value
Intercept	5.25809	0.991472	5.303
Body weight	0.718162	0.032913	21.82
Population	-0.08417	0.028751	-2.928
Year	1.366488	0.828957	1.662
Season LBS	-0.27777	0.246532	-1.127
Season NBS	-1.17233	0.29495	-3.975
Body weight : Population	0.002823	0.001411	2.001

Growth Variance (n = 939)			
Covariate	Estimate	Std. Error	t value
Va_Intercept^2	-2.97523	3.062519	-0.972
Va_Body weight	0.328392	0.112813	2.911
Va_Population	-0.09688	0.095093	-1.019
Va_Year	1.025712	2.386289	0.430
Va_Season LBS	1.225111	0.67382	1.818
Va_Season NBS	-1.07029	0.818132	-1.308
Va_Body weight : Population	0.002639	0.004907	0.538

Inheritance (n = 24)			
Covariate	Estimate	Std. Error	t value
Intercept	7.588469	7.899627	0.961
Body weight	0.185114	0.300344	0.616
Population	0.067904	0.378776	0.179
Year	-2.65679	1.785062	-1.540
Season LBS	0.504483	0.741140	0.681
Body weight : Population	-0.00216	0.016191	-0.134

Inheritance Variance (n = 24)			
Covariate	Estimate	Std. Error	t value

Va_Intercept^2	-3.20669	4.352113	-0.737
Va_Body weight	0.11621	0.162422	0.716
Va_Population	-0.04235	0.181871	-0.233
Va_Year	0.496626	1.000786	0.517
Va_Season LBS	0.009058	0.399965	0.023
Va_Body weight : Population	0.002341	0.007591	0.308

Recruitment (n = 1537)			
Covariate	Estimate	Std. Error	z value
Intercept^2	-4.84105	2.38727	-3.7
Body weight	0.26933	0.097367	2.766
Population	-0.09106	0.132204	-0.689
Year	-0.31752	0.35658	-0.701
Season LBS^2	0.743941	0.420162	0.6
Body weight : Population	0.003761	0.005579	0.674

Chapter 5

Movement patterns influence estimation error in home range size calculations

Abstract

Home range is an important concept to analyse animal space use and movement patterns at the individual and population level. Due to current constraints in data collection most home ranges are estimates, based only on a subset of the animal's true utilization distribution of space. Consequently, a home range estimate is likely to be inaccurate and the level of inaccuracy might vary depending on the underlying movement pattern. We simulated six different movement patterns, using a spatially explicit, individual based model to calculate home ranges based on real-time resolution. We then subsampled locations from the true home range at five different temporal resolutions, calculated the new home ranges and measured the mean and variation of the relative bias in core and full home range estimation. Across all models, bias in home range size estimation increased as temporal resolution decreased, resulting in more biased mean core and full home range size estimation and higher variation of home range size estimation at lower temporal resolution. The increase of variation at lower temporal resolution, the ratio of bias between full and core home range estimation and whether biased estimation tended to over- or underestimate true home range size varied between movement patterns. Our results highlight the advantage of understanding the movement pattern of a study species in order to assess potential inaccuracy of home range estimation. This accounts particularly for researchers who have to prioritise between high temporal resolution of data collection and number of different individuals monitored.

Key-words: home range, individual based model, kernel density estimation (KDE), movement pattern, temporal resolution

Introduction

Animal space use influences many life history processes including reproduction and survival, and thus ultimately the dynamics of a population (Gaines and McClenaghan Jr 1980; Fisher and Lara 1999; Getz, Oli et al. 2005; Booth, Montgomery et al. 2009). It is therefore important to understand how animals use space, but estimates of statistics describing movement patterns and home range size can often be inaccurate as they are based on a subset of spatio-temporal locations rather than on true utilization distribution of space. Here, we investigate how temporal resolution influences space use estimates for different types of movement patterns.

The space an animal needs to survive and reproduce is defined as its home range (Burt 1943). Home ranges can be derived using kernel density estimation (KDE) (Worton 1989), a method that accounts for variation in space use frequency within a home range better than other home range estimation methods (e.g. harmonic mean, MCP (Seaman and Powell 1996), see Seaman et al. (1999) for further references). The estimation error of the home range using KDE may depend on 1) the temporal resolution of sampling location fixes during the study period (henceforth temporal resolution), 2) the spatial structure of a home range or, 3) the number of individuals (in case of mean home range size estimation).

Increased number of location fixes (per unit time), i.e. higher temporal resolution, decrease the estimation error of KDE (Seaman, Millspaugh et al. 1999; Blundell, Maier et al. 2001). In addition, the spatial structure of a home range is likely to affect estimation error in KDE. At low temporal resolution, a

home range with a complex spatial structure (e.g. multiple activity centres) should be more sensitive to estimation error in home range size than a home range based on a homogenous distribution of location fixes. To our knowledge, this has only been investigated using a basic approach that assessed differences in KDE estimation between home ranges composed of 1, 4 and 16 bivariate normal distributions (Seaman, Millspaugh et al. 1999). The sampled proportion of a population is also likely to affect error in mean home range size estimation. Individual variation in home range size has been subject to many studies (for example Van Beest, Rivrud et al. (2011)). Yet only one study has assessed the effect of the number of individuals sampled on estimation error in mean home range size (Borger, Franconi et al. 2006). Both the mean and variance associated with home range sizes within and across populations are important in ecological research. For instance, analysing home range size variation between different groups in a population (e.g age class (Cederlund and Sand 1994) or sex (Herfindal, Linnell et al. 2005)) can help explain reproduction and recruitment. Additionally, assessing the minimal size of protected areas required to support a viable population is an example of how home range estimation can benefit conservation (Kramer and Chapman 1999; Linnell, Andersen et al. 2001).

High temporal resolution - ideally real-time resolution – and a large number of monitored individuals – ideally the entire (sub-)population – are clearly desirable, but sampling designs are often restricted in their temporal resolution, and sampled group size is limited by economic, labour or technological constraints. Given a fixed budget of any kind (e.g. time, money, equipment) researchers may have to prioritise an increase in temporal resolution over

sampled group size or vice versa. In many cases, it is likely that the best choice might depend on the movement pattern specific spatial structure of a home range, but to our knowledge the effect of the home range's spatial structure on estimation error has not been investigated.

In this study, we use a modelling approach to analyse how the error in home range size estimation of six different movement patterns depends on temporal resolution and sampled group size. In particular, we are interested in using temporal resolutions commonly used in the most popular monitoring methods, either mobile technologies (e.g. satellite and radio based techniques) or stationary technologies (e.g. trapping and PIT-based techniques). We hypothesise that a structurally more complex movement pattern will be more sensitive to reduced temporal resolution than a spatially more homogenous movement pattern.

Material and Methods

The methods we used are based on a study by Fieberg (2007), who assessed the performance of weighted kernels for spatial data collected with sampling designs that are used in telemetric studies by creating several sub-samples of spatial points from a modelled KDE. He then compared the spatial overlap between the true KDE and each sub-sample as an indicator of how well a sub-sample estimates the true KDE. Here we developed his method further to assess the estimation error of KDEs of home ranges created by different types of movement behaviour, with sampling frequencies that are characteristic of (small) mammal studies.

Simulations

Six different sets of movement behaviour were simulated over a 365-day period at a 15-minute resolution (96 location fixes per day) using the software Netlogo (Wilensky 1999). The arena is a 500 x 500 grid (250 000 cells) with its origin (0,0) in the bottom left corner. The population size for each simulation was 50. Individual movement per day can be described by one or more stochastic partial differential equations, all of the form:

$$\begin{pmatrix} dX(t) \\ dY(t) \end{pmatrix} = C_i \cdot \begin{pmatrix} a_{i,x} - X(t) \\ a_{i,y} - Y(t) \end{pmatrix} dt \ , \qquad (5.1)$$

where $(a_{i,x}, a_{i,y})$ is the local range of coordinates to which an individual can move during period *i* (see below) and C controls the movement speed (table 5.1). Locations were generated at sequential time steps $t_{i+1} = t_i + \Delta t$ by discretizing equation 1:

$$\mathrm{M} = \begin{pmatrix} x_{(t+1)} \\ y_{(t+1)} \end{pmatrix} = \begin{pmatrix} x_t \\ y_t \end{pmatrix} + C_i \cdot \begin{pmatrix} a_{i,x} - x_t \\ a_{i,y} - y_t \end{pmatrix} \Delta t. \qquad (5.2)$$

The local range *a* was defined as:

$$\begin{pmatrix} a_{i,x} \\ a_{i,y} \end{pmatrix} = \begin{pmatrix} (x_t + \varepsilon) > r_{i,x} > (x_t - \varepsilon) \\ (y_t + \varepsilon) > r_{i,y} > (y_t - \varepsilon) \end{pmatrix}, \qquad (5.3)$$

where $(r_{i,x}, r_{i,y})$ is the total range of coordinates to which an individual could move during period *i,* and ε is the radius of the circular area around the individual over which it has knowledge (table 5.1). In order to account for individual variation and random movement, the parameters of equation 2 were varied depending on the conditional equations:

$$p_M > q, \quad (5.4)$$

where *p* is the threshold value between 0 and 1 for the model *M* and *q* is a random number between 0 and 1 (table 5.1). In some models, individual transition stages exist to allow individuals to move from one defined area to another. The length of an individual transition stage z_i during period *i* is:

$$z_i = \sum_{z=1}^{n} \left(\begin{pmatrix} x_t \\ y_t \end{pmatrix} \neq \begin{pmatrix} r_{i,x} \\ r_{i,y} \end{pmatrix} \right). \quad (5.5)$$

With the 365 days x 96 daily fixes = 35040 location fixes per individual, I calculated a KDE of the simulated individual space use to generate individual full home ranges (95% isopleth).

KDEs were calculated using the package 'ks' in R (version 3.0.2, Core Development Team, Vienna, Austria). I used the plug-in estimator (Wand and Jones 1994) to obtain smoothing parameters for *x* and *y*. The core home range size of an individual was estimated by using the time-maximizing function developed by Van der Wal & Rodgers (2012). The resulting 'true' home ranges were compared to home range estimates from subsampled data sets to investigate the accuracy of home range size estimations across different sample designs (see section "Sampling design" below).

Movement behaviour

The six sets of movement rules can be described sufficiently with the above equations. Below, we provide additional conceptual information.

Random walk

"Random walk" simulates random movement. Random walks are rarely observed in animals. They occur, when animals forage in an area with homogenous food distribution and no inter- or intra-specific interaction. Here, we chose this simple movement lacking spatial structure as a base line model to compare it to movement patterns with spatial structure. In our simulation, all individuals were placed at the centre of the grid (250,250) at t_0, and location for each time step $t_i$was calculated via equation 2 (table 5.1).

Oriented walk

The model simulates movement behaviour along/towards a randomly distributed feature. This type of movement behaviour, for instance, can be found in many species with browsing foraging patterns (Etzenhouser, Owens et al. 1998), or in species that move from feature to feature to reduce predation risk (Tallmon and Mills 1994). In our model, a random number of cells between zero and one-third of the total number of cells (n_{total} =83333) were selected to represent such features. The cells including features were placed randomly across the arena. As before, all individuals were placed at the centre of the grid (250,250) at t_0, and location for each time step $t_i$was calculated via equation 2 (table 5.1). If $p_M < q$, ε is defined as a random number between one and five (table 5.1). If $p_M > q$, ε is defined as the minimum distance (i.e. number of cells) within a radius of five cells between (x_i, y_i) and ($x_{withfeature}$, $y_{withfeature}$). The range for ε was chosen to introduce heterogeneity in individual movement speed. If there are no cells with features within a radius of five cells, the individual moves according to $p_M < q$.

Central place forager (CPF)

A central place forager is based at a nest and conducts foraging trips from its nest (Orians and Pearson 1979). For simplicity, abundant and randomly distributed food availability was simulated by assigning one quarter of all cells as food cells ($x_{withfeature}$,$y_{withfeature}$). This way, food was abundant enough to avoid effects of the spatial structure of food availability and scarce enough to create the spatial dynamic of an individual moving increasingly further away from its nest. Each individual *f* is placed at its nest ($x_{f,nest,}y_{f,nest}$) at t_0 and depletes the local food resources. The location for each time step $t_i$was calculated via equation 2 (table 5.1). During period 1 and if $p_M > q$, ε is defined as the minimum distance (i.e. number of cells) between (x_i, y_i) and ($x_{withfeature}$,$y_{withfeature}$) and the individual moves towards ($x_{withfeature}$,$y_{withfeature}$) with a randomly selected speed between 1 – 5 cells/time step (table 5.1) to account for individual movement speed variation. Once the individual reaches a food cell, period 2 commences in which the individual returns to its nest (table 5.1). As soon as the animal reaches the nest, period 1 starts again.

Territorial behaviour

The territorial movement behaviour is simulated by combining two types of movement patterns. A territorial animal will spend a part of its daily time budget controlling or defending the border of its territory (period 1 in table 5.1) and the other part of its daily time budget moving through its territory (period 2 in table 5.1). (Ims 1995; Jedrzejewski, Schmidt et al. 2001). For reasons of simplicity, the daily time budget was divided equally between period 1 and 2. Each individual *f* has a territory of a randomly assigned radius between 50 and 200

cells to account for inter-individual variation in territory size. For simplicity, all territories were designed as a circular shape. At t_0, each individual is placed at the centre of its territory and the individual's location for each time step $t_i$was calculated as described in equation 2 (table 5.1). During period 1, the individual's total range of attraction $(r_{1,x}, r_{1,y})$ is restricted to the cells that are within the range of two cells of the territorial border (BT), defined as $x_{f,BT}, y_{f,BT}$. During period 2, the individual's *f* total range of attraction $(r_{2,x}, r_{2,y})$ is restricted to the cells within the territory. During both periods 1 and 2, the individual moves with a randomly varying speed of 1-5 cells/time step to account for individual movement speed variation.

2 Places

"2 places" simulates movement behaviour where the animal spends one part of its daily time budget in one area, which is followed by a transition period to another area, where it spends another part of its daily time budget, before it returns to the first area. This type of movement can be found in species that rest and forage in two different places (Henzi, Byrne et al. 1992; Chilvers 2008). At t_0 all individuals are placed randomly within $r_{1,x}, r_{1,y}$. The location for each time step $t_i$was calculated as described in equation 2 (table 5.1). Periods 1 and 3 are the transition periods where individuals move between the two areas (table 5.1). During period 2 and if $p_M > q$ the individual does not move (table 1). If $p_M < q$, the individual moves to a randomly selected neighbouring cell within $r_{1,x}, r_{1,y}$ (table 5.1). During period 4, individuals move within an area with one-fifth of its cells randomly assigned as features. In this period, individuals always

move to the closest cell with a feature (table 5.1), simulating foraging behaviour in an area with high food availability.

4 places

The model “4 places” is an extension of the “2 places” model where species move across four different areas per day (Jordan, Cherry et al. 2007). In our simulations, the daily movement pattern includes the transition periods 1,3,5,7 and 9 and the stationary periods 2,4,6,8 and 10 (table 5.1). At t_0 all individuals are placed randomly within$r_{1,x}, r_{1,y}$. The location for each time step $t_i$was calculated as described in equation 2 (table 5.1). Transition periods are structured equally to periods 1 and 3 in the “2 place” model, but differ in transiting speed between different areas (table 5.1) to simulate heterogeneity for different transition periods. Stationary periods are equivalent to periods 2 and 4 in the “2 place model” and only differ with respect to their location in the arena.

Table 5.1.a. Parameters that were used to generate location data for the three simulations random walk, oriented walk and central place forager. b Parameters that were used to generate location data for the three simulations territorial, 2 places and 4 places. **Period**: The number of different types of movement patterns within the daily time budget. **Time steps**: The allocation of time units to every period (total daily budget = 96 time steps). **z:** is the length of an individual transition stage z_i during period *i*. **Time interval:** The translation of time steps into a 24-hours scheme. $\boldsymbol{p_M}$: *p* is a threshold value between 0 and 1 for the model *M* in Eq. 4. **Eq. 4**: Conditional equation to account for random movement. Different movement rules depending on *q* , a random number between 0 and 1, being larger or smaller than *p*. For more details see equation 4 in the method section. $\boldsymbol{\varepsilon}$: Local sensing radius, i.e. radius of cells over which an individual has perfect knowledge. In some periods, ε is a randomly allocated number within a range of numbers to account for individual variation. **Min. dist**.: minimum distance to a particular feature. $\boldsymbol{x\ and\ y_{with\ feature}}$: coordinates of a particular feature. $\boldsymbol{r_{i,x}, r_{i,y}}$: Total range of coordinates that are accessible for an individual during period *i*. $\boldsymbol{x_{f,BT}, y_{f,BT}}$ & $\boldsymbol{x_{f,nest}, y_{f,nest}}$ & $\boldsymbol{x_{f,minT} - x_{f,maxT}}$**:** individual *f*'s coordinates (*x*,*y*) for its territorial border (*BT*), *nest* or the total extent of its territory (*T*) . $\boldsymbol{C_i}$**:** The movement speed, i.e. number of cells on x and y axis that can be crossed within one time step.

a Simulation	Period	Time steps	Time interval (hs)	p_M	Eq. 4	ε	$r_{i,x}, r_{i,y}$	C_i
Random walk	1	1 to 96	0000 - 2400	-	-	1	0 - 500	$\begin{pmatrix} 5 & 0 \\ 0 & 5 \end{pmatrix}$
Oriented walk	1	1 to 96	0000 - 2400	0.8	$p_M > q$	1 - 5	0 - 500	$\begin{pmatrix} \varepsilon & 0 \\ 0 & \varepsilon \end{pmatrix}$
					$p_M \leq q$	1 - 5	0 - 500	$\begin{pmatrix} \varepsilon & 0 \\ 0 & \varepsilon \end{pmatrix}$

Central place forager	1	1 to 96	0000 - 2400	0.8	$p_M > q$	min. dist. to $(x_{with\ feature}\ y_{with\ feature})$	0 - 500	$\begin{pmatrix} 1-5 & 0 \\ 0 & 1-5 \end{pmatrix}$
					$p_M \leq q$	1 - 5	0 - 500	$\begin{pmatrix} \varepsilon & 0 \\ 0 & \varepsilon \end{pmatrix}$
	2	1 to 96	0000 – 2400	-	-	1 - 5	$x_{f,nest}, y_{f,nest}$	$\begin{pmatrix} \varepsilon & 0 \\ 0 & \varepsilon \end{pmatrix}$
b Simulation	Period	Time steps	Time interval (hs)	p_M	Eq. 4	ε	$r_{i,x}, r_{i,y}$	C_i
Territorial	1	1 to 48	0000 - 1200	-	-	1 - 5	$x_{f,BT}, y_{f,BT}$	$\begin{pmatrix} \varepsilon & 0 \\ 0 & \varepsilon \end{pmatrix}$
	2	49 to 96	1215 - 2400	-	-	1 - 5	$x_{f,minT} - x_{f,maxT}$, $y_{f,minT} - y_{f,maxT}$	$\begin{pmatrix} \varepsilon & 0 \\ 0 & \varepsilon \end{pmatrix}$
2 places/ 4 places	1	z	z ·15	-	-	1	0 - 50	2 places: A = $\begin{pmatrix} 25 & 0 \\ 0 & 25 \end{pmatrix}$ 4 places: 2 · A
	2	z to 24	(z · 15) - 0600	0.8	$p_M > q$	0	0	$\begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}$
					$p_M \leq q$	1	0 - 50	$\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$

2 places	3	25 to (25 + z)	0615 – (0615 + z · 15)	-	-	1	250 - 500	$\begin{pmatrix} 25 & 0 \\ 0 & 25 \end{pmatrix}$
	4	(25 + z) to 96	(0615 + z · 15) – 2400	-	-	min. dist. to $(x_{with\ feature}\ y_{with\ feature})$	250 - 500	$\begin{pmatrix} \varepsilon & 0 \\ 0 & \varepsilon \end{pmatrix}$
4 places	3	24 to (25 + z)	0615 – (0615 + z · 15)	-	-	1	225 - 275	$\begin{pmatrix} 50 & 0 \\ 0 & 50 \end{pmatrix}$
	4	(25 + z) to 32	(0615 + z · 15) - 0800	-	-	min. dist. to $(x_{with\ feature}\ y_{with\ feature})$	225 - 275	$\begin{pmatrix} \varepsilon & 0 \\ 0 & \varepsilon \end{pmatrix}$
	5	33 to (33 + z)	0815 - (0815 + z · 15)	-	-	1	0 – 125, 375 – 500	$\begin{pmatrix} 50 & 0 \\ 0 & 50 \end{pmatrix}$
	6	(33 + z) to 72	(0815 + z · 15) - 1800	-	-	min. dist. to $(x_{with\ feature}\ y_{with\ feature})$	0 – 125, 375 – 500	$\begin{pmatrix} \varepsilon & 0 \\ 0 & \varepsilon \end{pmatrix}$
	7	73 to (73 + z)	1815 – (1815 + z · 15)	-	-	1	375 - 500	$\begin{pmatrix} 50 & 0 \\ 0 & 50 \end{pmatrix}$
	8	(73 + z) to 88	(1815 + z · 15) - 2200	-	-	min. dist. to $(x_{with\ feature}\ y_{with\ feature})$	375 - 500	$\begin{pmatrix} \varepsilon & 0 \\ 0 & \varepsilon \end{pmatrix}$
	9	89 to (89 +z)	2215 - (2215 + z · 15)	-	-	1	225 - 275	$\begin{pmatrix} 50 & 0 \\ 0 & 50 \end{pmatrix}$
	10	(89 +z) to 96	(2215 + z · 15) - 2400	-	-	min. dist. to $(x_{with\ feature}\ y_{with\ feature})$	225 - 275	$\begin{pmatrix} \varepsilon & 0 \\ 0 & \varepsilon \end{pmatrix}$

Sampling designs

We created different sampling designs to sub-sample the spatial points of the true space use at five different temporal resolutions and for ten different proportions of the population. The quantitative sampling design was structured as an incremental increase by 10%, starting at 10% of the population (n=5) to 100% of the population (n = 50). Within each temporal design, we determined a random starting day within the first week, and took one random location fix for the following intervals:

1) Fortnightly sample (= $n_{locationfixes}$ 26 - 27) : This approach simulates, for example, home range estimation based on fortnightly trapping, which is used in many small mammal studies.

2) Weekly sample (= $n_{locationfixes}$ 52). This sampling design simulates home range estimations based on a weekly relocation effort.

3) Daily sample (= $n_{locationfixes}$ 365). This design simulates a highly sparse network of stationary monitoring devices, currently used in our study site (Godsall, Coulson et al. 2014).

4) 12-hourly sample (= $n_{locationfixes}$ 730). This design simulates a denser network of the design above, where each individual is located twice a day, or a remote tracking device with low temporal resolution.

5) Hourly sample (= $n_{locationfixes}$ 8760). Such sampling effort can be achieved with a tracking device with medium - high temporal resolution.

The temporal sampling design (n = 5) and the quantitative designs (n= 10) produced a total number of 50 different designs for each type of movement patterns (n = 6). Every combination was re-sampled 500 times, creating a total number of 25 000 subsamples and a total number of 687 500 estimated home ranges. KDEs (95% isopleth) of the different samples were estimated using the same methods as described for KDE of the true home range (see "Simulations"). For every home range HR_i, the percentage of relative bias (PRB) to the mean of the true home range size $\acute{H}R_t$ was calculated:

$$\text{PRB} = (HR_i - \acute{H}R_t) / \acute{H}R_t * 100 \quad (5.6)$$

The effect of temporal resolution (i.e. location fixes) on PRB between different simulations was assessed by log-transforming explanatory (temporal resolution) and response (PRB) variable and fitting a linear model.

Results

Across all models, bias in home range size estimation increased as temporal resolution decreased, resulting in more biased mean home range size estimation and higher variation of home range size estimation at lower temporal resolution (Figures 5.1 – 5.2, table 5.2).

Core and full home range size estimates of all, but the central place forager model (CPF) model, over-estimated true mean home range size at lower temporal resolution. While true mean core and full home range size of CPF was over-estimated at intermediate temporal resolution (12-hourly, daily, weekly), it under-estimated mean full home range size at the lowest, bi-weekly temporal resolution (Figure 5.1, table 5.2). The increase (or decrease) of mean home range PRB at lower temporal resolution varied between simulations (table 5.2).

The lowest increase was found in the 2 places simulation, while the spatially most complex model, the 4 places simulation, showed the highest increase in estimation bias (table 5.2).

Generally, the tendency for bias to increase at lower temporal resolution was similar for core and full home range size estimation (table 5.2). There were, however, model specific differences regarding the extent to which variation and mean of home range size estimation changed at lower temporal resolution (Figures 5.1 – 5.2, table 5.2). In the “2 places” and “4 places” simulations, PRB of mean core home range size estimation was constantly lower than in mean full home range size estimation (table 5.2). In all other simulations, PRB in mean core home range size estimation was higher when compared to PRB of mean full home range size estimation (table 5.2). The variation of PRB at lower temporal resolution was in all simulations but the CPF simulation higher for core home range size estimation than for full home range size estimation (table 5.2). Due to high levels of variation in core home range size estimation, all simulations except for the “4 places” simulation estimated core home ranges that were smaller and larger than the true mean core home range (Figure 2, table 5.2). For full home range size estimations, in contrast, all simulations, except the territorial model and CPF, only estimated full home range sizes that were larger than the true mean full home range (Figure 5.1, table 5.2).

Patterns across all six different simulations remained the same at different population sizes, but variation in home range size estimation increased at lower population numbers.

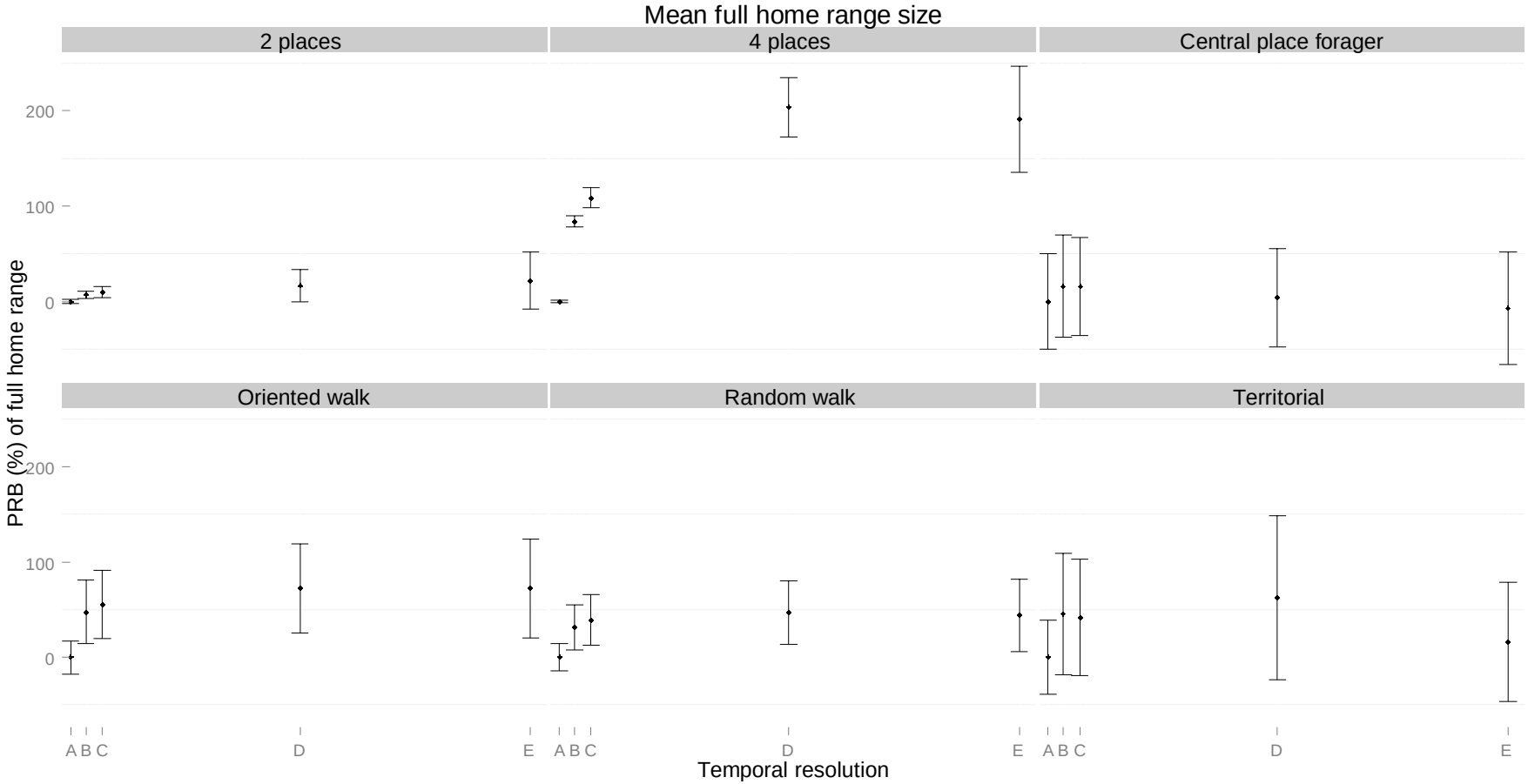


Figure 5.1. Percentage of relative bias (PRB) of mean full home range size (±1 SD) of all individuals (n = 50) for six different types of movement patterns and five different levels of temporal resolutions. **A**: Hourly, every 4 fixes; **B**: 12-hourly, every 48 fixes; **C**: daily, every 96 fixes; **D**: weekly, every 672 fixes; **E**: bi-weekly, every 1344 fixes.

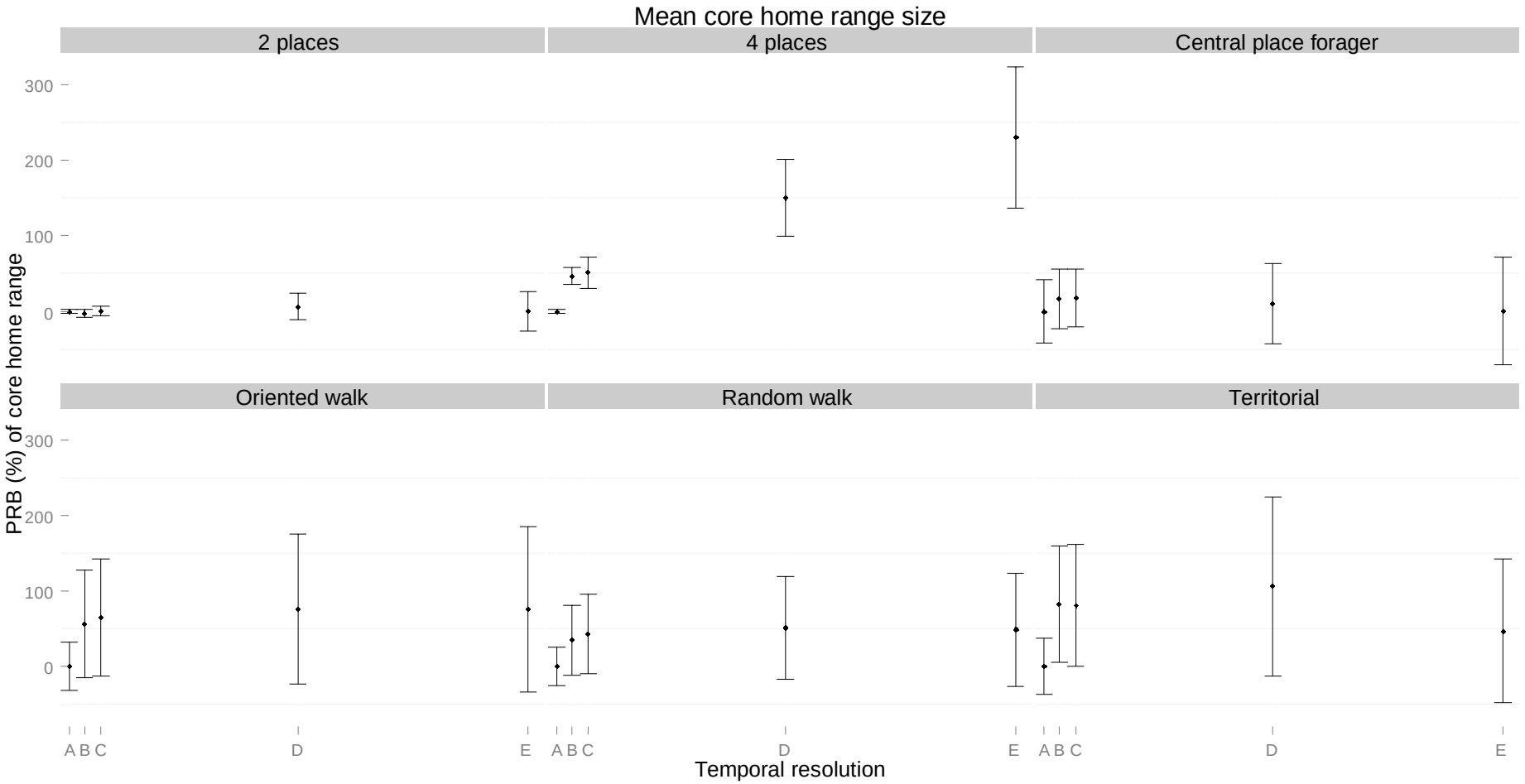


Figure 5.2. Percentage of relative bias (PRB) of mean core home range size (±1 SD) of all individuals (n = 50) for six different types of movement patterns and five different levels of temporal resolutions. **A**: Hourly, every 4 fixes; **B**: 12-hourly, every 48 fixes; **C**: daily, every 96 fixes; **D**: weekly, every 672 fixes; **E**: bi-weekly, every 1344 fixes.

Table 5.2. Mean percentage of relative bias (PRB) (± 1SD) for the six models of different movement patterns. Biased full and core home range size estimations over the true home range size are calculated for five different temporal resolutions (hourly, 12-hourly, daily, weekly and bi-weekly). **Slope:** The relationship of PRB as a function of temporal resolution was derived from a linear model.

Model	Hourly (± 1SD)		12-hourly (± 1SD)		Daily (± 1SD)		Weekly (± 1SD)		Bi weekly (± 1SD)		Slope (± 1SE)	
	Full	Core	Full	Core	Full	Core	Full	Core	Full	Core	Full	Core
2 places	0 (± 1.82)	0 (± 2.44)	7.06 (± 3.89)	-2.9 (± 5.11)	9.84 (± 6.05)	0.91 (± 6.57)	16.69 (± 16.78)	6.17 (± 17.42)	21.79 (± 21.77)	0.15 (± 26.28)	0.03 (± 0.22 x 10^{-3})	0.02 (± 0.30 x 10^{-3})
4 places	0 (± 1.18)	0 (± 2.45)	84.05 (± 5.96)	46.58 (± 11.24)	108.8 (± 10.84)	51.23 (± 20.43)	203.51 (± 31.26)	149.95 (± 50.87)	190.92 (± 55.48)	229 (± 93.41)	0.14 (± 0.50 x 10^{-3})	0.17 (± 1.32 x 10^{-3})
Random	0 (± 14.37)	0 (± 25.55)	31.56 (± 23.76)	34.99 (± 46.43)	39.28 (± 26.26)	43.16 (± 52.38)	47.14 (± 33.28)	51.54 (± 68)	44.11 (± 37.86)	48.58 (± 74.89)	0.03 (± 0.24 x 10^{-3})	0.03 (± 0.26 x 10^{-3}))
Oriented	0 (± 17.37)	0 (± 31.61)	47.74 (± 33.19)	56.89 (± 71.13)	55.25 (± 35.87)	64.58 (± 77.39)	72.34 (± 46.49)	76.09 (± 99.24)	72.4 (± 51.79)	75.31 (± 109.55)	0.06 (± 0.21 x 10^{-3})	0.05 (± 0.32 x 10^{-3})

Territorial	0 (± 38.78)	0 (± 36.91)	45.45 (± 63.74)	82.65 (± 76.69)	41.79 (± 61.16)	81.24 (± 80.74)	62.56 (± 86.15)	106.02 (± 118.31)	35.51 (± 62.59)	58.87 (± 95.37)	0.05 (± 0.25 x 10^{-3})	0.05 (± 0.40 x 10^{-3})
Central place forager	0 (± 49.86)	0 (± 42.02)	15.82 (± 53.61)	16.23 (± 39.1)	15.86 (± 51.40)	17.28 (± 38.12)	3.98 (± 51.41)	10.49 (± 52.93)	-6.96 (± 58.97)	0.6 (± 70.77)	-0.03 (± 0.66 x 10^{-3})	-0.02 (± 0.64 x 10^{-3})

Discussion

Home range size, as a proxy for animal space use, is a key parameter for many life history processes including reproduction and survival, and ultimately affects the dynamics of a population (Gaines and McClenaghan Jr 1980; Fisher and Lara 1999; Getz, Oli et al. 2005; Booth, Montgomery et al. 2009). In this study, we investigated how kernel density estimations (KDEs) of home ranges generated by six different movement patterns were affected by temporal resolution. Our results generally show that the mean and variation of percent relative bias (PRB) of home range size estimation increases as temporal resolution decreases. The high levels of PRB highlight the limitation of KDEs based on low temporal resolution for both individual and population (mean) home range size estimation.

Over- vs. underestimation

Our findings suggest that temporal resolution should be increased to the highest possible level – ideally real-time resolution – to minimise bias in home range estimation. Often, however, a trade-off between temporal resolution and number of individuals obliges researchers to prioritise one over the other. Our results stress that such decisions should be based on the species specific type of movement, as PRB at lower temporal resolution varies between the different spatial structures of home ranges.

Mean home range size was overestimated for five out of six movement patterns and only underestimated in the central place forager model (CPF) that used bi-weekly location fixes. Home range size can be overestimated when, at lower temporal resolutions, location fixes are included into KDE that would be

discarded as outermost 5% in a 95% KDE at real-time resolution. As hypothesized, overestimation is strongest for spatially more complex movement patterns, i.e. those with multiple activity centres. This is because over-estimation can occur at each activity centre, adding up to a higher total PRB as compared to spatially less complex movement patterns. In contrast to all other simulations, CPF full home ranges are underestimated at low temporal resolution. This could be due to a concentration of location fixes at the home range centre, the nest, and relatively few location fixes in the surrounding (foraging) area. At low temporal resolution, the likelihood of collecting a fix at the nest is much higher than in the surrounding environment, thereby leading to an underestimation of true home range size.

Information regarding over- or underestimation of mean home range size is important in assessing the validity of space use analyses. It is, however, incomplete without including the level of variation in home range size estimation. Due to high levels of variation it is possible, for example, that for a movement pattern with an overestimated mean home range size, an individual home range (at the same temporal resolution) is underestimated compared to the true mean home range size. Taking into account both, changes in mean PRB and amount of variation, some of our simulations, namely CPF and territorial, support the findings of Borger, Franconi et al. (2006). They argue that due to a consistency of variation across different level of temporal resolution, preferences should be given to high number of individuals in order to capture individual variation of home range size. Our results highlight the high levels of variation in home range size estimation even at high temporal resolution, thus favouring high numbers of individuals over high temporal resolution. Two other

simulations, random walk and oriented walk, illustrate cases where both the number of individuals and the temporal resolution could be prioritised, depending on resources. If high temporal resolution (i.e hourly location fixes) can be achieved, preferences should be given to temporal resolution over number of individuals, as mean and variation in PRB are considerably lower. In contrast, if the monitoring technology used only permits lower temporal resolution, number of individuals should be prioritised over temporal resolution, as variation of full home range size estimation is generally high across all lower temporal resolution levels. Lastly, for the spatially more complex simulations 2 places and 4 places priority should always be given to increase temporal resolution as it will decrease mean and variation of PRB and bring estimates closer to the true home range size.

Core vs. full home range

As full home range size estimation at low temporal resolution is often subject to severe bias, Seaman et al (1999) suggested focusing on mean core home range size for comparison between different groups. According to their simulations, core ranges were less biased than estimations of full home ranges, adding that core home ranges also contain the biologically more relevant information. Our results, in contrast, show that in most simulations the mean PRB of core home ranges is higher than the mean for the full home range PRB. Only in simulations with two or more spatially distinct activity centres (i.e. 2 places and 4 places simulation), mean full home range PRB is higher than mean core home range PRB. Core home ranges represent an individual's activity centre (Vander Wal and Rodgers 2012) where an increase by a small number of additional fixes will result in no or little increase in core home range

size. In simulations with multiple, yet spatially clear distinguishable activity centres, core home ranges have relatively little scope to be overestimated, as the main activity is restricted to a small, clearly defined area (i.e the activity centre). In other simulations, namely random walk, oriented walk and territorial, mean core home range PRB increases more than mean full home range PRB. This is caused by spatially more even distributed location fixes that can be included into core KDE at lower temporal resolution. Similarly, variation of PRB is higher for core home ranges than for full home ranges, due to higher number of possible combinations of location fixes at low temporal resolution. Only for the CPF simulation, variation of PRB at different temporal resolution levels remains similar between core and full home range, highlighting the importance of the central place for home range estimation in the CPF simulation.

Our results suggest that focussing on the core home range area in comparative studies is only advisable if the movement pattern of the focal species is known. In case of complex movement patterns with multiple centres of activities, focussing on the core home range has the potential to reduce PRB. In most of our simulations, however, the opposite was found; here a space use analysis of core home ranges would not only lose out on potential biologically relevant data of the periphery, but could also result in an even more biased estimation of home range size.

Practical application

Caution must be taken when using in-silico data to make inferences on in-situ conditions. We believe, however, that it is possible to extrapolate some of our findings on in-situ monitoring. For future space use analysis, especially for

unknown types of movement pattern, we recommend conducting a pre-analysis of home range estimates at high temporal resolution. If subsampling at lower temporal resolution increases the mean home range size estimations significantly, it is likely that the study species' home range is spatially complex with different centres of activity. In that case, we recommend maintaining a high temporal resolution, even at the costs of sampling fewer individuals, to avoid severe bias in home range size estimation. If the mean PRB does not increase significantly, we recommend increasing the number of individuals to capture more individual variation.

For small species where no high temporal resolution device, i.e satellite or radio based devices, are available or still uneconomical, researchers rely on stationary trapping to collect space use data and estimate home ranges. Trapping is rarely conducted more frequently than at weekly rates due to logistical constraints and to avoid a negative impact on the study species (Korn 1987). We show that data from such a low temporal resolution is likely to be located, at best, within a large range of variation and, in case of a spatially more complex home range structure, could overestimate home range size by up to 200%. In recent years, several projects aimed to improve the temporal resolution of small species monitoring (Wikelski, Kays et al. 2007; Wikelski, Moxley et al. 2010; Kays, Tilak et al. 2011). Our results highlight the necessity of such new technologies and we strongly recommend adapting technologies that increase temporal resolutions and decrease biased home range size estimations.

Chapter 6

Discussion

For biologists who work on rodent ecology these are exciting times. Over the last century, extensive research on this diverse taxon allowed us to substantially improve our understanding of its biology. Now with this concrete foundation, this thesis contributes novel findings on space use patterns and population dynamics of two common European rodents, *A. sylvaticus* and *M. glareolus*. In Chapters two and three, I show that predation risk seems to be the overarching driver of space use, across seasons and species. Perceived predation risk might also be a driver of inter-specific competition (Chapter 2). My research shows that space use drivers work on different spatial scales, affecting different parts of the home range (Chapter 2). Additionally, chapter 4 provides initial evidence for density dependent difference in body weight and how life history parameters affect population dynamics in wood mice.

Parallel to uncovering new aspects of rodent biology come remarkable advancements in methods and technologies. Increases in computational power, newly developed software, devices and models allow us to address ecological questions in a way that would have been impossible a few years ago. For many taxa, studies that combine in-silico with in-situ data are increasingly used to improve our understanding on individual space use patterns and population dynamics(DeAngelis and Gross 1992; Grimm, Revilla et al. 2005; Ellner and Rees 2006; Rees and Ellner 2009; Coulson 2012). The unique opportunity of combining in-situ and in-silico approaches has yet to be fully developed for

small mammal research. In chapters three, four and five, I demonstrate the use of two models and show how combining in-situ and in-silico data allows us to address unanswered questions and to test novel hypotheses. Advances in the field are not restricted to new methods, but also include new technologies that improve the quality and quantity of data collection. Fast developments of new remote tracking devices have improved our understanding of space use patterns in many taxa, while still excluding the majority of small mammals, birds and ectotherm species due to tag size and weight (Kays, Crofoot et al. 2015). My field data were collected by a combination of traditional data acquisition during trapping sessions and a novel monitoring technology using mobile RFID-tag data loggers that allow data collection without interfering with rodent natural behaviour.

In this chapter, I evaluate the main findings of my thesis, the limitations of my studies and the next steps that could be undertaken.

Predation risk, food availability and population density - three drivers of space use and population dynamics

In this thesis, I showed that predation risk is an important driver of space use patterns in *A. sylvaticus* and *M. glareolus*. Several studies have investigated predation risk, but focussed almost exclusively on a microhabitat scale or on behavioural responses to actual or perceived predation risks (Kotler 1984; Kotler, Brown et al. 1991; Korpimaki, Koivunen et al. 1996; Mandelik, Jones et al. 2003; Trebatická, Sundell et al. 2008). My study shows that the impact of predation risk extends beyond the short term scale of microhabitat selection and behavioural response to predators. More precisely, I found that the effect of

habitat features that are thought to reduce predation risk is key in explaining deviance in core and full home range size variation. While this adds new insights on space use drivers of our rodent study species, predation risk is known to be an important driver of home range size in other taxa, such as larger mammalian herbivores (Tufto, Andersen et al. 1996; Anderson, Forester et al. 2005). Despite the relevance of this variable, I could not quantify the actual predator density nor identify individual predator species, as cameras traps failed to function reliably and produce appropriate data. Instead predation risk was approximated as the proportion of dense shrub cover of *Rhododendron* and *Sasa*. The dense vegetation is thought to provide a physical and visual barrier to one of the main aerial predators, the tawny owl (Southern and Lowe 1968). Aerial hunters are not the only predators, as several ground hunting carnivores (e.g. fox, stoat and weasel) also prey on rodents. Habitat features that reduce predation risk from aerial hunters are known to be different from those reducing the success rate of ground hunting predators (Haapakoski, Sundell et al. 2015). However, it has also been shown that in the presence of both types of predators, microhabitat preferences are driven by avoidance of aerial hunters (Korpimaki, Koivunen et al. 1996). The assumption that dense cover reduces predation rates, was supported by data from our study site showing that areas of dense cover had higher densities and trapability of rodents (Malo, Godsall et al. 2013), and via similar findings in other studies on predation risk for small mammals (Kotler, Brown et al. 1991; Longland and Price 1991; Bowers and Dooley Jr 1993; Tallmon and Mills 1994). Many questions regarding the role of predation risk as a driver of space use remain unsolved and should be subject to further research. For example, do different predator species affect home

range sizes differently and does the importance of avoiding predators vary between seasons and sex? Presumably a holistic approach combining research on microhabitat selection, behavioural responses and drivers of home range size is required to address further questions on the effect of predation risk on space use.

Although predation risk appears to be an important space use driver, food availability is also a critical factor. In this thesis, I showed that variation in food availability drives home range size. Research has already started to address the effect of food availability on microhabitat selection and on survival and reproduction, and consequently on population dynamics (Mares, Watson et al. 1976; Cole and Batzli 1978; Hansen and Batzli 1978; Desy and Batzli 1989; Schradin, Schmohl et al. 2010; Emsens, Suselbeek et al. 2013; Schoepf, Schmohl et al. 2015). My research, however, higlights the importance of food as a driver of space use in rodentsat the home range size level, which has already been shown for larger species (Tufto, Andersen et al. 1996; Loveridge, Valeix et al. 2009; Van Beest, Rivrud et al. 2011). I also showed that home range size is adjusted every year or season to adapt to the quality and quantity of food available. For the purpose of this thesis, I tested the effect of food availability on home range size during the non-breeding season, when reproductive behaviour does not affect space use patterns. Future studies should attempt to assess the importance of food availability during the breeding season. How do individuals combine territorial needs with food requirements? How do rodents adjust to fluctuations in their summer diet, including invertebrates, which are more mobile and – most likely – less regular in their availability, compared to tree seeds? This again will require a holistic approach, merging microhabitat preferences,

food item selection and home range size variation of the focal rodent species with research on invertebrate availability and invertebrate movement dynamics.

Food availability and predation risk are both factors that can be approximated by the presence (or absence) of habitat features. Food is often directly provided by habitat features and rodents seem to choose ‘safe habitats’ by perceiving the potential presence of predators rather than reacting on the actual predators’ appearance. The effect of population density, in contrast, is directly driven by the quantity of conspecifics and competitors from other species. Many studies have investigated the effect of intra- and inter-specific density effects on space use patterns in rodents (Boonstra 1989; Gilbert and Krebs 1991; Eccard and Ylönen 2002; Eccard and Ylönen 2007; Eccard, Fey et al. 2011). I aimed to extend the existing literature in rodents by investigating whether bank vole home range size is not only negatively affected by high wood mouse densities, but that competition, that is otherwise reduced by partial niche separation, can increase if two species use similar habitat features to reduce predation risk. The apparent dominance of wood mice over bank voles also adds knowledge to ongoing research about the hierarchy in the forest community of European rodents (Flowerdew, Gurnell et al. 1985; Kleeberger 1985; Eccard and Ylönen 2002; Eccard and Ylönen 2007; Eccard, Fey et al. 2011; Eccard, Jokinen et al. 2011). Further research should aim to better understand what species outcompetes the other. As there is some evidence that the dominance of inter-specific competition might also be density driven (Eccard and Ylönen 2002), more detailed research on dynamic of population size and species interactions is needed.

Ecologists have long acknowledged that space use patterns are affected by multifactorial and interacting drivers. My findings contribute to our knowledge on space use drivers for two common European rodents but also highlight more general the need of assessing the importance of space use drivers for different parts of a species home range or territory. While research on a single space use driver or on one part of a home range can still provide valuable insights and can improve our understanding of a species' ecology, full understanding of space use patterns can only be achieved by assessing all known factors, their interaction and their varying impact on different parts of the space use. The challenge of future research on space use patterns, therefore, will be to acquire high quality data of space use behaviour and of all potential space use drivers.

In chapter 4, I demonstrate that intra-specific density can drive population dynamics by affecting reproduction and causing metabolic changes. My findings provide the first evidence in this taxon for seasonal and density-driven variation in the life history parameters, generation time and lifetime reproductive success. In addition, I found a positive density-dependence of sub-adult and juvenile body growth, so far unknown for non-microtine rodents. Taken together, these findings support the dynamic energy allocation hypothesis (Oli 1999) that aims to explain the Chitty effect as a result of density dependence and not as its driver (Burthe, Lambin et al. 2010). Density driven dynamics in wood mice highlight that the Chitty effect can also be found in taxa with population dynamics different to microtine rodents. Due to its novelty and the small effect size of my findings, this study should be replicated, ideally in different study

sites. Further research on density driven dynamics in other rodent species is now required to assess the generality of this pattern.

Caution here should be given to the methodology. In this thesis, I used body weight data collected during trapping to estimate growth rates. Additionally, I used pedigree data from Godsall (2015) to include heritability in my analysis. The quantity of data is exceptional for current in-situ studies on rodents. However, I still lacked any information on individual litter size and growth rate up to the juvenile age. Only at this age individuals are heavy enough to set off the trigger of a trap. Therefore, I used approximations for growth rate and litter size and the biological realism of my results supports the acceptability of their quality. Future studies should continue to analyse the two variables as a function of extrinsic and intrinsic parameters, including habitat data, individual-level data and population level data, that would allow to substantially improve our current understanding of rodent space use patterns and population dynamics. For example, my results showed that in juvenile and sub-adult wood mice growth rates are density dependent but I was unable to define more specifically the developmental stage when growth rates differed due to population density. Such data could be collected if nests could be individually monitored to record litter size and track growth rates of infants. In our study site, artificial burrows were tested but did not work reliably and were not accepted by rodents.

Core vs. periphery - a useful approach?

The idea of dividing the home range in core and periphery areas is as old as the home range concept itself (Burt 1943). However, in contrast to space use

research on mega fauna, it has received relatively little attention in small mammal research (but see for example (Godsall, Coulson et al. 2014)), mostly due to difficulties in the data collection. In this thesis, however, I showed that in bank vole the core and periphery home ranges are shaped by different space use drivers. Knowing that factors affect the inner and outer part of a home range differently, or might even be irrelevant for one part, has severe implications for our studies on rodent space use. For example, in chapter 2 I show that sex-based differences in spacing behaviour thought to be an important driver of home range size during breeding season are actually restricted to the periphery of a home range. The core home range, in contrast, does not show any sex-based size differences. Future research should assess if space use drivers, formerly attributed to the entire home range, are in fact restricted to parts of a home range.

I also highlighted that it can be advantageous to restrict space use analysis to the core home range. In chapter 5, I showed that for spatially complex home ranges, i.e. with multiple and spatially distinct cores, core home range size estimations are less biased than estimates of the full home range. For other space use patterns I found the opposite effect. Here, using only core home range estimations can lead to a greater bias in home range size estimation than using full home range estimates. Whether to focus on the core home range alone should, therefore, depend on species specific movement patterns.

In-situ and in-silico – together to a brighter future?

In this thesis, I used in-situ and in-silico methods to answer questions on the ecology of rodents. More specifically, I used two models, the Individual Based

Model (IBM) and the Integral Projection Model (IPM), to analyse space use patterns and population dynamics. The former has already been successfully used in research on rodent space use patterns (e.g. (Liu, Sibly et al. 2013; Tamburino and Bravo 2013)) but until now research has not used an IPM to analyse an r-selected species. By using an IBM, I demonstrated how modelling simple behavioural rules based on two drivers, predation risk and food availability, generate similar space use patterns to those observed in the field. By constructing an IPM, I was able to analyse the population dynamic of a wood mice population and to calculate life history parameters that currently cannot be obtained from in-situ studies. IPMs are increasingly used to analyse the relationship between a phenotypic trait (e.g. body mass) and the dynamic of a population (Coulson, Catchpole et al. 2001; Ellner and Rees 2006; Ozgul, Childs et al. 2010; Coulson 2012). They allow for an in-depth analysis of population dynamics, especially for parts of a population that are challenging to observe in the field. In contrast to other population simulations (e.g. matrix population models (Caswell 2001)) IPMs have the advantage of using continuous phenotypic traits that can examine continuous trait related changes in growth, reproduction and survival in a population. An IPM, therefore, can be used to follow a continuous trait distribution and the size and composition of a population over time. This data then allows examination of how a population is affected by the phenotypic-population dynamic interaction. As IPM functions are parameterised with fixed estimates, they require reliable and high quality data. In my analysis, I was only able to use a small number of individuals for the inheritance function (one part of the reproduction function) due to our inability to catch most offspring early enough to examine the juvenile growth rate. Other

studies will hopefully overcome this limitation of my study and provide larger sample sizes that are more representative of the population. However, using both models allowed me to address questions, for which my in-situ data alone would not have been accurate enough, and highlights the benefits of combining in-situ and in-silico approaches. As a result from my work within this thesis, further research should use in-silico methods to address more specific questions on space use patterns and population dynamics in rodents. One future direction is to use IBM to assess long term changes in food availability, caused by global change, on space use patterns on rodents. Alternatively, using an IPM could help to predict how long term changes in weather patterns would affect population size and composition of rodents.

The more the merrier - do we need to improve our data collection?

Temporal resolution of location fixes affects home range size estimation. In chapters 3 and 5, I showed that smaller sample sizes of location fixes, even if sampled at regular intervals, increased variation of home range size estimation and bias of mean home range size estimation. For simulations of different space use patterns and movement types, I showed that at low temporal resolution most space use patterns overestimate home range size and that the amount of overestimation increases with spatial complexity of the simulation. These findings could have implications for many space use analysis that rely on low temporal resolution, especially when comparing individuals or populations. Home range size can be used to provide advice on conservation strategies, to prevent the spread of disease or to succeed in pest management. If home range sizes are overestimated, the effect of a conservation strategy or a pest management based on a species' spatial distribution could be redundant.

However, having a biased home range estimate might be advantageous compared to not having a home range estimate at all, providing that all possible steps of avoiding mis-estimations have been taken. Unfortunately, some studies on animal space use continue to neglect the potential effect of sample size on their space use estimates. Assessing this effect can provide valuable insights what temporal resolution is required to reduce biased estimation. In lions (*Panthera leo*), for example, home range estimates based on hourly location fixes closely correlated with estimates based on one daily location fixes, reducing the amount of location fixes required for a home range estimates (Loveridge, Valeix et al. 2009). In this thesis, I reduced the risk of biased estimates by including sample size as a weighting factor. Additionally, the combined approaches of trapping data and the location fixes obtained from the mobile recording stations increased absolute sample size of location fixes and decreased the time period between two location fixes. To my knowledge, the temporal resolution and the sample size obtained from our study are unmatched by other field studies on rodents. This allowed me to compare seasonal space use patterns as well as differences between core and periphery home ranges.

Despite this improvement, additional technological developments are critical to improve our space use analysis. Many questions on space use cannot be addressed with current technology. For example, only near real-time temporal resolution will allow us to quantify the effect of inter- and intra-specific density on space use patterns or how spacing behaviour on the microhabitat scale is related to home range size. Especially for small mammal studies, developing devices that provide real time resolution, should be of highest priority. While this would have been a seemingly overambitious goal a few years ago, tracking and

monitoring technology is developing quickly, largely driven by advancements in the industrial sector. Soon there might be off-the shelf devices offering ultra-light, high resolution tags catapulting small mammal research to unprecedented spheres. These are indeed exciting times to study small mammals.

References

Aars, J. and R. A. Ims (2002). "Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles." Ecology **83**(12): 3449-3456.

Alatalo, R. V., D. Eriksson, L. Gustafsson and K. Larsson (1987). "Exploitation competition influences the use of foraging sites by tits: experimental evidence." Ecology **68**(2): 284-290.

Alibhai, S. and J. Gipps (1985). The population dynamics of bank voles. Symposia of the Zoological Society of London.

Anderson, D. P., J. D. Forester, M. G. Turner, J. L. Frair, E. H. Merrill, D. Fortin, J. S. Mao and M. S. Boyce (2005). "Factors influencing female home range sizes in elk (Cervus elaphus) in North American landscapes." Landscape Ecology **20**(3): 257-271.

Andrzejewski, R. and M. Mazurkiewicz (1976). "Abundance of food supply and size of the bank vole's home range." Acta Theriologica **21**(12): 237-253.

Andrzejewski, R. and J. Olszewski (1963). "Social behaviour and interspecific relations in *Apodemus flavicollis* (Melchior, 1834) and *Clethrionomys glareolus* (Schreber, 1780)." Acta Theriologica **7**(10): 155-168.

Athens, J. S. (2009). "*Rattus exulans* and the catastrophic disappearance of Hawai'i's native lowland forest." Biological Invasions **11**(7): 1489-1501.

Attuquayefio, D., M. Gorman and R. Wolton (1986). "Home range sizes in the wood mouse *Apodemus sylvaticus*: habitat, sex and seasonal differences." Journal of Zoology **210**(1): 45-53.

Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift and P. L. Sims (1996). "Mechanisms that result in large herbivore grazing distribution patterns." Journal of Range Management **49**(5): 386-400.

Barg, J. J., J. Jones and R. J. Robertson (2005). "Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas." Journal of Animal Ecology **74**(1): 139-149.

Barnett, A. and J. Dutton (1995). "Small Mammals." Expedition Field Techniques series, Expedition Advisory Centre, Royal Geographical Society. London.

Bartmann, S. and G. Gerlach (2001). "Multiple paternity and similar variance in reproductive success of male and female wood mice (*Apodemus sylvaticus*) housed in an enclosure." Ethology **107**(10): 889-899.

Bates, D., M. Mächler, B. Bolker and S. Walker (2015). "Fitting linear mixed-effects models using lme4." Journal of Statistical Software **37**(1): 1548-7660.

Batzli, G. O. and F. A. Pitelka (1970). "Influence of meadow mouse populations on California grassland." Ecology **51**(6): 1027-1039.

Bean, W. T., L. R. Prugh, R. Stafford, H. S. Butterfield, M. Westphal and J. S. Brashares (2014). "Species distribution models of an endangered rodent offer conflicting measures of habitat quality at multiple scales." Journal of Applied Ecology **51**(4): 1116-1125.

Benhamou, S. (1991). "An analysis of movements of the wood mouse (*Apodemus sylvaticus*) in its home range." Behavioural Processes **22**(3): 235-250.

Berger, K. M. and E. M. Gese (2007). "Does interference competition with wolves limit the distribution and abundance of coyotes?" Journal of Animal Ecology **76**(6): 1075-1085.

Bergstedt, B. (1965). "Distribution, reproduction, growth and dynamics of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Linne) in Southern Sweden." Oikos **16**(1): 132-160.

Bjørnstad, O. N. (2001). "Chitty cycles–at last!" Trends in Ecology & Evolution **16**(2): 72.

Blackburn, T. M., P. Cassey, R. P. Duncan, K. L. Evans and K. J. Gaston (2004). "Avian extinction and mammalian introductions on oceanic islands." Science **305**(5692): 1955-1958.

Blair, W. F. (1948). "Population density, life span, and mortality rates of small mammals in the blue-grass meadow and blue-grass field associations of Southern Michigan." American Midland Naturalist **40**(2): 395-419.

Blanckenhorn, W. U. (2000). "The evolution of body size: what keeps organisms small?" Quarterly Review of Biology **75**(4): 385-407.

Blundell, G. M., J. A. Maier and E. M. Debevec (2001). "Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates." Ecological Monographs **71**(3): 469-489.

Boon, A. K., D. Réale and S. Boutin (2008). "Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*." Oikos **117**(9): 1321-1328.

Boonstra, R. (1989). "Life history variation in maturation in fluctuating meadow vole populations (*Microtus pennsylvanicus*)." Oikos **54**(3): 265-274.

Boonstra, R. and P. T. Boag (1987). "A test of the Chitty hypothesis: inheritance of life-history traits in meadow voles *Microtus pennsylvanicus*." Evolution **41**(5): 929-947.

Boonstra, R. and M. Hochachka (1997). "Maternal effects and additive genetic inheritance in the collared lemming *Dicrostonyx groenlandicus*." Evolutionary Ecology **11**(2): 169-182.

Boonstra, R., C. J. Krebs and N. C. Stenseth (1998). "Population cycles in small mammals: the problem of explaining the low phase." Ecology **79**(5): 1479-1488.

Booth, W., W. Montgomery and P. Prodöhl (2009). "Spatial genetic structuring in a vagile species, the European wood mouse." Journal of Zoology **279**(3): 219-228.

Borger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari and T. Coulson (2006). "Effects of sampling regime on the mean and variance of home range size estimates." Journal of Animal Ecology **75**(6): 1393-1405.

Börger, L., N. Franconi, F. Ferretti, F. Meschi, G. De Michele, A. Gantz and T. Coulson (2006). "An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size." The American Naturalist **168**(4): 471-485.

Bowers, M. A. (1995). "Use of space and habitats by the Eastern chipmunk, *Tamias striatus*." Journal of Mammalogy **76**(1): 12-21.

Bowers, M. A. and J. H. Brown (1992). "Structure in a desert rodent community: use of space around *Dipodomys spectabilis* mounds." Oecologia **92**(2): 242-249.

Bowers, M. A. and J. L. Dooley Jr (1993). "Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects." Oecologia **94**(2): 247-254.

Bowler, D. E. and T. G. Benton (2005). "Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics." Biological Reviews **80**(2): 205-225.

Bowman, A. W. and A. Azzalini (1997). Applied smoothing techniques for data analysis: the kernel approach with S-Plus illustrations: the kernel approach with S-Plus illustrations. Oxford, Oxford University Press.

Brackin, M. F. (1978). "The relation of rank to physiological state in *Cnemidophorus sexlineatus* dominance hierarchies." Herpetologica **34**(2): 185-191.

Briner, T., W. Nentwig and J.-P. Airoldi (2005). "Habitat quality of wildflower strips for common voles (*Microtus arvalis*) and its relevance for agriculture." Agriculture, Ecosystems & Environment **105**(1): 173-179.

Bronson, F. and G. Perrigo (1987). "Seasonal regulation of reproduction in muroid rodents." American Zoologist **27**(3): 929-940.
Bronson, F. and S. Pryor (1983). "Ambient temperature and reproductive success in rodents living at different latitudes." Biology of Reproduction **29**(1): 72-80.
Brown, C., F. Burgess and V. A. Braithwaite (2007). "Heritable and experiential effects on boldness in a tropical poeciliid." Behavioral Ecology and Sociobiology **62**(2): 237-243.
Brown, J. L. and G. H. Orians (1970). "Spacing patterns in mobile animals." Annual Review of Ecology and Systematics **1**: 239-262.
Brown, J. S. (1988). "Patch use as an indicator of habitat preference, predation risk, and competition." Behavioral Ecology and Sociobiology **22**(1): 37-47.
Brown, J. S., J. W. Laundré and M. Gurung (1999). "The ecology of fear: optimal foraging, game theory, and trophic interactions." Journal of Mammalogy **80**(2): 385-399.
Buesching, C. D., C. Newman, R. Twell and D. W. Macdonald (2008). "Reasons for arboreality in wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*)." Mammalian Biology-Zeitschrift für Säugetierkunde **73**(4): 318-324.
Burt, W. H. (1943). "Territoriality and home range concepts as applied to mammals." Journal of Mammalogy **24**(3): 346-352.
Burthe, S. J., X. Lambin, S. Telfer, A. Douglas, P. Beldomenico, A. Smith and M. Begon (2010). "Individual growth rates in natural field vole, *Microtus agrestis*, populations exhibiting cyclic population dynamics." Oecologia **162**(3): 653-661.
Butet, A. and Y. Delettre (2011). "Diet differentiation between European arvicoline and murine rodents." Acta Theriologica **56**(4): 297-304.
Calhoun, J. B. and J. U. Casby (1958). Calculation of home range and density of small mammals. United States of America, US Department of Health, Education, and Welfare, Public Health Service.
Canova, L. (1993). "Resource partitioning between the bank vole *Clethrionomys glareolus* and the wood mouse *Apodemus sylvaticus* in woodland habitats." Bollettino Di Zoologia **60**(2): 193-198.
Capizzi, D. (2014). "Rating the rat: global patterns and research priorities in impacts and management of rodent pests." Mammal Review **44**(2): 148.
Casaer, J., M. Hermy, P. Coppin and R. Verhagen (1999). "Analysing space use patterns by Thiessen polygon and triangulated irregular network interpolation: a non-parametric method for processing telemetric animal fixes." International Journal of Geographical Information Science **13**(5): 499-511.
Caswell, H. (2001). Matrix population models, Wiley Online Library.
Catchpole, E. A., B. J. Morgan, T. Coulson, S. N. Freeman and S. D. Albon (2000). "Factors influencing Soay sheep survival." Journal of the Royal Statistical Society: Series C (Applied Statistics) **49**(4): 453-472.
Caughley, J., M. Bomford, B. Parker, R. Sinclair, J. Griffiths and D. Kelly (1998). Managing vertebrate pests: Rodents. Australia, Bureau of Resource Sciences Canberra
CDC. (2011). "Diseases from rodents." Retrieved 03/10/2015, 2015, from http://www.cdc.gov/rodents/diseases/index.html.
Cederlund, G. and H. Sand (1994). "Home-range size in relation to age and sex in moose." Journal of Mammalogy **75**(4): 1005-1012.
Charnov, E. L. (1976). "Optimal foraging, the marginal value theorem." Theoretical population biology **9**(2): 129-136.
Charnov, E. L. (1976). "Optimal foraging: attack strategy of a mantid." American Naturalist **110**(971): 141-151.
Chen, D. and M. W. Wang (2005). "Development and application of rodent models for type 2 diabetes." Diabetes, Obesity and metabolism **7**(4): 307-317.

Childs, D. Z., M. Rees, K. E. Rose, P. J. Grubb and S. P. Ellner (2004). "Evolution of size–dependent flowering in a variable environment: construction and analysis of a stochastic integral projection model." Proceedings of the Royal Society of London B: Biological Sciences **271**(1537): 425-434.

Chilvers, B. L. (2008). "Foraging site fidelity of lactating New Zealand sea lions." Journal of Zoology **276**(1): 28-36.

Chitty, D. (1967). "The natural selection of self-regulatory behaviour in animal populations." Proceedings Ecological Society of Australia **2**(5): 1-78.

Choquet, R., L. Rouan and R. Pradel (2009). Program E-SURGE: a software application for fitting multievent models. Modeling demographic processes in marked populations. United States of America, Springer**:** 845-865.

Christian, J. J. (1980). "Regulation of annual rhythms of reproduction in temperate small rodents." Testicular Development, Structure, and Function: 367-380.

Clarke, J. (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. and B. C. Sheldon (2010). "Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology." Trends in Ecology & Evolution **25**(10): 562-573.

Clutton-Brock, T. H. (1989). "Review lecture: mammalian mating systems." Proceedings of the Royal Society of London B: Biological Sciences **236**(1285): 339-372.

Clutton-Brock, T. H. and A. C. Vincent (1991). "Sexual selection and the potential reproductive rates of males and females." Nature **351**(6321): 58-60.

Cole, F. R. and G. O. Batzli (1978). "Influence of supplemental feeding on a vole population." Journal of Mammalogy **59**(4): 809-819.

Connell, J. H. (1961). "The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*." Ecology **42**(4): 710-723.

Cook, S. F. (1959). "The effects of fire on a population of small rodents." Ecology **40**(1): 102-108.

Corp, N., M. Gorman and J. Speakman (1999). "Daily energy expenditure of free-living male wood mice in different habitats and seasons." Functional Ecology **13**(5): 585-593.

Corriale, M. J., E. Muschetto and E. A. Herrera (2013). "Influence of group sizes and food resources in home-range sizes of capybaras from Argentina." Journal of Mammalogy **94**(1): 19-28.

Cottingham, K., B. Brown and J. Lennon (2001). "Biodiversity may regulate the temporal variability of ecological systems." Ecology Letters **4**(1): 72-85.

Coulson, T. (2012). "Integral projections models, their construction and use in posing hypotheses in ecology." Oikos **121**(9): 1337-1350.

Coulson, T., S. Albon, J. Pilkington and T. Clutton-Brock (1999). "Small-scale spatial dynamics in a fluctuating ungulate population." Journal of Animal Ecology **68**(4): 658-671.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley and B. T. Grenfell (2001). "Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep." Science **292**(5521): 1528-1531.

Coulson, T. and S. Tuljapurkar (2008). "The dynamics of a quantitative trait in an age-structured population living in a variable environment." The American Naturalist **172**(5): 599.

Cousin, X., T. Daouk, S. Péan, L. Lyphout, M.-E. Schwartz and M.-L. Bégout (2012). "Electronic individual identification of zebrafish using radio frequency identification (RFID) microtags." The Journal of Experimental Biology **215**(16): 2729-2734.

Cowen, R., C. Paris and A. Srinivasan (2006). "Scaling of connectivity in marine populations." Science **311**(5760): 522-527.

Crawley, M. C. (1969). "Movements and home ranges of *Clethrionomys glareolus* (Schreber) and *Apodemus sylvaticus* (L.) in North-East England." Oikos **20**(2): 310-319.
Crawley, M. J. (2012). The R book, John Wiley & Sons.
Creel, S. and N. M. Creel (2002). The African wild dog: behavior, ecology, and conservation, Princeton University Press.
Cross, J. R. (1973). Ecology and control of *Rhododendron ponticum* (L.). PhD, University of Dublin.
Cumming, G. S. and D. Cornélis (2012). "Quantitative comparison and selection of home range metrics for telemetry data." Diversity and Distributions **18**(11): 1057-1065.
Cuthill, I. C. and A. I. Houston (1997). "Managing time and energy." Behavioural Ecology: an Evolutionary Approach **1**(2): 97-120.
Cuyler, C. and N. A. Øritsland (2004). "Rain more important than windchill for insulation loss in Svalbard reindeer fur." Rangifer **24**(1): 7-14.
Dahlgren, J. P. and J. Ehrlén (2009). "Linking environmental variation to population dynamics of a forest herb." Journal of Ecology **97**(4): 666-674.
Davidson, A. D., J. K. Detling and J. H. Brown (2012). "Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands." Frontiers in Ecology and the Environment **10**(9): 477-486.
Davidson, A. D. and D. C. Lightfoot (2006). "Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland." Ecography **29**(5): 755-765.
Davidson, A. D., E. Ponce, D. C. Lightfoot, E. L. Fredrickson, J. H. Brown, J. Cruzado, S. L. Brantley, R. Sierra-Corona, R. List and D. Toledo (2010). "Rapid response of a grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock." Ecology **91**(11): 3189-3200.
De Larramendi, A. R. (1900). Diferencias morfológicas en un gradiente altitudinal de la cordillera cantábrica para la especie *Apodemus sylvaticus*, Universidad de Oviedo.
DeAngelis, D. L. and L. J. Gross (1992). Individual-based models and approaches in ecology: populations, communities and ecosystems, Chapman & Hall.
DeAngelis, D. L. and W. M. Mooij (2005). "Individual-based modeling of ecological and evolutionary processes." Annual Review of Ecology Evolution and Systematics **36**: 147-168.
Denton, P. W. and J. V. Garcia (2011). "Humanized mouse models of HIV infection." AIDS Reviews **13**(3): 135.
Desy, E. A. and G. O. Batzli (1989). "Effects of food availability and predation on prairie vole demography: a field experiment." Ecology **70**(2): 411-421.
Díaz, M., I. Torre, A. Peris and L. Tena (2005). "Foraging behavior of wood mice as related to presence and activity of genets." Journal of Mammalogy **86**(6): 1178-1185.
Dick, F. and H. Tevaearai (2015). "Significance and Limitations of the p Value." European Journal of Vascular and Endovascular Surgery **50**(6): 815.
Dickman, C. R. (1992). "Predation and habitat shift in the house mouse, *Mus domesticus*." Ecology **73**(1): 313-322.
Dickman, C. R. (1999). "Rodent-ecosystem relationships: a review." Ecologically-based management of rodent pests. ACIAR Monograph(59): 113-133.
Dobson, F. S. (1995). "Regulation of population size: evidence from Columbian ground squirrels." Oecologia **102**(1): 44-51.
Doggrell, S. A. and L. Brown (1998). "Rat models of hypertension, cardiac hypertrophy and failure." Cardiovascular Research **39**(1): 89-105.
Easterling, M. R., S. P. Ellner and P. M. Dixon (2000). "Size-specific sensitivity: applying a new structured population model." Ecology **81**(3): 694-708.

Ebensperger, L. A. and P. K. Wallem (2002). "Grouping increases the ability of the social rodent, *Octodon degus*, to detect predators when using exposed microhabitats." Oikos **98**(3): 491-497.

Eccard, J. A., K. Fey, B. A. Caspers and H. Ylönen (2011). "Breeding state and season affect interspecific interaction types: indirect resource competition and direct interference." Oecologia **167**(3): 623-633.

Eccard, J. A. and A. Herde (2013). "Seasonal variation in the behaviour of a short-lived rodent." BMC Ecology **13**(1): 259.

Eccard, J. A., I. Jokinen and H. Ylönen (2011). "Loss of density-dependence and incomplete control by dominant breeders in a territorial species with density outbreaks." BMC Ecology **11**(1): 16.

Eccard, J. A. and H. Ylönen (2002). "Direct interference or indirect exploitation? An experimental study of fitness costs of interspecific competition in voles." Oikos **99**(3): 580-590.

Eccard, J. A. and H. Ylönen (2007). "Costs of coexistence along a gradient of competitor densities: an experiment with arvicoline rodents." Journal of Animal Ecology **76**(1): 65-71.

Ecuyer-Dab, I. and M. Robert (2004). "Have sex differences in spatial ability evolved from male competition for mating and female concern for survival?" Cognition **91**(3): 221-257.

Ellner, S. P. and M. Rees (2006). "Integral projection models for species with complex demography." The American Naturalist **167**(3): 410-428.

Elton, C. S. (1924). "Periodic fluctuations in the numbers of animals: their causes and effects." Journal of Experimental Biology **2**(1): 119-163.

Emlen, J. M. (1966). "The role of time and energy in food preference." American Naturalist **100**(916): 611-617.

Emsens, W.-J., L. Suselbeek, B. T. Hirsch, R. Kays, A. J. S. Winkelhagen and P. A. Jansen (2013). "Effects of food availability on space and refuge use by a neotropical scatterhoarding rodent." Biotropica **45**(1): 88-93.

Epstein, J. M. (1999). "Agent-based computational models and generative social science." Generative Social Science: Studies in Agent-Based Computational Modeling **4**(5): 4-46.

Ergon, T., X. Lambin and N. C. Stenseth (2001). "Life-history traits of voles in a fluctuating population respond to the immediate environment." Nature **411**(6841): 1043-1045.

Estes, J., M. Riedman, M. Staedler, M. Tinker and B. Lyon (2003). "Individual variation in prey selection by sea otters: patterns, causes and implications." Journal of Animal Ecology **72**(1): 144-155.

Etzenhouser, M., M. K. Owens, D. Spalinger and S. B. Murden (1998). "Foraging behavior of browsing ruminants in a heterogeneous landscape." Landscape Ecology **13**(1): 55-64.

Fa, J. E., S. F. Ryan and D. J. Bell (2005). "Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests." Biological Conservation **121**(2): 167-176.

Festa-Bianchet, M., J.-M. Gaillard and J. T. Jorgenson (1998). "Mass-and density-dependent reproductive success and reproductive costs in a capital breeder." The American Naturalist **152**(3): 367-379.

Festa-Bianchet, M., J. T. Jorgenson, C. H. Bérubé, C. Portier and W. D. Wishart (1997). "Body mass and survival of bighorn sheep." Canadian Journal of Zoology **75**(9): 1372-1379.

Fieberg, J. (2007). "Kernel density estimators of home range: smoothing and the autocorrelation red herring." Ecology **88**(4): 1059-1066.

Fieberg, J. and L. Börger (2012). "Could you please phrase “home range” as a question?" Journal of Mammalogy **93**(4): 890-902.

Fisher, D. and M. Lara (1999). "Effects of body size and home range on access to mates and paternity in male bridled nailtail wallabies." Animal Behaviour **58**(1): 121-130.

Flowerdew, J. (1972). "The effect of supplementary food on a population of wood mice (*Apodemus sylvaticus*)." Journal of Animal Ecology **41**(3): 553-566.

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

Flowerdew, J., J. Gurnell and J. Gipps (1985). The Ecology of woodland rodents: bank voles and wood mice: the proceedings of a symposium held at the Zoological Society of London on 23rd and 24th of November 1984, Zoological Society of London.

Ford, R. G. and F. A. Pitelka (1984). "Resource limitation in populations of the California vole." Ecology **65**(1): 122-136.

Freund, J., A. M. Brandmaier, L. Lewejohann, I. Kirste, M. Kritzler, A. Krüger, N. Sachser, U. Lindenberger and G. Kempermann (2013). "Emergence of individuality in genetically identical mice." Science **340**(6133): 756-759.

Frost, S. K. and P. G. H. Frost (1980). "Territoriality and changes in resource use by sunbirds at *Leonotis leonurus* (Labiatae)." Oecologia **45**(1): 109-116.

Furukawa, R., K. Suzuki, T. Shimamoto and H. Yanagawa (2015). "Communal nesting of the small Japanese field mouse in tree cavities in early spring." Wildl. Biol **1**.

Gaines, M. S. and L. R. McClenaghan Jr (1980). "Dispersal in small mammals." Annual Review of Ecology and Systematics **11**(1): 163-196.

Ganskopp, D. C. and D. D. Johnson (2007). "GPS error in studies addressing animal movements and activities." Rangeland Ecology & Management **60**(4): 350-358.

Garnett, M. (1981). "Body size, its heritability and influence on juvenile survival among great tits, *Parus major*." Ibis **123**(1): 31-41.

Garten Jr, C. T. (1976). "Relationships between aggressive behavior and genic heterozygosity in the oldfield mouse, *Peromyscus polionotus*." Evolution **30**(1): 59-72.

Gaulin, S. J. and R. W. FitzGerald (1986). "Sex differences in spatial ability: an evolutionary hypothesis and test." American Naturalist **127**(1): 74-88.

Gese, E. M. and S. Grothe (1995). "Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming." American Midland Naturalist **133**(1): 36-43.

Getz, L. L., M. K. Oli, J. E. Hofmann, B. McGuire and A. Ozgul (2005). "Factors influencing movement distances of two species of sympatric voles." Journal of Mammalogy **86**(4): 647-654.

Getz, W. M. and C. C. Wilmers (2004). "A local nearest-neighbor convex-hull construction of home ranges and utilization distributions." Ecography **27**(4): 489-505.

Gilbert, B. S. and C. J. Krebs (1991). "Population dynamics of *Clethrionomys* and *Peromyscus* in Southwestern Yukon 1973-1989." Ecography **14**(4): 250-259.

Gipps, J. (1985). The behaviour of bank voles. Symposium of the Zoological Society of London.

Girard, I., J.-P. Ouellet, R. Courtois, C. Dussault and L. Breton (2002). "Effects of sampling effort based on GPS telemetry on home-range size estimations." Journal of Wildlife Management **66**(4): 1290-1300.

Gliwicz, J. (1981). "Competitive interactions within a forest rodent community in Central Poland." Oikos **37**(3): 353-362.

Gliwicz, J. (1988). "Seasonal dispersal in non-cyclic populations of *Clethrionomys glareolus* and *Apodemus flavicollis*." Acta Theriologica **33**(18): 263-272.

Godsall, B. (2015). Mechanisms of space use in the wood mouse, *Apodemus sylvaticus*. PhD, Imperial College

Godsall, B., T. Coulson and A. F. Malo (2014). "From physiology to space use: energy reserves and androgenization explain home-range size variation in a woodland rodent." Journal of Animal Ecology **83**(1): 126-135.

Gordon, A. G. (1992). Seed manual for forest trees. London, H.M.S.O.

Grant, P. (1972). "Interspecific competition among rodents." Annual Review of Ecology and Systematics **3**: 79-106.

Greenwood, P. J. (1978). "Timing of activity of bank vole (*Clethrionomys glareolus)* and wood mouse (*Apodemus sylvaticus)* in a deciduous woodland." Oikos **31**(1): 123-127.

Grimm, V. (1999). "Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future?" Ecological Modelling **115**(2-3): 129-148.

Grimm, V., U. Berger, F. Bastiansen, S. Eliassen, V. Ginot, J. Giske, J. Goss-Custard, T. Grand, S. K. Heinz, G. Huse, A. Huth, J. U. Jepsen, C. Jørgensen, W. M. Mooij, B. Müller, G. Pe'er, C. Piou, S. F. Railsback, A. M. Robbins, M. M. Robbins, E. Rossmanith, N. Rüger, E. Strand, S. Souissi, R. A. Stillman, R. Vabø, U. Visser and D. L. DeAngelis (2006). "A standard protocol for describing individual-based and agent-based models." Ecological Modelling **198**(1–2): 115-126.

Grimm, V., K. Frank, F. Jeltsch, R. Brandl, J. Uchmański and C. Wissel (1996). "Pattern-oriented modelling in population ecology." Science of the Total Environment **183**(1): 151-166.

Grimm, V., E. Revilla, U. Berger, F. Jeltsch, W. M. Mooij, S. F. Railsback, H. H. Thulke, J. Weiner, T. Wiegand and D. L. DeAngelis (2005). "Pattern-oriented modeling of agent-based complex systems: lessons from ecology." Science **310**(5750): 987-991.

Grodzinski, W. (1963). "Seasonal changes in the circadian activity of small rodents." Ekol Polska Ser B **9**: 3-17.

Grodziński, W. and K. Sawicka-Kapusta (1970). "Energy values of tree-seeds eaten by small mammals." Oikos **21**(1): 52-58.

Gula, R. and J. Theuerkauf (2013). "The need for standardization in wildlife science: home range estimators as an example." European Journal of Wildlife Research **59**(5): 713-718.

Gurnell, J. (1985). Woodland rodent communities. Symposium of the Zoological Society of London, London.

Gurnell, J. (1993). "Tree seed production and food conditions for rodents in an oak wood in Southern England." Forestry **66**(3): 291-315.

Gustafsson, T. O., C. B. Andersson and L. M. Westlin (1983). "Reproduction in laboratory colonies of bank vole, *Clethrionomys glareolus*, originating from populations with different degrees of cyclicity." Oikos **40**(2): 182-188.

Haapakoski, M., J. Sundell and H. Ylönen (2015). "Conservation implications of change in antipredator behavior in fragmented habitat: boreal rodent, the bank vole, as an experimental model." Biological Conservation **184**: 11-17.

Hacker, H. P. and H. S. Pearson (1944). "The growth, survival, wandering and variation of the long-tailed field mouse, *Apodemus sylvaticus*." Biometrika **33**(2): 136-162.

Hammer, W. (1906). "Epidemic disease in england – The evidence of variability and the persistence of type." The Lancet, II **167**(4307): 733-739.

Hansen, L. and G. O. Batzli (1978). "The influence of food availability on the white-footed mouse: populations in isolated woodlots." Canadian Journal of Zoology **56**(12): 2530-2541.

Hanski, I., A. Peltonen and L. Kaski (1991). "Natal dispersal and social dominance in the common shrew *Sorex araneus*." Oikos **62**(1): 48-58.

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

Hansson, L. (1988). "Parent-offspring correlations for growth and reproduction in the vole *Clethrionomus glareolus* in relation to the Chitty hypothesis." Zeitschrift für Säugetierkunde **53**(1): 7-10.

Hansteen, T. L., H. P. Andreassen and R. A. Ims (1997). "Effects of spatiotemporal scale on autocorrelation and home range estimators." Journal of Wildlife Management **61**(2): 280-290.

Hardenberg, A., B. Bassano, A. Peracino and S. Lovari (2000). "Male Alpine chamois occupy territories at hotspots before the mating season." Ethology **106**(7): 617-630.

Harris, D. B. (2009). "Review of negative effects of introduced rodents on small mammals on islands." Biological Invasions **11**(7): 1611-1630.

Harris, S., W. Cresswell, P. Forde, W. Trewhella, T. Woollard and S. Wray (1990). "Home-range analysis using radio-tracking data–a review of problems and techniques particularly as applied to the study of mammals." Mammal Review **20**(2-3): 97-123.

Harris, S. and D. W. Y. Yalden (2008). Mammals of the British Isles: handbook, Mammal society.

Harting, J. E. and N. West (1887). On the bank vole, *Arvicola glareolus* (Schreber).

Haugen, A. O. (1942). "Home range of the cottontail rabbit." Ecology **23**(3): 354-367.

Hayes, L. D. (2000). "To nest communally or not to nest communally: a review of rodent communal nesting and nursing." Animal Behaviour **59**(4): 677-688.

Hayes, L. D., A. S. Chesh and L. A. Ebensperger (2007). "Ecological predictors of range areas and use of burrow systems in the diurnal rodent, (*Octodon degus*)." Ethology **113**(2): 155-165.

Hedrick, A. V. (1988). "Female choice and the heritability of attractive male traits: an empirical study." American Naturalist: 267-276.

Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley and D. MACDONALD (2005). "Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation." Journal of Animal Ecology **74**(3): 455-463.

Henzi, S. P., R. W. Byrne and A. Whiten (1992). "Patterns of movement by baboons in the Drakensberg mountains: Primary responses to the environment." International Journal of Primatology **13**(6): 601-629.

Herfindal, I., J. D. Linnell, J. Odden, E. B. Nilsen and R. Andersen (2005). "Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*)." Journal of Zoology **265**(01): 63-71.

Hinkelman, T. M., J. L. Orrock and S. C. Loeb (2012). "Effect of downed woody debris on small mammal anti-predator behavior." Ethology **118**(1): 17-23.

Hisaw, F. L. and H. K. Gloyd (1926). "The bull snake as a natural enemy of injurious rodents." Journal of Mammalogy **7**(3): 200-205.

Hofer, H. and M. L. East (1993). "The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. II. Intrusion pressure and commuters' space use." Animal Behaviour **46**(3): 559-574.

Hoffmann, A., J. Decher, F. Rovero, J. Schaer, C. Voigt and G. Wibbelt (2010). Field methods and techniques for monitoring mammals. Manual on field recording techniques and protocols for all taxa biodiversity inventories and monitoring Sofia, Bulgaria, Pensoft Publishers**:** 482-529.

Holbrook, S. J. and R. J. Schmitt (1988). "The combined effects of predation risk and food reward on patch selection." Ecology **69**(1): 125-134.

Holm, J. C., T. Refstie and S. Bø (1990). "The effect of fish density and feeding regimes on individual growth rate and mortality in rainbow trout (*Oncorhynchus mykiss*)." Aquaculture **89**(3): 225-232.

Holmes, N. D., R. Griffiths, M. Pott, A. Alifano, D. Will, A. S. Wegmann and J. C. Russell (2015). "Factors associated with rodent eradication failure." Biological Conservation **185**: 8-16.

Hörnfeldt, B. (1994). "Delayed density dependence as a determinant of vole cycles." Ecology **75**(3): 791-806.

Hoset, K. S., J.-F. L. Galliard, G. Gundersen and H. Steen (2008). "Home range size and overlap in female root voles: effects of season and density." Behavioral Ecology **19**(1): 139-145.

Howerton, C. L., J. P. Garner and J. A. Mench (2012). "A system utilizing radio frequency identification (RFID) technology to monitor individual rodent behavior in complex social settings." Journal of Neuroscience Methods **209**(1): 74-78.

Howze, J. M. and L. L. Smith (2015). "Spatial ecology and habitat use of the coachwhip in a longleaf pine forest." Southeastern Naturalist **14**(2): 342-350.
Huang, B., T. W. Wey and D. T. Blumstein (2011). "Correlates and consequences of dominance in a social rodent." Ethology **117**(7): 573-585.
Hubbs, A. H. and R. Boonstra (1997). "Population limitation in arctic ground squirrels: effects of food and predation." Journal of Animal Ecology **66**(4): 527-541.
Hulme, P. E. (1994). "Post-dispersal seed predation in grassland: its magnitude and sources of variation." Journal of Ecology **82**(3): 645-652.
Ims, R. A. (1987). "Male spacing systems in microtine rodents." The American Naturalist **130**(4): 475-484.
Ims, R. A. (1988). "Spatial clumping of sexually receptive females induces space sharing among male voles." Nature **335**(6190): 541-543.
Ims, R. A. (1995). Movement patterns related to spatial structures. Mosaic landscapes and ecological processes, Springer**:** 85-109.
Ingles, L. G. (1961). "Home range and habitats of the wandering shrew." Journal of Mammalogy **42**(4): 455-462.
IUCN. (2015). "The IUCN Red List of Threatened Species." Version 2015-3. Retrieved 03/10/2015, from http://www.iucnredlist.org.
Jacob, J. and E. Tkadlec (2010). Rodent outbreaks in Europe: dynamics and damage. Rodent outbreaks: ecology and impacts. Los Banos, Philippines, International Rice Research Institute**:** 207-224.
Jędrzejewski, W., B. Jędrzejewska and L. Szymura (1995). "Weasel population response, home range, and predation on rodents in a deciduous forest in Poland." Ecology **76**(1): 179-195.
Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska and H. Okarma (2001). "Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Bialowieza primeval forest in Poland." Canadian Journal of Zoology **79**(11): 1993-2004.
Jennings, T. (1975). "Notes on the burrow systems of wood mice (*Apodemus sylvaticus*)." Journal of Zoology **177**(4): 500-504.
Jensen, S. P. (1993). "Temporal changes in food preferences of wood mice (*Apodemus sylvaticus* L.)." Oecologia **94**(1): 76-82.
Jensen, T. S. and O. F. Nielsen (1986). "Rodents as seed dispersers in a heath—oak wood succession." Oecologia **70**(2): 214-221.
John, A. (2014). "Rodent outbreaks and rice pre-harvest losses in Southeast Asia." Food Security **6**(2): 249-260.
Jordan, N. R., M. I. Cherry and M. B. Manser (2007). "Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence." Animal Behaviour **73**(4): 613-622.
Kai, F. and F. Walter (1998). "Seasonal variations of diet composition in farmland field mice *Apodemus spp*. and bank voles *Clethrionomys glareolus*." Acta Theriologica **43**(4): 379-389.
Karino, K. and Y. Haijima (2001). "Heritability of male secondary sexual traits in feral guppies in Japan." Journal of Ethology **19**(1): 33-37.
Katajisto, J. and A. Moilanen (2006). "Kernel-based home range method for data with irregular sampling intervals." Ecological Modelling **194**(4): 405-413.
Kaufman, D. W. and G. A. Kaufman (1982). "Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*)." Journal of Mammalogy **63**(2): 309-312.
Kays, R., M. C. Crofoot, W. Jetz and M. Wikelski (2015). "Terrestrial animal tracking as an eye on life and planet." Science **348**(6240): 2478.
Kays, R., S. Tilak, M. Crofoot, T. Fountain, D. Obando, A. Ortega, F. Kuemmeth, J. Mandel, G. Swenson, T. Lambert, B. Hirsch and M. Wikelski (2011). "Tracking animal location and

activity with an automated radio telemetry system in a tropical rainforest." Computer Journal **54**(12): 1931-1948.

Keating, K. A. and S. Cherry (2009). "Modeling utilization distributions in space and time." Ecology **90**(7): 1971-1980.

Keitt, T. H. (1997). "Stability and complexity on a lattice: coexistence of species in an individual-based food web model." Ecological Modelling **102**(2–3): 243-258.

Kelly, D., A. Geldenhuis, A. James, E. Penelope Holland, M. J. Plank, R. E. Brockie, P. E. Cowan, G. A. Harper, W. G. Lee, M. J. Maitland, A. F. Mark, J. A. Mills, P. R. Wilson and A. E. Byrom (2013). "Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change." Ecology Letters **16**(1): 90-98.

Kelt, D. A. and D. H. Van Vuren (2001). "The ecology and macroecology of mammalian home range area." The American Naturalist **157**(6): 637-645.

Kerley, G. and T. Erasmus (1991). "What do mice select for in seeds?" Oecologia **86**(2): 261-267.

Kermack, W. O. and A. G. McKendrick (1927). A contribution to the mathematical theory of epidemics. Proceedings of the Royal Society of London A: Mathematical, Physical and Engineering Sciences, The Royal Society.

Kernohan, B. J., R. A. Gitzen, J. J. Millspaugh, J. Millspaugh and J. Marzluff (2001). Analysis of animal space use and movements. Radio tracking and animal populations. San Diego, California, USA, Academic Press**:** 125-166.

Kie, J. G. and R. T. Bowyer (1999). "Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche." Journal of Mammalogy **80**(3): 1004-1020.

Kie, J. G., M. Jason, J. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J.-M. Gaillard and P. R. Moorcroft (2010). "The home-range concept: are traditional estimators still relevant with modern telemetry technology?" Philosophical Transactions: Biological Sciences **365**(1550): 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**(2): 259-299.

King, C. M. (1980). "The weasel *Mustela nivalis* and its prey in an English woodland." Journal of Animal Ecology **49**(1): 127-159.

King, C. M. (1985). Interactions between woodland rodents and their predators. Symposium of the Zoological Society of London.

Kjellander, P., A. Hewison, O. Liberg, J.-M. Angibault, E. Bideau and B. Cargnelutti (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**(3): 478-485.

Kleeberger, S. R. (1985). "Influence of intraspecific density and cover on home range of a plethodontid salamander." Oecologia **66**(3): 404-410.

Korn, H. (1986). "Changes in home range size during growth and maturation of the wood mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*)." Oecologia **68**(4): 623-628.

Korn, H. (1987). "Effects of live-trapping and toe-clipping on body weight of European and African rodent species." Oecologia **71**(4): 597-600.

Korpimaki, E., V. Koivunen and H. Hakkarainen (1996). "Microhabitat use and behavior of voles under weasel and raptor predation risk: predator facilitation?" Behavioral Ecology **7**(1): 30-34.

Koteja, P. and J. Weiner (1993). "Mice, voles and hamsters: metabolic rates and adaptive strategies in muroid rodents." Oikos **66**(3): 505-514.

Kotler, B. P. (1984). "Risk of predation and the structure of desert rodent communities." Ecology **65**(3): 689-701.
Kotler, B. P., J. S. Brown and O. Hasson (1991). "Factors affecting gerbil foraging behavior and rates of owl predation." Ecology **72**(6): 2249-2260.
Kramer, D. and M. Chapman (1999). "Implications of fish home range size and relocation for marine reserve function." Environmental Biology of Fishes **55**(1-2): 65-79.
Krebs, C. J. (1970). "Microtus population biology: behavioral changes associated with the population cycle in *M. ochrogaster* and *M. pennsylvanicus*." Ecology **51**(1): 34-52.
Krebs, C. J. (1978). "A review of the Chitty hypothesis of population regulation." Canadian Journal of Zoology **56**(12): 2463-2480.
Krebs, C. J. and J. H. Myers (1974). "Population cycles in small mammals." Advances in Ecological Research: 267-399.
Kruuk, L. E., J. Slate, J. M. Pemberton, S. Brotherstone, F. Guinness and T. Clutton-Brock (2002). "Antler size in red deer: heritability and selection but no evolution." Evolution **56**(8): 1683-1695.
LaFleur, M. and L. Gould (2009). "Feeding outside the forest: the importance of crop raiding and an invasive weed in the diet of gallery forest ring-tailed lemurs (*Lemur catta*) following a cyclone at the Beza Mahafaly special reserve, Madagascar." Folia Primatologica **80**(3): 233-246.
Lagos, V., L. Contreras, P. Meserve, J. Gutiérrez and F. Jaksic (1995). "Effects of predation risk on space use by small mammals: a field experiment with a Neotropical rodent." Oikos **74**(2): 259-264.
Larsson, K., H. P. v. d. Jeugd, I. T. v. d. Veen and P. Forslund (1998). "Body size declines despite positive directional selection on heritable size traits in a barnacle goose population." Evolution **52**(4): 1169-1184.
Larsson, T.-B., L. Hansson and E. Nyholm (1973). "Winter reproduction in small rodents in Sweden." Oikos **24**(3): 475-476.
Laver, P. N. and M. J. Kelly (2008). "A critical review of home range studies." Journal of Wildlife Management **72**(1): 290-298.
Lawson, E. J. G. and A. R. Rodgers (1997). "Differences in home-range size computed in commonly used software programs." Wildlife Society Bulletin **25**(3): 721-729.
Lefkovitch, L. (1965). "The study of population growth in organisms grouped by stages." Biometrics **21**(1): 1-18.
Leirs, H. (2003). "Management of rodents in crops: the pied piper and his orchestra." ACIAR Monograph Series **96**: 183-190.
Leslie, P. H. (1945). "On the use of matrices in certain population mathematics." Biometrika **33**: 183-212.
Letcher, B. H., J. A. Rice, L. B. Crowder and K. A. Rose (1996). "Variability in survival of larval fish: disentangling components with a generalized individual-based model." Canadian Journal of Fisheries and Aquatic Sciences **53**(4): 787-801.
Letnic, M., M. Crowther and F. Koch (2009). "Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator?" Animal Conservation **12**(4): 302-312.
Levin, S. A. (1992). "The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture." Ecology **73**(6): 1943-1967.
Lidicker Jr, W. Z. and R. S. Ostfeld (1991). "Extra-large body size in California voles: causes and fitness consequences." Oikos **61**(1): 108-121.
Lima, M., J. E. Keymer and F. M. Jaksic (1999). "El Nino–southern oscillation–driven rainfall variability and delayed density dependence cause rodent outbreaks in western South America: linking demography and population dynamics." The American Naturalist **153**(5): 476-491.

Lima, S. L., T. J. Valone and T. Caraco (1985). "Foraging-efficiency-predation-risk trade-off in the grey squirrel." Animal Behaviour **33**(1): 155-165.

Lima, S. L. and P. A. Zollner (1996). "Anti-predatory vigilance and the limits to collective detection: visual and spatial separation between foragers." Behavioral Ecology and Sociobiology **38**(5): 355-363.

Linnell, J. D. C., R. Andersen, T. O. R. Kvam, H. AndrÉN, O. Liberg, J. Odden and P. F. Moa (2001). "Home range size and choice of management strategy for lynx in Scandinavia." Environmental Management **27**(6): 869-879.

List, R. and D. W. Macdonald (2003). "Home range and habitat use of the kit fox (*Vulpes macrotis*) in a prairie dog (*Cynomys ludovicianus*) complex." Journal of Zoology **259**(1): 1-5.

Litvaitis, J. A., J. A. Sherburne and J. A. Bissonette (1986). "Bobcat habitat use and home range size in relation to prey density." Journal of Wildlife Management **50**(1): 110-117.

Liu, C., R. M. Sibly, V. Grimm and P. Thorbek (2013). "Linking pesticide exposure and spatial dynamics: an individual-based model of wood mouse (*Apodemus sylvaticus*) populations in agricultural landscapes." Ecological Modelling **248**: 92-102.

Löfgren, O. (1995). "Niche expansion and increased maturation rate of *Clethrionomys glareolus* in the absence of competitors." Journal of Mammalogy **76**(4): 1100-1112.

Longland, W. S. and M. V. Price (1991). "Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use?" Ecology **72**(6): 2261-2273.

Loveridge, A. J., M. Valeix, Z. Davidson, F. Murindagomo, H. Fritz and D. W. MacDonald (2009). "Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna."

Loveridge, A. J., M. Valeix, Z. Davidson, F. Murindagomo, H. Fritz and D. W. Macdonald (2009). "Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna." Ecography **32**(6): 953-962.

Lurz, P. W. W., P. J. Garson and L. A. Wauters (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.

Lyly, M., T. Klemola, E. Koivisto, O. Huitu, L. Oksanen and E. Korpimäki (2014). "Varying impacts of cervid, hare and vole browsing on growth and survival of boreal tree seedlings." Oecologia **174**(1): 271-281.

MacArthur, R. H. and E. O. Wilson (1967). The theory of island biogeography, Princeton University Press.

Macdonald, D. (2009). The encyclopedia of mammals. Oxford, Oxford University Press.

Madsen, T. and R. Shine (1999). "Rainfall and rats: Climatically-driven dynamics of a tropical rodent population." Australian Journal of Ecology **24**(1): 80-89.

Maher, C. R. and D. F. Lott (1995). "Definitions of territoriality used in the study of variation in vertebrate spacing systems." Animal Behaviour **49**(6): 1581-1597.

Malo, A. F., B. Godsall, C. Prebble, Z. Grange, S. McCandless, A. Taylor and T. Coulson (2013). "Positive effects of an invasive shrub on aggregation and abundance of a native small rodent." Behavioral Ecology **24**(3): 759-767.

Malo, A. F., F. Martinez-Pastor, G. Alaks, J. Dubach and R. C. Lacy (2010). "Effects of genetic captive-breeding protocols on sperm quality and fertility in the white-footed mouse." Biology of Reproduction **83**(4): 540-548.

Mandelik, Y., M. Jones and T. Dayan (2003). "Structurally complex habitat and sensory adaptations mediate the behavioural responses of a desert rodent to an indirect cue for increased predation risk." Evolutionary Ecology Research **5**(4): 501-515.

Mares, M., M. Watson and T. Lacher, Jr. (1976). "Home range perturbations in *Tamias striatus*." Oecologia **25**(1): 1-12.

Marsh, R. (1988). Rodent problems on the North American Continent. Rodent pest management. P. I, CRC Press**:** 1-11.

Mateo, J. A. and M. Cuadrado (2012). "Communal Nesting and Parental Care in Oudri's Fan-Footed Gecko (Ptyodactylus oudrii): Field and Experimental Evidence of an Adaptive Behavior." Journal of Herpetology **46**(2): 209-212.

Matthiopoulos, J. (2003). "The use of space by animals as a function of accessibility and preference." Ecological Modelling **159**(2): 239-268.

Maurice, C. F., S. Cl Knowles, J. Ladau, K. S. Pollard, A. Fenton, A. B. Pedersen and P. J. Turnbaugh (2015). "Marked seasonal variation in the wild mouse gut microbiota." ISME J **9**(11): 2423-2434.

McCarthy, T. M., T. K. Fuller and B. Munkhtsog (2005). "Movements and activities of snow leopards in Southwestern Mongolia." Biological Conservation **124**(4): 527-537.

McCormick, M. (2003). "Rats, communications, and plague: toward an ecological history." Journal of Interdisciplinary History **34**(1): 1-25.

MClEan, R. G. (2007). "Infectious diseases of wild rodents." Journal of Wildlife Diseases **43**(3): 558-559.

McManus, M. and J. Travis (1998). "Effects of temperature and salinity on the life history of the sailfin molly (Pisces: Poeciliidae): lipid storage and reproductive allocation." Oecologia **114**(3): 317-325.

McNay, R. S., J. A. Morgan and F. L. Bunnell (1994). "Characterizing independence of observations in movements of Columbian black-tailed deer." Journal of Wildlife Management **58**(3): 422-429.

Metcalf, C., K. Rose, D. Childs, A. Sheppard, P. Grubb and M. Rees (2008). "Evolution of flowering decisions in a stochastic, density-dependent environment." Proceedings of the National Academy of Sciences **105**(30): 10466-10470.

Mihok, S. (1981). "Chitty's hypothesis and behaviour in subarctic red-backed voles *Clethrionomys gapperi*." Oikos **36**(3): 281-295.

Miller, R. S. and C. Elton (1955). Activity rhythms in the wood mouse, *Apodemus sylvaticus* and the bank vole, *Clethrionomys glareolus*. Proceedings of the Zoological Society of London, London, UK, Zoological Society of London

Miller, T. E., S. M. Louda, K. A. Rose and J. O. Eckberg (2009). "Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient." Ecological Monographs **79**(1): 155-172.

Millspaugh, J. J., R. M. Nielson, L. McDONALD, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard and S. L. Sheriff (2006). "Analysis of resource selection using utilization distributions." Journal of Wildlife Management **70**(2): 384-395.

Monteiro, L. S. and D. S. Falconer (2010). "Compensatory growth and sexual maturity in mice." Animal Science **8**(2): 179-192.

Montgomery, W. (1989). "Population regulation in the wood mouse, *Apodemus sylvaticus*. I. Density dependence in the annual cycle of abundance." Journal of Animal Ecology **58**(2): 465-475.

Montgomery, W. and J. Gurnell (1985). The behaviour of *Apodemus*. Symposia of the Zoological Society of London, London, UK, Zoological Society of London.

Montgomery, W. I., W. L. Wilson and R. W. Elwood (1997). "Spatial regulation and population growth in the wood mouse *Apodemus sylvaticus*: experimental manipulations of males and females in natural populations." Journal of Animal Ecology **66**(5): 755-768.

Morales, J. M. and S. P. Ellner (2002). "Scaling up animal movements in heterogeneous landscapes: the importance of behavior." Ecology **83**(8): 2240-2247.

Morellet, N., C. Bonenfant, L. Börger, F. Ossi, F. Cagnacci, M. Heurich, P. Kjellander, J. D. Linnell, S. Nicoloso and P. Sustr (2013). "Seasonality, weather and climate affect home range

size in roe deer across a wide latitudinal gradient within Europe." Journal of Animal Ecology **82**(6): 1326-1339.
Mueller, T. and W. F. Fagan (2008). "Search and navigation in dynamic environments–from individual behaviors to population distributions." Oikos **117**(5): 654-664.
Murdock, G. P. (1967). "Ethnographic atlas: a summary." Ethnology **6**(2): 109-236.
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**(1): 75-84.
Nakata, K. (1998). "Regulation of reproduction in a natural population of the small Japanese field mouse, *Apodemus argenteus*." Mammal Study **23**(1): 19-30.
Newsome, T. M., G.-A. Ballard, C. R. Dickman, P. J. S. Fleming and C. Howden (2013). "Anthropogenic resource subsidies determine space use by Australian arid zone dingoes: an improved resource selection modelling approach." PLoS One **8**(5): e63931.
Nicieza, A. G. and N. B. Metcalfe (1997). "Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability." Ecology **78**(8): 2385-2400.
Nicolaus, M., K. M. Bouwman and N. J. Dingemanse (2008). "Effect of PIT tags on the survival and recruitment of great tits *Parus major*." Ardea **96**(2): 286-292.
Norrdahl, K. (1995). "Population cycles in northern small mammals." Biological Reviews **70**(4): 621-637.
Norrdahl, K. and E. Korpimäki (2002). "Changes in individual quality during a 3-year population cycle of voles." Oecologia **130**(2): 239-249.
Nowak, R. M. (1936). Walker's Mammals of the World, Bd. 1 & 2. Baltimore and London, The John Hopkins University Press.
Nyholm, N. E. I. and P. Meurling (1979). "Reproduction of the bank vole, *Clethrionomys glareolus*, in Northern and Southern Sweden during several seasons and in different phases of the vole population cycle." Ecography **2**(1): 12-20.
Nylin, S. and K. Gotthard (1998). "Plasticity in life-history traits." Annual Review of Entomology **43**(1): 63-83.
O'Connor, T. P. (1992). "Pets and pests in Roman and medieval Britain." Mammal Review **22**(2): 107-113.
Ogbu, O., E. Ajuluchukwu and C. Uneke (2007). "Lassa fever in West African sub-region: an overview." Journal of Vector Borne Diseases **44**(1): 1-11.
Ogle, D. (2012). FSA: Fisheries stock analysis. R package version 0.2–8.
Oli, M. K. (1999). "The Chitty effect: a consequence of dynamic energy allocation in a fluctuating environment." Theoretical Population Biology **56**(3): 293-300.
Orians, G. H. and N. E. Pearson (1979). "On the theory of central place foraging." Analysis of Ecological Systems **1**: 155-177.
Orrock, J. L., B. J. Danielson and R. J. Brinkerhoff (2004). "Rodent foraging is affected by indirect, but not by direct, cues of predation risk." Behavioral Ecology **15**(3): 433-437.
Ostfeld, R. S. (1990). "The ecology of territoriality in small mammals." Trends in Ecology & Evolution **5**(12): 411-415.
Ostfeld, R. S., C. G. Jones and J. O. Wolff (1996). "Of mice and mast." BioScience **46**(5): 323-330.
Ostro, L. E., T. P. Young, S. C. Silver and F. W. Koontz (1999). "A geographic information system method for estimating home range size." Journal of Wildlife Management **63**(2): 748-755.
Otis, D. L. and G. C. White (1999). "Autocorrelation of location estimates and the analysis of radiotracking data." Journal of Wildlife Management **63**(3): 1039-1044.
Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar and T. Coulson (2010). "Coupled dynamics of body mass and population growth in response to environmental change." Nature **466**(7305): 482-485.

Perea, R., R. González, A. San Miguel and L. Gil (2011). "Moonlight and shelter cause differential seed selection and removal by rodents." Animal Behaviour **82**(4): 717-723.

Perry, G. and T. Garland Jr (2002). "Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny." Ecology **83**(7): 1870-1885.

Previtali, M. A., M. Lima, P. L. Meserve, D. A. Kelt and J. R. Gutiérrez (2009). "Population dynamics of two sympatric rodents in a variable environment: rainfall, resource availability, and predation." Ecology **90**(7): 1996-2006.

Ramesh, T., R. Kalle and C. T. Downs (2015). "Sex-specific indicators of landscape use by servals: consequences of living in fragmented landscapes." Ecological Indicators **52**: 8-15.

Randolph, S. E. (1977). "Changing spatial relationships in a population of *Apodemus sylvaticus* with the onset of breeding." Journal of Animal Ecology **46**(2): 653-676.

Réale, D., M. Festa-Bianchet and J. T. Jorgenson (1999). "Heritability of body mass varies with age and season in wild bighorn sheep." Heredity **83**(5): 526-532.

Rees, M. and S. P. Ellner (2009). "Integral projection models for populations in temporally varying environments." Ecological Monographs **79**(4): 575-594.

Rey, P. J. (1995). "Spatiotemporal variation in fruit and frugivorous bird abundance in olive orchards." Ecology **76**(5): 1625-1635.

Rhees, R. W. and D. E. Fleming (1981). "Effects of malnutrition, maternal stress, or ACTH injections during pregnancy on sexual behavior of male offspring." Journal of Behavioural Physiology **27**(5): 879-882.

Riechert, S. E. (1979). "Games spiders play: II. Resource assessment strategies." Behavioral Ecology and Sociobiology **6**(2): 121-128.

Riska, B., T. Prout and M. Turelli (1989). "Laboratory estimates of heritabilities and genetic correlations in nature." Genetics **123**(4): 865-871.

Ritz, B. W. and E. M. Gardner (2006). "Malnutrition and energy restriction differentially affect viral immunity." The Journal of Nutrition **136**(5): 1141-1144.

Robinson, J. G. (1986). Seasonal variation in use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: implications for foraging theory. Washington, DC, Smithsonian Institution Press

Rodriguez, J. (1993). Roedores plaga: un problema permanente en América Latina y el Caribe. Consulta Latinoamericana sobre Biología y Control de Roedores Plaga, Santa Cruz, Bolivia, FAO.

Roland, C., J. Schmidt and J. Johnstone (2014). "Climate sensitivity of reproduction in a mast-seeding boreal conifer across its distributional range from lowland to treeline forests." Oecologia **174**(3): 665-677.

Rooney, S., A. Wolfe and T. Hayden (1998). "Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects." Mammal Review **28**(2): 89-98.

Rose, R. K. and M. S. Gaines (1976). "Levels of aggression in fluctuating populations of the prairie vole, *Microtus ochrogaster*, in Eastern Kansas." Journal of Mammalogy **57**(1): 43-57.

Ross, A. and R. Nisbet (1990). "Dynamic models of growth and reproduction of the mussel *Mytilus edulis* L." Functional Ecology **4**(6): 777-787.

Rowley, J. J. and R. A. Alford (2007). "Techniques for tracking amphibians: the effects of tag attachment, and harmonic direction finding versus radio telemetry." Amphibia-Reptilia **28**(3): 367-376.

Saitoh, T. (1990). "Lifetime reproductive success in reproductively suppressed female voles." Researches on Population Ecology **32**(2): 391-406.

Samuel, M. D., D. J. Pierce and E. O. Garton (1985). "Identifying areas of concentrated use within the home range." Journal of Animal Ecology **54**(3): 711-719.

Santos, S. M., M. P. Simões, M. da Luz Mathias and A. Mira (2006). "Vegetation analysis in colonies of an endangered rodent, the cabrera vole (*Microtus cabrerae*), in Southern Portugal." Ecological Research **21**(2): 197-207.

Santos, T. and J. Tellería (1997). "Vertebrate predation on holm oak, *Quercus ilex*, acorns in a fragmented habitat: effects on seedling recruitment." Forest Ecology and Management **98**(2): 181-187.

Schoepf, I., G. Schmohl, B. König, N. Pillay and C. Schradin (2015). "Manipulation of population density and food availability affects home range sizes of African striped mouse females." Animal Behaviour **99**(0): 53-60.

Schradin, C., G. Schmohl, H. G. Rödel, I. Schoepf, S. M. Treffler, J. Brenner, M. Bleeker, M. Schubert, B. König and N. Pillay (2010). "Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study." Animal Behaviour **79**(1): 195-203.

Schulte-Hostedde, A. I. and J. S. Millar (2004). "Intraspecific variation of testis size and sperm length in the yellow-pine chipmunk (*Tamias amoenus*): implications for sperm competition and reproductive success." Behavioral Ecology and Sociobiology **55**(3): 272-277.

Schweiger, S. and S. Boutin (1995). "The effects of winter food addition on the population dynamics of *Clethrionomys rutilus*." Canadian Journal of Zoology **73**(3): 419-426.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke and R. A. Gitzen (1999). "Effects of sample size on kernel home range estimates." Journal of Wildlife Management **63**(2): 739-747.

Seaman, D. E. and R. A. Powell (1996). "An evaluation of the accuracy of kernel density estimators for home range analysis." Ecology **77**(7): 2075-2085.

Seddon, N., W. Amos, R. A. Mulder and J. A. Tobias (2004). "Male heterozygosity predicts territory size, song structure and reproductive success in a cooperatively breeding bird." Proc Biol Sci **271**(1550): 1823-1829.

Seigers, R. and J. E. Fardell (2011). "Neurobiological basis of chemotherapy-induced cognitive impairment: a review of rodent research." Neuroscience & Biobehavioral Reviews **35**(3): 729-741.

Silverman, B. W. (1986). Density estimation for statistics and data analysis. London, CRC press.

Simmonds, E. G. and T. Coulson (2015). "Analysis of phenotypic change in relation to climatic drivers in a population of Soay sheep *Ovis aries*." Oikos **124**(5): 543-552.

Simons, A. M. and D. A. Roff (1994). "The effect of environmental variability on the heritabilities of traits of a field cricket." Evolution **48**(5): 1637-1649.

Sinervo, B., E. Svensson and T. Comendant (2000). "Density cycles and an offspring quantity and quality game driven by natural selection." Nature **406**(6799): 985-988.

Singleton, G. R. (2003). Impacts of rodents on rice production in Asia, IRRI discussion paper series.

Smaill, S. J., P. W. Clinton, R. B. Allen and M. R. Davis (2011). "Climate cues and resources interact to determine seed production by a masting species." Journal of Ecology **99**(3): 870-877.

Smith, M. H., C. T. Garten Jr and P. Ramsey (1975). "Genic heterozygosity and population dynamics in small mammals." Isozymes **4**: 85-102.

Smyth, M. (1966). "Winter breeding in woodland mice, *Apodemus sylvaticus*, and voles, *Clethrionomys glareolus* and *Microtus agrestis*, near Oxford." Journal of Animal Ecology **35**(3): 471-485.

Solla, D., R. Shane, R. Bonduriansky and R. J. Brooks (1999). "Eliminating autocorrelation reduces biological relevance of home range estimates." Journal of Animal Ecology **68**(2): 221-234.

Southern, H. and V. Lowe (1982). "Predation by tawny owls (*Strix aluco*) on bank voles (*Clethrionomys glareolus*) and wood mice (*Apodemus sylvaticus*)." Journal of Zoology **198**(1): 83-102.

Southern, H. N. and V. P. W. Lowe (1968). "Pattern of distribution of prey and predation in tawny owl territories." Journal of Animal Ecology **37**(1): 75-&.

Spritzer, M. D., D. B. Meikle and N. G. Solomon (2005). "Female choice based on male spatial ability and aggressiveness among meadow voles." Animal Behaviour **69**(5): 1121-1130.

St Clair, J. J. H. (2011). "The impacts of invasive rodents on island invertebrates." Biological Conservation **144**(1): 68-81.

Stapp, P., P. J. Pekins and W. W. Mautz (1991). "Winter energy expenditure and the distribution of southern flying squirrels." Canadian Journal of Zoology **69**(10): 2548-2555.

Steen, H., N. G. Yoccoz and R. A. Ims (1990). "Predators and small rodent cycles: an analysis of a 79-year time series of small rodent population fluctuations." Oikos **59**(1): 115-120.

Stenseth, N. C., H. Leirs, A. Skonhoft, S. A. Davis, R. P. Pech, H. P. Andreassen, G. R. Singleton, M. Lima, R. S. Machang'u, R. H. Makundi, Z. Zhang, P. R. Brown, D. Shi and X. Wan (2003). "Mice, rats, and people: the bio-economics of agricultural rodent pests." Frontiers in Ecology and the Environment **1**(7): 367-375.

Stokes, M. K., N. A. Slade and S. M. Blair (2001). "Influences of weather and moonlight on activity patterns of small mammals: a biogeographical perspective." Canadian Journal of Zoology **79**(6): 966-972.

Swihart, R. K. and N. A. Slade (1985). "Testing for independence of observations in animal movements." Ecology **66**(4): 1176-1184.

Tallmon, D. and L. S. Mills (1994). "Use of logs within home ranges of California red-backed voles on a remnant of forest." Journal of Mammalogy **75**(1): 97-101.

Tamburino, L. and G. Bravo (2013). "Mice in wonderforest: understanding mast seeding through individual-based modelling." Ecological Modelling **250**: 34-44.

Tarlow, E. M. and D. T. Blumstein (2007). "Evaluating methods to quantify anthropogenic stressors on wild animals." Applied Animal Behaviour Science **102**(3): 429-451.

Tesfatsion, L. (2003). "Agent-based computational economics: modeling economies as complex adaptive systems." Information Sciences **149**(4): 262-268.

Tew, T. E. and D. W. Macdonald (1994). "Dynamics of space use and male vigor amongst wood mice, *Apodemus sylvaticus*, in the cereal ecosystem." Behavioral Ecology and Sociobiology **34**(5): 337-345.

Thompson, R. L., C. L. Chambers and B. C. McComb (2009). "Home range and habitat of Western red-backed voles in the Oregon cascades." Northwest Science **83**(1): 46-56.

Tilman, D., P. B. Reich and J. M. Knops (2006). "Biodiversity and ecosystem stability in a decade-long grassland experiment." Nature **441**(7093): 629-632.

Trebatická, L., J. Sundell, E. Tkadlec and H. Ylönen (2008). "Behaviour and resource use of two competing vole species under shared predation risk." Oecologia **157**(4): 707-715.

Trombulak, S. C. (1985). "The influence of interspecific competition on home range size in chipmunks (*Eutamias*)." Journal of Mammalogy **66**(2): 329-337.

Tufto, J., R. Andersen and J. Linnell (1996). "Habitat use and ecological correlates of home range size in a small cervid: the roe deer." Journal of Animal Ecology **65**(6): 715-724.

Tuljapurkar, S. (1990). Population dynamics in variable environments. New York & London, Springer.

Udyawer, V., A. Chin, D. M. Knip, C. A. Simpfendorfer and M. R. Heupel (2013). "Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use." Marine Ecology Progress Series **480**: 171-183.

Urbanek, S. (2013). Rserve: binary R server. R package version 0.6-8.1.

Van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner and A. Mysterud (2011). "What determines variation in home range size across spatiotemporal scales in a large browsing herbivore?" Journal of Animal Ecology **80**(4): 771-785.

Van Dam, D. and P. P. De Deyn (2006). "Drug discovery in dementia: the role of rodent models." Nature Reviews Drug Discovery **5**(11): 956-970.

Van Winkle, W. (1975). "Comparison of several probabilistic home-range models." Journal of Wildlife Management **39**(1): 118-123.

Vander Wal, E. and A. R. Rodgers (2012). "An individual-based quantitative approach for delineating core areas of animal space use." Ecological Modelling **224**(1): 48-53.

Vickery, W. and J. Bider (1981). "The influence of weather on rodent activity." Journal of Mammalogy **62**(1): 140-145.

Volampeno, M. S. N., J. C. Masters and C. T. Downs (2011). "Home range size in the blue-eyed black lemur (*Eulemur flavifrons*): a comparison between dry and wet seasons." Mammalian Biology-Zeitschrift für Säugetierkunde **76**(2): 157-164.

Wakefield, E. D., T. W. Bodey, S. Bearhop, J. Blackburn, K. Colhoun, R. Davies, R. G. Dwyer, J. A. Green, D. Grémillet and A. L. Jackson (2013). "Space partitioning without territoriality in gannets." Science **341**(6141): 68-70.

Walker, E. P. (1975). Mammals of the World. Vol. 1. Baltimore, USA, Johns Hopkins Press.

Wallace, K., A. Leslie and T. Coulson (2013). "Re-evaluating the effect of harvesting regimes on Nile crocodiles using an integral projection model." Journal of Animal Ecology **82**(1): 155-165.

Wand, M. and M. Jones (1995). "Kernel Smoothing." Monographs on Statistics and Applied Probability **60**.

Wand, M. and M. Jones (1995). "Kernel Smoothing." Monographs on Statistics and Applied Probability

60.

Wand, M. P. and M. C. Jones (1994). Kernel smoothing, Crc Press.

Wang, M. and V. Grimm (2007). "Home range dynamics and population regulation: an individual-based model of the common shrew *Sorex araneus*." Ecological Modelling **205**(3–4): 397-409.

Wästljung, U. (1989). "Effects of crop size and stand size on seed removal by vertebrates in hazel *Corylus avellana*." Oikos **54**(2): 178-184.

Waterman, J. M. and M. B. Fenton (2000). "The effect of drought on the social structure and use of space in Cape ground squirrels, *Xerus inauris*." Ecoscience **7**(2): 131-136.

Watts, C. (1969). "The regulation of wood mouse (*Apodemus sylvaticus*) numbers in Wytham woods, Berkshire." Journal of Animal Ecology **38**(2): 285-304.

Webb, D. and J. King (1984). "Effects of wetting of insulation of bird and mammal coats." Journal of Thermal Biology **9**(3): 189-191.

Webb, D., W. Porter and P. McClure (1990). "Development of insulation in juvenile rodents: functional compromise in insulation." Functional Ecology **4**(2): 251-256.

White, G. C. and R. A. Garrott (1990). Analysis of wildlife radio-tracking data. san Diego, USA, Academic Press.

Wikelski, M., R. W. Kays, N. J. Kasdin, K. Thorup, J. A. Smith and G. W. Swenson (2007). "Going wild: what a global small-animal tracking system could do for experimental biologists." Journal of Experimental Biology **210**(2): 181-186.

Wikelski, M., J. Moxley, A. Eaton-Mordas, M. M. Lopez-Uribe, R. Holland, D. Moskowitz, D. W. Roubik and R. Kays (2010). "Large range movements of Neotropical orchid bees observed via radio telemetry." PLoS One **5**(5): e10738.

Wilbur, H. M. (1977). "Interactions of food level and population density in *Rana sylvatica*." Ecology **58**(1): 206-209.

Wilensky, U. (1999). NetLogo. Northwestern University, Evanston, IL. , Center for Connected Learning and Computer-Based Modeling.

Williams, J. D., W. Krueger and D. H. Harmel (1994). "Heritabilities for antler characteristics and body weight in yearling white-tailed deer." Heredity **73**(1): 78-83.

Williams, J. L., T. E. Miller and S. P. Ellner (2012). "Avoiding unintentional eviction from integral projection models." Ecology **93**(9): 2008-2014.

Winterhalder, B. (1983). "Opportunity-cost foraging models for stationary and mobile predators." The American Naturalist **122**(1): 73-84.

Wolff, J. O. (1993). "Does the "Chitty effect" occur in *Peromyscus*?" Journal of Mammalogy **74**(4): 846-851.

Wolff, J. O. (1996). "Population fluctuations of mast-eating rodents are correlated with production of acorns." Journal of Mammalogy **77**(3): 850-856.

Wolff, J. O. and P. W. Sherman (2008). Rodent Societies : An Ecological and Evolutionary Perspective. Chicago, US, University of Chicago Press.

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

Wolton, R. J. (1983). "The activity of free-ranging wood mice *Apodemus sylvaticus*." Journal of Animal Ecology **52**(3): 781-794.

Worton, B. (1987). "A review of models of home range for animal movement." Ecological Modelling **38**(3): 277-298.

Worton, B. J. (1989). "Kernel methods for estimating the utilization distribution in home-range studies." Ecology **70**(1): 164-168.

Worton, B. J. (1995). "Using Monte Carlo simulation to evaluate kernel-based home range estimators." Journal of Wildlife Management **59**(4): 794-800.

Zedrosser, A., B. Dahle and J. E. Swenson (2006). "Population density and food conditions determine adult female body size in brown bears." Journal of Mammalogy **87**(3): 510-518.

Zizkova, M. and D. Frytna (1996). "Reproduction in *Apodemus sylvaticus* (Rodentia: Muridae) in captivity." Acta Soc. Zool. Bohem **60**: 83-93.

Appendix

Satellites, telemetry and sensor networks - Monitoring technologies in biological application

Introduction

Understanding the drivers and consequences of animal space use and movement patterns is crucial to animal ecology, evolution and conservation, having been investigated both empirically and theoretically (Gaines and McClenaghan Jr 1980; Fisher and Lara 1999; Getz, Oli et al. 2005; Börger, Franconi et al. 2006; Schick, Loarie et al. 2008; Booth, Montgomery et al. 2009; Gautestad 2011; Gorini, Linnell et al. 2012). Information about space use and movement can only be reliably collected through direct observation or remote monitoring of individuals. In practice, however, direct observation is often impossible, logistically challenging, or prohibitively expensive. Therefore, researchers often rely on technologies that allow them to remotely collect high quality data, hence data with high spatial and temporal resolution, of animal space use and movement.

Over the last five decades, numerous methods have been developed to monitor animals and due to constant improvement many technologies collect data of increasing spatial and temporal resolution (Harris 1990; Harris, Cresswell et al. 1990; Tomkiewicz, Fuller et al. 2010; Bridge, Thorup et al. 2011; Recio, Mathieu et al. 2011; Matthews, Ruykys et al. 2013). Unfortunately, many technologies can only be used for animals larger than 300 grams, hence excluding many small mammal species from being monitored (Wikelski, Kays et al. 2007 2). For example, small mammals, such as our study population of wood mice, *Apodemus sylvaticus*, are too small for most monitoring technologies and spatial data has to be collected via trapping and RFID PIT tags. Currently, we are working on implementing a third

monitoring technology to improve the quality of our space use and movement data. Despite their limited applicability for smaller animals, the two most commonly used methods are satellite-tracking and ground based telemetry (Harris, Cresswell et al. 1990; White and Garrott 1990; Cagnacci, Boitani et al. 2010; Hebblewhite and Haydon 2010). Over the last decade, an additional monitoring technology, wireless sensor networks (WSN), has begun to be used (Buratti, Conti et al. 2009). These WSNs can be used to monitor many aerial, aquatic and terrestrial species, allowing questions about competition, foraging, home range, mating, migration, movement pattern and space use to be answered. This chapter discusses these three technologies. Section 1.2 gives an overview of the history and functionality of each technology. Section 1.3 reviews their application to animal monitoring as well as their current technical limitations. The chapter concludes in section 1.4 with a summary and an outlook on future technologies.

The empirical data that many monitoring technologies can collect are essential for ecologists and evolutionary biologists to test their hypotheses and for conservationists to successfully implement conservation strategies. However, many hypotheses can only be tested by monitoring animals over long time periods, which can be restricted by technical limitations of monitoring devices. In chapter III, I assess the impact of one central technical limitation, the temporal resolution, on the accuracy of monitoring data, used for space use analysis. Additionally, some hypotheses are difficult to test with empirical data alone. Animal behaviour determining space use and movement is usually influenced by many different factors and observational approaches have limited power to disentangle the relative importance of individual factors on the behaviour, which researchers are interested in. The limited power of observational data can be increased by combining it with a

modelling approach. Models can test for the impact of a single factor on a complex structure and are not restricted by technical limitations, imposed on many monitoring technologies. In chapter II, I present a modelling approach, parameterized with data from our study population of wood mice, to test the effect of food availability, composition and distribution on animal space use, which would be infeasible to test in-situ.

Weight – A problem unifying monitoring technologies

Most monitoring technologies track an object by attaching a signal-transmitting device to it. The transmitter determines the spatial and temporal resolution of the location estimations, but also the length of the time-series data can be collected for. The amount of time data can be collected for is critically dependent on battery power, which can at the same time influence spatial and temporal accuracy. In practice, more battery power translates into heavier transmitter. For ethical and scientific reasons, in terrestrial species the maximum weight of a transmitter is limited to 5% of the animal's body weight (Cochran 1980). This restriction aims to avoid changes in behaviour and fitness caused by the transmitter and any negative consequences for the animal's welfare. In aquatic environment this limits is not as clear defined as in terrestrial applications, with suggestions of maximal weight ranging from 1.5% up to 12% of the animal's body weight (Ross and McCormick 1981; Anglea, Geist et al. 2004). The 5% threshold signifies that current transmitters are too heavy to track animals with body weights below 20 grams and therefore exclude many mammal, bird and invertebrate species from being monitored. It is important to note that the smallest and lightest transmitter currently available often have short lifespans of few hours and relatively poor relocation accuracies (Rychlik, Ruczynski et al. 2010; Vinatier, Chailleux et al. 2010; Wikelski, Moxley et al. 2010).

These transmitters cannot be used to answer most questions about animal space use, movement pattern and behaviour. For larger animals, the species-dependent limit of tag weight results in a fixed maximum of battery power available. Therefore, either the transmitter's lifetime or the spatial and temporal accuracy have to be prioritised, depending on the study's requirements. A longer battery life can be important, because many of the biological processes of interest span extensive time periods and replacing the battery (or the transmitter) can be highly invasive or just infeasible. On the other hand, many biological questions can only be answered if movement data has a minimum spatial and temporal resolution. Often, both lifetime and tracking accuracy must be reduced below the desire of researchers to match the weight restriction of the transmitter. It is therefore an important task during the design process of a study, that the researcher chooses the monitoring technology and a trade-off between lifetime and tracking accuracy that best fit the study's requirement.

History and technology

Satellite-based technologies

ARGOS

ARGOS was established in 1978 as a co-operation between the French space agency Centre National d'Etudes Spatiales, the National Aeronautics and Space Administration and the National Oceanic and Atmospheric Administration (NOAA, USA). In 2006 the European Meteorological Satellite Organization (Eumetsat) joined and launched its first MetOp satellite with ARGOS compatibility. The ARGOS system includes four components: the transmitters, six satellites, 60 ground stations and two processing stations in France and the USA (figure 1). The satellites orbit Earth at an altitude of 850km with a Pole-to-Pole revolution approximately every 100 minutes.

The orbit provides higher latitudes with better coverage than equatorial areas. The revolution at the equatorial plane is fixed to local solar time and therefore guarantees that (static) transmitters are passed at the same local time every day. The transmitter emits a signal to the satellites at a frequency of 401.650 MHz ± 30 kHz, with repetition periods between 90 and 200 seconds and transmission duration of less than one second. To calculate the transmitter's location the ARGOS system uses the Doppler Effect, a physical phenomenon whereby a satellite moving towards a transmitter records a higher frequency of the signal wave than is actually emitted by the transmitter, the same frequency when it is perpendicular to the transmitter and a lower frequency when it is moving away from the transmitter (figure 2). If the satellite receives four or more signals during a flying over of the transmitter, it can estimate the transmitter's location. After initial localization estimation, only one message is required to estimate the next position. The accuracy level of the location is then recorded and, together with the location data, sent to the ground stations. The ground stations then forward the information to one of the processing centres that in turn, make the data available to licensed users.

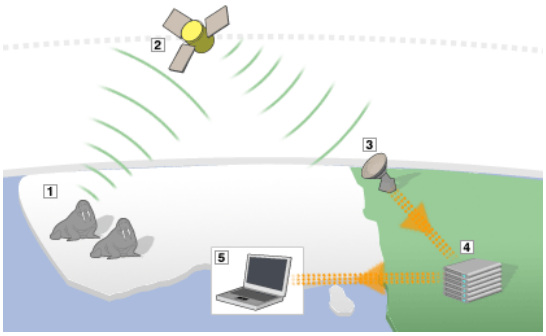


Figure 1: Different components of the ARGOS system. ARGOS transmitter attached to an object (1) transmit a signal that is detected by a satellite (2). The satellite sends information about (1) to the ground station (3). The information is then forwarded to the processing station (4) that makes it available to the user (5). Source: www.bbc.co.uk

GPS

GPS, established with the launch of an experimental satellite in 1978, is a satellite based localisation system used in both military and civil applications, owned by the United States of America and maintained by their Department of Defence. The

system contains three components: The satellites, the control segment and the user segment. Thirty satellites are currently in use, orbiting the Earth at an altitude of 20,200km. GPS satellites do not follow Earth's rotation but remain in a defined orbit. From every point on Earth, GPS devices are in principle able to detect nine satellites. GPS satellites transmit at frequencies of 1.57542 GHz and 1.2276 GHz, although only the higher frequency is available for civilian use. In contrast to the ARGOS system, GPS satellites do not detect broadcasting transmitters but constantly transmit signals that are detected by GPS receivers on Earth. The broadcast contains two codes- the course/acquisition code and the navigation message- that enable receiver units to calculate their own location. The coarse/acquisition code is transmitted constantly every millisecond, and is unique to every satellite. The navigation message, contains date, time, orbital information and data of the satellite's error correction. The navigation message is split up into five

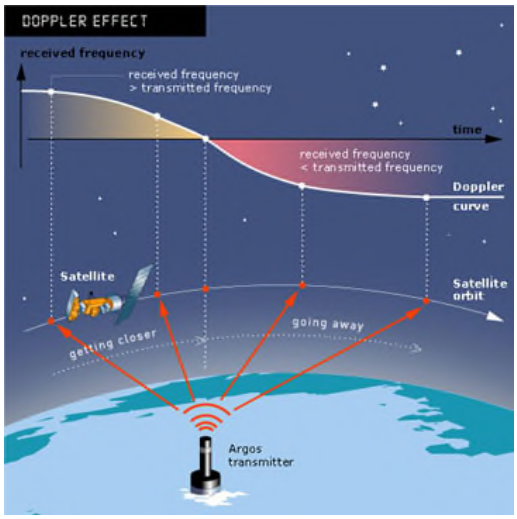


Figure 2: Calculation of location of an ARGOS transmitter using the Doppler Effect. The transmitter emits a signal at a specific frequency that is detected by the satellite. If the satellite is moving towards the transmitter the received frequency is higher than the transmitted frequency and lower when the satellite is moving away from the transmitter. If the satellite is perpendicular to the transmitter both frequency are equal. Source: www.argos-system.org

frames, which each take six seconds to be transmitted. The receiver uses information in the navigation message to calculate the satellite's position and the distance to the satellite by using the time difference in signal arrival. Time-of –Arrival is a method to estimate the distance between a transmitter and a receiver. By relating the signal frequency of the transmitter to the speed of light in a vacuum, the velocity of the signal can be calculated. The distance between receiver and transmitter is calculated, using the velocity and the signal's time of arrival at the receiver. The receiver then creates a virtual sphere with the radius equals to the receiver-transmitter distance as the radius. To estimate the position of a transmitter in a d-dimensional space, the minimum number of independent measurements required is d+1 (figure 3) (Watkins and Schevill 1972; Catipovic 1990).

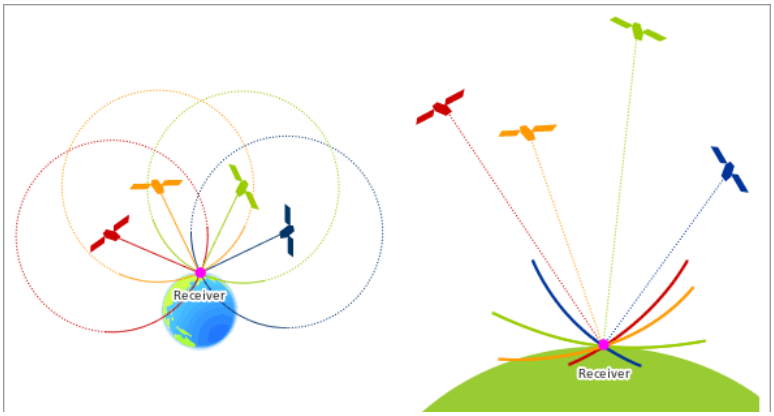


Figure 3: Calculation of the location of a GPS receiver. The receiver calculates position and distance for at least four satellites, using information transmitted by the satellites. Then it creates a virtual sphere for each satellite, with the radius equals to the distance to the satellite and the position of the satellite as the sphere's centre (left). Based on the assumption that the receiver is located somewhere on every sphere, the receiver's location is estimated as the intersection of at least four spheres (right). Source: www.jaxa.jp

Since the first launch of GPS satellites in 1978, accuracy has improved by including external, non-GPS satellite-based information into the localization process. Examples include the Satellite Based Augmentation System (SBAS), the European Geostationary Navigation Overlap Service (EGNOS) or the US-American Wide Area Augmentation System (WAAS) (Witte and Wilson 2005; Arnold and Zandbergen 2011). Alternatively, augmentation systems can also be ground based like the

Differential Global Positioning System (DGPS) (Bolstad, Jenks et al. 2005). For aquatic applications, where the transmitter has to be at the water surface for a sufficiently long period of time to estimate its position, fastloc GPS (or fast GPS) devices have been developed that reduces transmission time to less than 1 second (Hoenner, Whiting et al. 2012).

Telemetry

History

Wireless telemetric systems have been used since the early 1900s, with Bureau in 1930 being the first scientist to use a wireless device, *"the thermoradio sonde"*, to record weather data and send the information wirelessly to a receiver station (Zaitseva 1993). Since then telemetric systems have been used in many civil and military applications, especially during World War II and Cold War. Many telemetry-based applications have been replaced by satellite-based devices, but are still widely used for aerial applications, such as rockets and aircrafts (Kruk and Regan 1983). Since the early 1960s natural scientists started useing the technology for biological projects, both in aquatic and terrestrial applications (Campbell, Cyr et al. 1961; Lord, Cochran et al. 1962; Cochran and Lord 1963; Carey and Lawson 1973). The first biological applications were expensive and relied on military technology, but increasing demand and the development of off-the-shelf-components now give researchers easy and cheap access to telemetric technology (Naef-Daenzer, Fruh et al. 2005).

Technology

The telemetry technology used for biological applications can be classified into very-high frequency telemetry (VHF) mainly used for terrestrial projects, and acoustic telemetry, a technology primarily used for aquatic applications. Both technologies, however, follow the same basic idea: the tag or transmitter attached to the focal individual transmits a signal that is either a radio-frequency electromagnetic or acoustic wave, which is detected by one or more receivers. The receivers are either stationary or mobile, carried by the researcher or mounted on a vehicle. The signal can be used for localization of the transmitter or for recording the presence/absence of transmitters within the sensing radius of the receiver. Localization of the transmitter occurs via triangulation, either triangulation through time-of–arrival or trigonometric triangulation. Time-of-Arrival is discussed in detail in the GPS technology section and in figure 3. Trigonometric triangulation uses angles from at least two known points to the transmitter, where the distances between the two known points is known (figure 4). Thus, to estimate a two-dimensional position the signal has to be detected by at least two different receivers with known distances to each other, or by the same receiver in two different location. To make the second method as accurate as possible, it is crucial that the second measurement is taken before the target has moved to a new position that exceeds the localization error. In contrast to satellite-based technology, telemetry can

VHF

VHF is defined by the International Telecommunication Union as radio frequencies between 30-300MHz (*www.itu.int*). Each transmitter uses a separate frequency which, in the most basic applications, also serves as the transmitter's ID. For many applications, VHF receivers are mobile and carried by researchers following the transmitter. In recent years, advances in technology have resulted in more complex

(1)

set-ups with stationary towers receiving simultaneously signals from numerous tagged animals (Kays, Tilak et al. 2011). When VHF signals hit an object, other than the receiver, the signal slows down, gets absorbed or diffracted. Therefore, with increasing habitat structure and distance VHF signals become less detectable and spatial error increases. Elevation, vegetation, buildings and other features such as rocks and logs reduce the maximum distance at which the receiver can detect a signal and increase the spatial error in location estimation (Belant 2009; Rychlik, Ruczynski et al. 2010). With few exceptions, such as flat deserts, VHF signals are only reliable over short-distance transmission within the line of sight (Montgomery, Roloff et al. 2010).

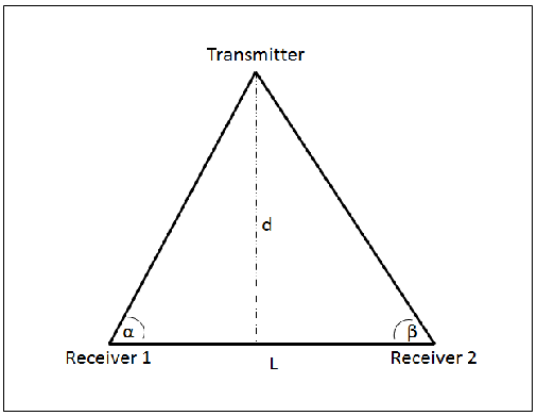


Figure 4: Trigonometric triangulation used for telemetric localization. With length L and the angles α and β distance d can be calculated using equation 1.

$$\frac{1}{d} = \frac{\sin(\alpha + \beta)}{L * sin\alpha * sin\beta}$$

Acoustic telemetry

Acoustic telemetry, in contrast, is mainly used for aquatic systems where electromagnetic waves are absorbed by (salt) water (Campbell, Cyr et al. 1961; Baggeroer 1984; Weiland, Deng et al. 2011). Transmitters attached or implanted in an individual send a unique acoustic signal that is detected by hydrophones. Frequencies span a broad range of at least 100 - 500 kHz (Deng, Weiland et al. 2011). Hydrophones are either stationary or mobile, for instance when installed on a boat or floating research station. Localization in water is more difficult than in terrestrial environment and reduces the spatial range over which acoustic signals

can be detected. For accurate position estimation, the maximum distance lies at approximately 100 meter (Grothues 2009).

Wireless sensor network (WSN)

History

Wireless sensors were developed in the late 1980s and early 1990s (Neukomm and Kundig 1990). During the mid-90s, increasing computational power allowed the development of more complex sensor networks. But only with reduction of weight and size of crucial components the start of the new century research of WSNs took off (Bult 2006; Kulkarni, Tilak et al. 2007; Buratti, Conti et al. 2009; Katiyar, Chand et al. 2010). Today, WSN is a collective term that refers to a diverse technology that is used in many different applications and the object of many research areas (Szewczyk, Polastre et al. 2004; Navarro, Davis et al. 2013).

Technology

General concept

WSN is a collective term for many different applications that have a single concept in common: A network of several sensors that can gather data and transmit them wirelessly. A WSN usually has three main components: one or several nodes, a sink and a gateway. A node is a small, low cost, low power, ‘intelligent’ sensing device. Each node can measure, detect, track and/or classify a physical quantity (for example temperature, pressure or humidity) or an object and send information via radio waves to a sink. Multiple nodes can use one sink, which can also be a node itself. The sink collects the data from the nodes and forwards it to the (remote) user

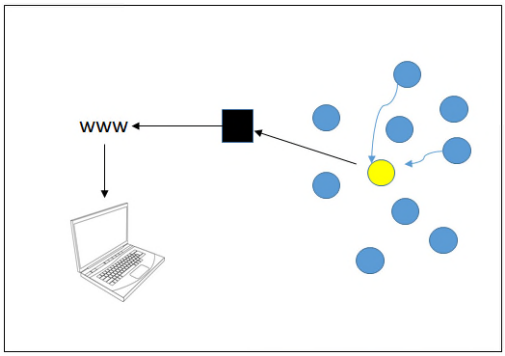


Figure 5: Basic concept of a WSN. Nodes (blue circles) send information to a sink (yellow circle). The sink bundles information and uploads it through the gateway (black box) to the internet ("www") where it can be downloaded by the remote user.

through the gateway (figure 5) (Akyildiz 2002; McErlean and Narayanan 2002; Balasubramanian and Aksoy 2004; Culler, Estrin et al. 2004; Melo, Pedrosa et al. 2009). The number of nodes and sinks in a WSN is theoretically unlimited and networks with several hundreds of nodes have been deployed successfully (Mainwaring, Culler et al. 2002). Besides the common concept and use of the same main components WSNs do not have a unique technological feature that makes them clearly distinguishable from other monitoring technologies. In fact they often incorporate different elements from other technologies. In many ways, WSNs are similar to widely used ad-hoc networks but can be distinguished from them by their less complex devices used (Balasubramanian and Aksoy 2004; Buratti, Conti et al. 2009). The different application WSNs can be used for are so diverse that sensing modalities, sensor design, and packaging vary from application to application (Balasubramanian and Aksoy 2004). For example, in-door and industrial applications require high measuring consistency, high data transfer rates, security and inter-operability, while outdoor applications have to incorporate a limited power supply and low amounts of data transfer as well as mechanisms for field calibration, diagnostic and monitoring tools (Whitehouse and Culler 2002; Zhao 2003).

Categorisation by WSN features

Due to the variability of WSN applications it is difficult to define clearly distinguishable types of WSNs. However, several distinctions can be made based on individual characteristics of a WSN:

A) **Data transmission via simple node-sink connection or multi-hop connection**: In simple structured WSNs each node must be positioned so that the sink is within its sensing range, while in multi-hop WSNs nodes can forward information to a neighbouring node, and so on until it reaches the sink. The latter is necessary in networks with sparsely distributed nodes and/or with nodes that have only a small sensing radius.

B) **Transmission rate**: The transmission rate from node to sink can vary from no transmission of data but local storage, to real-time transmission. Data transmission is usually more energy consuming than data acquisition. Many applications with limited energy supply vary the transmission rate, with regular intervals of high rates of data transmission and no data transmission (but data storage) in between (Guo, Corke et al. 2006; Rutishauser, Petkov et al. 2011).

C) **Node sink communication**: The communication between nodes and sink can be one-way, with nodes only transferring data to the sink, or two-ways, with nodes and sink able to send and receive information (Zhang, Sadler et al. 2004; Rutishauser, Petkov et al. 2011). The latter is particularly helpful if a specific node needs to be contacted to request data, or when, for example, a sampling protocol has to be updated.

D) **Mobility**: Both nodes and sinks can either be static or mobile (Kansal, Rahimi et al. 2004; Pon, Batalin et al. 2005; Song and Guizani 2006).

E) **Network structure**: WSNs can be categorised into star, mesh
tree networks (Szewczyk, Polastre et al. 2004; Buratti, Conti et a
Ellwood et al. 2012). Star networks have the most basic structure with one sink receiving information from all nodes (figure 5). In a mesh network several sinks are used and nodes have usually more than one sink in their sensing

radii. Star networks can suffer from a lack of scalability while mesh networks have theoretically no scalability limits (Chih-Yu, Yu-Chee et al. 2006). In cluster tree networks, several hierarchical levels are combined into one design (figure 6) (Mainwaring, Culler et al. 2002). One sink is the terminal for all the nodes within a cluster (Mainwaring, Culler et al. 2002). A cluster might be spatially defined, such that one sink covers a particular area and all nodes within that area use the same sink. Alternatively, the sink is connected to a pre-defined set of nodes that can only use the associated sink. Such pre-defined designs are especially used in application where the sink also collects data representative for the nodes in the cluster (Thorstensen, Syversen et al. 2004; Buratti, Conti et al. 2009).

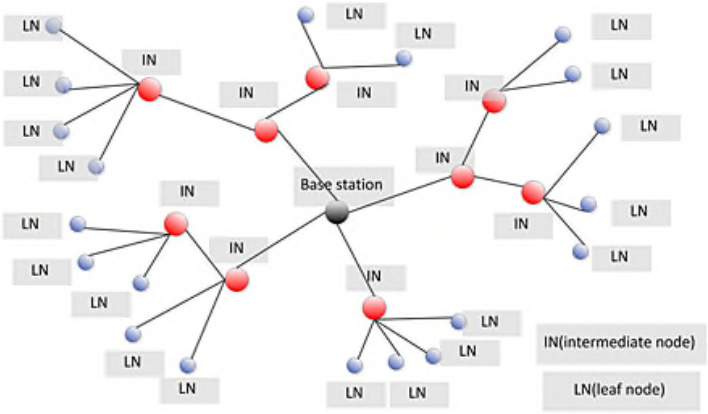


Figure 6: Design of a cluster tree WSN with hierarchical levels. Nodes (LN) within one cluster send data to cluster's sink (IN). The sink then forwards the data either directly or via another sink to the main sink (Base station). Source: Liu et al., 2012

F) **Tagged vs. untagged objects**: WSNs can also be distinguished by the node's ability to locate objects, which may be either tagged or untagged. In WSNs designed for tagged objects, a node can detect a tagged object or is the tagged object. In both cases additional technologies are usually used to estimate the object's position. In a way, these WSNs can be seen as extended networks of GPS-based or telemetry based devices. The advantage of such WSNs is that nodes can communicate, at least with the sink, and

more frequently with neighbouring nodes, too. This improves and simplifies data collection and makes it easier to adjust nodes to changes in the set-up or environment, for example, by updating the sampling protocol. Nodes in WSNs for untagged objects detect an object passing through its sensing radius by using light, infrared, acoustic or motion sensors. These work by comparing a measured value to a baseline value, and if this difference is larger than a pre-defined threshold the node reports the detection of an object to the sink. However, the object's identification, its exact position and its movement direction is unknown, so in principle all nodes have to continue to scan their sensing area. Constant node search for objects is energy consuming and reduces battery life span (Tsai, Chu et al. 2007; Tsukamoto, Ueda et al. 2009). The grouped design of nodes in cluster tree networks makes it easier to track untagged objects. Nodes within a cluster report a detection to the cluster's sink , which then activates the nodes, which are most likely to be close to the untagged object (Balasubramanian and Aksoy 2004; Barrenetxea, Fran et al. 2008). Tracking success increases if movement occurs in a regular pattern or in easily controllable check-points but decreases for objects with a random movement type pattern (Tao, Barolli et al. 2010).

The node

A node is the distinguishing element within a WSN. Many nodes are purpose-designed for specific applications and, so far, there is no market leader offering standardized devices (Buratti, Conti et al. 2009). Despite the lack of mass-producing brands and the specific requirements for each application, several hardware platforms have gained wider attention from researchers. Widely used platforms include MICA and MICA2 nodes (Malan, Fulford-Jones et al. 2004; Shen, Wang et

al. 2004; Zhang, Sadler et al. 2004), FLECK (Sikka, Corke et al. 2004), Zigbee (Kinney 2003) and TELOS platforms (figure 7) (Polastre, Szewczyk et al. 2005). Additional nodes have been developed at Harvard (Werner-Allen, Swieskowski et al. 2005), Intel (Kling 2004), MIT (Min, Bhardwaj et al. 2002), the Rockwell Science Centre (Agre, Clare et al. 2001), Motorola Labs (Hester et al. 2002) and by Pakanen et al. (2002). The main distinctions are different types of microcontrollers and communication devices, as well as differences in power consumption and chip memory. The platforms support a variety of technological add-ons such as GPS, radio, 3-axis-accelerometers, sensors measuring physical quantities and even own power sources such as solar cells (Akyildiz 2002; Thorstensen, Syversen et al. 2004; Zhang, Sadler et al. 2004). Explaining differences between the nodes in detail would go beyond this review but can be found at Polastre et al. (2005).

Figure 7: Example of a node, the TELOS platform. The node, excluding battery and packaging, measures 65 x 31 x 6 mm and weights 23 grams. It has a maximum transmission power of 1mW. Image: Polastre at al., 2005.

Many applications require nodes of small size, low weight and long lifetime. Factors, such as design, packaging and radio range, affect weight, size and lifetime, especially if the application is used outdoors. The most influential factor, however, is the battery. The choice of battery has implications for the device's weight and size, the choice of hardware, data collection and signal transmission (Goldsmith and Wicker 2002; Matthews, Hendrickson et al. 2002; Raghunathan, Schurgers et al. 2002; Barrenetxea, Fran et al. 2008; Buratti, Conti et al. 2009). Because of the high priority of power saving requirements nodes are normally designed to work in duty-cycles rather than in a constantly transmitting mode. To safe battery power a node is usually "sleeping". At regular intervals the node "wakes" and performs its task. It then

sends its ID, its data and, in the case of a multi-hop system, other node's data to the neighbouring node or the sink. In a two-way application the node waits for a signal from the sink or the neighbouring nodes and then returns to the power saving mode (Thorstensen, Syversen et al. 2004). Nodes working in duty-cycles have a much longer life span than constantly active nodes. However, in networks where duty-cycles of node and sink are not synchronized, data transmission can only be successful if both, node and sink, are by chance active at the same time. Additionally, there is the risk of data collision if two nodes send data at the same time to the same sink. Both problems do not exist in synchronized networks (for example those using GPS-based clocks) at the expenses of weight and battery lifetime. Additional research has been conducted on data collision, so that unsynchronized nodes transmitting to the same sink repeat data transmission until a slot is free and therefore avoid data loss due to collision (Szewczyk, Polastre et al. 2004; Polastre, Szewczyk et al. 2005). Additionally, algorithms have been developed that can prioritise transmission strategies (sample-and-send vs. sample-and-store) depending on the network activity and therefore reduce data collision(Balasubramanian and Aksoy 2004; Werner-Allen, Dawson-Haggerty et al. 2008; Zeynali, Mollanejad et al. 2011). For example, if nodes are designed to collect weather data and to track an object, a solution to reduce the risk of data collision could be that only tracking data is transmitted to the sink to guarantee successful tracking and the weather data would be stored at the node until the tracking process stops and network activity is low.

A node's lifetime is usually rather short given that batteries are generally small and light whilst powering multiple complex tasks. Once the node runs out of battery it can be recollected for additional data download, reprogramming and re-use. Ekici et al.

(2006) developed an algorithm that orders mobile sinks to visit (static) nodes before storage capacity or the end of battery lifespan is reached. In the case of mobile objects nodes can be designed to drop from the object after a pre-defined time period (Zhang, Sadler et al. 2004; Mennill, Doucet et al. 2012). In other applications, mobile nodes transmit data to the neighbouring node that has been close to the sink most recently thereby increasing the likelihood of successful data transmission (Balasubramanian and Aksoy 2004)

Application and limitation

Many studies have specific requirements for the monitoring device's weight, size, life time and the resolution of the collected data. Therefore, most devices are uniquely designed and programmed to fit the study's requirements. Due to the variety of devices, it is, therefore, difficult to provide generally valid information for each technology regarding the device's weight, resolution and life time. The following section is not exhaustive, but aims to give an overview of the main limitations of each technology, the questions that can be answered by using the technology and the species that can be monitored.

Satellite-based technologies

ARGOS

Transmitters with ARGOS technology allow location estimation with a spatial accuracy of 250m – 1500m. (Costa, Robinson et al. 2010; Dubinin, Lushchekina et al. 2010). The temporal resolution is set at one fixed point every 100 minutes per satellite. The latest generation of transmitters weigh 5g, making it possible to monitor species with a body weight as low as 100g (Bridge, Thorup et al. 2011). In practice,

however, the use of ARGOS technology is only feasible if the animal covers a distance between localization events that is larger than the spatial error of ARGOS resolution. In addition, the low temporal resolution also limits the extent to which ARGOS can be used in biological applications. The fix rate increases slightly with shorter distances to the poles, because at higher latitudes several satellites cover the same area and fix rates are not synchronized across satellites. The temporal resolution therefore increases, if the tracked animal is recorded at higher latitudes.

In recent years, ARGOS application are increasingly used in combination with other monitoring technologies, such as GPS, Pop-Archival-Tag (PAT), accelerometer and telemetry (Weimerskirch, Le Corre et al. 2005; Mate 2012; Thums, Whiting et al. 2013). Combinations of several technologies allow answering new questions, which could not be answered by using ARGOS devices alone. GPS and telemetry can increase the spatial and temporal resolution of the data, while accelerometers can be used to address behavioural questions, such as foraging or sleeping patterns. PATs estimate location using light levels rather than satellite technology, and also record depth and temperature (Hammerschlag, Gallagher et al. 2011).

ARGOS transmitters are mainly used to answer questions about animals that show large scale movement such as migrating birds and marine animals, and in particular marine mammals, turtles and sharks (Frydman and Gales 2007; Robinson, Bowlin et al. 2009; Bridge, Thorup et al. 2011; Guilford, Åkesson et al. 2011; Hammerschlag, Gallagher et al. 2011; Hoenner, Whiting et al. 2012; Seminoff, Benson et al. 2012). The technology cannot be used for species with movement patterns smaller than the minimal spatial error. Additionally, in marine systems the application of ARGOS technology is restricted to species that at least swim occasionally to the water's surface, where accuracy greatly increases with the time

spent at the surface (Hammerschlag, Gallagher et al. 2011). Its use is also restricted to address questions about general space use, movement and migratory behaviour, excluding questions about habitat use and intra-and inter specific behaviour.

GPS

Spatial accuracy of GPS technology is much higher than ARGOS-based application with a maximum resolution of currently 10m. In combination with additional augmentation systems, accuracy can increase up to 0.5m (Bolstad, Jenks et al. 2005). Temporal resolution of the fixes is technically not restricted and real-time resolution is possible. Use of GPS technology in many civilian and military sectors has led to considerable reduction of weight in GPS devices down to 22g (Bridge, Thorup et al. 2011). In practice, however, such high spatial and temporal accuracy is rarely achieved. Spatial accuracy is often reduced by topographical interferences and habitat features. Temporal resolution remotely near to real-time is technically possible but reduces the life span to a few weeks and increases weight to at least 600 grams (Eriksen, Wabakken et al. 2009). Similar, additional augmentation systems increase not only the accuracy but the weight by 50% to at least 32grams (Witte and Wilson 2005).

Many studies, nowadays, combine GPS technology with other tracking methods (Horback, Miller et al. 2012). Combinations of two technologies can be used to address new questions that cannot be answered by using only GPS-based devices or to improve accuracy by generating additional spatial points. Recent combinations of GPS devices and WSN technology make recapture to download data no longer necessary and reduce number of captures to two, one for the initial attachment and another for the final removal of the tag (Zhang, Sadler et al. 2004; Rodríguez, Negro

et al. 2012). The combination of GPS and accelerometer allows behavioural questions being addressed (Grünewälder, Broekhuis et al. 2012) and the combination of GPS and unmanned aerial systems allows the monitoring of foraging regions (Rodríguez, Negro et al. 2012). Additional spatial points for space use and movement analysis can be created by analysing stable isotope to reveal the origin of migrating species (Seminoff, Benson et al. 2012) or by colouring faeces for foraging behaviour analysis (Giroux, Dussault et al. 2012).

GPS technology enables biologists to answer a broad range of questions about movement patterns, home range size and use, migration, space and habitat use for many terrestrial animals with minimum body weight of 500 grams (Strandberg, Klaassen et al. 2010; Recio, Mathieu et al. 2011; Giroux, Dussault et al. 2012; Grünewälder, Broekhuis et al. 2012; Rodríguez, Negro et al. 2012; Shamoun-Baranes, van Loon et al. 2012). In addition, GPS transmitter can be used to monitor aquatic animals, if they return occasionally to the water's surface. The usability of GPS devices to answer questions about small scale behaviour, such as habitat use or intra- and inter-specific behaviour depends on the focal species and its movement range. It is possible for larger animals, where movement distances between two fixes are usually larger than the spatial error. Additionally, a higher maximum tag weight for larger animals allows to include augmentation systems to increase spatial accuracy and to use heavier batteries to increase the frequency of fixes. A high fix rate is particularly required to answer any questions about animal behaviour. For animals that only can be equipped with light transmitters, questions about general movement pattern and space use can be answered. GPS technology cannot be used to address questions about small scale movement pattern, space use and

inter- and intra-specific behaviour of small animals because of the low spatial and temporal resolution of light transmitters.

ICARUS- a look ahead

In 2002 the ICARUS project was founded, an initiative from a consortium of scientists, research institutions and funding bodies across the globe. Its ambitious goal is to install a highly sensitive receiver on the International Space Station (ISS) to provide global positioning of low-power (1 mW), low weight (<1 gr) tags with a relatively high accuracy of few kilometres to monitor migrating animals (Wikelski, Kays et al. 2007). If the initiative succeeds it would solve many of the limitations ARGOS and GPS based devices are facing at the moment. Tags would be light enough to attach them to species with a body weight of just 20grams that have not been monitored so far. The project has the potential to greatly extend our knowledge of the ecology of small, terrestrial animals. So far the final stage of the project has not been launched and it is not certain whether the large fund investments required to allow the project to continue will be available during a time when Western countries are cutting research budgets (Pennisi 2011).

Telemetry

VHF

Monitoring devices using very-high-frequency telemetry can estimate location with a spatial accuracy of 5-50 meter and, similarly to GPS technology, do not have temporal resolution technically restricted (Rychlik, Ruczynski et al. 2010; Bridge, Thorup et al. 2011). Devices of 300mg are now available, making VHF transmitters considerably lighter than acoustic telemetry devices and satellite-based transmitters

(Wikelski, Kays et al. 2007 2). Spatial accuracy remains to be a central limitation in VHF studies, as accuracies <50m are only achieved under ideal conditions or with complex, spatially restricted set-ups and powerful batteries, increasing the weight of the transmitter (Kays, Tilak et al. 2011). Although telemetry is not as strongly affected by vegetation as satellite based systems, vegetation, rock and elevations still increase localization error, make position estimation less reliable and decrease the maximum distance that a receiver can detect a transmitter (Belant 2009; Montgomery, Roloff et al. 2010; Rychlik, Ruczynski et al. 2010; Kays, Tilak et al. 2011). Frequency of fixes higher than one fix per hour reduce lifespan to 2-10 days for transmitters of 0.5 gram (Rychlik, Ruczynski et al. 2010). Short life span results in small number of spatial points which can lead to home range size estimates scaling with number of records (Wikelski, Moxley et al. 2010). In addition to limitations of accuracy and resolution, most VHF application still include the researcher to be in relatively close proximity to the focal individual. The high degree of manual labour is expensive, can lead to bias in sampling intervals and might also alter the tagged individual's behaviour (Fieberg 2007; Rowley and Alford 2007; Tarlow and Blumstein 2007). This is important in studies on small species that require, smaller batteries. Smaller batteries usually result in weaker signals which force the researcher to move even closer towards the tagged individual (Rychlik, Ruczynski et al. 2010).

In recent years, combinations of VHF with satellite-based technology and sensors for body temperature, pulse and behaviour recording accelerometers are increasingly used (Brøseth and Pedersen 2000; Sheppard, Preen et al. 2006; Soisalo and Cavalcanti 2006). In these applications, VHF is now mainly used to transmit the stored sensor data and not for location estimation, as GPS data is usually more spatially accurate (Sheppard, Preen et al. 2006).

VHF can be used to study individuals or small groups of many mammals, reptiles and invertebrates with body weights of only up to 10 grams. The technology helps answering questions about their behaviour, movement pattern, space use, resource use and migratory behaviour (Harris, Cresswell et al. 1990; Thompson, Hammond et al. 1991; Bobek, Simek et al. 2002; Hedin and Ranius 2002; Cadahía, Urios et al. 2005; Rittenhouse and Semlitsch 2007; Bridge, Thorup et al. 2011; Guilford, Åkesson et al. 2011; Way and Timm 2011; Grünewälder, Broekhuis et al. 2012; Trevelin, Silveira et al. 2013). Currently, VHF devices allow monitoring of many species with body weights too low for transmitters of other technologies, such as GPS-based devices. However, some approaches to monitor even smallest animals, for example small beetles and hymenoptera with sub-gram body weights, often exceed the tag-body weight ratio of 5% and can be as high as 1:1 (Vinatier, Chailleux et al. 2010; Wikelski, Moxley et al.). VHF cannot be used to answer questions that require a higher temporal resolution than one fix every few hours, thus excluding questions about small scale movement and space use, as well as intra- and inter-specific behaviour. Additionally, species with movement pattern that are smaller than the spatial error cannot be monitored. Finally, VHF is difficult to use for animals with inaccessible habitats, such as alpine species, and species that cover large areas and move quickly, therefore excluding many bird species from VHF tracking.

Acoustic telemetry

Acoustic telemetry devices reach a spatial accuracy of between 0.2 – 2m (Grothues 2009; Deng, Weiland et al. 2011; Afonso, Graca et al. 2012). Similar to other monitoring technologies, acoustic telemetry does not have a rate of fixes that is technically restricted and near-real time resolution is possible (Weiland, Deng et al.

2011). Weight of acoustic telemetric devices has been reduced over recent years and transmitters weighing three grams are now available (Stark, Jackson et al. 2005; Grothues, Able et al. 2012; Thums, Whiting et al. 2013). In practice, spatial accuracy usually depends on the proximity of the tag to the receiver. In some application, spatial accuracy can be as high as 0.02 – 0.2 m within a range of 100m from the receiver and drops sharply for distances larger than 100m (Weiland, Deng et al. 2011). As in many monitoring technologies, temporal resolution depends on battery and the life span of the transmitter. Life span for smaller transmitters varies between 14 days and 3 months, for near-real time resolution and position estimation (Brunnschweiler 2009; Simpfendorfer, Wiley et al. 2010; Thums, Whiting et al. 2013) and several years for presence/absence data (Afonso, Graca et al. 2012)

Several projects have aimed to combine different technologies such as echo sounding, VHF and satellite technology, with acoustic telemetry to increase the applicability. For example, echo sounding increases the distances and areas that can be monitored, and combinations of acoustic telemetry, satellite technology and VHF applied to amphibious mammals provide the opportunity to monitor them in both habitats (Thompson, Hammond et al. 1991; Lyons and Lucas 2002; Kelly, Badajos et al. 2010).

Acoustic telemetry is widely used to answer questions about animal behaviour, movement pattern, space use, resource use and migratory behaviour in many aquatic animals (Kilfoyle and Baggeroer 2000; Grothues 2009; Weiland, Deng et al. 2011). It is one of few tools that marine biologist and fishery scientists can use to collect data, because radar and satellite technologies - commonly used for terrestrial approaches - do not work underwater. Acoustic telemetry has helped identify migration routes, to analyse swimming behaviour of economically important fish

species and to assess the feasibility of conservation tools such as artificial coral reefs (Mellas and Haynes 1985; Clements, Jepsen et al. 2005; Bruce, Stevens et al. 2006; Reynolds, Powers et al. 2010; Clements, Hygnstrom et al. 2011; D'Anna, Giacalone et al. 2011). The high temporal resolution that acoustic transmitter can provide over several months, allows observation of intra- and inter-specific behaviour. In contrast to VHF, most acoustic receiver are stationary. Therefore, acoustic telemetry is only feasible if the individual remains within the receiver's sensing radius, such as coral reef species, or if movement patterns are sufficiently predictable that tagged animals repeatedly use the same routes (Weiland, Deng et al. 2011; Acolas, Rochard et al. 2012).

Wireless sensor networks

WSNs are used in many different areas and their applications are spreading so rapidly that there seems to be very few fields that would not benefit from this technology. Only in recent years, however, WSNs have begun to be used in biological applications. In other research areas, WSNs are already an important tool for data collection: Micro-climate control in buildings, nuclear, biological and chemical attack detection, agriculture, health monitoring, intelligent highway systems, emergency disaster response and home automation use wireless network to improve their performance (Cerpa, Elson et al. 2001; Intanagonwiwat, Estrin et al. 2002; Liu and Nicol 2002; Madden, Szewczyk et al. 2002; He, Huang et al. 2003; Patnode, Dunne et al. 2003; Akyildiz and Kasimoglu 2004; Bull, Limb et al. 2004; Younis and Fahmy 2004; Lee, Seo et al. 2006; Ong and Motani 2008; Mampentzidou, Karapistoli et al. 2012; Capella, Bonastre et al. 2013; Tseng, Lin et al. 2013). Military and security forces use WSNs to track enemies, detect illegal border crossing and monitor their own troops in conflict zones (Qi, Brady et al. 2006;

Tsai, Chu et al. 2007; Wittenburg, Terfloth et al. 2007; Chen, Zhou et al. 2013). WSN have even been used by researchers at Mecca to track pilgrim movements (Mohandes, Haleem et al. 2013).

In many ways, biological and environmental applications are more restricted than, for example, devices for industrial use. Weight and size constraints are even greater, it is more difficult to recollect the node for recharge, updating or maintenance, and outdoor conditions, animal behaviour and unpredictable movement patterns require even higher standards for packaging, data transmission, and tracking protocols. WSNs for untagged objects are widely used to monitor environmental phenomena at high temporal resolution and spatial accuracy. WSNs are currently in use to detect and monitor large scale environment patterns, such as volcano activity, changes in permafrost, fire spread, flooding or storms (Simic and Sastry 2003; Talzi, Hasler et al. 2007; Barrenetxea, Fran et al. 2008; Toriumi, Sei et al. 2008; Fabbri, Riihijarvi et al. 2009; Giorgetti, Lucchi et al. 2011; Sun and Jin 2011; Liu, Tan et al. 2013). Such networks collect high quality data, for example nodes used on volcanos record up to 100 different seismic intensities per second, while nodes remain cheap and small(Tan, Xing et al. 2010). For monitoring animals, WSNs for untagged objects have a limited applicability. Untagged animals are usually difficult to identify. WSNs for untagged objects can only be used to monitor individuals if their home range is within the sensing radius of a node or if they visit their nests regularly. Successful applications investigate, for example, the ecology of the sea birds on their remote breeding islands (Szewczyk et al. 2004). Nodes are placed inside of the birds' burrows and at the entrance, measuring weather data and, via infrared radiation, the presence of birds. Alternatively, WSN for untagged objects can detect general presence of animals, either at places that a frequently visit by animals, such as

certain points on migration routes, or places where animals are forced to use infrastructures, such as highways and railways safe passages (Garcia-Sanchez, Garcia-Sanchez et al. 2010).

WSNs for tagged objects, however, can identify and track individual animals (Mainwaring, Culler et al. 2002). It is therefore a powerful tool to understand movement pattern, space and habitat use, migration, mating, competition and foraging behaviour of many species (Cooke, Hinch et al. 2004). To date, WSNs have been used to monitor amphibians (Colonna, Ribas et al. 2012), birds (Mennill, Doucet et al. 2012), plants (Tolle and Culler 2005), turtles (Joshi, VishnuKanth et al. 2008) and mammals (Thorstensen, Syversen et al. 2004; Zhang, Sadler et al. 2004; Guo, Corke et al. 2006; Rutishauser, Petkov et al. 2011; Dyo, Ellwood et al. 2012). Depending on the application, nodes can weigh between less than 1 gram (Mennill, Doucet et al. 2012) and more than 1 kg (Zhang, Sadler et al. 2004) while sensing range varies between 15m and 3km and accuracy between 5m and several 100m (Thorstensen, Syversen et al. 2004; Zhang, Sadler et al. 2004; Guo, Corke et al. 2006; Mennill, Doucet et al. 2012).

The following three examples give an overview of how WSNs can be used for monitoring applications:

Rutishauser et al. (2011) developed the CARNIVORE system, to track solitary, carnivorous species and monitor their movement and space use. Spatial data points are collected using GPS-based technology and behavioural data is recorded with a 3-axis-acceleremoter. Due to the sparse network, solitary species create and the large territories that individuals can cover, the system was designed to operate only with periodic connectivity and store the data otherwise. Data can be transmitted to

the sink and to other nodes. The nodes, with a weight of 450 grams, are synchronized via GPS which reduces data loss due to collision. It also provides nodes with information about which of the neighbouring nodes connected most recently to the sink.

Similarly, the ZebraNet application includes a WSN that is designed to monitor movement and space use of large ungulates that cover large areas (Zhang et al., 2004). Node-to-node data flow is even more important as the system has no static sinks, since this is not feasible for species without constant home ranges. However, to ultimately collect the data researchers can use mobile sinks that have much larger ranges and can collect data from several individuals simultaneously. ZebraNet's nodes weigh approximately 1150grams and include rechargeable batteries and battery supporting solar cells. The latter does not only extend the nodes' lifetime but also improve its GPS performance. ZebraNet is particularly useful for mobile systems where it is difficult to install static sinks.

A contrasting approach uses a cluster tree network to monitor domestic sheep, hence called the "Electronic shepherd" (ES) (Thorstensen et al. (2004). ES is designed to monitor gregarious animals with consistent sub-group structures, where one sub-group (for example one mother sheep with her offspring) is defined as one cluster. ES has one main node attached to an individual per sub-group that collects spatial data. In addition, the main node receives data (for instance dead/alive or body temperature) from the other individuals, which carry a simpler node. The main node then forward all the compiled data to a terminal that makes it available to the user. ES provides an interesting approach using two types of nodes in one system. For studies in which it is not necessary or practically possible to collect all data from all individuals the ES concept could be successfully implemented.

At the time of writing research in all fields of the WSN technology is continuing {Katiyar, 2010 #1724;Low, 2013 #1722; Silicon Labs (http://www.silabs.com)}. Longer battery lifetime remains one of the biggest challenges in WSN applications and the main reason why only few long term studies using WSN technology have been conducted so far (Szewczyk, Osterweil et al. 2004). Further research will continue to see a reduction of node sizes and will eventually aim for more standardization of all parts of a WSN (Rabaey, Ammer et al. 2000; Buratti, Conti et al. 2009). Standardization of WSN components would enable larger scale production and would bring down costs per project (Costa, Robinson et al. 2010; Low 2013). Another part of ongoing research are nodes that can be reprogrammed remotely, so that protocols can be adjusted to local or changing conditions (Wang and Chandrakasan 2002; Dyo, Ellwood et al. 2012). Finally, other technologies exists such as Bluetooth, ANT technology or ultra wide bandwidth technology that could be implemented in WSNs to improve spatial and temporal resolution and increase the device's sensing radius (for a review see Buratti et al. (2009)).

Summary

Satellite-based tracking and telemetry are two powerful and widely used technologies to track animals. Recently, wireless sensor networks have begun to be used to monitor animals. Satellite-based systems have the great advantage of providing global coverage, at the expense of accuracy (ARGOS) and weight (GPS). Telemetry is much more spatially restricted and, in case of terrestrial telemetry, still depending to a large degree on researchers' sampling effort. The advantage of telemetry devices is the much lower weight, simpler set-up and lower costs. In addition, recent installations of static telemetric receivers seem to decrease the usually large spatial error.

In recent years, applications tend to combine different technologies to improve data acquisition and transmission. GPS-based systems now use terrestrial augmentation systems, practically telemetry, to improve accuracy. Terrestrial telemetry now often uses satellite-based systems for relocation and only uses telemetry to transmit the data to the receiver. WSNs for tagged objects use GPS to locate the node's position. The node then transmits the GPS data and additional information from its sensors (for example heart rate, body temperature or data from accelerometers), via telemetry to the sink or neighbouring nodes. The sink forwards the data, again via telemetry or satellite-based applications, to the remote user.

Despite the advantages across different technologies, most limitations are related to the weight of the device. In an application without weight limitations, data with a remarkably high spatial accuracy and with real-time resolution can be recorded over long periods of time. Unfortunately, weight does matter in most applications and the battery is usually the heaviest component of tracking device. It is an important task for future research to develop transmitters that are small and light enough to be carried by species smaller than 50 grams, while producing data with high spatial accuracy and temporal resolution. The author believes for two reasons that such transmitters are more likely to be based on a technology similar to static telemetric receivers (Kays, Tilak et al. 2011 649) than satellite-based technology such as ICARUS (Wikelski, Kays et al. 2007 2). First, even with a relatively low power demanding localization method as used by ARGOS application, terrestrial applications are generally less power demanding than satellite applications. Location data with similar spatial accuracy and temporal resolution but less power consumption can be recorded using telemetry-based application compared to satellite based technology. Second, excluding small migratory birds, currently most

small-bided species cannot be monitored at an adequate spatial and temporal resolution. In most cases their home range sizes can be covered by one or more automated receivers. Thus, a satellite-based application providing global coverage at the expense of weight and accuracy might no longer be an advantage, adding unnecessary costs and complexity to the technology. It seems hence more important to focus future research on light, small and long-lived transmitters that can estimate locations locally not globally and at high spatial accuracy and temporal resolution.

References

Acolas, M. L., E. Rochard, et al. (2012). "Downstream migration patterns of one-year-old hatchery-reared European sturgeon (Acipenser sturio)." Journal of Experimental Marine Biology and Ecology 430–431(0): 68-77.

Afonso, P., G. Graca, et al. (2012). "First observations on seamount habitat use of blackspot seabream (Pagellus bogaraveo) using acoustic telemetry." Journal of Experimental Marine Biology and Ecology 436: 1-10.

Agre, J. R., L. P. Clare, et al. (2001). Wireless integrated sensor network using multiple relayed communications, Google Patents.

Akyildiz, I. F. (2002). "Wireless sensor networks: a survey." Computer networks 38(4): 393-422.

Akyildiz, I. F. and I. H. Kasimoglu (2004). "Wireless sensor and actor networks: research challenges." Ad Hoc Networks 2(4): 351-367.

Anglea, S. M., D. R. Geist, et al. (2004). "Effects of acoustic transmitters on swimming performance and predator avoidance of juvenile Chinook salmon." North American Journal of Fisheries Management 24(1): 162-170.

Arnold, L. L. and P. A. Zandbergen (2011). "Positional accuracy of the Wide Area Augmentation System in consumer-grade GPS units." Computers & Geosciences 37(7): 883-892.

Baggeroer, A. B. (1984). "Acoustic telemetry-an overview." Oceanic Engineering, IEEE Journal of 9(4): 229-235.

Balasubramanian, S. and D. Aksoy (2004). Automatic registration for dynamic and reconfigurable sensor networks. Local and Metropolitan Area Networks, 2004. LANMAN 2004. The 13th IEEE Workshop on.

Barrenetxea, G., Fran, et al. (2008). The hitchhiker's guide to successful wireless sensor network deployments. Proceedings of the 6th ACM conference on Embedded network sensor systems. Raleigh, NC, USA, ACM: 43-56.

Belant, J. L. (2009). "Effects of antenna orientation and vegetation on global positioning system telemetry collar performance." Northeastern Naturalist 16(4): 577-584.

Bobek, M., J. Simek, et al. (2002). "Migration patterns of Black Storks (Ciconia nigra) from the Czech Republic as revealed by Satellite and VHF Telemetry." Le Bulletin AVES 40.

Bolstad, P., A. Jenks, et al. (2005). "A Comparison of Autonomous, WAAS, Real-Time, and Post-Processed Global Positioning Systems (GPS) Accuracies in Northern Forests." Northern Journal of Applied Forestry 22(1): 5-11.

Booth, W., W. Montgomery, et al. (2009). "Spatial genetic structuring in a vagile species, the European wood mouse." Journal of Zoology 279(3): 219-228.

Börger, L., N. Franconi, et al. (2006). "An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size." The American Naturalist 168(4): 471-485.

Bridge, E. S., K. Thorup, et al. (2011). Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. BioScience, American Institute of Biological Sciences. 61: 689-698.

Brøseth, H. and H. C. Pedersen (2000). "Hunting effort and game vulnerability studies on a small scale: a new technique combining radio-telemetry, GPS and GIS." Journal of Applied Ecology 37(1): 182-190.

Bruce, B., J. Stevens, et al. (2006). "Movements and swimming behaviour of white sharks (Carcharodon carcharias) in Australian waters." Marine Biology 150(2): 161-172.

Brunnschweiler, J. M. (2009). "Tracking free-ranging sharks with hand-fed intra-gastric acoustic transmitters." Marine and Freshwater Behaviour and Physiology 42(3): 201-209.

Bull, P., R. Limb, et al. (2004). "Pervasive Home Environments." BT Technology Journal 22(3): 65-72.

Bult, K. (2006). "The effect of technology scaling on power dissipation in analog circuits." Analog Circuit Design: 251-294.

Buratti, C., A. Conti, et al. (2009). "An Overview on Wireless Sensor Networks Technology and Evolution." Sensors 9(9): 6869-6896.

Cadahía, L., V. Urios, et al. (2005). "Survival and movements of satellite-tracked Bonelli's eagles Hieraaetus fasciatus during their first winter." Ibis 147(2): 415-419.

Cagnacci, F., L. Boitani, et al. (2010). "Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges." Philosophical Transactions of the Royal Society B: Biological Sciences 365(1550): 2157-2162.

Campbell, D. E., R. J. Cyr, et al. (1961). "Underwater Acoustic Telemetry." J Acoust Soc Am 33(11): 1681-1681.

Capella, J. V., A. Bonastre, et al. (2013). "In line river monitoring of nitrate concentration by means of a Wireless Sensor Network with energy harvesting." Sensors and Actuators B: Chemical 177(0): 419-427.

Carey, F. G. and K. D. Lawson (1973). "Temperature regulation in free-swimming bluefin tuna." Comparative Biochemistry and Physiology Part A: Physiology 44(2): 375-392.

Catipovic, J. A. (1990). "Performance limitations in underwater acoustic telemetry." Oceanic Engineering, IEEE Journal of 15(3): 205-216.

Cerpa, A., J. Elson, et al. (2001). "Habitat monitoring: application driver for wireless communications technology." SIGCOMM Comput. Commun. Rev. 31(2 supplement): 20-41.

Chen, J., L. Zhou, et al. (2013). "Human Motion Tracking With Wireless Wearable Sensor Network: Experience and Lessons." KSII Transactions on Internet & Information Systems 7(5).

Chih-Yu, L., T. Yu-Chee, et al. (2006). Message-efficient in-network location management in a multi-sink wireless sensor network. Sensor Networks, Ubiquitous, and Trustworthy Computing, 2006. IEEE International Conference on.

Clements, G. M., S. E. Hygnstrom, et al. (2011). "Movements of white-tailed deer in riparian habitat: Implications for infectious diseases." The Journal of Wildlife Management 75(6): 1436-1442.

Clements, S., D. Jepsen, et al. (2005). "Optimization of an acoustic telemetry array for detecting transmitter-implanted fish." North American Journal of Fisheries Management 25(2): 429-436.

Cochran, W. (1980). "Wildlife telemetry." Wildlife management techniques manual 4: 507-520.

Cochran, W. W. and R. D. Lord, Jr. (1963). "A Radio-Tracking System for Wild Animals." The Journal of Wildlife Management 27(1): 9-24.

Colonna, J. G., A. D. Ribas, et al. (2012). Feature subset selection for automatically classifying anuran calls using sensor networks. Neural Networks (IJCNN), The 2012 International Joint Conference on, IEEE.

Cooke, S. J., S. G. Hinch, et al. (2004). "Biotelemetry: a mechanistic approach to ecology." Trends in Ecology & Evolution 19(6): 334-343.

Costa, D. P., P. W. Robinson, et al. (2010). "Accuracy of ARGOS Locations of Pinnipeds at-Sea Estimated Using Fastloc GPS." Plos One 5(1): e8677.

Culler, D., D. Estrin, et al. (2004). "Guest Editors' Introduction: Overview of Sensor Networks." Computer 37(8): 41-49.

D'Anna, G., V. Giacalone, et al. (2011). "Movement pattern of white seabream, Diplodus sargus (L., 1758)(Osteichthyes, Sparidae) acoustically tracked in an artificial reef area." Italian Journal of Zoology 78(2): 255-263.

Deng, Z. D., M. A. Weiland, et al. (2011). "A Cabled Acoustic Telemetry System for Detecting and Tracking Juvenile Salmon: Part 2. Three-Dimensional Tracking and Passage Outcomes." Sensors 11(6): 5661-5676.

Dubinin, M., A. Lushchekina, et al. (2010). "Performance and accuracy of Argos transmitters for wildlife monitoring in Southern Russia." European Journal of Wildlife Research 56(3): 459-463.

Dyo, V., S. A. Ellwood, et al. (2012). "WILDSENSING: Design and deployment of a sustainable sensor network for wildlife monitoring." ACM Trans. Sen. Netw. 8(4): 1-33.

Eriksen, A., P. Wabakken, et al. (2009). "Encounter frequencies between GPS-collared wolves (Canis lupus) and moose (Alces alces) in a Scandinavian wolf territory." Ecological research 24(3): 547-557.

Fabbri, F., J. Riihijarvi, et al. (2009). Area Throughput and Energy Consumption for Clustered Wireless Sensor Networks. Wireless Communications and Networking Conference, 2009. WCNC 2009. IEEE.

Fieberg, J. (2007). "Kernel density estimators of home range: smoothing and the autocorrelation red herring." Ecology 88(4): 1059-1066.

Fisher, D. and M. Lara (1999). "Effects of body size and home range on access to mates and paternity in male bridled nailtail wallabies." Animal Behaviour 58(1): 121-130.

Frydman, S. and N. Gales (2007). "HeardMap: Tracking marine vertebrate populations in near real time." Deep Sea Research Part II: Topical Studies in Oceanography 54(3–4): 384-391.

Gaines, M. S. and L. R. McClenaghan Jr (1980). "Dispersal in small mammals." Annual Review of Ecology and Systematics 11(1): 163-196.

Garcia-Sanchez, A.-J., F. Garcia-Sanchez, et al. (2010). "Wireless Sensor Network Deployment for Monitoring Wildlife Passages." Sensors 10(8): 7236-7262.

Gautestad, A. O. (2011). "Memory matters: influence from a cognitive map on animal space use." Journal of theoretical biology 287: 26-36.

Getz, L. L., M. K. Oli, et al. (2005). "Factors influencing movement distances of two species of sympatric voles." Journal of Mammalogy 86(4): 647-654.

Giorgetti, A., M. Lucchi, et al. (2011). "Throughput per Pass for Data Aggregation from a Wireless Sensor Network via a UAV." Aerospace and Electronic Systems, IEEE Transactions on 47(4): 2610-2626.

Giroux, M.-A., C. Dussault, et al. (2012). "A New Way of Assessing Foraging Behaviour at the Individual Level Using Faeces Marking and Satellite Telemetry." Plos One 7(11): e49719.

Goldsmith, A. J. and S. B. Wicker (2002). "Design challenges for energy-constrained ad hoc wireless networks." Wireless Communications, IEEE 9(4): 8-27.

Gorini, L., J. D. Linnell, et al. (2012). "Habitat heterogeneity and mammalian predator–prey interactions." Mammal Review 42(1): 55-77.

Grothues, T. M. (2009). A review of acoustic telemetry technology and a perspective on its diversification relative to coastal tracking arrays. Tagging and Tracking of Marine Animals with Electronic Devices, Springer: 77-90.

Grothues, T. M., K. W. Able, et al. (2012). "Winter flounder (Pseudopleuronectes americanus Walbaum) burial in estuaries: Acoustic telemetry triumph and tribulation." Journal of Experimental Marine Biology and Ecology 438(0): 125-136.

Grünewälder, S., F. Broekhuis, et al. (2012). "Movement Activity Based Classification of Animal Behaviour with an Application to Data from Cheetah <italic>(Acinonyx jubatus)</italic>." Plos One 7(11): e49120.

Guilford, T., S. Åkesson, et al. (2011). "Migratory navigation in birds: new opportunities in an era of fast-developing tracking technology." The Journal of Experimental Biology 214(22): 3705-3712.

Guo, Y., P. Corke, et al. (2006). Animal Behaviour Understanding using Wireless Sensor Networks. Local Computer Networks, Proceedings 2006 31st IEEE Conference on.

Hammerschlag, N., A. J. Gallagher, et al. (2011). "A review of shark satellite tagging studies." Journal of Experimental Marine Biology and Ecology 398(1–2): 1-8.

Harris, R. B. (1990). "Tracking wildlife by satellite: current systems and performance." Fish and Wildlife technical report (USA).

Harris, S., W. Cresswell, et al. (1990). "Home-range analysis using radio-tracking data–a review of problems and techniques particularly as applied to the study of mammals." Mammal Review 20(2-3): 97-123.

He, T., C. Huang, et al. (2003). Range-free localization schemes for large scale sensor networks. Proceedings of the 9th annual international conference on Mobile computing and networking. San Diego, CA, USA, ACM: 81-95.

Hebblewhite, M. and D. T. Haydon (2010). "Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology." Philosophical Transactions of the Royal Society B: Biological Sciences 365(1550): 2303-2312.

Hedin, J. and T. Ranius (2002). "Using radio telemetry to study dispersal of the beetle< i> Osmoderma eremita</i>, an inhabitant of tree hollows." Computers and Electronics in Agriculture 35(2): 171-180.

Hoenner, X., S. D. Whiting, et al. (2012). "Enhancing the Use of Argos Satellite Data for Home Range and Long Distance Migration Studies of Marine Animals." Plos One 7(7): e40713.

Horback, K. M., L. J. Miller, et al. (2012). "The effects of GPS collars on African elephant (< i> Loxodonta africana</i>) behavior at the San Diego Zoo Safari Park." Applied Animal Behaviour Science 142(1): 76-81.

Intanagonwiwat, C., D. Estrin, et al. (2002). Impact of network density on data aggregation in wireless sensor networks. Distributed Computing Systems, 2002. Proceedings. 22nd International Conference on.

Joshi, A., I. N. VishnuKanth, et al. (2008). GPS-less animal tracking system. Wireless Communication and Sensor Networks, 2008. WCSN 2008. Fourth International Conference on.

Kansal, A., M. Rahimi, et al. (2004). Controlled mobility for sustainable wireless sensor networks. Sensor and Ad Hoc Communications and Networks, 2004. IEEE SECON 2004. 2004 First Annual IEEE Communications Society Conference on.

Katiyar, V., N. Chand, et al. (2010). "Recent advances and future trends in Wireless Sensor Networks." International Journal of Applied Engineering Research, Dindigul 1(3): 330-342.

Kays, R., S. Tilak, et al. (2011). "Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest." Computer Journal 54(12): 1931-1948.

Kelly, B. P., O. H. Badajos, et al. (2010). "Seasonal home ranges and fidelity to breeding sites among ringed seals." Polar Biology 33(8): 1095-1109.

Kilfoyle, D. B. and A. B. Baggeroer (2000). "The state of the art in underwater acoustic telemetry." Oceanic Engineering, IEEE Journal of 25(1): 4-27.

Kinney, P. (2003). Zigbee technology: Wireless control that simply works. Communications design conference.

Kling, R. (2004). Intel research mote.

Kruk, R. and D. Regan (1983). "Visual test results compared with flying performance in telemetry-tracked aircraft." Aviation, space, and environmental medicine 54(10): 906-911.

Kulkarni, K., S. Tilak, et al. (2007). Engineering challenges in building sensor networks for real-world applications. Intelligent Sensors, Sensor Networks and Information, 2007. ISSNIP 2007. 3rd International Conference on.

Lee, B.-H., K.-T. Seo, et al. (2006). Design of the Configurable Clothes Using Mobile Actuator-Sensor Network. Computational Science and Its Applications - ICCSA 2006. M. Gavrilova, O. Gervasi, V. Kumaret al, Springer Berlin Heidelberg. 3983: 288-295.

Liu, G., R. Tan, et al. (2013). Volcanic earthquake timing using wireless sensor networks. Proceedings of the 12th international conference on Information processing in sensor networks, ACM.

Liu, J. and D. M. Nicol (2002). Lookahead revisited in wireless network simulations. Parallel and Distributed Simulation, 2002. Proceedings. 16th Workshop on.

Lord, R. D., W. W. Cochran, et al. (1962). "Radiotelemetry of Respiration of a Flying Duck." Science 137(3523): 39-&.

Low, A. (2013). "Evolution of Wireless Sensor Networks for Industrial Control." Technology Innovation Management Review(May 2013: Technology Evolution).

Lyons, J. and M. C. Lucas (2002). "The combined use of acoustic tracking and echosounding to investigate the movement and distribution of common bream (Abramis brama) in the River Trent, England." Hydrobiologia 483(1-3): 265-273.

Madden, S., R. Szewczyk, et al. (2002). Supporting aggregate queries over ad-hoc wireless sensor networks. Mobile Computing Systems and Applications, 2002. Proceedings Fourth IEEE Workshop on.

Mainwaring, A., D. Culler, et al. (2002). Wireless sensor networks for habitat monitoring. Proceedings of the 1st ACM international workshop on Wireless sensor networks and applications. Atlanta, Georgia, USA, ACM: 88-97.

Malan, D., T. Fulford-Jones, et al. (2004). Codeblue: An ad hoc sensor network infrastructure for emergency medical care. International workshop on wearable and implantable body sensor networks.

Mampentzidou, I., E. Karapistoli, et al. (2012). Basic guidelines for deploying Wireless Sensor Networks in agriculture. Ultra Modern Telecommunications and Control Systems and Workshops (ICUMT), 2012 4th International Congress on.

Mate, B. (2012). Improved Satellite-Monitored Radio Tags for Large Whales: Dependable ARGOS Location-Only Tags and a GPS-Linked Tag to Reveal 3-Dimensional Body-Orientation and Surface Movements, OREGON STATE UNIV NEWPORT HATFIELD MARINE SCIENCE CENTER.

Matthews, A., L. Ruykys, et al. (2013). "The success of GPS collar deployments on mammals in Australia." Australian Mammalogy 35(1): 65-83.

Matthews, H. S., C. T. Hendrickson, et al. (2002). Energy impacts of wired and wireless networks. Electronics and the Environment, 2002 IEEE International Symposium on.

McErlean, D. and S. Narayanan (2002). Distributed detection and tracking in sensor networks. Signals, Systems and Computers, 2002. Conference Record of the Thirty-Sixth Asilomar Conference on.

Mellas, E. J. and J. M. Haynes (1985). "Swimming performance and behavior of rainbow trout (Salmo gairdneri) and white perch (Morone americana): effects of attaching telemetry transmitters." Canadian Journal of Fisheries and Aquatic Sciences 42(3): 488-493.

Melo, P., L. D. Pedrosa, et al. (2009). Interconnecting WSNs with Fast Moving Nodes: Experiments in Real-World Scenarios. Computer Communications and Networks, 2009. ICCCN 2009. Proceedings of 18th Internatonal Conference on.

Mennill, D. J., S. M. Doucet, et al. (2012). "A novel digital telemetry system for tracking wild animals: a field test for studying mate choice in a lekking tropical bird." Methods in Ecology and Evolution 3(4): 663-672.

Min, R., M. Bhardwaj, et al. (2002). "Energy-centric enabling tecumologies for wireless sensor networks." Wireless Communications, IEEE 9(4): 28-39.

Mohandes, M., M. A. Haleem, et al. (2013). "Pilgrim Tracking and Identification Using Wireless Sensor Networks and GPS in a Mobile Phone." Arabian Journal for Science and Engineering 38(8): 2135-2141.

Montgomery, R. A., G. J. Roloff, et al. (2010). "Can we accurately characterize wildlife resource use when telemetry data are imprecise?" The Journal of Wildlife Management 74(8): 1917-1925.

Naef-Daenzer, B., D. Fruh, et al. (2005). "Miniaturization (0.2 g) and evaluation of attachment techniques of telemetry transmitters." Journal of Experimental Biology 208(21): 4063-4068.

Navarro, M., T. W. Davis, et al. (2013). A study of long-term WSN deployment for environmental monitoring. Personal Indoor and Mobile Radio Communications (PIMRC), 2013 IEEE 24th International Symposium on, IEEE.

Neukomm, P. A. and H. Kundig (1990). "Passive Wireless Actuator Control and Sensor Signal Transmission." Sensors and Actuators a-Physical 21(1-3): 258-262.

Ong, L. and M. Motani (2008). "Myopic Coding in Multiterminal Networks." Information Theory, IEEE Transactions on 54(7): 3295-3314.

Patnode, D., J. Dunne, et al. (2003). WISENET - TinyOS based wireless network of sensors. Industrial Electronics Society, 2003. IECON '03. The 29th Annual Conference of the IEEE.

Pennisi, E. (2011). "Global Tracking of Small Animals Gains Momentum." Science 334(6059): 1042.

Polastre, J., R. Szewczyk, et al. (2005). Telos: enabling ultra-low power wireless research. Information Processing in Sensor Networks, 2005. IPSN 2005. Fourth International Symposium on.

Pon, R., M. A. Batalin, et al. (2005). Networked infomechanical systems: a mobile embedded networked sensor platform. Information Processing in Sensor Networks, 2005. IPSN 2005. Fourth International Symposium on.

Qi, H., D. J. Brady, et al. (2006). "Human Tracking With Wireless Distributed Pyroelectric Sensors." Sensors Journal, IEEE 6(6): 1683-1696.

Rabaey, J. M., M. J. Ammer, et al. (2000). "PicoRadio supports ad hoc ultra-low power wireless networking." Computer 33(7): 42-+.

Raghunathan, V., C. Schurgers, et al. (2002). "Energy-aware wireless microsensor networks." Signal Processing Magazine, IEEE 19(2): 40-50.

Recio, M. R., R. Mathieu, et al. (2011). "Lightweight GPS-Tags, One Giant Leap for Wildlife Tracking? An Assessment Approach." Plos One 6(12): e28225.

Reynolds, B. F., S. P. Powers, et al. (2010). "Application of Acoustic Telemetry to Assess Residency and Movements of Rockfish and Lingcod at Created and Natural Habitats in Prince William Sound." Plos One 5(8).

Rittenhouse, T. A. and R. D. Semlitsch (2007). "Distribution of amphibians in terrestrial habitat surrounding wetlands." Wetlands 27(1): 153-161.

Robinson, W. D., M. S. Bowlin, et al. (2009). "Integrating concepts and technologies to advance the study of bird migration." Frontiers in Ecology and the Environment 8(7): 354-361.

Rodríguez, A., J. J. Negro, et al. (2012). "The Eye in the Sky: Combined Use of Unmanned Aerial Systems and GPS Data Loggers for Ecological Research and Conservation of Small Birds." Plos One 7(12): e50336.

Ross, M. J. and J. H. McCormick (1981). "Effects of external radio transmitters on fish." The Progressive Fish-Culturist 43(2): 67-72.

Rowley, J. J. and R. A. Alford (2007). "Techniques for tracking amphibians: the effects of tag attachment, and harmonic direction finding versus radio telemetry." Amphibia-Reptilia 28(3): 367-376.

Rutishauser, M., V. Petkov, et al. (2011). "CARNIVORE: A Disruption-Tolerant System for Studying Wildlife." EURASIP Journal on Wireless Communications and Networking 2011(1): 968046.

Rychlik, L., I. Ruczynski, et al. (2010). "Radiotelemetry Applied to Field Studies of Shrews." Journal of Wildlife Management 74(6): 1335-1342.

Schick, R. S., S. R. Loarie, et al. (2008). "Understanding movement data and movement processes: current and emerging directions." Ecology letters 11(12): 1338-1350.

Seminoff, J. A., S. R. Benson, et al. (2012). "Stable Isotope Tracking of Endangered Sea Turtles: Validation with Satellite Telemetry and δ¹⁵N Analysis of Amino Acids." Plos One 7(5): e37403.

Shamoun-Baranes, J., E. E. van Loon, et al. (2012). "Analysis and visualization of animal movement." Biology Letters 8(1): 6-9.

Shen, X., Z. Wang, et al. (2004). Wireless sensor networks for industrial applications. Intelligent Control and Automation, 2004. WCICA 2004. Fifth World Congress on, IEEE.

Sheppard, J. K., A. R. Preen, et al. (2006). "Movement heterogeneity of dugongs,< i> Dugong dugon</i>(Müller), over large spatial scales." Journal of Experimental Marine Biology and Ecology 334(1): 64-83.

Sikka, P., P. Corke, et al. (2004). Wireless sensor devices for animal tracking and control. Local Computer Networks, 2004. 29th Annual IEEE International Conference on.

Simic, S. N. and S. Sastry (2003). Distributed environmental monitoring using random sensor networks. Information Processing in Sensor Networks, Proceedings. F. Zhao and L. Guibas. 2634: 582-592.

Simpfendorfer, C. A., T. R. Wiley, et al. (2010). "Improving conservation planning for an endangered sawfish using data from acoustic telemetry." Biological Conservation 143(6): 1460-1469.

Soisalo, M. K. and S. M. C. Cavalcanti (2006). "Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry." Biological Conservation 129(4): 487-496.

Song, C. and M. Guizani (2006). Energy Map: Mining Wireless Sensor Network Data. Communications, 2006. ICC '06. IEEE International Conference on.

Stark, K. E., G. D. Jackson, et al. (2005). "Tracking arrow squid movements with an automated acoustic telemetry system." Marine Ecology Progress Series 299: 167-177.

Strandberg, R., R. H. G. Klaassen, et al. (2010). "How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors." Biology Letters 6(3): 297-300.

Sun, J. and H. Jin (2011). Intelligent design in fire prevention based on WSN. Uncertainty Reasoning and Knowledge Engineering (URKE), 2011 International Conference on.

Szewczyk, R., E. Osterweil, et al. (2004). "Habitat monitoring with sensor networks." Communications of the Acm 47(6): 34-40.

Szewczyk, R., J. Polastre, et al. (2004). "Lessons from a sensor network expedition." Wireless Sensor Networks, Proceedings 2920: 307-322.

Talzi, I., A. Hasler, et al. (2007). PermaSense: investigating permafrost with a WSN in the Swiss Alps. Proceedings of the 4th workshop on Embedded networked sensors, ACM.

Tan, R., G. Xing, et al. (2010). Quality-driven volcanic earthquake detection using wireless sensor networks. Real-Time Systems Symposium (RTSS), 2010 IEEE 31st, IEEE.

Tao, Y., L. Barolli, et al. (2010). Impact of Mobile Event Movement on the Performance of Wireless Sensor Networks. Systems and Networks Communications (ICSNC), 2010 Fifth International Conference on.

Tarlow, E. M. and D. T. Blumstein (2007). "Evaluating methods to quantify anthropogenic stressors on wild animals." Applied Animal Behaviour Science 102(3): 429-451.

Thompson, D., P. Hammond, et al. (1991). "Movements, diving and foraging behaviour of grey seals (Halichoerus grypus)." Journal of zoology 224(2): 223-232.

Thorstensen, B., T. Syversen, et al. (2004). Electronic shepherd - a low-cost, low-bandwidth, wireless network system. Proceedings of the 2nd international conference on Mobile systems, applications, and services. Boston, MA, USA, ACM: 245-255.

Thums, M., S. D. Whiting, et al. (2013). "Tracking sea turtle hatchlings — A pilot study using acoustic telemetry." Journal of Experimental Marine Biology and Ecology 440(0): 156-163.

Tolle, G. and D. Culler (2005). "Design of an application-cooperative management system for wireless sensor networks." Proceedings of the Second European Workshop on Wireless Sensor Networks: 121-132.

Tomkiewicz, S. M., M. R. Fuller, et al. (2010). "Global positioning system and associated technologies in animal behaviour and ecological research." Philosophical Transactions of the Royal Society B: Biological Sciences 365(1550): 2163-2176.

Toriumi, S., Y. Sei, et al. (2008). Energy-Efficient Event Detection in 3D Wireless Sensor Networks.

Trevelin, L. C., M. Silveira, et al. (2013). "Use of space by frugivorous bats (Chiroptera: Phyllostomidae) in a restored Atlantic forest fragment in Brazil." Forest Ecology and Management 291(0): 136-143.

Tsai, H.-W., C.-P. Chu, et al. (2007). "Mobile object tracking in wireless sensor networks." Computer Communications 30(8): 1811-1825.

Tseng, C.-C., C.-L. Lin, et al. (2013). "SIP-enabled Surveillance Patrol Robot." Robotics and Computer-Integrated Manufacturing 29(2): 394-399.

Tsukamoto, K., H. Ueda, et al. (2009). "Deployment Design of Wireless Sensor Network for Simple Multi-Point Surveillance of a Moving Target." Sensors 9(5): 3563-3585.

Vinatier, F., A. Chailleux, et al. (2010). "Radiotelemetry unravels movements of a walking insect species in heterogeneous environments." Animal Behaviour 80(2): 221-229.

Wang, A. and A. Chandrakasan (2002). "Energy-efficient DSPs for wireless sensor networks." Signal Processing Magazine, IEEE 19(4): 68-78.

Watkins, W. A. and W. E. Schevill (1972). Sound source location by arrival-times on a non-rigid three-dimensional hydrophone array. Deep Sea Research and Oceanographic Abstracts, Elsevier.

Way, J. G. and B. C. Timm (2011). "Record Pack-density of Eastern Coyotes/Coywolves (Canis latrans x lycaon)." American Midland Naturalist 165(1): 201-203.

Weiland, M. A., Z. D. Deng, et al. (2011). "A Cabled Acoustic Telemetry System for Detecting and Tracking Juvenile Salmon: Part 1. Engineering Design and Instrumentation." Sensors 11(6): 5645-5660.

Weimerskirch, H., M. Le Corre, et al. (2005). "The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment?" Proceedings of the Royal Society B: Biological Sciences 272(1558): 53-61.

Werner-Allen, G., S. Dawson-Haggerty, et al. (2008). Lance: optimizing high-resolution signal collection in wireless sensor networks. Proceedings of the 6th ACM conference on Embedded network sensor systems. Raleigh, NC, USA, ACM: 169-182.

Werner-Allen, G., P. Swieskowski, et al. (2005). Motelab: A wireless sensor network testbed. Proceedings of the 4th international symposium on Information processing in sensor networks, IEEE Press.

White, G. C. and R. A. Garrott (1990). Analysis of wildlife radio-tracking data, Elsevier.

Whitehouse, K. and D. Culler (2002). Calibration as parameter estimation in sensor networks. Proceedings of the 1st ACM international workshop on Wireless sensor networks and applications. Atlanta, Georgia, USA, ACM: 59-67.

Wikelski, M., R. W. Kays, et al. (2007). "Going wild: what a global small-animal tracking system could do for experimental biologists." Journal of Experimental Biology 210(2): 181-186.

Wikelski, M., J. Moxley, et al. (2010). "Large range movements of Neotropical orchid bees observed via radio telemetry." Plos One 5(5).

Witte, T. H. and A. M. Wilson (2005). "Accuracy of WAAS-enabled GPS for the determination of position and speed over ground." Journal of Biomechanics 38(8): 1717-1722.

Wittenburg, G., K. Terfloth, et al. (2007). "Fence monitoring - Experimental evaluation of a use case for wireless sensor networks." Wireless Sensor Networks, Proceedings 4373: 163-178.

Younis, O. and S. Fahmy (2004). "HEED: a hybrid, energy-efficient, distributed clustering approach for ad hoc sensor networks." Mobile Computing, IEEE Transactions on 3(4): 366-379.

Zaitseva, N. A. (1993). "Historical developments in radiosonde systems in the former Soviet Union." Bulletin of the American Meteorological Society 74(10): 1893-1900.

Zeynali, M., A. Mollanejad, et al. (2011). "Novel hierarchical routing protocol in wireless sensor network." Procedia Computer Science 3(0): 292-300.

Zhang, P., C. M. Sadler, et al. (2004). Hardware design experiences in ZebraNet. Proceedings of the 2nd international conference on Embedded networked sensor systems. Baltimore, MD, USA, ACM: 227-238.

Zhao, F. (2003). "Collaborative In-Network Processing for Target Tracking." EURASIP Journal on Advances in Signal Processing 2003(4): 378.