Species Interactions: the interplay between conservation and research methods

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Declaration of authorship

The work presented in this thesis is my own. In each of the chapters presented here, I have developed the aims, concepts, and methodology, I performed the analyses, interpreted results, and wrote the manuscripts. During my thesis chapters, I have been lucky to collaborate with several excellent scientists. Below, I provide a full list of co-authors and a statement of their contributions for each chapter.

Chapter 1

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Chapter 2
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Contributions – JD and TC conceived and developed the model. MJ and RG coordinated the data collection. DK provided a cleaned dataset and supported developing the growth vital rates. JD performed the analysis and created the model. JD and TC interpreted the results. JD wrote the manuscript with the help of TC. All authors reviewed and approved the final manuscript.

Chapter 3
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Contributions – JD conceived and designed the study. SK and TC provided the dataset (collected by many different contributors). JD performed the analysis. JD wrote the manuscript with the help of SK and TC. All authors reviewed and approved the final manuscript.

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Contributions – SK, CL and AR conceived the study. AR and CL created the initial logger. AR, CL and JD constructed and maintained the loggers. JD and AR collected the data. JD and AR analysed the data. JD wrote the manuscript. All authors reviewed and approved the final manuscript. * joint first author

Chapter 5
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Contributions – JD and SK conceived the study. JD and AR collected the data. JD analysed the data. JD wrote the manuscript with support from SK. All authors reviewed and approved the final manuscript.

Chapter 6
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Dedicated to transgender youth, know that you are not alone. In this journey, you are embraced, cherished, and supported by a community that recognises your significance. May this thesis serve as a reminder that you possess the strength, resilience, and boundless potential to overcome any obstacle. Believe in yourself, for we believe in you wholeheartedly, and together, we will rewrite the narrative of possibility and inspire a world where your success knowns no bounds.



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Abstract

This doctoral thesis investigates the complex interplay between ecological diversity and research methods in the context of species interactions. By utilising two distinct ecological systems as case studies, I delve into the diverse approaches and techniques employed for analysing and collecting data on species interactions. The first system focuses on the dynamics between purinina/Tasmanian devils (*Sarcophilus harrisii*) and devil facial tumour disease (DFTD), exploring the utility of integral projection models (IPMs) in understanding interactions between host and pathogen. This study sheds light on the underlying demographic dynamics that have allowed purinina to coexist with DFTD and the broader ongoing implications for purinina populations. It additionally enhances our understanding of how research methods, specifically IPMs, can contribute to unravelling the complexities of species interactions in the face of disease outbreaks. The second system focuses on a wild small mammal community, investigating how different data collection techniques, namely count data and fine-scale RFID (Radio-Frequency Identification) logger data offer insights into different ecological questions. Comparing the outcomes of count data and RFID logger data analysis, the research highlights the strengths and limitations of each method, shedding light on their respective applications in ecological research. It demonstrates how the fine-scale data obtained from RFID loggers enable researchers to

investigate intricate social interactions, movement patterns, and resource utilisation in the small mammal community, complementing traditional count data analyses. Overall, this research provides a comprehensive exploration of the interdependence between conservation efforts, research methods, and species interactions. It elucidates the value of population level statistical models in understanding host-pathogen dynamics, using the case of purinina and DFTD as an illustrative example. Additionally, it demonstrates the diverse insights that can be gained by employing different data collection methods. The thesis not only advances our ecological understanding but also offers practical guidance for researchers by providing novel technology and mathematical models to their toolkit. The work presented here is diverse, but ultimately when collated contributes to answering a single question – what is the best way to understand how species interact?

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1

General Introduction

Monitoring the Intricacies of Species Interactions

J. R. Dale

Motivation behind thesis

Species interactions play a fundamental role in shaping ecosystems and driving evolutionary processes (Dobzhansky, 1950). Here I explore the importance of understanding interaction mechanisms in ecological research and how they offer insights into the dynamics of ecosystems and the coevolutionary processes that shape biodiversity patterns (Strauss & Irwin, 2004; Thompson, 2013). In recent years, there has been a growing recognition of the complexity inherent in species interactions, necessitating a deeper understanding of their ecological and evolutionary implications (Pocock et al., 2012). This has prompted researchers to develop advanced methods to study, model, and analyse species interaction datasets (Gravel et al., 2011; Bascompte & Jordano, 2014). In this thesis, I aim to delve into the world of species interactions, exploring their underlying mechanisms and unravelling the patterns that emerge from these intricate networks. By studying these interactions, we can gain a comprehensive understanding of ecosystem dynamics and how they may respond to environmental changes and disturbances. Through reciprocal adaptations and interactions, species shape each other's evolutionary trajectories, leading to the development of specialised traits and the formation of tight ecological dependencies (Strauss & Irwin, 2004; Thompson, 2013). Understanding species interactions aids conservationists and managers in identifying key species and their roles within ecosystems. By focusing on protecting or managing these species, they can promote the overall health and resilience of the ecosystem (Mouquet et al., 2013). In addition, endangered species often rely on specific interactions with other species for their survival, such as pollination (Memmott et al., 2007), seed dispersal (Escribano-Avila et al., 2018), or predator-prey relationships (Suzuki et al., 2022). Furthermore, when ecosystems have been degraded or disturbed, understanding species interactions is essential for successful ecological restoration. By reintroducing key species or establishing appropriate species interactions, conservationists can enhance the recovery of ecosystems and promote their long-term sustainability (Hobbs et al., 2006). By understanding the dynamics of these interactions, we can develop effective management strategies to protect biodiversity and maintain vital ecosystem functions (Díaz et al., 2019).

At the core of species interactions lie the fundamental concepts of symbiosis, competition, consumption, and mutualism (Dobzhansky, 1950; Machicote, Branch & Villarreal, 2004; Thompson, 2013; Bascompte & Jordano, 2014; Curtsdotter et al., 2018; Mikula et al., 2018). Each of these presents a unique set of interactions and outcomes. This thesis deals primarily with how species can coexist through parasitic and competitive interactions. Parasitic relationships occur when one organism (the parasite or pathogen) benefits at the expense of another organism (the host). Parasites may live on or within their hosts, causing varying degrees of harm or even death. Examples include

ticks, fleas, and tapeworms (Dobzhansky, 1950). The coexistence between the purinina[1]/Tasmanian devil (*Sarcophilus harrisii*) and devil facial tumour disease (DFTD) is an example of a host-pathogen species interaction that has had significant ecological and evolutionary implications. DFTD is a transmissible cancer that affects purinina, causing the growth of facial tumours that eventually lead to death (Jones et al., 2008). Despite the severity of the disease, some purinina have shown varying degrees of resistance or immunity to DFTD, allowing for the coexistence of the species (Jones et al., 2018). This resistance is partly due to genetic variation among individuals, which provides a subset of the population with the ability to mount an immune response against the cancer cells (Storfer et al., 2010). These resistant individuals can survive and reproduce, passing on their advantageous traits to their offspring. The disease significantly reduces the fitness and population size of the host species, which is a characteristic outcome of parasitic interactions (Smith, Acevedo-Whitehouse & Pedersen, 2009). However, the presence of resistant individuals within the purinina population allows for some individuals to persist and maintain the species' survival despite the ongoing parasitic pressure.

Competition arises when two or more species compete for limited resources such as food, territory, or mates. Interspecific competition can lead to niche differentiation, where species evolve to occupy different ecological niches, minimising direct competition (Gravel et al., 2011). Here we use a small mammal system comprised of three species, the wood mouse (*Apodemus sylvaticus*), the yellow necked mouse (*A. flavicollis*) and the bank vole (*Myodes glareolus*) to explore the coexistence mechanisms across short- and long-term time scales. These species have developed strategies to partition their niches to avoid direct competition (Viviano, Scarfo & Mori, 2022). By utilising different habitats, feeding preferences, activity patterns, microhabitats, and reproductive strategies, these species minimise direct competition and reduce the risk of resource depletion (Guilia et al., 2022). This allows them to coexist in the same ecological community while sharing common resources and maintaining population stability over time.

Numerous explanations have been proposed to elucidate the coexistence of certain species while it is lacking in others (Chesson, 2000). Modern coexistence theory (MCT) is a framework that aims to explain how multiple species with similar ecological requirements can stably coexist in the same landscape (Chesson, 1994, Chesson, 2000). The concept of MCT was formalized by Chesson (1994) and Chesson (2000) to identify key differences and processes that play a crucial role when species exhibit variations and multiple processes are at work. Essentially, MCT provides a broad structure that connects real coexistence with simple explanations.

[1] Words such as purinina and lutruwita are palawa kani. palawa kani is a reconstructed language from a variety of language groups within lutruwita/Tasmania. This language purposely does not use capital letters as per the guidelines from the Tasmanian Aboriginal Centre (TAC). I use palawa kani words exclusively where appropriate within the rest of this thesis.

Several mechanisms associated with MCT have been identified as crucial facilitators of coexistence. These mechanisms include competition for limited resources (Tilman et al., 1982; Brown, 1989; MacArthur, 1970; Letten et al., 2017), shared predators (Paine, 1966; Janzen, 1970; Holt & Lawton, 1994), mutualists (Johnson & Bronstein, 2019), and temporal fluctuations in environmental conditions (Chesson, 1994, 2003). These mechanisms generally involve a shared or distinct separation of ecological niches, which often requires a trade-off between environmental tolerance and competitive dominance (Chesson, 2008; Chesson, 2009; Mittelbach & McGill, 2019). To maintain stable coexistence, it is crucial for species to possess significant ecological distinctions (Chesson, 2000a). This phenomenon is known as niche partitioning and occurs across four dimensions: resources, predators (and other natural adversaries), time, and space (Mittelbach & McGill, 2019). Clesson's (2000b) coexistence framework expands and extends on the concept of niche partitioning and states that: a pair of species can coexist only if each species can invade a steady-state populations of its competitor (Chesson 2011; Godwin et al., 2020)

MCT, along with consumer-resource models like the Lotka-Volterra models, have significantly enhanced our comprehension of species coexistence (Chesson, 2000b). These frameworks provide valuable insights into the dynamics of coexistence, particularly the intricate relationship between niche breadths and the maintenance of species within an ecological community. Ongoing research in this field aims to unravel the complexities underlying niche breadths and their influence on coexistence patterns (Chesson, 2013).

Through the exploration of parasitism/pathogenicity, coexistence, and competition, we will gain valuable insights into the evolutionary forces and population dynamics driven by these interactions. Understanding these complex relationships requires robust methodologies and meticulous scientific inquiry, which can shed light on the intricate mechanisms and ecological consequences of species interactions. This thesis utilises three methods of studying how species interact, chosen from a suite of methodologies currently employed in the field of ecology and evolutionary dynamics (Table 1). I focus specifically on field surveys, behavioural observations, and mathematical models. However, it is important to note that the field of studying species interactions is vast and encompasses a wide range of methodologies. The selection of these three methods was based on their suitability and relevance to the study systems under investigation. Through our research, we aimed to push the boundaries of these study methods, leveraging their strengths, and building upon prior knowledge to provide valuable tools for researchers who are interested in studying how species interact at different levels. By refining and expanding these methods, this work contributes to the advancement of understanding how species interact.

Table 1 Methods of studying how species interact.

Method	Description and Suitability	Data Output	Key Reference Material
Observational study	Involves observing and documenting species interactions in their natural environment – without manipulations. Suitable for studying natural interactions in complex ecosystems.	Qualitative or quantitative observations of species interactions, species composition and community structure	Paine, 1996
Experimental study	Involves manipulating conditions or factors to test specific hypotheses about species interactions. Useful for testing specific hypotheses and manipulating conditions.	Experimental data including measurements, counts, and observations which can be analysed statistically	Connell, 1961
Field surveys (*Ch 3*)	Involves collecting data through systematic sampling or observations in the field to study species interactions. Commonly used to gather data on species interactions in natural habitats.	Data on species abundance, presence/absence, behaviour or ecological parameters collected from field observations	Gotelli & Ellison, 2013
DNA barcoding	Involves using DNA sequences to identify species and study their interactions in various ecological communities. Particularly useful for identifying species and their interactions in diverse communities.	DNA sequences or genetic information used for species identification, diversity assessments and interaction analyses	Hebert et al., 2003
Stable isotope analysis	Utilises isotopic signatures to trace energy and nutrient flows in food webs, revealing species interactions. Helps elucidate trophic interactions and energy flow in food webs.	Isotopic ratios used to infer trophic interactions, diet composition and energy transfer pathways	Fry, 2006
Network analysis	Analyses complex networks of interactions among species, providing insights into patterns and dynamics. Suitable for studying complex networks of mutualistic interactions.	Network structure, interaction strengths and centrality measures to characterise species interactions	Bacompte & Jordano, 2014

Behavioural observations (*Ch 4 & 5*)	Involves observing and documenting behavioural interactions among species to understand their social dynamics. Useful for studying communication and social interactions among species.	Behaviour sequences, or frequency data on species interactions and behaviours	Danchin et al., 2008
Mathematical modelling (*Ch 2 & 3*)	Uses mathematical equations and models to simulate and predict populations dynamics and species interactions. Valuable for simulating and predicting population dynamics and species interactions.	Simulated data on population sizes, growth rates or interactions dynamics based on model parameters and simulations.	May, 1974
Remote sensing	Utilises satellite imagery and other remote sensing technologies to study spatial patterns and habitat interactions. Useful for assessing habitat suitability and landscape-scale interactions.	Spatial data, such as vegetation indices, land cover, classifications, or habitat suitability maps, indicating species-environment interactions.	Pettorelli et al., 2011

In the dynamic landscape of the 21st century, humanity faces a myriad of new and novel challenges, including the rapid transformation of ecosystems and therefore the increasing complexity of species interactions (Tylianakis et al., 2008; Pocock et al., 2012; Bascompte & Jordano, 2014; Hendry et al., 2010; Schleuning et al., 2020). As we strive to understand and mitigate the consequences of these challenges, it is paramount that we employ best practice methods, both in the field and through rigorous statistical analyses, to study species interactions. By staying at the forefront of scientific advancements and employing innovative techniques, we can uncover hidden patterns and mechanisms, revolutionise our understanding of species interactions, and generate novel insights that can inform effective conservation strategies (Poisot et al., 2015; Vázquez et al., 2017).

This thesis aims to contribute to this growing field of research by providing and applying a suite of tools for researchers and conservation managers to employ to understand how species interact and to monitor and build ecosystem resilience. To do this, I will focus on two broad themes: the interactions between purinina/Tasmanian Devils and devil facial tumour disease (DFTD) in lutruwita/Tasmania, and niche partitioning and cycles in wild small mammals in England. These two examples represent distinct cases of how species interact with each other and their environment, shaping the demography of the species (McCallum et al., 2009; Lambin et al., 2010; Lambin & Meyfroidt, 2011). Ultimately, this research will enhance our understanding of the intricate web of life and inform conservation and management strategies to protect and sustain biodiversity.

The overarching theme and narrative of this thesis was ultimately dictated by datasets that were readily available. The Covid-19 pandemic restricted my ability to undertake my planned field work in the UK. The work presented here is based on data that was already collected than enabled me to ask interesting questions about species interactions.

Using biological demography to untangle complex demographic puzzles: a case study of the purinina/Tasmanian Devil

The field of ecology seeks to understand the interactions between organisms and their environment. One of the most fascinating aspects of ecology is the dynamic nature of these interactions, which can change over time influenced by natural and human-induced factors (Chesson, 1994). Host-pathogen species interactions encompass a wide range of relationships between organisms that can have significant impacts on both the host and the pathogen involved (Johnson et al., 2013). A unique host-pathogen interaction is observed between the purinina/Tasmanian devil (*Sarcophilus harrisii*) and devil facial tumour disease (DFTD). DFTD is a transmissible cancer that spreads between conspecifics through biting, resulting in the decline of purinina populations in lutruwita/Tasmania, where they are endemic (Loh et al., 2006). They play an important ecological role as scavengers and predators, controlling the populations of other species, such as wallabies and possums (Hawkins et al., 2006). However, since the initial incursion of DFTD in 1996, their population has declined by more than 80% (Hamede et al., 2015). The tumours, which primarily grow on the face and mouth of infected individuals, eventually lead to starvation and death (McCallum, 2008). The impact of DFTD on purinina populations has been the subject of extensive research and conservation efforts (see specifically: Pye, Woods & Kriess, 2016 and Hawkins et al., 2006). Despite some success in controlling the disease through genetic recovery and captive breeding programs, the long-term prognosis for purinina remains uncertain (Hawkins et al., 2006).

The purinina provides a compelling case study of a species that has demonstrated resilience in the face of low population numbers through a disease outbreak (Hawkins et al., 2006). The introduction of DFTD pushed the species to the brink of extinction (Brüniche-Olsen et al., 2013). However, recent studies have revealed that despite this, purinina has exhibited remarkable recovery and an ability to coexist with a disease with a high fatality rate (McCallum et al., 2008). The ability of the purinina to survive at low population numbers and low survival rates post DFTD incursion can be attributed, in part, to increased individual growth and reproductive rates (Lachish, Jones & McCallum, 2006; Lachish, McCallum & Jones, 2009, Hamede et al. 2023). Reproductive compensation has been observed in response to disease impacts via a reduction in the age of sexual maturity of females (an increase in precocial breeding) over time (Lachish, McCallum & Jones, 2009). Understanding the

compensatory response of purinina to DFTD through demographic mechanisms and mathematical models is crucial for species management. By employing mathematical models, researchers can quantitatively assess how the disease affects different demographic parameters. Through mathematical modelling, researchers can simulate various scenarios and explore hypothetical management strategies to evaluate their potential outcomes (Brook et a., 2000). This enables the development of effective species management plans that consider the long-term viability and resilience of the purinina population. By understanding the demographic mechanisms underlying the compensatory response, scientists can identify interventions that support the purinina population's recovery and reduce the disease's impact. Integral projection models (IPMs) can serve as powerful tools to understand these compensatory responses and the demographic mechanisms underpinning them (Ellner & Rees, 2006). IPMs integrate information on an individual's traits, such as body size, age, or reproductive status, and their influence on vital rates (e.g., survival, reproduction) into a unified framework (Morris & Doak, 2002). By incorporating individual-level variation and trait-dependent processes, IPMs allow researchers to explore the complex relationships between demographic parameters and compensatory responses. These models can capture the effects of disease on different life stages and traits, enabling a more comprehensive understanding of how DFTD influences population dynamics (Figure 1). For example, IPMs can reveal how disease-induced mortality affects survival rates differently based on an individual's body size or age. In the case of purinina, IPMs provide a powerful tool to investigate the impact of DFTD on population viability. These models can incorporate disease-related factors such as disease transmission rates, disease-induced mortality rates, and changes in reproductive rates due to disease-induced stress (McCallum et al., 2009). By simulating different scenarios we will be able to tease out the underlying demographic factors that have allowed this species to coexist with DFTD.

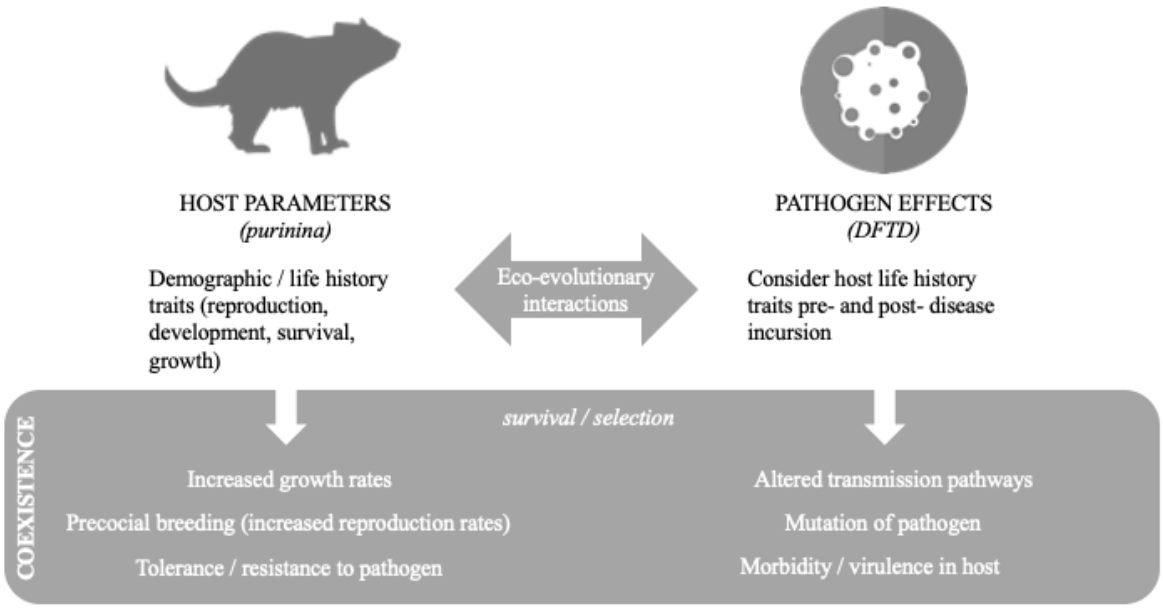


Figure 1 Mechanisms that have aided in the perceived coexistence between purinina and DFTD

Understanding the demographic factors that allow species to persist at low survival rates is an important research topic for several reasons. It provides valuable insights into the mechanisms underlying species' persistence, helps inform conservation strategies, and contributes to our understanding of ecosystem dynamics (Siepielski & McPeek, 2010). Studying how species persist at low survival rates can also provide evolutionary insights. It helps us understand the selective pressures and adaptations that shape a species' ability to survive and reproduce under challenging circumstances. This knowledge enhances our understanding of evolutionary processes and can potentially inform strategies for managing threatened or endangered species. In addition, through understanding the specific factors that contribute to a species' survival, researchers can create more accurate models to evaluate population viability. This information allows for better-informed decisions about conservation actions, such as habitat protection, population management, or reintroduction programs.

In summary, the utilisation of biological demography has emerged as a powerful tool in unravelling the intricate conservation puzzles, we face today. By studying the vital rates, population dynamics, and life history traits of species, researchers can gain invaluable insights into the factors that influence their survival and reproduction (Ellner & Rees, 2006). This knowledge not only enhances our understanding of ecological processes but also aids in the development of effective conservation strategies. Biological demography allows us to identify critical bottlenecks, predict population trends, and prioritize conservation efforts where they are most needed. In addition, understanding the demographic mechanisms enabling a species to survive at low population numbers is essential for

effective conservation efforts. The ability of purinina to rebound from the brink of extinction despite low population numbers and the challenges posed by DFTD underscores the importance of investigating population dynamics and employing tools like IPMs (McCallum et al., 2007). By utilising these models, scientists can gain valuable insights into the resilience and recovery potential of endangered species, aiding in the development of targeted and evidence-based conservation strategies (Morris & Doak, 2002).

Having explored the methodology and data collection techniques employed in our first study system, we now shift our focus towards our second study system, a woodland community of small mammals in England. Here, we delve deeper into the intricate process of data collection and examine how the specific type of data gathered can provide valuable insights into understanding species interactions. By carefully selecting and analysing the data collected about this system, we can effectively address various research questions pertaining to the intricate dynamics and relationships between species.

Broad and fine scale species interactions: a comparison, highlighting small mammals

Species interactions occur at various scales, ranging from broad-scale interactions that involve entire communities to fine-scale interactions that occur between individual species (Novella-Fernandez et al., 2021). Understanding the nuances and consequences of these interactions is crucial for unravelling the complexity of ecological systems. Here I compare broad and fine-scale interactions, with a particular emphasis on the role of small mammals as an exemplar study system.

Broad-scale species interactions encompass interactions that occur at the community level or involve a wide range of species (Begon, Townsend, & Harper, 2014). These interactions shape the structure, composition, and functioning of ecological communities, exerting profound effects on ecosystem processes (Sinclair, Fryxell, & Caughley, 2006). Factors such as competition, predation, and mutualism influence the dynamics of broad-scale species interactions. For instance, in a forest ecosystem, small mammals such as mice, voles, and shrews may compete for limited resources, including food, shelter, and nesting sites (Begon, Townsend, & Harper, 2014). Interspecific competition can lead to shifts in population sizes and distributions, as well as alterations in community composition and species diversity (Connell, 1983). Additionally, small mammals can serve as prey for larger predators, contributing to the regulation of predator-prey dynamics across the ecosystem (Sinclair, Fryxell, & Caughley, 2006). Their role as both competitors and prey influences energy flow, nutrient cycling, and trophic interactions within the broader ecological context (Polis & Strong, 1996). Long-term and broad count data provides an understanding of the dynamics and changes within ecosystems over time. By capturing information about species abundance, diversity, and distribution, this method enables scientists, conservationists, and policymakers to make informed

decisions, protect biodiversity, and maintain the health of ecosystems. The continued collection and analysis of this form of data is essential for addressing current and future environmental challenges. This format of data is complemented by short time frame detailed species interaction data. Both types of datasets in ecology supplement each other by providing different levels of detail and context, allowing for a more comprehensive understanding of ecological patterns and processes. Fine-scale datasets provide detailed information on species interactions, community dynamics, and habitat-specific factors. Integrating these datasets allows researchers to bridge the gap between large-scale patterns and local-scale processes, resulting in a more holistic understanding of ecosystems and facilitating effective conservation and management strategies.

Fine-scale species interactions occur at a more localised level, often involving direct interactions between specific species or individuals (Feng, Chen & Wang, 2021). These interactions often occur in response to immediate environmental conditions, such as changes in resource availability (Batzil, 2001), predation risk (Lazenby, Mooney & Dickman, 2015), or reproductive opportunities (Kelt et al., 2019). Despite their brevity, short time frame species interactions can have significant impacts on individual fitness, population dynamics, and community structure. By studying fine-scale species interactions, ecologists gain insights into the intricate web of relationships that underpin the functioning of ecosystems, enabling better conservation and management strategies (Feng, Chen & Wang, 2021). For example, small mammal species, such as mice and voles, may engage in rapid competition for food resources. For instance, in a limited food patch, multiple individuals may scramble to gather seeds, fruits, or insects within a short time frame (Batzil, 2001). Studying these rapid exchanges contributes to our understanding of the complex social, ecological, and evolutionary processes that shape small mammal populations and their interactions with their environment. Exploring the intricacies of short time frame species interactions deepens our understanding of the complex ecology of small mammals and their dynamic role within ecosystems.

Small mammals hold particular significance within the discipline of species interactions due to their role in ecosystem functions and their remarkable diversity across the world. They occupy a wide range of ecological niches within ecosystems, displaying an array of adaptations, behaviours, and life history strategies. Here I compare broad and fine-scale species interactions, with a particular focus on small mammals. By delving into the literature, we can explore the significance of these interactions in shaping ecological communities and the role small mammals play in these processes. Comparing, long-term studies of broad counts of individual small mammals to fine-scale, shorter time scale studies of minute interactions between small mammals involves considering the advantages and limitations of each approach (Table 2).

Table 2 Examples from the literature demonstrating the advantages of long-term count based studies and fine scale interactions

Long-term studies of broad counts of individual small mammals	
Advantages	*Limitations*
• Capturing population dynamics: Long-term studies can provide insights into population size, density, and changes over time. For example, a long-term study on small mammals in a North American hardwood forest found that population fluctuations were influenced most strongly by density (Fryxell et al., 1998). • Large-scale patterns: Long-term studies can identify broad-scale patterns and associations. For instance, a study on small mammal community structure in a Brazilian forest revealed how abiotic factors, such as vegetation type and structure, influenced species composition and abundance (Melo et al., 2011). • Statistical power: By studying many individuals, long-term studies can achieve high statistical power. For example, a long-term study on a population of white-footed mice (*Peromyscus leucopus*) demonstrated the strong influence of predator abundance on mouse population dynamics (Marcello, 2005).	• Lack of detail: Long-term studies often focus on population-level trends and may overlook fine-scale interactions. This limitation was highlighted in a study on the effect of trap confinement on behaviour and 'personality' measurements in deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*). Camera traps placed facing the trap to record behaviour didn't correlate with the behaviour recorded through the trapping regime (Brehm, Tironi & Mortelliti, 2020). • Limited ecological context: Long-term studies may not capture the full complexity of ecological interactions. A study in Germany modified their trapping regime due to by catch of the endangered Eurasian harvest mouse (*Micromys minutus*) and Eurasian Water Shrew (*Neomys fodiens*) but could not draw ecological conclusions as to why these species were becoming increasingly common by catch (Hotopp et al., 2022). • Time-consuming and costly: Conducting long-term studies requires significant resources. Waudby, Petit & Gill (2019) created an extensive tool in which to perform a cost-benefit analysis for small mammal trapping, showing that sherman traps (the most common trapping technique)

	was the least efficient in answering scientific questions and the costliest.
Fine-scale, shorter time scale studies of interactions between small mammals	
Advantages	*Limitations*
• Detailed behavioural insights: Fine-scale studies provide a more in-depth understanding of specific interactions. For example, a study on the acoustic communication of deer mice (*Peromyscus maniculatus*) revealed a complex vocal repertoire involved in territoriality and mate attraction (Pasch et al., 2013). • Ecological context: Fine-scale studies often consider the broader ecological context. A study in Israel used unmanned aerial vehicles to study the activity of Levant voles (*Microtus guentheri*) and house mice (*Mus musculus*) as well as their impact on commercial crops (Keshet et al., 2022). • Statistical power: As these type of studies can collect large amounts of data even across short time scales, the scope of analysis is wider and often more accurate. A studying in the Italian alps compared live trapping and radio tracking of yellow necked mice (*Apodemus flavicollis*) for creating social networks (Perkins et al., 2009). Radio tracking produced more informative networks even in periods of low density.	• Limited generalisability: Fine-scale studies may focus on specific populations or locations. For example, a study on the social organisation of prairie voles (*Microtus ochrogaster*) investigated a single population, limiting the generalisability of their findings (Getz & Carter, 1996). • Potential confounding factors: Fine-scale studies can struggle with isolating and controlling all relevant variables. A study on mating behaviour in house mice (*Mus musculus*) highlighted the challenge of disentangling the effects of genetic relatedness and familiarity on mate choice (Sherborne et al., 2007). • Feasibility: As this is an emerging field accessing the materials or off-the-shelf components for these types of studies can be a major limiting factor. For example, Harrison & Kelly (2022) estimated a single commercial RFID logger could cost between £950 to £1,600. Another study used drones to track small animals which can cost upwards of £5000 (Berardi, 2016)

By comparing these two approaches, researchers can gain a more comprehensive understanding of small mammal ecology. Long-term studies provide valuable information about population trends, responses to environmental changes, and broad-scale patterns across different habitats and regions. They can identify factors affecting population size and provide insights into population regulation (Fryxell et al., 1998; Perkins et al., 2009; Brehm, Tironi & Mortelliti, 2020; Hotopp et al., 2022).On

the other hand, fine-scale studies focus on individual behaviours and interactions, allowing researchers to investigate the proximate mechanisms underlying social dynamics, resource use, and communication strategies within small mammal populations (Perkins et al., 2009; Pasch et al., 2013; Keshet et al., 2022)

Replicable and accessible novel applications of technology at the forefront of research

As demonstrated, there are many benefits to using fine scale datasets to understand the intricacies of how species interact with each other. However, accessing the technology and resources necessary to undertake such studies can be difficult to develop or replicate (Dell'omo, Shore, Lipp, 1998; Harrison & Kelly, 2022). Advancements in technology have opened new avenues for research and have led to novel applications in ecology (Harrison & Kelly, 2022). One such advancement is using remote microchip identification. Implanting small microchips under the skin of small mammals can provide individual identification and allow researchers to track their movements and interactions. This method enables detailed observations of social interactions, territorial behaviour, and dominance hierarchies among individuals. First conceptualised by Dell'omo, Shore and Lipp in 1998, the use of microchips to monitor small mammals has grown substantially in recent years. The seminal study used a bulky system comprised of a decoder, two car batteries and a waterproof box and produced accurate temporal activity plots for three species of small mammal. There are numerous potential applications of this technology in studying wild communities, with the potential of providing valuable insights into the behaviour, movement, and interactions of various species in their natural habitats. These same basic components have been honed and modified due to their popularised use in stock management and other industry scale operations, and researchers can now purchase of-the-shelf RFID systems (Harrison & Kelly, 2022). A major drawback of this is that they can be quite costly and difficult to modify.

Through the need to understand social networks of small mammals we designed an independent ultra-low power and low-cost RFID logger that can be built with minimal prior knowledge of coding and construction. This logging system has been used to untangle various facets of how small mammals interact with each other longitudinally and at a landscape level, and it could hold further benefits for researchers seeking to answer similar questions. Within this thesis I provide a detailed explanation of how to source the components for this system, build it and monitor its efficacy in a field setting. As well as examples of the data it can attain and questions it could be applied to. Replicability forms the bedrock of scientific progress. We wish to empower others to reproduce these loggers and use them in their own studies. This accessibility expands the reach of scientific research beyond well-funded institutions, enabling researchers from diverse backgrounds and geographic locations to contribute to

the field. Embracing the culture of open knowledge exchange empowers researchers to collectively push the boundaries of scientific understanding and address complex challenges facing our world.

Overarching theme of thesis

The interactions between and within species play a fundamental role in shaping ecological communities. In this thesis, we focus on two broad themes in species interactions: the impact of disease on populations, using the example of purinina and DFTD, and the role of niche partitioning and cycles in wild small mammals in England.

This research aims to contribute to filling knowledge gaps in the species interaction literature by investigating two distinct ecological phenomena. Through examining devil facial tumour disease (DFTD) in lutrwuita and its implications for driving demographic shifts in the host organism, purinina, I will showcase a novel modelling tool used to understand how the species has so far coexisted with a contagious cancer (Loh et al., 2006). Secondly, through investigating niche partitioning and cycles in wild small mammals in England I reveal insights into community assembly and coexistence dynamics. By addressing these research topics, I aim to enhance our understanding of the complexity of interactions, the context dependency of species interactions, the effects on biodiversity, the processes driving community assembly, and the role of non-trophic interactions. The study of species interactions has a long history in ecology and has been the subject of intensive research in recent decades. However, many questions remain unanswered about the mechanisms underlying species interactions, their ecological consequences, and their implications for conservation and management. The findings from the investigation of DFTD in lutruwita will contribute to our understanding of the complexity of species interactions in the face of disease outbreaks. The results will provide insights into the mechanisms underlying disease transmission and demography facilitated genetic rescue. The study on niche partitioning and cycles in wild small mammals in England will shed light on community assembly processes and the factors influencing species coexistence.

Thesis Structure

Through extensive research, critical analysis, and systematic investigation, this thesis aims to shed light on the underlying principles, theories, and methodologies relevant to the field. Each chapter of this thesis focuses on a specific dimension of species interactions presenting a cohesive and in-depth examination of its key components. The chapters are organized in a manner that ensures a coherent

narrative, allowing readers to follow the research process, evidence-based findings, and conclusions reached throughout the study.

Chapter 2 focuses on the purinina (*Sarcophilus harrisii*), a marsupial that has been severely affected by a contagious cancer, DFTD. Despite the devastating effects of DFTD on purinina populations, some populations have persisted and even recovered. I investigate the coexistence mechanisms that have allowed purinina to survive in the face of this deadly disease. Research has shown that genetic diversity plays an important role in the ability of purinina to survive the disease. Additionally, some purinina may have developed behavioural or immune responses that help them resist or tolerate DFTD. Other factors that contribute to purinina coexistence with DFTD include habitat characteristics and prey availability. Using Integral Projection Models (IPMs) I highlight the importance of certain demographic vital rates that contribute to the species self-facilitated genetic-population rescue. Our models show that at reduced survival rates, purinina can increase reproduction rates in order to minimise the risk of population crashes, which affirms what has been observed in the literature.

Chapter 3 explores the long-term cyclic dynamics of wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*) in Wytham Woods, a deciduous forest in Oxfordshire, UK. Using a 23-year dataset, we investigate the factors that drive the cyclic patterns in these two small mammal species and explore the potential consequences of these patterns for the forest ecosystem. Small mammal populations, such as wood mice and bank voles, often show cyclic patterns over time. These cycles are thought to be driven by a combination of biotic and abiotic factors, including predator-prey interactions, food availability, and climate. In Wytham Woods, a 23-year study found that wood mice and bank voles showed a consistent 3-4 year cycle, with wood mice peaking before bank voles. This pattern was attributed to the fact that wood mice are more generalist feeders and thus better able to cope with food scarcity than bank voles, which are more specialized. Additionally, the study found that predation and weather conditions may also play a role in the cyclic dynamics of these small mammal populations.

Chapter 4 presents a low-cost method of rapidly sampling movement data of wild animals using Radio-Frequency Identification (RFID) loggers with Passive Integrated Transponder (PIT) tags injected into the animals. We demonstrate the applicability of this method in a field experiment with small mammals and discuss its potential for broader use in ecological studies. Radio-Frequency Identification (RFID) technology has become increasingly popular in wildlife research due to its ability to track individual animals without causing harm. Researchers have used RFID tags to study a wide range of species, from small mammals to large predators. In recent years, researchers have begun using Passive Integrated Transponder (PIT) tags, which can be injected into an animal's body and are less invasive than traditional methods such as collaring. A recent study demonstrated the

efficacy of PIT tags in tracking movement data of small mammals. The study also developed a low-cost method of using RFID loggers to collect data, which could make this technology more accessible to researchers with limited budgets.

Chapter 5 investigates the spatiotemporal niche partitioning of bank voles, wood mice, and yellow-necked mice (*Apodemus flavicollis)* in Wytham Woods. Using a combination of field observations and statistical analyses, we examine how these three species coexist in the same habitat by partitioning their space and time. Spatio-temporal niche partitioning is a key mechanism that allows multiple species to coexist in the same habitat. In Wytham Woods, bank voles, wood mice, and yellow-necked mice are all found in the same area but partition their space and time in different ways. A study found that bank voles prefer to occupy habitats with high vegetation cover and are more active during the day, while wood mice and yellow-necked mice prefer habitats with low vegetation cover and are more active during the night. The study also found that the three species have different diets, with bank voles feeding more on invertebrates and wood mice and yellow-necked mice feeding more on seeds and fruits. These differences in habitat use and diet may allow the three species to coexist in the same habitat without competing for resources.

Together, these chapters offer insights into the complex and fascinating world of wildlife ecology and highlight the importance of interdisciplinary approaches to understanding and conserving our natural world. This thesis will use a combination of field studies, experimental manipulations, and mathematical modelling to investigate the dynamics of species interactions in these two contexts, and to explore the ecological and evolutionary mechanisms that drive these interactions. By integrating empirical and theoretical approaches, this thesis will provide new insights into the complex and dynamic nature of species interactions, and their implications for ecology and conservation.

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2

Modelling the population dynamics and life history of Tasmanian Devils prior to the emergence of DFTD

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Abstract

Tasmanian devil facial tumour disease (DFTD) is a transmissible cancer that fatally affects the purinina/Tasmanian Devil (*Sarcophilus harrisii*) and has led to widespread population decline. The disease is in most cases non-recoverable and has affected the population size and structure of the species across its range. Here we detail the building of a pre-disease emergence integral projection model (IPM) and describe the baseline purinina demographics in a pre-diseased population. We undertook a sensitivity analysis to population vital rates, which reveal that at low densities purinina are expected to increase development and reproductive rates, speeding up their life history, which may play a key role in this host-pathogen coexistence. We used our baseline population model to emulate the effects of DFTD through perturbating the survival and growth vital rates of the purinina population. This perturbation showed that populations with low densities tended to have higher development and growth rates, a trend observed in populations post DFTD emergence. This demographic model can be used to investigate how further population perturbations may impact the purinina population, including the effects of increased DFTD load in a population.

Introduction

Emerging infectious diseases increasingly threaten wildlife populations and are complex to model due to the fluctuations in mutations and strains (Gandon, Day, Metcalf, & Grenfell, 2016). Most studies focus on managing short-term epidemic properties, such as controlling early outbreaks. Predicting long-term endemic characteristics with limited retrospective data is more challenging. Here we developed an IPM to explore the population dynamics of a population of wild purinina[2]/Tasmanian devils (*Sarcophilus harrisii*, Family Dasyuridae, a marsupial carnivore now restricted to the island of lutruwita/Tasmania, Australia. Prior to the emergence of DFTD. The model produced in this paper aims to quantify the population dynamics prior to disease emergence using a two-decade longitudinal study of purinina by the University of Tasmania.

Demography underpins many contemporary challenges in ecology from understanding species' distributions to the fate of biodiversity under climate change (Merow et al., 2014). Demographic models can do this because demography links the processes that affect individuals to population- and community-level patterns (Lachish, McCallum, & Jones, 2009). IPMs provide a framework within which we can analyse the dynamics of population structure by continuous characters, such as body

[2] Echoing the footnote in Chapter 1, words such as purinina and lutruwita are palawa kani. palawa kani is a reconstructed language from a variety of language groups within lutruwita/Tasmania..

size (or a proxy for size such as head width) (Rees, Childs, & Ellner, 2014). Construction of an IPM requires identification of associations between a continuous character and (i) survival, (ii) growth, (iii) inheritance and (iv) reproduction. IPMs have emerged as a powerful tool for quantifying how the vital rates of individuals (i.e. survival, growth and fecundity) govern such higher-level properties, partly because the models can be constructed very flexibly from regression models. To construct a model depicting general population demography prior to DFTD emergence, we parametrised our IPM using data collected across the island of lutruwita before DFTD was first noted during regular sampling trips.

To predict how a population will respond to external pressures on its life history, it is necessary to model the system prior to perturbation (Metcalf, Graham, Martinez-Bakker, & Childs, 2016). For example, a pre-disease emergence model of a host population will provide a deeper understanding of the population dynamics of a species in the absence of disease, and through perturbation analysis we can explore how populations are expected to respond to an emerging disease. One commonly used modelling approach for understanding population demography is Integral Projection Models (IPMs) (Coulson, Tuljapurkar, & Childs, 2010; Ellner & Rees, 2006; Lachish et al., 2020; Merow et al., 2014; Rees & Ellner, 2009; Traill, Schindler, & Coulson, 2014; Wallace, Leslie, & Coulson, 2013). These models are often used to explore the implications of population-scale changes in survival, growth, inheritance, and reproduction (Ellner & Rees, 2006). Predicting the impact of disease on demography of a species is important because it aids in understanding the potential impacts of the disease on a population or ecosystem. Cattadori et al. (2005) demonstrated the importance of understanding how disease can affect life history traits in wild populations. The study showed that a parasite infection in a wild population of rodents led to reduced body condition, growth, and reproduction, which in turn led to reduced population growth rates. These findings highlighted the potential impacts of disease on population dynamics and the need to consider the effects of disease when managing populations. More recently, a study by Johnson et al. (2020) highlighted the importance of considering the effects of disease on population dynamics in endangered species management. The study showed that disease-induced reductions in survival and fertility can have significant impacts on the viability of endangered species populations, and that disease management strategies may need to be prioritized to ensure the long-term persistence of these populations.

The purinina/Tasmanian Devil is the largest extant marsupial carnivore following the extinction of the thylacine (*Thylacinus cynocephalus*), with wild populations restricted to the island state of lutruwita/Tasmania, Australia. Listed as Endangered (IUCN, 2008), purinina have experienced long-term (over the last 20,000 years) density fluctuations correlated with environmental changes resulting in low genetic diversity in surviving populations (Brüniche-Olsen, Jones, Austin, Burridge, & Holland, 2014). The species disappeared from the mainland of Australia approximately 3200 years ago (White et al., 2018). Climate variation, a prolonged hot and dry El Nino, reduced populations to a

small part of their range (Morris, Kearney, Johnson, & Brook, 2022) and correlated with a genetic bottleneck following a decline in population in Tasmania (Brüniche–Olsen et al., 2018;). Remaining mainland populations may have disappeared due to competition with the placental Dingo (*Canis dingo*) introduced to Australia in the same time period (Archer & Clayton, 1984; Letnic et al., 2012) and expanding human populations (Johnson & Wroe, 2003). Within lutruwita, populations severely reduced from the early 1900s, recovering during the 1960s (Guiler, 1983) with postulated causes unconfirmed but ranging from disease (McCallum & Dobson, 1995) to persecution (Guiler, 1983). The current major threats to the species are road traffic strikes (Jones, 2000) and a transmissible cancer, Tasmanian devil facial tumour disease (DFTD) (Cunningham et al., 2021). purinina are generalists in their habitat choices and can inhabit coastal areas to sub-alpine heathland although they avoid dense wet moorlands and scrubs (Cunningham et al., 2021). They thrive in wet and dry sclerophyll forests where habitat is fragmented into a mosaic of forests and grassland (indicative of long-term Indigenous management and use of the landscape). purinina have a complex life history in which they give birth to a large amount (20-30 individuals) of offspring but only have 4 teats in their pouch to allowing for suckling and development into weaned juveniles (Russell et al., 2019). Like all marsupials, young are born in the embryonic stage, the vagina dumps the young into the cloaca and they emerge in a stream of fluid across their mother's body. They then remain in the pouch to complete development, initially firmly attached to the teat, releasing this as they mature. This r-selected life history strategy means that population recovery may be able to survive better in unstable environments and recover more effectively from population disturbances than K-selected species. This may be the underlying mechanism that has enabled purinina to recover from multiple population crashes in recent decades (Brüniche–Olsen et al., 2018).

Within the purinina study system we wanted to understand the biological mechanisms underpinning the perceived coexistence in this host-pathogen system. Using pre-disease vital rates, we will demonstrate what the population demography of purinina might have been prior to DFTD emergence. Through elasticity and sensitivity analyses we attempt to reproduce the changes DFTD has had on population dynamics that have been observed in the field. Cunningham et al. (2021) describe the observable effects of DFTD ~23 years after the first observed cancer in wukalina/Mt William in the NW of lutruwita. Initial rapid decline in population numbers is often the first impact of the disease, which leads to decreased reproduction and genetic diversity. We model a population of the purinina prior to the emergence of DFTD. We predict that as DFTD is spread by mature recruited individuals, populations with long-term disease prevalence will have a population dominated by larger younger individuals participating in precocial breeding as yearlings, which is what was observed. A key test of the efficacy of our model as a useful tool to researchers and conservation managers of this species will be how well the pre-disease model can predict these effects when perturbed. The model produced

here may be used to explore whether we could have predicted how a disease that impacts survival might impact purinina life history and demographics.

Methods

Description of model

All populations consist of individuals, which can be measured on several continuous and discrete characters. At any point in time, a population can be characterized by a distribution of character values. This distribution can change with time as the environment fluctuates (Coulson, 2012). All population biology parameters describe an aspect of a character distribution or its dynamics: some, like λ (the finite growth rate) and the strength of selection, describe change in the character distribution over a time step; others, like R0 (the average number of new infections generated by a single infected individual in a susceptible populations), describe aspects of the dynamics of cohorts; whilst yet others, like heritability, describe how character distributions correlate (or not) across generations (Coulson et al., 2010). Integral projection models project the temporal dynamics of distributions of phenotypic traits and can be used to simultaneously study the dynamics of all these parameters.

We developed a single-sex Integral Projection Model (IPM) for a population of female purinina that had not yet been exposed to DFTD. The model is formulated to reflect the ecology and population dynamics of purinina and predict dynamics and life history within a disease-free population. We assume an annual breeding cycle, with time iterated forward on a yearly time step. The dynamics of the purinina populations are defined by an IPM that links changes in the distribution of individual phenotypes to demographic outcomes at the population level. We use head width measurements as the focal trait (Z) as it correlates with body size (Ruiz-Aravena et al., 2018). Maximum head width is measured over the zygomatic arch and is a standard and precise measure of body size in the purinina as it is less likely to be influenced by environmental fluctuations and external variables compared to other body size measurements such as tooth and weight measurements (Jones, 1995). Here we illustrate the survival, growth, reproduction, and investment in offspring functions, and explain how they were parametrised.

In many populations, demographic rates are influenced by both size and age. For each year, the IPM iterates the distribution of head width (Z) at time t, $H(Z,t)$ to the distribution of head width at time t+1, $H(Z',t+1)$ using the following equation:

$$H(Z',t+1) = \int_{\Omega} [D(Z'|Z,t)R(Z,t) + G(Z'|Z,t)S(Z,t)]H(Z,t)dZ$$

where the survival function $S(Z,t)$ is the probability that individuals with head width Z survive from time t to time $t+1$, the growth function $G(Z'|Z,t)$is the probability that those individuals of head width Z at time t that survive grow to size Z' at time t+1. The reproduction function $R(Z,t)$calculates the number of offspring produced by an individual of size Z between time t and $t+1$ that survive to recruit to the population at time $t+1$. The offspring investment function $D(Z'|Z,t)$ gives the probability that an offspring born to an individual of head width Z is of head width Z' at time $t+1$. Individuals can be characterised in terms of one or more state variables that explain variation in vital rates, in the case of our model, survival, reproduction, inheritance and growth.

Functions

Survival $S(z,t)$ *& Reproduction* $R(z,t)$

The functions making up the survival and reproduction kernels can be estimated by regression; for example, size-dependent survival and fecundity can be fitted by generalized linear or non-parametric models and growth by regression models (Metcalf et al., 2016).

$$S(z,t) = \frac{1}{1+e^{-(a_s+b_s\,z+\rho_s N_t)}}$$

where $S(z,t)$ is the predicted probability of survival given a specific character value z; a_s and b_s are respectively an intercept and slope describing the linearised association between the character (head width) and expected survival. We can also include a density-dependent term ($+\rho_s\ N$) to account for the negative effect of intra-specific competition on purinina survival (Pemberton et al., 1993,).

Breeding occurs annually over a single time step, such that all reproductive costs to individuals (i.e. costs of pregnancy, parturition, and lactation) are assumed to occur over a single month. As purinina do not usually breed in their first year of life, we set a threshold size for breeding in the model equal to the minimum head width of two-year-old female breeders (~70cm: Jones et al., 2008). Individuals must be above this threshold head width to breed. A density dependence term was included in the reproduction function to account for density-dependent fecundity, where the birth rate falls as competition increases.

Mortality is high in the first year of life – Lachish et al. (2007) demonstrated 45% mortality per year before their second year. Given we are interested in recruitment we model "recruited" as being binomially distributed with a 1 representing the successful production of a recruit and a 0 representing a failure to do so.

$$R(z,t) = \left(\frac{1}{1+e^{-(a_r+b_r\,z+r_r N_t)}}\right)$$

where $R(z,t)$ is the predicted probability of reproduction given a specific character value z; a_s and b_s are respectively an intercept and slope describing the linearised association between the character (head width) and expected reproduction.

Growth $G(z'|z,t)$ *& Inheritance* $D(z'|z,t)$,

The head width growth function describes how the character value changes among surviving individuals from time t to $t+1$. Growth is probabilistic and not deterministic and as such not all individuals that had the same head width at time t will have identical head widths at time $t+1$. This means that each head width at time t requires a probability distribution of possible head width at time $t+1$. The aim of this is to work out the expected distribution of head width at time $t+1$ among survivors, given their distribution of head width at time t. We did this by working out the distribution of expected head width at time $t+1$ for each head width at time t before summing these distributions together. The mathematical notation to describe this is $\int G(z'|z,t)H(z,t)\,dz$. Here the z is head width at time t and z' is head width at time $t+1$. The | symbol means 'given' or 'conditional on'. $G(z'|z,t)$ is consequently a function describing how head width at time t maps to head width at time $t+1$ among those individuals that survive. To statistically estimate $G(z'|z,t)$ we work out the expected (predicted) head width at time $t+1$ for a given head width at time t: $E(z')$. To do this we collated pairs of head width measured at time t and $t+1$ from the same individual and regressed the head width at time $t+1$ against head width at time t. In the case of the purinina a linear regression for the form of the fitted data adequately:

$$E(z') = a_g + b_g z$$

The next step in constructing $G(z'|z,t)$ required squaring the residuals around the $E(z')$ fit and modelling these as a function of head width. If the association is linear, we can estimate this function as:

$$\sigma^2(z') = a_{gv} + b_{vg} z$$

we can then combine the functions $E(z')$ and $\sigma^2(z')$ to construct the character growth function:

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

Identical logic to that used to construct the function $G(z'|z,t)$ is used to identify $D(z'|z,t)$, except instead of initially regressing head width at time $t+1$ against head width at time t, we regress the head widths of recruits that enter the population at time $t+1$ against that of parents at time t. As we are dealing with only the female component of the population, we work with maternal head width at time t in this example.

Sensitivity Analysis

We performed a sensitivity analysis to assess how model predictions varied by altering parameter values and quantified the effect of each parameter on the final model outcome. We varied the value of each individual parameter by a standardised measure of 1%, (Coulson, 2012) running a separate

model each time and recording the carrying capacity of purinina after the model reached equilibrium (after 5000 iterations).

Study System

Since the extinction of the thylacine (*Thylacinus cynocephalus*) in the 1930s, the purinina acts as the top predator on the island of lutruwita. The purinina is now listed as threatened primarily due to the emergence of a transmissible cancer, devil facial tumour disease (DFTD). DFTD is almost 100% lethal and devils show nearly universal susceptibility to the transmissible cell line, which is transmitted by biting during common social interactions (Hamede, McCallum, & Jones, 2013; McCallum et al., 2009). Since its discovery in 1996, DFTD has spread across ~95% of the purininas geographic range and has caused localized declines exceeding 90% in most areas with long-term infection (Lazenby et al., 2018; Storfer et al., 2018). purinina-DFTD host-pathogen system provides perhaps a singular, but generalizable, example of a long-term ecological study with documented rapid evolution, as well as community-level consequences of top predator loss (Cunningham et al., 2021; Epstein et al., 2016; T. A. Hollings, 2013; T. Hollings, Jones, Mooney, & McCallum, 2014). In this model reproduction occurs once a female reaches a certain head width (head width), the social complexity of breeding in devils is not well understood so we assume each individual has the same chance of reproducing once the appropriate head width has been reached.

Parameterisation

The model described above has been parameterised for a disease-free population to simulate population dynamics prior to disease emergence. All parameters were derived from the extensive two-decade longitudinal study of purinina, undertaken by the University of Tasmania and the Tasmanian Government's Save the Tasmanian Devil Program. Trapping and demographic sampling methods are described in Lazenby et al. (2018) and are the ongoing standardised capture-recapture procedures for the entire state. Custom made standardised baited PVC traps (Hamilton et al., 2020) were placed systematically around the state totalling (10,761 trap nights for this dataset). Six (6) sites were identified as suitable for this model development based on the time period of data available prior to DFTD emergence, puthimiluna/Freycinet National Park, wukalina/Mt William National Park, West Pencil Pine, Takone, paytanarung/Black River and maytim/Arthur River. Forty traps were deployed temporarily at each site for a ten-day period, on tracks and pathways that would be used by purinina. Each individual wass uniquely identified with a microchip (a 12mm PIT tag, inserted subcutaneously) and at each sampling event demographic head width information is taken including: head width (mm, measured behind the cranial arch), weight (kg), tail width (mm, measured at the base of the tail), head of pouch young if present and if uncurled from the embryonic state at birth.

To create the parameters for the initial model the data were filtered to only include timepoints prior to DFTD emergence in the landscape. This allows us to develop a density dependant model to reflect the demographics of a non-diseased population. We can test the viability and efficacy of the model by simulating disease emergence in populations and compare the IPM kernel to the actual population shifts reflected in the collected data. As our model is non-spatial, and because the annual movement of adult devils between sites is not widely known, we made the simplifying assumption that the simulated devil population was resident year-round.

All statistical analysis was carried out in R (version 4.2.2, R Core Team, 2022), packages of note are described where relevant.

To estimate survival parameters, we used the package RMark (version 3.0.0, Laake, 2013) which is an interface for the program MARK the most widely used application currently available for parameter estimation. Standardising for age we used the Cormack-Jolly-Seber (CJS) mark recapture method to estimate survival rates (Laake, 2013). The CJS model calculates the survival of tagged individuals over time by using recapture rates and estimating survival and recapture probabilities using a maximum likelihood estimate. We estimated age-specific survival through correcting for recapture probability, and then correlating age to an average value.

Growth parameter estimates were developed by Kerlin et al. (unpublished data) using a von Bertalanffy growth function relating head width (body size) to age. Head width is a standardised measurement that experts in purinina ecology collectively agree is the most accurate indicator of age and condition (Jones, 1995).

The reproduction and growth parameters were estimated through visualisations of the raw data and fitting linear regression models with a Poisson error structure. The growth functions assumed all head width measures of recruits were drawn from a distribution with a mean and variance determined from raw data and the current literature, namely Lachish et al. 2009. Head width at sexual maturity was set at 69.4mm (log 4.24) based on an average body size of when an individual was recorded reproducing for the first time.

A slope parameter for density was included in the reproduction vital rate and omitted from survival, inheritance, and growth. This was to give a weighted importance to reproduction, as from field observations we know DFTD directly affects reproduction rates in an infected population. (Lazenby et al., 2018)

Results

Parameter estimates (Table 1) were found for survival, reproduction, growth, and inheritance. We ran our pre-disease emergence model until equilibrium, and population equilibrium was reached at 931 individuals. Head width (body size) influenced survival and growth, but not reproduction or inheritance. We incorporated density-dependence into reproduction given findings in the literature (Lachish et al., 2020). We also set the variance term to 0.1 as per Coulson, Gaillard, & Festa-Bianchet, 2005.

Table 1 Parameters for Vital Rate Functions

Parameter	Intercept	Head width slope	Density Dependence slope	Variance term
Survival	-0.4855082	0.3809523		
Reproduction	0.7		-0.001	
Growth	2.1373	0.5496		0.1
Inheritance	4			0.1

Stable size distribution w(z)

The stable size distribution of the pre-disease emergence purinina population (Fig 1) when the deterministic model is evaluated at different densities. This shows that the mean and variance of head width change with density. The median head width of the population was ~90mm.

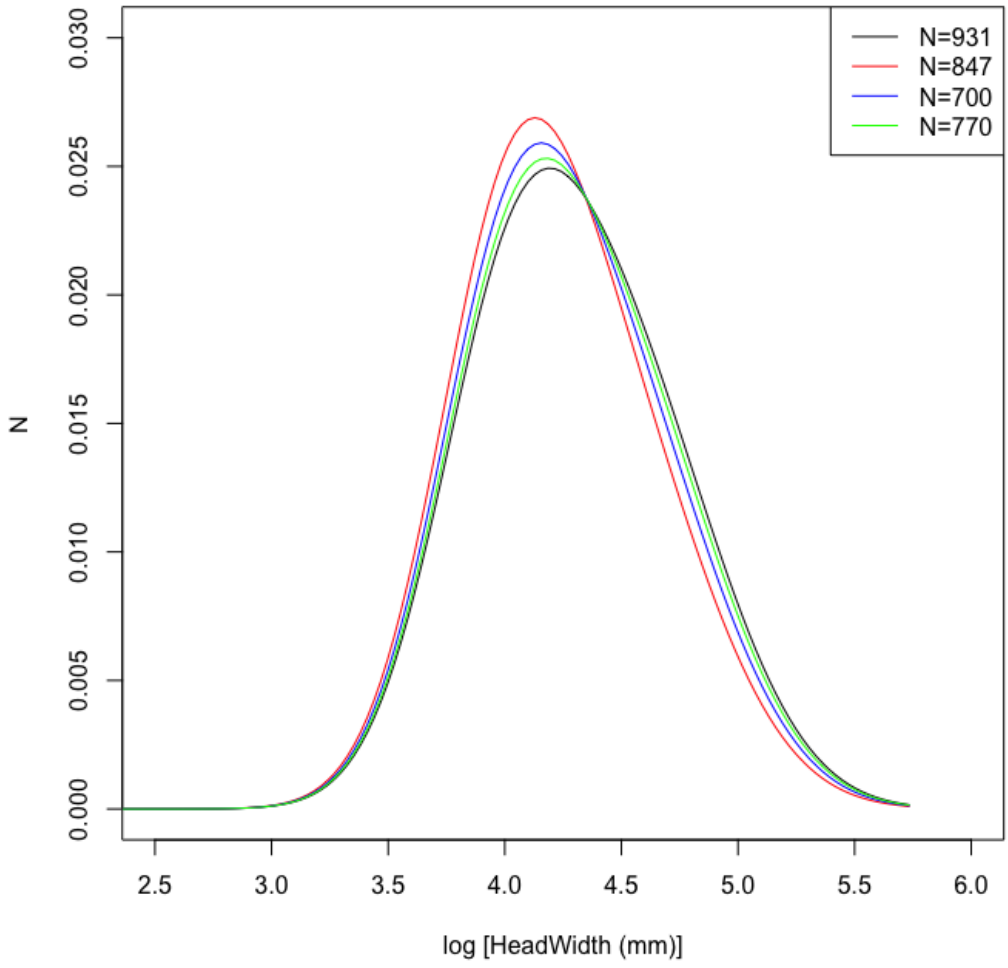


Figure 1 The effect of different population densities on head width (body size).

Sensitivity Analysis

Perturbating all vital rate parameters (Table 1) by ±1% showed that different parameters can have different effect on the final model estimates across a range of densities. As density increased, the sensitivities of λ to parameters in the survival, growth, reproduction, and inheritance functions all decreased (Figure 2).

By holding N constant, we converted the density dependent model into a density-independent model. Then we could draw conclusions about the sensitivity of the asymptotic population growth to each fixed N value.

The population growth rate (λ) was most sensitive to terms in the growth function, the size of offspring when they recruited to the population (in this populations case, when they were first trapped and tagged as subadults), and the intercept of the survival function. Each one of these sensitivities tended to increase at lower density, but with the largest increase seen in parameters in the growth function. A decline in survival rates consequently negatively impacts the population, but the high

sensitivity of lambda to growth, means a population could partly mitigate decreased survival by increased individual growth, if growth increases as survival declines and if this increased growth rate leads to higher survival rates or age-related fecundity shifts.

As purinina population size decreased, reproductive rates increase due to the density dependent term in the reproduction function (Table 1) but this change is predicted to have little impact on the population growth rate.

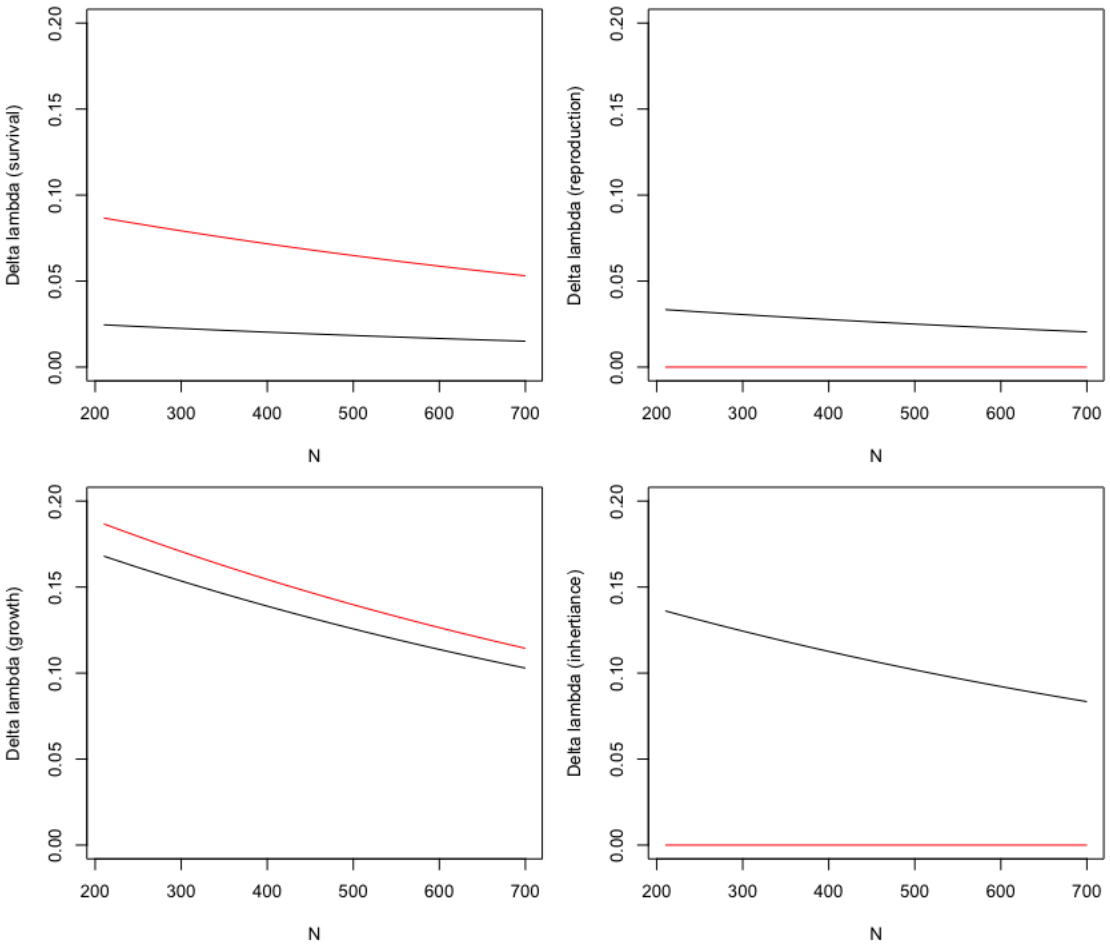


Figure 2 Sensitivities of the population growth rate to parameters in the (a) survival, (b) reproduction, (c) growth and (d) inheritance functions. Red lines represent the head width slope and black the intercept.

Discussion

In this paper we developed a density-dependent integral projection model (IPM) for purinina/Tasmanian devils pre-DFTD emergence and parameterised it using a multi-decade long data set from across the island state of lutruwita/Tasmania. This model was produced to understand population demographics prior to the emergence of DFTD. The model revealed that a decline in population size caused by a reduction in survival and consequently population density, could result in

an increase in individual body size growth rates (Figure 2 c). The resulting increased growth could partially buffer the population from the negative effects of the cause of population decline, in this case DFTD. Accelerated growth is a positive demographic trait as animals can reach sexual maturity at a younger age and larger animals will have higher survival rates.

DFTD has had a significant impact on the demography of purinina. Spread through direct transfer of live cancerous cells through conspecific contact (primarily intraspecific aggression (Hamede et al., 2013), DFTD is amongst only a handful of known transmissible cancers (Belov, Jones, & Cheng, 2015; Ujvari, Gatenby, & Thomas, 2016; Ujvari, Papenfuss, & Belov, 2016) and since its emergence has reduced average life expectancy at birth from five years to two (Epstein et al., 2016; Farquharson et al., 2018; Lachish et al., 2009). Transmission of DFTD is largely frequency dependent (Deakin, Waters, & Graves, 2010; Lachish et al., 2009; McCallum et al., 2009), making transmission possible at very low host densities (McCallum et al., 2009). Since its discovery in the mid-1990s, the disease has spread rapidly and has caused a major decline in the purinina population, with estimates suggesting a decline of 60-80% (Cunningham et al., 2021). The decline in the purinina population has consequences for the ecosystem in which they live, as they play an important role as top predators in structuring both the consumptive and scavenging components of the ecosystem and in protecting smaller biodiversity (Cunningham et al., 2020).
Conservation efforts, such as the establishment of insurance populations, are ongoing to try and save the species from extinction (Hogg et al., 2019). The impact of the disease on individual purinina is severe, with many individuals dying within months of showing symptoms. This has resulted in a change in the age structure of the population, with fewer older individuals and a higher proportion of younger, less experienced individuals (Jones et al., 2008; Lachish et al., 2009). The decline in population size and the altered age structure of the population has had cascading effects on the purinina role in the ecosystem, and on their behaviour and social dynamics. DFTD is known to effect density of purinina across their range, reduced density is known to affect this species in several ways. As the population size of the purinina decreases, the distance between individuals will increase, leading to reduced social interaction and possibly mating opportunities (limiting reproductive potential). This leads to a decline in genetic diversity and an increased risk of inbreeding, which will have negative flow on effects on the health and fitness of the population (Hamilton et al., 2020). The decline in population size may also increase the risk of extinction, as small populations are more susceptible to stochastic events such as disease outbreaks, natural disasters, and genetic drift. Finally, reduced density can also affect the behaviour and social dynamics of the purinina, as they may become more solitary and less likely to engage in communal behaviours (Lazenby et al., 2018). The results of our pre disease emergence IPM show that perhaps these impacts and the resulting population decline could have been predicted prior to the appearance of DFTD.

Using elasticity and sensitivity analyses, our final model showed the key effects that DFTD has ultimately had on purinina. As density declines, reproduction increases and so too do individual growth rates. Individuals reach sexual maturity faster, consequently they can reproduce at a younger age. Additionally, they increase reproduction at lower densities, most likely because more food resources are available. If we had used this same dataset and modelled the population prior to disease emergence, we would have predicted that increased growth rates would have had the potential to help buffer the populations from some of the negative effects of decreased survival caused by DFTD. Thus, if growth rates increase at low densities, then this would act to increase the finite population growth rate, which has also been found in other studies of population demography (Kerlin et al. unpublished data). This may also be a consequence that our model was trained on populations pre-DFTD emergence which have a relatively stable structure. The sensitivity analysis predicts that an increase in individual growth rate should have a strong positive effect on the population growth rate, which may contribute to population recovery. The mechanisms behind this are high survival rates with increased growth, and precocial breeding observed in wild purinina populations (Russell et al., 2019).

We were interested in the population dynamics in purinina prior to the emergence of DFTD. Plastic demographic and life history changes have been observed in response to disease emergence. Most notably, precocial breeding (breeding as yearlings is strongly associated with years since DFTD emergence (Jones et al., 2008). Prior to DFTD emergence sexual maturity was reached as 2-year-olds, as our model illustrates when survival is reduced purinina are growing to a bigger head width earlier and achieving sexual maturity faster. This buffers the population from some of the effects of DFTD and other negative pressures on the populations. A key concern in the conservation and management of this species is whether localised or widespread extinction is likely to occur. Early frequency dependent models suggested that diseased induced extinction was probable in areas with high disease prevalence (Epstein et al., 2016; McCallum et al., 2009). There is increasing evidence that rapid evolutionary changes have taken place in infected purinina populations, particularly in loci associated with disease resistance and immune response (Epstein et al., 2016; McCallum et al., 2009; Storfer et al., 2018). Therefore, despite high lethality, the rate of epidemic increase appears to be slowing and predictive modelling may be useful to understand demographic changes in response to the genetic evolution in response to DFTD emergence (Patton et al., 2020). We analysed our model with sensitivity analysis to mimic the effects of DFTD through exploring how the population growth rate is influenced by each demographic function at different densities. Our assumption was that an increase in mortality will decrease density, and this could impact growth and reproduction. This approach gives us the mathematical freedom to predict how a particular type of perturbation might impact a population.

Our final parameterised model describes a population growth rate that is most sensitive to individual growth rates, particularly at low densities. This response has been observed in populations affected by DFTD, where early breeding is a consequence of more rapid growth in response to a reduced population density and reduced food competition (Jones et al., 2008). Demonstrating this mechanism in populations before the onset of disease could suggest that it is a beneficial recovery mechanism that has proven effective in previous population declines. Prior to the emergence of DFTD, purinina exhibited slow growth rates relative to post-disease emergence population and reached sexual maturity typically around two to three years old. The formation of facial tumours impedes the animal's ability to feed properly, in response, infected purinina may overcompensate by consuming more food and increasing their overall energy intake. This increased nutrition can result in faster growth rates, allowing infected individuals to reach sexual maturity at an earlier age compared to healthy individuals. The early age of sexual maturity in response to DFTD is an adaptation that maximizes reproductive opportunities before succumbing to the disease. By maturing earlier, infected individuals have a better chance of reproducing and passing on their genetic material before the tumours become debilitating or fatal. However, the early sexual maturity in response to DFTD comes with its own set of challenges. One significant concern is the potential for reduced overall lifespan and reproductive output. Since infected purinina allocate more energy towards growth and reproduction at a younger age, they may experience accelerated aging and reduced longevity. Additionally, early sexual maturity may lead to smaller body size and lower overall fitness, as these individuals may not have had sufficient time to develop fully before beginning to reproduce. This may have flow on consequences if DFTD is excluded from populations that have coexisted with the disease for decades.

Another hypothesis that may be gleaned through this model is that the species r-selected life history may play a critical role in their resilience to population fluctuations. By producing many offspring, purinina increase their chances of at least some individuals surviving in harsh conditions or during disease outbreaks. Even if a significant portion of the population perishes, the large number of offspring can compensate for the loss. purinina also exhibit high dispersal behaviour, with individuals ranging over large areas. This behaviour allows for the colonisation of new habitats and the establishment of subpopulations. In the face of adversity, individuals can disperse to areas with more favourable conditions, reducing competition and increasing overall population resilience. These traits provide the species with the ability to rebound and adapt to changing environmental conditions, although they may also pose challenges in specific circumstances.

Bruniche-Olsen et al. (2014) investigated population trends in purinina over recent time. Climatic changes caused three major declines in populations and colonisation caused a further major population decline resulting in decreased genetic variability. Each event triggered population declines

in the order of 78-90%, like what has been observed in DFTD infected populations. Historic fluctuations of this magnitude may have resulted in purinina evolving response mechanisms to support population recovery, such as precocial breeding (Russell et al., 2019).

The current literature on purinina life history demographics is focused on post DFTD emergence. Our model gives us insight into the demographic patterns pre-emergence and can be used as a tool to predict how they may respond to other threatening events that impact the demography of the species. The model we have constructed is a simplification of real-world population dynamics. We do not incorporate environment stochasticity or external environmental pressures. We acknowledge that these are omissions of important factors that can have substantial influences on any population, nonetheless there is no reason to expect how incorporation of additive environmental effects would alter our results. This model sought to explore the population dynamics of purinina without external pressures of a disease epidemic. Our results can be used to provide a baseline understanding of population dynamics, which can be manually perturbated in response to external conditions to understand how a population may respond to extrinsic pressures if the effect of one of the parameters is approximately known.

The development and implementation of an IPM to elucidate the mechanisms enabling purinina to persist under conditions of low survival rates represents a valuable addition to the toolkit for managing their recovery from DFTD. By capturing the complexities of purinina population dynamics, this model offers insights into the underlying processes that contribute to their survival, providing a comprehensive understanding of the species' response to disease and other challenges. The IPM's ability to incorporate various factors, such as age-specific survival rates, reproductive output, and in the future disease prevalence, allows for a more accurate representation of the devil's population dynamics than simpler models. Furthermore, this model holds great potential for future work, as it can serve as a predictive tool for forecasting population fluctuations. By considering different scenarios and manipulating key parameters, we can assess how varying conditions and management strategies may influence the devil's long-term viability. Such predictions can inform proactive conservation efforts, facilitating adaptive management and enhancing the prospects for the recovery and persistence of purinina populations in the face of ongoing threats.

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3

Understanding cyclic dynamics and interspecific competition in a community of wild small mammals

Dale, J. R., Knowles, S., Coulson, T.

Abstract

This chapter explores the long-term population cycles of wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*) in Wytham Woods, a deciduous woodland located in Oxfordshire, UK. The study analysed population data collected over a period of 28 years, from 1984 to 2012, to investigate the factors driving the cyclical fluctuations observed in these small mammal populations.

We found that both species exhibited cyclical population patterns, with peaks occurring approximately every three to four years. The cycles were found to be synchronous between the two species, indicating a shared driver of population dynamics. An unknown perturbation around 1970 caused a steep decline in the bank vole population, and consequently a destabilisation of their long-established cycles. Here we use autoregressive moving average models (ARIMA) and wavelet coherent analyses to determine trends, cycle lengths and overarching population dynamics. We report a stable trend in wood mice but a negative trend in bank voles. Using wavelet analysis, we show that both wood mouse and bank vole cycles were lost after the 1990s, which is consistent with dampening cycles of similar small mammals across Europe.

The findings of this study have significant implications for our understanding of population dynamics in woodland ecosystems. By identifying the key drivers of population cycles in these species, this research contributes to the development of more accurate predictive models of population dynamics, which can aid in the management and conservation of these ecosystems. The study also highlights the importance of long-term monitoring programs for understanding the complex dynamics of natural systems.

Introduction

Wild small mammals are known to exhibit cyclic population dynamics, where their numbers oscillate over multi-year timescales (Andreassen et al., 2021). These cycles are typically driven by changes in food availability, predation, and disease, among other factors. For example, the populations of lemmings and voles in the arctic tundra are known to undergo cyclic fluctuations, with peak abundance occurring every three to five years (Krebs, 2013). In these species, the cycles are thought to be driven by changes in the availability of their primary food source, which is dependent on the timing and extent of snow cover. Similarly, the populations of the deer mouse and the cotton rat in North America exhibit cyclic patterns, with peak abundance occurring every two to four years (Turchin & Batzli, 2001). Understanding the factors that drive these cycles is important for predicting and managing populations of wild small mammals, which can have significant impacts on ecosystems. Charles Elton was a pioneering ecologist who proposed one of the earliest theories to explain the cyclic population dynamics of small mammals. Elton's theory, which he first proposed in the 1920s, suggested that these cycles were driven by changes in food availability, which in turn were influenced by predation and other factors (Elton, 1924). According to this theory, when the population of small mammals was low, there would be an abundance of food resources and little competition for them. This would lead to a rapid increase in the small mammal population. As the population grew, however, competition for food would increase, and predators would become more effective at hunting the small mammals. Eventually, the small mammal population would reach a peak and begin to decline, as food resources became scarce, and predation increased. Elton's theory has been refined over the years, but it remains an important framework for understanding the cyclic population dynamics of small mammals and other species. Alfred Lotka was another seminal researcher who made significant contributions to the study of small mammal population dynamics, particularly regarding the mathematical modelling of these cycles. Lotka's work focused on the interactions between predator and prey populations, and he developed a set of equations that could be used to predict the cyclic patterns of these populations over time. His models considered factors such as the rate of predation and the reproductive rates of both predators and prey. Lotka's models were among the first attempts to quantify and predict the cyclic dynamics of small mammal populations, and they continue to be used and refined by ecologists today. Complementary to the work undertaken by Lotka, Vito Volterra proposed that the population dynamics of small mammals are influenced by predation and resource availability, and that these interactions could be modelled mathematically using a system of differential equations. He also suggested that the cycles observed in small mammal populations were driven by the interaction between these factors. The Lotka-Volterra model, which combines both of their approaches to modelling predator-prey interactions, is still widely used today to understand the dynamics of animal populations, including small mammal cycles.

More recently, ecologists such as Smith (2019) have explored the role of disease in driving small mammal population cycles. This research has shed light on the impact of diseases on small mammal populations and their cyclic dynamics. Additionally, investigations have been conducted to examine the role of climate (Johnson et al., 2020) and other environmental factors (Davis et al., 2018) in influencing small mammal population cycles. These studies have contributed to our understanding of the complex interactions underlying the cyclic dynamics of small mammals. Mathematical models developed by researchers like Caswell (2000) have also played a significant role in elucidating these dynamics. Despite ongoing research, the precise mechanisms that drive small mammal population cycles remain a subject of debate and continued investigation. Many hypotheses in addition to those formulated by Elton have been put forth to explain the cyclic nature of small mammal populations, across a wide geographic range. These include behavioural shifts (Voipio, 1950a, 1950b; Chitty, 1960, 1967; Krebs, 1964, 1979, 1985; Charnov & Finerty, 1978; Getz, 1978; Abramsky & Tracy, 1979; Gaines et al., 1979; Stenseth, 1983; Hestbeck, 1982; Halle & Lehmann, 1987; Gliwicz, 1990); habitat changes (Southern, 1979; Bondrup-Nielsen & Ims, 1988); predation pressure (Elton, 1924; Shelford, 1943; Pearson, 1966; Erlinge et al., 1983; Hansson, 1984; Hansson & Henttonen, 1988); disease (Elton, 1924); physiology (Christian 1950, 1978; Mihok et al., 1985); fire (Bowman et al., 2017), or a multifaceted combination of the above (Elton, 1924; Lidicker, 1978; 1988).

Understanding small mammal cycles holds importance for several reasons. Small mammals are integral components of many ecosystems, and their population dynamics can exert considerable impacts on other species and ecosystem processes. For instance, during population booms, small mammals can consume substantial amounts of vegetation, leading to alterations in plant communities and ecosystem structure. Furthermore, small mammal outbreaks can have significant economic and public health implications, as some species can cause damage to crops and infrastructure or serve as carriers of diseases transmissible to humans. By studying the cyclic population dynamics of small mammals, researchers can gain insights into the factors influencing these patterns and develop models to forecast future cycles. This information can inform land management decisions, including the timing and strategies for controlling small mammal populations to mitigate adverse effects. Moreover, comprehending small mammal cycles enhances our understanding of ecosystem processes and the interconnectedness of species within ecosystems. Furthermore, studying small mammal population dynamics can provide valuable insights into broader ecological and evolutionary inquiries, such as the factors influencing species interactions, predator-prey dynamics, and the evolution of life history traits. Overall, understanding small mammal cycles constitutes an important component of ecological research and holds implications for a wide range of fields, from conservation biology to public health.

Wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*) are two common species of small mammals that coexist in many woodland ecosystems. Here we investigate their long term

sympatry in Wytham Wood. Wytham is a research forest located near Oxford, England, which has been the site of numerous studies on the population dynamics and ecology of small mammals. Researchers have been conducting studies in the forest since the 1920s, and the site is now one of the longest-running ecological studies in the world. Studies in Wytham have contributed significantly to our understanding of small mammal population cycles and the factors that influence them (Table 1). Here, we use a 50-year timeseries of Wytham's small mammal community, comprised of wood mice and bank voles to understand population trends and cycles. Capture-mark-recapture surveys were undertaken between 1948-1999.

Table 1 Review of studies on small mammals in Wytham
* Denotes studies that use the same data presented here

Title	Species	Factor(s)	Key conclusions	Year(s)	Reference
Prior to 1948					
Aspects of the population and feeding ecology of *Microtus agrestis* the field vole	Field vole	Various, but with a focus on the boom-bust cyclic population dynamics	Predictable peaks at various times of year support the 'density dependant' hypothesis proposed by Chitty (1952)	~1938-1940	Richards, 1985 (thesis submission)
Voles, mice and lemmings & The health and parasites of a wild mouse population	Field vole, bank vole, wood mouse and lemmings	Species interactions and parasite loading	Foundation body of work which led to the establishment of the current study	1926-1938	Elton, 1942 & Elton et al., 1931
During 1948-1999					
Impacts of woodland deer on small mammal ecology	Bank vole and wood mouse	Ungulate presence, vegetation structure and small mammal perturbation	Intensive deer management and exclusion promote understory regeneration, leading to more stable bank vole numbers.	1949-1999	Flowerdew & Ellwood, 2001*
Dynamics of space use and male vigor amongst wood mice, *Apodemus sylvaticus*, in the cereal ecosystem	Wood mouse	Territoriality and ranging patterns	Home range size fluctuates annually based on breeding condition and among the sexes.	1987-1992	Tew & MacDonald, 1994
Field and laboratory experiments on the social behaviour and population dynamics of the wood mouse (*Apodemus sylvaticus*)	Wood mouse	Sociality driving populations fluctuations	Aggression within a population hinders immigration and juvenile survival. Provides a biotic explanation for population declines in spring and summer.	Various	Flowerdew, 1974
A yardstick for measuring populations of small mammals	Bank vole and wood mouse	Accuracy of small mammal trapping	Simple index trapping can give an adequate estimate of small mammal numbers. Generally, one can assume that the captures represent 50% (at best) of the total population	1952-1969	H.N Southern, 1970*
The regulation of wood mouse (*Apodemus sylvaticus*) numbers in Wytham Woods, Berkshire	Wood mouse	Weather patterns and masting	(1) When masting crops fail, wood mice numbers decrease significantly. (2) low dispersal rates of individuals indicate the core drivers of populations are abiotic rather than biotic	1952-1965	Watts, 1969*
The foods eaten by wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*) in Wytham Woods, Berkshire	Bank voles and wood mouse	Dietary patterns	Similar diets between both species (potentially leading to niche competition). Both prefer woodland edges and open pastures.	1964-1965	Watts, 1968
A study of a wood mouse population in Wytham Woods, Berkshire	Wood mouse	Population dynamics and dispersal	(1) High food yields may predict greater ranging patterns (2) Increased activity correlated with the breeding condition of females	1950-1951	Miller, 1958
Post 1999					
Woodland Recovery after Suppression of Deer: Cascade effects for Small	Bank vole and wood mouse	Ungulate presence, vegetation structure and	Increased complexity in understory vegetation promotes small mammal populations.	2001-2003 and 2010	Bush et al., 2012

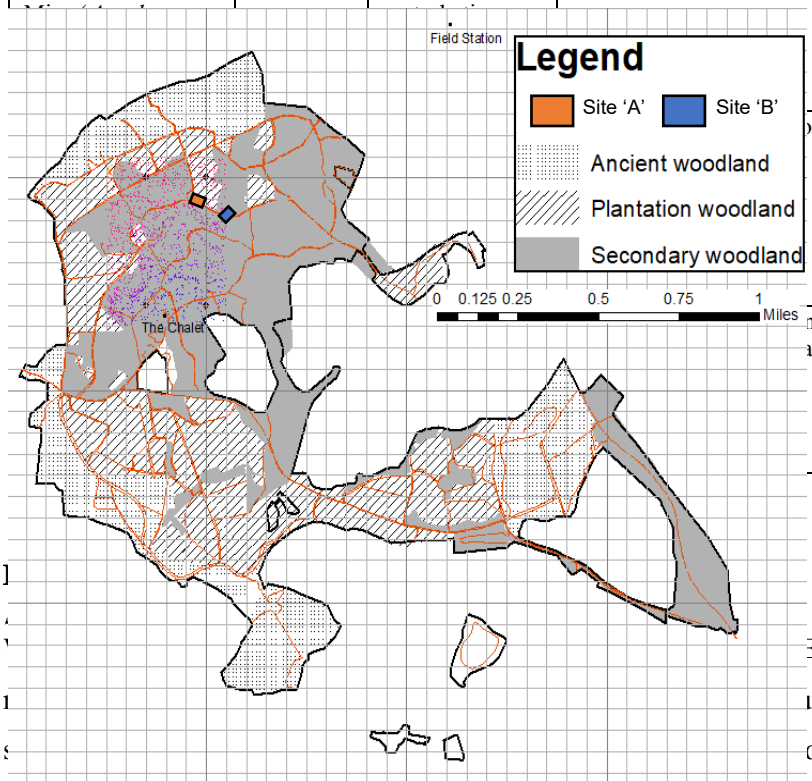


Figure 1 Map of Wytham Woods (Shapefile credit: Wytham ECN, Earthwatch, University of Oxford, 1994). Demonstrating the matrix of habitats within Wytham, this map shows the location of the two plots within the woods.

The plots were chosen for their proximity to accessible rides.

As they are geographically close together, in all analyses they are grouped and treated as a single site.

ngland (51.77°N, -1.33°E). It is a

ıral landscapes located in

d and is used primarily for ecological research. The two sites within this study were in secondary woodland dominated by Sycamore (*Acer pseudoplatanus*), Ash (*Fraxinus excelsior*), and Oak (*Quercus robur*) (Figure 1).

Field Methods

Between 1948 and 1999, small mammals were caught biannually at the end of May/beginning of June and in December (following standardised methods outlined in Southern, 1964, 1970; Flowerdew et

al., 2003). In each trapping event, two 50m x 30m grids set 35m apart (together totalling 4.9 ha in size) were index trapped with 150 traps/trapping event(Figure 1). Index trapping involves capturing small mammals without giving individuals unique identifiers or recording any measurements. Longworth traps were pre-baited for two nights prior to trapping, and then visited one evening and one morning. Traps were baited with whole oats, and hay was provided as nesting material. At each trapping event, the weather on pre-baiting days and trapping days was recorded. During the 1976-1992 period, animals were marked with fur clips, weighed to the nearest 0.5g with a Salter spring balance, sex and reproductive status was also determined, whilst the animal was being handled. The protocol for each site, involved two nights of pre-baiting and then an evening and morning trapping. Animals were marked with a toe clip and each site had a specific ear clip pattern to determine if individuals were moving between the sites.

Statistical Analysis

All analyses were carried out in the statistical freeware R version 3.5.0 (R Core Team, 2019). The population count was log transformed for all analyses to minimise the effect of outliers.

Buishand range test

A homogeneity test was used to look for change points in time series. This assesses the point at which the time series deviates from a previously observed trend (R package: *trend* Pohlert, 2018). Several methods can be applied to determine change points (Hawkins, 1977; Buishand, 1982; Kim & Siegmund, 1989; Chen & Gupta, 2001; Radziejewski et al., 2000; Lund et al., 20002; Rodionov, 2004; Seidal & Lanzante, 2004; Menne et al., 2005; Bryson et al., 2012; Gallagher et al., 2012; Li & Lund, 2012). The test works by calculating the difference between the maximum and minimum values of a time series data over non-overlapping sub-intervals of the series. The test statistic is then calculated as the maximum of the absolute deviations of the differences from their median value. Under the null hypothesis of no trend in the data, the test statistic follows a standard normal distribution.

$$S_0^* = 0 \; and \; S_k^* = \sum_{i=1}^{k} (Y_i - \bar{Y}), \quad k = 1,2, \dots, n$$

where Y_i is the ith observation. If the series is homogeneous, then S_k^* fluctuates around zero. If there is a break in year K, then S_k^* reaches a maximum (negative shift) or minimum (positive shift) near the year $k = K$. n is the length of the time series.

The test statistic is defined as:

$$Range = \frac{[max\ S_k^* - min\ S_k^*]}{s}$$

where s is the sample standard deviation. The computed value of $R/\sqrt{n}$ is compared to critical values given by Buishand (1982).

Wavelet analysis

The wavelet transform is a method of converting a function (or signal) into another form, which can make features of a time series more easily visible. It represents a numerical time series in the frequency domain. The amplitude of the spectrum allows for visualisation of the frequency content of the timeseries and is more useful for comparing signals to each other – as well as for isolating meaningful frequency peaks. Wavelets are a useful tool when attempting to understand the presence of a potential frequency change across time – in other words, a change in the numerical dynamics. To perform this analysis an overarching 'mother' wavelet is used to compare the timeseries against, we used the R package *WaveletComp* (Rosch & Scmidbauer, 2018) which uses the Mortlet wavelet as the 'mother' wavelet – as it is a continuous, complex-valued wavelet which preserves information:

$$\psi(t) = \frac{1}{(\sqrt{(s)} \times \psi(\frac{t-u}{s})}$$

where $\psi(t)$is the wavelet function, u is the translation parameter, a is the scaling parameter, and $\sqrt{(s)}$is a normalization factor that ensures that the wavelet function has unit energy.

The wavelet equation describes how the wavelet function is dilated and translated in time and frequency domains. By varying the scaling and translation parameters, wavelet functions can be used to analyse signals and data at different scales and resolutions, making them a powerful tool in a variety of fields, including signal processing, image processing, and data compression.

Autoregressive moving average models

The 'predictable' cyclic pattern over time means that small mammal populations are ideal for fitting to time-series models. Understanding the core driving dynamics within such a system is complex. Such cyclical or repeating datasets are often fit with autoregressive integrated moving average (ARIMA) models, including, stock shares: (Jarrett & Kyper, 2011)(Jarret & Kyper, 2011); wind speed: (Lui, Tian & Li, 2012)(Lui, Tian, & Li, 2012); electricity prices: (Contreras et al., 2003); foreign exchange markets: (Tseng, Tzeng, Yu, & Yuan, 2001)(Tseng et al., 2001); wheat production: (Iqbal et al., 2005); human populations: (Saboia, 1977)(Saboia, 1977); lnfectious disease spread: (Liu,

Luan, Yin, & Zhu, 2015)(Liu et al., 2015); el niño oscillation and malaria spread: (Fuller et al., 2009)(Fuller, Troyo, & Beier, 2009). By importing prior collected data as a 'training dataset', ARIMAs can detect population trends based on the linearity of the data. Further, auto-regressive integrated moving average models (ARIMA), can be used to investigate the effects of abiotic factors in bank vole and wood mouse cycles. Initially an ARIMA model in isolation of any covariates was created, to determine the autoregressive and moving average values for each population (R packages: *forecast* (Hyndman et al., 2019; *tseries* Trapletti & Hornik, 2018). To develop an ARIMA model, the first step is to determine whether the time series data is stationary or non-stationary. We can diagnose whether the data is stationary from a run sequence plot which can be detected from an Augmented Dickey-Fuller (ADF) test. Generally, non-stationarity is shown by an autocorelation plot that slowly decays, and then the differencing approach should be applied. Differencing can eliminate the changes from time series data and make the data more stable. Secondarily the Akaike information criterion (AIC) is used for parameter estimation, as a rule of thumb, the lower the AIC value the better the model fits the data.

Autoregressive (AR) models are a regression of a time series against the lagged value of that series.

$$y_t = c + \varphi_1 y_{t-1} + \varphi_2 y_{t-2} + \cdots + \varphi_p y_{t-p} + e_t \qquad e_t \sim white\ noise$$

Where;

φ_1 and φ_2 are parameters for the model and φ_p is the predictor values.

c is the average of the changes between consecutive observations. If c is positive, then the average change is an increase in the value of y_t. Thus, y_t will tend to drift upwards. However, if c is negative, y_t will tend to drift downwards.

A moving average (MA) model is a regression model, but instead of regressing against dated observations, we regress against lagged errors. The last 'q' errors are used as predictors in the equation.

$$y_t = c + e_t + \varphi_1 e_{t-1} + \varphi_2 e_{t-2} + \cdots + \varphi_q e_{t-q} + e_t$$

These equations combined for the Autoregressive Moving Average (ARMA) model, where the last p observations and the last q errors are all used as predictors in the equation.

$$y_t = c + \varphi_1 y_{t-1} + \cdots + \varphi_p y_{t-p} + \varphi_1 e_{t-1} + \cdots + \varphi_q e_{t-q} + e_t$$

ARMA models can only be fit to stationary data. ARIMA (*p,q,d*) models account for this, by imbedding differencing in the model construction essentially removing any temporal trends. To apply an ARIMA model to data, the value of *p*, *q*, and *d* must be calculated (as well as whether to include the constant '*c*' – the intercept).

The value of *d*: estimating by considering autocorrelation plots. When the autocorrelations die out quickly, the appropriate value of *d* has been found.

The value of *p* and *q*: determined from the partial autocorrelations of the appropriately differenced series. If the partial autocorrelations cut off after a few lags, the last lag with a large value would be the estimated value of *p*. If they do not cut off, you either have a moving average model ($p = 0$ & $q = 0$) or an ARIMA model with positive *p* and *q* values.

Models are fit using the three step Box-Jenkins method. 1) identifying the values of *p*, *q*, and *d;* 2) estimating phis using maximum likelihood techniques and back casting; and 3) diagnostic checking for inadequacies by considering the autocorrelations of the residual series. These steps are applied until step 3 provides no further improvement to the model.

Trends, density dependence and population growth

The Ricker map, also known as the Ricker model, is a mathematical model that describes the dynamics of a population over time. It is a discrete-time dynamical system that is often used to model the growth and decline of animal and plant populations.

The Ricker model is defined by the following equation:

$$N(t+1) = N(t) \times \exp(r - a \times N(t))$$

where $N(t)$ is the population size at time t, r is the intrinsic growth rate of the population, and a is a parameter that represents the strength of density dependence in the population growth. The Ricker map assumes that the population size in each time step is determined by the previous population size and a random factor that is drawn from a probability distribution.

Results

A total of 14,850 trap nights (99 trapping sessions with 150 traps set at each session), resulted in 3006 wood mouse captures and 4426 bank vole captures.

Demographic information (1979-1999)

During the study period (1979-1999) 1113 bank vole (Figure 2 b) were captured. Including 515 females, 596 males and 2 juveniles (of unidentified sex). 415 evening captures, 698 morning captures.

Of the females, 94 individuals were imperforate, 3 lactating, 72 perforate, 23 pregnant, 1 pregnant and lactating. 1128 wood mice (Figure 2 a) were capture overall, comprising of 538 females, 587 males, 7 juveniles (of unidentified sex). 17 evening captures, 1118 morning captures. And of the females, 98 were imperforate, 2 lactating, 83 perforate, 1 plugged, 42 pregnant).

(a) (b)

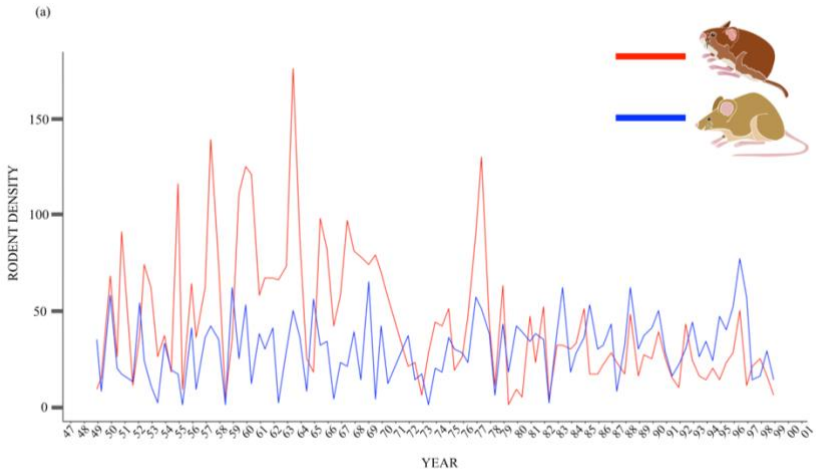




Figure 2 Across[illegible] refer to each species with a [illegible] implify result interpretation. (a) wood mice, and (b) bank vole.

In

Th[illegible]minary insights int[illegible]cles is apparent an[illegible]across all seasons (F[illegible]winter, which wi[illegible]ere generally m[illegible]om 1978 to the co[illegible]



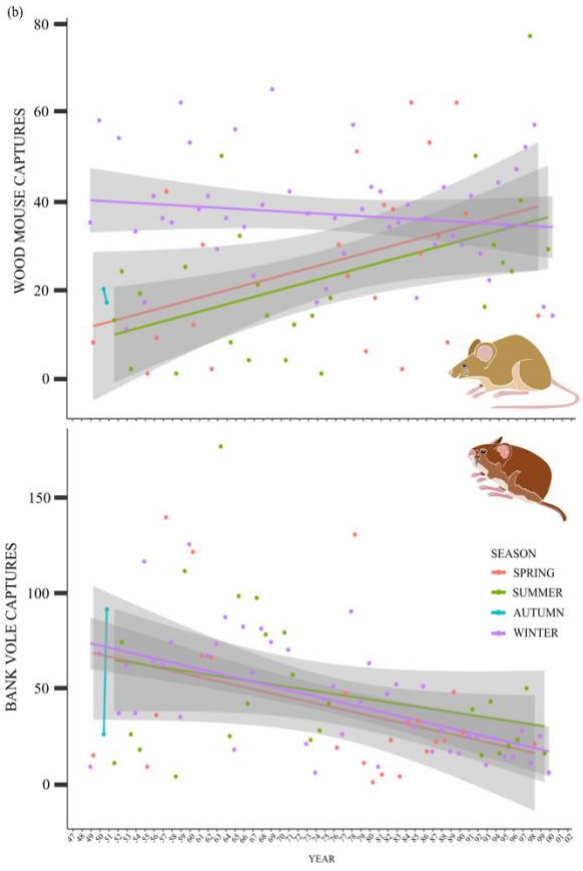


Figure 3 Capture rates over the whole time series, and per species, per season (a) Basic capture plot, showing the collapse and subsequent dampened cycles of the vole population (blue line). Along-side the relatively stable wood mice population cycles (red line). (b) Plots of captures per season. Showing the collapse in the vole cycles was consistent across seasons. Wood mice captures were higher in winter on average than in summer. Potentially indicating high overwinter survival.

Buishand range test

A change in trend was detected in August 1970 for the bank voles (critical value: 1.55, $p<0.001$) followed by a trend change in the wood mice in May 1976 (critical value: 1.55, $p<0.01$) (significance values determined by critical values in Buishand, 1982). Figure 4 shows the dynamic shifts for each species and at which time point it occurred. The wood mice (Figure 4 a) trend shifted positively, and the cycles become longer. Inversely, the bank voles (Figure 4 b) negatively shifted, and their cycles became shorter. The y-axis on the plot is the adjusted partial sum, or the cumulative deviation from the mean for the k^{th} observation. In other words, the y-axis shows the total deviation from the mean, considering all the observations up to a particular point (K^{th} observation). It gives us an idea of how the individual values differ from the average value, considering all the previous values. The x-axis "Index" is a time variable with time step 1=1948, and time step 99=1999.

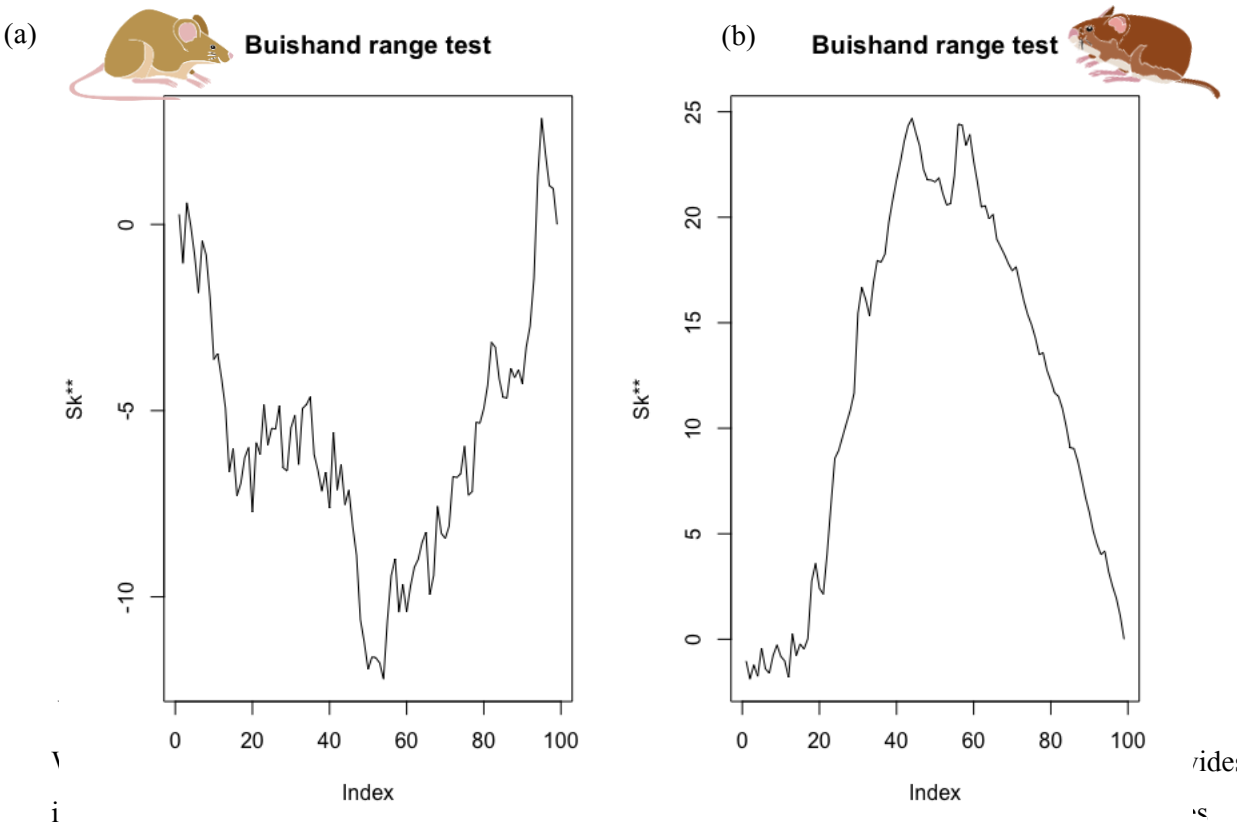


Figure 4 Buishand range test and associated plots visualising trend changes
The Buishand range test assess the point in time that the time series deviates from the *normal* or previously observed trends.

(a) The population trend of wood mice positively shifted (and lengthened) in May 1976 ($p<0.01$)
(b) The population trend of bank voles negatively shifted (and shortened) in August 1970 ($p<0.001$). This preceded the change in the wood mice, and perhaps the trend shift in bank voles encouraged the trend shift in wood mice.

information about the characteristics and dominant frequencies of each cycle. Lastly, to demonstrate the accuracy of the wavelet coherency analysis the transformed and reconstructed dataset is provided (wood mice: Figure 5 d and, bank voles: Figure 5 h). To interpret these plots we look for regions of coherence, or areas where there are bright colours, this indicates a time-frequency interval or a cycle. We compare the coherence plot with the wavelet power spectra of each individual cycle looking specifically for similarities or differences in the dominant cycles and power distributions. Our analysis and visualisations provide a statistical significance measure in the global wavelet power spectrum (wood mice: Figure 5 b and, bank voles: Figure 5 f) which allows us to interpret the coherence values reliably. For example, we can see that bank voles have two significant cycles ($p>0.05$).

The wavelet coherency plots show a dominant 1-year cycle and a sub-dominant 2-year cycle in wood mice (Figure 5 a). The yearly wood mouse cycles appear consistent across much of the time series until post 1980 where all cycles appear to disappear. But this is explained by the reconstructed timeseries (Figure 5 d) which flattens at the end – possibly due to the shifted amplitude in the time series – this is also true for the bank voles coherency plots (Figure 5 e) and reconstruction (Figure 5 h). Bank voles had a dominant 4-year cycle and a sub-dominant 8-year cycle (Figure 5 e), the voles also experienced two 'bouts' of annual cycles around 1948-1952 and 1978-1979. The decade between 1960 and 1970 show an absence of all recognised significant cycles.

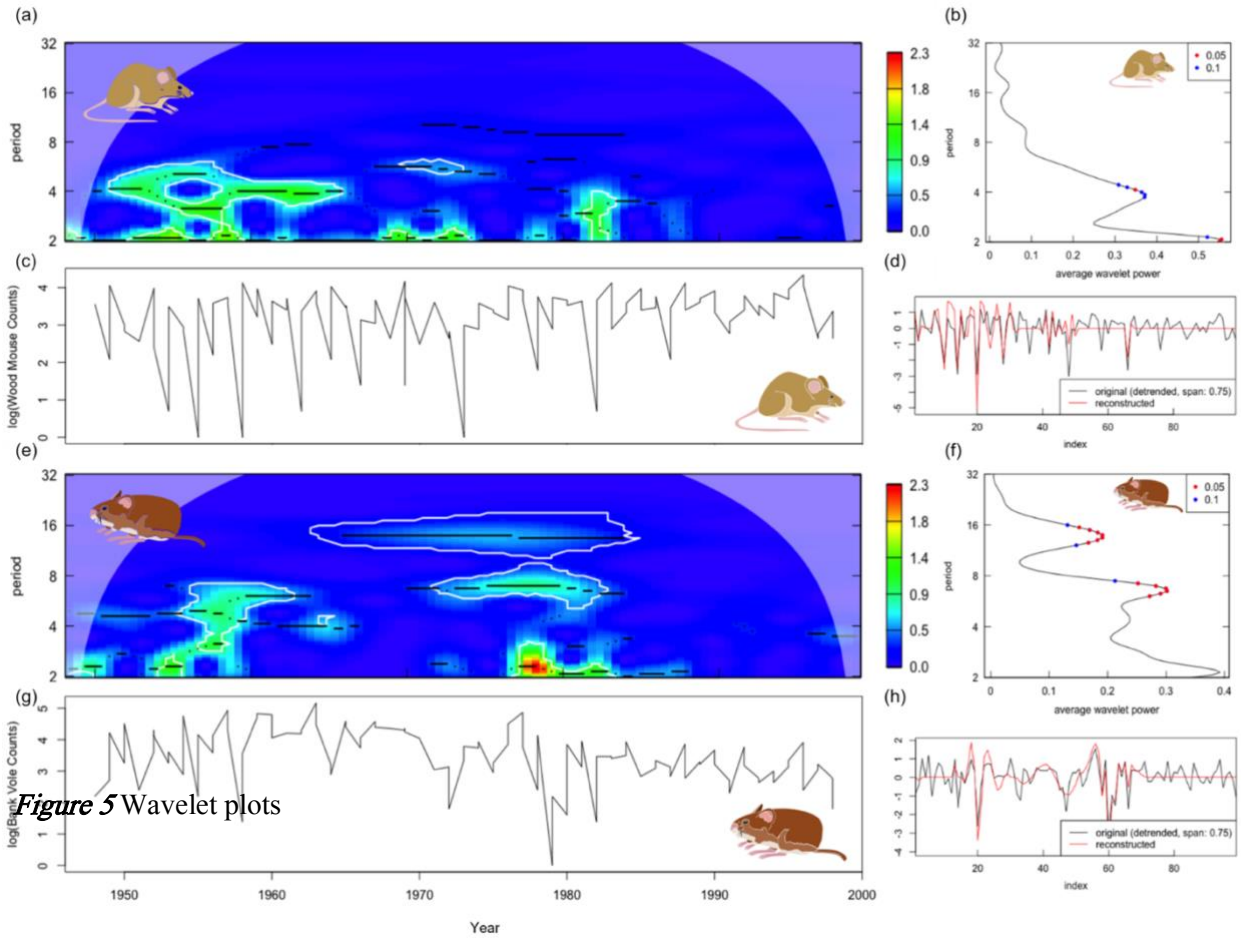


Figure 5 Wavelet plots

- ***(a)*** and ***(e)*** Wavelet coherency plots for logged timeseries ***(a - wood mouse + e bank vole)*** period lengths having statistically significant coherence and cross-wavelet power are outlined in white solid lines. The y axis denotes the period of the cycles – in this case, as captures of wood mice and bank voles occurred twice a year **period 2 = 1 year, period 4 = 2 years** and so on. For each point in time and for each period length, wavelet power is indicated with darked red indicating higher power and darker blue indicating lower power. The shaded areas on the plots indicate the cone of influence – results in these shaded areas may be influenced by spurious patterns at either end of the time series.
- ***(b)*** and ***(f)*** Global wavelet spectra for the logged time series for both species. Significant wavelet power is indicated by blue (significance level of 0.1) and red dots (significance level of 0.05).
- ***(c)*** and ***(g)*** Logged time series for both species.
- ***(d)*** and ***(h)*** Wavelet transform was used to reproduce the original time series to assess how well the transform read and fit the data. Only the periods whose average power was found significant over the entire timeseries. The black lines show the original, detrended data, the red lines show the reconstructed data.

Autoregressive integrated moving average (ARIMA) models

Table 2 shows the results for the Augmented Dickey-Fuller Test (ADF) for both wood mice and bank voles. The significance level prove that both timeseries are non-stationary. Additionally, the AIC values are presented here, justifying the choice of the models (the lowest AIC value indicating the best fit). The combination of ARIMA model parameter estimates (p, q, and d) that provided the best fit each species are 2,1,7 for wood mice and 7,1,7 for bank voles. In an ecological context, the p, d, and q values in an ARIMA model are useful in describing the temporal dynamics of a particular ecological variable, in our case the population size of wood mice and bank voles.

The p parameter represents the autoregressive component of the model, capturing the effect of past values of the ecological variable on the current value. It tells us how much a population in the present year is influenced by its size in the previous year. Therefore, the bank vole population was more influenced by its size in the previous year compared to the wood mice, as their p parameter value was higher.

The q parameter represents the moving average component of the model, capturing the effect of random fluctuations or noise on the current value of the ecological variable. For example, if the population size of a species is affected by stochastic factors such as weather or disease outbreaks, then a larger value of q would be appropriate to capture this randomness. A q value of 1 means that the current observation is being influenced by the previous years forecast errors. The moving average component helps capture any remaining patterns or dependencies in the data that are not explained by the autoregressive (AR) or differencing (I) components.

The d parameter represents the number of times the ecological variable needs to be differenced to make it stationary. This is important because ecological variables often exhibit non-stationary behaviour due to changes in environmental conditions, such as climate or habitat availability.

Differencing can help remove any trends or seasonality in the data and make it easier to model. This value is the same for both species. In ecological terms, a d value of 7 in an ARIMA model indicates that the time series requires differencing seven times to achieve stationarity. Differencing is a technique used to remove trends and seasonality from a time series, making it stationary. Stationarity implies that the statistical properties of the time series, such as the mean and variance, do not change over time. By applying differencing, we subtract the previous observation from the current one, which can be done multiple times until the resulting series becomes stationary. Each differencing operation reduces the impact of long-term trends and dependencies. A value of 7 for the differencing component indicates that it took seven consecutive differencing operations to make the time series stationary. This suggests that both the wood mice and bank vole time series exhibited a significant trend or seasonality that required repeated differencing to remove.

Table 2 ADF and AIC values used for model identification

AUGMENTED DICKEY-FULLER TEST	
t-statistic (wood mouse)	Prob.*
-4.5444	0.01
t-statistic (bank vole	Prob.*
-3.8464	0.01
AIC VALUES OF ARIMA (p,q,d)	
Wood mouse	
ARIMA (p,q,d)	AIC
2,1,7	-603.24
2,1,3	-566.66
2,1,1	-562.02
AIC VALUES OF ARIMA (p,q,d)	
Bank vole	
ARIMA (p,q,d)	AIC
7,1,7	-221.42
7,1,1	-195.46
0,1,0	-151.7

Density-dependence and relationships between the two species

After exploring the population shifts and general long-term trends, we wanted to understand the mechanisms underlying the demography of each species. Ricker models were created pre (Figure 6) and post (Figure 7) the population trend shifts (1970 for wood mice and 1976 for bank voles). To analyse the relationship between population size and growth rate and determine density dependence in a population. In these scatterplots population size is represented on the x-axis, and growth rate is on

the y-axis. If the growth rate increased with increasing population size, it suggests positive density dependence, indicating that population growth is enhanced as the population density increase. Conversly, if the growth rate decreases with increasing population size, it suggests negative density dependence, where population growth is inhibited as density increases. These models show strong density dependence for mice (Adj $R^2 = 0.02$, $p = 0.04$), but not for voles. The wood mice map also suggests that the population has compensatory dynamics. This refers to modes of change in response to the environment, and can occur in the presence, or absence of a long trend in the environment (Gonzales and Loreau, 2009). We can identify compensatory dynamics through Ricker maps as the dynamics often result in stable population dynamics, meaning the population size tends to fluctuate around a stable equilibrium point. We see signs of stability in the wood mice plots as they tend to converge toward a particular point or value over time. This may infer that the phases of population growth and decline in wood mice might be in response to continuous environmental pulses/fluctuations. To understand this further a self-exciting threshold autoregressive (SETAR) model was fitted to each species, divided by season (Figure 7 wood mice, Figure 8 bank voles).

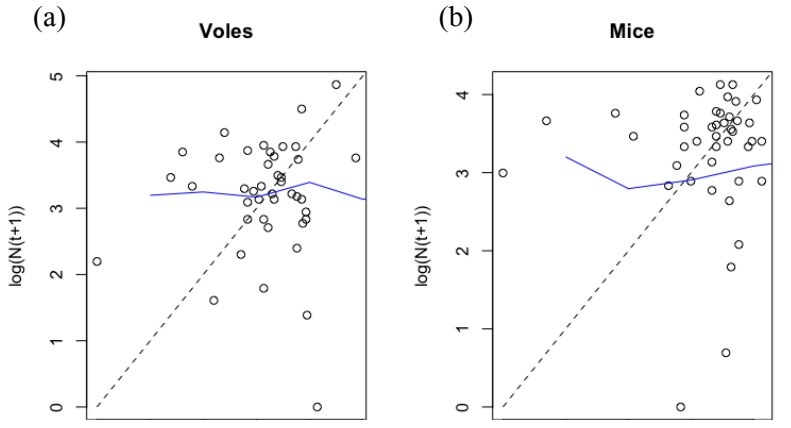


Figure 6 Ricker Maps for Bank Voles and Wood Mice pre-trend shifts
This figure showcases the pre shift population trend of (a) bank voles and wood mice (b) using a Ricker map model incorporating density dependence before a shift occurs. The x-axis represents time, denoted as t, while the y-axis represents the population size at the next time step, t+1.

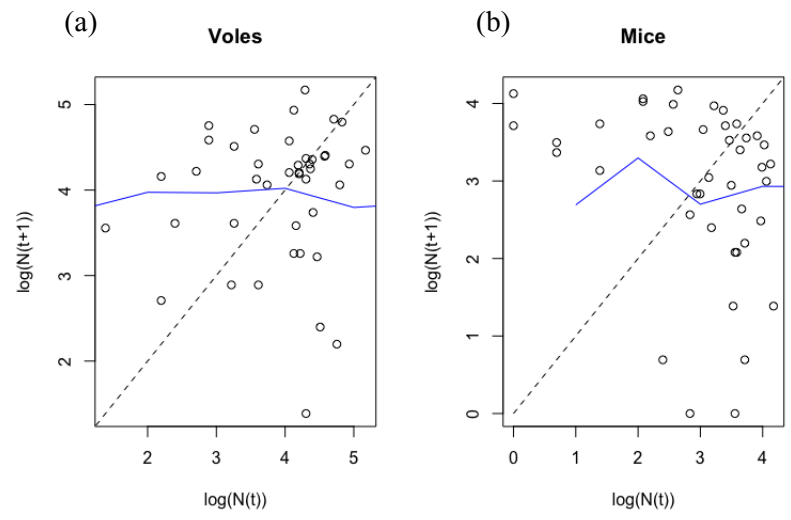


Figure 7 Ricker Maps for Bank Voles and Wood Mice post-trend shifts
This figure showcases the post shift population trend of (a) bank voles and wood mice (b) using a Ricker map model incorporating density dependence before a shift occurs. The x-axis represents time, denoted as t, while the y-axis represents the population size at the next time step, t+1.

We applied a SETAR model to investigate the dynamics of wood mouse populations. The SETAR model is a valuable tool in ecology as it captures nonlinearities and regime shifts in ecological systems. It is particularly useful for analysing data with distinct thresholds or breakpoints, where the relationship between variables changes abruptly. The x-axis in these plots is time, representing the chronological order of the observations. The y-axis is the residuals, the differences between the observed number of individuals and the models predictions. In Figure 8 a, representing winter wood mice population trends, the SETAR model revealed two distinct regimes. The first regime is characterized by a stable equilibrium. However, beyond a certain threshold, the model identified a second regime with an increasing population size. This finding suggests that certain environmental conditions during winter, such as temperature or food availability, may trigger an increase in the wood mouse population. Figure 8 b depicting wood mice in summer shows a similar stable primary regime, followed by a decline in population size. This suggests that specific ecological factors, such as predation pressure or resource scarcity, may contribute to a decline in wood mice numbers during this period.

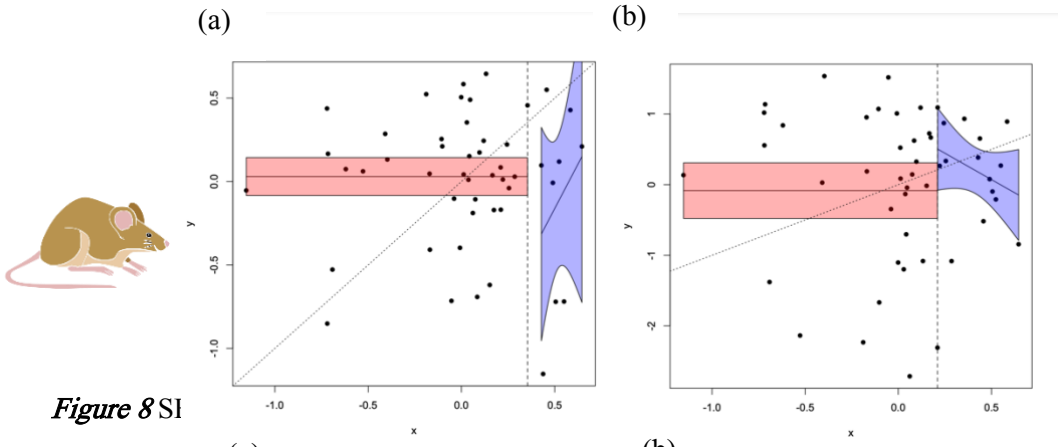


Figure 8 SI

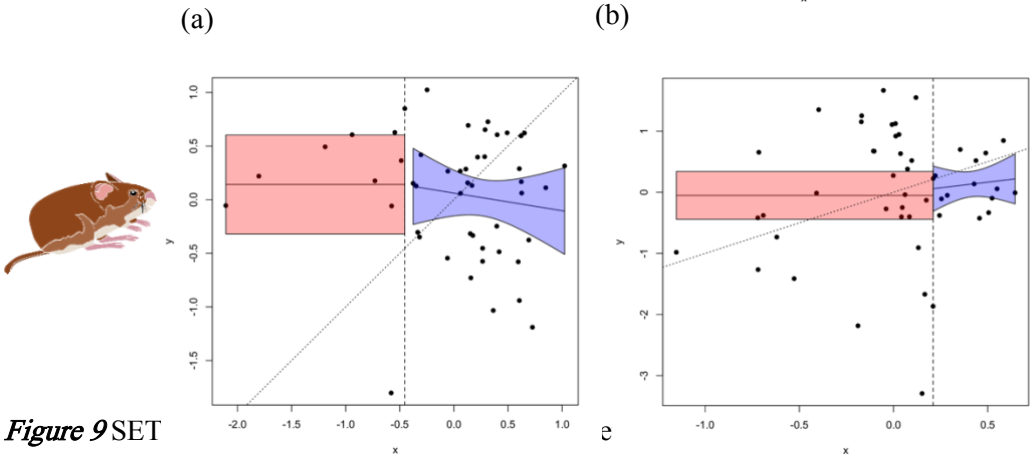


Figure 9 SET

In Figure 9 a, representing bank vole populations in winter, the SETAR model identified two distinct regimes. The first regime displayed a relatively stable population size, suggesting an equilibrium

state. Beyond a certain threshold, the model identified a second regime where the population size did not exhibit a notable increase or decrease. This indicates that during winter, the bank vole population remains relatively stable, possibly influenced by factors such as habitat suitability or resource availability. This stable trend was also observed in summer (Figure 9 b). These findings highlight the differences in the population dynamics of bank voles and wood mice, indicating that both species respond differently to seasonal changes.

Discussion

Understanding the cyclic dynamics of small mammal populations and their implications for population and community dynamics has been a long-standing area of interest (Andreaseen et al., 2021). Here we used a range of statistical approaches to gain insights into the long-term dynamics observed in two sympatric populations of small mammals in the UK. By studying the dymanics underlying the cycles in these species, we aimed to unravel the factors influencing cycles and crashes in small mammal populations. Mathematical models provide a valuable framework for examining the complex dynamics of small mammal populations. Through phase effect identification, models can pinpoint changes in cycles and determine the underpinning biological mechanisms shaping population dynamics. Here we sought to further understand the cyclic dynamics of bank voles and wood mice and further understand the pressures driving these cycles. We chose to use a combination of methods to be able to understand the trends and cyclic dynamics more readily in this small mammal community.

The results of this study add to a growing body of literature on the population dynamics of small mammals and provide insights into the mechanisms driving long-term population cycles in wood mice and bank voles. The observed changes in population trends in the two species, with wood mice showing longer cycles and bank voles showing shorter and declining cycles, suggest that they may have different population dynamics and responses to environmental changes. Similar studies have investigated population cycles of small mammals in different ecosystems and geographical locations. For example, a study by Korpimäki et al. (2005) found that bank voles in northern Finland showed a 3-4 year population cycle, which was influenced by climate and predator-prey interactions. Another study by Krebs et al. (2001) investigated population cycles of small mammals in the boreal forests of Canada and found that the cycles were driven by food availability and predator–prey interactions.

The wavelet coherency analysis in this study revealed a dominant 1-year cycle and a sub-dominant 2-year cycle in wood mice. This is consistent with previous studies that have found that annual environmental factors, such as rainfall and temperature, drive population cycles in wood mice (Krebs et al., 2001; Krebs and Myers, 1974). However, the absence of significant cycles in bank voles

suggests that their population dynamics may be driven by different mechanisms, such as food availability, predation, or disease (Andreaseen et al., 2021). Wood mouse dynamics were characterised by fading 1-year cycles early in the timeseries, and towards the end of the dataset cycles appeared to begin to reestablish. Conversely – bank vole dynamics were generally characterised by 4-year cycles. The cycles then became weaker and less frequent, and a new set of cycles with lower densities started again in the late 1990s. Bank voles also had a significant 8-year cycle which may be due to natural varying peak amplitude in cycles (Framstad et al., 1993, Hellstedt et al., 2006) or perhaps an abiotic pressure causing a dampening in the cycles. Fading cycles and disturbed dynamics was simultaneously observed in alpine voles in the 1980s and 1990s due to climatic changes resulted in greater irregularities in period length, higher occurrences of short increase phases, and a decrease in cycle amplitude (Hanski et al., 1993; Hanski & Henttonen, 1996; Oksanen & Henttonen, 1996; Angerbjorn et al., 2001; Hornfeldt, 2004; Kausrud et al., 2008).

Bank voles in this system entered a period of extended low density post 1978 which lasted until the conclusion of the study (~20 years). This is a common phenomenon within cyclic populations (Andreassen et al., 2021), where these periods may last between 1-3 years, whereas eruptive populations can experience extended lows often lasting over 10 years (Singleton et al., 2007). Eruptive dynamics are characterised by sudden and dramatic population explosions followed by crashes and are more commonly associated with species like lemmings (*Lemmus spp.*) rather than bank voles. The profile of this species (Figure 2 a) is more indicative of eruption than regular cycles. Bank voles are widely accepted to be cyclic in nature (Andreaseen et al., 2021) so it is a more plausible conclusion that the observed crash and dampening of this species is a transition to non-stationary population dynamics (Henden et al., 2009). The dynamics quantified here for bank voles are characteristic of non-stationary dynamics in small mammals, and indicate that this populations behaviour and wider ecological interactions will exhibit continuous changes over time consistent with a collapse of cyclicity (Ims et al., 2008; Singleton et al., 2009).

The ARIMA models show a ~4 decade negative trend in the bank vole population and no overall trend in the wood mouse population. In this context a negative trend refers to a decreasing pattern, suggesting that the original time series had a decreasing trend. This shift in trend in bank vole numbers occurred in August 1970 (Figure 4). This cycle dampening has been well documented in the northern hemisphere. Ims et al. (2008) summarised the dampening cycles of eight microtine vole species. The changes in vole dynamics were all linked to decreased winter survival. Shifting from one cycle to another is an expected phenomenon in ecosystems, which themselves are dynamic. Abiotic changes have the capacity to trigger flow on disruptions to trophic interactions. Voles are a single cog in a complex ecological machine, but small mammals are at the core of many terrestrial food chains, as a limiting food resource for predator species. Indeed, the changed regime of voles and lemmings in

northern Europe has led to significant decline in predator populations (Ims et al., 2005). These cyclic collapses should be cause for concern, as climate change inevitably continues to alter the dynamics of even the most basal species in trophic systems. The ARIMA model values I estimated (p,q,d) showed that the demography patterns of the two populations differed, with wood mice have shorter cycles (Figure 5) and being more influenced by the previous time step than bank voles. This is consistent with previous studies that have found that small mammal populations can exhibit memory-based behaviour and population dynamics (Turchin et al., 1999; Henttonen et al., 2018). However, the mechanisms underlying these differences in memory-based behaviour between the two species are not well understood and require further investigation.

The Ricker Maps and SETAR models showed strong density dependence for wood mice, but not for bank voles. This is consistent with previous studies that have found that small mammal populations can exhibit strong density dependence, whereby population growth rates decline as population density increases (Turchin et al., 1999; Bjørnstad et al., 1999). However, the absence of density dependence in bank voles suggests that their population dynamics may be less susceptible to fluctuations in population density. Density dependence can equally be a regulatory or destabilising force (Lee & Strauss, 2016), and testing for it can determine whether the dynamics of the population are stationary (Turchin, 1995). Both direct and delayed density-dependence are necessary to generate cycles (Stenseth, 1999) but density-dependent factors can interact with or become subordinate to stochastic perturbations and environmental trends. By using a Ricker model, we were able to create a 1-dimensional density-dependence matrix plot, to determine the point at which density dependence hits a critical point. While vole population changes seem to be tied to abiotic factors, wood mice dynamics appear to be much more influenced by density-dependence. Figure 5 b shows the basic pattern of density dependence in the wood mouse population by a standard plot of log (population growth rate) against log (population numbers). Inferring that population growth rate declines as population size increases, because of intraspecific competition. There is also variation around this trend which is greater at high population density. Voles – and other more diurnal small mammals are more intrinsically tied to and limited by their abiotic surroundings as they rely on biomass cover for protection from predators (Ims et al., 2005). This may explain why the dynamics of voles appears more volatile than that of the wood mice – who are predominately crepuscular/nocturnal.

This study highlights the significance and effectiveness of count data in addressing complex research questions. The dataset utilised in this study possesses several noteworthy attributes that contribute to its utility and power. First and foremost, the longitudinal nature of the data allows for the examination of trends and patterns over an extended period. This temporal dimension provides valuable insights into the dynamics and fluctuations within the small mammal populations under investigation. Furthermore, the simplicity in the structure of the data proves advantageous for analysis. By

exclusively relying on crude counts of individuals, the study demonstrates the ability of count data to yield valuable information. Count data, in its raw form, allows researchers to directly observe and quantify the abundance or scarcity of specific species or populations. This simplicity enables researchers to explore various aspects of population dynamics, such as changes in abundance, distribution, or diversity, without the need for extensive data pre-processing or manipulation. Overall, the study underscores the potential of count data to address a wide range of research questions pertaining to ecological dynamics. By harnessing the simplicity of the dataset, researchers can extract meaningful insights into the fluctuations, trends, and underlying processes governing the populations of interest.

It is worth noting that the dataset presented here has been previously used to understand important ecological pressures on small mammal dynamics. Including: how increased deer populations impact small mammal abundance (Flowerdew & Ellwood, 2001); the predation rates and diet preferences of Tawny Owls (Southern & Lowe, 1982); and, understanding movement of Tawny Owls and territory allocation of fledgling chicks in parallel to small mammal populations (Southern, 1970), as well as being referenced in '*The Mammals of Wytham Woods*' (Beusching et al., 2010, within: Savill et al., 2010). In addition to this, other analogous studies in Wytham detail a picture of the functional role that wood mice and bank voles play in Wytham (Table 1). From the literature available on bank voles and wood mice in Wytham (and elsewhere), it is clear the two species have coexisted for many years to some degree (Table 1), perhaps through space partitioning in times of high resource competition (Buesching et al., 2008), behavioural partitions (Brouard et al., 2015), or dietary partitioning (Watts, 1968). From results in Southern (1970) and Flowerdew & Ellwood (2001) an unknown perturbation caused a dramatic decline in the bank voles, and consequently a destabilisation of the multiannual cycle. These studies reported an approximate 2-5 year-long trough and peak cycle in both species (bank voles: Boonstra, 1994; wood mice: Beusching et al., 2010) shifts in 1970 (Figure 4), resulting in the bank voles steadily decreasing in abundance. Flowerdew & Ellwood (2001) and Bush et al. (2012) reach the conclusion that increased deer-grazing supressing understory vegetation restricts vole movement based on suitable habitat. This conclusion was reached as the fencing and consequent restriction of deer movement coincided with the reduced density of voles. The cycles presented here using quantitative methods are a more accurate representation of the true cycles of the species due to the availability and diversity of statistical approaches.

In summary, by fitting mathematical models applied to long-term simple trapping data we deconstruct the component trends underlying population fluctuations in a community of small mammals and discuss the wider implications of these findings. Through decades of research, scientists have made significant strides in understanding the factors that drive cyclic fluctuations in small mammal populations, including environmental factors, predation, and disease dynamics. In addition, the

development of mathematical models, such as the Lotka-Volterra and ARIMA models, has enabled researchers to make predictions about future population cycles and to assess the potential impacts of environmental change on small mammal populations. Despite these advances, much remains to be learned about small mammal cycles, particularly considering ongoing environmental change and the complex interplay of factors that influence these cycles. Future research in this area will be critical for understanding the dynamics of small mammal communities, and for informing management strategies to understand the role small mammals have on ecosystem stability and health.

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4

An ultra low-power, cost-effective RFID solution for studying wild small mammal behaviour

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Abstract

Understanding the behaviour of wild mammals is vital for understanding ecological dynamics and species conservation, but current methods for monitoring the activity of some species is hampered by their small size and often nocturnal lifestyles. Radio Frequency Identification (RFID) technology offers a promising approach to collect behavioural data from such species, but existing solutions often suffer from limitations such as high-power consumption, labour, and cost. Here we present the development of an innovative ultra-low-power, cost-effective RFID solution specifically designed for studying the behaviour of wild small mammals. Our solution minimises power consumption to achieve prolonged battery life, enabling long-term behavioural monitoring without the need for frequent device maintenance. We also employ cost-effective RFID tags and readers, making the system accessible for a range of researchers and projects. To validate the performance and demonstrate a range of uses for our RFID solution, we conducted a field study monitoring a population of wild small mammals, using our loggers to characterise activity patterns, space use, and social interactions. Through use of this passive monitoring system, we demonstrate how it allows the collection of high-resolution data on individual behaviour and inter-individual interactions in space and time, with minimal disturbance. This ultra-low-power, cost-effective RFID solution therefore offers a practical and scalable approach to studying wild small mammal behaviour, with potential for broad application in ecological, conservation and epidemiological studies.

Introduction

Studying small mammal behaviour, space use and movement has historically presented several challenges (Hughey et al., 2018). Their small size, elusive and often nocturnal behaviour can make it difficult to accurately track movement, behaviour and habitat use (Harkins, Keinath & Ben-David, 2019). Traditional techniques for monitoring larger mammals, such as camera traps or visual surveys, may have limited detection ranges for small mammals and struggle to capture their fast movements, especially at night (Glen et al., 2013; Hughey et al., 2018). Trapping-based studies offer valuable insights but suffer from coarse temporal and spatial resolution (Flowerdew et al., 2003). Intensive trapping is also labour-intensive and poses welfare concerns as repeated capture alters animal foraging behaviour and has been associated with weight loss (Suazo et al., 2005) and an increased risk of mortality in some species (Soulsbury et al., 2020). Radio-tracking is another commonly employed technique for studying small mammal movements, but also suffers from some important limitations in terms of animal welfare, cost, logistics, data quantity and quality (Soulsbury et al., 2020; Robinson et

al., 2023). Use of radio transmitters can negatively impact animal welfare in small mammals, as attachment typically requires anaesthesia with its associated risks, and attached transmitters can impact the behaviour and social interactions of tracked individuals by adding weight, affecting balance, and protruding from the body, potentially impeding movement and burrowing (Hummell, Li & Mullinax, 2022; Robinson et al., 2023). Effectively monitoring transmitted signals can also be challenging in certain habitats (Rado & Terkel, 1989; Briner et al., 2003; Robinson et al., 2023). Radio signal can be disrupted by dense vegetation or uneven terrain and signal is lost when animals enter burrows, and once the transmitter battery runs out, limiting the possible duration of monitoring. Radio-tracking is also time-consuming, relatively expensive, and necessitates regular monitoring and maintenance of transmitters (Hummell, Li & Mullinax, 2022). These logistical challenges and resource requirements often lead to small sample sizes and short monitoring periods, impeding the implementation of population-wide and long-term approaches (Robinson et al., 2023).

More recently, researchers have adopted Radio-Frequency Identification (RFID)-based methods to monitor the activity patterns and space use of a variety of wild animals. The use of RFID technology in understanding the activity patterns of animals has been developed and honed over the past 30 years (Table 1). Passive RFID monitoring methods rely on tagging individuals with a small passive integrated transponder (PIT) tag and then setting out detectors to monitor their locations and behaviour over time (Balogh & Turcåni, 2015). This approach can be useful for studying behaviour in the wild over relatively long periods of time, for monitoring health and well-being after release from captivity (Ross et al., 2022), or to detect and record specific events, such as when an individual enters or exits a specific area (Briggs, Robstad & Rosell, 2021) or when they eat or drink (Harrision & Kelly, 2022). Passive monitoring of small mammals via PIT tags and a set of loggers has several advantages over other available methods. PIT tags are already frequently used as an inexpensive means of uniquely and permanently identifying individuals in capture-mark-recapture studies (Brehm et al., 2019), such that use of loggers can easily be added to existing research setups. PIT tags are physically small such that they can be used with smaller animals than radio transmitters, and do not require collars or anaesthesia (Balogh & Turcåni, 2015). Once animals are tagged, monitoring is entirely passive such that there is no interference with behaviour (Kuenzi, Zumbrun & Hughes, 2005). Overall, PIT tag-based monitoring systems such as those in Table 1 offer a variety of methods for studying animal behaviour that are logistically simpler and less time-consuming than radio-tracking, maximise animal welfare and data validity, and allow large numbers of animals to be monitored simultaneously with minimal disturbance, broadening the range of questions that can be asked.

Table 1 Summary of papers that describe the development of RFID logging systems designed for monitoring wild species/systems.

Study system/ Species	Description of RFID and PIT system	Outcomes of study	Reference
Small Mammals			
Prarie Vole (*Microtus ochrogaster*) and Eastern Meadow Vole (*Microtus pennyslyvanicus*)	Two separate readers and antennae systems. Antenna were positioned perpendicular along runways. Set for 3 months. PIT tags used were AVID Identity brand (no specific KHz)	First large-scale proof of concept of RFID logging in monitoring small mammals with 893 individuals being tagged and monitored. The readers weren't weatherproof so on-going maintenance was required to ensure the loggers functioned appropriately.	Heper & Batzli (1996)
Wood Mice (*Apodemus sylvaticus*), Bank Voles (*Myodes glareolus*) and Field Vole (*Microtus agrestis*)	Eight antennae positioned under a circular feeding station. Centrally powered by 2 12V car batteries and operated by an electronic decoder with a storage system. Set for 3 weeks. Generic PIT tag.	This study represents the first application of a remote logging system to study a community of wild animals. The study incorporated mechanisms to prevent replicated detection and provided a simple design that could be easily replicated.	Dell'omo, Shore & Lipp (1998)
Deer Mice (*Peromyscus maniculatus*), Southern Red Back Voles (*Myodes gapperi*) and Northern Short-Tail Shrews (*Blarina brevicauda*)	Reader and antenna (Priority1 rdifcoil – 160a) mounted atop plexiglass. Records stored on SD memory card. No information on power source PIT tags from RFIDLOG.	Wild animal behavioural monitoring paired with data from a remote trail camera	Brehm et al. (2019)
Grey Squirrel (*Sciurus carolinensis*)	A modified bait hopper with a 134kHz antenna at the entrance. A data logger (powered by 5 AA batteries) positioned at rear of hopper. PIT tags sourced from Identichip.	Novel application of a hopper and bait weigh station to measure bait uptake as a form of pest control.	Beatham et al., 2021
Other small-medium sized mammals			
Northern Quolls (*Dasyurus hallucatus*) and Quenda (*Isodon fusciventer*)	Off-the-shelf 'RFIDlog animal tag RFID data logger' by Priority1, powered by 6 X rechargeable AA batteries in a battery pack (powered for 31 hours / charge). Antenna ('RFIDcoil-160A RFID coil antenna') placed around circular entrance to nest box and read 134.2kHz PIT tags.	A low cost per unit RFID logging system, that can capture behavioural and demographic metrices	Harrison & Kelly, 2022
Eurasian Beaver (*Castor fiber*)	Off-the-shelf Trovan LID650 fixed readers with custom built BTS-ID antennas. Powered by 30-Ah batteries, replaced every 3 nights. Antennas fixed to entrance to beaver lodges, with the readers being placed in waterproof boxes. PIT tags through Avid Identification Systems	The use of antenna systems over a lodge/burrow entrance to record occupancy and dispersal patterns.	Briggs, Robstad & Rosell (2021)
Other Taxa (Amphibians, Reptiles, Birds and Arthropods)			
Toad (*Bufo spinosus*) and Ground Beetles (*Carabus nemoralis* and *Carabus coriaceus coriaceus*)	Tunnel system with four antennas (134.kHz) inside the system, with a centrally located reader. Antennas have a read range of 3cm. PIT tags from Biolog-Tiny were used.	Demonstrated use of PIT tag use in insects	Testud et al., 2019
Giant girdled lizard/Sungazer (*Smaug giganteus*)	FDX-A PIT tags and compatible reader system. Antenna wired to reader and surround burrows. Reader programmed to ignore animals resting under antenna. Powered	Demonstrated use of remotely transmitting data through a cellular network. And use of logging technology for burrow use investigation.	Wade (2018)

	by a single 50W solar cell and a 12V 100Ah lead-acid battery. Deployed for ~ 5 months (w/out charging). Surrounded in custom waterproof boxes. Data transmitted remotely using cellphone engines.		
Spotted Salamander (*Ambystoma maculatum*) and Marbled Salamander (*Ambystoma opacum*)	Use of RFID antenna to 'sweep' a landscape to locate burrowed animals.	Demonstrates the ability of RFID systems to be used to locate subterranean animals	Hamed, Ledford & Laughlin (2008)
Black-capped Chickadees (*Poecile atricapillus),* Tufted Titmice (*Baeolophous bicolor*), White-breasted Nuthatches (*Sitta carolinensis*), and House Finches (*Carpodacus mexicanus*).	Off-the-shelf Amtel Corporation antenna with a self-developed microprocessor. Reader turns on for short periods of time to 'sweep' for PIT tags. Powered by a 12V lead-acid battery with a field life of 2 weeks logging. Antenna is tightly coiled magnet wire and attached to a bird porch connected to a feeder. Reads 125kHz PIT tags.	Very low cost design and low power consumption due to only being triggered at set times, not whenever an animal interacts with the antenna.	Bridge & Bonter, 2011

Several RFID logging-based monitoring systems have been specifically developed for monitoring small mammals (Heper & Batzli, 1996; Dell'omo, Shore & Lipp, 1998; Brehm et al., 2019; Beatham et al., 2021). However, existing solutions have some notable limitations. Existing loggers often have high power consumption, such that running them continuously requires large heavy batteries and frequent recharging (Beatham et al., 2021). They also typically have a short read range (less than 20cm) which means animals must pass through a relatively small circular detector to be recorded, which can limit versatility and ease of use (Briggs, Robstad & Rosell, 2021). Finally, commercially available solutions are expensive, limiting the numbers used and scope of studies possible (Harrison & Kelly 2022). We therefore perceived a need for an RFID logger that is low-power (to reduce logistical effort in recharging batteries), has a versatile detector with a long read range, and is low cost, such that it is feasible to deploy a set of loggers capable of providing large-scale monitoring of an entire population or community of small mammals. Here, we document the development and testing of such a device, that can be used to collect a variety of behavioural data from wild small mammals and potentially other animals, including activity patterns, space use (home ranges), social networks and survival data. We describe its design features and construction such that other researchers may replicate it. We then demonstrate the type of data this system can collect, through a 10-month monitoring study in a wild community of small mammals.

Methods

Description of the logger

The logger is comprised of three main parts: an RFID reader (antenna), a PIR sensor, and a weatherproof box of electronic components, including the printed circuit board (PCB), battery and SD card (Figure 1 a). For use in our study site's woodland environment, we rested each logger on a 15cm high wooden table with non-magnetic stainless steel wire legs, with the PIR sensor pointing downwards towards the ground through a small hole made in the table (Figure 1 b). Table 1 lists each design requirement we had during development, and how our final design achieved it. Principle among these was that the logger should have low power consumption, which is primarily achieved by the logger being activated by a passive infrared (PIR) sensor. As the antenna draws a considerable amount of power from the battery, PIR activation conserves a large amount of power compared to continuous operation. The PIR sensor monitors continuously for 'movement' and is triggered when a warm moving object (>5°C above ambient temperature), such as a rodent, moves within its range (~28cm when ambient temperature is 20°C, Figure 1 c). The table on which the logger sits, as well as a small ring of rubber above the sensor act to shield it from excessive triggering from sunlight on vegetation, and rain droplets which can otherwise reduce sensitivity (Figure 1). When the PIR sensor is triggered, the logger wakes up from sleep mode, performs a self-check, records the date and time and within 1.5 seconds activates the antenna which begins recording any PIT tags within range together with associated time stamp data (to one second). The logger waits for an initial period of 10s for a valid RFID tag read or another PIR trigger. If either occurs, the logger remains on for another 15s, up to a maximum of 60 seconds of PIR/RFID tag inactivity, before returning to sleep. The logger cannot be retriggered for 10s immediately after the 60 second maximum triggering period, to avoid over triggering. During sleep mode, the logger will activate periodically (e.g. every 4 hours) to record temperature, check battery voltage and record and send (if connected to a wireless system) an 'I am alive' signal that indicates it is functioning properly.



Figure 1 (a) Logger system and labelled parts in the lab (b) logger in the field and (c) read range of the antenna.

To further conserve power, the logger can also be programmed to only operate at certain times of day. PIR activation means the logger can operate on small Li-ION batteries, minimising logger weight (1.5kg) so they can be easily moved around during fieldwork. To enable versatile logger use in which animals do not have to walk through an RFID coil, we use a large flat reader with a 0.09m^2 oscillating detection field, that has a vertical read range of approximately 28cm (when using a 12mm PIT tag). Tag ID and time-stamp are stored on a standard microSD card. If fitted, time-stamped information can also be sent using a packet wireless system via a wireless transceiver, as established at our own study site. This allows one to observe logger activity remotely in real-time and monitor technical issues such as a decrease in voltage (indicating battery replacement is required) as well as animal activity. Further details on individual components and logger construction can be found in Supplementary Material 1.

Table 2 Logger design requirements and features that contribute to meeting low power low cost system

Design requirement	Features enabling design requirement
Low power consumption, and ability to run continuously for long periods without battery change	• PIR activation • Long in-field life using rechargeable Li-ION battery • Unnecessary component functions removed (e.g. beeping mechanism of antenna – which also may have startled the animals) • Programmable to only operate at certain times of day • Possible to connect two Li-ION battery packs simultaneously for extra-long running time
Collection of environmental metadata	• On-board temperature sensor at negligible extra cost • Standard digital, analogue and I2C interfaces allowing use of additional sensors (e.g. humidity, pulse, light)
Ability to accurately, reliably record small mammal activity	• Long range antenna (~28cm vertical read range with 12mm tags), which turns on and functional rapidly (within 1.5s of activation) • On-board real time calendar-clock • High temporal resolution of data recording
Simple, accurate data storage and access	• Data stored on standard MicroSD card that is easily removed • Remote access to data possible via optional wireless transceiver
Adaptable and easy to mould to various project needs	• Option for on or off-board antenna (reader connected to device or in a separate wired container) • Optional remote wireless communication • Open-source and user-modifiable code • Separate large flat antenna to enable versatile positioning (movement through circular reader not required) • Separate PIR detector to allow for versatile positioning • Standard RS232 serial interface for configuration, programming and diagnosis • Standard digital, analogue and I2C interfaces allowing use of additional sensors (e.g. humidity, pulse, light)

	• Standard circuit board interfaces allowing generic antennas and sensors to be used • Highly adaptable firmware and electronics system to meet research requirements
Lightweight and easy to move	• Total weight of typical system 1.5kg

Lab performance test

We tested performance of the completed logger design in the lab before field testing. Li-ION batteries are known to function best at temperatures between +20 to +40°C (Gu et al., 2022), but can function from -20°C to +40°C (Yaakov et al., 2010). To measure thermal tolerance of our unit, we exposed the logger to these temperature extremes (through use of a freezer and full summer sun exposure for 30 days). The logger demonstrated functionality even at these thermal extremes. We also confirmed read range and what conditions might affect the antennas read range. Key specifications and measured performance parameters of the final logger design are given in Table 3.

Table 3 Key specifications (attributes) of the RFID logger.

Battery life	3000 triggers (including periodic activation during sleep, PIR triggers, tag reads). In our study this meant that batteries needed recharging every 3 months
Weight	1.5kg
RFID antenna range	280mm (axial orientation 12 x 2.1mm injectable glass tag, EM4102 IC or series, FDX-B) Potential to cause interference: electrical noise from power supplies and electronics, data communication cables, mains wiring, magnetic materials, 125kHz radio interference, speed of mouse/PIT tag entering the field.
Temperature sensitivity	Demonstrated functional at temperatures (recorded inside electronics box of): Field: -7°C to 45°C Lab: -20°C to >50°C
Cost per unit (parts only)	c.£ 350 (as of July 2023)
Power Consumption	120mA (operational at 11.1V) when active
Power Consumption	30uA (In sleep mode with one PIR active, 11.1V)
PIT tag compatibility	Only 125 kHz FDX-B RFID tag

Field performance test

Small-scale field pilot study

Field performance tests were carried out in Wytham Woods, a mixed deciduous woodland near Oxford, UK (51.77 °N, -1.33°E). We first performed a small pilot study using 25 loggers, to test and optimise logger performance under field conditions. This pilot study identified several optimisations in logger design and deployment that were implemented in future work.

First, it was important that the antenna was placed at least 10-15cm away from the electronics box to avoid interference with reader performance. Second, we made several adjustments to ensure loggers were weatherproof for long periods. We added a small rubber washer as a PIR sensor 'rain protector' to prevent raindrops accumulating on the PIR sensor lens and reducing sensitivity. We also improved in-box humidity control and minimised the risk of water ingress to the electronics box. At first, the weatherproof enclosure was completely sealed. However, wide temperature changes in the field caused the pressure within the enclosure to change and over time and draw in water through the seals. Additional protection including wrapping the enclosure in heavy duty cling film and including silica gel inside the enclosure as a simple and effective way to reduce humidity. With these modifications, we achieved a weatherproof and humidity-controlled solution that could be left in the field for long periods without condensation forming on the electronics. Finally, during pilot studies we optimised use of a proprietary packet radio wireless mesh network to monitor logger performance, identify loggers being over-triggered (e.g. by sunlight), monitor battery status, local temperature and identify loggers which were no longer operating and required checking.

Large-scale field performance test

We next conducted a larger test of field performance, by deploying 60 loggers over a 10-month period on a 160m x 160m plot called 'Holly Hill' (51.77 °N, -1.33°E) in Wytham Woods, Oxford. Over the same period we regularly trapped and PIT-tagged the more abundant wood mice (*Apodemus sylvaticus*), as well as the less abundant bank voles (*Myodes glareolus*) and yellow-necked mice (*Apodemus flavicollis*). Our goals were two-fold: first, to test the quality of data an array of loggers could provide on temporal, spatial, and social activity patterns in a community of small mammals. And second, to use the collected behavioural data, in conjunction with regular faecal sampling, to explore the transmission ecology of the gut microbiota in wild mice. Here we report results from the first aim, while those from the second are reported elsewhere (Raulo et al. *in prep*).

An array of 60 loggers (Figure 2, red dots) were positioned in an even chequerboard design, with loggers placed in the middle of every fourth 10 x 10 m grid cell across the 2.56 ha study grid. Additionally, loggers were rotated fortnightly throughout the whole study period (February-November 2019) by moving each logger one cell (=10 m) north (increasing numbers in y axis). This way each grid cell had a logger (green triangle) for two weeks every two months. In this design, each logger had a set territory

that it would cover repeatedly over the course of the study. An example of such a logger territory is highlighted blue in Figure 2.

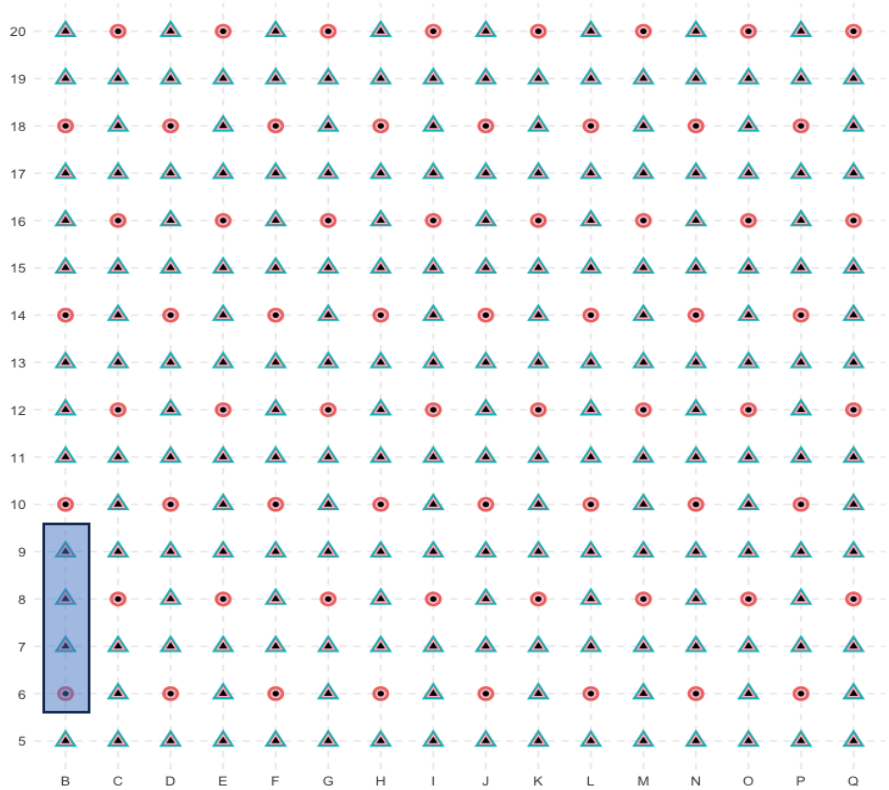


Figure 2 Logger distribution and rotation design during the large-scale field performance test, showing an example of a single loggers 'territory' (blue highlighted box).

We used the wireless monitoring system to inform battery replacements during this study. When a logger battery dropped below 10V during the weekly rotation and logger data quality check, it was removed, charged and replaced in the same grid cell. Rodent trapping sessions were conducted every 2-4 weeks. During each trapping session, one small Sherman trap (16 cm L × 5•8 cm W × 6•5 cm D) was placed in each selected 10 m × 10 m grid cell (n = 80–140 per session). Traps baited with eight peanuts, a slice of apple and non-absorbent cotton wool for bedding were set at dusk and collected at dawn, with all animals processed, sampled and then released inside the 100m^2 grid cell where they were captured. As part of processing, captured individuals were identified to species, sexed, weighed, and aged (juvenile or adult) based on size and pelage characteristics. When large enough (over ~12g), rodents were subcutaneously injected with a 12 mm × 2 mm RFID 125kHz PIT tag. Ear punches were collected from all mice and stored in ethanol at -20°C to provide genetic material for host genotyping. Faecal samples for gut microbiota analysis were collected from traps and frozen at -80°C within 8 hours of collection and between trapping sessions any traps showing evidence of rodent contact were sterilised by washing with bleach.

Statistical Analysis

We performed a range of analyses to demonstrate the capabilities of RFID loggers in understanding the ecology and demography of wild rodent populations, as well as their technical performance over the study period. All analysis and reporting was done in the statistical freeware R (Version 4.2.2, R Core Team, 2022). Prior to publication all code will be made publicly available in a GitHub repository. We define the following terms to describe key aspects of the logger data:

(i) **Tag Read**: when an individual animal was recorded by the logger (PIT tag was recorded)
(ii) **Trigger**: when an 'activity' was recorded on the SD Card, either (1) by an animal and a tag was read, (2) the sensor was triggered but no tag was read, or (3) an "I'm alive" signal was sent.
(iii) **PIR Trigger**: When an animal or other warm object triggered the PIR
(iv) **Tag minute**: unique combinations of PIT tag and each minute in the dataset. Where multiple reads of the same tag occurred at the same logger in the same minute, they were condensed to this unit for further analysis.

Temporal activity patterns

We defined "activity" as the cumulated period animals were detected by the logging systems, regardless of their behaviour. We limited pseudoreplication bias by counting any repeated measures in a 5-minute period as one single "PIR Trigger". The plots were generated using the *overlap* function in the *overlap* R package (Ridout & Linkie, 2009).

Home Range & Social Networks

We quantified home ranges from logger data using a spatial point-based kernel utilisation density estimator implemented using the *adehabitatHR* package in R (Calenge, 2006). We used data from individuals with a minimum of 5 unique observation locations with a maximum of 25% observations touching the edge of the study area. Smoothing of the kernels was performed with the default "*href*" setting. Home range boundaries were delineated at the 75% level to provide an estimate of the 'core' home range, i.e., the smallest area you could expect to find an individual in with 75% probability. The home ranges of 9 male and 9 female wood mice were randomly selected for visualization purposes.

We derived social networks from the large-scale field performance test using custom methods for estimating social associations from spatiotemporal co-occurrence data. Following the principles of animal social network analysis (Croft et al., 2008; Krause et al., 2015), individuals are nodes in the network and edge weight was based on the strength of social association. We used a custom measure of social association, the "Adjusted simple ratio index" or Adjusted SRI (Raulo et al., 2021). This captures the frequency of incidents when two individuals were observed 'associated' relative to the frequency they were observed in general. Here, 'associated' meant observed within 12 hours of each other at the same logger location during the same night, where night was defined as the 16-h period from 4pm to 8am, since this is the daily period when all three rodent species are active (See Figure 4). These instances of association were then used to calculate an association index defined as:

$$Adjusted\ SRI\ = \frac{X}{[X + y_{AB}\ + yA\ + yB],}$$

where X = the number of nights in which individuals A and B were observed associated (in the same location within 12 h of each other), y_{AB} is the number of nights in which A and B were *both* observed but not associated (observed at the same location but more than 12h apart), y_A and y_B are the number of nights in which both were known to be alive but only A or B was observed respectively. Accounting for lifespan overlap in this metric allows us to summarise the temporally fluctuating social structure of the rodent populations in one static social network. The social network was plotted using the R package *igraph* (Csardi, 2014).

Results

Technical performance of loggers in the large-scale field test

Over 10 months the 60 loggers were deployed across the Wytham Woods grid. Data from temperature sensors inside the loggers indicated the loggers operated at temperatures (inside the electronics box) ranging from -7°C to 45°C in the field, while a microclimate station nearby recorded ambient temperatures over the same period of approximately -6°C to 36.5°C.

Although we aimed to replace logger batteries when voltage dropped to 10V on our wireless monitoring system, it is possible their performance could have been reduced prior to this point. We therefore analysed the relationship between logger battery voltage and PIR trigger rate (Figure 3). This revealed a clear decline in PIR triggers below 10V, confirming that battery recharge or replacement at this voltage is desirable. While they can record PIR triggers below 10V, the rate is noticeably reduced, suggesting incomplete data is being collected. Above 12.5V there was also a decline in PIR triggers, but we suspect this is due to logger batteries typically being replaced (and being at maximum voltage) in the middle of the day, when rodent activity is at a minimum.

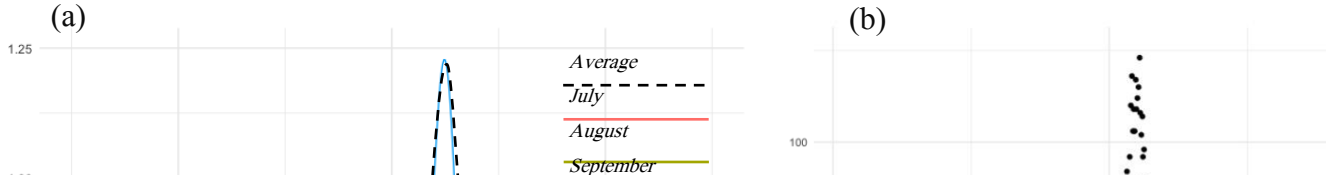


Figure 4 (a) Voltage (V) plotted against the relative density of PIR triggers (all kinds of triggers excluding "I am alive" signals), coloured by season (b) Number of PIR triggers (related to animal tags, excluding "I am alive" signals) plotted against Battery Level (V).

The results displayed in Figure 5 exhibit three distinct plots representing the unique passive infrared (PIR) hits per species versus the total PIR hits per species (as a proxy for minimum number known alive) faceted for three different rodent species: (a) yellow-necked mouse, (b) wood mouse, and (c) bank vole. All three plots demonstrate a positive association, indicating a strong correlation between unique PIR hits and total rodent density.

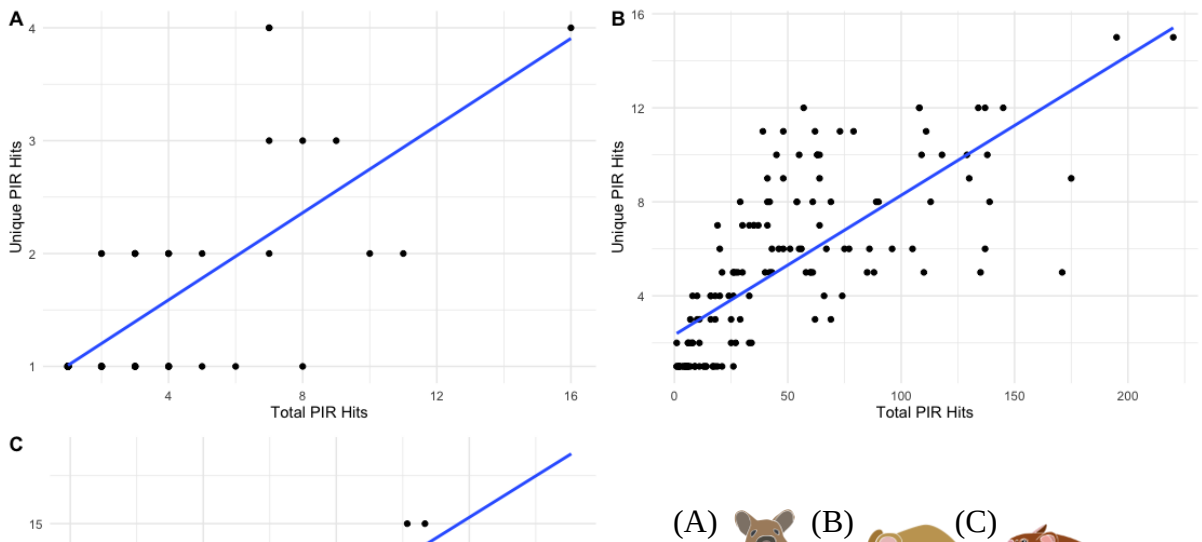


Figure 5 Unique PIR hits are strongly correlated with the total rodent density, suggesting that the movement patterns of individual rodents are closely tied to the overall density of the population in the area. **a** Yellow Necked Mouse **b** Wood Mouse and **c** Bank Vole

Logger-based characterisation of small mammal behaviour

Time-series data and survival

Figure 6 displays time-series of logging records for the complete assemblage of small mammals tagged during the study period. These plots highlight how these RFID loggers can generate high resolution data on individual presence within a defined spatial area, that could be used to infer survival patterns among individuals at a population-wide scale.

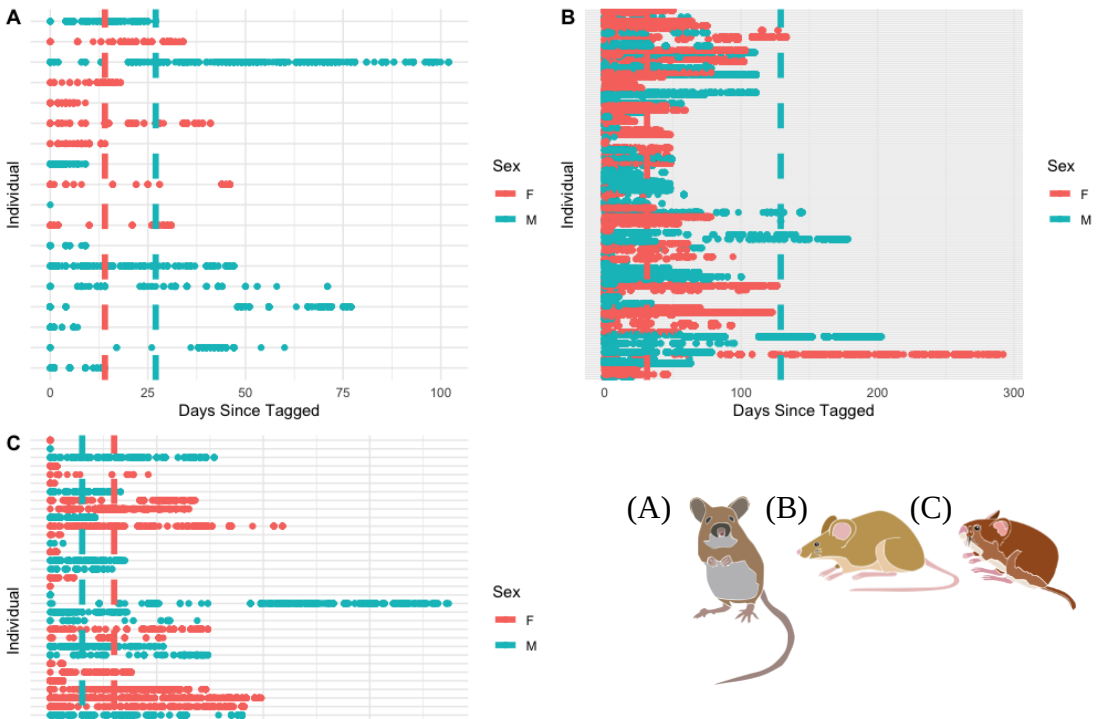


Figure 6 Individual Animal Loggings showing that these loggers could provide useful data for ephemeral populations and survival analyses. **a** Yellow Necked Mouse **b** Wood Mouse and **c** Bank Vole. Female individuals are coloured in coral and male are coloured in blue. Dashed lines are coloured by sex and denote median values.

Temporal activity patterns

Temporal activity profiles for individuals with at least 60 logger records over the study period are shown in Figure 7. Each plot depicts the density of logger records for an individual (on the y-axis) by time of day (on the x-axis). These logger-derived data clearly reveal differences in the temporal niche of the three rodent species (with mice more nocturnal and voles more diurnal), as well as variation among individuals within each species in their daily activity patterns. Yellow-necked mice and wood mice exhibit remarkably similar, nocturnal temporal niches, displaying activity patterns concentrated during the night, while bank voles show activity throughout the day with slightly more activity in early hours of the morning. For all three species, individual variation is apparent, with some individuals active at a narrow range of times (peaky profiles), while others are recorded at widely varying times of day (flat profiles).

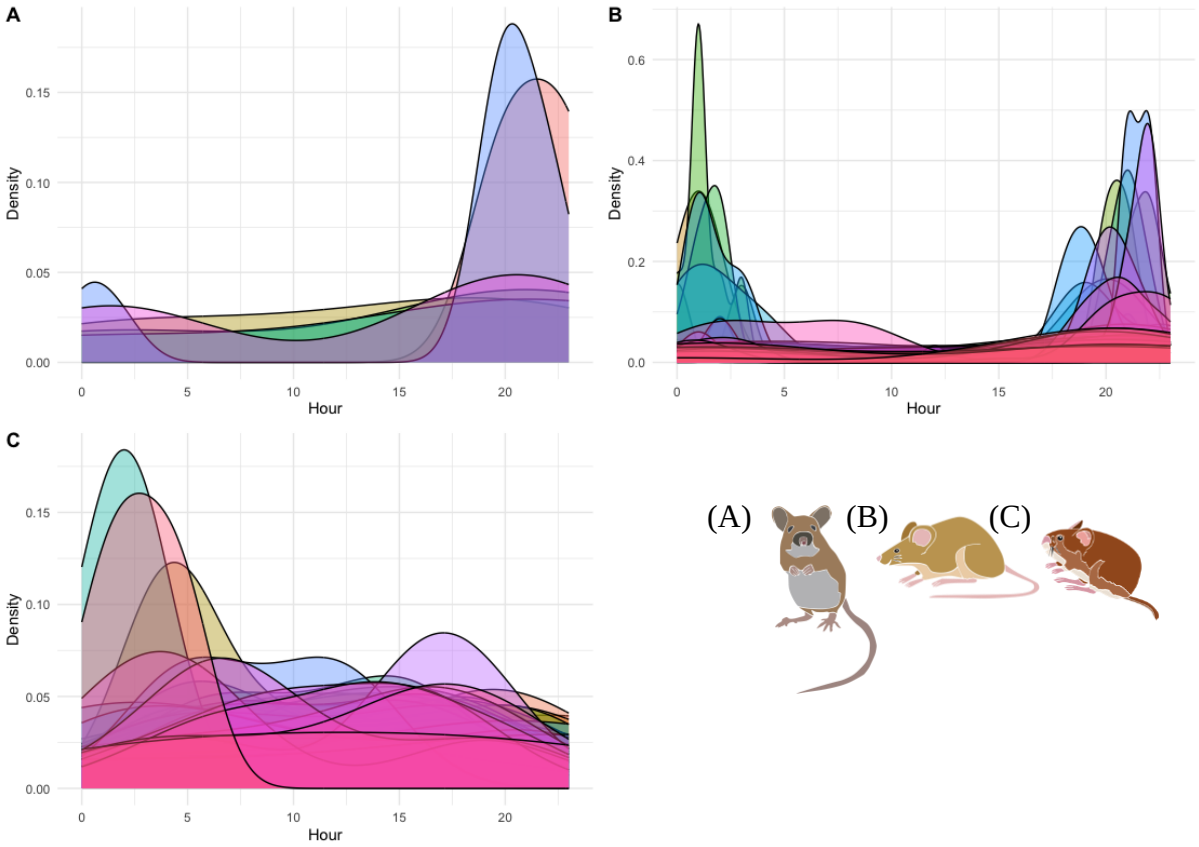


Figure 7 Individual temporal activity profiles These findings highlight the distinct temporal patterns and levels of intraspecific variation among sympatric small mammal species, shedding light on their individual behaviour and niche specialisation. The dataset was filtered to those individuals who had 60 or more PIT tag reads across the study. **a** Yellow Necked Mouse **b** Wood Mouse and **c** Bank Vole

Home range characterisation & social network development

Logger data could be readily used to infer home ranges for large numbers of each rodent species. Kernel-density home range estimates for a selection of 9 male and 9 female wood mice are shown both separately (Figure 8) and in spatial context (Figure 9). These revealed distinct patterns, such as the home ranges of male wood mice exhibiting greater overlap compared to those of females. This observation suggests that male wood mice have a higher degree of spatial proximity and potentially share common areas within their home ranges. In contrast, female wood mice display less overlap, indicating a greater degree of territoriality or individual space utilisation. These data highlight the capability of our RFID loggers to capture high resolution data on space use of many wild rodent individuals simultaneously.



Figure 8 Kernel density estimation for a single female wood mouse

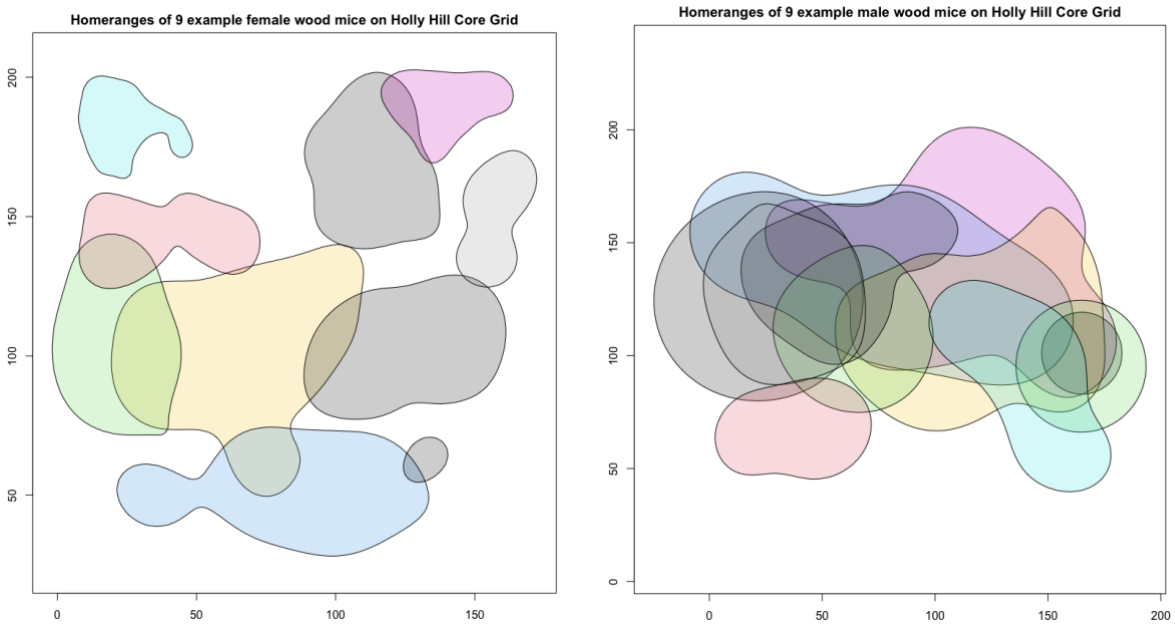


Figure 9 Home ranges (75% kernels of utilisation distributions) of an example subset of 18 wood mice across the study area (a) female and (b) male. Female wood mice are more territorial and consequently have less overlapping home ranges than males.

Our RFID logging system offers exceptional spatial and temporal resolution for studying social networks (Figure 10). The ability to track individuals with high precision enhances the scope of understanding of how social interactions occur in specific locations and with arcuate real-time meta data. The spatial and temporal resolution offered by RFID logging systems enables researchers to explore questions related to social proximity, spatial patterns of interaction, and the influence of physical environments on social dynamics.

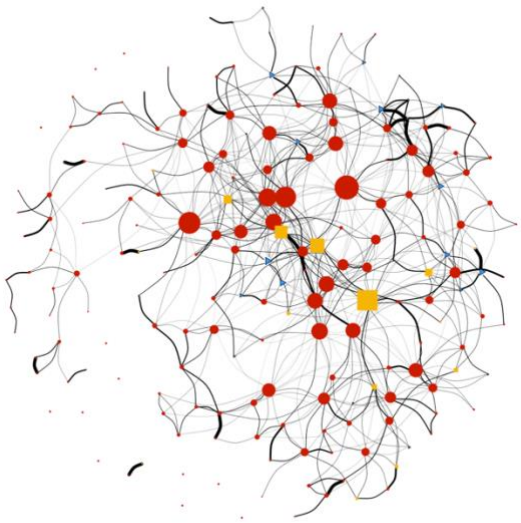


Figure 10 Nodes are individual rodents, wood mice (red), yellow-necked mice (yellow) or bank voles (blue). Edges are measures of social association (Adjusted SRI). Node size reflects an individual's degree i.e. the number of social connections (larger = more connections), and line thickness denotes social association strength (thicker = higher Adjusted SRI). Nodes are arranged in a standard spring layout, such that closely connected individuals appear closer.

Discussion

Understanding the animal behaviour at an individual level is vital for many ecological applications, as well as effective implementation of conservation management strategies. However, the financial constraints associated with collecting such data often pose a significant obstacle. To overcome these, we have developed an affordable, low-power remote logging system. Our design provides a cost-effective solution for monitoring wild small mammals with RFID technology (approximately 36% cheaper than comparable off-the-shelf commercial systems at the time of writing, e.g. Microchips Australia: LID650 reader & ANTSQR300 antenna quoted between $900–1500 AUD), making it accessible to a broad range of researchers and conservation practitioners. We also illustrate how a set of these loggers can identify PIT-tagged wild small mammals over an extended period in the field, enabling the calculation of several insightful behavioural metrics, including activity levels throughout the day, preferred habitats, social networks, and the extent of their territorial boundaries.

We highlight the use of this logging system in constructing home ranges (Figure 8 and 9) and social networks (Figure 10). These social networks can enable the monitoring of key epidemiological factors such as contact networks, population dynamics, and spatial distribution of rodents, which are often

significant contributors to disease transmission. With the ability to capture detailed data on rodent behaviour, including nesting patterns, foraging habits, and social interactions, this RFID logging system may offer a deeper understanding of the ecological and behavioural drivers behind disease outbreaks. This knowledge can inform targeted intervention strategies, such as implementing effective rodent control measures, predicting disease hotspots, noting key individual hubs for disease outbreaks, and evaluating the impact of interventions on disease transmission dynamics.

The RFID loggers developed here can also help advance reliable and precise ecological research. First, by reducing the per unit cost, these loggers encourage the implementation of larger-scale, more robust experimental designs. For instance, in our own study, we utilised 60 loggers to monitor a 2.56-hectare grid for a period of 10 months. Their low power consumption meant we could leave them in the field for approximately three months without needing a battery recharge, reducing the human workload during fieldwork and thus increasing what was achievable. Third, by recording individual identities, these RFID loggers researchers to investigate behaviour at the individual level within populations and across contexts. This is not possible with some other methods for monitoring small mammals, such as camera trapping. For example, in a recent 2023 study conducted in Austria, camera traps were used to determine temporal activity patterns of wood mice and bank voles (Probost & Probost, 2023). Although that study yielded interesting findings regarding inter-species density suppression, it could not capture individual-level data, and struggled to differentiate between species with similar physical characteristics. In contrast, our RFID logger-derived data allowed us to observe not only distinct temporal niches among species, but also clear individual variation in daily activity patterns among members of each rodent species. Individual-level behavioural data is essential in many subfields of biology. For example, individuals often vary in movement or contact patterns and thus propensity to transmit infections, making it important to record individual behaviour in epidemiological studies. RFID technology has the potential to play a vital role in population monitoring for demographic studies by providing essential information about individual activity and density. The presented logger system accurately generated temporal profiles for all three small mammal species examined, offering detailed estimates of home range for the most abundant species within the community. This highlights the system's potential for future use and expansion. In conservation, being able to identify individual-specific behaviour is crucial when monitoring threatened or vulnerable species, and if individuals differ in their behavioural responses to a common intervention. Fourth, as logger-based monitoring is entirely passive, the acquired data should provide a more accurate representation of natural small mammal behaviour than methods like radio-tracking, which involve much more human disturbance. Finally, the RFID loggers designed here are also easily customizable and modifiable to suit specific research aims or studies, and they require relatively simple servicing and maintenance. Overall, the use of these RFID loggers can enhance ecological research by enabling the collection of high resolution, large-scale and individual-level behavioural datasets on small mammal movements, at a reasonable cost.

As well as providing high resolution individual-level data, analysis of the data from our PIR-triggered RFID loggers also suggested another application of PIR sensors in ecological monitoring. We detected a strong correlation between the rate of PIR triggers and overall population density (Figure 5). This finding suggests that the remote loggers utilised in this study effectively capture the movements and activities of most of the population for each species. This illustrated that where species or individual-level information is *not* required, a set of PIR-sensors without RFID readers may provide an even more cost-effective and lower-power means of estimating or monitoring total rodent density. In order to accurately capture rodent density, any such PIR sensor arrays would have to be set up in a way that is rodent-targeted (e.g. only active at night, pointing towards the ground from a low level, shielded from other forms of PIR activation such as light glinting off vegetation).

While our RFID loggers eliminate the need for a human observer in the field, data collection still necessitates some human effort, in charging and often in rotating loggers to achieve even and broad spatial coverage. Our study benefited from the packet radio wireless mesh for direct data reception and altering to specific loggers in need of charging. We recommend future studies incorporating our RFID loggers to explore the potential of this within their own studies to enhance data collection efficiency through automation. Such advancements also open up various possibilities for remote trapping of targeted individuals or access-limited nest boxes based on individual identity. If a wireless monitoring system was not in place voltage can be checked manually on SD cards, through a battery low warning light or simply by triggering the PIR sensor to confirm operation of the logger. Throughout both field trials we checked the functionality of every logger fortnightly in addition to the wireless monitoring system.

The technology we developed here may not be novel, the key strength for this system is its versatility. What sets our system apart is its adaptable design, which lends itself to easy modifications. For instance, the square antenna that we currently employ can be effortlessly swapped out for a circular antenna, enabling us to monitor burrows or tree hollows with precision. Moreover, the system's flexibility allows for the incorporation of solar panels, reducing the need for frequent charging and maintenance. This innovative feature ensures uninterrupted functionality in remote locations. Additionally, the same PCB board can be utilised for handheld RFID monitoring, providing a convenient and portable solution. Furthermore, we can extend the application of our system to other types of monitoring systems, such as selective trapping based on PIT tags. In essence, our RFID logging system serves as a versatile platform that can be customized to meet a wide range of monitoring needs.

Here I presented the development of an RFID logging system that showcases its functionality in capturing community dynamics and behavioural metrics. The system successfully tracks and records

interactions among individuals equipped with RFID PIT tags, providing valuable insights into social networks and behavioural patterns. Through extensive field experimentation and analysis, we demonstrate the system's high accuracy in data collection, enabling comprehensive monitoring of community dynamics. Furthermore, we highlight promising future directions for the RFID logging system, including enhancements in data analysis techniques, integration with other technologies, and its potential impact on diverse domains such as behavioural ecology, and epidemology. By successfully implementing our RFID loggers in real-world scenarios, we were able to capture behavioural metrics. With their potential to contribute significantly to various fields, these RFID loggers will open new avenues for exploring ecological dynamics.

This chapter serves as a comprehensive guide for researchers interested in leveraging the capabilities of our RFID logging system and paves the way for exciting advancements in understanding and harnessing community dynamics.

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Supplementary Material

1. *Logger Parts and Operation*

The antenna and tag compatibility

The logger can be connected to any type of antenna which outputs RS232 serial data. The standard long-range reader we have used is a self-tuning 300 x 300mm sealed unit taking up to 120mA of current at 12V with a read range of almost 30cm (when using a 12mm PIT tag). The antenna is designed to read EM4102 integrated circuit family, Manchester encoded, FDX-A tags which operate at 125 kHz. The

reader requires about 1.5 seconds to self-tune and during power-up the large inrush current is controlled by the firmware preventing the battery voltage from dropping below a minimum threshold.

The passive infrared detector (PIR)

The current consumption of the PIRs is around 15uA. There are many PIR modules available and current consumptions vary. Ideally the total sleep current should not exceed 100uA to preserve battery life and so PIRs with an operating current of up to 50uA are recommended. The ultra-low power PIR is sealed in a metal tube and the electronics made waterproof using resin. The PIR is very sensitive and can be triggered by moving warm objects of >5ºC above the average thermal background. The PIR is designed to compensate for and not be triggered by slow changes in background ambient thermal conditions. The PIR can be triggered by sunlight, moving objects (vegetation) and warm air currents. It is recommended that the PIR be kept shaded from direct sun or sunlight reflections to prevent false triggers and the plastic sensor lens kept free of water (e.g. raindrops) otherwise the sensitivity of the PIR will be reduced. During laboratory tests we found that allowing the PIR to settle (manually covering the sensor) for 10s will allow the PIR to re-calibrate its sensitivity level.

Main logger circuit board and battery

The central component of the system is the main microprocessor circuit board. The dimensions of the circuit board are 102 x 69mm and it consists of several elements, including the main microprocessor, an SD card holder, interfaces, sensor and power connectors, a real-time clock-calendar, and space for an optional wireless transceiver module (Supp Material 2). The custom-designed circuit board aims to minimise power consumption of the logger, averaging around 0.01W during a 3-month trial period. This power consumption is significantly lower compared to commercially available single board computers like the Raspberry Pi (a Pi Zero typically requires 0.9W). Achieving such low power consumption is possible by utilizing low power Arduino or similar microprocessors. A 2500mAh 11.1V Li-ION battery is used to meet the high-power demand of the antenna, and should provide a useful field life of approximately 2500-3000 activations (including periodic activations to communicate the logger is functioning normally, set here to every 4h, PIR triggers and tag reads). See Results section for empirically measured field-life in our study system. We have proven in a further field trial that it is possible to diode-link an additional battery to increase operational lifetime.

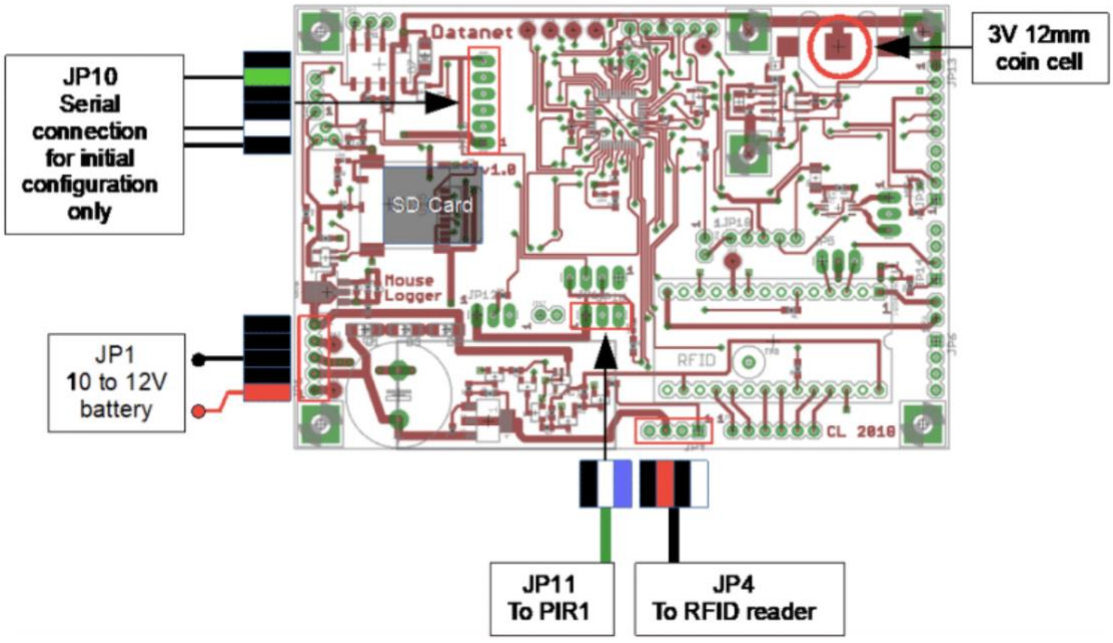
The logger is designed to function reliably until the battery reaches 8.0V, after which it shuts down to protect the battery from over discharge. The logger is fully programmable, allowing it to be customized for different applications and research areas. It includes a real-time clock-calendar backed up by a separate battery (a12mm 3V coin cell), a precise temperature sensor, a voltage reference, a motor driver for motor control, two serial RS232 interfaces, two analogue-to-digital inputs (ADCs), two I2C serial interfaces, a power relay for switching applications, two independent power regulators for the sensors

and microprocessor, and a programmable digital interface with indicator LEDs. Data is recorded onto a standard microSD card and can optionally be transmitted wirelessly. The configuration of the logger is determined by a text file on the SD card, and the date and time can be updated using a standard serial connection.

Serial interface and optional wireless communication

The loggers can be tested and monitored using a standard 3.3V TTL RS232 serial interface. The firmware presents the user with options to update the date and time, the check the operation of the PIR detector, on-board temperature sensor, antenna, and SD card. The same interface can be used to connect to a wireless system to allow remote monitoring of data. All data recorded on the SD card are also sent to the TTL-RS232 port allowing a TTL-RS232 compatible wireless module to be connected e.g. LoRa (LoRa Alliance, 2023). In this study we used a custom-built proprietary low power packet-radio system to upload real-time data, the details of which are not included here.

2. *Circuit Board Schematics*



5

Detection of spatiotemporal partitioning of a wild small mammal community using fine scale individual movement data

J. R Dale, A. Raulo, C. Lamberth, S. Knowles, T. Coulson

Abstract

Understanding how different species coexist in a given habitat is a central question in ecology. In this study, we investigated the spatiotemporal niche partitioning of three small mammal species, wood mice, bank voles and yellow-necked mice, in two UK woodland sites. Using RFID loggers placed across grids, we quantified the temporal activity patterns and space use patterns of each species, and tested whether they showed any evidence of niche partitioning.

We found that wood mice and yellow-necked mice exhibited very similar temporal activity patterns, being more active at night and less active during the day, whereas bank voles were active more frequently throughout the day. This suggests that the two mouse species may be sharing a temporal niche, potentially avoiding competition by using the same resource at different times. In contrast, bank voles may be exploiting a different resource or facing less competition by being active during the day.

We also found a strong negative correlation between the space use of bank voles and both mouse species, indicating that bank voles occupy areas where the other two species were more abundant. This suggests that spatial niche partitioning may also be occurring, with the three species displaying segregated use of space at a fine spatial scale.

Overall, our results provide evidence for spatiotemporal niche partitioning among these three sympatric small mammal species, facilitating their coexistence.

Introduction

Niche partitioning is a crucial process in which sympatric species divide the available resources in their environment, including food, space, and time. This phenomenon plays a significant role in shaping species interactions within ecological communities (Vacher et al., 2016; Maziarz et al., 2023). By engaging in niche partitioning, species can minimise direct competition and promote coexistence by specialising in different aspects of their environment (Vacher et al., 2016). Furthermore, this process enhances ecological stability by reducing the likelihood of competitive exclusion (Holt, 2013).

When multiple species with similar resource requirements coexist without niche partitioning, competition can arise, leading to the dominance of a single species and the exclusion of others from the ecosystem (Gause, 1934; Grant, 1972; Sozio & Mortelliti, 1978; Kneitel, 2008; Holt, 2013). Niche partitioning protects against such competitive exclusion, preserving a more balanced and stable community structure (Anarasekare, 2003; Kneitel, 2008; HilleRisLambers et al., 2012). In this study, we delve into the spatiotemporal niche partitioning exhibited by an assemblage of wild small mammals. Our objective is to gain insight into how multiple species with similar resource needs can coexist harmoniously.

Spatiotemporal niche partitioning refers to the phenomenon whereby organisms occupying distinct spatial and temporal niches within an ecosystem (Dayan & Simberloff, 2005; Scriven et al., 2016). The process involves the segregation of populations based on factors such as resource requirements, behaviour, and physiological adaptations (Schoener, 1974). Spatial niche partitioning occurs when different species or populations occupy specific spatial habitats or microhabitats within the ecosystem (Schoener, 1974; Balaz et al., 2016). This spatial segregation can be influenced by factors such as resource availability, environmental conditions, or interspecies interactions (Amori et al., 2015; Balaz et al., 2016). For example, one species may occupy the upper canopy of a forest, while another species resides in the understory, effectively utilising different vertical layers of the habitat (Eccard & Ylonen, 2003). On the other hand, temporal niche partitioning entails the temporal segregation of species or populations, with each occupying a distinct time window for activity sych as resource acquisition or reproduction (Greenwood, 1978; Carothers & Jaksic, 1984). This temporal separation can occur on a daily, seasonal, or annual scale. For instance, some animals may exhibit diurnal behaviour, being predominantly active during the day, while others adopt nocturnal activity patterns, reducing direct competition for resources.

By examining the spatiotemporal niche partitioning patterns in this common assemblage of small mammals, we aim to shed light on the mechanisms that facilitate their coexistence and resource utilisation. Understanding these dynamics will provide valuable insights into the maintenance of diverse and stable ecological communities.

Bank voles (*Myodes glareoulus*), yellow-necked mice (Apodemus flavicollis), and wood mice (Apodemus sylvaticus) are small granivorous mammals that are commonly found living in sympatry in mixed forest ecosystems across Europe (*Poland:* Andrzejewski & Olszewski, 1963; *Germany:* Abt & Bock, 1998; *United Kingdom:* Buesching et al., 2008 *Vienna:* Mitter, Sumasgutner & Gamauf, 2015, *Italy:* Viviano, Scarfo & Mori, 2022; *Austria:* Probst & Probust, 2023). These are common model species for ecological studies and present an ideal study system for examining coexistence through spatiotemporal niche partitioning, given their similar ecological requirements and extensive records of coexistence (Grum & Bujalska, 2000; Hile & Mortelliti, 2011). Previous research has shown that these small mammal species partition their niches in various ways, including temporally (Probst & Probst, 2023), spatially (Jancewicz & Gliwicz, 2017), vertically (Buesching et al., 2008), and in terms of food use (Chibowski et al., 2022). These established niche axes form the foundation of coexistence within this community. Here, we delve deeper into the well-established niches in the literature, aiming to identify the fundamental dynamics that drive the spatial and temporal partitioning. Leveraging a cutting-edge technology, we unveil a groundbreaking application that

details the most precise and comprehensive depiction to date of how these three species successfully coexist.

In this study, our aim was to develop a minimally invasive, low-cost remote tool to understand species interactions. We employed the remote Radio Frequency Identification (RFID) loggers described in Chapter 4 to gain insights into the intricacies of small mammal movement. RFID loggers are powerful tools for studying niche partitioning in wild systems, as they provide detailed information on individual animal movements and behaviours. This chapter applies the logging system to explore niche partitioning of species along both temporal and spatial axes within this sympatric small mammal community.

Methods

Site Descriptions

The temporal and spatial niche partitioning was assessed in two locations within the UK where wood mice, bank voles and yellow-necked mice are sympatric: Silwood Park (51.4091° N, 0.6392° W) and Wytham Woods (51.7773° N, 1.3399° W). Silwood Park is a 100-hectare woodland and research campus owned by Imperial College London, located in the village of Sunninghill near Ascot, Berkshire, The woodland at Silwood Park is predominantly composed of broad-leaved trees such as oak, beech, and cherry, and is an important site for conservation biology, ecology, and evolutionary biology research. Wytham Woods is an ancient semi-natural woodland located approximately 5 miles west of Oxford, England. The woodland covers an area of approximately 1000 acres and is characterised by its diverse range of flora and fauna. The woodland is primarily composed of oak, beech, and ash trees, with smaller populations of birch, holly, and hazel also present. Wytham Woods is a Site of Special Scientific Interest (SSSI) and is owned and managed by the University of Oxford. The woodland has been the subject of numerous ecological and conservation studies due to its unique characteristics and long-standing history. Wytham Woods is a well-preserved example of semi-natural ancient woodland, having been covered in forest for over 8000 years.



Figure 1 Location of study, blue representing Wytham Woods in Oxford University and black representing Silwood Park at Imperial College London

Field Methods

Wood mice, Yellow-necked mice and bank voles were trapped using sma
Sherman traps one night every 2-4 weeks. Across both sites the traps were
to ensure even coverage across the grids. Traps were set at dusk and, collected at dawn. Upon trapping, mice were injected subcutaneously with a passive tracking tag (PIT-tag) for permanent identification, demographic data on mouse individuals were recorded (sex based on anogenital distance, age based on weight and pelage colour). Traps showing sign of small mammal contact were washed and sterilised using bleach between trapping sessions. After processing, animals were returned in the same 10 m x 10 m grid cell they were captured in, no later than 8 hours post capture.

RFID Logger Descriptions

In Silwood, data was collected over a one-year period (Nov 2014–Dec 2015) in a 2.47 ha (130 m x 190 m) mixed woodland plot called Nash's Cops. A set of nine custom built PIT-tag loggers were distributed across the trapping grid and regularly rotated to ensure even spatial coverage. Loggers consisted of a box with paired entrance-exit tubes, that recorded the time-stamped presence of any small mammal that entered. A larger plastic box encapsulated a smaller wooden box filled with sawdust and baited with a single peanut, and peanut oil was rubber around the tube entrances as a small lure. Due to the design of the loggers, they were cleaned during each rotation with 70% ethanol. Loggers were rotated systematically using a sampling design that ensured even spatial coverage, with each logger covering a spatial 'territory' that it was cycled through. Rotations occurred between 10am-2pm and were performed 2-7 times a week except for days where trapping occurred, where the loggers were deliberately not rotated. Data from the day after a trapping night were excluded from analysis as behaviour may not have been natural at this time. Further details on the loggers and their rotation are provided in Raulo et al., 2021.

In Wytham data was collected over a 10-month period (January 2019 – October 2019) on a 2.56ha plot (160 m x 160 m). Here, we tagged and tracked small mammal movements using a set of 60 custom-built motion-activated PIT-tag loggers (see Chapter 4). These updated loggers were not baited with any kind of lure and were evenly distributed across the grid and rotated fortnightly.

Statistical Analysis

All statistical analyses were conducted using the R statistical freeware (version 4.1.0, R Foundation for Statistical Computing, Vienna, Austria, R Core Team, 2022).

Circular Plots – density diagrams

To investigate the temporal niche partitioning of the three species in detail, we generated circular plots using kernel hours. Kernel hours represent the proportion of time that a species spends active during each hour of the day, weighted by the intensity of activity during that hour. Here we use kernel density estimates (KDE) to extrapolate in which time bracket each species spends the most time. KDE work by approximating the stationary utilisation distribution $p(\boldsymbol{r})$ of the individual, i.e. its time budget spent with respect to hour r, with a sum of "kernels", i.e. unimodal distributions k centred around each recorded hour $\{\boldsymbol{r_i}\}$.

$$\hat{p}(\boldsymbol{r}, \{\boldsymbol{r_i}\}, \sigma_B) = \frac{1}{N}\sum_{i=1}^{N} k\,(r, r_i, \sigma_B)$$

The parameter σ_B, is the bandwidth and controls the spread of each kernel around each recorded hours, and therefore ultimately the degree of smoothing of the resulting distribution. The circular plots were generated using the *circular* function in the *circular* R package (Agostinelli & Lund, 2002).

Activity Overlap Plots

We first calculated the proportion of time that members of each species were active during each hour of the day. We then plotted the activity patterns of the three species using Activity Overlap plots, which show the degree of temporal overlap in activity between pairs of species. As with the circular plots, these plots similarly use KDE. The plots were generated using the *overlap* function in the *overlap* R package (Ridout & Linkie, 2009). The proportion of overlap is calculated through Dhat4 [Δ_4] which works best when the smallest sample has at least 50 observations.

$$\widehat{\Delta}_4 = \frac{1}{2}\left(\frac{1}{n}\sum_{i=1}^{n} min\left\{1, \frac{\hat{g}(x_i)}{\hat{f}(x_i)}\right\} + \frac{1}{m}\sum_{i=1}^{m} min\left\{1, \frac{\hat{f}(y_i)}{\hat{g}(y_i)}\right\}\right)$$

where n, m are the sample sizes and I is the indicator function (1 if the condition is true, 0 otherwise)

Watsons U^2 test

To test for differences in temporal niches among between the three species, we used Watson's U^2 test. This test compares the distribution of activity across the 24 hours of the day between two groups.

$$U^2 = \frac{n_1 n_2}{N^2}\left[\sum d_k^2 - \frac{(\sum d_k)^2}{N}\right]$$

where;

$N = n_1 n_2$

d_k = difference between two cumulative frequencies

We used the *watson.test* function in the *circular* R package (Agostinelli & Lund, 2002) to conduct the test for each pair of species.

Coefficient of Overlap

To assess the effect of ecological niche on temporal overlap, we estimated the coefficient of overlap between all species' probability densities using a Dhat estimator [Δ_4] (Ridout & Linkie, 2009). We calculated the 95% confidence intervals using smoother bootstrap with 100 resamples (Ridout & Linkie, 2009). This is a descriptive method, and is best summarised in conjunction with a Watsons U^2 test.

Actograms

We created Actogram plots for each species, which display the daily activity patterns over the course of the year. We included sunrise and sunset times in the plots to provide context for the activity patterns. The Actogram plots were generated using the *actogrammr* function in the *ActCR* R package (Di et al., 2019).

Grid Spatial Plots

To investigate the spatial niche partitioning of the three species, we created grid spatial plots. These plots display the density of activity for each species across the study area, with each 10 m x 10 m grid cell representing a specific location. The density of activity is calculated by summarising (per 5 minute interval) the corrected amount of activity per day on the grid. The plots were generated using the *spatstat* R package.

Spatial correlation

To quantify the degree of spatial niche partitioning among the three species, we calculated spatial correlation coefficients between each pair of species using the *spatcor* function in the *spatstat* R package (Baddeley, Rubak & Turner, 2015). The spatial correlation table was generated using the *corr.test* function in the *psych* R package. (Revelle, 2023)

Results

Overall, we recorded rodent activity over 380 sampling days in Silwood and 126 days in Wytham. From the individuals trapped and PIT-tagged in Silwood the loggers recorded 86 wood mice (Figure 2 a), 30 yellow necked mice (Figure 2 c), and 54 bank voles (Figure 2 b), and in Wytham 93 wood mice, 6 yellow necked mice and 36 bank voles.

(a) (b) (c)

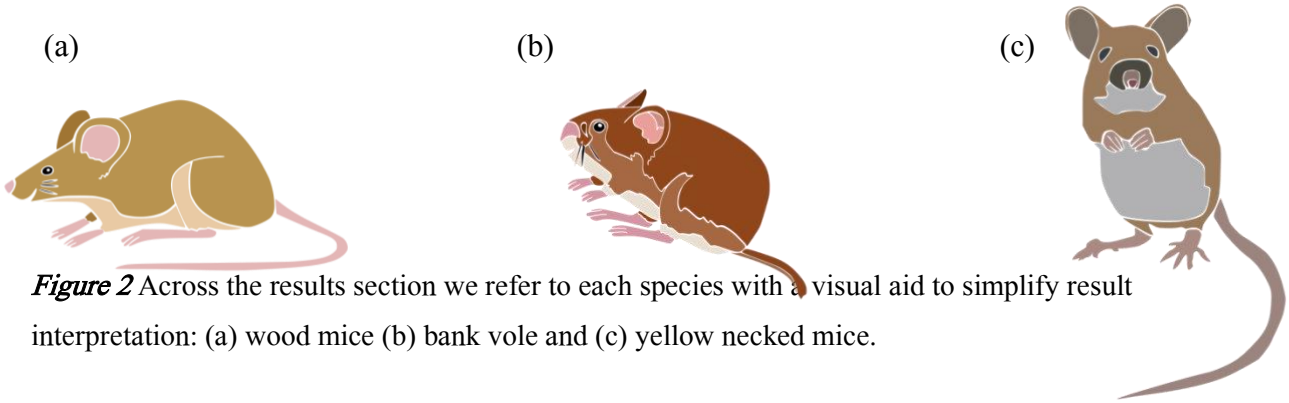
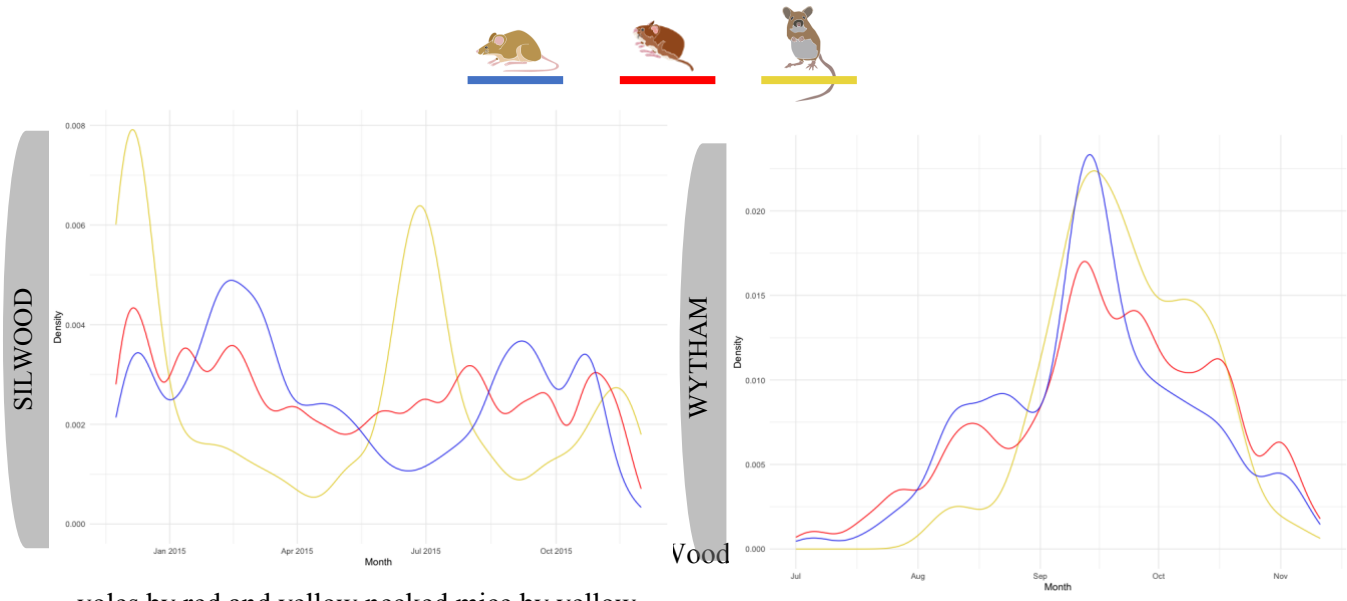


Figure 2 Across the results section we refer to each species with a visual aid to simplify result interpretation: (a) wood mice (b) bank vole and (c) yellow necked mice.

Population density plots revealed that in Wytham, all three species exhibit a uniform single peak, with Autumn having the highest density for all species. In Silwood, bank voles and wood mice had similar synchronistic densities across the study period, whereas yellow necked mice exhibited an explosive density followed by periods of extended lows. Silwood was studied over a longer period of time so we can see the cyclic dynamics typical of each species, whereas in Wytham we track each species during a singular cycle.



voles by red and yellow necked mice by yellow.

We initially set out to understand the temporal patterns for each species and used density diagrams through kernel density estimators at each time point in a 24-hour window (Figure 4). For both sites the patterns are visually similar, with bank voles demonstrating pattern of consistent activity across day and night hours. Wood mice and yellow necked mice had a very similar temporal niche pattern, with both species being more active between 1800 hours and 0600 hours. In Wytham, bank voles exhibited a distinct and stable activity pattern with no clear peaks of activity and activity was consistent across most hours. In Silwood, their activity peaks at around 1500 hours to 1800 hours. In Wytham, wood mice were primarily active during the evening and nighttime, with reduced activity

during the early morning hours. The peak of activity for wood mice in Wytham was around 1900 hours. This pattern was replicated at Silwood, where wood mice also exhibited increased activity during the evening and nighttime, wood mice in Silwood have an activity peak around 1800 hours. Like the wood mouse, the yellow-necked mice were most active during the evening and nighttime hours, with decreased activity during the early morning hours. Their period of peak activity also aligns with wood mice at both sites.

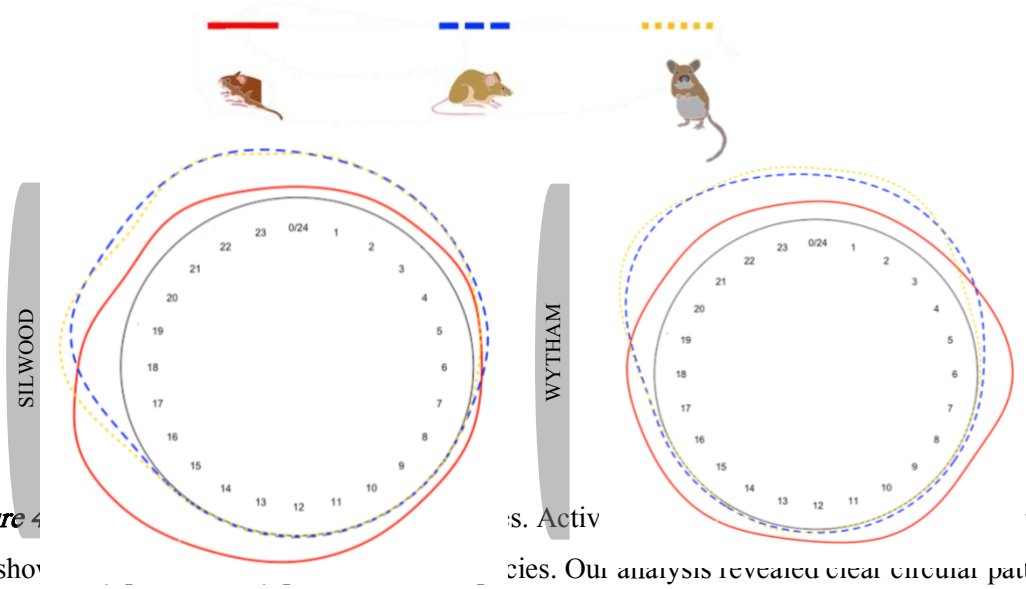
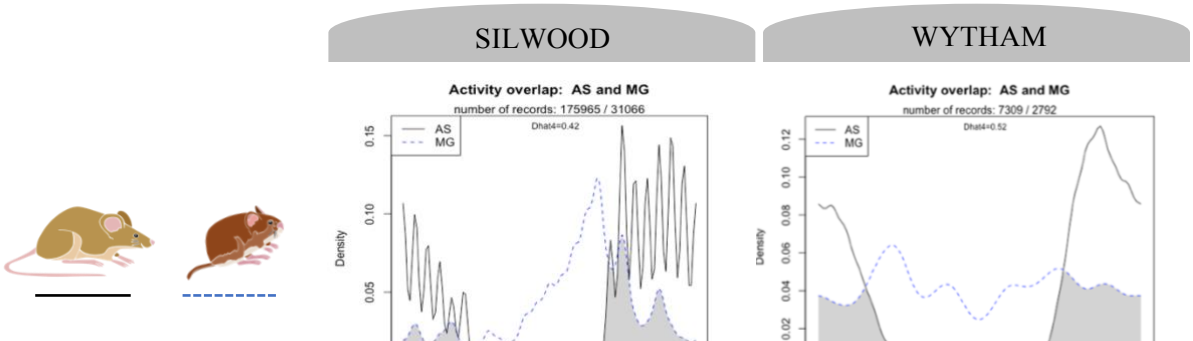


Figure 4 s. Activ of the day sho cies. Our analysis revealed clear circular patterns in the activity of all three species at both sites. Despite some variations in the intensity of activity between the species, the general pattern was similar for each species at both sites.

To understand these patterns further we created temporal activity overlap plots (Figure 5). Each species temporal niche was plotted against the other species to determine the amount of overlap in time use. We used Dhat4 (Δ_4) as a vector of the amount of density overlap at each time of observation. Dhat4, also known as the D4 statistic, is a measure of dissimilarity or distance between two temporal activity patterns. It quantifies the dissimilarity between two time series by comparing the observed activity levels at each time point. The temporal niches of each species were highly consistent across sites. Wood mice and bank voles had low overlap (Wytham; Dhat4: 0.52, Silwood; Dhat4: 0.42, Figure 5), as did yellow necked mice and bank voles (Wytham: 0.45, Silwood: 0.46, Figure 5). However the *Apodemus* species Yellow necked had high Dhat4 values, signifying significant temporal overlap (Wytham: 0.91, Silwood: 0.87, Figure 5).



Using a Watsons U^2 test we compared the distributions of each paired overlap to statistically validate these temporal partitioning findings. The test was conducted to determine whether there are significant differences among bank voles, wood mice, and yellow necked mice. As expected, only bank voles had a significantly different temporal distribution with the *Apodemus* species, whereas there was no significant difference in temporal distribution between the *Apodemus* species (Table 1). The daily activity pattern of bank voles and wood mice, and bank voles and yellow-necked mice were both significantly different (wood mice: Watsons U^2 test $p < 0.001$, yellow-necked mice: Watsons U^2 test $p < 0.001$), indicating that the circular distributions of voles and mice are statistically distinct. However, the daily patterns of activity for the yellow-necked mice and wood mice were not statistically distinguishable (Watsons U^2 test $p > 0.05$).

Table 1 Differences in temporal activity between species pairs in each location using Watsons U^2-Test

Note: * denotes a significant difference ($p < 0.001$)

The results in Table 2 show the temporal overlap in activity patterns for all three species at Silwood and Wytham based on Dhat4 values (Δ_4). We wanted to further investigate how each species spends their time and whether another species activity inhibits or depresses the activity of another. Here I extend the pairwise use of a Dhat4 measurement to identify when no overlaps occurred, and to include a measurement of when all species were active. The overlap of individual species being active in isolation is low, with bank voles having the highest values due to their diurnality quantified in Figure 4 and Table 1. These are most useful when additionally compared with the Watson U^2 test

	SILWOOD			WYTHAM		
	U^2	Critical Value	p-value	U^2	Critical Value	p-value
	645.52	162.64	<0.001*	48.341	21.325	<0.001*
	3.7348	38.23	>0.05	0.4489	0.2277	>0.05
	511.72	105.79	<0.001*	6.4092	5.9272	<0.001*

results.

Table 2 Temporal overlap in activity patterns, based on Δ_4 estimates from kernel density analysis. Approximate 95% bootstrap confidence intervals in parentheses.

		SILWOOD	WYTHAM
Bank Vole		0.11 (*0.09 – 0.13*)	0.15 (*0.13-0.22*)
Wood Mouse		0.04 (*0.03 – 0.06*)	0.03 (*0.01- 0.06*)
Yellow Necked Mouse		0.09 (*0.08 – 0.11*)	0.07 (*0.02- 0.26*)
Bank Vole-Wood Mouse		0.87 (*0.85 – 0.88*)	0.84 (*0.81- 0.85*)
Bank Vole – Yellow Necked Mouse		0.82 (*0.80 – 0.84*)	0.79 (*0.69- 0.83*)
Wood Mouse – Yellow Necked Mouse		0.89 (*0.87 – 0.91*)	0.91 (*0.86- 0.94*)
Bank Vole – Wood Mouse – Yellow Necked Mouse		0.80 (*0.78 – 0.81*)	0.78 (*0.72 – 0.82*)

Actograms were created for each site (Figure 6) to visualise any seasonal variation in activity patterns. Each data point was an "active point" in light hours or dark hours (data sourced from local weather stations). As expected, the longer Silwood dataset confirmed the temporal niche overlap with wood mice and yellow necked mice, and that they are predominately active in 'dark' hours. In Wytham this trend is less apparent, and wood mice were more active in light hours than their Silwood counterparts. Across both sites, bank voles displayed their characteristic activity pattern, being active throughout the day and night. In line with expectations, the mice species exhibited a correlation with changes in daylight hours, showing predominantly nocturnal activity across seasons. A noteworthy finding emerged when the population of yellow necked mice increased in Wytham: wood mice exhibited a shift towards diurnal behaviour. This suggests a potential compensatory dynamic, potentially driven by the wood mice's adaptive response to avoid competition with the larger yellow necked mice.

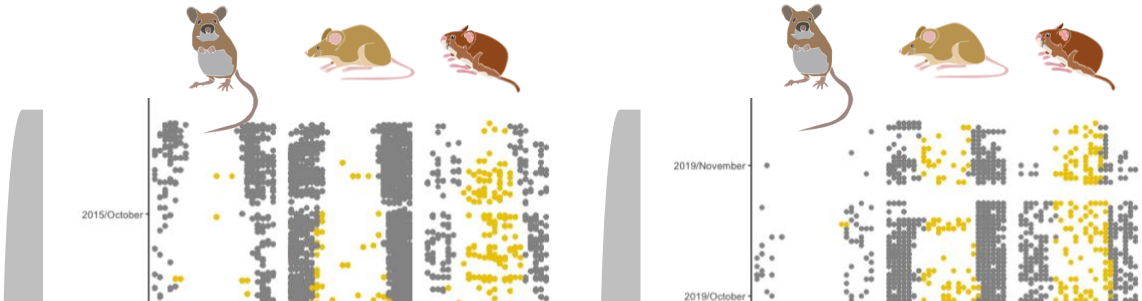


Figure 6 Actograms for each species at each site. The yellow dots represent an activity point in daylight hours, the grey represent an activity point in darkness.

RFID loggers are also well suited to monitoring spatial niches, and as there is clear overlap in the temporal niches of the wood mice and yellow necked mice, we turned to investigating how each species uses space to understand the possible mechanism underlying their coexistence in woodland ecosystems. The correlation coefficients in Table 3 reveal an interesting spatial relationship between the three species. A correlation coefficient is a statistical measure that quantifies the strength and direction of the relationship between two variables and ranges from -1 to +1. The correlation coefficient indicates the degree to which the variables move together or vary inversely. When the coefficient is close to +1, it suggests a strong positive correlation, meaning that as one variable increases, the other variable tends to increase as well. Conversely, when the coefficient is close to -1, it indiciates a strong negative correlation, implying that as one variable increases, the other variable tends to decrease. A correlation coefficient of 0 suggests no linear relationship between the variables. In Wytham, bank voles and wood mice had a strong negative correlation (-0.95), meaning that when one species was present the other species rarely was. Wood mice and yellow necked mice avoided each other in a similar way, but this negative relationship was much stronger in Silwood (-0.75) than Wytham (-0.32) possibly due to the small number of yellow necked mice in Wytham. There was no relationship between bank vole and yellow necked mouse spatial use (0.02 at both sites).

Table 3 Pairwise Spatial Correlation Coefficients between the three focal species in Silwood and Wytham Approximate 95% bootstrap confidence intervals in parentheses.

		SILWOOD	WYTHAM
Bank Vole-Wood Mouse		-0.68 (*-0.65- -0.70*)	-0.95 (*-0.90- 0.1*)
Bank Vole – Yellow Necked Mouse		0.02 (*0.01-0.03*)	0.02 (*0.01-0.03*)
Wood Mouse – Yellow Necked Mouse		-0.75 (*-0.70- -0.80*)	-0.32 (*-0.24- -0.35*)

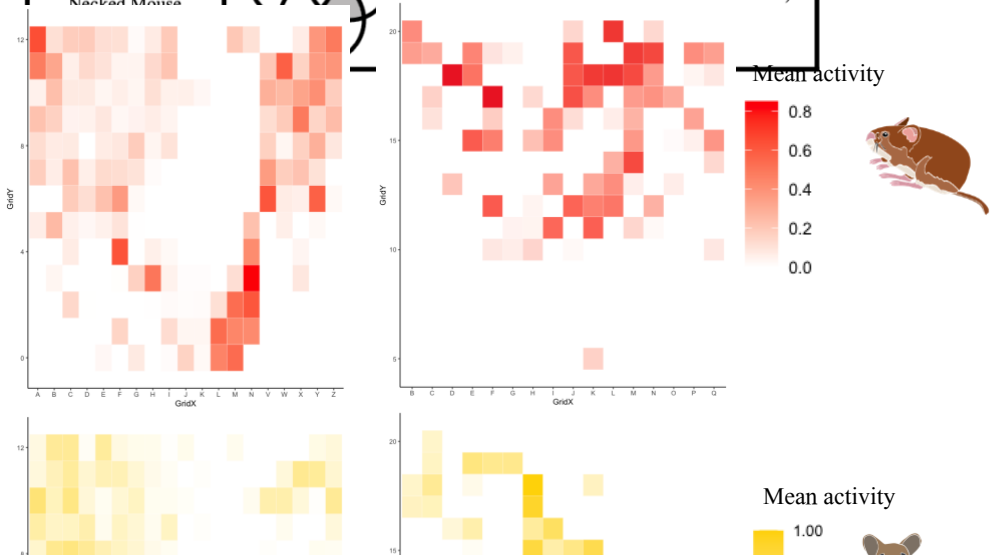


Figure 7 Spatial Plots for each species in Wytham and Silwood. The opaquer the square the higher the number of unique PIR hits that occurred in that square over the study period. To avoid confounding density with number of hits, hits were summarised into 5-minute periods so if an animal was sat under a logger for an extended period of time this could be excluded from the analysis. Visually there is some distinction between the wood mice and bank voles across both sites.

Discussion

Bank voles (*Myodes glareolus*), wood mice (*Apodemus sylvaticus*) and yellow-necked mice (*Apodemus flavicollis*) are sympatic small mammal species that coexist across Europe (Eriksson, 1984; Wolton & Flowerdew, 1985; Grum & Bujalska, 2000). The partitioning of their ecological niches has been the focus of several studies in recent years (Buesching et al., 2008; Schirmer et al., 2019, Probost & Probost, 2023). However, the work presented here is one of the first to directly compare the temporal and spatial niches of all three species and does so at high temporal and spatial resolution using state-of-the-art RFID monitoring technology. Our findings revealed notable patterns in both temporal and spatial distributions among these species. Specifically, we found that wood mice and yellow necked mice exhibited similar temporal niches, displaying comparable predominately nocturnal temporal patterns. Anecdotally, wood mice seemed to become increasingly diurnal towards the end of the study as shown in the Actograms (Figure 6). This corelated with a spike in overall small mammal abundance (Figure 2) and could be tied to the increased overall small mammal density on the grid. Bank voles demonstrated a non-selective pattern, indicating a temporal niche that differed significantly from the *Apodemus* species (Table 1). These temporal niches were also observed in a Mediterranean population of yellow necked mice and bank voles (Viviano, Scarfo & Mori, 2022). Through analysing camera trap images, the authors proposed the minimal disturbance to the study area may encourage the species to maintain natural behaviours. They observed a 22% overlap of yellow necked mice and bank voles' temporal niches, our study showed a 45% overlap and a 46% overlap in Silwood and Wytham respectively. Our sites were much smaller (0.001 of the size of their survey site) and are active working research forests, such that human activity during the day may have some impact on animal behaviour. However, there is merit in ensuring the study area remains as undisturbed as possible, especially for diurnal species.

In comparing the KDE circular activity patterns observed in the bank vole, wood mouse, and yellow-necked mouse it was found that they were consistent across both sites (Figure 4). This suggests that these patterns are inherent to each species and are not significantly influenced by the site specific conditions. The similarities in activity patterns between the two sites may indicate that these species exhibit similar circadian rhythms or are responding to common environmental cues that regulate their activity. The proportional activities were also similar between both sites, with yellow-necked mice and wood mice has a high degree of overlap in their activity patterns, and a high proportional occurrence of all three species together. Furthermore, bank voles showed a higher tendency for exclusive activity, indicating potential differences in their habitat preferences or behaviour compared to the *Apodemus* species. Small mammals that are non-selective or more active during the day, exhibit a greater intrinsic linkage to and reliance on their abiotic surroundings, as they depend on

biomass cover as a means of protection against predators. This observation may elucidate the comparatively higher volatility in the population dynamics of voles, which our data suggested are cathemeral (active during day and night) in contrast to the predominantly crepuscular/nocturnal *Apodemus* species. The temporal niches of these species suggest a clear degree of temporal niche partitioning that would facilitate coexistence of the voles and *Apodemus* species.

Regarding the spatial relationships, our analysis revealed intriguing patterns among the species. In Wytham, bank voles and wood mice exhibited a strong negative correlation in space across a relatively small area (Table 3), indicating that their presence was effectively mutually exclusive. The negative spatial correlation between bank voles and wood mice in both study sites suggests that there may be some space resource partitioning between these species. This may also be due to differences microhabitat preferences, with voles preferring dense understories and mice preferring more open landscapes (Hansson and Henttonen, 1985). We intend to explore the spatial preferences of all three species and habitat features at a later date. This finding is consistent with previous studies that have found negative correlations between these two species (Hansson and Henttonen, 1985). Surprisingly, the activity level of wood mice and yellow necked mice showed a negative spatial correlation and was stronger in Silwood (-0.75) than in Wytham (-0.32). This is the first reporting of any form of spatial separation for the *Apodemus* species. Ruetter et al. (2003) showed that both the yellow-necked mouse and the wood mouse in the Swiss alps were more generalists in their habitat preference. However, this work represents the first fine scale quantification of a negative spatial correlation between these two species. This negative correlation may be due to competitive interactions, resource partitioning, or other ecological factors and deserves further investigation.

Interestingly, there was no discernible relationship between the space use of bank voles and yellow necked mice. This finding indicates the existence of an underlying mechanism that allows these two species to spatially coexist. One plausible explanation could be the arboreal nature of the yellow necked mouse, as their utilisation of different vertical strata within the woodland might facilitate coexistence with the ground-dwelling bank voles (Beusching et al., 2008) and also likely their very different diets, with bank voles feeding on vegetation with *Apodemus* mice are more granivorous and omnivorous (Grüm and Bujalska, 2000). Figure 7 corroborates these findings, with visual gaps between areas of high activity between wood mice and the yellow necked mice and voles. This study demonstrates intriguing patterns of spatiotemporal niche partitioning among bank voles, wood mice, and yellow necked mice, which provide a foundation for future research exploring the complex interactions and mechanisms driving niche partitioning and coexistence in small mammal communities.

Our investigation is congruent with an observed surge in the population density of yellow-necked mice in the Wytham system, attributable to their ongoing northward expansion (Marsh, 1999). This occurrence substantiates the principles of contemporary coexistence theory, emphasising the intricate dynamics between species and their capacity to acclimate and prosper within evolving habitats. Through our examination of the interrelationships between yellow-necked mice and their sympatric species, our study elucidates the ecological ramifications of this latitudinal advancement and furnishes valuable insights into the delicate equilibrium of coexistence in a swiftly transforming ecological milieu.

The modern coexistence theory (MCT) offers valuable insights when trying to understand the invasion of a new sympatric species into a landscape (Chessen, 1994). This theory examines the mechanisms and factors that contribute to species coexistence and can provide a framework for studying the dynamics of invasive species in an ecosystem (Chessen, 2000a).
MCT emphasises the importance of species traits and their influence on competitive interactions (Chessen, 2000b). Each species possesses unique characteristics, such as morphology, physiology, and behaviour, that shape their ability to utilise resources and cope with environmental conditions. When a new species invades a landscape, its traits and how they differ from the resident species can have significant implications for coexistence. For example, the invader might have a novel feeding strategy or in the case of yellow necked mice, higher rates of arboreality (Buesching et al., 2008), allowing it to exploit resources that were previously unavailable to the resident species. Understanding these trait differences is crucial for predicting the outcome of the invasion and the long-term dynamics of the invaded ecosystem, and would be an interesting path of further investigation leading on from this study.

The congruence in spatiotemporal niches observed between two distinct sites, one characterized by a longstanding coexistence of yellow-necked mice and sympatric species (Silwood), and the other reflecting a recent establishment of the species (Wytham), provides evidence of the adaptability and plasticity exhibited by the community in facilitating the coexistence of invading species. This phenomenon underscores the dynamics of species interactions and underscores the potential for coexistence even in the context of novel ecological challenges. Such findings contribute to our understanding of the ecological resilience and capacity for niche accommodation demonstrated by these small mammal species, shedding light on their ability to adapt to and integrate invasive species within established ecological frameworks.

Our results also demonstrate the effectiveness of RFID remote loggers in studying the spatiotemporal niche partitioning of small mammals. Firstly, one of the key advantages of using RFID remote loggers is the ability to compare niche axes for an entire assemblage of small mammals. By conducting

analogous and regular trapping trips, we ensured that we captured a comprehensive representation of the small mammal community across both Silwood and Wytham, allowing us to study their niche partitioning in a more comprehensive manner. The fine-scale data collected by the RFID logging systems plays a crucial role in unravelling the complexities of population and community dynamics, providing valuable insights into niche differences and other intricate questions. By capturing detailed information at a localised level, such data enables researchers to delve deeper into the factors driving ecological patterns and processes. Fine-scale information enhances the resolution and realism of ecological models, allowing for more reliable predictions about species responses, community dynamics, and ecosystem functioning. By leveraging the benefits of fine-scale data, scientists can gain deeper insights into the intricate mechanisms shaping ecological communities and improve our ability to address environmental challenges and promote sustainable management practices.

Furthermore, the continuous monitoring capability offered by RFID remote loggers has been instrumental in our research. Unlike traditional trapping methods that are limited to specific time intervals, the loggers enabled us to record small mammal activities at all times of the day across the entire study site. This comprehensive temporal coverage facilitated a thorough understanding of how the spatiotemporal niche partitioning patterns may vary throughout the day or across different seasons. By capturing data round-the-clock, we were able to identify and analyse potential variations in time and space resource utilisation during different periods, shedding light on the fine-scale temporal dynamics of small mammal niche partitioning.

Based on the findings of this study on spatiotemporal niche partitioning in wood mice, bank voles, and yellow-necked mice in Wytham Woods and Silwood Park, there are several suggestions for future research. Firstly, further investigation could explore the specific ecological mechanisms underlying the spatiotemporal niche partitioning patterns observed in this study. For instance, it would be interesting to investigate the role of resource availability, arboreality, predation pressure, and other biotic and abiotic factors in shaping the distribution and behaviour of these three small mammal species. One could also direct further work to understanding the behavioural mechanisms behind the spatiotemporal niche partitioning, investigating whther there is active avoidance by one species by another. Yellow necked mice in particular are known to use vertical space to avoid interspecific competition (Buesching et al., 2008), investigating this with the RFID logging system described here would give further information about how species coexist in a landscape. Secondly, given the potential impact of immigration on resident species behaviour and ecology observed in this study, future research could explore the spatiotemporal niche partitioning dynamics between species in areas where one or more species have recently immigrated. Such studies could shed light on how resident species respond to and adapt to new ecological conditions and how these responses affect the overall community structure and dynamics. Lastly, studies could explore the broader implications of

spatiotemporal niche partitioning patterns observed in this study for ecosystem functioning and conservation. For example, investigating the impact of changes in small mammal species composition on ecosystem processes such as seed dispersal and soil nutrient cycling could help inform conservation and management strategies.

Overall, this study provides valuable insights into the spatiotemporal niche partitioning of wood mice, bank voles, and yellow-necked mice in two fairly typical deciduous woodlands in the UK. The findings suggest there are definite spatiotemporal partitions in play promoting a level of coexistence between these three sympatric species. Future research could investigate the role microhabitat structure has in determine space use, the mechanisms underlying these patterns and explore the potential impact of immigration on the behaviour and ecology of resident species. The results from this study have important implications for the conservation and management of small mammal populations. The spatiotemporal niche partitioning of these three species suggests that they are actively avoiding direct competition for resources. This may be an important factor in maintaining biodiversity in these ecosystems, as competition for resources can lead to species displacement and ultimately reduce the diversity of the ecosystem (Soininen et al. 2007; Tilman 1982). This research also demonstrates the effectiveness of RFID remote loggers in studying the fine-scale behaviour and spatiotemporal niches of small mammals. Through the ability to compare niches, continuous monitoring, accurate individual identification, and analysis of trends across different time scales, these loggers have proven to be a powerful tool for unravelling the complex dynamics of small mammal communities and their ecological interactions in relation to resource utilisation and habitat preferences.

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6

General Discussion

How do species interact?

In this thesis, I investigated the mechanisms underlying species interactions in two distinct ecological contexts: the interactions between purinina/Tasmanian devils and Devil Facial Tumour Disease (DFTD) in Tasmania, and niche partitioning and cycles in wild small mammals in England. I had the overarching aim of exploring the diverse range of systems and methods to showcase the extensive ways in which one can address the fundamental question of how species interact. By employing two distinct systems, I aimed to capture the breadth of ecological interactions that occur across different habitats. Furthermore, I utilised a multitude of research methods, including field observations, and mathematical modelling techniques, to uncover the intricate dynamics of species interactions. Through this exploration, my thesis aimed to demonstrate the richness and complexity of the interactions between species, shedding light on the intricacies of ecological systems and offering valuable insights for conservation and ecosystem management. In chapter 2 I demonstrated the utility of integral projection models (IPMs) as valuable tools for integrating ecological and epidemiological concepts, enabling the prediction of disease dynamics and their impact on host populations. By incorporating demographic and epidemiological processes, these models provide a comprehensive understanding of the interplay between hosts and pathogens (McCallum, 2008; Metcalf et al., 2015; Epstien et al., 2016). They offer insights into how disease transmission and host population responses to pathogens are influenced by various factors, such as host demographics, pathogen virulence, and environmental conditions (Wilber et al., 2016). Host-pathogen IPMs are particularly useful for studying emerging infectious diseases and aiding in the design of effective disease management strategies (Wilber et al., 2022). The model in Chapter 2 revealed that devil population growth rates were the most important factor influencing devil survival in the face of the disease. This finding has important implications for conservation efforts aimed at protecting purinina in the wild. It suggests that efforts to increase devil growth rates, for example through the provision of supplemental food or reduction of external pressures such as road strikes, could be an effective strategy for mitigating the impact of DFTD on purinina populations.

In chapters 3 and 5 I used communities of small mammals to demonstrate coexistence axis measured at different scales and resolution (Vance, 1984). In chapter 3 I show several important findings that explain the population dynamics of wood mice and bank voles. Firstly, both bank voles and wood mice populations exhibited a noticeable trend shift, indicating significant changes in their dynamics over time. Notably, the population cycles observed in bank voles resembled those of eruptive populations, suggesting boom-and-bust cycles characterised by irregular fluctuations (Bush et al., 2012). Moreover, the transition to non-stationary population dynamics indicated that the vole population is subject to changing conditions and not in equilibrium. This has implications for the stability and resilience of the ecosystem, as well as conservation and management effort (Chock,

Shier & Grether, 2022). In contrast, the population dynamics of wood mice were found to be density-dependent, meaning their numbers were influenced by population density. However, bank voles did not exhibit significant density-dependent regulation. These contrasting responses suggest that wood mice and bank voles employ distinct strategies for population regulation, with potential implications for community dynamics and management approaches. Overall, these findings emphasize the complexity of population dynamics and highlight the importance of considering species-specific and ecological factors when studying and managing animal populations. In chapter 5 I use data from two woodland ecosystems to show that the community of sympatric small mammals partition their temporal and spatial niches to enable coexistence. These results confirm previous studies on these species (Buesching et al., 2006; Jancewicz & Gliwicz, 2017; Chibowski et al., 2022; Probst & Probst, 2023) and answers further questions surrounding their dynamics. By comparing two communities at different sites using the same methods I could conclude that the niche partitioning wasn't site species and is probably similar across their range (O'Connell & Hallett, 2019). Additionally, using remote RFID logging systems I was able to quantify the negative spatial relationship between bank voles and wood mice and wood mice and yellow necked mice. I hypothesise that the negative relationship between wood mice and yellow necked may be density driven as the avoidance patterns were stronger in Silwood which had a higher density of both *Apodemus* species. Chapter 3 revealed that wood mice are strongly density dependant, and our findings in Chapter 5 allude to a species that exhibits niche plasticity under different density conditions. Suggesting that density is a core driver of broad and fine scale dynamics in wood mice. This is similar to the findings in other similar species regarding shifts in spatial niches as density changes. A study on white footed mice (*Peromyscus leucopus*) and eastern deer mice (*Peromyscus maniculatus nubiterrae*) found that sizes of home ranges were marginally negatively associated with population density. Additionally, aggression and territorial defense were density dependent and occurred only when populations exceeded 25 to 30 mice/ha (Wolff, 2011). Understanding these density-dependent relationships in wood mice provides insights into the mechanisms that regulate population dynamics (Probst & Probst, 2023). It also has implications for conservation and management efforts aimed at maintaining healthy and sustainable populations (Chock, Shier & Grether, 2022). For example, as population density increases, competition for limited resources intensifies. The density dependant wood mice may experience reduced resource availability per individual, leading to decreased reproductive success, lower birth rates, and increased mortality (Skogland, 1985; Row et al., 2014). Additionally, higher densities result in more frequent encounters and interactions between individuals, including aggression and competition for mates (Brouard et al., 2015). These intraspecific interactions further affect reproductive success and social dynamics, shaping the demographics of the wood mouse population.

Chapter 3 and.5 also serve as a crucial exploration of the comparative value of diverse data types and study durations in elucidating various aspects of population dynamics. They detail how research

approaches can address specific inquiries concerning the interactions within species populations and highlight how the convergence of results from different methodologies can enhance our comprehension of the multifaceted levels at which these interactions occur (Southern, 1970). The comparative analysis of different data types and study durations within population dynamics research is of paramount importance. It allows researchers to effectively address diverse questions, encompassing long-term trends and short-term events, ultimately fostering a more profound comprehension of species interactions.

Studying how species interact in ecological systems requires data that capture the dynamics and patterns of their movements and interactions. Two types of data commonly used in this context are count data and more fine-scale movement network data. Each approach has its advantages and disadvantages, which can influence the conclusions drawn from the research. Count data, which record the number of interactions or occurrences of a specific event, provide a coarse-grained perspective on species interactions. One of the advantages of count data is their simplicity. They are relatively easy to collect and analyse, making them accessible for researchers with limited resources or expertise. Count data can reveal broad patterns of species interactions, such as the frequency or intensity of interactions, which can be useful for understanding the overall structure and functioning of ecological networks. As demonstrated with the use of longitudinal trapping data in this thesis, count data can help identify patterns of species turnover and assess the stability of ecological communities over time. The broad-scale patterns derived from count data can inform theoretical models and hypotheses related to species coexistence.

In contrast, more fine-scale datasets, are able to capture detailed interactions between individuals, provide a richer and more mechanistic view of species interactions. Fine-scale data allows for the analysis of individual-based processes, such as dispersal, foraging, or social interactions, enabling a deeper understanding of the underlying mechanisms driving ecological patterns. They are particularly valuable for studying animal behaviour and how it relates to ecological dynamics. By tracking individual movements and interactions, researchers can examine the role of spatial dynamics, resource partitioning, and individual behaviour in shaping species coexistence.

The integration of findings from both approaches facilitates a multi-dimensional perspective on population dynamics and coexistence. By combining the broad-scale perspectives provided by count data with fine-scale researchers can gain a deeper understanding of the complex interactions and mechanisms that drive species coexistence in ecological communities. This integrated approach enables the refinement and validation of theoretical models and contributes to our knowledge of how species interact and persist in dynamic ecosystems.

Chapter 5 demonstrated the functionality and versatility of the RFID logging system developed in Chapter 4. RFID logging, a technology based on Radio Frequency Identification, has the potential to revolutionise the study of small mammal behaviour, and has already been used to study diverse systems (Brehm et al., 2019; Betham et al., 2021; Briggs, Robstad & Rosell, 2021; Harrison & Kelly, 2022). This non-invasive and high-resolution tracking method allows researchers to monitor the movement, habitat use, and social interactions of individual animals over extended periods of time. RFID logging provides detailed insights into the behaviour and ecology of small mammals, revealing patterns of movement, home range sizes, and interaction networks (Kays et al., 2011). It has proven valuable in understanding the factors that influence disease transmission dynamics, such as contact rates among individuals and habitat preferences (Ford et al., 2017). Furthermore, RFID technology facilitates the tracking of individual animals within complex ecological networks, elucidating the role of specific individuals in disease spread and population dynamics (Wade, 2018). The RFID logging system described in Chapter 4 offers several advantages over other systems in the current literature that make it suitable for replication and versatile for studying various systems. Our system's versatility lies in its adaptability to different study designs and the ability to adjust based on the behaviour of the animals being studied. Researchers can easily modify the parameters of the system to suit the specific requirements of their study. For example, they can change the design of antenna, the entire system only weights 1.5kg so it can be installed in trees as easily as on the forest floor, and the circuit board is fully customisable. This flexibility allows researchers to customize the system to match the scale and scope of their research. The ease of adjusting the system is crucial for adapting to the behaviour of the animals being studied. Animals may exhibit unexpected patterns or behaviours that require modifications to the tracking parameters. The RFID logging system allows researchers to adapt to these changes quickly and easily, ensuring that the data collected remains accurate and relevant throughout the study duration. These qualities in addition with the simplicity of construction make it a valuable tool for researchers in a wide range of fields.

In conclusion, although this thesis may not provide a definitive answer to the multifaceted question of how species interact, it serves as a valuable compendium and handbook, highlighting the cutting-edge statistical and field methods employed in addressing this central inquiry within community ecology. By synthesising and presenting the current state of the art methods, this work represents a collective endeavour towards untangling the complexities of species interactions. It contributes significantly to the scientific community's ongoing exploration of this captivating field and provides a solid foundation for future research. Understanding the dynamics of species interactions is crucial for gaining insights into the intricate webs of life within ecosystems and ultimately advancing our knowledge and conservation efforts.

Future directions

This work presents several useful tools for researchers and conservationists to add to their arsenal of techniques to study and manage species. There are many ways in which these tools could be developed and built upon to answer a diverse range of questions, specifically the integral projection model (Chapter 2) and the RFID logging system (Chapter 4).

The IPM developed in Chapter 2 provides a powerful tool for understanding and predicting population dynamics, allowing for more informed decision-making and targeted conservation efforts (Ellner & Rees, 2006; Metcalf et al.,2012). By utilising and expanding upon the model, researchers and conservationists can gain insights into the vital rates and life history traits of the purinina population (Ellner & Rees, 2006). This information serves as a baseline model, capturing the species' reproductive output, survival rates, and other key parameters (Wallace, Leslie & Coulson, 2012; Wilber et al., 2016; van Benthem et al., 2017). Armed with this knowledge, managers can then assess how various perturbations, such as habitat loss, disease outbreaks, or climate change, might impact the purinina population (Metcalf et al., 2012). The IPM allows for the exploration of different scenarios and the simulation of potential population responses to these perturbations (Ellner & Rees, 2006). Researchers can input alternative values or scenarios into the model and evaluate the potential effects on vital rates and overall population dynamics (Coulson et al., 2017). This approach provides a quantitative framework to estimate population trajectories under different conditions, thereby enabling a more comprehensive understanding of how the purinina may respond to changes in its environment. Integrating disease dynamics of DFTD into the baseline integral projection model provided in Chapter 2 represents a crucial and promising avenue for future research (Metcalf et al., 2016; Clark et al., 2016). By incorporating the intricate complexities of DFTD transmission, disease progression, and host mortality into an integral projection model, researchers can gain valuable insights into the long-term impacts of the disease on purinina populations. Such an integrated approach would allow for the evaluation of disease-induced changes in vital rates, such as survival and reproduction, and the subsequent population-level consequences (Merow et al., 2014). Moreover, this modelling framework could facilitate the assessment of potential management interventions, such as vaccination or culling strategies, and their effectiveness in mitigating the disease's impact on purinina demography (Metcalf et al., 2016). Furthermore, the IPM can help identify critical life stages or demographic parameters that are particularly vulnerable to perturbations (Plard et al., 2015; Griffith et al., 2016; Vindenes et al., 2016). By pinpointing these vulnerable points, researchers and conservationists can focus their efforts on developing targeted interventions and conservation strategies. For example, if the model reveals that juvenile survival has a significant impact on population growth, conservationists can prioritise actions that enhance juvenile survival rates, such as reducing mortality rates or providing supplementary food sources (Plard et al., 2015). A 2018 study

used an IPM to determine the vulnerability of macroalga to climate change and warming sea levels (Capdevila et al., 2018). Their results found that warming effects during early life stages of the algae reduced their resilience to ongoing perturbations. Ultimately, by utilising the IPM researchers and conservationists can better understand the species' vulnerabilities, identify effective management strategies, and take proactive measures to safeguard the future of the purinina.

The availability of high-resolution tracking techniques, including RFID logging systems, will continue to enhance our ability to collect fine-scale data on individual movements and behaviours. A promising direction for RFID logging systems that was highlighted in this thesis is the simultaneous study of multiple species. This approach enables researchers to investigate species interactions and community dynamics, which are crucial for understanding ecosystem functioning and conservation planning. By identifying key ecological relationships, such as predator-prey dynamics or mutualistic interactions, conservation efforts can be better tailored to preserve the delicate balance of species within an ecosystem.

This work also highlights the utility of using small mammals as a focal species in studies focused on species interactions. The field of species interactions is dominated by larger iconic mammal species (Kelt et al., 2019), these species tend to attract more attention and interest due to their visibility and position as flagship species in conservation programs (Kelt et al., 2019). Small mammals however an ideal taxon for testing the efficacy of novel applications of technology due to their relative abundance, the expansive baseline knowledge of their biology, and their well-established part of a functioning ecosystem as a prey species. Small mammals exhibit a high degree of abundance and diversity in various ecosystems worldwide. They often have large population sizes, occupying diverse habitats ranging from forests to grasslands, and even urban environments. This abundance provides researchers with ample opportunities to observe and study their interactions with other species. Additionally, small mammals have been extensively studied by scientists over many years. They have served as model organisms in numerous ecological studies, resulting in a wealth of available data on their biology, behaviour, and population dynamics. This existing knowledge base provides a solid foundation for designing and interpreting experiments focused on species interactions. Researchers can build upon this foundation to investigate how small mammals respond to and influence other species within their ecological communities. Moreover, small mammals play critical roles in ecosystem functioning. They are often important prey species for a wide range of predators, as such, changes in the abundance or behaviour of small mammal populations can have cascading effects throughout the food web. In conclusion, although small mammals may often be overlooked in terms of studying complex species interactions they are an ideal focal taxon and within this thesis have provided an exemplary case of how well suited they are for studying complex questions surrounding species interactions and coexistence mechanisms.

Conclusions

Overall, the findings of this study underscore the importance of understanding the mechanisms underlying species interactions in different ecological contexts. By identifying the key drivers of species interactions, and the ecological and evolutionary processes that shape them, we can gain new insights into the dynamics of ecological communities and develop more effective strategies for conservation and management. Taken together, the findings of this study provide new insights into the mechanisms underlying species interactions, and their implications for ecology and conservation. By integrating empirical and theoretical approaches, and studying species interactions in different ecological contexts, we can gain a more comprehensive understanding of the dynamics of ecological communities and develop more effective strategies for preserving biodiversity and ecosystem function.

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