DAVIS EXPEDITION FUND

REPORT ON EXPEDITION / PROJECT

Expedition/Project Title:	Shared spaces - shared parasites? How space-use contact-structure, and behaviour affects within and between species parasite transmission in a wild small mammal community
Travel Dates:	July – October 2020
Location:	Edinburgh, Scotland
Group Members:	Agata Delnicka, Sam Hillman, Lucy Barnard, Katie McCabe
Aims:	Establishing how shared space-use, contact structure and behaviour of bank voles, *Myodes glareolus*, and wood mice, *Apodemus sylvaticus*, affect parasite burden, infection status and disease transmission of a range of parasites. (see detailed aims in 'Aims' section)

Photography consent form attached: (*please refer to your award letter)*

☐ Yes
☒ No

Outcome (a minimum of 500 words):-

Shared spaces - shared parasites? How space-use contact-structure, and behaviour affects within- and between-species parasite transmission in a wild small mammal community

Davis Expedition Fund Report 2021

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Introduction

Host-parasite systems are inherently structured in space. As we are only too aware from the COVID-19 pandemic, an individual's infection risk depends on how close and for how long they spend near infected individuals, which is defined as a contact. These contacts can drive localised transmission events that then scale up to drive parasite dynamics at the host population level, influencing how fast a parasite spreads and the spatial distribution of infection 'hotspots' (Bansal et al., 2010; Sah et al., 2018). To manage the spread of infectious diseases we therefore need to understand how individual infectivity, susceptibility, and movement interact to drive parasite spatiotemporal dynamics at the host population level.

Recent advancements in individual wildlife monitoring tools have greatly enhanced our ability to follow individuals, measure possible contacts, and build networks of contacts that can begin to determine how animals interact (Boyland et al., 2013; Craft, 2015; White et al., 2017). However, our ability to define and accurately measure contacts between individuals, based on how close and for how long they interact, has until recently been limited to studies of large mammals due to the size and cost of the technology. These focused studies typically measure contacts between individuals that could result in successful transmission and then they build networks to investigate their implications for transmission of a single, target parasite species within one possible host species. This approach has been incredibly useful for determining how fast pathogens spread in a population, and what type of contacts result in transmission (Bansal et al., 2010, 2007; Ferrari et al., 2011).

However, while this approach has become the norm due to the practical limitations of available technology and field methods, there are two potential problems. Firstly, most wild animals and humans can be infected by multiple parasite species which include a wide range of species, from macro-parasites (ie. helminths, ectoparasites) to micro-parasites (i.e. viruses, protozoans, bacteria, etc), and with very diverse transmission modes (ie. vector-borne, environmental, direct, sexual, etc) (Griffiths et al., 2011). Importantly, coinfection, or simultaneous infection with more than one parasite species, is common in wildlife and can alter host susceptibility and transmission at both the individual-level and the population-level (Knowles et al., 2013). Examples can be seen in many systems, such as in wild buffalo where coinfection with bovine tuberculosis and brucellosis (two bacterial pathogens) reduces the transmission potential of bovine tuberculosis but has no effect on brucellosis transmission (Gorsich et al., 2018) . This diverse parasite community will include directly-transmitted viruses spread only through close physical contact to environmentally-transmitted helminths that can remain viable in the soil for weeks, where contacts may be best measured based on shared space use between hosts (**Table 1**).

Secondly, most real-world communities include both multiple host and multiple parasite species. Given that many parasites can infect more than one host species, there is potential for both within and between species transmission when multiple host species share the same environment (Woolhouse et al., 2001). The degree to which these parasites are transmitted between host species can vary: from true multi-host parasites that frequently transmit between species, such as the causative agent of Lyme disease, *Borrelia* bacteria, being transmitted via ticks between deer,

rodents, humans and other species (Franke et al., 2013; Hofmeester et al., 2016)**;** to more rare cross-species transmission events called ‘spillovers’, like the Ebola virus spillover suggested to be from bats to humans leading to outbreaks in human populations (Rewar and Mirdha, 2014). Importantly, the multi-host nature of many parasites and diseases complicates disease control efforts since there are many possible disease reservoirs present which often need to be treated at the same time for successful eradication (Viana et al., 2014).

In order to understand the spread of parasites in natural systems we need to embrace the complexity, and study multi-parasite, multi-host systems. Crucially, measuring transmission in natural populations can be very difficult (Cable et al., 2017), but by integrating knowledge of the host’s social behaviours, in particular contacts and space-use, we can begin to understand and predict how different parasites with different biologies and transmission modes may be driven by within- and between-host transmission.

In addition, both abiotic factors and landscape structure can shape where parasites and pathogens infect hosts in space, and how animals move within that space will determine which parasites they are exposed to. Microclimatic variables (such as temperature and humidity, which act on small spatial scales) or the availability of a suitable habitat can determine parasite infection risk/abundance, especially for parasites with environmentally-transmitted propagules (eg. helminths) or those relying on intermediate-hosts with narrow habitat ranges (eg. liver flukes are more abundant in wet fields due to snails’ habitat range) (Mas-Coma et al. 2008; Albery et al. 2019). As such, we might expect that individuals which overlap in their space-use might also be more likely to be infected with the same parasite communities or have similar parasite burdens; these patterns may be strongest for environmentally or vector-borne parasites, specifically those with limited off-host movement like ticks or fleas. Spatial autocorrelation in disease prevalence/burdens is pervasive among wild populations due to these types of factors, yet is often understudied (Albery et al. 2021).

Exposure to parasites and pathogens is mediated, in part, by the space that the hosts move in as well as who they contact and potentially contract infection from. Therefore, an individual’s behaviour and personality can be a driver of how infection spreads within a population and can lead to the heterogeneities we observe in infection status and burdens of hosts. For example, ‘bolder’ deer mice, *Peromyscus maniculatus*, (defined by higher travel distances, time spent in exposed areas, and more likely to engage in aggressive behaviours) were three times more likely to be infected with Sin Nombre virus (SNV) than shyer individuals (Dizney and Dearing 2013). In golden-mantled ground squirrels, *Callospermophilus lateralis*, personality of individuals was found to be correlated with space-use as well as sociability - where bolder individuals had larger core areas, more access to preferred resources, and were also more sociable (Aliperti et al. 2021). Clearly, the link between the social and spatial contexts is common, and incorporating both into the disease analyses can help us gain more insight into disease dynamics (Emch et al. 2012).

Table 1: *Parasites commonly found in wood mice (Apodemus sylvaticus) and blank voles (Myodes glareolus) and their respective type and transmission mode (Behnke et al., 2001; Callejón et al., 2010; Clerc et al., 2018; Feore et al., 1997; Lewis and Ball, 1982; Loxton et al., 2016; Noyes et al., 2002; Withenshaw et al., 2016)*

Parasite	**Type**	**Transmission mode**	**Host (wood mice/ bank voles/ both)**
Heligmosomoides polygyrus	Nematode	Environmental	Wood mice
Heligmosomoides glareoli	Nematode	Environmental	Bank voles
Trichuris muris	Nematode	Environmental	Both
Eimeria hyngaryensis	Protozoan	Environmental	Wood mice
Eimeria cernae	Protozoan	Environmental	Bank voles
Cowpox virus	Virus	Direct Contact	Both
Bartonella species	Bacteria	Vector-borne	Both
Trypanosoma grossi	Protozoan	Vector-borne	Wood mice
Trypanosoma evotomys	Protozoan	Vector-borne	Bank voles

In addition to being able to determine how shared space use and contacts impact parasite transmission in a multi-host community, it is important to ask what definition of a ‘contact’ (eg. direct, non-direct, brief encounter, longer lasting interaction) most accurately predicts localised transmission events. And does this definition of a contact differ by parasite transmission mode or based on the methods and technology used for assessing animal movement? To address these questions we must be able to gather high-quality and precise data on animal movement and contacts across a community and cross-reference this data with longitudinal host parasite intensity and prevalence data. We can then use this to build contact networks of host contacts to examine if shared space-use (**Fig. 1A**) over time or direct contact (**Fig. 1B**) can determine localised transmission events and population-level spread.

We addressed these questions using two complementary technologies and common behavioural assays.

First, we used a set of stationary loggers that record the presence of an individual based on its RFID tag. Secondly, we also trialed using a newly developed Bluetooth-based technology to measure individual movement patterns and between-hosts contacts of two wild small mammals - wild wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*). This technology has been successfully deployed on starlings and small mammals in Africa (Kirkpatrick et al., 2021) yet due to problems with this technology in our system we were unable to use this for this experiment like we proposed (see methods section). Lastly, we also used two behavioural assays: i) an open-field test, to quantify behaviours as proxies of individuals' personalities such as boldness, and exploration of novel environments; and ii) a choice assay, in order to see if individuals show odour preference for same or other species' odours, and if this is associated with the species/strains of pathogens which are shared between host species.

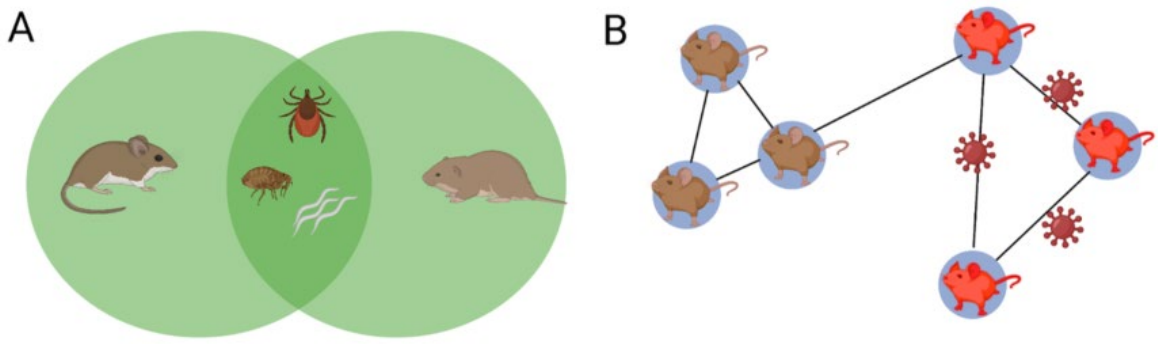

Figure 1 ***(A)****Does overlap in home range between different animals (either of the same species, or different) result in sharing of parasites? We predict that if this is true then it is more likely to be the case for vector-borne or environmentally-transmitted parasites - here represented by the tick, flea, and helminth worms in the shaded overlap of home ranges.* ***(B)*** *Contact networks are commonly used to study parasite transmission of parasites where the nodes (circles) representing individual hosts are connected to each other via edges (lines). We want to know how well the structure of the contact network and which definitions of a contact best predict the spread of parasites between infected individuals (red mice) and non-infected individuals (brown mice). We predict that this effect will be stronger for parasites which are transmitted by direct contact (eg. viruses)*

Wood mice and bank voles are common, indigenous rodents that are highly prevalent throughout the UK and are known to occupy similar woodland habitats. Both are known to be infected by multiple parasite species, with multiple transmission modes (environmentally transmitted, vector-borne, direct contact; **Table 1**). Using this study system we set out to answer the following questions:

Aims

1. Do wood mice and bank voles show overlap in space-use with individuals of the same or different species in the woodland community, and is this shared space dependant on host sex and/or species?
2. Does space-use overlap and contact networks predict parasite infection and burdens of wild wood mice and bank voles? Do these patterns vary by parasite type (eg. ectoparasites like ticks and fleas, endoparasites like helminths or viruses)?
3. How do results of common behavioural assays (eg. open-field tests) compare to estimates of home-range sizes and space-use overlap, generated from a) trapping data and b) stationary loggers?
4. Are we able to use choice assays to determine what host species/individuals are more repelled/attracted to odours of different host-species, thereby preventing/allowing interspecies parasite transmission?

Methods

Small mammal trapping, identification, and data collection

We used an established local woodland field site (Penicuik, **Fig 2**) to live-trap wild wood mice and bank voles from July to September 2021. Our trapping grid consisted of a 9x9 array with 10m spacing between traps, to give 81 total trapping points each of which had two Sherman small mammal traps (B. Sherman Traps, Inc, Florida) to give a total of 162 traps across the grid (**Fig 3**). We trapped on three nights (Monday to Thursday) every other week throughout the field season to allow time for preparation for future trapping and for lab work and data analysis in the non-trapping weeks. During the trapping weeks, traps were baited with bird seed, carrot, and cotton bedding, and were opened after late afternoon and checked early morning the following day for captures. At first capture each wood mouse and bank vole was tagged with a Passive Integrated Transponder (PIT/RFID) tag (Avid Identification Systems, California, USA) with a Unique Identifier number to allow for future identification when recaptured and longitudinal tracking of individual animals throughout the field season. At each capture we collected detailed information about each animal, including age, mass, sex, age, body length, and reproductive status. Each animal was checked for ectoparasites, with the number of ticks, fleas, and mites recorded, and at the first capture of each week a blood sample was taken for immunological assays and identification of blood-borne parasites. Animals under 14g were released without being tagged, but mass, sex, and body length were recorded. Faecal samples of PIT-tagged animals were collected from the traps at each trapping opportunity and were stored in 10% formalin to be used to assess GI (gastrointestinal) parasite burden using a salt-solution flotation technique. Blood samples were separated into serum and blood pellet, with serum stored at -80°C and blood pellet stored at -20°C. We will extract DNA from the ear tissue and blood samples to be later used to test for vector- borne parasites, such as *Bartonella* spp., *Borrelia burgdorferi*, *Anaplasma phagocytophilum, Babesia microti* .

Space-use tracking and proximity-logging

Across our grid we aimed to measure space-use and contact using two proximity-logging technologies:(i) static PIT-tag host-proximity loggers ('Stations'); and (ii) mobile Bluetooth host-proximity loggers ('Proxlog').

Both of these loggers record when a tagged animal comes into contact with a logger, but the Stations are in permanent locations across the grid (**Fig 3**) while the Proxlogs will be attached to individual mice and voles. These Proxlogs would have allowed us to record interactions across the whole grid, giving a level of detail about both intraspecific and interspecific species interactions rarely seen before. These Proxlogs would have allowed us to measure, for the first time, both (i) the duration and frequency of intraspecific contacts and (ii) the spatial location and movement patterns for each animal.

However, after COVID-related shortages and delays in obtaining the Proxlogs as well as after trailing them in controlled settings, we **concluded that these were unsuitable to use on animals and we were not able to include them in our experiment, and recorded the space-use and contacts using Stations only.**

To compensate for this, we designed and used two different behavioural tests (below) to give us a level of detail on individual behavioural traits and how these are associated with parasite infection status and parasite burdens.

Additionally, with the permission of the land owners, we decided to leave the station loggers in their positions on the trapping grid to keep logging space-use and contacts of tagged individual animals beyond our last trapping date. This was done to increase the sample size of the dataset, follow the animals for a longer time period, and capture any seasonal changes in space-use of the animals. As such, **we are still waiting to collect this data fully and to start any analysis involving the data from these loggers.**

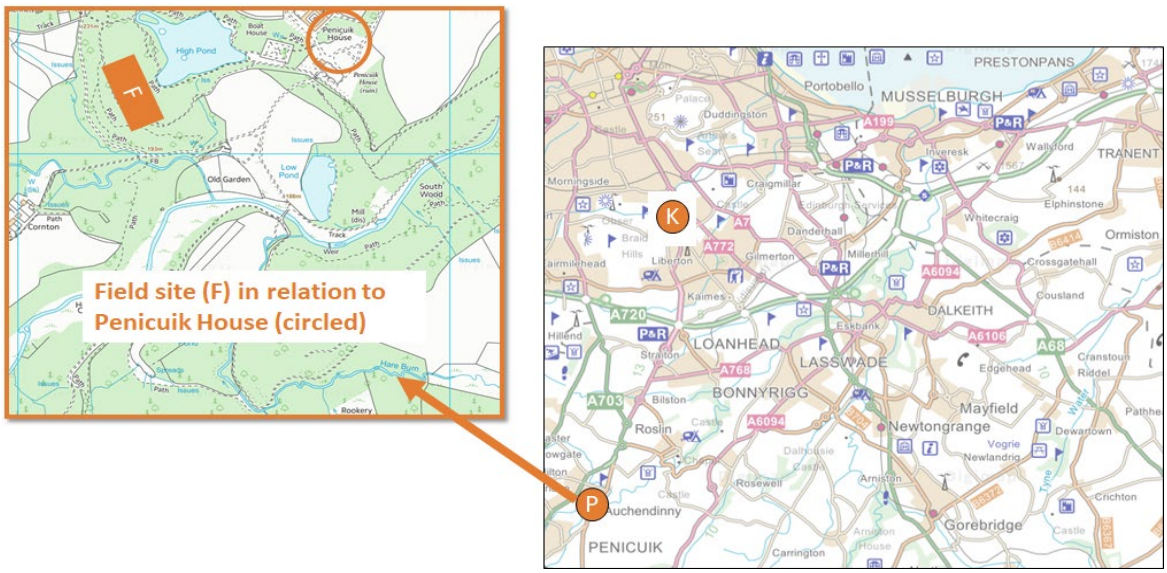

Figure 2. *A map of our field site at Penicuik (**P**), Scotland (55°49'N 3°15'W) in relation to Edinburgh and King's Buildings Campus (**K**), Edinburgh. We have*

previously worked at this field site and have full permission from the landowner and manager.

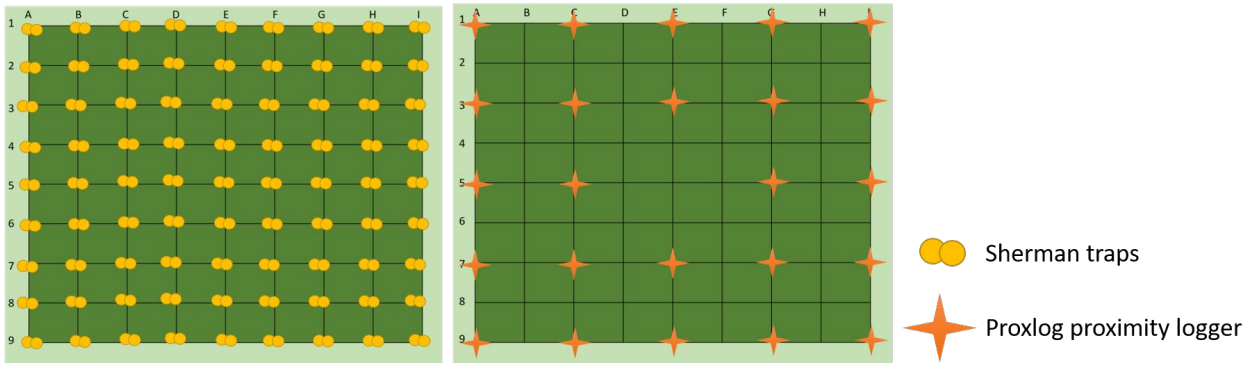

Figure 3. *Layout of the 9x9 trapping grid and Proxlog proximity logger layout to be used. Points are labeled from 1 to 9 on the Y-axis and A to I on the X-axis to allow for unique identification of all trapping points for data analysis. Proximity loggers and Sherman traps will both be on the same trapping grid but are shown here separately for ease of display.*

Behavioural tests - open-field and choice experiments

Tagged wood mice and bank voles were subjected to two behavioural assays, 1) an open field test and/or 2) a choice test to assess their exploratory behaviour and preferences. A single test (open field or choice) was carried out on the second within-week capture of each animal, after they were taken out of the trap but before any processing/samples have been taken to reduce stress to the animals within the behavioural test. The test was repeated on the same animal upon recapture, but a maximum of two tests were done on the same animal within a week (one of each kind), with only one behavioural test conducted on an animal in a single day.

Briefly, in the open field test **(Fig 4)** an animal was put into one of the corners of the open-field arena and the animal was allowed to explore the arena for 5 minutes while being video recorded. Next, we collected the following data: (i) time taken to first move, (ii) time spent moving, (iii) how many lines the animal has crossed (grid drawn on the bottom of the arena), and (iv) what behaviours the animal displays recorded as proxies for exploration of novel environment, boldness, and behavioural differences. After the 5 minutes test, the animal was taken out of the box by being transferred into a handling bag, metadata was collected, and the animal was released at the site of capture.

In the choice experiment, the animals were allowed to explore a Y-shaped maze **(Fig 4)** where at the end of each of the 3 arms there was either (i) used bank vole bedding, (ii) used wood mouse bedding or (iii) sterile bedding - in order to see if animals show odour preference. The bank vole and wood mouse bedding was obtained from the live-trapped caught bank voles/wood mice the day before and was placed at the end of each arm of the Y-maze behind a wall with holes in it so that the animal cannot directly contact it, but can smell it. At the start of the test, an animal was placed in the middle area of the Y maze and was allowed to explore the arms of the box for 5 minutes while being video recorded; the following data was collected during this time: (i) time spent in each preference zone, (ii) number of times entered into the preference zones, and (iii) how many times the animal has directly touched

the barrier at the end of the 3 arms of the box was recorded. After the 5 minutes test the animal was taken out and transferred into a handling bag, metadata was collected and then the animal was released at the site of capture. All tests were recorded so that the behaviour of animals was not influenced by the presence of observers and the tests were carried out underneath a tarp for cover to reduce effects of light, overhead-movement, fear of predation for the animals.

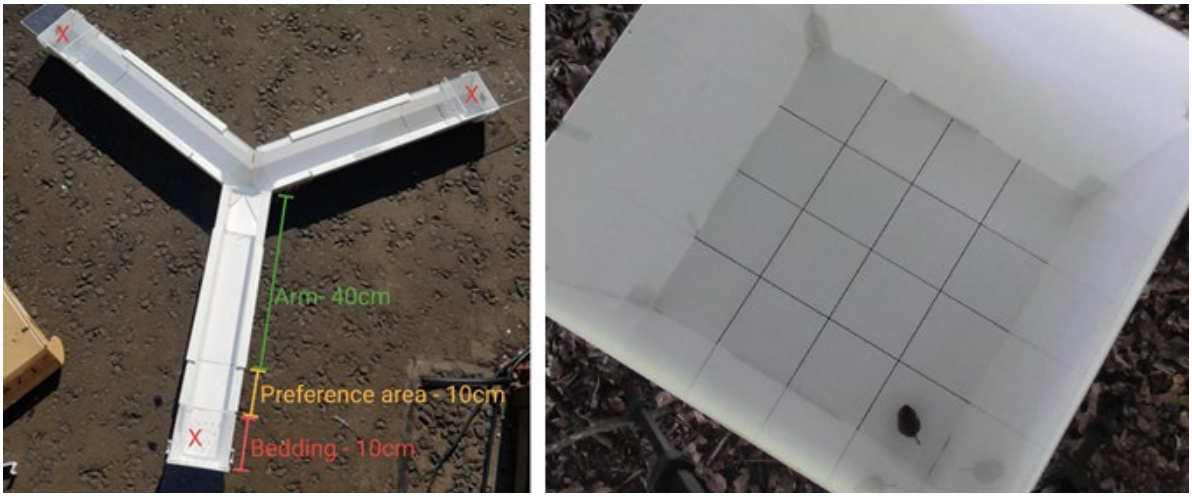

Figure 4 *- The choice Y-maze design (left) and open- field (right) during one of the behavioural assays, with a bank vole in the lowest corner of the open-field arena.*

Future Data Analysis

Space-use, contacts and disease transmission

As explained above, we are yet to obtain the data coming from the stationary loggers compiling contacts and space-use data, hence here we present the future data analysis we will carry out.

From the field data and the proximity-logging data we will compute home range sizes and home range overlaps for each tagged animal, and statistically test using GLMMs if there is an effect of species, sex, or other demographic variable on home range size or overlap. Home range overlap here is defined as the proportion of the home range of an animal that is covered by another animal, and we will be able to examine both inter- and intraspecific interactions with this data. Home range size and overlap will be computed using kernel utilisation distribution methods in R, using the package *adehabitathr* (Calenge, 2019; c.f. Worton, 1989)**.**

We will then model both inter- and intra-specific interactions using network modelling techniques. The data collected will allow for network models of interactions between animals, which can be further subset to look at interactions between different sexes and between different animal species. This will allow us to examine for the first time in our system how two small mammal species interact across shared space. Network modelling will be computed again using R.

Once these models are set up we will model parasite transmission within our populations and test how intra- and inter-species contacts and space-use overlap

predict parasite burden and infection status for our focal parasite species (**Table 1**), and if there is an effect of species, sex, or other demographic variable on burden and infection status. This will be done by extracting different network/node attributes from the networks described above and we will test whether these attributes predict the burdens/infection status of different parasites using generalised linear mixed models (GLMMs) in R.

Video analysis

The collected videos will be watched by a single/two observers to reduce observer bias as much as possible. This data will be used in GLMMs combined with the morphometric data of the individual animal (collected from the trapping data) and the parasite burdens of said individual (from processed tissue/blood samples/trapping data) to test for associations between these measures.

With the data from the choice experiment specifically, we will be able to relate the infection status of the multi-host vector-borne pathogens, such as the different species and variants of *Bartonella* (Withenshaw et al. 2016), to how 'discriminatory' the animal appears to be in choosing the bedding coming from the same or other species of small mammal (ie. whether animals which more often choose the bedding of the different species are more likely to be infected with a 'shared' variant of *Bartonella*).

Preliminary results

Trapping summary

Over the course of the 13 week experiment (5 July - 1 October 2021) we had 8 trapping weeks. We had 147 captures of wood mice and bank voles and this included 46 unique, tagged individuals (ie. those which were over 14g). We captured more bank voles than wood mice over the course of the experiment, who constituted 79% of all captures and 67% of the tagged animals (**Table 2; Fig 5**), and we did not capture any wood mice juveniles (**Table 3**).

We collected 69 ectoparasite samples (65 tick samples; 4 flea samples), where each sample contains a pool of all ectoparasites from an individual animal on a given trapping day. We also collected 166 faecal samples, which will be used for faecal egg counts (FEC) to diagnose and quantify infecting gastrointestinal parasites, and 81 blood and 41 tissue samples, which will be used for diagnosing infecting vector-borne parasites.

Table 2: *Summary of trapping results, grouped by the species trapped and processed (BV= bank voles; WM= wood mouse), the samples taken, and summary of ectoparasite counts and prevalence.*

Species	Sex	No. captured	No. of unique individuals	No. blood samples collected	Mean tick burden	Tick prevalence	Flea prevalence
BV	F	79	20	35	0.95	0.30	0.16
BV	M	38	11	18	1.29	0.45	0.21
WM	F	10	4	5	1.50	0.50	0.00
WM	M	20	11	13	1.05	0.55	0.10

Table 3 : *Numbers of bank voles and wood mice trapped of different age classes (J= juvenile; SA= sub-adult; A= adult). The age of the animal was based on the size, weight and pelage colour of the animal.*

Species	Age	No. of captures
BV	A	94
BV	J	10
BV	SA	29
WM	A	23
WM	SA	7

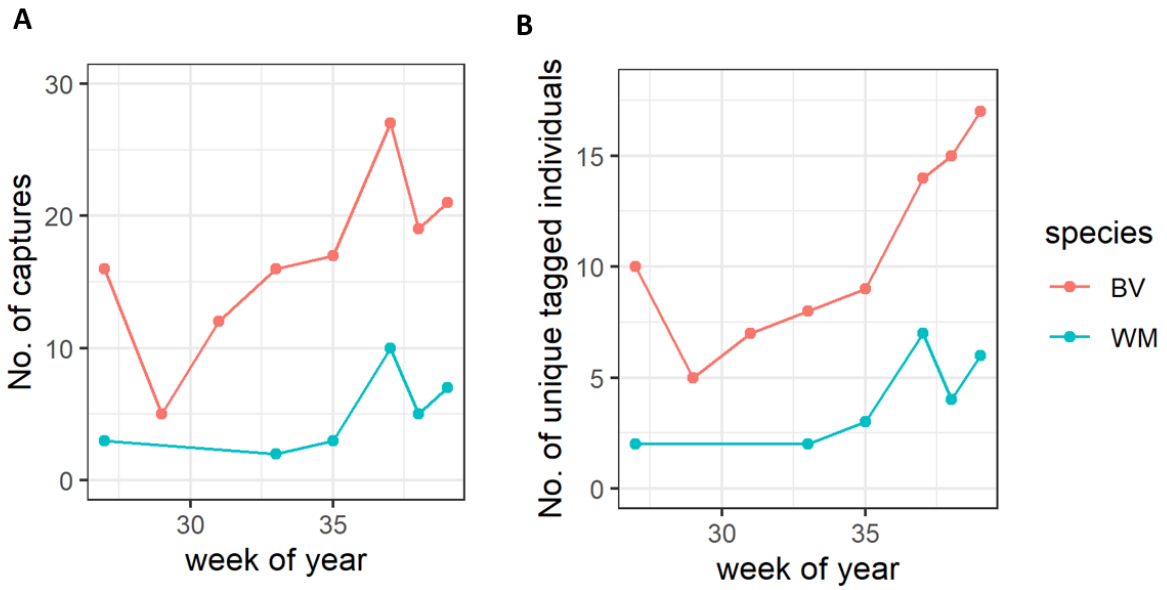

Figure 5: *Numbers of A) total animals trapped and B) unique individuals trapped per trapping week, shown over the course of the 13 week experiment, starting in July (27th week of year) and ending in October (39th week of year). Red points represent bank voles (BV) and blue points represent wood mice (WM).*

Participant involvement and additional project outcomes

Agata Delnicka and Sam Hillman - *PhD students*
Agata and Sam both contributed to the organisation of the fieldwork, and were responsible for the running of this including communicating with the landowners, supervising field assistants, obtaining all required permissions and were responsible for the wellbeing and use of animals in his experiment. They are responsible for the processing and testing of samples, as outlined above, and will be the key members analysing the obtained data.

The data obtained from this field season will be a part of a larger project with plans to repeat it in 2022, giving us a larger, more robust sample size- this will inform Agata's and Sam's PhD work and we expect to publish these results as research papers. Effort will be made to make all of our data open-source.

Katie McCabe, Lucy Barnard - *Field Assistants*
Katie and Lucy were enthusiastically involved in all parts of the fieldwork carried out, and this work could not have happened without their hard work and the funds provided by the Davis Expedition Fund which allowed them to gain invaluable research experience.

They gained experience in data recording, setting up trapping sites, working with animals, carrying out behavioural assays as well as laboratory techniques and processing the collected samples.

Additionally, both Katie and Lucy got a chance to explore the parts of research that they found most interesting. Katie was heavily involved in carrying out the behavioural assays, watching the videos and recording behaviours shown, as well in suggesting ways to improve this aspect of the experiment. Lucy got a chance to

further explore and develop her data analysis skills by analysing a dataset from a previous experiment with similar types of data using the same type of stationary loggers as were used in this experiment; she focused on assessing the activity patterns of wood mice over time (daily patterns) in relation to the experimental treatment on the trapping grids, using logger data.

Acknowledgments

We would like to thank the Davis Expedition Fund for providing the funding necessary for allowing two great field assistants- Katie McCabe, Lucy Barnard- to work on this project and help us achieve a successful field seasons. Thanks should also go to Jess Hall, Ivan Bialy, Josh Rey, Rowan Bancroft and other volunteers who helped with the fieldwork and organisation of this project. Finally, we would like to thank Amy B Pedersen for her advice and supervision at all points of the planning, organisation, and running of this experiment.

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