
The drivers of survival and spatiotemporal activity of a woodland rodent

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1 Declaration

Due to multiple occasions of Covid-19 outbreaks in the cities of where me and my supervisor Dr Aurelio Malo currently reside in, Hong Kong and Madrid, it was extremely difficult to organise a time when we could both travel to the UK for field work. Consequently, we organised a 3 week trip to Alcalá University in Madrid, where I was able to receive the full training for trapping and RFID-tagging rodents in the Valdenazar forest, Guadalajara. This allowed me to appreciate and understand the research methodology conducted at Silwood Park campus as it follows the exact same methodological process in Madrid. To perform survival and activity analysis, I was provided with the study site shapefiles, trapping and data logger data from 2010 to 2013. During our meetings, Dr Malo provided many important insights on the potential approaches to data analysis and the interpretation of predation risk effects on individual activity. He supported the idea of incorporating generalized linear mixed effect (GLMM) models and also suggested to exploit program MARK through RMark for predicting individual survival estimates. As both GLMM models and program MARK require a specific data structure, I was responsible for the processing and cleaning of raw data, making use of the shapefiles with GIS, in addition to fitting the processed data to the correct models and model analysis.

Word count: 5491

2 Abstract

Animal activity patterns are critical to understanding species adaptation to environmental fluctuations. Variation in individual activities through space and time can influence survival probability, which is a crucial component in population biology. Most published studies have so far focused on the relationship between activity data and environmental variation or an animal's behavioural state. In this study, we investigate individual activity patterns of a wild wood mouse population in Nash's Copse at a fine spatio-temporal resolution, relating survival probabilities to individual activity and further deduce the drivers of survival and activity. We focus on wood mice behaviour and predict that mice will reduce predation risk under three environmental conditions, *Rhododendron ponticum*, fallen logs and moonlight intensity, all of which have been suggested to impact predatory success. The daily activity rate for each individual was based on four indicators, consisting of the total number of encounters, different number of locations visited, total distance travelled and activity time. A mean activity rate was also estimated for each captured individual based on their calculated daily active time and distance travelled. We found that the interaction between predation risk and activity rate were important in predicting the daily survival estimates of wood mice. Additionally, activity rate was observed to increase with rhododendron covers and logs, indicating that activity rate is related to predation risk since individuals frequently displayed high activity rates under rhododendron. Surprisingly, the effects of rhododendron with activity rate had a diminutive effect on survival, this is likely the consequence of a high competition intensity individuals suffer from. Furthermore, during clear nights, wood mice activity was found to significantly decrease, but when individuals were under rhododendron patches, their activity increased substantially. However, when predation risk was not considered, two of the individual activity indicators were observed to have decreased in association with rhododendron and fallen logs, this is probably due to the spatial partitioning of wood mice to avoid competition and an increase in foraging efficiency. Finally, these results offer explanations behind the drivers of survival and activity patterns under a complex environmental interaction, which has an applied value in assessing whether habitat changes can impact wood mouse abundance and distribution within woodlands, their predation populations and the rate of woodlands regeneration.

3 Introduction

Animal activity patterns reflect a major aspect of their behaviour and ecology (Frey et al. 2017). Various patterns can be observed throughout a wide range of taxa as a result from adaptations to environmental fluctuations (Steele et al. 2006; Allen & Singh 2016). They can not only discern potential effects from the interactions between environmental variables, but also provide important information on the species natural history, ecological niche and conservation management actions (Avgar et al. 2013; Miller et al. 2019; Tang et al. 2019). Besides, studying these activity patterns is integral to understanding population dynamics as they significantly affect survival rate, which is a crucial component in population biology (Tamarin & Malecha 1971; Morales et al. 2010). Throughout an individual's lifetime, it will have disparate spatial and temporal movement behaviours depending on the resource availability, intensity of competition and predation risks. These between individual variation will influence population dynamics and affect fitness components. Recognizing these patterns will help explain and predict survival rates for conspecifics living under different environmental conditions. Consequently, this makes studying the activity patterns and survival rates between individuals extremely important (Colchero et al. 2019; Moiron et al. 2020; White & Wagner 2021).

To date, the activity of large carnivores and their prey have primarily been the focus of most studies, whilst the small mammal communities remain substantially unexplored (Viviano et al. 2021). Considering that only a few published studies consist of a design system with individual spatiotemporal activity of a high resolution in conjunction with multiple environmental factors (Godsall et al. 2014), and with most of these studies having almost identical objectives, which is to solely relate activity patterns to environmental variations and the animal's behavioural states (DeMars et al. 2013). We still have an insufficient amount of information on the complex interactive environmental effects on species activity and survival (Weber & Hoekstra 2009; Godsall et al. 2014). In this study, we analyse location data of a wild wood mouse population, *Apodemus sylvaticus*, to relate survival probabilities to individual activity, and further infer the drivers of survival and activity patterns at both the spatial and temporal scales.

Given that rodents constitute around half of the mammalian species and have adapted to a wide range of environments, it is no surprise that they are of great interest to countless research topics and are one of the first organisms to be focused upon in multi-year studies (Auffray, Renaud & Claude 2009; Hayes et al. 2017). Rodents are commonly known to have negative impacts on human societies as they are agricultural pests and transmitters of pathogens for both humans and other domestic species. Similarly, they play important roles in the regulation of other ecosystem processes. Through the combined effects of granivory, herbivory, dispersing and caching seeds, the spatial distribution and the regeneration rate of woodlands can be affected heavily upon (Ostfeld, Manson & Canham 1997; Malo et al. 2013; López-Sánchez et al. 2019). Rodents are also a stable food source for many terrestrial and aerial predators, enabling the transfer of energy from primary producers to higher food trophic levels. It has been ascertained in several population ecology studies that a drop in rodent abundance can bring about a cascade effect, causing predators to display dietary switches onto more vulnerable prey and having adverse effects on the ecosystem (Coulson & Malo 2008; Schmidt, Rush & Ostfeld 2008; Malo et al. 2013). Moreover, these small mammals are recognized as income breeders, with typical life history traits of short life spans, large litter sizes and reaching maturation early (Diaz & Alonso 2003). These traits make them an especially suitable model organism to explore questions on the drivers of survival in the wild, as their short life spans allow for the tracing of complete life trajectories in a year. Likewise, their

high densities within a relatively small area permits sufficient data collection to derive robust survival estimates and driver effects (Wolton 1985; Malo et al. 2013; Godsall et al. 2014).

Traditionally, data from wood mouse populations and survival studies have been collected using live-trapping techniques (Tanton 1965; Romairone et al. 2018; Navarro-Castilla & Barja 2019). However, many challenges emerge when we depend entirely on trapping data to answer ecological questions. Since small mammals such as rodents have a particularly high risk of mortality in traps, this could affect data analyses and create a bias in results. Trap saturation could also pose a problem as population density could be severely underestimated when an inadequate number of traps are placed (Romairone et al. 2018). Furthermore, the capture probabilities of wood mice vary with season, habitat types and behaviours, often causing data to under-represent trap-shy individuals (Tanton 1965; Malo et al. 2013). Lastly, it has been frequently observed that there is a considerable lack of recaptures in wood mouse studies, which may again cause inaccurate population estimates and result in some of these single data points to be treated as outliers (Tanton 1965). To lessen these potential problems trapping creates, we use a novel system of mobile transponder readers (hereafter data loggers) at a study site with detailed measurements of microhabitat features. Unlike trapping, a single data logger can detect multiple individuals without inducing additional stress on the animals (Godsall et al. 2014; Bolaños, LeDue & Murphy 2017). Thus, the collected data logger data would consist of a better representation of the population. The presence of individuals with RFID passive integrated transponder (PIT) tags will be recorded at a fine spatio-temporal scale and their movement patterns analysed along with individual-level attributes and environmental variables.

Much of a rodent's behaviour is heavily shaped by predator avoidance and ecological niche partitioning between conspecifics and species with similar niches (Bouskila 1995; Schirmer et al. 2020). Here, we focus on individual variation of wood mouse activity in minimising predation risks. Habitat features, in particular, *Rhododendron ponticum* (hereafter rhododendron), are viewed as a high quality territory. The thick shrub covers are able to function as a refuge from one of their primary predators, tawny owls, thus positively affecting rodent abundance. Rhododendron covers have also been discovered to house a higher density of individuals compared to open woodlands and during breeding seasons, larger mice evict smaller individuals for these safety areas (Malo et al. 2013; Godsall et al. 2014). Having said that, as fewer ground flora exist in rhododendron patches (Brouard et al. 2020), wood mice often forage in open woodlands, relying on their natural speed and agility to evade predators (Plesner Jensen & Honess 1995). Recently, it has been suggested that in the absence of rhododendron, wood mice tend to utilise fallen logs as a protective structure and an escape path with sound absorption surfaces (Malo et al. 2013; Li et al. 2020). While these rodents exhibit predator avoidance behaviours and are active during times when predators are less active (Jacob & Brown 2000), their temporal activity patterns are also affected by abiotic factors. Previous studies have displayed moonlight illumination to alter rodent foraging activities as brighter nights escalate predatory success (Plesner Jensen & Honess 1995; Pratas-Santiago et al. 2016).

To investigate the spatial and temporal variations in wood mouse behaviour under the interactions of environmental factors, we estimated individual activity to quantify the rate of different habitat usage which allowed us to relate survival to activity rate. Firstly, regarding the effects of protective features such as rhododendron and moonlight intensity on aerial predation, we predicted that those individuals that spent significantly more time under rhododendron or have reduced their time spent on clear nights would present higher survival probability. Secondly, knowing that predation risk can modify rodent behaviours and potentially influence survival (Farnworth et al. 2019), we predicted a positive association between activity rate and survival probability. Thirdly, we predicted wood mice to exhibit an increase in spatiotemporal activity under protective microhabitat structures and during periods of low lunar illumination as a reflection of predation risk alleviation.

4 Methods

4.1 Study site

The study site was established in a 2.47 hectare plot at Imperial College’s Silwood Park campus adjacent to Ascot in Berkshire, United Kingdom (OS grid ref.: SU 9430 6920). According to the National Vegetation Classification System, the site is categorized as W11, *Quercus petraea*–*B. pubescens*–*Oxalis acetosella* woodland (Pigott et al. 2000). The habitat was composed of the dominant tree species, *Betula pubescens*, while the main shrub layer species were rhododendron and common hazel (*Corylus avellana*). During spring, the ground layer was covered with bluebell (*Hyacinthoides non-scripta*), but during autumn and summer, it was covered with bracken (*Pteridium aquilinum*) instead. An isolated patch of bamboo was also present at the edge of the site.

4.2 Data description and collection

The plot was separated into 247 100m² quadrats and data were collected for approximately 3 years, between 23 March 2010 to 12 March 2013. At the start, woodland rodents were trapped once every week until 10 November 2010, when trapping sessions were conducted fortnightly. All trapped individuals had their phenotypic traits measured, tagged with RFID tags and released at where they were originally trapped.

The collection of location data occurred when PIT-tagged individuals were in close vicinity of data loggers, which are transponder readers made of plastic crates with entrances at opposite ends. When PIT-tagged rodents entered a data logger, the entrance times at $\frac{1}{16}^{th}$ of a second resolution along with their identities based on the unique PIT-tag numbers were recorded. As such, each row in the database denotes an individual detection record, accompanied with the date of detection, the precise location of the data logger, the tag number, species, sex and entrance time. Five data loggers were employed from 28 March 2010 to 6 June 2010 and afterwards, ten data loggers were used until 12 March 2013. To prevent individuals biasing their activity patterns to acquire potential food sources from data loggers, they were randomly moved to a precise location at a new quadrant within the study site every day and had their new coordinates updated in the data base. Further trapping and data logger details can be accessed in the following study (Godsall et al. 2014). All procedures together with the usage of animals strictly followed the guidelines provided by the Imperial College London ethical committee and Home Office UK.

4.3 Data preparation

The map of the study site (Supporting Information Fig.S1) was produced with the GIS platform in R version 4.1.0 (R Core Team, 2021), utilising the shapefiles obtained from ArcGIS v9.3. All shrubs, fallen logs, stumps and ground-layer plant species were overlaid onto the map at a 1m^2 scale resolution. The percentage of moonlight illumination data was obtained from an online calculator created by the company “Manatechs” ltd (Manatechs n.d.). Here, we focus on the two microhabitat features, rhododendron patches and quadrant log volume, suggested to have weighty impacts on wood mouse survival and activity patterns. The coordinates of each detection record was pinpointed onto the study site map, manifesting which 100m^2 quadrant the data logger was located at the time of detection and whether it was under a rhododendron patch. The quadrant log volume is defined as the total fallen log and stump volume inside the 100m^2 quadrant, both the log and stump volumes were calculated with the cylinder formula, $\pi r^2 l$, where r is the radius and l is the length of logs.

Overall, two separate data sets were sourced to investigate the additive and interactive effects of environmental constituents on survival probability and spatiotemporal activity. The data set utilised for survival probability predictions only encompassed data logger detections, whereas both trapping and data logger records were combined for spatiotemporal activity calculations to maximise the chance of deriving an accurate inference on the drivers of individual activity patterns.

4.3.1 Survival data

To formulate survival models, the data set was first processed and merged to comprise individual capture history and covariates. Each wood mouse was paired with six key covariates to account for their effects on individual survival probability. The capture history is a sequence of zeroes and ones only, with zeroes implicating the animal was not observed and one displaying the individual was detected on a given occasion. Each position in the capture history represents successive days in three years. For example, 1001 would represent the individual was detected on the first day and gone unnoticed until the fourth day.

The individual covariates appended to the capture history were sex, weight, rhododendron, quadrant log volume, lunar illumination percentage and rate of activity. Each detection record holds the quadrant log volume, moonlight and the presence or absence of rhododendron. The log and moonlight covariates were averaged across all detections for each individual whilst the detections under rhododendron were summed and divided by the total number of detections for each individual. Since weight could only be measured during trapping sessions, we matched the individuals by their PIT-tag number to the trapping data set and calculated the mean for each individual. Lastly, the individual activity rate was estimated by dividing the total daily distance travelled by the daily active time, where distance and activity time were calculated between subsequent detections in 24 hours.

4.3.2 Activity data

Regarding the spatiotemporal activity data, there were four response variables analysed: the total number of encounters, the total number of unique locations visited, the total distance travelled and the total activity time. We provide the following definitions associated with the elucidation of environmental drivers on spatiotemporal activity. *Encounter*: registered when an individual was captured in a trap or entered a data logger. *Total encounters*: the total number of encounters per recorded day. *Unique locations*: the total number of encounters at a different location per recorded day. *Total distance*: the total distance travelled in metres between subsequent encounters per recorded day. *Total active time*: the calculated time difference in minutes between the first and last encounter per recorded day. To calculate the distance and activity time for each individual, several data points (0.2% of data) were omitted due to the absence of recorded minutes when an individual was encountered. Furthermore, as wood mice are strictly nocturnal animals (Greenwood 1978), we decided to shift all encounter time by 7 hours to capture activity patterns during the hours of darkness. Lastly, 20 metres were added to individuals revisiting the same locations after 15 minutes, with the assumption that they had left and returned to the same 100m² quadrant.

Similarly, to investigate the effects of rhododendron and lunar illumination on spatiotemporal activity, we also estimated the activity rate for each captured individual by dividing the total distance travelled in metres by activity time in minutes for each encountered day. To ensure accurate examinations of the differences in activity rate between open woodlands and protective covered areas, we averaged the mean activity rate for each day and throughout an individual's lifetime to obtain activity rate estimates. These approximated individual activity rates were exploited for both survival and activity analyses.

4.4 Statistical analysis

All statistical analyses were performed using R version 4.1.0 (R Core Team, 2021) and program MARK (White & Burnham 1999). First, to test the effects of predation risk and activity rate on survival, we accessed program MARK through the RMark package (Laake 2013) and implemented Cormack-Jolly-Seber (CJS) models to estimate the apparent survival of marked individuals in the study population at a daily sampling interval. We conducted a number of models comprising of each individual covariates and their pairwise interactions to reveal their relative significance on survival predictions. The resulting models were ranked based on the Akaike Information Criterion (AICc) scores and we considered all models with an AICc score difference of no greater than 6 to be equally supported (Harrison et al. 2018).

Second, to explore the underlying relationship between activity rate and microhabitat structures, we used a correlation test. For the reason that rodents may still view open woodlands with a high log volume as a risky foraging area relative to rhododendron patches (Hinkelman, Orrock & Loeb 2012; Malo et al. 2013), we only tested rhododendron against individual mean activity rate. A Spearman's Rank-Order Correlation test was utilised as the assumption of variable normality for Pearson correlation was not fulfilled.

Third, we constructed GLMMs using the glmmTMB (Brooks et al. 2017) and lme4 (Bates et al. 2015) packages to scrutinize the effects of each individual environmental factor on spatiotemporal activity patterns. Due to the sex differences in home range sizes and potential testosterone-related behavioural changes in males during the breeding season (Godsall et al. 2014), the influence of spatiotemporal components on activity patterns were tested separately for each sex. Four GLMMs were built for both sexes and the response variables were divided into two groups, count data (*Total encounters* and *Unique locations*) and continuous non-negative data (*Total distance* and *Total active time*). For count data of both sexes, *Total encounters* were fitted with a quadratic parameterization of negative binomial distribution and a log link function. *Unique locations* were fitted with a generalized poisson family to handle under-dispersed data and avoid biasing effects on parameter estimates. For the continuous data, since successive detections are required in a single day to calculate *Total distance* and *Total active time*, this resulted in an abundance of zeroes as a large proportion of individuals were detected once a day only. Hence, these zero-inflated continuous data were fitted with a binomial-Gamma hurdle model, modelling the zeroes separately from the non-zero values, with a particular focus on the non-zero values.

All the initial mixed models incorporated rhododendron cover, quadrant log volume, moonlight illumination, data logger and trapping effort as fixed effects, with individual identity and yearly differences between seasons as random effects. In consideration of the minuscule data logger detection range on PIT-tagged rodents and the changes in data logger and trapping efforts during the course of the study. It is therefore not possible to standardise location data accession between individuals. To account for these potential confounding effects, the number of data loggers and trapping sessions were included as fixed effects in all GLMMs. Again, AICc scores were used for model selection, comparing the AICc values between models fitted with a different distribution or a link function, and model reduction (Harrison et al. 2018). Furthermore, multicollinearity amongst predictors was inspected with variance inflation factor and predictors with a high correlation were excluded.

5 Results

Throughout the three years of study period, there were a total of 9328 encounter records of *A. sylvaticus* with 400 unique individuals. Separately, the number of male and female observations were 5724 with 234 unique individuals and 3604 with 166 unique individuals respectively. On average, each individual was captured and detected 48.7 times, with male encounters at 52.1 times and females at 43.4 times. The proportion of individuals encountered under rhododendron was 0.39 ± 0.01 and the mean moonlight illumination was $48.65\% \pm 1.27$ on all encountered days.

5.1 Survival estimates

After running 17 CJS models, two best models were selected based on AICc scores and displayed significant statistical interactions between moonlight with activity rate and rhododendron with activity rate (Supporting Information Tab.S1). For both models, the results indicated strong evidence for activity rate as a predictor of survival under two environmental conditions, moonlight and rhododendron, with an elevated activity rate resulting in an increase in survival estimates. Using the estimates extracted from the model incorporated with moonlight and activity rate interaction, the daily survival probability for each individual was 0.95 ± 0.05 and with the maximum increase in activity rate, the survival estimate rapidly rose up to 0.999 ± 0.002 . However, when the interaction between moonlight illumination and activity rate was considered, using the maximum activity rate under an average moonlight illumination, survival estimates significantly reduced down to 0.002 ± 0.001 (Fig. 1a & 1b). For the second model, with *rhododendron* and activity rate interaction, *rhododendron* was discovered to increase survival estimates by at most, 1%, from 0.98 ± 0.003 to 1.00 ± 0.004 (Fig. 1c). In an attempt to explain this minuscule effect from rhododendron, estimates were drawn from the model incorporated with the interaction of rhododendron and mouse weight. With increasing rhododendron cover, survival estimates decreased from 0.95 ± 0.03 to 0.87 ± 0.28 . Conversely, an increase in mouse weight with rhododendron cover raised survival probability from 0.95 ± 0.03 to 1.00 ± 0.03 (Fig. 2a & 2b).

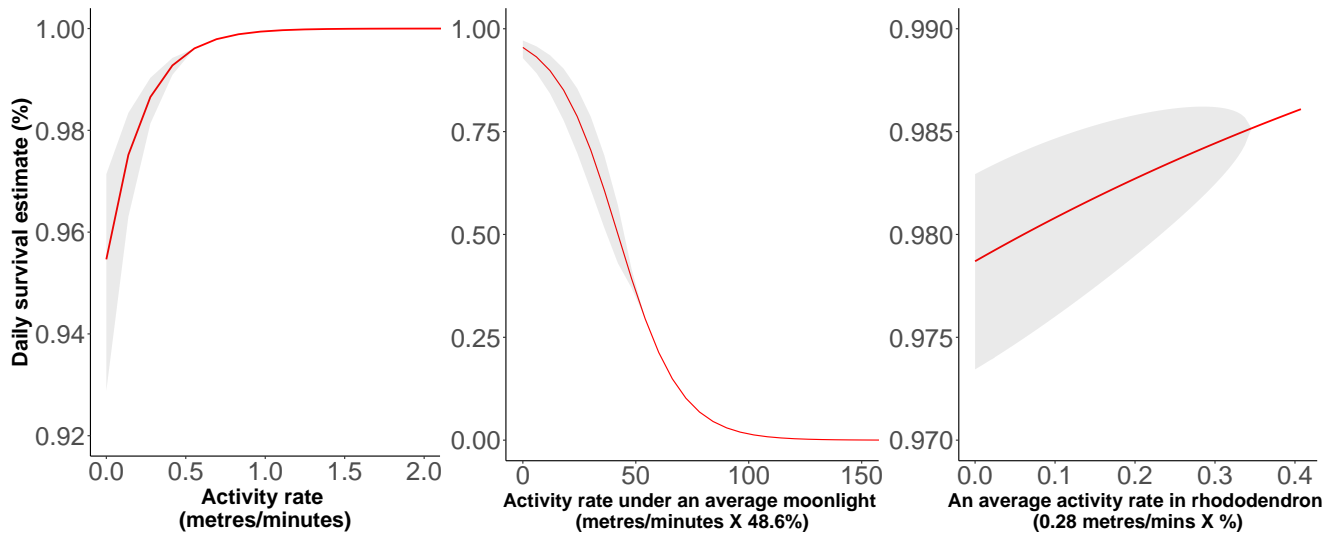


Figure 1. Effects of activity rate (a), activity rate under an average moonlight intensity of 48.6% (b) and an average activity rate of 0.28 metres per minute under rhododendron cover (c) on the daily survival probability of wood mouse, a total of 400 individuals were included and the shaded regions denote 95% confidence intervals.

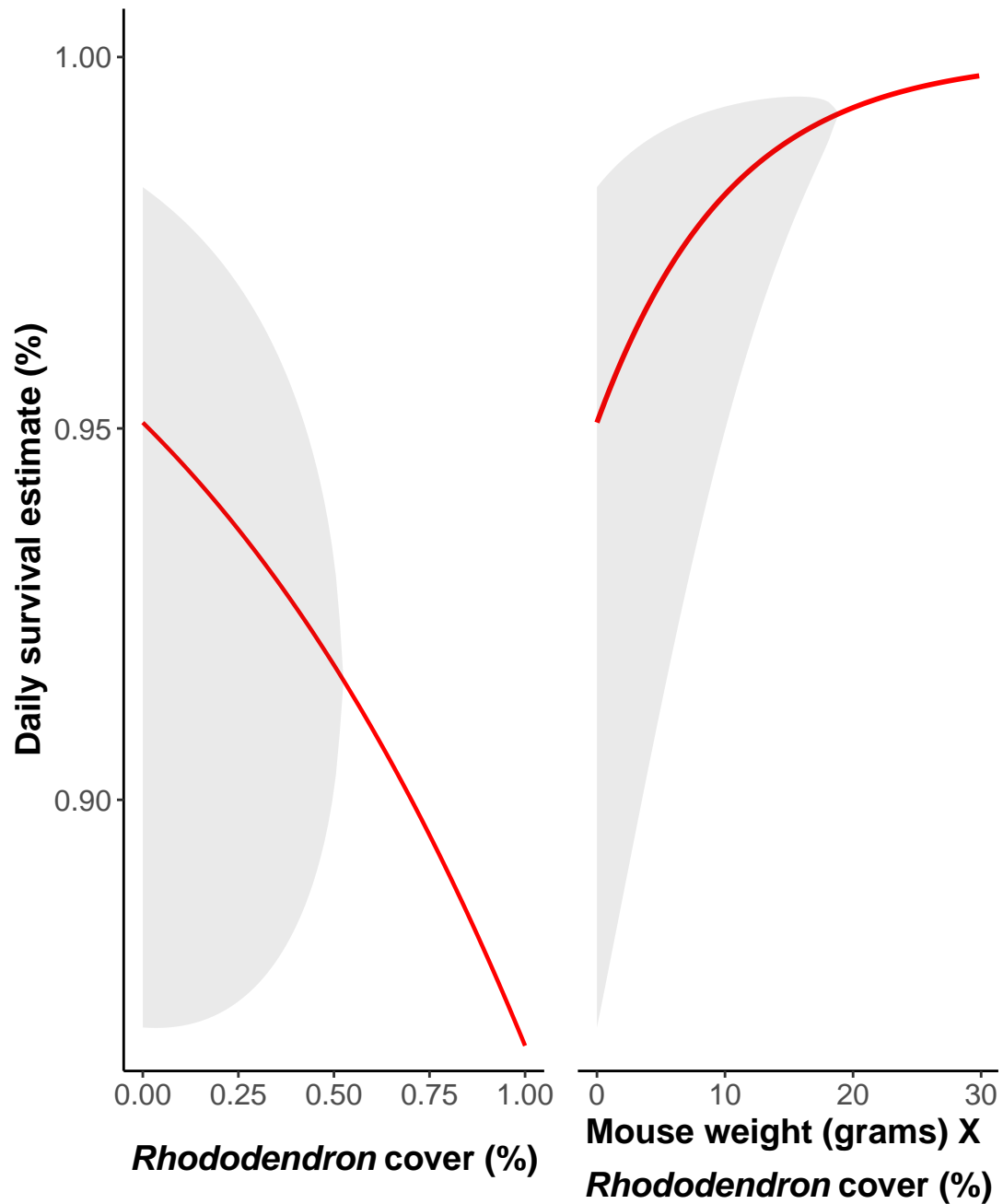


Figure 2. Effects of rhododendron (a) and rhododendron with mouse weight (b) on the daily survival estimate of wood mouse, a total of 400 individuals were included and the shaded regions denote 95% confidence intervals.

5.2 Spatiotemporal activity

Expectedly, a significant positive relationship was uncovered between activity rate and rhododendron cover (Fig.3, $R = 0.26$, $p < 0.0001$). Next, following GLMMs term reduction and reaching a final best model, both sexes displayed similar predictive patterns in the face of five integrated fixed effects: *rhododendron*, log volume, moonlight illumination, *rhododendron* X log volume and *rhododendron* X moonlight. The total number of encounters and new locations visited were negatively affected by an increase in rhododendron covers, log volumes and moonlight illumination, whilst an increase in both the interactions of *rhododendron* X log volume and *rhododendron* X moonlight uplifted total encounters and locations visited. Conversely, wood mice exhibited a drop in distance travelled and active time with the escalation in rhododendron cover, log volume and moonlight illumination, whilst the interactive fixed effects resulted in an elevation in those two response variables. Two additional fixed effects proved to have significant effects on females only, they were data logger and trapping efforts. With increasing logger and trapping effort, there was an increase in the total encounter records and new locations visited (Fig.4 & Supporting Information Tab.S2).

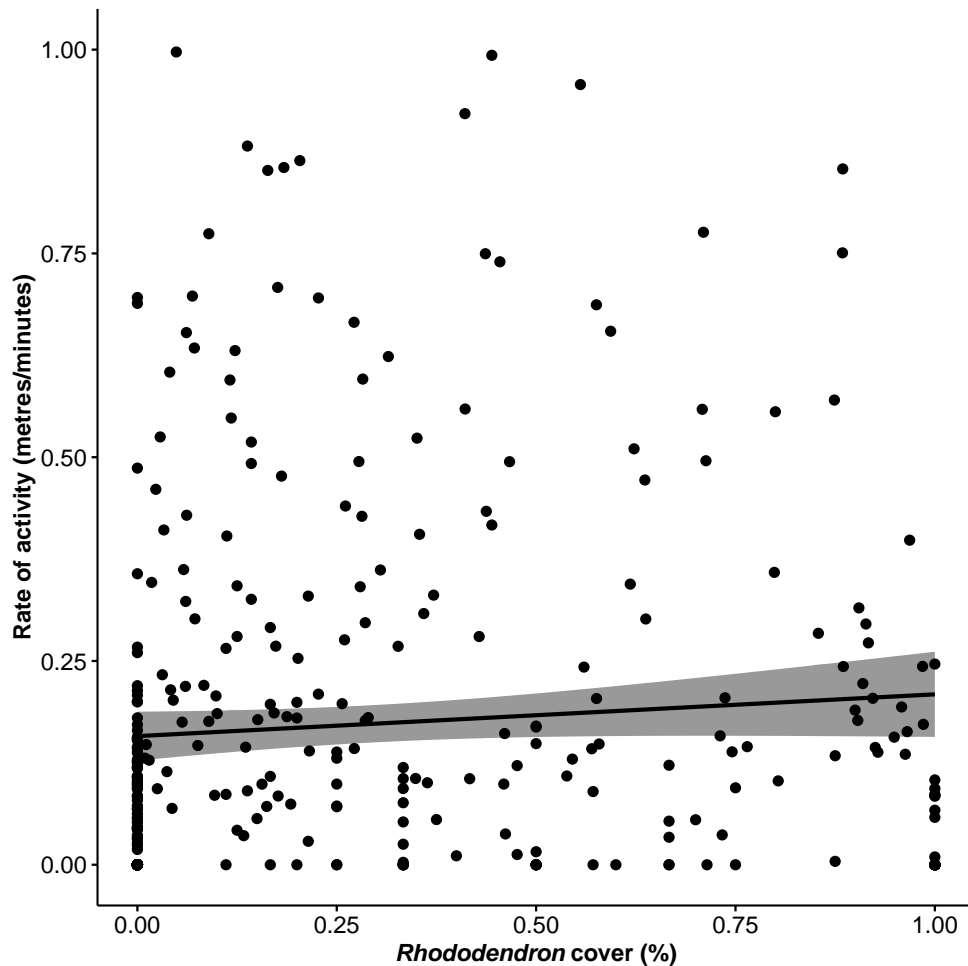


Figure 3. Result of the Spearman's Rank-Order correlation test between the rate of individual activity change in respect to rhododendron coverage, $R = 0.26$, $p < 0.0001$. A total of 400 individuals were included and the shaded region denotes 95% confidence intervals.

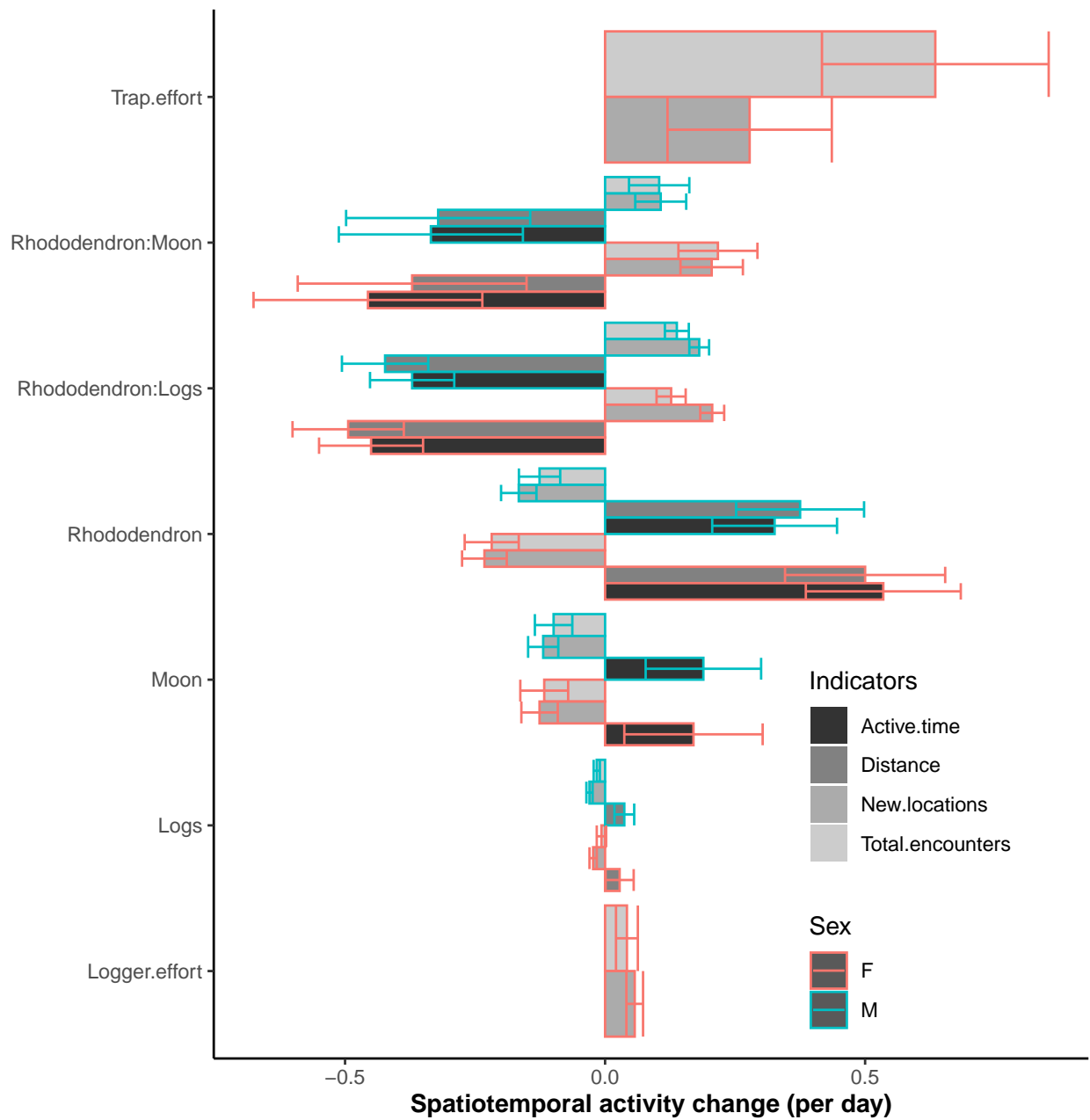


Figure 4. Featuring the estimated effect sizes from 8 GLMMs separated by sex, with 7 total incorporated fixed effects on individual spatiotemporal activity changes. The 4 indicators of spatiotemporal activity (response variables) are the total number of encounters, new locations visited, distance travelled and activity time per day. The sample size was 9328 and the error bars represent the corresponding standard error of estimates.

6 Discussion

In this study, we investigated how individual rodent activity determine survival. We show that survival, a key demographic parameter in population ecology, can be explained by the effects of predation risk and competition intensity on individual activity of a wild wood mouse population at a fine spatiotemporal resolution. Our CJS models and AICc ranking model approach suggest that predation risk and activity rate are significant predictors of survival.

Predation is one of the most prominent selective forces that acts on prey animals and can alter their behaviours. In particular, when prey animals such as rodents are capable of assessing the level of predation risk in relation to the environment and adjust their locomotory behaviours accordingly. For instance, indirect predation cues such as moonlight intensity and microhabitat structures that allow predatory detection or attacks can remarkably influence the activity patterns of rodents (Bowers & Dooley 1993; Farnworth et al. 2019; Gigliotti et al. 2020). Here, a high rate of activity indicates that an individual had travelled a significant distance during a short period of time. Our top two CJS models showed that activity rate was a strong predictor of survival only when the interactions between the two indirect predation cues, moonlight and rhododendron, were considered. Since wood mice were discovered to utilise covered areas more heavily compared to open habitats to lessen predation risk from tawny owls (Todd, Tew & Macdonald 2000). This implies that the rate of activity corresponds to their exposure to varying degrees of predation pressure, therefore, a high activity rate would be displayed when rodents experience the least amount of predation pressure as high rates of activity aid in predatory detection. Which explains our model estimates as both models suggest that a high activity rate reflects a high daily survival estimate. But when moonlight intensity, the factor which elevates Tawny owls' predatory success (Kotler, Brown & Hasson 1991), was taken into account, individual survival estimates decreased dramatically. The result (Fig. 1b) simulated a scenario where individuals exhibited increasingly high activity rates despite experiencing a constant predation pressure from their main aerial predator, thus causing their chance of survival to drop promptly.

On the other hand, our second CJS model (Fig. 1c) predicted an increasing rhododendron cover alongside a constant activity rate would raise individual survival estimates. Given the importance of the dense protective cover rhododendron shields from tawny owl predation, wood mice were allowed to increase foraging or mate-seeking behaviours freely which consequently, would further increase their survival probabilities (Korslund & Steen 2006; Navarro-Castilla, Barja & Díaz 2018). It is important to note that rhododendron patches have a lower density of seed producing trees and a lower invertebrate abundance compared to open woodlands (Malo et al. 2013; Brouard et al. 2020). Rhododendron therefore does not increase food availability, which means that the increase in survival was most probably associated with its structure in reducing predation risk.

There is appreciable evidence from our correlation test that the rate of individual activity increases with rhododendron cover, signifying that the rate of landscape usage under rhododendron is substantially higher due to a reduced predation risk. However, as *rhododendron* was only shown to impact daily survival estimates at a small scale, we extracted CJS model prediction results from *rhododendron* and mouse weight interactions to decipher this minuscule effect. Malo et al. (2013) demonstrated that wood mice highly prefer rhododendron covers compared to open woodlands, to the point where rhododendron patches housed a significantly higher density of individuals and larger adults competitively exclude

smaller juveniles and subadults to open woodlands. The observed negative relationship between *rhododendron* and daily survival estimates was likely caused by the high competitive intensity individuals experience under rhododendron. In populated areas, subordinate individuals were perceived to face an inflated mortality risk in the presence of other dominant individuals (Eccard & Ylönen 2007; Hernández et al. 2018). This would also explain the interaction between weight and rhododendron, in which increasingly weighted individuals would have a higher competitive advantage, resulting in dominant wood mice establishing their territories in rhododendron patches and displaying higher survival probabilities. This suggests that, although rhododendron improves individual survival estimates from aerial predation, there also exists a cost in living under rhododendron for subordinate individuals who suffer more from the consequence of competition.

The GLMMs indicated that both sexes were affected similarly by environmental variations. In general, the pairwise interactions between the environmental factors had positive effects on the total number of encounters and different locations visited whereas the other two responses, total distance travelled and activity time, were negatively influenced. But when the environmental factors were investigated in isolation, their results showed opposite patterns to the responses mentioned above. Unsurprisingly, predation risk had a considerable impact on wood mice activity. During brighter nights, individuals predominantly visited fewer places and different locations to minimize predation risk. Individuals were also discovered to be active for a longer period of time, this coincides with the results of a behavioural study which revealed a higher illumination intensity would induce more vigilance in rats and cause them to explore at a lower speed, resulting in a longer activity time (Farnworth et al. 2019). Nonetheless, when rhododendron cover was incorporated with moonlight, the effects on individual activity patterns fully reversed. As previously mentioned, rhododendron functions as a refuge from aerial predators (Malo et al. 2013), thus permitting individuals to visit more and different areas freely in response to the diminished predatory threat.

Past studies have proposed that areas with large quantities of fallen logs can provide nesting sites and protection from predators as a silent getaway (Lin & Shiraishi 1992; Malo et al. 2013). In view of the protective functionalities both rhododendron and logs possess, individuals were detected to visit more and different data loggers with more surrounding logs and rhododendron. However, although wood mice were found to travel longer distances in quadrants with a high log volume, they were also detected to visit fewer places in those quadrants, which is probably related to their seed recovering efficiency. With seeds as one of wood mice main food sources during the breeding season, cache hoarding of seeds in a scatter manner is a popular behaviour displayed by them (Muñoz & Bonal 2008; Godsall et al. 2014). Seeds cached near fallen logs were significantly more likely to be recovered as the fallen logs can act as a potential landmark (Ribeiro & Vieira 2016). As such, wood mice would be able to find buried seeds without the need to scout the area multiple times.

The decrease in the number of encounters and new locations visited under rhododendron covers, where adult mice preferentially cluster under, could be explained by competition intensity. In the absence of high predation risk, wood mice might perform spatial partitioning at these highly valued microhabitats to reduce encounter rates with conspecifics or species with a similar niche. Similarly, a reduction in individual travelled distance and activity time were observed when *rhododendron* with fallen logs and moonlight effects were included. It has been reported that rhododendron patches encompass more seed

caches, especially with seed species of a higher nutritious value (Godsall et al. 2014). This would entail less time and effort spent in foraging activities due to the clumped distribution of seed caches.

Interestingly, an increase in trapping and data logger efforts significantly elevated the total number of encounters and new locations visited for females only. *A. sylvaticus* shows a polygynous mating system, so contrary to males that hold large territories to overlap with as many female's territories as possible, females tend to occupy a small territory size with high quality (Bartmann & Gerlach, 2001). This means that as more trapping sessions and data loggers were employed, the devices were more likely to be in the vicinity of a female territory, resulting in a greater number of female encounters.

It is worth mentioning that CJS model predictions only provide apparent survival estimates, the calculated values do not differentiate death from permanent emigration, which can be problematic with species that move long distances (Barbour et al. 2013). Even though the home range sizes of wood mice were discerned to be smaller in deciduous woodland (Attuquayefio, Gorman & Wolton 1986), with past studies showing an average home range size to be noticeably smaller than our study site (Korn 1986; Godsall et al. 2014), care should still be taken when interpreting the results as they could represent underestimates of true survival.

Moreover, live trapping was utilised for wild rodent measurements and PIT-tagging. Since trapping instigates varying degrees of stress to captured individuals in accordance to different confinement time, this might impact their behavioural responses such as activity time (Brehm, Tironi & Mortelliti 2020). We attempted to avoid unequal stress induction amongst wood mice by releasing trapped individuals in the same order in which traps were set up to minimise this effect. In addition, as our study data only consisted of ground-level activity, we could only investigate the arboreal behaviours displayed by wood mice indirectly through the measurements of fallen logs and stump volume in each quadrant. For future references, both traps and data loggers should be placed above ground surface to confidently infer arboreality.

Despite being limited to ground-level activity detections and the potential behavioural effects from live trapping, our findings demonstrated that predation risk and activity rate may be the most powerful factors to account for in the predictions of wood mice survival. We showed that the individual activity rate was associated with the rodent's assessment of predation risk, with higher activity rates occurring in the absence of high predation pressure, which is influenced by rhododendron cover. Notably, both sexes displayed similar responses to environmental variations, where an increase in moonlight illumination generally decreased wood mice activity, but when individuals were under rhododendron cover, an opposite pattern was discovered. Furthermore, when predation risk was not considered, individual activity decreased in relation to rhododendron and logs volume due to a higher seed recovering efficiency and spatial partitioning to avoid competition. To conclude, spatiotemporal fluctuations in environmental factors related to predation risk were shown to have a prominent role in determining wood mice survival and activity patterns, with climate change's continual effect on the invasiveness of rhododendron (Manzoor et al. 2018; Manzoor, Griffiths & Lukac, 2021), this study can help in making predictions on the future distributions of wood mice within woodlands, their predation populations and woodland regeneration in the UK.

7 Data and Code Availability

All the data sets, R scripts, results and a description of the general data analysis workflow can be found in the following repository:

<https://github.com/billy999cmee/CMEECoursework/tree/main/MainProject>

8 References

- Allen, A. M. Singh, N. J. (2016) Linking Movement Ecology with Wildlife Management and Conservation. *Frontiers in Ecology and Evolution*, **3**, 155.
- Attuquayefio, D. K., Gorman, M. L. Wolton, R. J. (1986) Home range sizes in the Wood mouse *Apodemus sylvaticus*: habitat, sex and seasonal differences. *Journal of Zoology (1987)*. **210 (1)**, 45-53.
- Auffray, J., Renaud, S. Claude, J. (2009) Rodent Biodiversity in Changing Environments. *Kasetsart*. **43**, 83-93.
- Avgar, T., Mosser, A., Brown, G. S., Fryxell, J. M. Mysterud, A. (2013) Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *The Journal of Animal Ecology*. **82 (1)**, 96-106.
- Barbour, A. B., Ponciano, J. M., Lorenzen, K. O'Hara, R. B. (2013) Apparent survival estimation from continuous mark–recapture/resighting data. *Methods in Ecology and Evolution*. **4 (9)**, 846-853.
- Bartmann, S. Gerlach, G. (2001) Multiple Paternity and Similar Variance in Reproductive Success of Male and Female Wood Mice (*Apodemus sylvaticus*) Housed in an Enclosure. *Ethology*. **107 (10)**, 889-899.
- Bolaños, F., LeDue, J. M. Murphy, T. H. (2017) Cost effective raspberry pi-based radio frequency identification tagging of mice suitable for automated in vivo imaging. *Journal of Neuroscience Methods*. **276**, 79-83.
- Bouskila, A. (1995) Interactions Between Predation Risk and Competition: A Field Study of Kangaroo Rats and Snakes. *Ecology (Durham)*. **76 (1)**, 165-178.
- Bowers, M. A. Dooley, J. L. (1993) Predation Hazard and Seed Removal by Small Mammals: Microhabitat versus Patch Scale Effects. *Oecologia*. **94 (2)**, 247-254.
- Brehm, A. M., Tironi, S. Mortelliti, A. (2020) Effects of trap confinement on personality measurements in two terrestrial rodents. *PLoS ONE*. **15 (1)**
- Brouard, M. J., Knowles, S. C. L., Dressen, S., Coulson, T. Malo, A. F. (2020) Factors affecting woodland rodent growth. *Journal of Zoology (1987)*. **312 (3)**, 174-182.
- Colchero, F., Jones, O., Conde, D. A., Hodgson, D., Zajitschek, F., Schmidt, B. R., Malo, A. F., Alberts, S. C., Becker, P. H., Bouwhuis, S., Bronikowski, A. M., Vleeschouwer, K. M., Delahay, R. J., Dummermuth, S., Fernández-Duque, E., Frisenvænge, J., Hesselsøe, M., Larson, S., Lemaître, J., McDonald, J., Miller, D. A. W., O'Donnell, C., Packer, C., Raboy, B. E., Reading, C. J., Wapstra, E., Weimerskirch, H., While, G. M., Baudisch, A., Flatt, T., Coulson, T., Gaillard, J. Regan, H. (2019) The diversity of population responses to environmental change. *Ecology Letters*. **22 (2)**, 342-353.

- Coulson, T. Malo, A. (2008) Population biology Case of the absent lemmings. *Nature (London)*. **456** (7218), 43-44.
- DeMars, C. A., Auger-Méthé, M., Schlägel, U. E. Boutin, S. (2013) Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. *Ecology and Evolution*. **3** (12), 4149-4160.
- Diaz, M. Alonso, C. L. (2003) Wood Mouse *Apodemus sylvaticus* Winter Food Supply: Density, Condition, Breeding, and Parasites. *Ecology (Durham)*. **84** (10), 2680-2691.
- Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**(1), 1-48. doi:10.18637/jss.v067.i01.
- Eccard, J. A. Ylönen, H. (2007) Costs of Coexistence along a Gradient of Competitor Densities: An Experiment with Arvicoline Rodents. *The Journal of Animal Ecology*. **76** (1), 65-71.
- Farnworth, B., Meitern, R., Innes, J. Waas, J. R. (2019) Increasing predation risk with light reduces speed, exploration and visit duration of invasive ship rats (*Rattus rattus*). *Scientific Reports*. **9** (1), 3739.
- Frey, S., Fisher, J. T., Burton, A. C., Volpe, J. P. Rowcliffe, M. (2017) Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sensing in Ecology and Conservation*. **3** (3), 123-132.
- Gigliotti, L. C., Slotow, R., Hunter, L. T. B., Fattebert, J., Sholto-Douglas, C. Jachowski, D. S. (2020) Habitat complexity and lifetime predation risk influence mesopredator survival in a multi-predator system. *Scientific Reports*. **10** (1), 17841.
- Godsall, B., Coulson, T., Malo, A. F. Montgomery, I. (2014) From physiology to space use: energy reserves and androgenization explain home-range size variation in a woodland rodent. *The Journal of Animal Ecology*. **83** (1), 126-135.
- Greenwood, P. J. (1978) Timing of Activity of the Bank Vole *Clethrionomys Glareolus* and the Wood Mouse *Apodemus Sylvaticus* in a Deciduous Woodland. *Oikos*. **31** (1), 123-127.
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J. Inger, R. (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ (San Francisco, CA)*. **6** e4794.
- Hayes, L. D., Ebersperger, L. A., Kelt, D. A., Meserve, P. L., Pillay, N., Viblanc, V. A. Schradin, C. (2017) Long-term field studies on rodents. *Journal of Mammalogy*. **98** (3), 642-651.
- Hernández, M., Navarro-Castilla, Á, Piñeiro, A. Barja, I. (2018) Wood mice aggressiveness and flight response to human handling: Effect of individual and environmental factors. *Ethology*. **124** (8), 559-569.

- Hinkelman, T. M., Orrock, J. L., Loeb, S. C. (2012) Effect of Downed Woody Debris on Small Mammal Anti-Predator Behavior. *Ethology*. **118** (1), 17-23.
- Jacob, J., Brown, J. S. (2000) Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. *Oikos*. **91** (1), 131-138.
- Korn, H. (1986) Changes in Home Range Size during Growth and Maturation of the Wood Mouse (*Apodemus sylvaticus*) and the Bank Vole (*Clethrionomys glareolus*). *Oecologia*. **68** (4), 623-628.
- Korslund, L., Steen, H. (2006) Small Rodent Winter Survival: Snow Conditions Limit Access to Food Resources. *The Journal of Animal Ecology*. **75** (1), 156-166.
- Kotler, B. P., Brown, J. S., Hasson, O. (1991) Factors Affecting Gerbil Foraging Behavior and Rates of Owl Predation. *Ecology (Durham)*. **72** (6), 2249-2260.
- Laake, J.L. (2013). RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.
- Li, M., Van Renterghem, T., Kang, J., Verheyen, K., Botteldooren, D. (2020) Sound absorption by tree bark. *Applied Acoustics*. **165**, 107328.
- Lin, L., Shiraishi, S. (1992) Home Range and Microhabitat Utilization in the Formosan Wood Mouse, *Apodemus semotus*. *Journal of the Faculty of Agriculture, Kyushu University*. **37** (1), 13-27.
- López-Sánchez, A., Peláez, M., Dirzo, R., Fernandes, G. W., Seminatore, M., Perea, R., Flory, L. (2019) Spatio-temporal variation of biotic and abiotic stress agents determines seedling survival in assisted oak regeneration. *The Journal of Applied Ecology*. **56** (12), 2663-2674.
- Malo, A. F., Godsall, B., Prebble, C., Grange, Z., McCandless, S., Taylor, A., Coulson, T. (2013) Positive effects of an invasive shrub on aggregation and abundance of a native small rodent. *Behavioral Ecology*. **24** (3), 759-767.
- Manatechs. (n.d.) *Moon phases and lunar CALENDAR, AUGUST 2021 (Ascot, United Kingdom)*. Available from: <https://sunsetsunrisetime.com/moon/ascot> [Accessed 5th July 2021]
- Manzoor, S. A., Griffiths, G., Iizuka, K., Lukac, M. (2018) Land Cover and Climate Change May Limit Invasiveness of *Rhododendron ponticum* in Wales. *Frontiers in Plant Science*. **9**, 664.
- Manzoor, S. A., Griffiths, G., Lukac, M. (2021) Land use and climate change interaction triggers contrasting trajectories of biological invasion. *Ecological Indicators*. **120**, 106936.
- Michael A Steele, Steve Manierre, Theresa Genna, Thomas A Contreras, Peter D Smallwood, Michael E

- Pereira. (2006) The innate basis of food-hoarding decisions in grey squirrels: evidence for behavioural adaptations to the oaks. *Animal Behaviour*, **71** (1), 155–160.
- Miller, H. J., Dodge, S., Miller, J. Bohrer, G. (2019) Towards an integrated science of movement: converging research on animal movement ecology and human mobility science. *International Journal of Geographical Information Science : IJGIS*. **33** (5), 855-876.
- Moiron, M., Laskowski, K. L., Niemelä, P. T. Gurevitch, J. (2020) Individual differences in behaviour explain variation in survival: a meta-analysis. *Ecology Letters*. **23** (2), 399-408.
- Mollie E. Brooks, Kasper Kristensen, Koen J. van Benthem, Arni Magnusson, Casper W. Berg, Anders Nielsen, Hans J. Skaug, Martin Maechler and Benjamin M. Bolker (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, **9** (2), 378-400.
- Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H. Haydon, D. T. (2010) Building the bridge between animal movement and population dynamics. *Philosophical Transactions. Biological Sciences*. **365** (1550), 2289-2301.
- Muñoz, A. Bonal, R. (2008) Are you strong enough to carry that seed? Seed size/body size ratios influence seed choices by rodents. *Animal Behaviour*. **76** (3), 709-715.
- Navarro-Castilla, Á Barja, I. (2019) Stressful living in lower-quality habitats? Body mass, feeding behavior and physiological stress levels in wild wood mouse populations. *Integrative Zoology*. **14** (1), 114-126.
- Navarro-Castilla, Á, Barja, I. Díaz, M. (2018) Foraging, feeding, and physiological stress responses of wild wood mice to increased illumination and common genet cues. *Current Zoology*. **64** (4), 409-417.
- Ostfeld, R. S., Manson, R. H. Canham, C. D. (1997) Effects of Rodents on Survival of Tree Seeds and Seedlings Invading Old Fields. *Ecology (Durham)*. **78** (5), 1531-1542.
- Pigott, C.D., Ratcliffe, D.A., Malloch, A.J.C., Birks, H.J.B., Proctor, M.C.F., Shimwell, D.W., Huntley, J.P., Radford, M.J., Wiggington, M.J. Wilkins, P. (2000). *British plant communities*. Cambridge: Cambridge University Press.
- Plesner Jensen, S. Honess, P. (1995) The influence of moonlight on vegetation height preference and trappability of small mammals. *Mammalia (Paris)*. **59** (1), 35-42.
- Pratas-Santiago, L. P., Gonçalves, A. L. S., da Maia Soares, A. M. V Spironello, W. R. (2016) The moon cycle effect on the activity patterns of ocelots and their prey. *Journal of Zoology (1987)*. **299** (4), 275-283.
- Ribeiro, J. F. Vieira, E. M. (2016) Microhabitat selection for caching and use of potential landmarks for seed recovery by a neotropical rodent. *Journal of Zoology (1987)*. **300** (4), 274-280.

- Robert H Tamarin and Spencer R Malecha. (1971) The population biology of hawaiian rodents: demographic parameters. *Ecology*, **52** (3), 383–394.
- Romairone, J., Jiménez, J., Luque-Larena, J. J. Mougeot, F. (2018) Spatial capture-recapture design and modelling for the study of small mammals. *PloS One*. **13** (6), e0198766.
- R Core Team (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Schirmer, A., Hoffmann, J., Eccard, J. A. Dammhahn, M. (2020) My niche: individual spatial niche specialization affects within- and between-species interactions. *Proceedings of the Royal Society. B : Biological Sciences*. **287** (1918), 20192211.
- Schmidt, K. A., Rush, S. A. Ostfeld, R. S. (2008) Wood Thrush Nest Success and Post-Fledging Survival across a Temporal Pulse of Small Mammal Abundance in an Oak Forest. *The Journal of Animal Ecology*. **77** (4), 830-837.
- Tang, X., Tang, S., Li, X., Menghe, D., Bao, W., Xiang, C., Gao, F. Bao, W. (2019) A Study of Population Size and Activity Patterns and Their Relationship to the Prey Species of the Eurasian Lynx Using a Camera Trapping Approach. *Animals (Basel)*. **9** (11), 864.
- Tanton, M. T. (1965) Problems of Live-Trapping and Population Estimation for the Wood Mouse, *Apodemus sylvaticus* (L.). *The Journal of Animal Ecology*. **34** (1), 1-22.
- Todd, I. A., Tew, T. E. Macdonald, D. W. (2000) Arable habitat use by wood mice (*Apodemus sylvaticus*). 1. Macrohabitat. *Journal of Zoology (1987)*. **250** (3), 299-303.
- Viviano, A., Mori, E., Fattorini, N., Mazza, G., Lazzeri, L., Panichi, A., Strianese, L. Mohamed, W. F. (2021) Spatiotemporal Overlap between the European Brown Hare and Its Potential Predators and Competitors. *Animals (Basel)*. **11** (2), 562.
- Weber, J. N. Hoekstra, H. E. (2009) The evolution of burrowing behaviour in deer mice (genus *Peromyscus*). *Animal Behaviour*. **77** (3), 603-609.
- White, G.C. Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, 120–138.
- White, S. L. Wagner, T. (2021) Behaviour at short temporal scales drives dispersal dynamics and survival in a metapopulation of brook trout (*Salvelinus fontinalis*). *Freshwater Biology*. **66** (2), 278-285.
- Wolton, R. J. (1985) The ranging and nesting behaviour of Wood mice, *Apodemus sylvaticus* (Rodentia: Muridae), as revealed by radio-tracking. *Journal of Zoology (1987)*. **206** (2), 203-222.

9 Supplementary Information

Study site at Nash's Copse

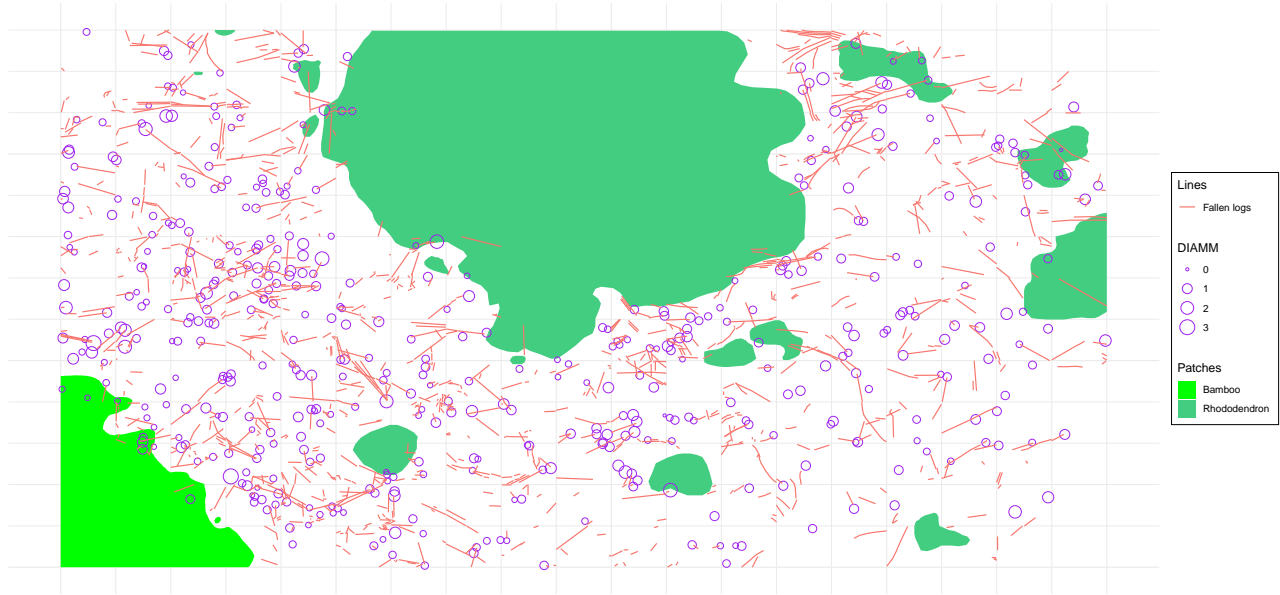


Figure S1. Map of the 2.47 hectare plot at Nash's Copse in Silwood Park Campus. The study site is separated into 247 100m² quadrants, featuring rhododendron, bamboo patches, stump (diameter in metres) and fallen logs.

Model	Npar	DeltaAICc	Weight	Deviance
Moon * Activity	5	0.00000	8.671590e-01	30904.37
Activity * <i>Rhododendron</i>	5	4.07500	1.130378e-01	30908.44
Activity * Weight	5	9.04100	9.437795e-03	30913.41
Activity	3	17.99637	1.072106e-04	30926.37
Activity * Logs	5	20.26700	3.444892e-05	30924.63
Weight * <i>Rhododendron</i>	5	22.73900	1.000893e-05	30927.11
<i>Rhododendron</i>	3	36.30237	1.135377e-08	30944.67
Weight	3	37.03137	7.885694e-09	30945.40
Moon * <i>Rhododendron</i>	5	38.17900	4.442569e-09	30942.55
Sex * Weight	5	39.15300	2.729812e-09	30943.52
Sex * <i>Rhododendron</i>	5	39.34600	2.478697e-09	30943.71
Weight * Logs	5	39.45800	2.343705e-09	30943.83
Moon	3	55.77537	6.708602e-13	30964.15
Intercept	2	56.23982	5.318348e-13	30717.97
Logs	3	56.99537	3.645125e-13	30965.37
Moon * Logs	5	58.96500	1.361481e-13	30963.33
Sex * Logs	5	59.44600	1.070444e-13	30963.81

Table S1. Results of 17 CJS models using program MARK, each model was incorporated with either one or two of the following individual covariates - moonlight intensity, *rhododendron*, logs, sex and activity rate. The table presents the model fixed covariates, number of parameters, delta AICc between models, model weight and the deviance.

	Total.enc(M)	Total.enc(F)	New.loc(M)	New.loc(F)	Distance(M)	Distance(F)	Act.time(M)	Act.time(F)
(Intercept)	0.697 (0.063)	-0.111 (0.262)	0.327 (0.096)	-0.458 (0.210)	0.354 (0.188)	1.130 (0.610)	0.372 (0.187)	0.293 (0.168)
<i>Rhododendron</i>	-0.126 (0.039)	-0.218 (0.052)	-0.166 (0.034)	-0.232 (0.043)	0.375 (0.123)	0.500 (0.154)	0.326 (0.120)	0.535 (0.150)
Logs	-0.016 (0.007)	-0.007 (0.009)	-0.030 (0.006)	-0.023 (0.007)	0.037 (0.019)	0.028 (0.028)		
Moon	-0.099 (0.036)	-0.117 (0.046)	-0.119 (0.029)	-0.126 (0.035)			0.189 (0.111)	0.170 (0.133)
<i>Rhododendron</i> :Logs	0.138 (0.023)	0.127 (0.028)	0.181 (0.020)	0.206 (0.023)	-0.423 (0.084)	-0.494 (0.107)	-0.371 (0.081)	-0.451 (0.101)
<i>Rhododendron</i> :Moon	0.104 (0.023)	0.217 (0.076)	0.107 (0.049)	0.205 (0.060)	-0.321 (0.177)	-0.371 (0.221)	-0.335 (0.177)	-0.456 (0.220)
Logger.effort		0.042 (0.021)		0.057 (0.016)				
Trap.effort		0.635 (0.217)		0.278 (0.158)				
AICc	19244.09	11779.71	14072.81	8131.39	38291.94	21349.46	46006.20	26643.47
Num.of.obs.	5724	3604	5724	3604	5724	3604	5724	3604
Num.of.ID	234	166	234	166	234	166	234	166
Total.seasons	9	9	9	9	9	9	9	9
Var: ID	0.074 (0.271)	0.064 (0.253)	0.112 (0.335)	0.117 (0.342)	0.769 (0.877)	0.499 (0.707)	0.036 (0.190)	0.063 (0.251)
Var: season	0.025 (0.158)	0.053 (0.230)	0.070 (0.265)	0.049 (0.221)	0.198 (0.445)	0.131 (0.362)	0.029 (0.169)	0.032 (0.179)

Table S2. Comparison of 8 GLMM models on wood mouse spatiotemporal activity. Data logger and trap efforts only affected females, whilst moonlight did not have significant effects on daily distance travelled and neither did logs quadrant volume on daily activity time.