Personality, Movement, and Infection in a Wild Population of Bank Voles (*Myodes glareolus*)

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Abstract

Personality affects many life decisions and potentially has major consequences on ecological and evolutionary processes. Personality-dependent local movement affects interactions between individuals, resource acquisition, and the risk of encountering predators and pathogens. Thus, differences in behavioral types can have larger consequences on fitness. Here, I investigated personality-dependent local movement, Puumala (PUUV) infection, and overwintering survival of a wild population of bank voles (*Myodes glarolus*). Voles were captured and tagged in a field site in Northeastern Sweden. I evaluated personality using standardized tests in field, collected mouth swab samples for PUUV analysis, and recorded local movement using an automated technology for logging PIT-tagged voles. Anxiety- and stress-tolerant voles visit the human dwellings more than the forest and thus exhibit a habitat preference. Moreover, the stress and anxiety-tolerant voles occupying the human dwelling to a larger degree were temporally closer to each other posing a potential risk for encountering pathogens. However, no PUUV was detected, indicating that infection risk was low and that neither of the habitats act as an infection hub or refugia during the study period. Furthermore, overwintering survival showed tendencies of being positively affected by anxiety- and stress-tolerance. However, the mechanisms behind this remain undetermined. Consequently, this pilot study provides evidence for personality-dependent local movements and provides a compelling argument for further long-term studies of the interaction between personality-dependent movement and ecological factors as well as their effect on survival.

Keywords: Animal personality, Behavior, Infection, Movement, *Myodes glareolus*, Puumala orthohantavirus

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Abbreviations

AIC	Akaike's Information Criterion
BLUP	Best linear unbiased predictor
FA	Factor analysis
GLM	Generalized linear model
HFRS	Hemorrhagic fever with renal syndrome
LMM	Linear mixed model
NE	Nepthopathia epidemica
PUUV	Puumala orthohantavirus

1. Introduction

Animal personality (AP) has gained interest in recent years and been shown to exist throughout the animal kingdom (Boyer et al., 2010, Coleman and Wilson, 1998, Dingemanse et al., 2003, Ducatez et al., 2012, Lantova et al., 2011, Myers and Krebs, 1971, Nilsson et al., 2014). It is defined as consistent inter-individual differences in behavior and is analogous to the term ‘behavioral syndrome’ which refers to suites of correlated behaviors (Lantova et al., 2011, Nilsson et al., 2014, Sih et al., 2004). Thus, personality traits include behavioral traits such as boldness, exploration, activity, sociability and aggression, whereas behavioral syndromes refer to correlations between such traits, e.g. the boldness-activity-aggression syndrome where bold individuals are more active and aggressive than shyer individuals (Dingemanse et al., 2007, Wolf and Weissing, 2012). Personality affects many life decisions and potentially has major consequences on ecological and evolutionary processes (Nilsson et al., 2014, Sih et al., 2004, Wolf and Weissing, 2012).

1.1. Animal Personality and Movement

Movement is one important aspect of an animal’s life that is impacted by personality (Cote et al., 2010, Hoset et al., 2011, Myers and Krebs, 1971, Nilsson et al., 2014, Patrick and Weimerskirch, 2014, Schirmer et al., 2019). There are often systematical differences in habitat use, activity patterns and foraging styles between behavioral types, i.e. a specific combination of behavioral tendencies such as being bold and active (Boon et al., 2008, Pearish et al., 2013, Sih et al., 2004, Wolf and Weissing, 2012). Most research, however, has focused on the effect of personality on dispersal and large-scale movements, leaving the effects on local movements largely understudied (Nilsson et al., 2014, Schirmer et al., 2019). Nevertheless, personality traits affect not only movement between habitats but also the distribution of individuals within habitats (Kobler et al., 2009, Wilson, 1998, Wolf and Weissing, 2012). Behavioral type-environment correlations result in non-random spatial distribution of individuals and, thus, non-random interactions between individuals (Pruitt and Ferrari, 2011, Pruitt and Modlmeier, 2015, Wolf and Weissing, 2012). Bank voles (*Myodes glareolus*), for example, exhibit personality-dependent space use and movement with bolder individuals occupying larger areas and moving longer distances than shyer conspecific (Schirmer et al., 2019). Additionally, bolder individuals spatially overlap with fewer conspecific and differ from shyer individuals in their choice of microhabitat (Schirmer et al., 2019).

A key question that is understudied in movement ecology and personality studies is how personality covaries with movement strategies in the wild (Nilsson et al., 2014). Individual differences in foraging behavior offer a key opportunity to study consistency of local movements and several studies have found personality-dependent local movements by studying foraging behavior (Patrick and Weimerskirch, 2014, Van Overveld and Matthysen, 2010). Fast exploring great tits (*Parus major*), for example, reacted quicker and shifted to other foraging areas sooner when food resources decrease than their slow-exploring conspecifics (Van Overveld and Matthysen, 2010). Consequently, personality differences in movement may have larger consequences on fitness (Nilsson et al., 2014). High activity and exploration could be advantageous in a heterogeneous environment if it increases the chance of finding important resources (Wolf et al., 2007). Nevertheless, fitness costs associated with increased risk of encountering predators and parasites may counterbalance this advantage (Boyer et al., 2010, Sih et al., 2004, Wilson et al., 1993).

1.2. Personality and Pathogens

Although many ecological factors have been postulated to shape animal personality and behavioral syndromes, attention has mainly focused on resources competition and predation, leaving other ecological factors unexplored (Barber and Dingemanse, 2010). In fact, other ecological factors may have major influences on the evolution of animal personalities, pathogens being one such potentially important factor (Barber and Dingemanse, 2010). The behavior of an individual has implications for the level of pathogen exposure and variation in behavior will consequently lead to differences in exposure (Barber and Dingemanse, 2010, Hart, 1990). Personality differences and personality-dependent space use have been found to affect parasite load and infection probability (Boyer et al., 2010, Dizney and Dearing, 2013, Wilson et al., 1993). For example, bolder North American deer mice (*Peromyscus maniculatus*) are more likely to be infected by Sin Nombre virus than shy conspecifics (Dizney and Dearing, 2013), and bold and active Siberian chipmunks (*Tamias sibiricus*) occupy larger areas and have a higher parasite load (Boyer et al., 2010). On the other hand, pathogens may also affect host behavior to increase transmission efficiency (Barber and Dingemanse, 2010).

Pathogen infections have substantial potential impacts on the host animals' fitness because they can both directly and indirectly harm the host (Barber and Dingemanse, 2010, Read, 1990). Hence, avoiding pathogens may have similar fitness pay-offs as predator avoidance (Barber and Dingemanse, 2010). Similar to the effect of variation in predation, the threat of pathogen infection across populations of host species leads to the evolution of morphology and behavior (Barber and Dingemanse, 2010, Reimchen, 1994).

With regards to exposure to pathogens and resource competition, personality differences in space use can have broad consequences on individuals (Nilsson et al., 2014). Personality, including boldness and activity, has been found to affect survival probability, but the effect depends on population dynamics and other ecological factors, such as habitat use (Boon et al., 2008, Foster et al., 2017, Haage et al., 2017, Homberger et al., 2021, Piquet et al., 2018, Richardson et al., 2019, Santicchia et al., 2018, Vanden Broecke et al., 2021, Yli-Renko et al., 2015).

1.3. Zoonotic diseases

Zoonotic diseases, i.e. diseases transmitted from vertebrate animal hosts to humans and vice versa, constitute the majority of known human pathogens (Khalil et al., 2014, Woolhouse and Gowtage-Sequeria, 2005). Such diseases result in great socio-economic costs and, due to anthropogenic land-use changes, their incidence and risk to our society is increasing (Chomel et al., 2007, Gottdenker et al., 2014, Khalil et al., 2014). Increased transmission and proportion of pathogen host species in disturbed areas are likely to be mediated by behavioral, ecological, and life-history trait of host species (Gibb et al., 2020, Gottdenker et al., 2014). Because the magnitude of these trends is especially strong for rodents, they have been pointed out as a globally important reservoir host (Gibb et al., 2020, Han et al., 2015).

1.3.1. Puumala orthohantavirus and bank voles

Puumala virus (PUUV) is an *orthohantavirus* that causes nephropathia epidemica (NE), a mild form of hemorrhagic fever with renal syndrome (HFRS), in humans (Kallio et al., 2007, Olsson et al., 2010). There are more than 10 000 cases annually of HFRS in Europe and most of these are NE (Vaheri et al., 2013). Human infection mainly occurs through inhalation of the viral particles excreted or secreted by infected rodents (Khalil et al., 2014). Bank voles, the only known reservoir host of PUUV, is one of the most abundant and widespread mammal species in Europe (Mitchell-Jones, 1999, Olsson et al., 2010). Transmission among bank voles occurs horizontally through direct and indirect contact and is density-dependent (Dobly et al., 2012, Gavrilovskaya et al., 1990, Kallio et al., 2006). The virus is chronic for the vole and can be infectious for the duration of life (Kallio et al., 2007, Meyer and Schmaljohn, 2000).

Although PUUV previously has been thought to be asymptomatic in bank voles, Kallio et al. (2007) showed that PUUV in fact decreases their overwinter survival.

Furthermore, previous studies have shown that bank vole population density and winter weather conditions predict NE incidents among humans, with an increasing risk of NE during high population density and rainy winters (Khalil et al., 2014). Sipari et al. (in print) have shown that rainy early winter promote PUUV transmission among bank voles, and Khalil et al. (2014) suggest that the increase of NE during rainy winters is caused by movement of voles into human dwellings due to decreased access to food and hiding places. In fact, juvenile and subadult bank voles infected by PUUV have shown higher mobility than uninfected conspecific (Escutenaire et al., 2002). Nevertheless, how environment and behavioral traits affect the movement of voles, pathogen transmission among voles and subsequent human infection by PUUV remains unsolved (Khalil et al., 2014).

2. Aim and objectives

As the movement of animals has been shown to correlate with certain personality traits or behavioral syndromes, it is of interest to investigate which voles move into human dwellings in search of resources and what behavioral characteristics they possess. Furthermore, from a human health point of view, it is imperative to examine if the individuals that move into human dwellings are more or less likely to carry and/or be infected by zoonotic pathogens, specifically PUUV. Therefore, I investigated (see also **Figure 1**):

1) What individual variation in local movements (habitat use and activity patterns) bank voles exhibit.
2) If individual variation in movement can be explained by personality differences.
3) If there is an interaction between infection, personality, and local movements.
4) If overwintering survival is affected by PUUV infection, personality, and local movements.

I hypothesized that voles exhibit individual variation in movement and that active, explorative, and bold voles move into human dwellings and are more likely to carry PUUV. The effects of PUUV, personality and movement on survival are harder to predict as the increased survival from movement into human dwelling could be counteracted by infection risks and thus result in a seemingly similar survival compared to voles that move in the adjacent forest.

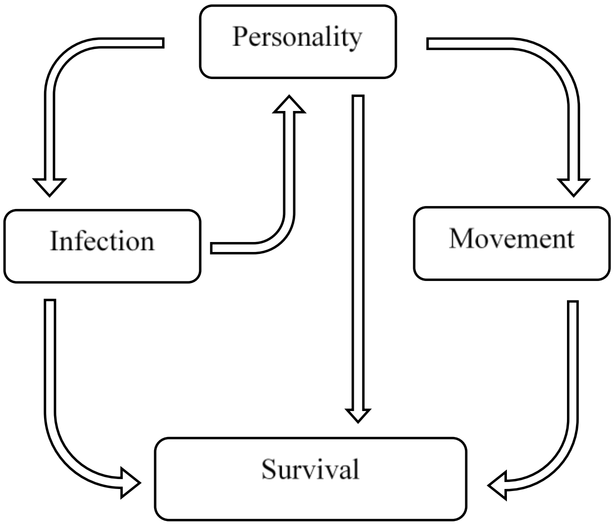

Figure 1: *Flow chart of variables under investigation showing the potential interaction between personality, infection and movement and their subsequent effects on survival.*

3. Methods

3.1. Study species

Bank voles are widely distributed in Europe (Mitchell-Jones, 1999). They occupy a variety of habitats and can tolerate anthropogenic disturbance (Ecke et al., 2002). Population densities vary seasonally and at especially northern latitudes with a 3-4 year cycle (Hörnfeldt, 2004). Females are territorial, especially during the breeding season in April-October when they reduce their home ranges (Koskela et al., 1997). Males, on the other hand, are not territorial and often overlap with various female territories (Andrezejewski and Mazurkiewicz, 1976, Mazurkiewicz, 1971). Bank voles have a polyphasic activity rhythm with higher activity during twilight but some activity throughout the course of the day (see appendix 1).

3.2. Data collection

In broad terms, data collection consisted of three parts: 1) trapping, swabbing for PUUV and tagging voles, 2) conducting arena experiments, and 3) tracking movements using ‘vole boxes’. I conducted vole trapping for personality tests during the winter of 2020/2021 which was a year of low bank vole population densities (Ecke and Hörnfeldt, 2021). I captured voles

***Figure 2**: Aerial photograph of the field site with location of stations for trapping and monitoring of rodent movement. Yellow dots show 'vole boxes' in the human dwelling and blue dots show 'vole boxes' in the adjacent forest. Red dots show where the traps were located. Source: ESRI, Maxar, GeoEye, Earthstar Geographics, CNES/AIRbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.*

at one field site in Umeå, Northeastern Sweden by using 14 traps (Ugglan, Grahnab, Sweden) placed in two different habitats: 1) in or near human dwellings, and 2) adjacent mixed coniferous and deciduous forest (**Figure 2**). This field site was chosen because it is known to previously having had a large bank vole population infected with PUUV (personal communication Frauke Ecke). I covered the traps with a plastic box to provide easy access after snowfall and baited them with sunflower seeds and apples and placed a ball of wood shavings for shelter. I conducted a first block of trapping and personality testing over a four-week period in November consisting of four separate trapping sessions. Each trapping session included two nights of trapping. I set up the traps in the afternoon of day one and then checked in the evening of day one, morning, afternoon, and evening on day two as well as the morning and (occasionally) the afternoon of day three. Finally, I collected the traps after the morning or afternoon check of day three. One more trapping session was conducted in the beginning of February. Every captured individual was tagged with a passive integrated transponder (PIT), sexed, weighed, mouth swabbed for future analysis of PUUV-shedding and exposed to an arena test for assessing personality. PIT tags where inserted underneath the skin of healthy individuals giving each individual a unique bar code that can be detected by a scanning device emitting a low-frequency radio signal. PIT-tagging is a widely adopted method of tagging small mammals and, if inserted correctly, PIT-tags will remain with the individual throughout its life span and not affect its behavior (Schooley et al., 1993). Mouth swabbing, personality test and weighing were repeated once for each session for every caught individual. To reduce stress and potential effects of the voles' behavior, I conducted the arena tests on recaptured voles at least one day after an individual had been PIT-tagged. To investigate repeatability of vole behavior, the personality tests were repeated the next session if a vole was recaptured.

Permission to trap and handle animals has been obtained from the Swedish Environmental Protection Agency (SEPA, latest permission: NV-07483-19) and from the Animal Ethics Committee in Umeå (latest permission: Dnr A2-2018).

3.2.1. Arena personality test

Figure 3: Arena experiment set up consisting of an arena divided into 16 sections and a pipe connected to it with a door at each end.

The arena test combines two commonly used tests for personality: the *dark-light test* and the *open-field test* and thus allowed me to test the personality of the voles in field (Archer, 1973, Herde and Eccard, 2013). The test setup consists of a circular arena (1.30 m diameter and 30 cm height plus ~10 cm extra glass plate attached) divided into 16 sections and has an opaque plastic pipe attached to it (**Figure 3**). At each end of the pipe there is a swing door. The procedure starts with connecting the trap to the tube attached to the arena and recording the time it takes for the vole to exit the trap and enter the tube. This was done to avoid handling of the voles and thus minimize human interference with the animals. Thereafter, the latency to enter the arena from the tube was recorded (*dark-light test*). If the individual did not enter within 5 minutes, it was gently forced into the open arena. The vole was then observed for 5 minutes in the arena (*open-field test)*. While in the arena several behaviors were recorded: 1) latency to enter the middle section, 2) number of sections explored, 3) number of crossings between sections, 4) number of crossings into middle area, and 5) the behavior or activity (running, jumping, grooming, scanning or no activity) for each 10-second interval.

To reduce interference by the observer a camera was set up to record the whole arena experiment and the behavior of the vole was observed both during and after the experiment. The test was only conducted in daylight and good weather conditions, to avoid behavioral changes caused by rain or other environmental factors. The arena experimental setup was executed in accordance with Schirmer et al. (2019) noting down jumping, grooming, running, sitting and moving head scanning, climbing, rearing as well as biting for “active” behavior and sitting and doing nothing as “non-active” behavior.

3.2.2. Vole boxes

__Figure 4__: 'Vole box' set up. The top picture shows the camera trap facing a box placed in the human dwelling and the bottom picture shows the tube going through the box where voles can run through.

To record vole movement (habitat use and activity patterns) without human interference boxes with a receiver for detecting PIT-tags were placed at the field site (**Figure 4**). The boxes have a tube running through them and record individuals that enter the tube. Five of these boxes were placed in human dwellings and five in the adjacent forest. They were then baited regularly with sunflower seeds and dried apples before and after every session. At each vole-box a camera trap was placed facing the two entries of the tube going through the box and set to film individuals entering and exiting the box. These videos were used to verify number and length of visits by voles. Data from these boxes on number of visits, length of visits and time between visits was then determined for each tagged individual.

The boxes were up and running during the whole trapping block in November. The tubes were cleaned and disinfected with ethanol before the start of each session. Some problems with the batteries occurred which might have resulted in missing data for some time occasions but could not be confirmed. The boxes were placed in a cluster close by traps in each habitat (forest and indoor habitat). Because this method of recording movement is in development, this placement was done to ensure that trapped and tagged individuals would be recorded. In each cluster, boxes were placed at least 5 meters apart in places where voles were presumed to travel (e.g. sheltered shed and wood pile in the human dwellings, and next to log or holes in the ground in the forest). Nevertheless, due to difficulties in finding suitable spots for the box and camera trap, two boxes in the indoor habitat were placed less than 5 meters apart (~4 meters). Furthermore, the location of one box and accompanying camera trap were moved due to the complete absence of vole visits to this box and the trap located nearby.

The ‘vole box’ antenna records ~6 times per second if an individual is continuously staying underneath the antenna. One antenna is located at each side of the tube making it possible to determine which side of the box the animal is entering and exiting. Thus, and with help from camera trap footage, it is possible to determine how long the individual is staying inside the tube feeding.

3.2.3. Infection detection

The inside of the vole's mouth was swabbed for detecting PUUV-infection. This method detects if an individual is currently shedding the virus. Because the animals may not always shed the virus (Hardestam et al., 2008), samples were taken from recaptured animals once every session. I preserved the samples in virus transport media (VTM) and stored them in -80°C until analysis at the Department of Virology, Umeå University.

Upon analysis, extraction of viral RNA was performed using QIAmp® Viral RNA Mini Kit (QIAGEN, Hilden, Germany) in accordance with the manufacturer's protocol (Spin Protocol). The extracted RNA was then converted to cDNA using the Revert Aid RT kit (Thermo Fisher Scientific, Vilnius, Lithuania) following the manufacturer's instructions and, subsequently, a nested PCR was performed targeting the S gene of the Puumala orthohantavirus as described by Milhano et al., (2017). As such, a two-step PCR was performed using the Phusion Green Hot Start II High-Fidelity PCR Master Mix (Thermo Fisher Scientific, Vilnius, Lithuania). Thereafter, the PCR product was analyzed by gel electrophoresis using 3% agarose in 1x TAE with GelRed (Biotium In. Hayward, CA, US), purified with ExoSAP-IT kit (Thermo Fisher Scientific, Vilnius, Lithuania) and sent to Eurofin Genomics (Germany) for Sanger sequencing. Finally, the obtained sequences were aligned to previously identified Puumala orthohantavirus strains in GenBank using the Basic Local Alignment Search Tool (BLAST) provided by National Center for Biotechnology Information.

3.3. Statistical analyses

All statistical analyses were done in RStudio (R Core Team, 2021).

3.3.1. Local movements

I analyzed differences in movement – habitat use and activity patterns (specifically, time since previous vole visit, length of visits and number of visits per day in each habitat) – from logged visits in the vole boxes with linear mixed models (LMMs) using the *lmer* function from the *lme4* package (Bates et al., 2015). I included habitat, vole, and time after baiting as fixed factors and time as a random factor. I included time after baiting as fixed to control for any differences in activity that might have been caused by the amount of food available in the vole boxes. Furthermore, including time as random controlled for any differences in activity over the trapping season. Because of difficulties to interpret the biological meaning of three-way interactions I excluded the three-way interaction between habitat, vole, and baiting before running the model. Moreover, I excluded non-significant interactions from the final models. Because there were uncertainties with the validation of some visits to the vole boxes, I constructed a set of rules used for extracting the visits from the data loggers. I ran analyses based on 6 different extraction assumptions. Because the results were qualitatively similar for all datasets, I only present the results from the combination of two extraction rules. I chose the data set with different extraction assumptions for “outside” data loggers and “inside” datalogger because this minimized the error in number of visits. However, because there were fewer validated visits for the outside, the uncertainty may be higher for the extracted visits from the forest loggers. After running the models, I conducted post hoc tests on the interactions that had a significant effect on the foraging behavior using the *glht* function from the *multcomp* package (Hothorn et al., 2008). A total of 10 out of 11 tagged voles visited the vole boxes and were included in these analyses.

3.3.2. Multivariate analysis of personality

A total of 16 observations of nine voles (with repeated measures of 5 voles) were included in the multivariate analysis. From arena-experiment data, I calculated the proportions spent doing each behavior and included this value in the analysis. I applied a principal component analysis (PCA) using the *prcomp* function form the *stats* package (R Core Team, 2021) and factor analysis (FA) using the *fa* function from the *psych* package (Revelle, 2020) to the correlation matrix of 15 behavioral variables, reducing the number of variables to a few principal components/factors. To determine the number of components and factors retained I used the Kaiser-Guttman criterion (i.e. eigenvalue > 1) (Kaiser, 1991). The results of the two analyses were similar, however, because the FA discriminated better among personality traits, I continued further analysis using the results from this analysis. To enhance interpretability of the factor loadings, I applied varimax rotation to the FA which maximizes the variance of the loadings within the factor analysis and thus better distinguishes the behavioral variables into separate components. I then calculated the factor scores using the Bartlett method of estimating factor scores. I decided to use the Bartlett method because it produces unbiased estimates of the true factor score by using maximum likelihood method estimates, a statistical method which produces estimates that are the most likely to represent the “true” factor scores (DiStefano et al., 2009).

I ran a repeatability analysis of a selection of the data (voles with multiple personality measurements), using *rptR* package and *rpt* function (Stoffel et al., 2017). Because a single value of each personality trait per vole is needed for analysis in the generalized mixed models and survival analysis, I used best linear unbiased predictors (BLUPs) from LMMs with FA scores as dependent variable with test occasion as fixed factor and individual voles as random factors. Additionally, for FA1 I included freezing temperature as a fixed factor since this determined if the personality trait was repeatable or not.

3.3.3. Personality effects on local movements

I analyzed the effect of personality on local movements using LMMs with personality (FA) scores and habitat as fixed factors and individual vole as random factors (to account for non-independence of data points). I included the interaction between habitat and personality to investigate potential differences in the slope of activity by personality in the two different habitats. I explored the effect of personality on proportion spent in human dwelling with generalized linear models (GLMs) with BLUP personality scores as fixed factors, using the *glm* function from the *stats* package (R Core Team, 2021). However, because I derived the proportion spent in human dwellings from the ‘number of visits’ data and because I excluded variation in vole personality using the BLUP scores, I decided to only keep the LMM analyses which similarly analyzed this aspect of movement.

3.3.4. Survival

I ran survival models using a robust method from the RMarked package (Laake, 2013). In the full model I constructed estimated survival based on sex, body weight, proportion spent in human dwelling, BLUP personality scores, and on the interaction between proportion spent in human dwellings and each personality factor. I then constructed all possible variations of simpler models and selected the most parsimonious model using the Akaike's Information Criterion for small sample size (AICc) and choosing models with ΔAICc ≤ 2 as having substantial support (White and Burnham, 1999, Burnham and Anderson, 2004). Because only trapping was repeated in February of 2021 to check if voles had survived or remained in the location over the winter, I used only the trapping data for the survival analysis.

4. Results

I trapped and recorded a total of eleven voles with a total number of 1412 visits in the ‘vole boxes’ and conducted personality experiments on nine of these (**Table 1**). Eight of the caught voles visited boxes in the human dwellings and six visited boxes in the adjacent forest. One vole did not visit any box, likely because it was caught and tagged on the last day of fieldwork. None of the saliva samples tested positive for PUUV infection and thus shows that none of the voles were shedding viral particles during the course of my study. Because no vole was infected by PUUV I excluded the infection aspect from my analysis.

***Table 1**: Descriptive information for all captured and tagged voles. M = Male, F = Female.*

	Vole										
Variable	***1***	***2***	***3***	***4***	***5***	***6***	***7***	***8***	***9***	***10***	***11***
Sex	M	M	M	M	F	F	M	M	M	M	F
Body weight	14.9	13.4	16.7	16.1	20.6	14.0	15.8	15.0	15.1	23.5	14.0
Proportion spent in human dwelling	0.00	1.00	1.00	0.00	1.00	0.56	0.95	1.00	1.00	0.69	0.00
Number of visits to vole boxes	56	3	275	63	65	312	263	8	332	35	0
Number of arena tests	1	1	2	1	1	4	2	0	2	2	0

4.1. Local movements

4.1.1. Number of visits

All factors (habitat, vole, and baiting) affected the number of visits by voles to the boxes. This included more visits in human dwellings than forests (df = 276.07, F-value = 48.25, P-value < 0.001, **Figure 5**), and a difference in number of visits between voles, with some making more visits than others (df = 274.44, F-value = 14.79, P-value < 0.001, **Figure 7**). Furthermore, number of visits depended on food availability in the vole boxes as shown by the decrease in number of visits with days after baiting (df = 281.90, F-value = 4.22, P-value = 0.041, **Figure 6**). Lastly there was an interaction between habitat and vole with a difference in behavior where certain voles made more visits in one habitat than the other (df = 276.07, F-value = 21.06, P-value < 0.001, **Figure 8**).

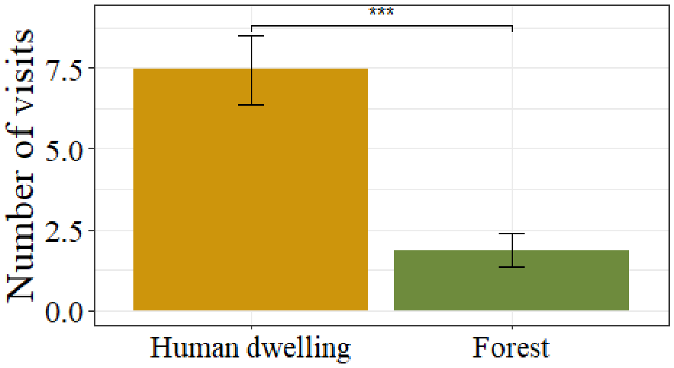

Figure 5: *Mean number of visits (+- standard error) by voles per day in the 'vole boxes' in the human dwelling versus adjacent forest. Plots show original data that has not been logarithmized. Stars represent significance level.   *** = <0.001*

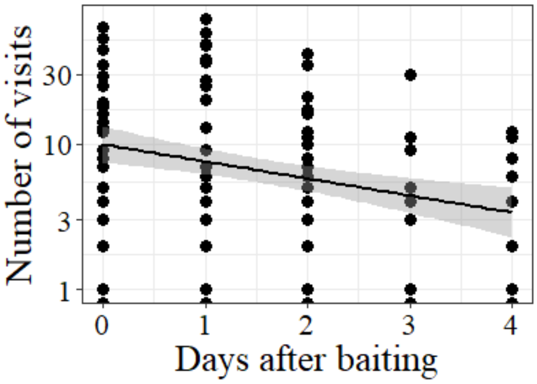

***Figure 6**: Mean number of visits per day made by voles in the 'vole boxes' by time after baiting. ‘0’ indicates day of baiting and 1-4 indicates how many days after baiting has occurred. Plots show original data that has not been logarithmized.*

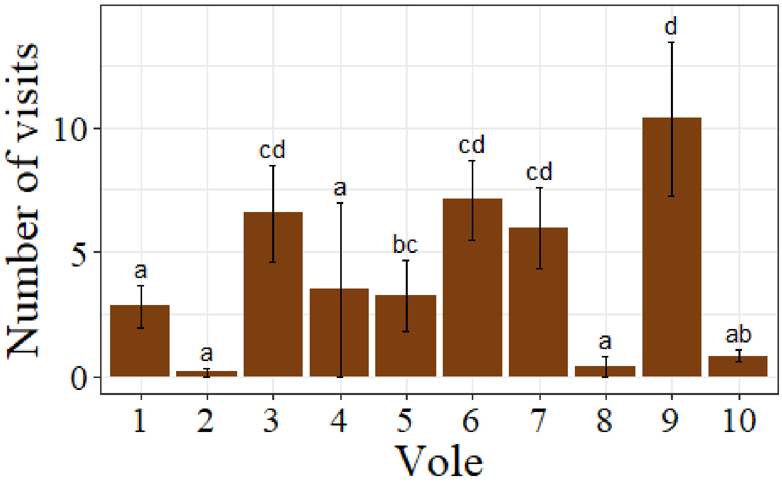

Figure 7: *Mean number of visits (+- standard error) made per day in the 'vole boxes' by each vole. Letters indicate differences among groups. If voles share the same letter, they do not differ in number of visits made to the boxes and if they do not share any letters, they are significantly different from each other. Plots show original data that has not been logarithmized.*

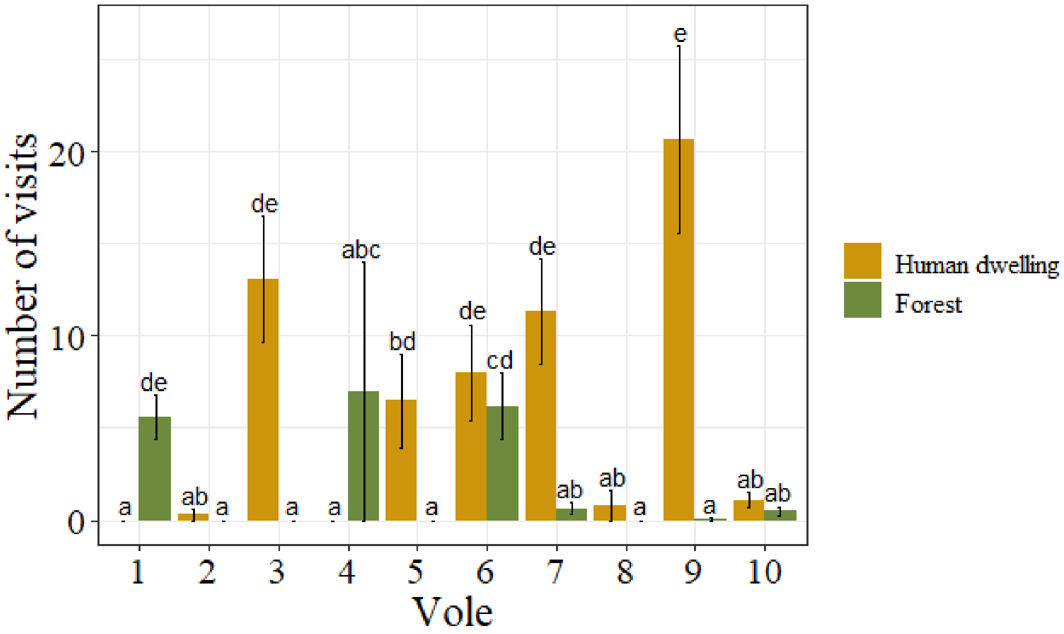

Figure 8: *Mean number of visits (+- standard error) per day in the 'vole boxes' made by each vole in the human dwelling versus adjacent forest. Letters indicate differences among groups. If voles share the same letter, they do not differ in number of visits made to the boxes and if they do not share any letters, they are significantly different from each other. Plots show original data that has not been logarithmized.*

4.1.2. Length of visits

All main effects affected the length of visits to the vole boxes. Visits were longer in the forest than in the human dwellings (df = 100.28, F-value = 5.94, P-value = 0.017, **Figure 9**) and, on average, vole '3' made longer visits than vole '9' (df = 95.34, F-value = 2.17, P-value = 0.031, **Figure 11**). The interaction between habitat and vole (df = 98.69, F-value = 6.57, P-value < 0.001, **Figure 12**) showed that only the length of visits for vole '9' in the human dwelling was lower than the visits by vole '6' in the forest. Similar to the number of visits, the length of visits depended on food availability and decreased with days after baiting (df = 59.82, F-value = 19.92, P-value < 0.001, **Figure 10**).

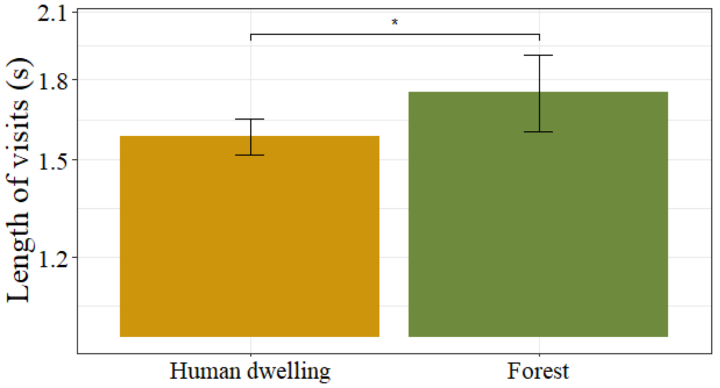

Figure 9: *Mean length of visits (in seconds) (+- standard error) made by voles in the 'vole boxes' in the human dwelling and the adjacent forest. * = level of significance p < 0.05.*

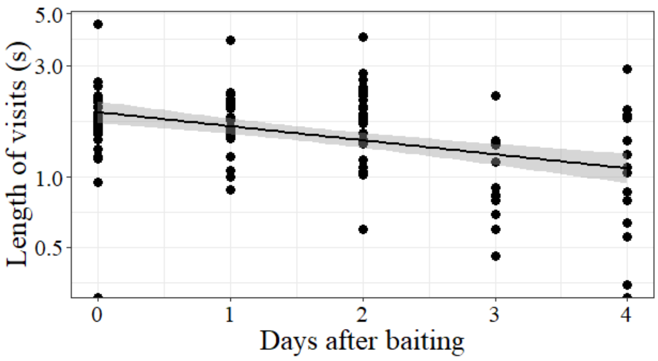

Figure 10*: Mean length of visits (in seconds) made by voles in the 'vole boxes' by time after baiting. '0' indicates day of baiting and 1- 4 indicates how many days after baiting has occurred.*

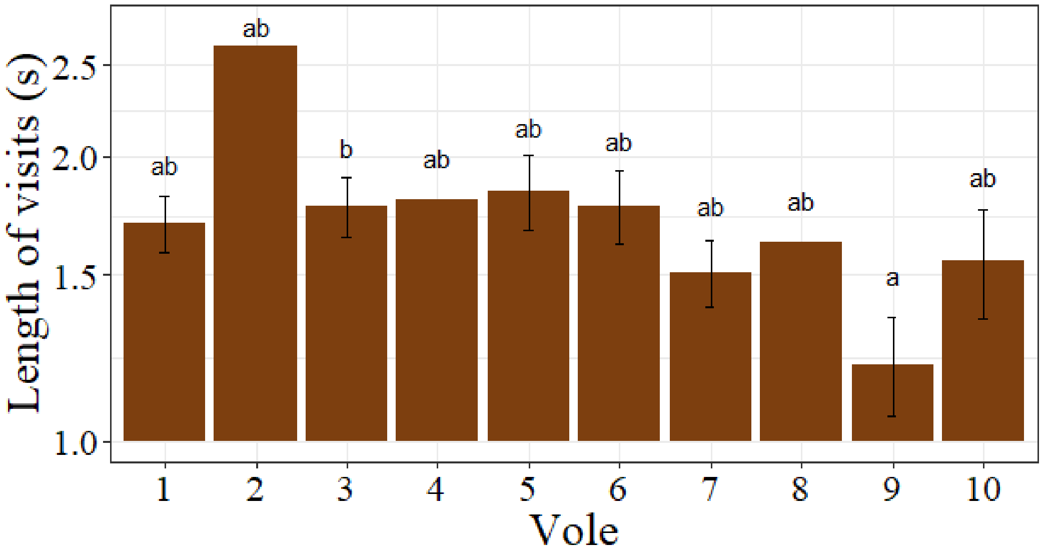

Figure 11: *Mean length of visits (in seconds) (+- standard error) for each vole in the 'vole boxes'. Letters indicate differences among groups. If voles share the same letter, they do not differ in number of visits made to the boxes and if they do not share any letters, they are significantly different from each other.*

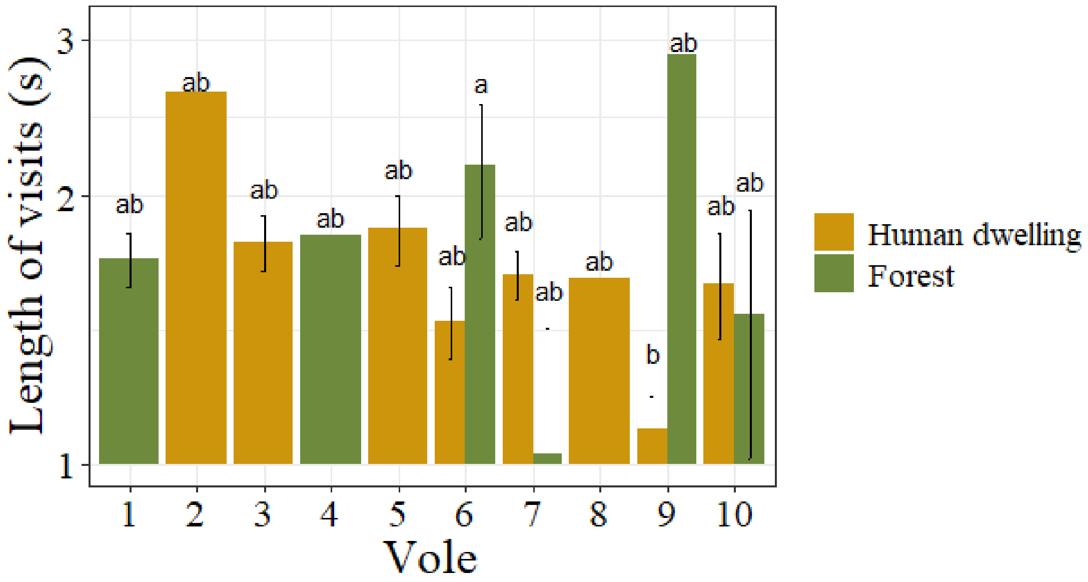

Figure 12: *Mean length of visits (in seconds) (+- standard error) made by each vole in the human dwelling versus the adjacent forest Letters indicate differences among groups. If voles share the same letter, they do not differ in number of visits made to the boxes and if they do not share any letters, they are significantly different from each other.*

4.1.3. Time since visit by another vole

Time since previous vole visit tended to differ between the habitats (df = 90.92, F-value = 3.79, P-value = 0.055, **Figure 13**) and voles (df = 92.11, F-value = 1.76, P-value = 0.087, **Figure 15**). The time since previous vole visit was shorter in the human dwelling than the forest and vole ‘4’ had longer time since previous vole visit than vole ‘3’, ‘6’ and ‘10’. There was, however, no interaction between these factors. Furthermore, there was an increase in time between visits by different voles with increased time after baiting (96.99, F-value = 7.47, P-value = 0.007, **Figure 14**).

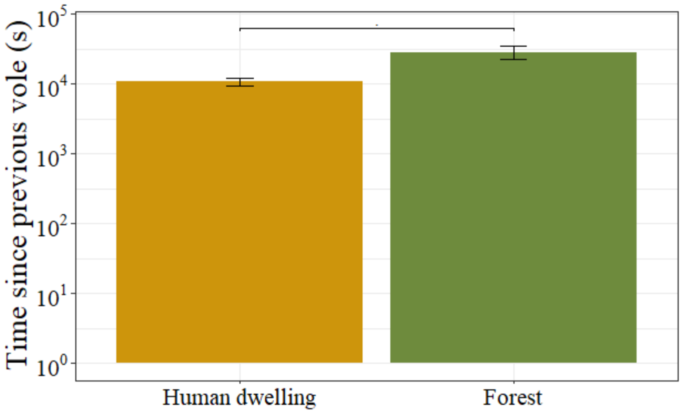

Figure 13: *Mean time (in seconds) (+- standard error) since previous visit by another vole (i.e. time between visits by different voles) in the 'vole boxes' in the human dwelling versus adjacent forest.*

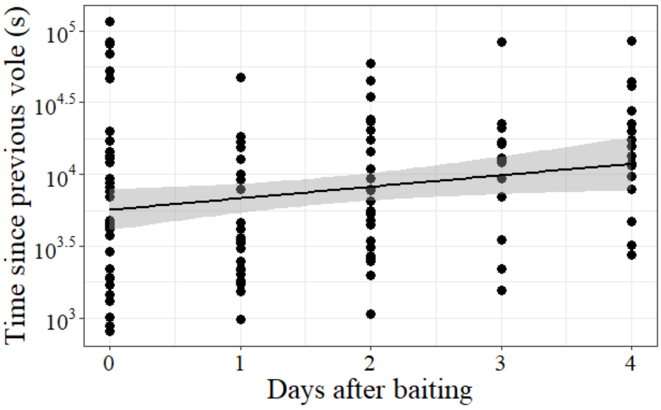

Figure 14: *Mean time (in seconds) since previous visit by another vole (i.e. time between visits by different voles) in the 'vole boxes' by time after baiting. '0' indicates day of baiting and 1- 4 indicates how many days after baiting has occurred.*

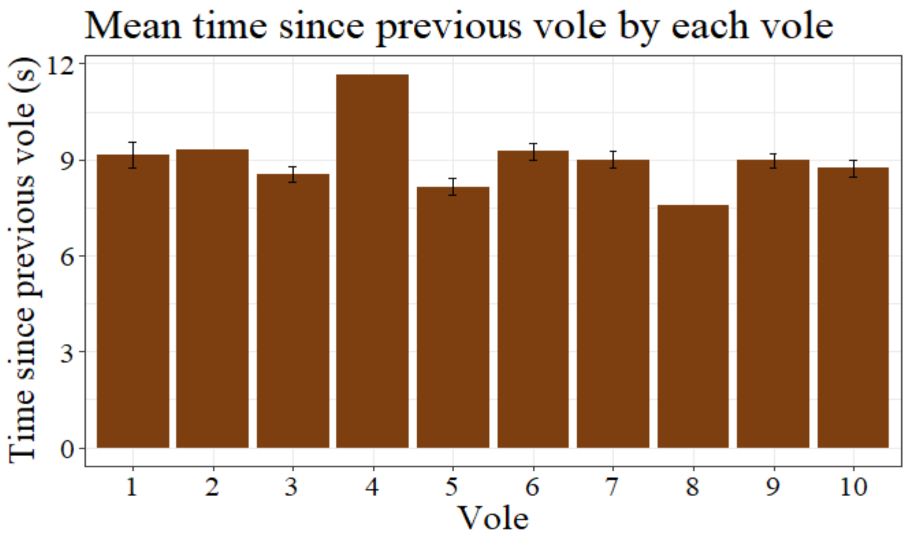

Figure 15*: Mean time (in seconds) (+- standard error) since previous visit by another vole in the 'vole boxes' (i.e. time between visits by different voles) for each vole (1-10).*

4.2. Personality

I retained three FA factors from the arena experiments which explained 60% of the total variance (**Table 2**). The first factor (FA1) included high positive loadings for number of sections explored, number of crossings, proportion spent jumping and running and a negative loading of proportion spent doing nothing (**Table 2**). I interpreted this factor as overall activity. The variables that loaded positive for the second factor (FA2) included proportion spent climbing and searching as well as the number of jumps, whereas latency of entering the tube and proportion spent doing nothing loaded negatively (**Table 2**). This factor therefore likely reflects escaping behavior. Lastly, the third factor (FA3) was characterized by negative loadings for proportion spent grooming, biting, and scanning (**Table 2**) and thus, likely reflects anxiety and stress (sensu Brehm et al., 2020, Mogil, 2019). Because higher values reflect less anxiety and stress, I referred to this trait as ‘anxiety- and stress-tolerance’. The repeatability analysis on the selected dataset showed that FA2 (R = 0.573, D = 3.28, df = 1, P = 0.0352, **Table 2**) and FA3 (R = 0.699, D = 5.29, df =1, P = 0.0107, **Table 2**) were repeatable over time. Nevertheless, because two out of seven repeated arena experiments were conducted at temperatures below 0°C and seemed to considerably affect the voles’ behavior by increasing their thermoregulating behavior, I decided to run another model controlling for below 0°C. The results from this model demonstrated that all factors were significantly repeatable over time (FA1: R= 0.551, D = 2.79, df = 1, P = 0.0473; FA2: R = 0.855, D = 11.1, df = 1, P < 0.0004; FA3: R = 0.577, D = 3.55, df = 1, P = 0.0297, **Table 2**).

Table 2: *Factor analysis (FA) loadings for behaviors in arena test, including repeatability of the factors. FA scores larger than 0.4 in absolute value are in bold. Repeatability scores in bold indicate significant repeatability over time.*

Behavior	***FA1***	***FA2***	***FA3***
Latency tube	-0.225	**-0.613**	0.187
Latency arena	-0.283	-0.092	0.333
Latency mid area	0.014	-0.292	0.273
Number of sections	**0.689**	-0.067	-0.121
Number of crossings all	**0.888**	-0.043	0.142
Number of crossings mid	**0.909**	0.011	0.107
Number of jumps	**0.752**	**0.539**	0.141
Proportion jumping	**0.540**	0.295	-0.100
Proportion running	**0.940**	-0.073	0.113
Proportion grooming	-0.279	-0.145	**-0.624**
Proportion scanning	-0.002	-0.287	**-0.623**
Proportion climbing	-0.169	**0.905**	0.121
Proportion rearing	-0.069	**0.842**	0.351
Proportion biting	-0.011	0.27	**-0.479**
Proportion nothing	**-0.55**	**-0.727**	0.267
% Total variance	29.2	20.6	10.2
% Repeatability	0	**57.3**	**69.9**
% Repeatability, controlled for < 0°C	**55.1**	**85.5**	**57.7**

Table 3: *Table 3: Personality scores obtained from best linear unbiased prediction (BLUP) analysis of FA1-3.*

	Vole										
Personality trait	***1***	***2***	***3***	***4***	***5***	***6***	***7***	***8***	***9***	***10***	***11***
Activity (FA1)	-1.06	0.41	0.31	1.36	0.39	0.05	-0.44	NA	0.77	-0.69	NA
Escaping behavior (FA2)	-1.00	0.98	0.39	0.23	0.97	0.18	-0.56	NA	0.39	-0.40	NA
Anxiety- and stress-tolerance (FA3)	-1.39	-0.58	0.01	-0.20	0.46	0.22	0.75	NA	0.56	-1.54	NA

4.2.1 Effect on indoor movement

Linear mixed models showed that FA3 in interaction with habitat had a significant effect on number of visits to vole boxes (df = 17.94, F = 9.28, P = 0.007, **Figure 16**), with an increase in number of visits for higher scores of FA3 in the human dwelling compared to in the forest. Furthermore, similar to number of visits, linear mixed models showed that only FA3 in interaction with habitat had a significant effect on time since previous vole visit (df = 9.52, F = 10.43, P = 0.01, **Figure 17**), with shorter time between visits in the human habitat than the forest for more anxiety- and stress-tolerant voles. However, none of the personality traits had any effect on mean time spent per visit.

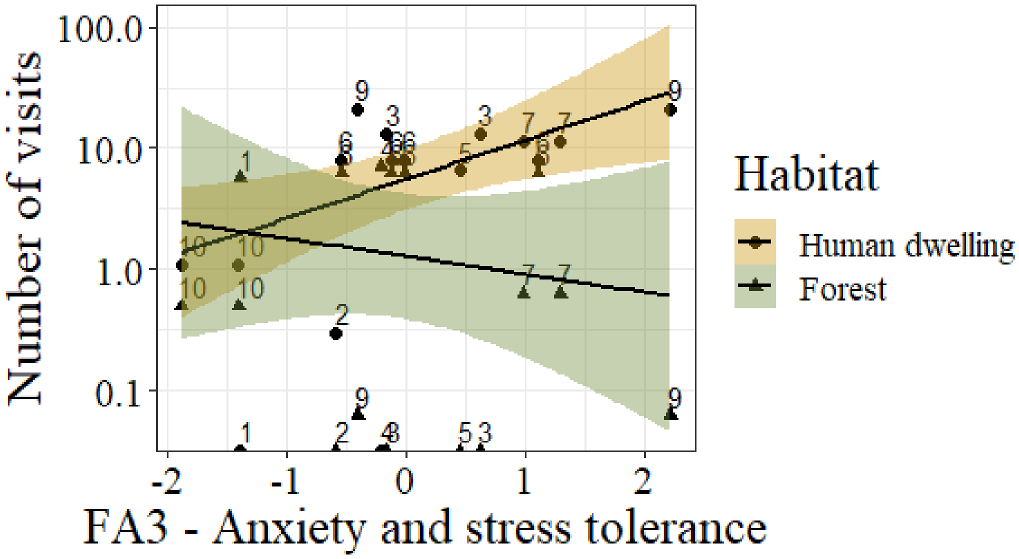

Figure 16: *The effect of anxiety and stress tolerance (FA3) on number of visits made per day by voles in the 'vole boxes' in the human dwelling versus adjacent forest. Lower x-values represents more anxious voles and higher values represents less anxious, i.e. more anxiety and stress tolerant voles. Numbers denote individual voles.*

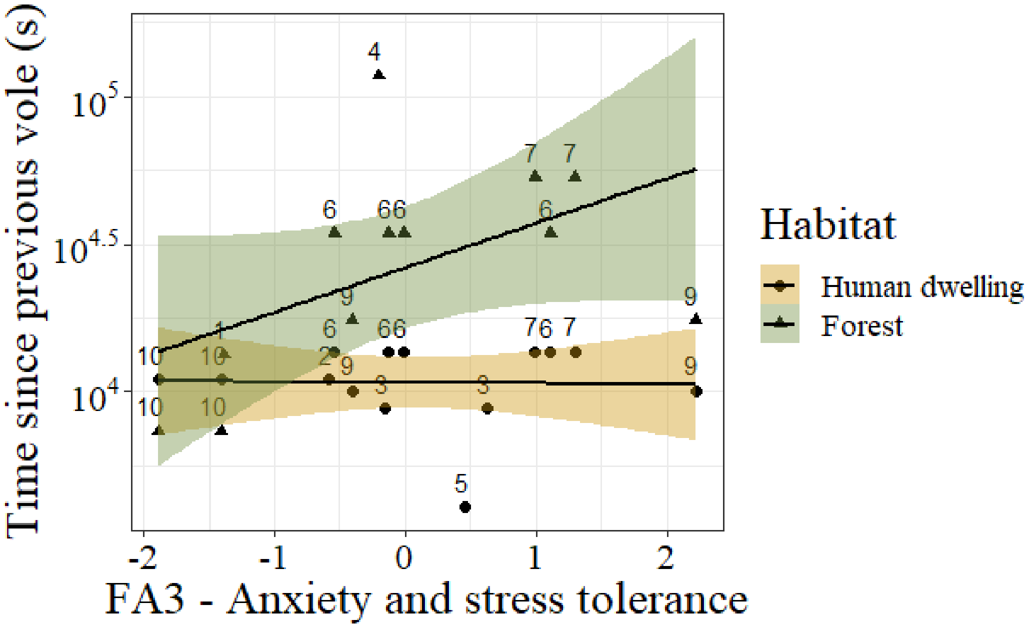

__Figure 17__: The effect of anxiety and stress tolerance (FA3) on the time (in seconds) since previous visit by another vole (i.e. time between visits by different voles) to the 'vole boxes' in the human dwelling versus adjacent forest. Lower x-values represents more anxious voles and higher x-values represent less anxious voles, i.e. more anxiety and stress tolerant voles. Numbers denote individual voles.

4.3. Survival

Model selection determined two models as equally good at explaining survival probability of voles (**Table 4**). Model A showed a negative effect of flight behavior (FA2) and a positive effect of stress- and anxiety-tolerance (FA3) on overwintering survival (**Table 5**). Model B showed a positive effect of anxiety- and stress-tolerance (FA3) and a negative effect of proportion spent in human dwellings (Prop.IN) on survival of the voles (**Table 6**). However, predicted survival was equal for all values of the different factors because of large confidence intervals and standard errors.

Table 4: *Best models of survival (S). Models include escaping behavior (FA2), anxiety- and stress-tolerance (FA3), and proportion spent in human dwelling (Prop.IN) as explanatory variables. AIC = Akaike's Information Criterion for small sample size; ΔAICc = difference between AICc value from model with smallest value.*

Model	*Explanatory variable*	*Number of parameters*	*AICc*	*ΔAICc*	*weight*	*Deviance*
A	~FA2 + FA3	12	34.349	0.000	0.500	4.109
B	~FA3 + Prop.IN	12	34.349	0.000	0.500	4.109

Table 5: *Summary of model estimates for model A with escaping behavior (FA2) and anxiety- and stress-tolerance (FA3) as explanatory variables.*

	estimate	*Standard error*	*Lower control limit*	*Upper control limit*
(Intercept)	38.87	462.80	-868.21	945.95
Escaping behavior (FA2)	-19.04	254.31	-517.48	479.40
Anxiety- and stress-tolerance (FA3)	29.00	366.42	-689.18	747.17

Table 6: *Summary of model estimates for model B with anxiety- and stress-tolerance (FA3) and proportion spent in human dwelling (Prop.IN) as explanatory variables.*

	estimate	*Standard error*	*Lower control limit*	*Upper control limit*
(Intercept)	83.42	199.18	-306.97	473.82
Anxiety- and stress-tolerance (FA3)	23.39	54.90	-84.21	130.99
Proportion spent in human dwelling	-66.47	167.15	-394.09	261.16

5. Discussion

5.1. Local movements

As I hypothesized, the voles in my study demonstrate individual variation in local movements. Animals have been shown to exhibit a wide range of intraspecific variation in local movements, from habitat use to activity patterns and foraging styles (Kobler et al., 2009, Kobler et al., 2011, Pearish et al., 2013, Sih et al., 2004). In my study individual variation in local movements was primarily evident from the difference in number of visits made to the ‘vole boxes’ with some voles making more visits to the boxes than others (**Figure 7**). This can be interpreted as a difference in level of activity. Because the voles most likely visit the boxes in search for food (but potentially also for protection from predators), corroborated by the correlation between local movement variables and baiting (**Figure 6**, **Figure 10**, **Figure 14**), this activity could to some extent be interpreted as foraging activity. Therefore, I will hereafter refer to it as ‘foraging activity’; not to be confused with the ‘activity’ personality trait (FA1). Although voles overall seem to differ in their foraging activity, the interaction between vole and habitat (**Figure 8**) suggests that foraging activity was habitat dependent. This interaction clearly shows that some voles have a habitat preference and make more visits in one habitat than the other, whereas others are more flexible and visit both habitats equally. Similar intraspecific variation in space use among bank voles has been found by previous research. Schirmer et al. (2019) found intraspecies variation in microhabitat preference, distances moved and size of home range. Additionally, these variations in movements were personality dependent (Schirmer et al., 2019).

Although there seems to be a general difference with more and shorter visits in the human dwelling and few but longer visits in the forest (**Figure 5**, **Figure 9**), the length of visits may not fully be explained by clear individual differences among voles. Only voles ‘3’ and ‘9’ differed in the length of visits (**Figure 11**), however, both mainly foraged in the human dwellings (**Figure 8**). Local habitat structures and other environmental factors could explain why voles make longer visits in the forest than in the human dwelling. In many rodent species, microhabitat structures have been found to affect foraging behavior (Doherty et al., 2015, Jacob and Brown, 2000, Kotler et al., 1991). Based on visual observation of camera trap footage of the ‘vole boxes’, I noticed that voles in the human dwelling tended to quickly run in to grab food and leave to eat it elsewhere but that this did not seem to occur in the forest. Predation risk, competition, and hiding places provided by local habitat structures have been found to affect foraging behavior in gerbils (Kotler et al., 1991) and could explain why voles in my study differ in behavior between the habitats. To assess the effect of environmental factors on foraging behavior it would be necessary to examine microhabitat structures around the boxes and accurately determine levels of inter- and intraspecific competition as well as predation risks. Nevertheless, if differences in environmental factors of the two habitats were the only reasons for behavioral differences, the interaction between vole and habitat should show a change in behavior for voles visiting both habitats. This, however, does not seem to be the case. The interaction only shows that vole ‘9’ made significantly shorter visits in the human dwelling than vole ‘6’ in the forest (**Figure 12**). Therefore, the general difference in length of visits between the two habitats seems to be driven by the habitat-specific behavior of these two voles. The driving factor of the differences between these individuals remain undetermined.

Time between visits by different voles was shorter in the human dwelling than the adjacent forest (**Figure 13**) and dependent on food availability (baiting) (**Figure 14**). This could reflect the higher abundance (one more vole) and foraging activity in the human dwelling. When there are more voles that make more visits, the time between these visits should logically be shorter. Since there is no clear individual variation among voles (**Figure 15**), this effect seems to be mainly habitat dependent. Consequently, my results demonstrate that voles in the human dwelling are temporally closer to each other. Khalil et al. (2017) suggest that habitats with certain microhabitat structures act as corridors where voles will travel. Such places may increase encounter rates between infected and susceptible individuals as well as exposure to environmental PUUV and, thus, function as infection hubs (Khalil et al., 2017). The risk of being infected by PUUV could, therefore, be higher in the human dwelling where voles are temporally closer to each other. Such places may also serve as infection ‘refugia’, i.e. key habitats were PUUV persist during low densities of host populations (Khalil et al., 2017). This is especially relevant to my study because the population was in transition between a low and increase phase of the population cycle in the winter of 2020/21 and thus had a low density. I could, however, not determine that the human dwelling acts as an infection hub or refugia because none of the voles were infected with PUUV. My data is only based on one location in northern Sweden. Replicated studies conducted over several years are thus needed to determine if this is a general phenomenon or an anomaly. Furthermore it is necessary to point out that baiting the boxes may be manipulating the environment and, subsequently, affect the voles’ behavior, movement, and infection risk by attracting them to a specific place where the chance of encountering and infecting each other could be higher (Forbes et al., 2015, Boutin, 1990, Robb et al., 2008). This could be an issue for the study and I, therefore, suggest that future studies avoid baiting the boxes to prevent manipulation of vole behavior as well as excluding food availability which is a factor that can be difficult to control.

5.2. Personality

Many species exhibit individual variation in space use regarding foraging, including locations travelled to and search strategies used to find food (Nilsson et al., 2014). Individual differences in foraging behavior therefore offer a key opportunity to study consistent individual variations in movement (Nilsson et al., 2014). Because the bank voles in my study exhibit individual differences in local foraging related movements, my study system provides an opportunity for studying how personality traits co-vary with movement strategies in the wild. Here, I was able to show that anxiety- or stress-tolerance influences local movement strategies. Stress- and anxiety-tolerant voles make more visits in human dwellings than the adjacent forest, compared to their less tolerant conspecific (**Figure 16**). Thus, stress- and anxiety-tolerance appears to have an effect on habitat preference. Similar personality dependent habitat preferences have previously been found in other animals as well as bank voles (Kobler et al., 2009, Pearish et al., 2013, Schirmer et al., 2020). In piscivorous pike (*Esox lucius*) three behavioral types determine habitat preferences and likely contribute to decreased intraspecific competition (Kobler et al., 2009). The two behavioral types with the lowest activity levels prefer habitats in the littoral zone whereas the behavioral type with the highest activity level use all zones (Kobler et al., 2009). Previous research on bank voles has found that individuals vary in movement, space use and habitat choice based on their level of boldness and activity (Schirmer et al., 2019, Schirmer et al., 2020). Different behavioral types occupy different individual ecological niches and could thus reduce intraspecific competition (Schirmer et al., 2020). Similarly, the different behavioral types in wild population of voles in my study may decrease competition by moving and foraging in different habitats. It is possible that stress-tolerant voles are able to cope with the presumably more stressful environment of the human dwelling and, thus, move into this habitat in search for potentially better resources. Since this habitat posed no increased risk of infection, other ecological factors, such as predation and competition (Barber and Dingemanse, 2010), need to be examined as potential factors interacting with personality and, together, affecting movement strategies. On the other hand, it is possible that occupying a stressful environment affects the individual’s tolerance to such stressful factors.

Consequently, manipulative experimental studies are needed to disentangle the dilemma of cause-and-effect.

Furthermore, stress- and anxiety-tolerant voles visited the boxes sooner after the visit of another vole in the human dwelling than in the forest (**Figure 17**). This result could simply reflect the trends of number of visits, because when voles make more visits in one habitat there will naturally be shorter time between these visits. Consequently, these results show that stress- and anxiety-tolerant voles move and forage more in the human dwelling and are temporally closer to each other and thus potentially facing higher risks of encountering pathogens. Ultimately, this confirms my hypothesis of personality-dependent local movement (although not the same traits as I predicted) and support the growing evidence of studies showing personality-dependent movement strategies in wild animals and bank voles specifically (Dammhahn and Almeling, 2012, Dingemanse et al., 2003, Schirmer et al., 2019, Schirmer et al., 2020). Furthermore, foraging activity has been suggested to be an important aspect of individual specialization, i.e. individual variation in food resource use, and thus a key link between animal personality and individual specialization (Bolnick et al., 2003, Toscano et al., 2016). As such, the interaction between personality and local foraging movement determined in my study may indicate that there could be personality-dependent individual specialization. This would be an interesting topic to explore further in future studies.

‘Activity’ (FA1) was only repeatable when I controlled for if the tests had been conducted at freezing temperatures (**Table 2**) and, contrary to my hypothesis and previous research (Boyer et al., 2010, Kobler et al., 2009), did not correlate with activity in the ‘vole boxes’ or local movement strategies. Therefore, it seems reasonable to assume that the activity of the voles in the arena depends on weather conditions. This raises the question of whether the arena experiment can accurately assess movement patterns in the wild. Additionally, this might suggest that activity as a personality trait could be context-dependent, as has been shown by various studies in other species (Coleman and Wilson, 1998, van Oers et al., 2005). If this is true, it may be necessary to evaluate activity under various contexts to get a better understanding of this trait and how it affects individuals and populations.

5.3. Infection

In my study no PUUV infection was detected and, thus, I cannot determine personality dependent infection probability. Contrarily, this seems to suggest no difference in infection probability based on either animal personality or local movement, which contradicts my hypothesis as well as previous research (Boyer et al., 2010, Dizney and Dearing, 2013, Wilson et al., 1993) Furthermore, this contradict previous suggestions that indoor movements by voles would increase infection risks for bank voles and humans (Sipari et al., Khalil et al., 2014). In multimammate mice, however, Morongo virus infection was first found not to correlate with individual variation in exploratory behavior and activity but later determined to correlate with exploration and host density (Vanden Broecke et al., 2018, Vanden Broecke et al., 2019). Therefore, other ecological factors not examined in this study may be important for the prevalence of PUUV infection and association with behavioral syndromes. Several reasons could explain why I found no infection. Firstly, the bank vole population in my study was small at the time of data collection because it was in a transition between low and increase phase of the population cycle. Thus, in combination with few recorded cases of infected voles in the previous year at the same site (Unpublished data Rodents and Disease group SLU Umeå), this could explain why I found no cases of PUUV among the voles in the winter of 2021. In northern Europe PUUV infected bank voles have been found to be most abundant in mid-winter during years of increase and peak host densities (Voutilainen et al., 2016). As my study was conducted between the low and increase phase, my results are consistent with these findings. This demonstrates the importance of long-term studies over the course of one or several full population cycles is needed. Nevertheless, my results seem to indicate that neither the forest or the human dwelling act as an infection refugia, i.e. key habitats where PUUV persist during low densities of host populations (Khalil et al., 2017).

Despite being infected, voles may only occasionally shed viral particles (Hardestam et al., 2008). Taking saliva samples to detect viral shedding and determine infection status could, therefore, result in false negatives and add uncertainties to infection status. Furthermore, by only analyzing for PUUV infection, I have ignored any other pathogens the voles may carry. Because of this, I suggest that future studies include other methods of pathogen detection. Nevertheless, the benefits of better pathogen detection have to be weighed against the negative effect on animal health from using more invasive approaches needed for e.g. blood samples.

5.4. Survival

Personality-dependent survival has been found for various animal species (Foster et al., 2017, Homberger et al., 2021, Moiron et al., 2020, Richardson et al., 2019, Santos et al., 2015, Yli-Renko et al., 2015). Boldness, for example, increases survival probability for snails (*Chlorostoma funebralis*), hihi (*Notiomystis cincta*), and grey partridges (*Perdix perdix*), whereas activity has been found to lower survival probability for marine isopods *Idotea balthica* (Foster et al., 2017, Homberger et al., 2021, Richardson et al., 2019, Yli-Renko et al., 2015). For bank voles, factors such as PUUV infection, population density, food availability and predation risk have previously been found to affect overwintering survival (Haapakoski et al., 2012, Kallio et al., 2007). Through model selection I found two models that explained overwintering survival equally well **Table 4**). These showed a negative effect of escaping behavior and proportion spent in human dwelling and a positive effect of anxiety- and stress-tolerance on survival (**Table 5**, **Table 6**). Because I cannot make biological sense of the negative effect of escaping behavior on survival, I will exclude this from further discussions.

Firstly, it is important to point out that, because of the low sample size and subsequent large confidence intervals, predicting survival based on these models is not possible. Prediction uncertainties may additionally arise from the way in which the model estimates survival. The Robust model of survival calculates the final survival probability based on each previous capture event (Cooch and White, 2019). It is possible that an individual is not (re)captured (but alive) at a certain occasion and then (re)captured at a later occasion. If this individual is absent at the final capture event, the model will estimate a higher survival probability than for an individual that was absent at the final event but continuously present and trapped before this. This occurs because the model takes into account that the individual may only be absent and not dead (Cooch and White, 2019). In other words, as the likelihood of being absent but alive increases, the likelihood of being absent and dead decreases. Therefore, poor capture probability for some voles, along with small sample size, increases difficulties in estimating survival. Nevertheless, these uncertainties in survival predictions clearly show the need for long-term studies based on several study sites to be able to construct models that can accurately predict survival.

Nevertheless, the models produced indicate some trends of what may be affecting bank vole overwintering survival and provides a foundation for future studies. Because only anxiety- and stress-tolerance (FA3) was included in both models, I believe this to be the most reliable factor for overwintering survival. The positive effect of stress-tolerance on survival probability is consistent with research made by Vanden Broecke et al. (2021) who found that less stress sensitive Multimammate mice (*Mastomys natalensis*) had a higher survival probability in the decrease phase of the population cycle, presumable because they take more risks in the wild. It is likely that animals that have higher anxiety- and stress-tolerance are better at coping with other environmental stress factors, such as resource shortage, higher competition and increased risk of predation and infection. Consequently, these results support my hypothesis of personality-dependent survival as well as the current scientific conjecture that personality may have wider consequences on fitness (Nilsson et al., 2014).

The positive effect of stress-tolerance together with a negative effect of proportion spent in human dwelling may seem contradictory because my analysis of personality and movement showed that more anxiety and stress-tolerant individuals make more visits in the human dwelling than the forest. The combination of these results, however, may indicate that there are opposing forces acting on the survival of the voles. Voles that are able to cope with a stressful environment may be moving into the human dwelling to escape higher interspecific competition of food resources. This may come at a cost of , for example, increased mortality from predation. Haapakoski et al. (2012) found that harsh winter conditions with low food availability and predation risk caused behavioral changes in bank voles that negatively affected overwintering survival. Additionally, it could come at a cost of increased intraspecific competition. In fact, the 'vole box' data showed that more voles visit the human dwelling, and, from the camera trap footage, it appeared like more squirrels and mice visit the boxes in the forest and more cats visit the boxes in the human dwelling. Similar trade-offs have been found in bank voles and striped field mice (*Apodemus agrarius*), where reduced intraspecific competition for bolder individuals came at the cost of increased interspecific competition (Schirmer et al., 2020). Consequently, including more ecological factors and looking at the broader ecological community would be important for future studies on personality dependent movement and survival of bank voles.

When interindividual variation in habitat selection covaries with fitness and is heritable, it can represent alternative tactics available to adaptive evolution (Fortin et al., 2008, Leclerc et al., 2014, McLoughlin et al., 2006). As such, the personality dependent movement and its effect on survival may have larger evolutionary consequences. It is necessary to point out that the interactions between personality, movement, infection, and survival are mediated by underlying mechanisms in physiology and/or life-history. In bank voles, for example, personality has been found to correlate with body mass, depending on mtDNA type and sex (Šíchová et al., 2014). With this in mind, and because of the uncertainty in predicting overwintering survival, the trends indicated by these models provide a compelling argument for future research to continue investigating personality-dependent movement, infection, and survival as well as the underlying mechanisms mediating the interactions between these factors.

6. Conclusion

I was able to determine personality-dependent local movements in bank voles captured and observed at my study site which supports previous studies on animal personality in bank voles (Schirmer et al., 2019). This was manifested as interindividual differences in habitat preference where more anxiety- and stress-tolerant voles showed higher foraging activity in the human dwelling than the adjacent forest. High competition and increased risk of predation and infection could explain why voles in the human dwelling are more anxiety- and stress-tolerant. Despite these voles being temporally closer to each other there seemed to be no increased risk of PUUV infection, which would suggest that the human dwelling is not acting as an infection hub or refugia. Furthermore, anxiety- and stress-tolerance may have positively affected survival and supports previous studies on personality-dependent survival (Vanden Broecke et al., 2021). Due to low sample size and large variation, further research is needed to investigate factors affecting overwintering survival.

It is necessary to point out that my study is based on eleven voles from only one location in the winter of 2020/21. Such a low sample size – though compensated by high number of recordings per individual – poses a concern for the validity of the statistical tests and results. My results should therefore be considered with caution and not be generalized. Costs and benefits of different personality types may not be temporally stable (Dingemanse et al., 2004). Hence, detailed longitudinal studies are required to investigate the relationship between local movement strategies, personality and fitness (Nilsson et al., 2014). The results from this pilot study provides an important baseline for future studies that investigate the interplay between animal personality, movement, and other ecological factors in wild rodents.

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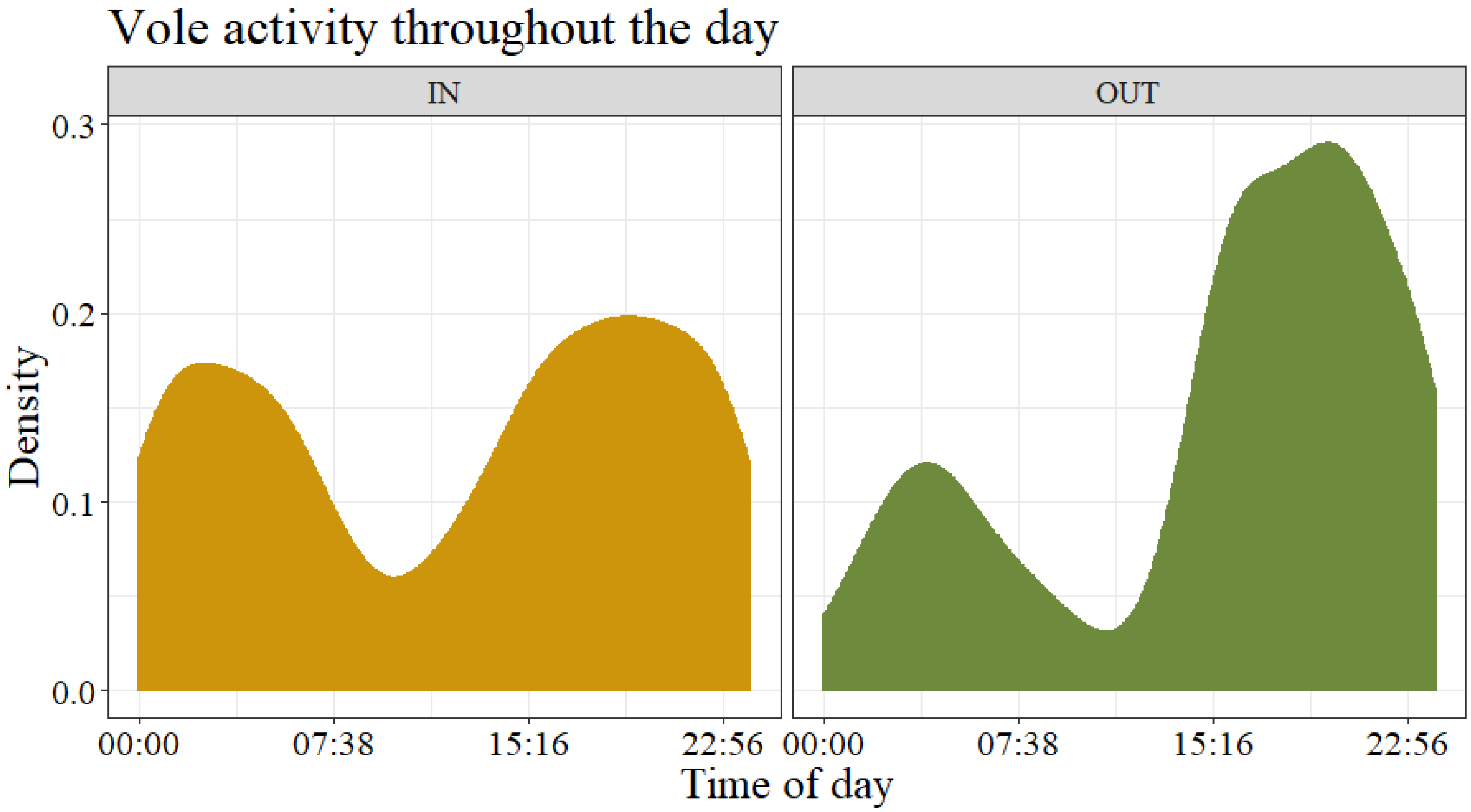
Appendix 1

Appendix 1: Daily activity pattern by voles in the ‘vole boxes’ showing an increase in activity at twilight and before sunrise as well as some activity throughout the course of the day. Graphs are separated by habitat. IN = human dwelling, and OUT = forest.



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