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# Ecological Consequences of Personality in a Guild of Terrestrial Small Mammals: From Trappability to Seed Dispersal

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# ECOLOGICAL CONSEQUENCES OF PERSONALITY IN A GUILD OF TERRESTRIAL SMALL MAMMALS: FROM TRAPPABILITY TO SEED DISPERSAL

By

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B.S. University of New Hampshire, 2014

A THESIS

Submitted in Partial Fulfillment of the

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(in Wildlife Ecology)

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December 2018

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# ECOLOGICAL CONSEQUENCES OF PERSONALITY IN A GUILD OF TERRESTRIAL SMALL MAMMALS: FROM TRAPPABILITY TO SEED DISPERSAL

By Allison M. Brehm

Thesis Advisor: Dr. Alessio Mortelliti

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
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Individual animals exhibit consistent behavioral tendencies over time and across contexts that have been termed *personalities*. Personality encapsulates an individual's unique way of behaving and responding to life's challenges, and since individuals vary in both personality type and their ability to exhibit behavioural plasticity, there are important links between an individual's personality and its response to a changing environment; resulting in the study of animal personalities becoming increasingly popular in recent years. Previous research suggests that personality traits measured through standardized behavioural tests predict trappability (i.e. 'trap happiness' versus 'trap shyness'). This relationship has been explored only within single species and never across environments, but it is essential to understand this link, because if personality drives trap response this suggests that samples obtained through active trapping methods are behaviorally-biased (perhaps weighing more heavily on the bold individuals) – violating any assumption of a random sample. Further, if personality traits predict trappability, it would be possible to extract personality data from long-standing mark-recapture datasets by using trappability as a proxy for personality. My thesis contributes to this growing field by

clarifying the relationship between trappability and personality in Chapter 1, and by demonstrating a critical relationship between personality and an essential ecosystem process: *seed dispersal* in Chapter 2. To meet these goals, we designed a large-scale field experiment to measure personality and trappability in five small mammal species and across varying forest types. Using standardized tests, we quantified behaviour in deer mice (*Peromyscus maniculatus*), Southern red-backed voles (*Myodes gapperi*), American red squirrels (*Tamiasciurus hudsonicus*), woodland jumping mice (*Napaeozapus insignis*), and Northern short-tailed shrews (*Blarina brevicauda*). Using this same experimental design, we performed a detailed seed predation experiment to observe interactions with seeds by known-individuals across different forest treatments. Chapter 1 shows that, although we identified personality in all five of target species, personality traits did not predict different aspects of trappability, suggesting that our work examined a random-subset of the population (i.e. not behaviorally-biased) and that trappability cannot be used as a proxy for personality. In Chapter 2, we remotely observed interactions with seeds and assessed whether personality traits influenced key decisions in a natural environment and at vital stages of the dispersal process. Ultimately, this research provides the first evidence that personalities influence four critical stages of seed predation and dispersal by scatter-hoarding small mammal, and that conserving behavioral diversity could maintain a diversity of ecological functions by conserving individuals with certain personality traits.

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# MIND THE TRAP: LARGE-SCALE FIELD EXPERIMENT SHOWS THAT TRAPPABILITY IS NOT A PROXY FOR PERSONALITY*

* Brehm, A. M., & Mortelliti, A. (2018). Mind the trap: large-scale field experiment shows that trappability is not a proxy for personality. *Animal Behaviour, 142*, 101–112. https://doi.org/10.1016/j.anbehav.2018.06.009

## INTRODUCTION

Behavioural tendencies often vary consistently among individuals and this variation is known as personality (Carere and Maestripieri 2013; Sih et al. 2004). Personalities have been observed in multiple species and across taxa: from insects (Pruitt and Modlmeier 2015), fish (Wilson et al. 1993; 2011) and reptiles (Carter et al. 2012), to birds (Dingemanse et al. 2003; Garamszegi et al. 2009) and mammals (Blumstein et al. 2013; Boon et al. 2007; Montiglio et al. 2012; Réale et al. 2000) and can have important implications for the fitness of the individual (Dingemanse and Réale 2005; Smith and Blumstein 2008). Because individuals vary in both personality type and their ability to exhibit behavioural plasticity (Dingemanse et al. 2010), there are important links between an individual's personality and its response to a changing environment (Sih et al. 2011). This has resulted in an increasing focus on the study of animal personalities in the field of behavioural ecology and, more recently, conservation biology (Candolin and Wong 2012).

Personality has been measured in several ways and in both field and laboratory settings (see Carter et al. (2013) and Gosling et al. (2001) for summaries of existing methods using standardized tests and Dammhahn and Almeling (2012) for an example using behavioural observations of non-captured animals). Although these methods are often quite inexpensive in terms of the materials and equipment required, tests like open-field (Archer 1973; Walsh and Cummins 1976), hole-board (Careau et al. 2011; Martin and Réale 2008, Menzies et al. 2013), and mirror-image stimulation (Boon et al. 2008; Svendsen and Armitage 1973) are time-consuming to perform and require additional time in the laboratory to quantify the behaviours observed, making them expensive in terms of labor costs.

More recently, correlations between an individual's personality and other measurable aspects of behaviour have been identified, including dispersal distance and exploration of the environment (Dingemanse et al. 2003; Wilson 1998), extra-territorial behaviours (Boon et al. 2008) and commonly, trappability (Krebs and Boonstra 1984). Trappability encompasses measures such as the propensity (or latency) to enter a trap, the probability of being captured, and trap response (a systematic trapping bias in which certain individuals become either more or less likely to be trapped after the initial capture) (Nichols et al. 1984). Trappability can also encompass characteristics such as the number of different traps utilized and can give insight into aspects of an individual's territory size or space use (Boon et al. 2008; Kanda and Hatzel 2015). Differing individual responses to trapping are common and have resulted in terms such as "trap-happy" and "trap-shy" becoming widespread descriptors to explain the reaction of different animals to trapping methods (Nichols and Pollock 1983).

In some studies, trappability has been shown to be consistent within individuals, and this consistency has been quantified using repeatability (Boyer et al. 2010; La Coeur et al. 2015; Réale et al. 2000). Statistically, repeatability can be defined as the proportion of total phenotypic variation accounted for by individual differences after controlling for the potential impacts of fixed-effects (Dingemanse et al. 2010; Dingemanse and Dochtermann 2013; Nakagawa and Schielzeth 2010).  When the proportion of the total variance accounted for by differences within individuals is small in relation to the variance attributed to differences between individuals, this is evidence for personality. Trappability has also been shown to correlate significantly with other aspects of personality such as boldness or risk-taking in bighorn ewes *Ovis canadensis* (Réale et al. 2000), Namibian rock agamas *Agama planiceps* (Carter et al. 2012), and bluegill sunfish *Lepomis macrochirus* (Wilson et al. 2011); activity levels in American red squirrels *Tamiasciurus hudsonicus* (Boon et al. 2008) and Siberian chipmunks *Tamias sibiricus* (Boyer et al. 2010); exploratory behaviours in collared flycatchers *Ficedula albicollis* (Garamszegi et al. 2009; and reduced fear response in Japanese quail *Coturnix japonica* (Mills and Faure 2000). See Biro and Dingemanse (2008), Biro (2013), Merrick and Koprowski (2017), and Stuber et al. (2013) for more thorough reviews.

Though these relationships have been observed in a number of species, these findings have encouraged some studies to use trappability directly as an index of other personality traits. For example, this has been done either by relying on the consistency of trappability in only a subsample of individuals (Boyer et al. 2010), supposing that trappability is consistent within individuals (Montiglio et al. 2012), or assuming a relationship between trappability and repeatable behaviours based on the findings of others (La Coeur et al. 2015; Patterson and Schulte-Hostedde 2011).

There is an issue with these above scenarios, because the relationships between trappability and personality observed in previous studies are context and species specific, meaning they lack a sound basis for generalization. Further, not all have calculated the repeatability of trappability, which is concerning because trappability has been shown to vary with changes in resource abundance and availability (Adler and Lambert 1997) as well as species abundance (Royle and Nichols 2003). In fact, trappability has also been shown to vary among and between sexes, age classes, study areas, seasons, and years (Adler and Lambert 1997; Byrne et al. 2012; Silver et al. 2004; Tuyttens et al. 1999) which may complicate the calculation of repeatability. This lack of repeatability estimates means also that there can be no direct comparison between studies. For trappability to be considered personality, it must be repeatable (e.g. a trap shy individual should consistently behave in a trap-shy manner) (Bell et al. 2009; Dingemanse and Dochtermann 2013; Nakagawa and Schielzeth 2010). Additionally, to consider trappability a proxy for a specific personality trait such as boldness, activity, or exploration, the trait should have been quantified independently of the trapping itself, and trappability must be found to correlate significantly with that trait.

Further, as several studies have suggested (Biro 2013; Biro and Dingemanse 2008; Carter et al. 2012; Stuber et al. 2013), if certain individuals are consistently trapped more often than others (i.e. trap-happy individuals), this will result in sampling methods representing a disproportionate number of individuals with a certain personality type; resulting in non-random and potentially behaviourally-biased samples. This would be troublesome for studies utilizing behavioural observations or life-history information from captured individuals. However, if trappability is not a repeatable measure, it is likely that the trappability of individuals is contingent upon many factors and may be changing constantly, reducing the negative effects of trap-response on the validity of data.

It is critical to resolve this ambiguity and extend our understanding of the relationship between trappability and personality. Confirming, as previous studies have suggested, that trappability is a measure of personality and is highly correlated with other personality traits would support the use of trappability as a proxy for traits that are usually expensive and time-exhaustive to measure. Ultimately, it may also be possible to use existing datasets, such as long-time series of capture-mark-recapture data, to explore questions relating to personality and population dynamics (Ogawa et al. 2017). Finally, this might indicate the need for a shift in the way animals are captured for behavioural studies; perhaps requiring the use of multiple different trapping approaches to limit the inherent behavioural bias caused by passive trapping methods (Biro 2013).

To fill this knowledge gap, we developed a large-scale field experiment involving multiple species (5 small mammal species belonging to 2 orders and 4 families) living in contrasting environments (i.e. forestry treatments). To the best of our knowledge, we are among the first studies to compare the relationship between personality and trappability simultaneously in multiple species and to concurrently investigate how these relationships might vary across environments.

The main objective of this study was to determine whether trappability reflected personality in five small mammal species and could be used as a proxy for these traits (see Figure 1.1 for a conceptual diagram). We hypothesized that individuals who showed increased activity/locomotion and exploratory behaviours in an open-field test would also show increased trappability; in line with studies by Boon et al. (2008), Boyer et al. (2010), Dingemanse et al. (2003), and Garamszegi et al. (2009). Particularly, we predicted that behaviours related to activity in the open-field test would be positively correlated with an increased number of captures and with captures occurring earlier in the trapping session. We also predicted that behaviours related to exploration would correlate positively with the number of different traps that an animal used. Further, since previous studies have found evidence for a relationship between personality traits and trappability among multiple taxa, we predicted that we would see similar results across all five study species, confirming that trappability can be used as a proxy for correlated personality traits.

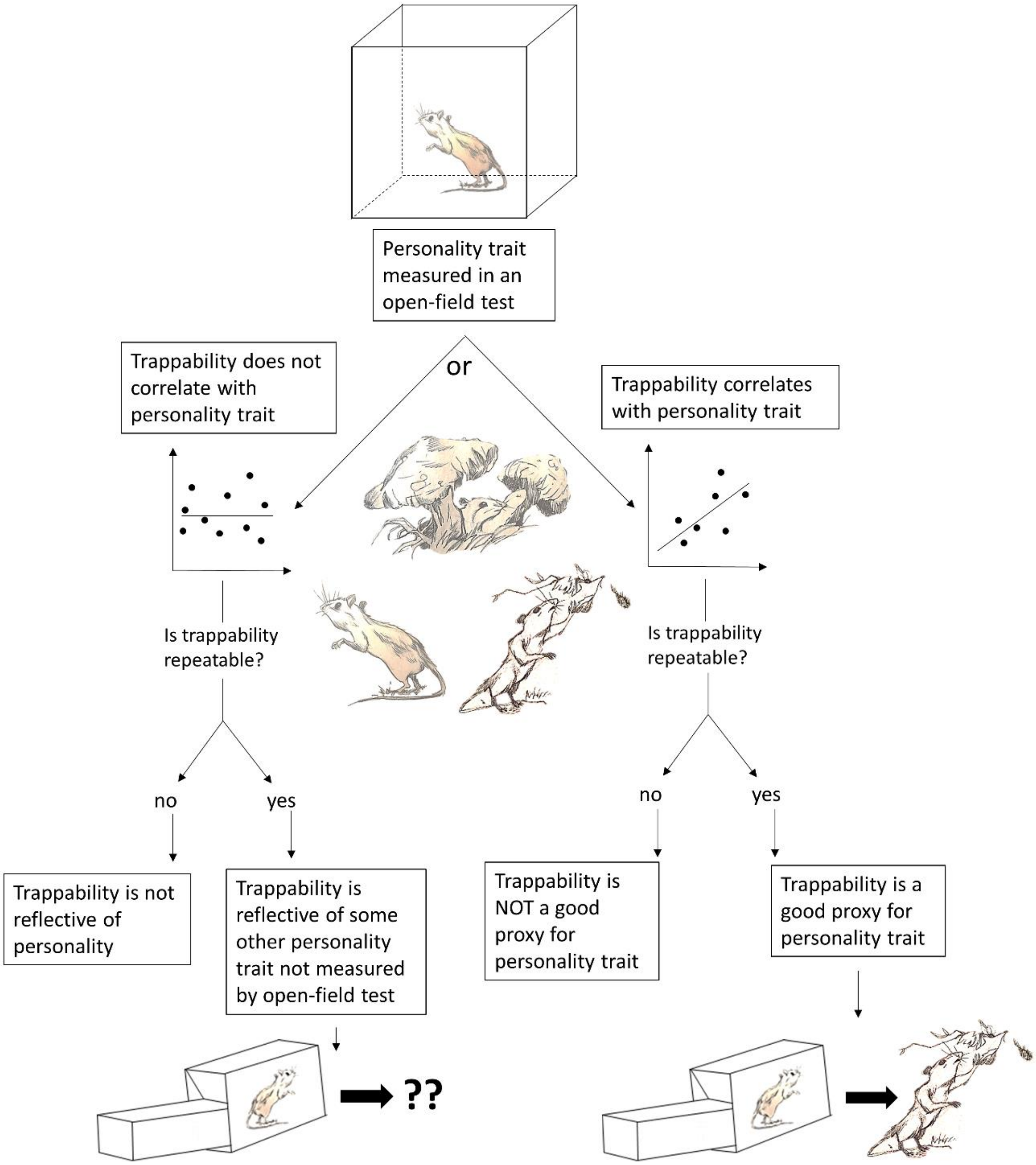

***Figure 1.1*** *Conceptual diagram of the study. Trappability can be used as a proxy for a personality trait (as measured in an open-field test) if trappability is both repeatable and significantly correlated with this trait. If trappability is repeatable but not correlated with personality as measured in an open-field test, this suggests that trappability might be reflective of some other aspect of personality. See introduction for more information.*

## METHODS

### *Study site*

This study was conducted in the Penobscot Experimental Forest (PEF, 44 053’ N, 68 039’ W). This is a 1,578-hectare Forest Service experimental forest located in the towns of Bradley and Eddington, Maine, USA on the east side of the Penobscot River and the southern edge of the Acadian Forest (a mixed conifer-deciduous forest) (Rowe 1972) (Figure A1.1). Species composition in the experimental forest varies by treatment but is dominated by shade-tolerant conifers. Common species include eastern hemlock (*Tsuga canadensis*), balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), white pine *(Pinus strobus*) and northern white cedar (*Thuja occidentalis*) (Kimball 2014). Different areas of the PEF have been managed with contrasting silvicultural treatments with each logged separately and replicated twice in a random experimental design. Each management unit averages 8.5 hectares in size (range = 8.1-16.2 hectares) and close to 25 hectares of forest (retained in two separate units) has remained unmanaged since the late 1800s and serves as reference area (Brehm AM, personal observation; Brissette and Kenefic 2014).

### *Contrasting forestry treatments*

We trapped small mammals in three contrasting silvicultural treatments and used two areas of old growth forest as controls. The treatment areas were as follows: even-aged forest (treatment 1, two replicates), two-stage shelterwood with retention (treatment 2, two replicates) and selection cutting (treatment 3, two replicates).

These three forestry treatments generated highly contrasting habitat types for small mammals: ranging from a forest that was relatively absent of shrubby or herbaceous understory, with a dense canopy and low light-levels in treatment 1, to a forest composed of a mosaic of mossy understory, downed woody material, open, grassy patches, small saplings, and large standing residuals in treatment 3. See the glossary in supplementary materials for further information about the forestry treatments used.

***Small mammal trapping***

We analyzed data collected from June – November 2016 in a fully controlled and replicated field experiment, and additional data for a subset of individuals captured from June – September 2017 was included to increase sample size. All trapping, handling, and marking procedures were approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC number A2015_11_02). We implemented a large-scale capture-mark-recapture experiment on eight study grids (two control grids in reference areas and three treatment grids with replicates). Each trapping grid was 0.81 hectares in area (considerably smaller than the area of the treatment) and consisted of 100 flagged points spaced ten metres apart. Grids were positioned at or close to the center of the treatment area to minimize edge effects. The mean distance between grids was approximately 1.47 km, and the mean distance between duplicate grids of the same treatment was approximately 1.17 km (Figure A1.1).

Longworth traps were placed at each point (100 Longworth in total) and Tomahawk traps were placed at every other point in an alternating fashion (50 Tomahawk in total, spaced approximately 20 metres apart). Longworth traps were baited with a mixture of sunflower seeds, oats, and freeze-dried mealworms and were bedded with cotton squares. Tomahawk traps were baited with a mixture of peanut butter and sunflower seeds. We checked Longworth traps twice a day (once just after sunrise and once in the late afternoon) and Tomahawk traps were set just after sunrise, checked in late afternoon, and closed overnight. By checking traps twice a day, we have attempted to limit the amount of time that animals must spend inside our traps. However, Fletcher and Boonstra (2006) found that, while live trapping did induce a stress response in voles, the time spent inside the trap had no effect on stress levels. For this reason, we do not think that this was a factor in the behaviour exhibited by the animals in this study. We trapped at each grid for 3 consecutive days and ran grids in duplicate treatments simultaneously. Grids were revisited after one month (five trapping sessions in total). For logistical reasons, squirrels were trapped from June – September only.

Target species for this study were the deer mouse (*Peromyscus maniculatus*), the Southern red-backed vole (*Myodes gapperi*), the American red squirrel (*Tamiasciurus hudsonicus*), the woodland jumping mouse (*Napaeozapus insignis*), and the Northern short-tailed shrew (*Blarina brevicauda*). All individuals were marked with National Band Small Animal Ear Tags – Style 1005-1 and Biomark MiniHPT8 PIT tags (inserted subcutaneously at the mid-back). Shrews have no external ears and thus were marked with a small individual haircut instead of an ear tag. Animals were anesthetized with Isoflurane prior to tagging and all tagging equipment was sanitized with 70% isopropyl alcohol in-between animals. We measured body weight using Pesola Lightline Spring Scales (100g and 1000g). Sex, age class, and reproductive status were recorded for every individual. Squirrel ear tags were threaded with a unique colour combination of coloured pipe cleaners (males) or coloured wire (females) for identification at a distance as in Boon et al. (2007).

### ***Behavioural tests***

Before we handled or processed animals, we measured personality in individuals using an open-field test. This is a standardized test used to measure activity, exploration, and stress responses in a novel environment (Hall 1934; Hall and Ballechey 1932; Walsh and Cummins 1976). All tests were performed at a base area in the home grid of the focal individual using a standardized procedure. For squirrels, we followed a protocol similar to that of Boon et al. (2007) and the open field test box was a (90 x 90 x 90 cm) white box with a clear acrylic lid through which behavioural trials were recorded with a Nikon CoolPix S3700 digital camera. For mice, voles, and shrews we used a smaller white box of dimensions (46 x 46 x 50 cm) and this size is consistent with open-field arenas used in similar studies (Polissidis et al. 2017; Zimprich et al. 2014). Test boxes were placed on a level platform and underneath a tarp to control for light levels and amount of canopy cover (see supplementary material for a diagram the of test arena setup).

The focal animal was captured, transferred directly from the trap into a plastic bag, and then released into the center of the test arena. Squirrels were transferred directly from the trap into the arena. A 5-minute trial began when the observer started the video recording and then left the test area and became silent (mean = 15 seconds). After five minutes passed, the observer ended the recording and removed the individual from the box using a plastic bag or net. After each trial, the test box was cleaned with 70% isopropyl alcohol and wiped with a dry cloth. This allowed us to control the test environment and ensure that we were observing an individual’s response to the novel environment rather than the response to the scent of a previous test individual. Animals were tested only once during each three-day trapping session, but we tested individuals again when they were recaptured during subsequent sessions.

We analyzed the videotaped trials and quantified behaviours of interest using JWatcher V1.0 (Blumstein and Evans 2010). We used an ethogram similar to those by Boon et al. (2007) and Martin and Réale (2008). See Table 1.1 for further details about the behaviours measured. Video analysis was performed by two different observers, and we tested inter-rater agreement by calculating Cohen’s Kappa coefficient. Because some videos ran slightly shorter than 5 minutes, we extracted the proportion of time that an individual spent performing each of the behaviours of interest and used these proportions for further analyses.

**Table 1.1** List of behaviours measured in an open field test. Study species included deer mice (*Peromyscus maniculatus*), American red squirrels (*Tamiasciurus hudsonicus*), Southern red-backed voles (*Myodes gapperi*), woodland jumping mice (*Napaeozapus insignis*) and Northern short-tailed shrews (*Blarina brevicauda*). A brief definition, biological interpretation, and a non-exhaustive list of studies utilizing this behavioural measurement are included along with the abbreviation used in analyses*.

| **Behaviour** | **Abbrev.** | **Definition/Biological Interpretation** | **Sources** |
|---|---|---|---|
| Center | Prop.c | Locomotion is occurring in center portion of open field arena; (thigmotaxis) suggests risk-taking and boldness; not used for *Tamiasciurus hudsonicus* | Eccard and Herde (2013); Gracceva et al. (2014); Prut and Belzung (2003) |
| Groom | Prop.g | Self-grooming behaviour; indicative of stress and negatively related to high-activity | Boon et al. (2007); Choleris et al. (2001); Martin and Réale (2008); Prut and Belzung (2003); |
| Hang | Prop.h | Hanging from walls or ceiling of arena; related to high levels of activity; used only for *Tamiasciurus hudsonicus* and *Napaeozapus insignis* | Boon et al. (2007); Martin and Réale (2008) |
| Sniff/Chew | Prop.n | Sniffing and chewing of the walls/floor of arena; generally correlated with other exploratory behaviours | Boon et al. (2007); Choleris et al. (2001) |

## Table 1.1 Continued

| | | | |
|---|---|---|---|
| Jump | Prop.j | Jumping at the sides of the arena; correlated with other behaviours indicating high levels of activity | Boon et al. (2007);<br>Boyer et al. (2010);<br>Choleris et al. (2001) |
| Move | Prop.m | Locomotor activity (i.e. the animal's location in the arena is changing); typically characterized by running, walking, or jumping. This behaviour acted as a "state" and could occur at the same time as other active-behaviours (i.e. jumping) | Boyer et al. (2010);<br>Gracceva et al. (2014);<br>Hoset et al. (2011);<br>Martin and Réale (2008) |
| Rear | Prop.r | Forelegs leave the floor of the arena; positively related to high levels of activity | Choleris et al. (2001);<br>Martin and Réale (2008); Prut and Belzung (2003) |
| Vigilance | Prop.v | Quadripedal vigilance behaviour; used only for *Tamiasciurus hudsonicus* | Boon et al. (2007);<br>Martin and Réale (2008) |
| Stationary | Prop.s | Absence of locomotor activity. This behaviour acted as a "state" and could occur at the same time as other sedentary-behaviours (i.e. grooming) | Boon et al. (2007);<br>Choleris et al. (2001);<br>Prut and Belzung (2003) |
| Stationary. corner | Prop.s.corner | Location of stationary state in arena; close-proximity to two walls of arena | |
| Stationary. edge | Prop.s.edge | Location of stationary state in arena; close-proximity to one wall of arena | |

**Table 1.1 Continued**

| | | |
|---|---|---|
| Stationary. center | Prop.s.center | Location of stationary state in arena; in center portion of arena |

** Because some open-field videos ran shorter than 5 minutes, we extracted the proportion of time that the animal performed each of the behaviours of interest. These proportions were retained for analyses.*

### ***Data analyses***

Rather than run a Principal Component Analysis (PCA), as is often done in studies of animal personality (Boon et al. 2007; Martin and Réale 2008), we decided to use the raw behavioural variables for further analyses. While the main advantage of using PCA is that it enables total independence between components, this comes at a price because components can be difficult to interpret biologically. In the case of our study, having correlated variables would not impact our ability to investigate repeatability of behaviours or to estimate relationships with trappability. Therefore, to retain all repeatable behaviours and avoid the possibility of missing a correlation between the behaviours of interest and trappability, we used the raw variables themselves for further analyses.

To determine whether individuals behaved consistently, we used R package lme4 (Bates et al. 2014) to run univariate mixed-effects models. We included potential confounding factors as covariates in the models. Specifically, we included sex, average weight, treatment, and session. We did not include sex in the models for *B. brevicauda* because shrews cannot be sexed externally. As dependent variables, we used the proportion of time spent performing each behaviour of interest and ran separate mixed-effects models for each behavioural variable (Zuur et al. 2009). Since proportional response variables used in these analyses were not binary, we logit transformed them (Warton and Hui 2011) to meet the assumptions of normality. Individual identity was included as a random-effect in the models. We then calculated the intra-class correlation coefficients (or repeatabilities) from the model outputs by dividing the among-individual variance by the total variance (equal to the among-individual variance plus the residual variance). We used this value to determine if individual's values for each of the behavioural variables were repeatable (i.e., whether a large portion of the total variance could be attributed to differences between individuals, rather than to differences among repeated observations of the same individual) (Cleasby et al. 2015; Dingemanse and Dochtermann 2013). It should be noted that these should be considered "adjusted repeatabilities" since our linear mixed models contained fixed effects (Nakagawa and Schielzeth 2010) and hereafter we use the terms "repeatability" and "adjusted repeatability" interchangeably. We obtained 95% confidence intervals using parametric bootstrapping with 1 000 simulations using the R package "rptR" (Stoffel et al. 2017), and repeatability estimates were deemed insignificant if the lower estimate of the confidence interval approached very close to zero (Houslay and Wilson 2017). We assessed model fit by visually inspecting qq-plots, histograms of the residuals, and plotting the fitted values against the residual values.

We used four different measures of trappability in this study. These included two repeated measures: the number of captures in a trapping session (CAP), and the night of the first capture in the session (FIRST). For example, if an individual was captured three times in a session and the first capture was on the second trap night, this individual would be given a score of three for CAP and two for FIRST during this session. We also used two non-repeated measures: the total number of captures (corrected for trap days present in the population)

(NUMCAP), which can be interpreted as the overall capture probability, and the total number of traps used (MAXTRAPS). We examined if CAP and FIRST were repeatable by running univariate mixed-effects models with each of the measures of trappability as dependent variables (Dingemanse and Dochtermann 2013; Houslay and Wilson 2017). Where response variables were counts, we used glmer analyses with Poisson error distributions, and for proportions, we used a logit transformation on the response variable (Warton and Hui 2011). We included potential confounding factors as covariates in the models. Specifically, we included sex, average weight, treatment, session, the proportion of inactive traps, and a variable which equaled the distance of the trap that the animal was captured in to the center of the trapping grid (which we named Dist.center in the models; Table A1.2). This variable was included to help us control for edge effects since animals living at the edge of trapping grids are potentially exposed to fewer traps and to less diversity of trapping locations (Boon et al. 2008; Efford 1998). We included individual identity as a random-effect in the models. We then compared the full models to identical linear models (absent of random-effects) and used likelihood-ratio tests (obtained through ANOVA analyses) to determine whether the effect of individual identity improved the models significantly (Lessells and Boag 1987; Martin and Réale 2008). From the univariate models, we calculated the adjusted repeatabilities. We obtained 95% confidence intervals using parametric bootstrapping with 1000 simulations, and repeatability estimates were deemed insignificant if the lower estimate of the confidence interval approached very close to zero. We also ran univariate models predicting the two non-repeated trappability measures, including one extra fixed-effect: the total number of trap-days that the individual was present in the population (to control for the fact that these measures are strongly related to the time present in the population).

To determine whether an individual's personality influenced its trappability, we used a Bayesian approach with Markov Chain Monte Carlo multivariate generalized linear mixed-effects models. Our analyses were performed predominantly following methods described by Dingemanse and Dochtermann (2013) and using measures of personality (the repeatable behavioural variables) and trappability as dependent variables. We used the R package "MCMCglmm" (Hadfield 2010). For each species, we ran multiple models, pairing each repeatable behavioural variable with each of the two repeated measures of trappability (we scaled these response variables to help with model-fit and ease of interpretation (Houslay and Wilson 2017). Models also included sex, average weight, treatment, session, the proportion of inactive traps, and distance to the center of the grid as fixed-effects. Individual identity was included as a random-effect in the models. We used non-informative (parameter expanded) inverse Wishart priors for both individual and residual variance of the raw behavioural variables and the trappability variables (prior specifications: R-structure degree of belief (nu) = 0.002; G-structure degree of belief = 2.0, alpha.mu = rep(0, 2), alpha.V = diag(25^2, 2, 2) (Hadfield 2015; Houslay and Wilson 2017; Ólafsdóttir and Magellan 2016). Exploration using flat and weakly informative priors had little or no effect on our model estimates. Models were run with a burn-in of 25 000 and subsequent 1 000 000 iterations (thinning interval of 500). We visually inspected plots of traces and posterior distributions to confirm convergence (Hadfield 2010) and calculated the autocorrelation between samples using the R package "coda" (Plummer et al. 2006). Autocorrelation was ≤ 0.02 for the majority of estimates and ≤ 0.07 for all estimates. Because the raw behavioural variables and trappability variables were not measured at the same time, we constrained the within-individual covariances in the models to equal zero (Dingemanse and Dochtermann 2013).

Variance components from model outputs are constrained to be positive in MCMCglmm, so 95% credible intervals that exclude zero cannot be interpreted to indicate statistical significance. Therefore, we decided to standardize the model covariances between the dependent variables to a scale from -1 to 1 by dividing the corresponding covariance between the two variables by the product of the square root of their variances (these methods are described by Houslay and Wilson (2017)). These methods allowed us to obtain the correlation between the two traits. We determined whether this correlation was significant by assessing the 95% confidence interval of the correlation and considering confidence intervals which excluded zero to signal a significant correlation (Dingemanse and Dochtermann 2013; Hadfield et al. 2010; Ólafsdóttir and Magellan 2016).

We assessed whether the repeatable behavioural variables correlated with our two non-repeated measures of trappability following similar methods as above, however, as outlined by Houslay and Wilson (2017), we fixed the within-individual variance in the non-repeated measures to equal a very small positive number – since a trait measured only once has no within-individual variance. We included the same fixed-effects as in the univariate models but tested for an effect of trapping session on the behavioural variables only – because these variables were measured repeatedly. Further, we included the additional fixed-effect of trap days present in the population.

### ***Further exploration of trappability***

To investigate whether the size of our dataset might limit our ability to make significant predictions about the repeatability of trappability, we utilized three large datasets collected from April 2011 to February 2013 in the Viterbo Province, central Italy (Sozio and Mortelliti 2016). These datasets contain a total of 8109 captures from 47 718 trap nights, and 2802 observations from 2055 *Apodemus flavicollis,* 1928 observations from 1468 *Apodemus sylvaticus*, and 1601 observations from 1121 individual *Myodes glareolus*. These species are the Eurasian counterparts of the deermouse and the Southern red-backed vole. Using these data, we calculated trappability using the same variables (CAP and FIRST) from our own study. We estimated the adjusted repeatability of the trappability variables from all three datasets using the R package "rptR" (Stoffel et al. 2017) and models included trapping session and weight as fixed-effects and the random-effect of ID.

All above analyses were performed using R version 3.25. The additional package "dplyr" was used for data manipulation (R Core Team 2016; Wickham and Francois 2016).

### *Ethical Note*

All trapping, handling, and marking procedures were approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC number A2015_11_02). Small mammal traps were checked twice a day to limit the amount of time that captured animals spent inside traps. Bedding was refreshed when necessary, and animals were always provided with fresh, high calorie bait. All individuals were anesthetized with Isoflurane prior to tagging, and tagging equipment was sanitized with 70% isopropyl alcohol in-between animals. Animals were released to the exact location of capture immediately post-processing. All small mammal handling was done by trained researchers, and steps were taken to limit the stress that animals would endure (such as minimizing noise and processing times). During inclement weather, traps were kept dry, and bedding was replaced. In cold weather, the amount of bedding provided was increased.

## RESULTS

### *Captures*

From June through November 2016, we had a total of 10 449 Longworth trap nights and 4708 Tomahawk trap days, calculated as follows: 8 trapping grids x 3 trap days x 100 Longworth traps x 5 months (minus inactive traps), and 8 trapping grids x 3 trap days x 50 Tomahawk traps x 4 months (minus inactive traps). In total, we had 1657 total small mammal captures. We captured and tagged 687 unique individuals, including 246 deer mice (*Peromyscus maniculatus),* 237 Southern red-backed voles (*Myodes gapperi*), 58 American red squirrels (*Tamiasciurus hudsonicus*), 60 woodland jumping mice (*Napaeozapus insignis*) and 86 Northern short-tailed shrews (*Blarina brevicauda*). From June – September 2017, we totaled 6831 Longworth trap nights and captured an additional 29 jumping mice and 74 shrews.

### *Personality*

We quantified behaviour in an open-field test for 189 deer mice, 170 voles, 42 squirrels, 58 jumping mice and 87 shrews. After removing data from a small number of videos (such as videos from unknown individuals or where weather or noise conditions deemed the results untrustworthy), our final dataset included 261 observations from 170 individual deer mice, 231 observations from 168 individual voles, 80 observations from 41 individual squirrels, 72 observations from 57 individual jumping mice, and 113 observations from 84 individual short-tailed shrews.

*P. maniculatus* showed strong evidence of personality, with significant repeatability for 7 out of the 10 behaviours of interest. Individuals were consistent across tests taken one or more months apart in the amount of movement, jumping, rearing, passing through the center of the arena, grooming, and time spent stationary in the arena. See Table 1.2 for a summary of behavioural variables, mean and range statistics, and repeatability estimates. Further results are shown in Table A1.1. Individual *M. gapperi* were significantly repeatable for the proportion of time spent stationary in the center of the arena. For *T. hudsonicus,* we found that hanging on the walls and ceiling of the arena, jumping, rearing, time spent vigilant, as well as time spent stationary vs moving were all significantly repeatable behaviours among tests taken one or more months apart. For *N. insignis,* we found that individuals were consistent in the amount of time that they spent moving vs stationary in the open-field arena. *B. brevicauda* were significantly repeatable for four behaviours: passing through the center of the arena, jumping, moving, and stationary (Table 1.2).

**Table 1.2** Repeatability estimates for target behaviours measured in an open field test. Study species included in deer mice (*Peromyscus maniculatus*), Southern red-backed voles (*Myodes gapperi*), American red squirrels (*Tamiasciurus hudsonicus*), woodland jumping mice (*Napaeozapus insignis*) and Northern short-tailed shrews (*Blarina brevicauda*).

| ***P. maniculatus*** | | | | ***N. insignis*** | | | |
|---|---|---|---|---|---|---|---|
| Behaviour | Mean | Range | Repeatability (95% CI) | Behaviour | Mean | Range | Repeatability (95% CI) |
| **Center** | 0.06 | (0, 0.17) | **0.28 (0.13, 0.49)** | Center | 0.04 | (0, 0.16) | 0.15 (0, 0.75) |
| **Groom** | 0.11 | (0, 1.0) | **0.45 (0.30, 0.62)** | Groom | 0.12 | (0, 0.76) | 0.35 (0.06, 0.80) |
| **Jump** | 0.20 | (0, 0.81) | **0.37 (0.20, 0.55)** | Hang | 0.04 | (0, 0.25) | 0.22 (0, 0.76) |
| **Move** | 0.81 | (0, 0.99) | **0.41 (0.25, 0.59)** | Jump | 0.19 | (0, 0.63) | 0.22 (0, 0.78) |
| Sniff | 0.25 | (0, 0.80) | 0.23 (0.06, 0.45) | **Move** | 0.68 | (0, 0.99) | **0.48 (0.23, 0.84)** |
| **Rear** | 0.50 | (0, 0.90) | **0.45 (0.30, 0.63)** | Sniff | 0.24 | (0, 0.77) | 0 (0, 0.67) |
| **Stationary** | 0.18 | (0, 1.0) | **0.48 (0.32, 0.65)** | Rear | 0.34 | (0, 0.67) | 0.29 (0.03, 0.79) |
| **S. corner** | 0.17 | (0, 1.0) | **0.52 (0.39, 0.68)** | **Stationary** | 0.30 | (0, 1.0) | **0.38 (0.13, 0.82)** |
| S. edge | 0.01 | (0, 0.18) | 0.08 (0, 0.30) | **S. corner** | 0.21 | (0, 1.0) | **0.50 (0.25, 0.87)** |

## Table 1.2 continued

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| S. center | 0.00 | (0, 0.35) | 0.03 (0, 0.26) | **S. edge** | 0.08 | (0, 1.0) | **0.67 (0.51, 0.91)** |

| ***M. gapperi*** | | | | ***B. brevicauda*** | | | |
|---|---|---|---|---|---|---|---|
| Behaviour | Mean | Range | Repeatability (95% CI) | Behaviour | Mean | Range | Repeatability (95% CI) |
| Center | 0.04 | (0, 0.25) | 0.25 (0.07, 0.52) | **Center** | 0.08 | (0, 0.61) | **0.48 (0.27, 0.77)** |
| Groom | 0.21 | (0, 0.95) | 0.11 (0, 0.38) | Groom | 0.01 | (0, 0.33) | 0 (0, 0.47) |
| Jump | 0.04 | (0, 0.42) | 0.05 (0, 0.35) | **Jump** | 0.18 | (0, 0.60) | **0.49 (0.29, 0.76)** |
| Move | 0.44 | (0, 0.99) | 0.22 (0.04, 0.48) | **Move** | 0.85 | (0, 1.0) | **0.42 (0.14, 0.71)** |
| Sniff | 0.39 | (0, 1.0) | 0.04 (0, 0.32) | Sniff | 0.56 | (0, 1.0) | 0.14 (0, 0.57) |
| Rear | 0.29 | (0, 0.81) | 0.14 (0, 0.42) | Rear | 0.43 | (0, 0.97) | 0 (0, 0.47) |
| Stationary | 0.55 | (0.01, 1.0) | 0.22 (0.02, 0.49) | **Stationary** | 0.15 | (0, 1.0) | **0.42 (0.13, 0.73)** |
| S. corner | 0.47 | (0, 1.0) | 0.10 (0, 0.39) | S. corner | 0.12 | (0, 1.0) | 0.14 (0, 0.57) |
| S. edge | 0.07 | (0, 1.0) | 0 (0, 0.27) | | | | |
| **S. center** | 0.01 | (0, 0.49) | **0.28 (0.10, 0.54)** | | | | |

***T. hudsonicus***

| Behaviour | Mean | Range | Repeatability (95% CI) |
|---|---|---|---|
| Groom | 0.05 | (0, 0.75) | 0.29 (0.05, 0.62) |
| **Hang** | 0.01 | (0, 0.42) | **0.77 (0.65, 0.89)** |
| **Jump** | 0.04 | (0, 0.65) | **0.50 (0.24, 0.75)** |
| **Move** | 0.09 | (0, 0.93) | **0.37 (0.12, 0.68)** |
| Sniff/Chew | 0.21 | (0, 0.92) | 0.23 (0, 0.58) |
| **Rear** | 0.08 | (0, 0.80) | **0.43 (0.19, 0.71)** |
| **Vigilance** | 0.55 | (0, 0.99) | **0.40 (0.11, 0.68)** |
| **Stationary** | 0.82 | (0, 1.0) | **0.41 (0.14, 0.70)** |
| S. corner | 0.51 | (0, 1.0) | 0 (0, 0.41) |

**Table 1.2 continued**

| | | |
|---|---|---|
| S. edge | 0.26 (0, 1.0) | 0.10 (0, 0.46) |
| S. center | 0.04 (0, 1.0) | 0.04 (0, 0.44) |

Units for mean are the proportions of time spent performing each behaviour. Repeatability was calculated from univariate mixed-effects models with identity included as a random-effect. Parametric bootstrapping was used to calculate confidence intervals. (N =261 observations from 170 individual deer mice, N = 231 observations from 168 individual voles, N = 80 observations from 41 individual squirrels, N = 72 observations from 57 individual jumping mice and N = 113 observations from 84 individual shrews). See methods for more information.

### ***Repeatability of trappability***

For all five species, we found that neither CAP (the number of captures in a trapping session) nor FIRST (the night of first capture in a trapping session) was a significantly repeatable measure of trappability and that the inclusion of identity as a random-effect did not improve the models when compared with likelihood-ratio tests (see Table 1.3 for repeatability estimates, 95% CI, and results of likelihood-ratio tests, and see Table A1.2 for the median and interquartile range (IQR) of trappability variables). Outputs from univariate models predicting repeated and non-repeated measures are detailed below.

**Table 1.3** Correlation between behavioural variables and four different measures of trappability. Study species included deer mice (*Peromyscus maniculatus*), American red squirrels (*Tamiasciurus hudsonicus*), Southern red-backed voles (*Myodes gapperi*), woodland jumping mice (*Napaeozapus insigni*s) and Northern short-tailed shrews (*Blarina brevicauda*). These measures of trappability include two repeated measures: the number of captures in a session (CAP) and the night of the first capture in a session (FIRST), and two non-repeated measures: the total number of captures (corrected for days present in the population) (NUMCAP), and the total number of traps used (MAXTRAPS). Repeatability estimates for the repeated measures are shown and significant estimates are seen in bold.

| ***P. maniculatus*** | | | | | | | |
|---|---|---|---|---|---|---|---|
| **CAP** | Estimate | 95% CI | *P* | **FIRST** | Estimate | 95% CI | *P* |
| Repeatability | 0.00 | (0, 0.10) | --- | Repeatability | 0.00 | (0, 0.11) | --- |
| LRT | <0.001 | --- | 1.00 | LRT | <0.001 | --- | 1.00 |
| Corr. with Prop.c | -0.21 | (-0.96, 0.48) | --- | Corr. with Prop.c | -0.02 | (-0.82, 0.86) | --- |
| Corr. with Prop.g | 0.13 | (-0.61, 0.80) | --- | Corr. with Prop.g | 0.05 | (-0.70, 0.91) | --- |
| Corr. with Prop.j | 0.11 | (-0.61, 0.86) | --- | Corr. with Prop.j | -0.26 | (-0.98, 0.51) | --- |
| Corr. with Prop.m | 0.00 | (-0.67, 0.79) | --- | Corr. with Prop.m | -0.10 | (-0.90, 0.71) | --- |
| Corr. with Prop.r | -0.10 | (-0.80, 0.65) | --- | Corr. with Prop.r | 0.17 | (-0.69, 0.91) | --- |
| Corr. with Prop.s | -0.01 | (-0.79, 0.68) | --- | Corr. with Prop.s | 0.17 | (-0.61, 0.91) | --- |

## Table 1.3 continued

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Corr. with Prop.s.corner | 0.00 | (-0.70, 0.73) | --- | Corr. with Prop.s.corner | -0.21 | (-0.54, 0.95) | --- |

| **NUMCAP** | Estimate | 95% CI | *P* | **MAXTRAPS** | Estimate | 95% CI | *P* |
|---|---|---|---|---|---|---|---|
| Repeatability | --- | --- | --- | Repeatability | --- | --- | --- |
| LRT | --- | --- | --- | LRT | --- | --- | --- |
| Corr. with Prop.c | -0.09 | (-0.68, 0.47) | --- | Corr. with Prop.c | 0.03 | (-0.52, 0.52) | --- |
| Corr. with Prop.g | 0.10 | (-0.24, 0.42) | --- | Corr. with Prop.g | 0.01 | (-0.37, 0.42) | --- |
| Corr. with Prop.j | -0.14 | (-0.65, 0.20) | --- | Corr. with Prop.j | 0.04 | (-0.44, 0.46) | --- |
| Corr. with Prop.m | -0.06 | (-0.52, 0.48) | --- | Corr. with Prop.m | -0.14 | (-0.62, 0.31) | --- |
| Corr. with Prop.r | 0.02 | (-0.56, 0.77) | --- | Corr. with Prop.r | 0.01 | (-0.43, 0.51) | --- |
| Corr. with Prop.s | 0.09 | (-0.29, 0.50) | --- | Corr. with Prop.s | 0.00 | (-0.43, 0.38) | --- |
| Corr. with Prop.s.corner | 0.11 | (-0.27, 0.47) | --- | Corr. with Prop.s.corner | 0.05 | (-0.37, 0.51) | --- |

***M. gapperi***

| **CAP** | Estimate | 95% CI | *P* | **FIRST** | Estimate | 95% CI | *P* |
|---|---|---|---|---|---|---|---|
| Repeatability | 0.00 | (0, 0.11) | --- | Repeatability | 0.00 | (0, 0.12) | --- |
| LRT | 2.58 | --- | 0.28 | LRT | <0.001 | --- | 1.00 |

**Table 1.3 continued**

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Corr. with Prop.s.center | 0.07 | (-0.52, 0.64) | --- | Corr. with Prop.s.center | 0.22 | (-0.57, 0.94) | --- |
| **NUMCAP** | Estimate | 95% CI | *P* | **MAXTRAPS** | Estimate | 95% CI | *P* |
| **Repeatability** | --- | --- | --- | Repeatability | --- | --- | --- |
| **LRT** | --- | --- | --- | LRT | --- | --- | --- |
| Corr. with Prop.s.center | -0.03 | (-0.33, 0.31) | --- | Corr. with Prop.s.center | -0.27 | (-0.97, 0.45) | --- |
| ***T. hudsonicus*** | | | | | | | |
| **CAP** | Estimate | 95% CI | *P* | **FIRST** | Estimate | 95% CI | *P* |
| Repeatability | 0.00 | (0, 0.10) | --- | Repeatability | 0.00 | (0, 0.03) | --- |
| LRT | 0.19 | --- | 0.66 | LRT | 0.05 | --- | 0.83 |
| Corr. with Prop.h | -0.23 | (-0.95, 0.53) | --- | Corr. with Prop.h | -0.03 | (-0.84, 0.75) | --- |
| Corr. with Prop.j | -0.28 | (-0.95, 0.49) | --- | Corr. with Prop.j | 0.19 | (-0.69, 0.93) | --- |
| Corr. with Prop.m | -0.32 | (-0.96, 0.50) | --- | Corr. with Prop.m | 0.39 | (-0.39, 0.99) | --- |
| Corr. with Prop.r | -0.30 | (-0.99, 0.50) | --- | Corr. with Prop.r | 0.42 | (-0.32, 0.99) | --- |
| Corr. with Prop.v | 0.08 | (-0.70, 0.82) | --- | Corr. with Prop.v | -0.30 | (-0.99, 0.57) | --- |
| Corr. with Prop.s | 0.33 | (-0.45, 0.98) | --- | Corr. with Prop.s | -0.37 | (-0.99, 0.38) | --- |

## Table 1.3 continued

| **NUMCAP** | Estimate | 95% CI | *P* | **MAXTRAPS** | Estimate | 95% CI | *P* |
|---|---|---|---|---|---|---|---|
| Repeatability | --- | --- | --- | Repeatability | --- | --- | --- |
| LRT | --- | --- | --- | LRT | --- | --- | --- |
| Corr. with Prop.h | 0.10 | (-0.73, 0.91) | --- | Corr. with Prop.h | -0.37 | (-0.99, 0.40) | --- |
| Corr. with Prop.j | 0.21 | (-0.63, 0.99) | --- | Corr. with Prop.j | -0.42 | (-1.0, 0.35) | --- |
| Corr. with Prop.m | 0.27 | (-0.63, 0.99) | --- | Corr. with Prop.m | -0.39 | (-1.0, 0.53) | --- |
| Corr. with Prop.r | 0.22 | (-0.66, 0.96) | --- | Corr. with Prop.r | -0.37 | (-0.99, 0.40) | --- |
| Corr. with Prop.v | -0.09 | (-0.89, 0.79) | --- | Corr. with Prop.v | 0.15 | (-0.70, 0.97) | --- |
| Corr. with Prop.s | -0.27 | (-0.98, 0.60) | --- | Corr. with Prop.s | 0.57 | (-0.15, 1.0) | --- |

***N. insignis***

| **CAP** | Estimate | 95% CI | *P* | **FIRST** | Estimate | 95% CI | *P* |
|---|---|---|---|---|---|---|---|
| Repeatability | 0.00 | (0, 0.15) | --- | Repeatability | 0.00 | (0, 0.14) | --- |
| LRT | <0.001 | --- | 1.00 | LRT | <0.001 | --- | 1.00 |
| Corr. with Prop.m | 0.03 | (-0.84, 0.85) | --- | Corr. with Prop.m | 0.18 | (-0.71, 0.94) | --- |
| Corr. with Prop.s | 0.01 | (-0.85, 0.84) | --- | Corr. with Prop.s | -0.16 | (-0.98, 0.69) | --- |

## Table 1.3 continued

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Corr. with Prop.s.corner | 0.14 | (-0.74, 0.92) | --- | Corr. with Prop.s.corner | -0.25 | (-0.97, 0.62) | --- |
| Corr. with Prop.s.edge | -0.19 | (-0.97, 0.60) | --- | Corr. with Prop.s.edge | 0.15 | (-0.95, 0.93) | --- |
| **NUMCAP** | Estimate | 95% CI | *P* | **MAXTRAPS** | Estimate | 95% CI | *P* |
| **Repeatability** | --- | --- | --- | Repeatability | --- | --- | --- |
| **LRT** | --- | --- | --- | LRT | --- | --- | --- |
| Corr. with Prop.m | -0.08 | (-0.70, 0.60) | --- | Corr. with Prop.m | -0.04 | (-0.87, 0.87) | --- |
| Corr. with Prop.s | 0.02 | (-0.82, 0.75) | --- | Corr. with Prop.s | 0.13 | (-0.76, 0.92) | --- |
| Corr. with Prop.s.corner | -0.08 | (-0.79, 0.70) | --- | Corr. with Prop.s.corner | 0.16 | (-0.69, 0.98) | --- |
| Corr. with Prop.s.edge | 0.09 | (-0.48, 0.60) | --- | Corr. with Prop.s.edge | -0.03 | (-0.82, 0.81) | --- |
| ***B. brevicauda*** | | | | | | | |
| **CAP** | Estimate | 95% CI | *P* | **FIRST** | Estimate | 95% CI | *P* |
| Repeatability | 0.00 | (0, 0.13) | --- | Repeatability | 0.00 | (0, 0.12) | --- |
| LRT | <0.001 | --- | 1.00 | LRT | <0.001 | --- | 1.00 |
| **Corr. with Prop.c** | **0.60** | **(0.23, 0.97)** | --- | Corr. with Prop.c | -0.15 | (-0.88, 0.65) | --- |
| Corr. with Prop.j | 0.24 | (-0.32, 0.94) | --- | Corr. with Prop.j | 0.03 | (-0.79, 0.83) | --- |

**Table 1.3 continued**

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Corr. with Prop.m** | **0.56** | **(0.10, 0.99)** | --- | Corr. with Prop.m | -0.06 | (-0.82, 0.77) | --- |
| **Corr. with Prop.s** | **-0.57** | **(-1.0, -0.16)** | --- | Corr. with Prop.s | 0.06 | (-0.79, 0.85) | --- |

| **NUMCAP** | Estimate | 95% CI | *P* | **MAXTRAPS** | Estimate | 95% CI | *P* |
|---|---|---|---|---|---|---|---|
| Repeatability | --- | --- | --- | Repeatability | --- | --- | --- |
| LRT | --- | --- | --- | LRT | --- | --- | --- |
| **Corr. with Prop.c** | **-0.64** | **(-0.99, -0.09)** | --- | Corr. with Prop.c | 0.10 | (-0.53, 0.67) | --- |
| Corr. with Prop.j | -0.37 | (-1.0, 0.43) | --- | Corr. with Prop.j | 0.25 | (-0.39, 0.90) | --- |
| Corr. with Prop.m | -0.61 | (-1.0, 0.05) | --- | Corr. with Prop.m | 0.26 | (-0.54, 1.0) | --- |
| Corr. with Prop.s | 0.61 | (-0.04, 1.0) | --- | Corr. with Prop.s | -0.16 | (-0.94, 0.64) | --- |

*Full models included sex, average weight, treatment, session, the proportion of inactive traps, and the distance from the center of the trapping grid as fixed-effects. "Proportion inactive" refers to the proportion of traps available at a grid which were found inactive. Models for MAXTRAPS and NUMCAP also included the total days in the population as a fixed-effect. Scores for repeatability were calculated from univariate mixed-effects models with identity included as a random-effect. Parametric bootstrapping was used to calculate confidence intervals. Likelihood ratio tests were used to compare mixed-effects models to identical linear models (absent of random-effect). Markov Chain Monte Carlo multivariate glmms were used to estimate correlations. (N =261 observations from 170 individual deer mice, N = 231 observations from 168 individual voles, N = 80 observations from 41 individual squirrels, N = 72 observations from 57 individual jumping mice and N = 113 observations from 84 individual shrews. See methods for further details.

Trappability in *P. maniculatus* was influenced by the time of the season, with the number of captures per session (CAP) increasing as the trapping season progressed (β = 0.101, SE = 0.046, *P* = 0.027). We found an effect of sex on the maximum number of traps used (MAXTRAP), and females tended to use a greater number of traps overall (β = -0.246, SE = 0.084, *P* = 0.003). We found a positive effect of the total days in the population on the maximum number of traps used (β = 0.103, SE = 0.011, *P* < 0.001), and a negative effect of this variable on the overall capture probability (NUMCAP) (β = -0.025, SE = 0.003, *P* < 0.001). We found that overall capture probability was lower in treatment 1, even-aged forest, when compared to the reference areas (β = -0.097, SE = 0.041, *P* = 0.018). Finally, we found a negative effect of the distance to the center of the trapping grid on the overall capture probability (β = -0.019, SE = 0.008, *P* = 0.018), indicating that individuals living closer to the center of the grid had an increased probability of capture.

Our results show that for *T. hudsonicus*, individuals present in the population for longer had generally lower scores for overall capture probability (NUMCAP) (β = -0.375, SE = 0.034, *P* < 0.001), and used a greater maximum number of traps (β = 0.142, SE = 0.020, *P* < 0.001). See supplementary material for full results from univariate models predicting trappability.

In *M. gapperi*, CAP was positively affected by average weight (β = 0.025, SE = 0.011, *P* = 0.026), was higher in females than in males (β = -0.216, SE = 0.100, *P* = 0.032), and increased as the trapping season progressed from early summer into autumn (β = 0.102, SE = 0.050, *P* = 0.043). We found that males generally had a lower overall probability of capture (β = -0.161, SE = 0.064, *P* = 0.013), and that individuals present in the population for longer had lower scores for overall capture probability (β = -0.052, SE = 0.009, $P < 0.001$), and used a greater maximum number of traps (β = 0.155, SE = 0.012, $P < 0.001$).

In *B. brevicauda,* CAP was lower in treatment 3, selection cutting, when compared to the reference areas (β = -0.568, SE = 0.261, $P = 0.029$). As in *T. hudsonicus,* individuals present in the population for longer had generally lower scores for overall capture probability (NUMCAP) (β = -0.037, SE = 0.008, $P < 0.001$), and used a greater maximum number of traps (β = 0.092, SE = 0.011, $P < 0.001$).

Finally, for *N. insignis,* individuals with a greater number of days in the population had lower scores for overall capture probability (β = -0.074, SE = 0.007, $P < 0.001$), and used a greater maximum number of traps (β = 0.043, SE = 0.019, $P = 0.022$), but overall capture probability was also negatively affected by average weight (β = -0.014, SE = 0.006, $P = 0.027$).

### ***Behavioural variables and trappability***

The repeatable behavioural variables did not correlate significantly with either of the two repeated trappability measures for *P. maniculatus, M. gapperi, T. hudsonicus, or N. insignis*. Our results do show for *B. brevicauda*, however, that CAP is correlated positively with the proportion of time spent moving and passing through the center ($r = 0.56$ (0.10, 0.99); and $r = 0.60$ (0.23, 0.97) respectively) and, unsurprisingly, is correlated negatively with the proportion of time spent stationary in the arena ($r = -0.57$ (-1.0, -0.16)). We do acknowledge, however, the wide confidence intervals for these estimates.

For the two non-repeated measures MAXTRAP and NUMCAP, we found no correlations between any of the repeatable behavioural variables in four of the five study species. In *T. hudsonicus*, however, the overall capture probability (NUMCAP) was positively correlated with the time spent stationary in the open-field arena ($r = 0.72$ (0.43, 0.98), and correlated negatively with the proportion of time spent moving, jumping, and rearing (*r* = -0.61 (-0.94, -0.24); *r* = -0.49 (-0.90, -0.13); and *r* = -0.56 (-0.93, -0.19), respectively).

### ***Results from analysis on Eurasian species***

For 2802 observations from 2055 *Apodemus flavicollis*, 1928 observations from 1468 *Apodemus sylvaticus*, and 1601 observations from 1121 individual *Myodes glareolus*, trappability was not a repeatable trait (repeatability for CAP = 0, CI (0, 0.049), 0 (0, 0.042), and 0 (0, 0.059), respectively; and for FIRST = 0 (0, 0.042), 0 (0, 0.058), and 0 (0, 0.05)).

## DISCUSSION

Through a fully controlled and replicated field experiment, we explored the link between trappability and personality simultaneously across five small mammal species and in four contrasting environments. We measured numerous target behaviours in *Peromyscus maniculatus*, *Tamiasciurus hudsonicus*, *Myodes gapperi*, *Napaeozapus insignis* and *Blarina brevicauda* and found significant repeatability in these traits (i.e. personality) for all five species. Through multivariate mixed-effects modelling we showed that in 81 out of 88 combinations of personality traits with trappability, personality was not a predictor of trappability. It should also be noted that in most cases where personality did predict trappability, confidence intervals were large. Further, we assessed the repeatability of these trappability measures and found that in all cases trappability was not repeatable; in other words, trappability lacked a necessary requirement to be considered ‘personality’. Moreover, we investigated the repeatability of trappability for three additional small mammal datasets from Central Italy and, consistent with the results from our main study, found that trappability was not a repeatable trait.

*P. maniculatus* had significant repeatability in seven out of ten behaviours measured. The amount of time that individuals spent moving, jumping, passing through the center, and rearing all suggest that individual deer mice are consistent in the amount of activity and exploration that they perform, and these results are comparable to an activity-component of personality identified in other studies (Boon et al. 2007; Michelangeli et al. 2016; Patterson and Schulte-Hostedde 2011). Additionally, grooming behaviour and time spent stationary in the arena are indicative of a stress-response (Daniels et al. 2004; Kalueff and Tuohimaa, 2004) and have been identified as personality in previous studies (Martin and Réale, 2008).

In deer mice we found that, despite significantly repeatable behaviours indicating both activity and exploration, none of the variables were correlated with trappability. In fact, our results suggest that trappability changes throughout the season, with individuals entering traps significantly more often later in the summer and early autumn than they did in late spring and early summer. These results are consistent with findings by Tuyttens et al. (1999) and Byrne et al. (2012). Our results also suggest that forest type can influence trappability and that males use a smaller number of traps overall than do females. This result may be explained, however, by the fact that there were a greater number of males in the population with only one capture event than there were females (31 compared to 13). It is possible that these were young dispersing males.

To the best of our knowledge, our study is the first to explore personality in the woodland jumping mouse. While our sample size for this species was relatively small, we found evidence for an activity-related component of personality (Boon et al. 2007; Michelangeli et al. 2016; Patterson and Schulte-Hostedde 2011). Specifically, individuals either consistently moved throughout the open field arena or were stationary (mainly on the edges and in the corners). Our results do not show any evidence for an effect of activity levels on trappability, however, and full results of model outputs can be found in Table A1.2. Instead, our results suggest an effect of weight on trappability. Specifically, heavier individuals had a lower overall probability of capture after controlling for trap days present in the population. This result contrasts with findings by Adler and Lambert (1997) and Tuyttens et al. (1999).

Individual Southern red-backed voles were significantly repeatable for one behaviour indicating the level of activity. This result is consistent with studies on the common vole, *Microtus arvalis* (Eccard and Herde 2013), as well as the root vole, *Microtus oeconomus* (Hoset et al. 2011), which both found activity components of personality. In line with our findings from the other study species, our results suggest that trappability in *M. gapperi* is time-dependent, is influenced by weight, and varies between the sexes. In late summer and early fall, individuals were captured more often than early in the trapping season. This result may be indicative of a sensitivity of red-backed voles to seasonal pressures, as was found by Eccard and Herde (2013) in the common vole. This result may also be linked to age-related changes, and this is supported by the result that trappability was positively correlated with weight. Since many individuals born early in the season reached maturity by early fall, we could not tease apart these two possible effects. It is likely that age-related differences in trappability exist separately from seasonal-effects, because age-related behavioural differences have been found in the root vole (Hoset et al. 2011).

Personality in *T. hudsonicus* has been well documented in previous studies (Boon et al. 2007; 2008) and our results provide further evidence for the consistent behavioural differences between individual American red squirrels. Squirrels were consistent in behaviours which may suggest levels of activity, exploration, and impulsiveness (as defined in Boon et al. 2007; 2008). These were: moving, rearing, jumping, and hanging from the walls and ceiling of the open-field arena. While our findings suggest strongly that red squirrels exhibit consistent differences in their amount of activity and exploration, these behaviours did not predict either the relative propensity for an individual to be trapped (defined by the number of captures in a trapping session), or the relative latency to be captured (defined by the variable FIRST). Further, neither of these trappability measures was repeatable, indicating that they may not be reflective of personality. These behaviours suggesting activity and exploration (characterized by movement, jumping, and rearing) were significantly correlated to the overall capture probability of individual red squirrels. Specifically, more active individuals had a lower probability of capture compared to squirrels that spent more time stationary in the arena. This result contrasts the findings of previous studies of American red squirrels (Boon et al. 2008), but does not necessarily suggest that capture probability can be used as a proxy for personality since this is a non-repeated measure and thus, its repeatability cannot be investigated. Understanding the relationships between activity levels and trappability of red squirrels requires further investigation. There is no correlation between activity levels and trappability on a short-term scale (i.e. within each trapping session), but when data are pooled to reflect the entire trapping season, these relationships emerge. Our results suggested that red squirrels, in general, were more active in the early summer months than they were in late summer and early autumn (Table A1.2), but since we know that activity levels are a component of personality (and thus are consistent within individuals through time), this shift could be explained by the fact that more active individuals are trapped more often later in the trapping season. This could be because active squirrels are allocating proportionally more time and energy to other activities in late spring and early summer (i.e. breeding and rearing young) and, thus, may be less likely to utilize anthropogenic food resources provided by traps. Again, future work should explore these relationships.

Northern short-tailed shrews showed consistency in four different behaviours: passing through the center of the arena, jumping, moving, and stationary. These behaviours suggest consistency in activity level, and the proportion of time spent avoiding the center area of the arena vs passing through the center also indicates thigmotaxis (Polissidis et al. 2017). As for our other four study-species, none of these trappability variables were repeatable in short-tailed shrews and, thus, cannot be interpreted to indicate personality. Also in line with the majority of our findings, 13 out of the 16 combinations of personality variables with trappability indicated no evidence of a correlation between personality and trappability in short-tailed shrews. Of the three significant correlations found, it is worth noting that the confidence intervals were wide – almost spanning from -1 to 0 in all-cases. These findings included a positive correlation between the amount of activity performed in the open-field test and the number of captures per trapping session.

Nevertheless, since none of the trappability measures were repeatable in *B. brevicauda*, they cannot be considered personality or used as a proxy for the traits with which they correlate. In fact, there were significant differences in trappability between the forest treatments. These results could be due to differing levels of available food resources or cover, or to contrasting small mammal densities. Future work will investigate these points.

### ***Trappability and personality***

Our empirical results strongly suggest that great caution should be exerted if planning to use trappability as a proxy for personality traits measured by standard methods. In five different small mammal species, encompassing four different families of rodents and one shrew, we explored personality in an open-field test and simultaneously measured trappability. Our results indicate that none of these species has the two requirements needed to consider trappability a proxy for personality; for trappability to be repeatable and to correlate significantly with a measurement of personality. Further, these results suggest that trappability is not reflective of personality because in all instances the adjusted repeatability was equal to zero. Additionally, results from identical analyses run on three large small mammal datasets from an independent study conducted in central Italy support these findings. Our results also strongly indicate that it is not appropriate to use estimates of trappability obtained from long-term capture-mark-recapture datasets to explore questions relating to personality and population dynamics.

Our findings contrast those of previous studies on the American red squirrel (Boon et al. 2008) and a similar study species, the Siberian chipmunk (Boyer et al. 2010). While Boon et al. (2008) did not directly test the repeatability of trappability in female red squirrels, they did observe significant positive correlations between measures of trappability and activity levels – while we observed the opposite trend. Boon et al. (2008) admit that, because their study was performed during only one single trapping year, it is possible that the trappability and habitat use of each animal in that year was influenced by the animal's state. In our study these data were also obtained from one trapping season and so the implications for yearly state on trappability exist. However, our study having sampled individual red squirrels across distinct forest types decreases this possibility – as squirrels living under different conditions are exposed to differing levels of resources (which may simulate differences in resource availability over distinct trapping years). As stated previously, future work should examine these trends. Regardless, the contrast in results found by these two studies supports the requirement to measure personality and trappability separately and confirm repeatability of both before considering trappability as a proxy for personality traits.

Boyer et al. (2010), on the other hand, did confirm repeatability of trappability in the Siberian chipmunk. Note, however, that this study utilized only one measure of trappability per trapping year and estimated repeatability across these two measures. While this is a perfectly fine approach for the Siberian chipmunk, the species used in our study are more transient; commonly captured in only two or three trapping sessions due to high mortality rates and a short lifespan. As such, a more appropriate measure is one taken within a more limited time scale. A benefit of this approach is that it allows for the potential confounding effects to be more closely controlled for. For example, in our study, we were able to capture seasonal variability in trappability that other studies (utilizing only one measure of trappability per trapping year) could not incorporate. Further, we can assume population closure during each trapping session which means that our trappability estimates are not biased due to temporary movements (i.e. attributing trap-shyness to individuals who may temporarily emigrate from the trapping grid).

To use trappability as a proxy for a personality trait, trappability and personality must be measured and examined for repeatability in the specific study population. This is because a key element of personality is repeatability, or the proportion of total phenotypic variation accounted for by individual differences after controlling for the potential impacts of fixed-effects (Dingemanse and Dochtermann 2013; Dingemanse et al. 2010; Nakagawa and Schielzeth 2010). When the variance accounted for by differences among individuals is small in relation to the variance attributed to differences between individuals, this is good evidence for personality. Consequently, although a specific personality trait might predict trappability, it is incorrect to consider trappability a component of personality unless trappability itself is repeatable. This relationship should also be examined through time, as results from previous studies in a population may not hold true across years as environmental pressures and population dynamics change.

### ***Conclusions***

Our findings, comprising results from four rodent species and one shrew living in varying forest types, clearly demonstrate that trappability measurements cannot be used as proxies for personality because they are not repeatable, and are largely uncorrelated. We emphasize that these results do not necessarily imply that trap-happy or trap-shy individuals do not exist. Rather, our results suggest that these trapping biases can have complex relationships with age, weight, and sex of individual animals depending on the study system. Further, our results suggest that these biases may be constantly changing; contingent upon external factors instead of consistent within individuals over time. This contingency has strong effects on trappability and even when confounding factors are controlled for using mixed effects models, it may mask any consistency in this behaviour. As our work has shown, the trappability of small mammals can vary between sexes and between individuals of different weights and living in different environments. Our work also reveals the effect that season can have on the trappability of individuals. This is not to say that trappability can never be considered a characteristic of personality where it has been found to be repeatable (Boyer et al. 2010; La Coeur et al. 2015; Réale et al. 2000), but researchers should not take a blind approach when using trappability as a proxy for other personality traits.

# CHAPTER 2:
# FOOD FOR THOUGHT: ECOLOGICAL CONSEQUENCES OF PERSONALITY IN A GUILD OF TERRESTRIAL SMALL MAMMALS

## INTRODUCTION

Plants cover over 30% of the Earth's surface and, despite being sessile organisms, they have managed to colonize even the most inaccessible locations, and have shifted their ranges in response to geological and climate changes throughout time (Bonan, 2008; Ridley, 1930). Every single plant arrived at its emergence site via some mechanism of dispersal, and an estimated 50-90% of seed producing plants rely on animal modes of dispersal (Estrada & Fleming, 1986; Howe & Smallwood, 1982). Through millions of years of coevolution, animals have utilized the rich resources found in these seeds; in-turn providing an essential ecosystem function (Herrera, 2002; Vander Wall, 2010) by dispersing seeds away from the mother plant. *Scatter-hoarding* mammals are one such group of seed predators and dispersers; by caching surplus seeds in small hoards they promote dispersal (Jansen, Bongers, & Hemerik, 2004; Vander Wall, 2010). Scatter-hoarding behavior involves several key decisions (Figure 2.1) such as which seed to select, whether to consume the seed immediately or cache it for later consumption as well as where to cache a seed to maximize chances of retrieving it while minimizing pilferage risk (Lichti, Steele, & Swihart, 2015). Surprisingly, although variation among individuals is a prerequisite for evolution, very little is known about the impact of individual-level variation on seed dispersal; a process that has cascade effects on the whole ecosystem. This has been highlighted as a fundamental ecological question (Sutherland et al., 2013).

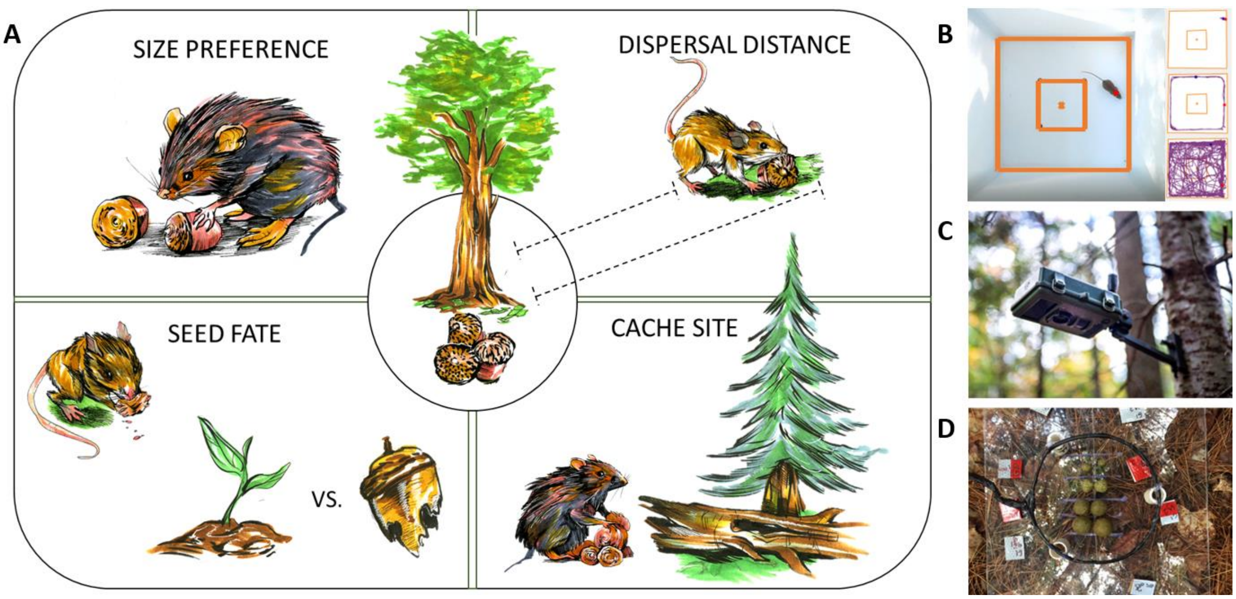

**Figure 2.1. Concept of the study. (A)** Effects of personality are explored at four key stages of seed dispersal. **(B)** Personality is measured in an open field test using ANY-maze® behavioral software. Example trajectories of three individuals show differences in activity (see Table B2.1 for further information). **(C)** High-definition trail cameras record interactions with seeds. **(D)** A seed experiment identifies known individuals while they choose between seeds of varying sizes. Flagged seeds allow for cache recovery.

Understanding the impacts of individual-level variation on the process of seed dispersal is critical (Zwolak, 2018) because not only can this variation result in ecological consequences, it can also have evolutionary implications. Small mammals are pervasive seed predators and dispersers and can harvest up to 95% of the seeds available in their territory (Lobo, 2014). This exerts selective pressures on certain seed attributes that scale up to ecosystem and community-level changes in plant species composition and drive evolution of seed traits (Jansen et al., 2002; Vander Wall, 2010). If certain individuals are contributing disproportionately to this process or providing rare outcomes (i.e. through selection of larger seeds or increased dispersal distance)

(Nathan, 2006) this will alter our understanding of the mechanistic foundations of seed dispersal, as well as the importance of individual behavioral variation to seed selection (Bolnick et al., 2011; Bolnick et al., 2003; González-Varo & Traveset, 2016).

Previous research has primarily examined how traits of seeds and environmental attributes influence the processes of seed predation and seed dispersal (i.e. via handling costs and predation risk) both at the interspecific and intraspecific level (Lichti et al., 2015; Zwolak, 2018). However, no study has examined variation in seed dispersal due to *personality* (Zwolak, 2018), which refers to consistent inheritable differences in behavioral tendencies among conspecifics (Dall, Houston, & McNamara, 2004; Sih, Bell, Johnson, & Ziemba, 2004). This is surprising because personalities are ubiquitous across taxa (Pennisi, 2016) and result in consistent differences in activity levels, exploration, and the propensity to take risks (Carere & Maestripieri, 2013) that ultimately affect individual fitness and other ecological parameters (Boon, Reale, & Boutin, 2008; Careau, Thomas, Humphries, & Re, 2008; Montiglio, Garant, Pelletier, & Réale, 2012; Smith & Blumstein, 2008). Consequently, it is extremely likely that small mammal personalities will influence numerous key decisions during seed dispersal because personality encapsulates an individual's unique way of behaving and responding to life's challenges (Réale et al., 2010). Since one of the greatest challenges in the life of a scatter hoarder is to collect and maintain seed caches, personality may drive certain individuals to contribute disproportionately to this key process (Zwolak, 2018).

If personalities influence seed dispersal this would mean that certain individuals are more important for maintaining ecosystem functioning than others. Identifying and conserving these individuals and preserving the behavioral diversity within a population will be a critical step for protecting this vital service to ecosystems (Correa et al., 2015; Dirzo et al., 2014). Further, if land-use change modifies the effect of individual-level variation on seed dispersal, habitat alteration could have unexpected consequences on this ecosystem-level process. During an era of rapid global change, understanding these processes is more important than ever, and maintaining this behavioral diversity is increasingly important when habitat modifications alter the distribution of behavioral phenotypes present in populations (Duckworth, Belloni, & Anderson, 2015; Miranda, Schielzeth, Sonntag, & Partecke, 2013), possibly resulting in the loss of “nonstandard” dispersers (Ran Nathan, 2006).

The goal of this study was to test the relationship between personality traits and key decisions at four vital stages of seed dispersal (Figure 2.1), and to determine whether these relationships varied across forests that have been manipulated with different silvicultural treatments. Accordingly, we conducted a large-scale, fully replicated field experiment wherein we trapped small mammals in three different forest types using mark-recapture techniques and measured personality in 648 free-ranging individuals using three standardized tests and an advanced behavioral tracking software (Figures A2.1 & A2.2). Previous work on this study population has confirmed that we are trapping a random subset of the population; that is, our work is not biased towards certain personality types – a major strength of this study (Brehm & Mortelliti, 2018). Then, in a seed predation experiment (Figure B2.3) we remotely observed interactions with artificial seeds (i.e. synthetic seeds of controlled mass with identical shape, quality, and odor – which will be referred to as ‘seeds’ hereafter)(Jansen et al., 2004; McGlothlin, Moore, Wolf, & Brodie, 2010; Steele et al., 2014) and assessed whether personality traits influenced key decisions in a natural environment and at vital stages of the dispersal process; ranging from the initial choice of seed size to the dispersal distance and fate of the seed.

## METHODS

### *Study Site and Small Mammal Trapping*

We conducted this study in the Penobscot Experimental Forest (PEF, 44° 51’ N, 68° 37’ W) which is located at the southern edge of the Acadian Forest in east-central Maine, U.S.A (Figure B2.4). The PEF is an experimental forest where forest units were chosen at random and logged separately with different silvicultural treatments (minimum of two replicates per treatment). Management units average 8.5 ha in size (range 8.1 – 16.2 ha) and nearly 25 ha of forest (retained in two separate units) has remained unmanaged since the late 1800s and serves as reference (Brehm & Mortelliti, 2018; Brissette & Kenefic, 2014).

As part of a fully controlled and replicated field experiment, we implemented a large-scale capture-mark-recapture study on six trapping grids: two control and four experimental. Control grids were located in the reference old-growth forest and experimental grids were located in either even-aged forest (two replicates) or two-stage shelterwood with retention (two replicates). Each trapping grid was 0.81 ha in area and consisted of 100 flagged points spaced 10 m apart. We positioned Longworth traps at each flagged point, bedded traps with cotton, and baited traps with a mixture of sunflower seeds, oats, and freeze-dried mealworms. Grids were positioned close to the center of the management unit to minimize edge effects (mean distance between grids was 1.44 km and mean distance between duplicate grids was 1.45 km; far greater than the movements of our target species). We trapped at each grid for 3 consecutive days and nights and grids were revisited after 1 month (five trapping sessions in total each year). We analyzed data collected from individuals over two trapping seasons (June – October 2016, 2017).

### ***Behavioral Tests***

We used three standard behavioral tests to measure personality in trapped individuals (Figure B2.1): an emergence test to measure boldness (Brown & Braithwaite, 2004; Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013), an open field test to assess activity and exploration in a novel environment (Perals, Griffin, Bartomeus, & Sol, 2017; Walsh & Cummins, 1976) and a handling bag test to measure docility and the response to being handled (Boon, Réale, & Boutin, 2007; Martin & Réale, 2008; Montiglio et al., 2012; Taylor, Boutin, Humphries, & Mcadam, 2014). At a base area in the home grid of the focal individual, we performed all tests in the order above before handling or marking. First, the animal was transferred directly from the trap of capture into a clean, empty Longworth trap. This trap was then placed into a box sized 46 x 46 x 50 cm. To create a more natural environment, the inside of the box had been painted light brown with a small amount of debris (dead leaves and pine needles) placed on the floor. The box was placed underneath a tarp to control for light levels and canopy cover. A digital camera (Nikon CoolPix S3700) was mounted facing the opening of the Longworth trap, and the observer locked the trap door open before leaving the test area. After three minutes, the observer returned and ended the test. Individuals were caught in a plastic bag and then released into the center of the open field arena.

A five minute open-field test was performed in an arena of dimensions 46 x 46 x 50 cm, placed on a level platform with light levels controlled (Brehm & Mortelliti, 2018). After five minutes, the animal was caught in a four-liter plastic bag and the observer suspended the bag into the open field test to control the visual surroundings. The observer measured the proportion of time that the individual spent immobile for 1 minute (referred to as handling time hereafter). Once behavioral tests were complete, animals were anesthetized with isoflurane and marked with

PIT tags (Biomark MiniHPT8) and either a small animal eartag or a distinctive haircut (i.e. for shrews, which have no external ears). We recorded the sex, weight (measured using a 100 g Pesola Lightline spring scale), body length, tail length, reproductive status, and age class. Animals were released at the exact site of capture. Traps used for emergence tests and the open-field test box were cleaned thoroughly with 70% isopropyl alcohol and wiped with a dry cloth in-between all tests. Behavioral tests were performed once monthly to ensure that animals would not habituate to the tests.

To analyze the videotaped emergence tests, we recorded whether or not the animal emerged (defined as all four feet having left the trap), the latency (in seconds) to emerge, the latency to go to the end of the Longworth tunnel, and the total time spent at the end of the tunnel before emerging. Open field tests were analyzed using the behavioral tracking software, ANY-maze ® (version 5.1; Stoelting CO, USA). See Table B2.1 for an ethogram of the behaviors measured and Figure B2.2 for an example of trajectories.

### ***Seed Experiments***

To record observations of seed choice in our marked populations, we performed a detailed seed experiment (Figure B2.3) during the months of July – October 2017, which is when seeds are naturally available. After the 3 consecutive day/night trapping period was completed each month, we deployed 106 seed experiment stations in our trapping grids (~18 stations per trapping grid). Target species were the deer mouse (*Peromyscus maniculatus),* the southern red-backed vole (*Myodes gapperi),* and the northern short-tailed shrew (*Blarina brevicauda).* At each seed station, we mounted a trail camera (Bushnell 119740 14MP Nature View HD) ~1 m above the ground and pointed it towards the forest floor to record videos of all small mammal seed choices and interactions with seeds. We placed a 30 x 30 cm piece of transparent plexiglass on the forest floor, and atop this plexiglass, we presented artificial seeds of four controlled masses (P. A. Jansen et al., 2004; McGlothlin et al., 2010; Steele et al., 2014). This allowed us to control for shape, odor, and quality; attributes that typically covary in real seeds (Smallwood & Peters, 1986; Wang, Ye, Cannon, & Chen, 2013). Artificial seeds were made using raw organic pumpkin seeds that had been pulverized into powder and a mixture of pure gelatin powder and water. The four distinct seed masses were 1, 3, 6, and 9 grams. Each artificial seed was formed into a ball, and seeds of the same mass were inspected to ensure that shape and size were consistent. Two seeds of each mass were placed at the station, and we randomly rotated the location of these seeds on the plexiglass, so that seeds were in a different order at each seed experiment station (Figure B2.3).

To allow for specific behavioral observations and seed choices to be associated with the individual who made them, we utilized a permanent RFID reader to scan and identify individuals marked with PIT tags (RFIDLOG dual animal tag rfid data logger). Mounted atop the plexiglass was an antenna (Priority1 rfidcoil – 160a) which attached to the reader located in a dry bag ~1 m away. These antennas were built to measure at an operating frequency of 134.4 kHz; the optimal operating frequency of the antenna. Records were automatically stored inside an SD memory card along with the exact date and time of the visit. To allow for easy relocation of dispersed seeds, we connected a 10cm long thin piece of copper thread to each seed, and at the end of the thread we attached a flag made of DOT-C2 grade reflective tape. Each flag was uniquely labeled and each seed’s location on the plexiglass was recorded for ease of identification in videos.

Each morning, an observer visited the seed experiment stations and recorded which seeds had been removed and which remained untouched at the site. Seeds that had been consumed at the site were recorded and removed. Seeds that had been removed from the site were relocated with the aid of a flashlight. The exact location of recovery was recorded by measuring the direct distance and bearing from the center of the seed station. We noted the location of recovery as either: at the seed station, on the ground relatively in the open, at the base of a tree, down a hole, underneath or next to CWD, or underneath or next to fine woody debris (FWD). Each recovered seed was classified as either ≥50% consumed, or <50% consumed (including 100% intact seeds). Seed stations were left active at a site for an average of 3 days and nights but were removed early if no seeds remained.

### ***Microhabitat Measurements***

Habitat structure is an important determinant of foraging activity by small mammals (Orrock, Danielson, & Brinkerhoff, 2004). Consequently, in July 2017, we recorded detailed microhabitat measurements at each seed experiment site (Dueser & Shugart, 1978; Mortelliti & Boitani, 2007). A ‘site’ was defined as the 5 m radius surrounding each experiment. At each site, field technicians measured numerous microhabitat variables, including canopy cover, shrub cover, and coarse woody debris (Table B2.2).

### ***Cone Abundance***

Seed abundance is known to influence foraging decisions by scatter-hoarding small mammals (Lobo, Green, & Millar, 2013; Vander Wall, 2010; Zhang, Cheng, Xiao, & Zhang, 2008). To quantify seed abundance in our study area, one observer surveyed all trapping grids during the first week of October 2017 to calculate an index of cone abundance (a proxy for seed abundance)(Broome, Summers, & Vanhala, 2016; Nixon & Worrell, 1999). In each trapping grid, cone counts were taken along ten parallel 1m-wide transects (van Riper & Cole, 2004). We focused on the three most common cone-types. These were: *Pinus strobus* and *Pinus resinosa,* white and red pine, *Abies balsamea*, balsam fir, and *Picea glauca* and *Picea rubens,* white and red spruce. Only cones that had fallen during 2017 were recorded (cones from previous years could be distinguished easily due to color and the presence of rot). Cones were counted only if the spine was still attached, and cone spines that were missing scales were also counted.

### *Analysis of seed videos*

Video observations from the seed experiments allowed us to observe and record detailed measures about interactions with seeds and choices made by small mammals. We played seed experiment videos back in the laboratory and recorded the following variables of interest: the total number of seconds that the individual spent at the seed station, the latency to choose a seed, the size of the first choice seed, the number of seconds consuming the first choice seed, the total number of seconds consuming seeds at the site, whether the seed was eventually removed from the site or consumed at the site, and the size of the removed seed. We then combined these observations with corresponding data obtained in the field (i.e. the distance that the seed was removed, the cache site, and the fate of the seed), and matched observations with visits by known individuals (via PIT reads).

## *Data Analyses*

### *Personality assessment*

To determine which behavioral variables could be considered personality, we used R package lme4 (Bates et al., 2014) to run univariate mixed-effects models and included potential confounding factors as covariates in the models. Specifically, we included sex, silvicultural treatment, trapping session, and body condition (calculated using the scaled mass index (Peig & Green, 2009)). We did not include sex in the models for *B. brevicauda* because shrews cannot be sexed externally. As dependent variables, we used the behavior of interest and ran separate mixed-effects models for each behavioral variable. We logit transformed the response variable when it was proportional (Warton & Hui, 2011; Zuur, Leno, Walker, Saveliev, & Smith, 2009) to meet the assumption of normality. Individual identity was included as a random effect in the models to account for the proportion of the variance that can be attributed to differences among individuals (Gelman & Hill, 2007; Zuur et al., 2009). We then calculated the adjusted repeatabilities (Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010) from the model outputs by dividing the among-individual variance by the total variance (equal to the among individual variance plus the residual variance). Statistically, repeatability refers to the proportion of the total phenotypic variation that can be attributed to individual differences (Dingemanse & Dochtermann, 2013; Dingemanse, Kazem, Réale, & Wright, 2010; Nakagawa & Schielzeth, 2010). Practically, this means that when differences between repeat measurements from the same individual are small in comparison to differences between individuals, this is good evidence for personality. We obtained 95% confidence intervals using parametric bootstrapping with 1000 simulations using the R package 'rptR' (Stoffel et al., 2017), and if the lower estimate of the confidence interval approached close to zero, we deemed the interval insignificant (Houslay & Wilson, 2017). We assessed normality by visually inspecting Q–Q plots and histograms of the residuals, and by plotting the fitted values against the residual values. Further details are described by Brehm and Mortelliti (2018).

After determining which variables were repeatable at the individual level and could, therefore, be considered part of an animals' personality, we examined the repeatable behavioral variables and explored the literature to assess which personality attributes they characterized. For full descriptions of the variables, the tests from which they were attained, and the sources we used to interpret them, see Table B2.1.

### ***Personality and seed choice***

To assess whether personality influenced decisions regarding seed predation and dispersal, we used a nested hypothesis testing approach (Burnham & Anderson, 2002) using mixed-effects models in R package *lme4* (Bates et al., 2015). Dependent variables that were numeric or integers were assessed for normality and log10 transformed if necessary. Binomial variables were examined using generalized linear mixed effects models with a binomial family and a logit link. Count variables were generally right-skewed and were examined using generalized linear mixed effects models with a negative binomial family.

We ran models using the variables obtained from the seed experiments (e.g. latency to choose, size choice, and distance dispersed) as dependent variables. First, in a base model we imposed covariates to control for the availability of each seed size since this variable has the potential to influence the seed choice, as well as the latency to make this choice (Cooper & Millspaugh, 1999; Manly, McDonald, Thomas, McDonald, & Erickson, 2002; Richardson, Lichti, & Swihart, 2013). Depending on the response variable, it was necessary to impose other control variables into the base model as well (Table B2.4). We checked whether models containing the imposed covariates fit the data better than the null model by comparing AICc scores, and models within 2 Delta AICc of the top model were considered to have equal support (Buckland, Burnham, & Augustin, 1997; Burnham & Anderson, 2002). The necessary imposed covariates were retained throughout the rest of the model selection process.

We first ran a model set comprised of six models: a null model (including imposed covariates), and one including each of the following: sex, body condition, reproductive status (either reproductively active or not), trapping session, and silvicultural treatment. We compared these models by AICc and, again, models within 2 Delta AICc of the top model were considered to have equal support (Burnham & Anderson, 2002). If two or more models showed better support than the null, we tested for an additive effect of these variables. Next, we retained the top model from this model set and tested it against six new models; adding one new microhabitat variable to each (Table B2.2). Again, if two or more models showed better support than the null, we tested for additive effects of these variables.

Next, we retained the top model from this model set and tested it against new models, each containing the additive effect of one personality variable (Table B2.1). By using this method, we intended to control for as much variability in the data as possible before introducing our personality covariates. We also tested for non-linear effects of personality (specifically, quadratic, exponential, and logarithmic) (Chavel, Imbeau, Mazerolle, & Drapeau, 2017; Pinheiro & Bates, 2000). Last, we tested the hypotheses that the relationship between personality and seed decisions would vary depending on sex, trapping session, and silvicultural treatment. To do this, we ran models including interactions between personality and sex, session, and treatment. We retained all models within 2 Delta AICc of the top model and used model averaging (Burnham & Anderson, 2002) to obtain estimates and confidence intervals.

We examined categorical response variables using multilevel, multinomial logistic regression models (Koster & McElreath, 2017). These models were fitted and plotted using *Rstan* (the interface to software Stan) and *rethinking* packages for R (McElreath 2016, Stan Development Team 2018). *Rstan* uses Hamiltonian Monte Carlo methods for parameter estimation; a preferred method for complex models because they allow adequate mixing of the posterior distribution in relatively fewer iterations of the chains (Monnahan, Thorson, & Branch, 2017). To facilitate good mixing of the Hamiltonian Monte Carlo chains, we provided weakly informative priors for the fixed effect parameters and variance-covariance matrices (Koster &

McElreath, 2017; McElreath, 2016a). For all models, we used three chains of 2000 iterations (including 1000 warm-up iterations)(Koster & McElreath, 2017; McElreath, 2016b). We evaluated model convergence and adequate mixing by inspecting traceplots and checking the number of effective samples (n_eff) and the Gelman-Rubin convergence diagnostic (Rhat) (McElreath, 2016b).

Similar to our procedures using *lme4*, we began by fitting a base model with seed availability covariates as fixed effects (i.e. the availability of each seed size) (Cooper & Millspaugh, 1999; Manly et al., 2002; Richardson et al., 2013) and individual ID as a random effect. We compared this base model to models containing the additional effects of sex, body condition, body weight, reproductive status, session, and treatment using the Widely Applicable Information Criterion (WAIC), (McElreath, 2016b) and for models within 2 Delta WAIC, we tested for additive effects among covariates. We continued the procedure; adding in microhabitat variables and then personality variables. As pointed out by Koster & McElreath (2017), when dealing with multinomial multilevel models, interpretation of coefficients is not straightforward and may be misleading, therefore we based our inference on the final probability of selection and its 89% percentile intervals.

## RESULTS

We examined behavioral data from standardized tests (Figure B2.1) for 705 observations from 295 individual deer mice (*Peromyscus maniculatus*), 646 observations from 244 southern red-backed voles (*Myodes gapperi),* and 246 observations from 109 northern short-tailed shrews (*Blarina brevicauda)* and found significant repeatability for a majority of behaviors (Table B2.4). Personality was a key predictor variable in the top model(s) for one or more species at all four key stages of seed dispersal (Figure 2.1; Table B2.5). Further, personality variables appeared in 84% of top models, and model fit for the top model was moderately high on average for the three species (mean $R^2 = 0.35$, Table B2.5).

Personality influenced seed size preference in all three study species (Table B2.5; Figure 2.2; Figure B2.5). Distance of seed dispersal and amount of seed consumed were affected by personality in both deer mice and voles (Figure 2.3) and personality also predicted cache location in voles (Figure 2.4). We found that personality variables also influenced the interaction of small mammals with seeds. Specifically, behaviors such as the latency to choose a seed, the time spent consuming seeds at the site, and the probability of removing a seed from the site (Table B2.5). Additionally, several microhabitat variables influenced seed predation decisions including: meters of coarse woody debris present at the seed experiment site, percent canopy cover, cone availability, shrub cover, and variables associated with visibility such as moon phase and sky condition (Table B2.5).

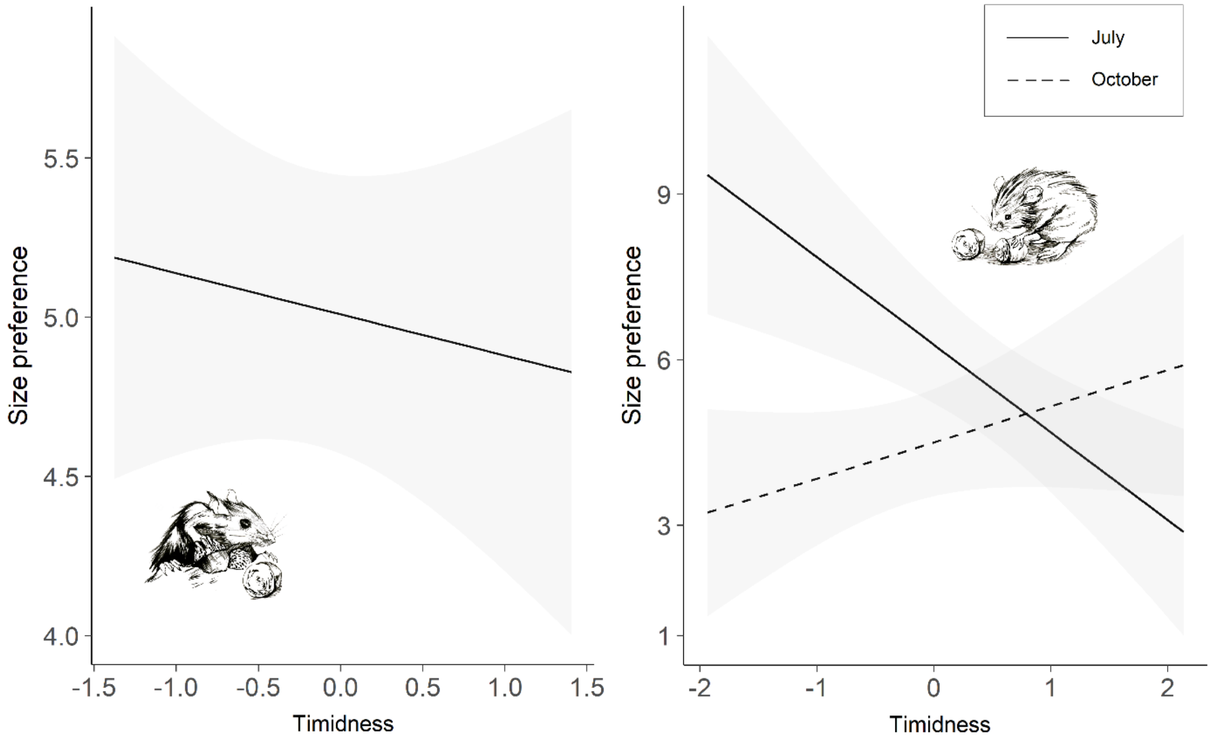

**Figure 2.2. Effects of personality on size preference** in *P. maniculatus* (left) and *M. gapperi* (right). Results were obtained from linear mixed-effects models with identity included as a random effect. Model-averaged 95% CIs are shown.

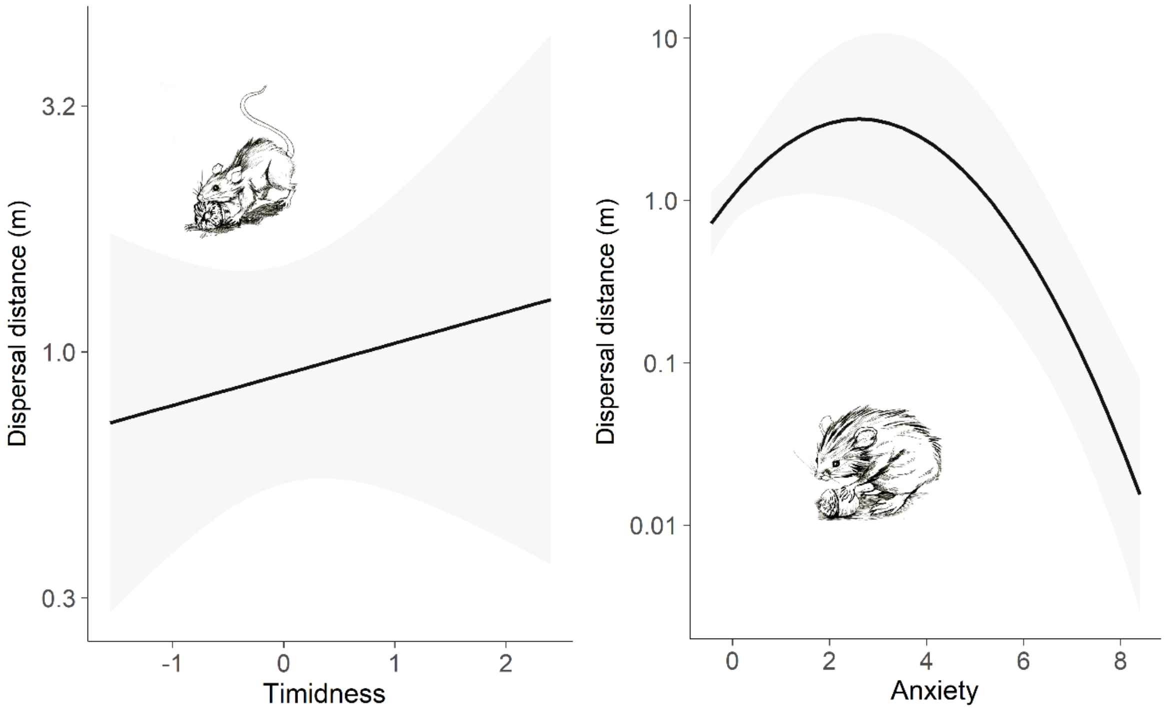

**Figure 2.3. Effects of personality on seed dispersal distance** in *P. maniculatus* and *M. gapperi*. Results were obtained from linear mixed-effects models with identity included as a random effect. Model-averaged 95% CIs are shown.

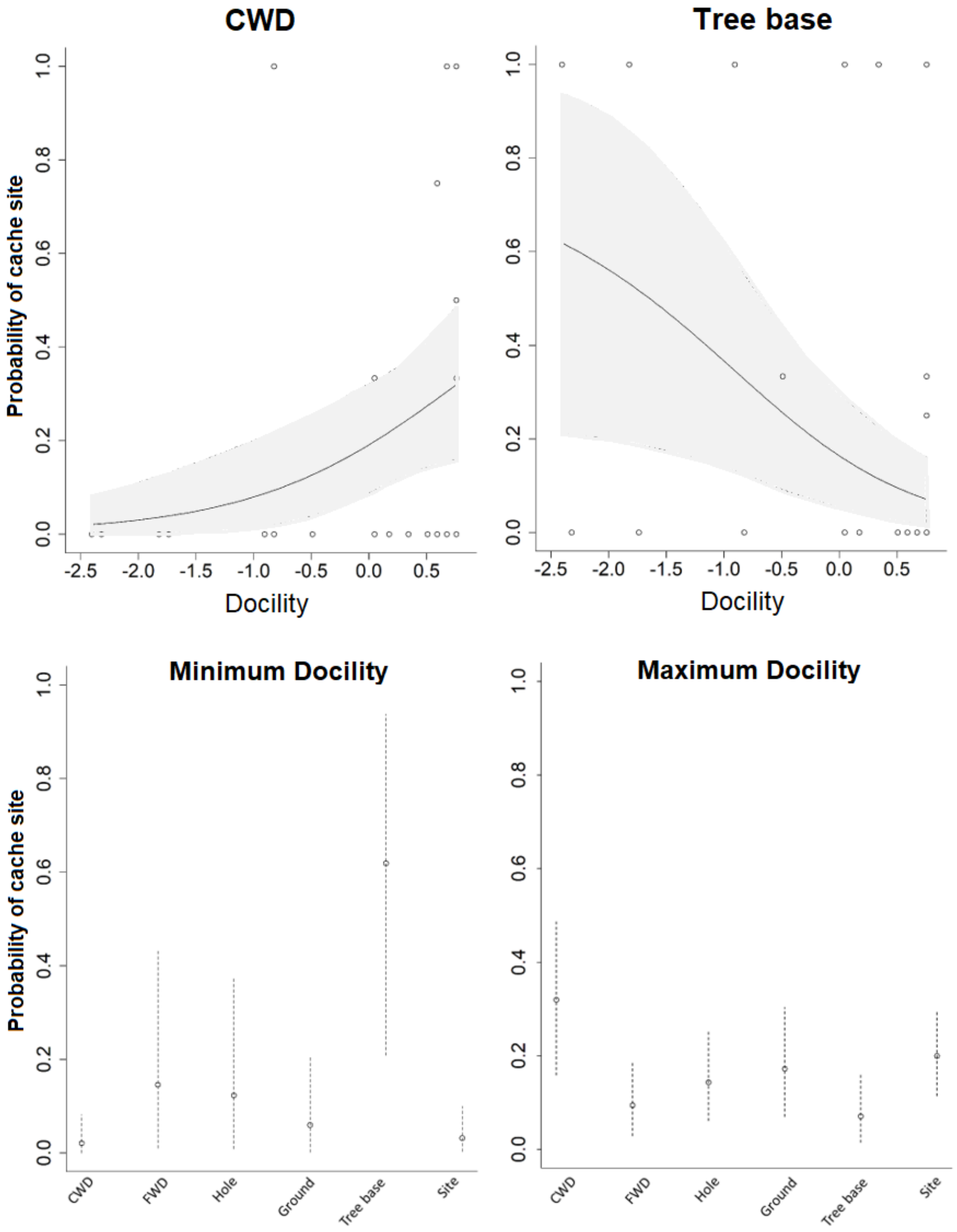

**Figure 2.4. Personality influences cache location in *M. gapperi*.** Results were obtained from multinomial mixed-effects models with identity included as a random effect. 89% percentile intervals are shown.

## DISCUSSION

Our empirical results show, for the first time, that individual personality affects all four core stages of seed dispersal: seed preference, dispersal distance, cache site, and seed fate. Decisions made by individuals are driven by their personality and can result in predictable ecological consequences, such as the chances of a seed surviving or being dispersed in an optimal site for germination. While our results do not suggest that silvicultural treatments mediate the relationships between personality and seed predation decisions, we provide evidence that populations with different distributions of personality types (Figure B2.5) will ultimately provide different contributions to this ecosystem process.

A scatter hoarder's preference for seed size is intricately related to nutrient content and metabolic requirements (Jansen et al., 2004), handling time and body size (Muñoz & Bonal, 2008), and predation risk (Lichti et al., 2015); resulting in complex costs and benefits to small mammals. Our results indicate that an individual's personality plays a key role in this decision-making process (Figure 2.2; Figure B2.6). Specifically, boldness in mice and voles influenced the size preference of seeds; timid mice generally removed smaller seeds than bold ones, and in voles, we found that in early/mid-summer, bold voles chose to remove larger seeds than timid voles. In autumn, however, this relationship was reversed, and timid voles chose larger seeds. Seasonal shifts in behavior are not uncommon, and as an example previous research on the common vole*, Microtus arvalis*, has shown that individuals exhibit seasonal behavioral plasticity because they benefit from bold/risk-taking personalities in the summer and a shy/cautious personality in the winter (Gracceva et al., 2014). Our results also indicated that anxiety/stress in mice influenced size preference; and less anxious mice had an increased probability of choosing a risky 9g seed over safer but less rewarding options. Last, our results suggested that activity levels influence size preference by shrews and voles. The least active shrews preferred the largest seed option over the smaller ones, and the most active voles had an increased probability of choosing 3g seeds, and a decreased probability of choosing 9g seeds. High activity has been shown to coincide with increased metabolism and thus increased requirement of resources (Careau et al., 2008). Our results from shrews and voles suggest a tradeoff between resource requirement and handling time. While the 9g seed option offers the highest energy payoff, it is possible that individuals with higher metabolic needs prefer smaller seed options because these seeds still offer a relatively high metabolic payoff while being easy to handle and disperse allowing the individual to obtain resources more quickly. These relationships between boldness, anxiety, activity, and size preference have implications for differing selective pressures on large or small seeds depending on the dominant personalities in the population.

Aside from size preference, several other decisions were influenced by activity level. Specifically, active deer mice were more likely to remove seeds from the site and consumed a greater proportion of the seed in the end compared to less active mice (likely due to higher metabolic requirements) (Table B2.5) (Careau et al., 2008). This suggests that highly active individuals might contribute more to seed predation and, thus, less to dispersal.

Dispersal distance of seeds is a complex metric influenced by several traits of the environment, seed, and the disperser (Jansen et al., 2004; Lichti et al., 2015; Muñoz & Bonal, 2008), and is critical to plant recruitment (Dirzo et al., 2014; Ran Nathan, 2006) by decreasing density-dependent mortality near the mother tree (P. A. Jansen, Bongers, & Van Der Meer, 2008; P. A. Jansen, Visser, Joseph Wright, Rutten, & Muller-Landau, 2014; R. Nathan & Muller-landau, 2000). Our results provide evidence that dispersal distance depends on an individual's response to stress (Figure 2.3) and that anxious individuals contribute far less to dispersal than those with low anxiety (moving seeds less than half the distance). Though the contributions by a single small mammal won't result in ecosystem level shifts in dispersal, these rare dispersal events are critical and have disproportionate effects on gene flow, regeneration rates, and range expansion (Ran Nathan, 2006; Zwolak, 2018). One previous study has observed a relationship between "boldness" and the spatial pattern between caches (Dochtermann & Jenkins, 2007), however repeatability was not assessed so it remains unclear whether these measurements constituted personality (Bell, Hankison, & Laskowski, 2009).

The location in which a seed is cached often depends on the risk of cache pilferage (Muñoz & Bonal, 2011; Steele et al., 2014) and traits of the seed (Wang & Corlett, 2017) and this placement impacts the effectiveness of the seed's dispersal by moderating seedling establishment. Often, small mammals can increase germination probability by transporting seeds to optimal sites for germination (Vander Wall, 2010; Wenny, 2001). Our results show that docility (Taylor et al., 2014) is a personality trait which influences the location of cache placement by voles (Figure 2.4). Specifically, docile individuals were more likely to cache seeds among coarse woody debris (which offer several benefits to seedlings) (Fukasawa, 2012; Harmon et al., 1986) and also provide important refuge to small mammals (Fauteux, Imbeau, Drapeau, & Mazerolle, 2012). By contrast, the least docile individuals were more likely to transport seeds to the base of a tree; an area where density dependent mortality is common (P. A. Jansen et al., 2014). Docility, therefore, moderates a disperser's contribution to seedling establishment.

This study provides the first evidence that personality traits influence all critical stages of seed predation and dispersal by scatter-hoarding small mammals. Not only does this imply that personality may be a mechanism influencing forest structure and composition at local/population scales, but also that it may affect processes like long-distance dispersal and plant species range-shifts. Our study provides empirical evidence that conserving behavioral diversity could in-turn maintain a diversity of ecological functions by conserving individuals with certain personality types that are more likely to cache seeds in optimal sites for germination or disperse seeds further from the mother tree. A paradigm shift towards promoting behavioral diversity within populations should be a critical target for conservation. Not all individuals are equal when it comes to the ecological consequences of personality on seed dispersal.

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# APPENDIX A CHAPTER 1 SUPPLEMENTARY MATERIALS

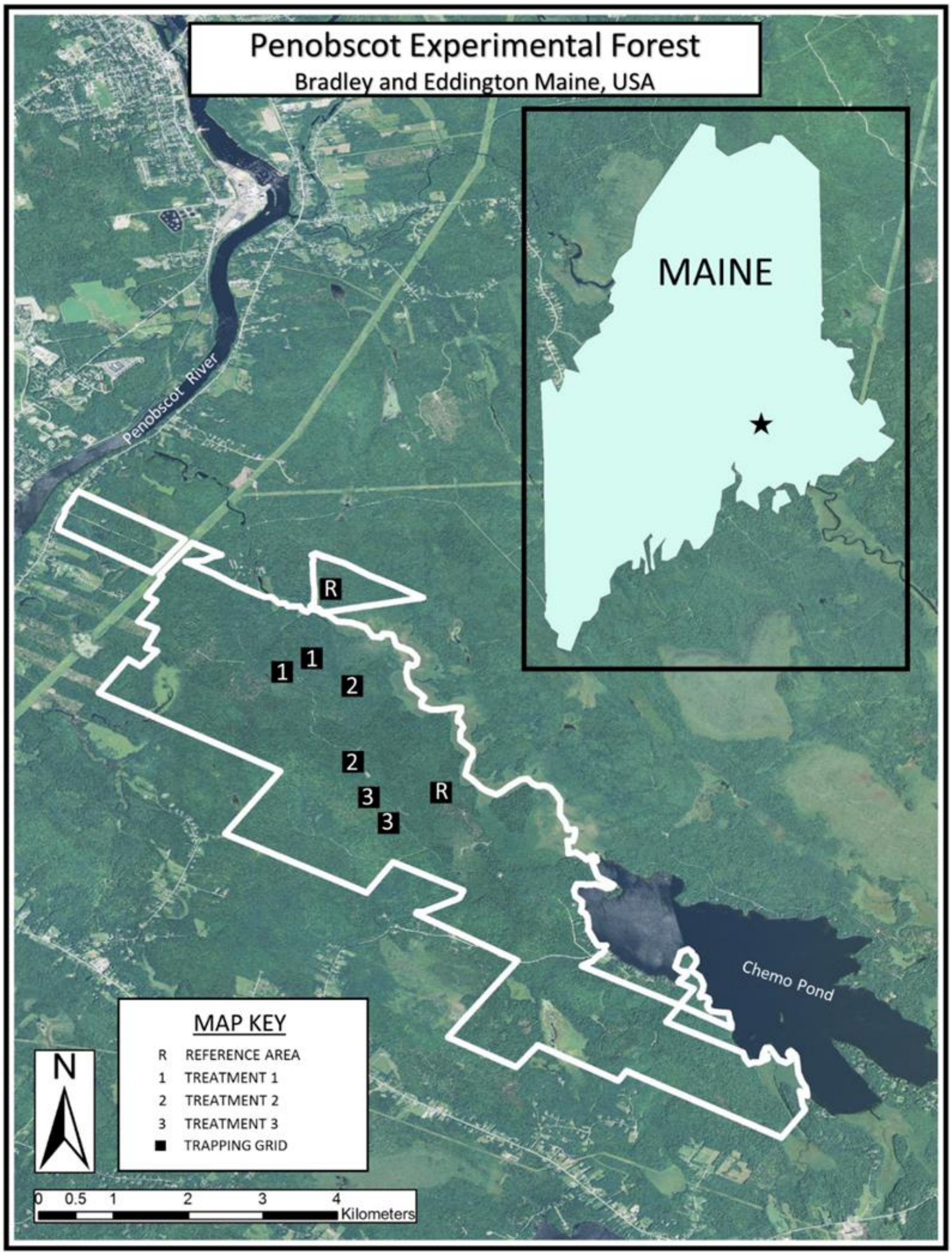

**Figure A1.1** Map of study area at the Penobscot Experimental Forest (PEF, 44 053’ N, 68 039’ W) in Bradley and Eddington, Maine, USA. Treatment and reference areas are shown. Details about treatments are described in the methods section.

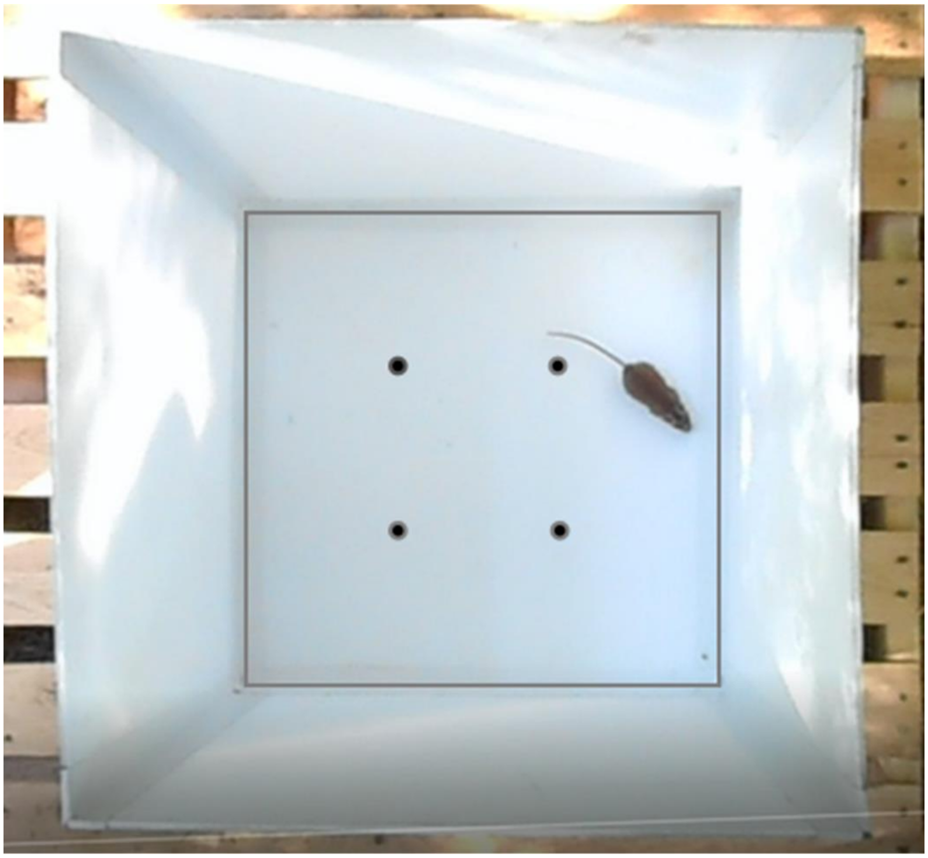

**Figure A1.2** Open-field test arena. A 46 x 46 x 50 cm box was placed on a level wooden-platform in the home-grid of the test animal. Above the arena, a tarp controlled for light levels and canopy cover. Squirrel box dimensions were 90 x 90 x 90 cm. See introduction and methods for further detail about open-field tests.

**Table A1.1** Model output and variance structures from univariate mixed-effects models* predicting repeatable behaviours. Study species included deer mice (*Peromyscus maniculatus*), American red squirrels (*Tamiasciurus hudsonicus*), Northern short-tailed shrews (*Blarina brevicauda*), Southern red-backed voles (*Myodes gapperi*), and woodland jumping mice (*Napaeozapus insignis*).

| ***P. maniculatus*** | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Prop.c** | β | St. Error | *P* | **Prop.g** | β | St. Error | *P* |
| (Intercept) | -2.464 | 0.289 | <0.001 | (Intercept) | -3.926 | 0.599 | <0.001 |
| **Avg.Weight** | -0.032 | 0.016 | **0.044** | **Avg.Weight** | 0.110 | 0.034 | **0.001** |
| SexM | 0.027 | 0.084 | 0.751 | **SexM** | -0.378 | 0.175 | **0.031** |
| Treatment 1 | 0.114 | 0.161 | 0.491 | Treatment 1 | 0.665 | 0.344 | 0.055 |
| **Treatment 2** | 0.299 | 0.120 | **0.014** | Treatment 2 | -0.117 | 0.256 | 0.647 |
| Treatment 3 | 0.091 | 0.111 | 0.415 | Treatment 3 | -0.174 | 0.237 | 0.464 |
| Session | 0.021 | 0.038 | 0.582 | Session | -0.045 | 0.073 | 0.538 |
| **Variance** | **ID** | 0.116 | | | **ID** | 0.764 | |
| | **Residual** | 0.289 | | | **Residual** | 0.940 | |
| **Prop.j** | β | St. Error | *P* | **Prop.m** | β | St. Error | *P* |
| (Intercept) | -0.336 | 0.545 | 0.538 | (Intercept) | 3.811 | 0.661 | <0.001 |
| **Avg.Weight** | -0.125 | 0.030 | **<0.001** | **Avg.Weight** | -1.170 | 0.037 | **<0.001** |
| SexM | 0.117 | 0.159 | 0.463 | SexM | 0.264 | 0.193 | 0.172 |
| Treatment 1 | -0.075 | 0.308 | 0.809 | Treatment 1 | -0.516 | 0.377 | 0.174 |
| Treatment 2 | 0.252 | 0.229 | 0.273 | Treatment 2 | 0.312 | 0.280 | 0.268 |
| Treatment 3 | 0.329 | 0.212 | 0.123 | Treatment 3 | 0.078 | 0.260 | 0.764 |
| Session | 0.099 | 0.069 | 0.150 | **Session** | 0.186 | 0.082 | **0.024** |
| | **ID** | 0.521 | | **Variance** | **ID** | 0.859 | |
| | **Residual** | 0.896 | | | **Residual** | 0.218 | |

## Table A1.1 continued

| **Prop.r** | β | St. Error | *P* | **Prop.s** | β | St. Error | *P* |
|---|---|---|---|---|---|---|---|
| (Intercept) | 0.858 | 0.369 | 0.028 | (Intercept) | -3.910 | 0.653 | <0.001 |
| **Avg.Weight** | -0.061 | 0.022 | **0.006** | **Avg.Weight** | 0.174 | 0.040 | **<0.001** |
| SexM | 0.008 | 0.113 | 0.943 | SexM | -0.297 | 0.190 | 0.120 |
| **Treatment 1** | -0.665 | 0.222 | **0.003** | Treatment 1 | 0.544 | 0.378 | 0.152 |
| Treatment 2 | -0.056 | 0.165 | 0.751 | Treatment 2 | -0.241 | 0.281 | 0.392 |
| Treatment 3 | -0.189 | 0.153 | 0.218 | Treatment 3 | -0.104 | 0.260 | 0.691 |
| Session | 0.061 | 0.047 | 0.200 | **Session** | -0.196 | 0.078 | **0.013** |
|  | **ID** | 0.319 |  |  | **ID** | 0.978 |  |
|  | **Residual** | 0.392 |  |  | **Residual** | 1.047 |  |

| **Prop.s.corner** | β | St. Error | *P* |
|---|---|---|---|
| (Intercept) | -4.119 | 0.672 | <0.001 |
| **Avg.Weight** | 0.174 | 0.038 | **<0.001** |
| SexM | -0.367 | 0.195 | 0.061 |
| Treatment 1 | 0.419 | 0.392 | 0.288 |
| Treatment 2 | -0.262 | 0.291 | 0.370 |
| Treatment 3 | -0.109 | 0.270 | 0.688 |
| Session | -0.152 | 0.079 | 0.055 |
| **Variance** | **ID** | 1.115 |  |
|  | **Residual** | 1.029 |  |

***T. hudsonicus***

| **Prop.h** | β | St. Error | *P* | **Prop.j** | β | St. Error | *P* |
|---|---|---|---|---|---|---|---|
| (Intercept) | -3.998 | 1.488 | 0.012 | (Intercept) | -2.524 | 2.326 | 0.284 |
| Avg.Weight | -0.005 | 0.009 | 0.547 | Avg.Weight | -0.011 | 0.014 | 0.421 |
| SexM | 0.376 | 0.233 | 0.115 | SexM | 0.298 | 0.378 | 0.435 |

## Table A1.1 continued

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Treatment 1 | 0.075 | 0.423 | 0.860 | Treatment 1 | 0.296 | 0.664 | 0.659 |
| Treatment 2 | 0.195 | 0.414 | 0.642 | Treatment 2 | 0.341 | 0.645 | 0.601 |
| Treatment 3 | 0.001 | 0.436 | 0.998 | Treatment 3 | 0.074 | 0.666 | 0.912 |
| Session | 0.033 | 0.049 | 0.512 | Session | -0.064 | 0.110 | 0.563 |
| **Variance** | **ID** | 0.490 | | | **ID** | 0.854 | |
| | **Residual** | 0.148 | | | **Residual** | 0.847 | |

| **Prop.m** | β | St. Error | *P* | **Prop.r** | β | St. Error | *P* |
|---|---|---|---|---|---|---|---|
| (Intercept) | -0.131 | 2.536 | 0.959 | (Intercept) | -2.313 | 2.537 | 0.367 |
| Avg.Weight | -0.019 | 0.015 | 0.215 | Avg.Weight | -0.009 | 0.015 | 0.543 |
| SexM | 0.305 | 0.410 | 0.462 | SexM | 0.657 | 0.412 | 0.119 |
| Treatment 1 | 1.269 | 0.723 | 0.086 | **Treatment 1** | 1.579 | 0.724 | **0.035** |
| Treatment 2 | 1.347 | 0.700 | 0.061 | Treatment 2 | 0.981 | 0.702 | 0.170 |
| Treatment 3 | 0.523 | 0.717 | 0.470 | Treatment 3 | 0.741 | 0.722 | 0.311 |
| **Session** | -0.492 | 0.134 | **<0.001** | **Session** | -0.395 | 0.128 | **0.003** |
| | **ID** | 0.798 | | | **ID** | 0.900 | |
| | **Residual** | 1.337 | | | **Residual** | 1.183 | |

| **Prop.v** | β | St. Error | *P* | **Prop.s** | β | St. Error | *P* |
|---|---|---|---|---|---|---|---|
| (Intercept) | -7.212 | 3.946 | 0.076 | (Intercept) | -0.984 | 3.860 | 0.800 |
| Avg.Weight | 0.044 | 0.023 | 0.070 | Avg.Weight | 0.025 | 0.023 | 0.278 |
| **SexM** | -1.712 | 0.639 | **0.011** | SexM | -0.670 | 0.626 | 0.290 |
| Treatment 1 | 0.826 | 1.125 | 0.468 | Treatment 1 | -2.072 | 1.101 | 0.067 |
| Treatment 2 | 0.637 | 1.090 | 0.563 | Treatment 2 | -1.367 | 1.067 | 0.207 |
| Treatment 3 | 1.111 | 1.119 | 0.329 | Treatment 3 | -0.759 | 1.095 | 0.493 |
| Session | 0.343 | 0.204 | 0.099 | **Session** | 0.541 | 0.199 | **0.008** |
| | **ID** | 2.037 | | | **ID** | 1.977 | |
| | **Residual** | 3.074 | | | **Residual** | 2.899 | |

## Table A1.1 continued

| ***B. brevicauda*** | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Prop.c** | β | St. Error | *P* | **Prop.j** | β | St. Error | *P* |
| (Intercept) | -3.421 | 0.912 | <0.001 | (Intercept) | -0.946 | 1.233 | 0.445 |
| Avg.Weight | 0.008 | 0.052 | 0.874 | Avg.Weight | -0.059 | 0.071 | 0.403 |
| Treatment 1 | 0.235 | 0.343 | 0.495 | Treatment 1 | 0.820 | 0.464 | 0.081 |
| Treatment 2 | 0.656 | 0.373 | 0.082 | Treatment 2 | 0.563 | 0.504 | 0.267 |
| Treatment 3 | -0.195 | 0.388 | 0.616 | **Treatment 3** | 1.295 | 0.525 | **0.016** |
| Session | 0.051 | 0.102 | 0.621 | Session | -0.238 | 0.137 | 0.086 |
| **Variance** | **ID** | 0.573 | | | **ID** | 1.071 | |
| | **Residual** | 0.615 | | | **Residual** | 1.096 | |
| **Prop.s** | β | St. Error | *P* | **Prop.m** | β | St. Error | *P* |
| (Intercept) | -2.752 | 2.012 | 0.175 | (Intercept) | 2.764 | 2.011 | 0.173 |
| Avg.Weight | 0.038 | 0.115 | 0.743 | Avg.Weight | -0.038 | 0.115 | 0.741 |
| Treatment 1 | -0.701 | 0.757 | 0.357 | Treatment 1 | 0.693 | 0.757 | 0.363 |
| Treatment 2 | -1.089 | 0.823 | 0.189 | Treatment 2 | 1.087 | 0.822 | 0.190 |
| Treatment 3 | -0.908 | 0.858 | 0.293 | Treatment 3 | 0.907 | 0.858 | 0.293 |
| Session | -0.046 | 0.232 | 0.844 | Session | 0.043 | 0.232 | 0.853 |
| **Variance** | **ID** | 2.459 | | | **ID** | 2.452 | |
| | **Residual** | 3.414 | | | **Residual** | 3.414 | |

| ***M. gapperi*** | | | |
|---|---|---|---|
| **Prop.s.center** | β | St. Error | *P* |
| (Intercept) | -4.489 | 0.284 | <0.001 |
| Avg.Weight | 0.006 | 0.010 | 0.521 |
| SexM | -0.011 | 0.094 | 0.907 |
| **Treatment 1** | 0.365 | 0.157 | **0.021** |

## Table A1.1 continued

| | | | |
|---|---|---|---|
| Treatment 2 | 0.034 | 0.143 | 0.812 |
| Treatment 3 | 0.139 | 0.121 | 0.251 |
| Session | -0.054 | 0.042 | 0.197 |
| **Variance** | **ID** | 0.118 | |
| | **Residual** | 0.297 | |

***N. insignis***

| **Prop.m** | β | St. Error | *P* | **Prop.s** | β | St. Error | *P* |
|---|---|---|---|---|---|---|---|
| (Intercept) | 3.707 | 1.814 | 0.045 | (Intercept) | -3.945 | 1.785 | 0.031 |
| Avg.Weight | -0.058 | 0.059 | 0.329 | Avg.Weight | 0.058 | 0.057 | 0.319 |
| SexM | 0.756 | 0.567 | 0.189 | SexM | -0.729 | 0.549 | 0.192 |
| Treatment 1 | 0.035 | 1.290 | 0.978 | Treatment 1 | -0.194 | 1.249 | 0.878 |
| Treatment 2 | -0.447 | 1.231 | 0.718 | Treatment 2 | 0.270 | 1.191 | 0.822 |
| Treatment 3 | -0.016 | 1.250 | 0.990 | Treatment 3 | 0.051 | 1.212 | 0.967 |
| Session | -0.579 | 0.307 | 0.065 | **Session** | 0.664 | 0.311 | **0.037** |
| **Variance** | **ID** | 2.019 | | **Variance** | **ID** | 1.535 | |
| | **Residual** | 2.214 | | | **Residual** | 2.545 | |

| **Prop.s.corner** | β | St. Error | *P* | **Prop.s.edge** | β | St. Error | *P* |
|---|---|---|---|---|---|---|---|
| (Intercept) | -4.054 | 1.682 | 0.019 | (Intercept) | 0.062 | 0.193 | 0.748 |
| Avg.Weight | 0.084 | 0.054 | 0.129 | Avg.Weight | -0.003 | 0.007 | 0.702 |
| SexM | 0.144 | 0.528 | 0.786 | SexM | -0.109 | 0.067 | 0.110 |
| Treatment 1 | -1.022 | 1.201 | 0.399 | Treatment 1 | 0.082 | 0.153 | 0.595 |
| Treatment 2 | -0.375 | 1.145 | 0.745 | Treatment 2 | 0.086 | 0.146 | 0.559 |
| Treatment 3 | -0.210 | 1.163 | 0.857 | Treatment 3 | 0.047 | 0.147 | 0.750 |
| Session | 0.274 | 0.282 | 0.335 | Session | 0.020 | 0.023 | 0.396 |

**Table A1.1 continued**

| | | | | | |
|---|---|---|---|---|---|
| **Variance** | **ID** | 1.822 | **Variance** | **ID** | 0.047 |
| | **Residual** | 1.823 | | **Residual** | 0.007 |

*Models included individual identity as a random-effect. (N =261 observations from 170 individual deer mice, N = 231 observations from 168 individual voles, N = 80 observations from 41 individual squirrels, N = 72 observations from 57 individual jumping mice and N = 113 observations from 84 individual shrews). See methods for more information.

**Table A1.2** Model output and variance structures from univariate mixed-effects models* predicting four measures of trappability. Study species included deer mice (*Peromyscus maniculatus*), American red squirrels (*Tamiasciurus hudsonicus*), Southern red-backed voles (*Myodes gapperi*), Northern short-tailed shrews (*Blarina brevicauda*), and woodland jumping mice (*Napaeozapus insignis*). These measures of trappability include two repeated measures: the number of captures in a session (CAP) and the night of the first capture in a session (FIRST), and two non-repeated measures: the total number of captures (corrected for days present in the population) (NUMCAP), and the total number of traps used (MAXTRAPS). Median and interquartile range (IQR) are included.

| ***P. maniculatus*** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **CAP** | β | St. Error | *P* | **FIRST** | β | St. Error | *P* |
| | Intercept | 0.660 | 0.338 | 0.051 | Intercept | 0.595 | 0.355 | 0.094 |
| | Avg.weight | -0.007 | 0.017 | 0.689 | Avg.weight | 0.008 | 0.018 | 0.665 |
| | SexM | -0.138 | 0.091 | 0.129 | SexM | -0.030 | 0.096 | 0.756 |
| | Prop.inactive | 0.792 | 0.815 | 0.331 | Prop.inactive | -1.489 | 0.996 | 0.135 |
| | Treatment 1 | -0.255 | 0.174 | 0.143 | Treatment 1 | 0.268 | 0.165 | 0.103 |
| | Treatment 2 | -0.085 | 0.121 | 0.483 | Treatment 2 | 0.175 | 0.131 | 0.184 |
| | Treatment 3 | -0.128 | 0.115 | 0.265 | Treatment 3 | 0.119 | 0.124 | 0.339 |
| | **Session** | 0.101 | 0.046 | **0.027** | Session | -0.027 | 0.048 | 0.565 |
| | Dist.center | -0.020 | 0.032 | 0.528 | Dist.center | -0.028 | 0.034 | 0.408 |
| **Variance** | **ID** | 0.000 | | | **ID** | 0.000 | | |
| | **Median** | 2 | **IQR** | 2 | **Median** | 2 | **IQR** | 1 |

## Table A1.2 continued

| | **NUMCAP** | β | St. Error | *P* | **MAXTRAPS** | β | St. Error | *P* |
|---|---|---|---|---|---|---|---|---|
| | Intercept | 1.122 | 0.084 | <0.001 | Intercept | 0.390 | 0.314 | 0.215 |
| | Avg.weight | -0.005 | 0.004 | 0.197 | Avg.weight | -0.017 | 0.016 | 0.283 |
| | SexM | -0.015 | 0.022 | 0.500 | **SexM** | -0.246 | 0.084 | **0.003** |
| | **Total_days** | -0.025 | 0.003 | **<0.001** | **Total_days** | 0.103 | 0.011 | **<0.001** |
| | Prop.inactive | 0.113 | 0.208 | 0.588 | Prop.inactive | -0.080 | 0.962 | 0.934 |
| | **Treatment 1** | -0.097 | 0.041 | **0.018** | Treatment 1 | -0.250 | 0.155 | 0.106 |
| | Treatment 2 | -0.042 | 0.031 | 0.174 | Treatment 2 | -0.025 | 0.114 | 0.830 |
| | Treatment 3 | -0.015 | 0.029 | 0.599 | Treatment 3 | 0.060 | 0.106 | 0.569 |
| | Session | -0.013 | 0.011 | 0.246 | Session | 0.044 | 0.041 | 0.278 |
| | **Dist.center** | -0.019 | 0.008 | **0.018** | Dist.center | -0.012 | 0.029 | 0.674 |
| **Variance** | **ID** | --- | | | **ID** | --- | | |
| | **Residual** | --- | | | **Residual** | --- | | |
| | **Median** | 0.667 | **IQR** | 0.333 | **Median** | 2 | **IQR** | 2 |

***T. hudsonicus***

| | **CAP** | β | St. Error | *P* | **FIRST** | β | St. Error | *P* |
|---|---|---|---|---|---|---|---|---|
| | Intercept | -0.579 | 1.293 | 0.654 | Intercept | 1.100 | 1.193 | 0.356 |
| | Avg.weight | 0.002 | 0.007 | 0.770 | Avg.weight | 0.000 | 0.007 | 0.967 |

## Table A1.2 continued

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | SexM | -0.033 | 0.189 | 0.860 | SexM | -0.134 | 0.177 | 0.448 |
| | Prop.inactive | 4.198 | 4.390 | 0.339 | Prop.inactive | 4.884 | 4.203 | 0.245 |
| | Treatment 1 | 0.468 | 0.403 | 0.246 | Treatment 1 | -0.398 | 0.317 | 0.210 |
| | Treatment 2 | 0.329 | 0.392 | 0.401 | Treatment 2 | -0.268 | 0.294 | 0.361 |
| | Treatment 3 | 0.455 | 0.383 | 0.235 | Treatment 3 | -0.261 | 0.290 | 0.369 |
| | Session | 0.087 | 0.083 | 0.292 | Session | -0.039 | 0.079 | 0.625 |
| | Dist.center | 0.006 | 0.064 | 0.925 | Dist.center | -0.029 | 0.058 | 0.621 |
| **Variance** | **ID** | 0.000 | | | **ID** | 0.000 | | |
| | **Median** | 1 | **IQR** | 1 | **Median** | 2 | **IQR** | 1 |
| | **NUMCAP** | β | St. Error | *P* | **MAXTRAPS** | β | St. Error | *P* |
| | Intercept | 3.538 | 1.883 | 0.064 | Intercept | 0.011 | 0.934 | 0.991 |
| | Avg.weight | -0.003 | 0.011 | 0.765 | Avg.weight | 0.000 | 0.005 | 0.996 |
| | SexM | -0.005 | 0.283 | 0.986 | SexM | -0.007 | 0.122 | 0.954 |
| | **Total_days** | -0.375 | 0.034 | **<0.001** | **Total_days** | 0.142 | 0.020 | **<0.001** |
| | Prop.inactive | 6.815 | 7.322 | 0.355 | Prop.inactive | 4.322 | 3.275 | 0.187 |
| | Treatment 1 | 0.361 | 0.531 | 0.499 | Treatment 1 | 0.249 | 0.254 | 0.328 |
| | Treatment 2 | 0.723 | 0.500 | 0.153 | Treatment 2 | 0.128 | 0.239 | 0.591 |
| | Treatment 3 | 0.891 | 0.497 | 0.077 | Treatment 3 | 0.239 | 0.237 | 0.314 |

## Table A1.2 continued

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Session | -0.057 | 0.125 | 0.650 | Session | -0.013 | 0.056 | 0.820 |
| | Dist.center | 0.086 | 0.093 | 0.360 | Dist.center | -0.047 | 0.043 | 0.276 |
| **Variance** | **ID** | --- | | | **ID** | --- | | |
| | **Residual** | --- | | | **Residual** | --- | | |
| | **Median** | 0.5 | **IQR** | 0.25 | **Median** | 4 | **IQR** | 3 |
| ***M. gapperi*** | | | | | | | | |
| | **CAP** | β | St. Error | *P* | **FIRST** | β | St. Error | *P* |
| | Intercept | 0.223 | 0.351 | 0.524 | Intercept | 0.902 | 0.362 | 0.013 |
| | **Avg.weight** | 0.025 | 0.011 | **0.026** | Avg.weight | -0.014 | 0.012 | 0.233 |
| | **SexM** | -0.216 | 0.100 | **0.032** | SexM | 0.017 | 0.112 | 0.876 |
| | Prop.inactive | -0.903 | 0.770 | 0.241 | Prop.inactive | 0.876 | 0.641 | 0.172 |
| | Treatment 1 | 0.072 | 0.164 | 0.660 | Treatment 1 | -0.067 | 0.180 | 0.708 |
| | Treatment 2 | -0.007 | 0.158 | 0.966 | Treatment 2 | -0.037 | 0.167 | 0.826 |
| | Treatment 3 | 0.075 | 0.126 | 0.549 | Treatment 3 | -0.144 | 0.141 | 0.307 |
| | **Session** | 0.102 | 0.050 | **0.043** | Session | -0.098 | 0.053 | 0.065 |
| | Dist.center | -0.022 | 0.014 | 0.107 | Dist.center | 0.010 | 0.015 | 0.500 |
| **Variance** | **ID** | <0.001 | | | **ID** | 0.00000 | | |

### Table A1.2 continued

| | **Median** | 2 | **IQR** | 2 | **Median** | 1 | **IQR** | 1 |
|---|---|---|---|---|---|---|---|---|
| | **NUMCAP** | β | St. Error | *P* | **MAXTRAPS** | β | St. Error | *P* |
| | Intercept | 0.928 | 0.217 | <0.001 | Intercept | 0.215 | 0.294 | 0.465 |
| | Avg.weight | 0.008 | 0.008 | 0.292 | Avg.weight | -0.004 | 0.010 | 0.736 |
| | **SexM** | -0.161 | 0.064 | **0.013** | SexM | -0.007 | 0.080 | 0.935 |
| | **Total_days** | -0.052 | 0.009 | **<0.001** | **Total_days** | 0.155 | 0.012 | **<0.001** |
| | Prop.inactive | -0.309 | 0.429 | 0.473 | Prop.inactive | -0.105 | 0.767 | 0.891 |
| | Treatment 1 | 0.073 | 0.106 | 0.492 | Treatment 1 | -0.160 | 0.133 | 0.229 |
| | Treatment 2 | -0.030 | 0.098 | 0.758 | Treatment 2 | 0.096 | 0.127 | 0.450 |
| | Treatment 3 | 0.016 | 0.082 | 0.843 | Treatment 3 | 0.133 | 0.103 | 0.199 |
| | Session | -0.010 | 0.032 | 0.756 | Session | 0.034 | 0.039 | 0.383 |
| | **Dist.center** | -0.024 | 0.009 | **0.005** | Dist.center | -0.014 | 0.011 | 0.195 |
| **Variance** | **ID** | --- | | | **ID** | --- | | |
| | **Residual** | --- | | | **Residual** | --- | | |
| | **Median** | 0.8 | **IQR** | 0.4 | **Median** | 2 | **IQR** | 3 |
| ***B. brevicauda*** | | | | | | | | |
| | **CAP** | β | St. Error | *P* | **FIRST** | β | St. Error | *P* |
| | Intercept | -0.150 | 0.615 | 0.807 | Intercept | 0.618 | 0.637 | 0.332 |
| | Avg.weight | 0.053 | 0.032 | 0.094 | Avg.weight | -0.017 | 0.034 | 0.622 |

## Table A1.2 continued

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Prop.inactive | -0.134 | 0.484 | 0.782 | Prop.inactive | -0.071 | 0.527 | 0.893 |
| | Treatment 1 | -0.253 | 0.199 | 0.202 | Treatment 1 | 0.243 | 0.250 | 0.330 |
| | Treatment 2 | -0.321 | 0.219 | 0.143 | Treatment 2 | 0.309 | 0.261 | 0.236 |
| | **Treatment 3** | -0.568 | 0.261 | **0.029** | Treatment 3 | 0.390 | 0.277 | 0.159 |
| | Session | 0.055 | 0.076 | 0.474 | Session | -0.045 | 0.078 | 0.564 |
| | Dist.center | -0.005 | 0.049 | 0.924 | Dist.center | 0.012 | 0.053 | 0.823 |
| **Variance** | **ID** | 0.00000 | | | **ID** | 0.00000 | | |
| | **Median** | 2 | **IQR** | 1 | **Median** | 1 | **IQR** | 1 |
| | **NUMCAP** | β | St. Error | *P* | **MAXTRAPS** | β | St. Error | *P* |
| | Intercept | 0.325 | 0.268 | 0.228 | Intercept | 0.043 | 0.462 | 0.925 |
| | Avg.weight | 0.017 | 0.015 | 0.247 | Avg.weight | 0.025 | 0.025 | 0.306 |
| | **Total_days** | -0.037 | 0.008 | **<0.001** | **Total_days** | 0.092 | 0.011 | **<0.001** |
| | Prop.inactive | -0.002 | 0.216 | 0.993 | Prop.inactive | 0.031 | 0.319 | 0.922 |
| | Treatment 1 | 0.107 | 0.096 | 0.268 | Treatment 1 | 0.260 | 0.160 | 0.104 |
| | Treatment 2 | -0.105 | 0.103 | 0.311 | Treatment 2 | -0.003 | 0.180 | 0.987 |
| | Treatment 3 | 0.023 | 0.115 | 0.845 | Treatment 3 | -0.170 | 0.230 | 0.459 |
| | Session | -0.036 | 0.034 | 0.293 | Session | -0.037 | 0.054 | 0.486 |
| | Dist.center | 0.000 | 0.022 | 0.996 | Dist.center | 0.019 | 0.036 | 0.589 |
| **Variance** | **ID** | --- | | | **ID** | --- | | |

## Table A1.2 continued

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Residual** | --- | | | **Residual** | --- | | |
| | **Median** | 0.667 | **IQR** | 0.5 | **Median** | 3 | **IQR** | 2 |
| ***N. insignis*** | | | | | | | | |
| | **CAP** | β | St. Error | *P* | **FIRST** | β | St. Error | *P* |
| | Intercept | 0.733 | 0.768 | 0.340 | Intercept | 0.917 | 0.635 | 0.149 |
| | Avg.weight | -0.018 | 0.025 | 0.478 | Avg.weight | 0.001 | 0.021 | 0.979 |
| | SexM | -0.117 | 0.219 | 0.592 | SexM | 0.099 | 0.183 | 0.589 |
| | Prop.inactive | -0.775 | 1.016 | 0.446 | Prop.inactive | 0.790 | 0.730 | 0.280 |
| | Treatment 1 | -0.215 | 0.494 | 0.663 | Treatment 1 | -0.076 | 0.397 | 0.848 |
| | Treatment 2 | -0.019 | 0.452 | 0.966 | Treatment 2 | -0.137 | 0.371 | 0.712 |
| | Treatment 3 | 0.031 | 0.459 | 0.945 | Treatment 3 | -0.382 | 0.391 | 0.329 |
| | Session | 0.065 | 0.140 | 0.642 | Session | -0.102 | 0.116 | 0.378 |
| | Dist.center | -0.021 | 0.065 | 0.741 | Dist.center | 0.015 | 0.053 | 0.775 |
| **Variance** | **ID** | 0.00000 | | | **ID** | 0.00000 | | |
| | **Median** | 1 | **IQR** | 1 | **Median** | 2 | **IQR** | 2 |
| | **NUMCAP** | β | St. Error | *P* | **MAXTRAPS** | β | St. Error | *P* |
| | Intercept | 0.699 | 0.213 | 0.002 | Intercept | 0.313 | 0.707 | 0.658 |
| | **Avg.weight** | -0.014 | 0.006 | **0.027** | Avg.weight | 0.005 | 0.022 | 0.822 |
| | SexM | -0.108 | 0.056 | 0.058 | SexM | 0.018 | 0.185 | 0.921 |
| | **Total_days** | -0.074 | 0.007 | **<0.001** | **Total_days** | 0.043 | 0.019 | **0.022** |

## Table A1.2 continued

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Prop.inactive | 0.304 | 0.241 | 0.212 | Prop.inactive | -0.967 | 0.966 | 0.317 |
| | Treatment 1 | -0.003 | 0.132 | 0.980 | Treatment 1 | 0.193 | 0.436 | 0.658 |
| | Treatment 2 | 0.187 | 0.121 | 0.128 | Treatment 2 | 0.268 | 0.395 | 0.497 |
| | Treatment 3 | 0.192 | 0.132 | 0.152 | Treatment 3 | 0.257 | 0.432 | 0.552 |
| | Session | 0.018 | 0.035 | 0.610 | Session | 0.000 | 0.117 | 0.998 |
| | Dist.center | 0.007 | 0.016 | 0.651 | Dist.center | -0.034 | 0.053 | 0.520 |
| **Variance** | **ID** | --- | | | **ID** | --- | | |
| | **Residual** | --- | | | **Residual** | --- | | |
| | **Median** | 0.667 | **IQR** | 0.667 | **Median** | 2 | **IQR** | 2 |

*Models included sex, average weight, treatment, session, the proportion of inactive traps, and distance from the center of the trapping grid as fixed-effects. "Proportion inactive" refers to the proportion of traps available at a grid which were found inactive. (N =261 observations from 170 individual deer mice, N = 231 observations from 168 individual voles, N = 80 observations from 41 individual squirrels, N = 72 observations from 57 individual jumping mice and N = 113 observations from 84 individual shrews). See methods for more information.

## Table A1.3 Glossary of Forestry Treatments

| Treatment | Description | Source |
|---|---|---|
| **Even-aged silviculture** | Used to create stands of trees that are of all the same age-class and size. This treatment can result in a very dense canopy due to the close-proximity of trees. | Brissette and Kenefic (2014) |
| **Two-stage shelterwood** | Used commonly to increase growth and vertical structure, as well as provide downed wood and snags. It is accomplished by retaining large trees from the older cohort and then applying an even-aged cut. | Brissette and Kenefic (2014) |
| **Selection cutting** | A regeneration method used in uneven-aged stands to harvest mature timber and tend to the immature classes. Because selection cutting can be used to remove single trees as well as groups of trees, these forests can have a highly variable, patchy structure. | Brissette and Kenefic (2014) |

# APPENDIX B CHAPTER 2 SUPPLEMENTARY MATERIALS

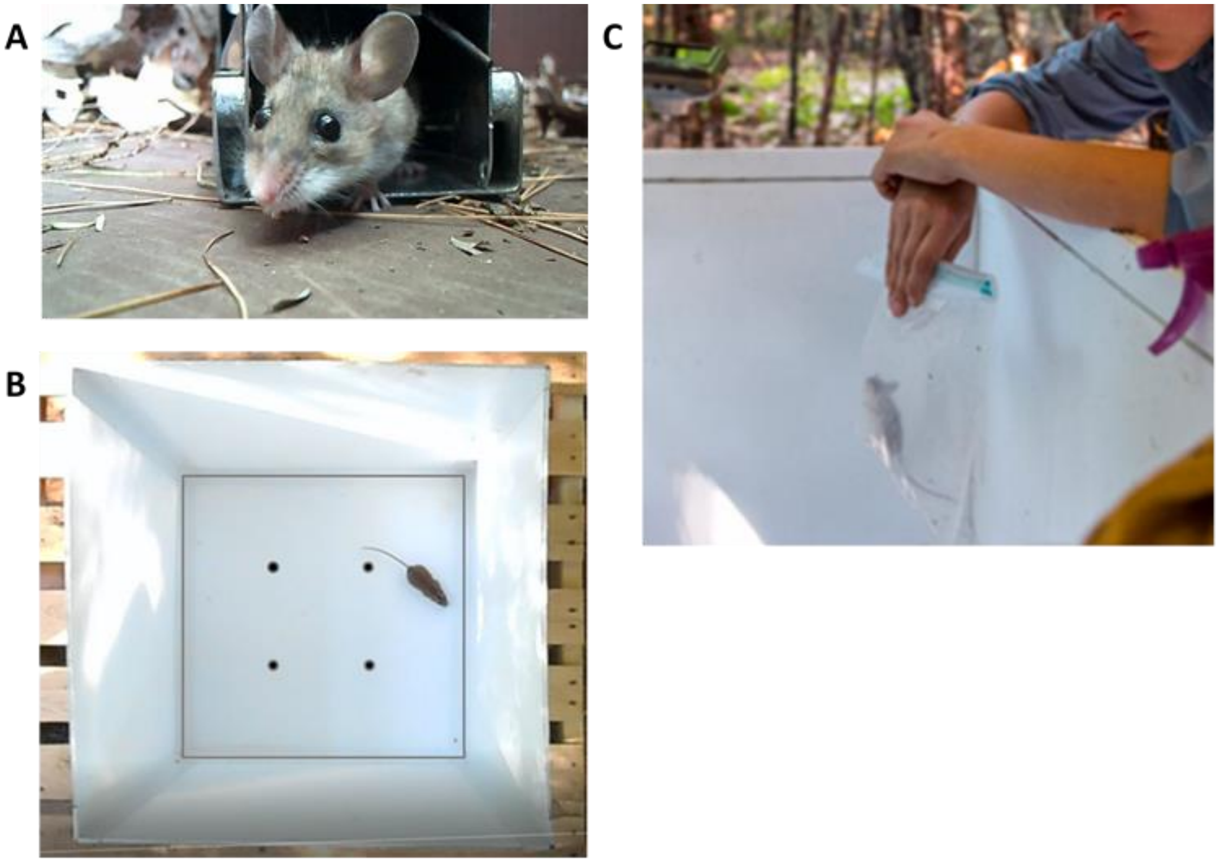

**Figure B2.1 Three behavioral tests used to assess personality of *P. maniculatus, M. gapperi,* and *B. brevicauda.*** (**A**) An individual emerges from a Longworth trap in an emergence test. (**B**) An individual in motion during an open field test. (**C**) An observer suspends an individual over a controlled arena during the handling bag test.

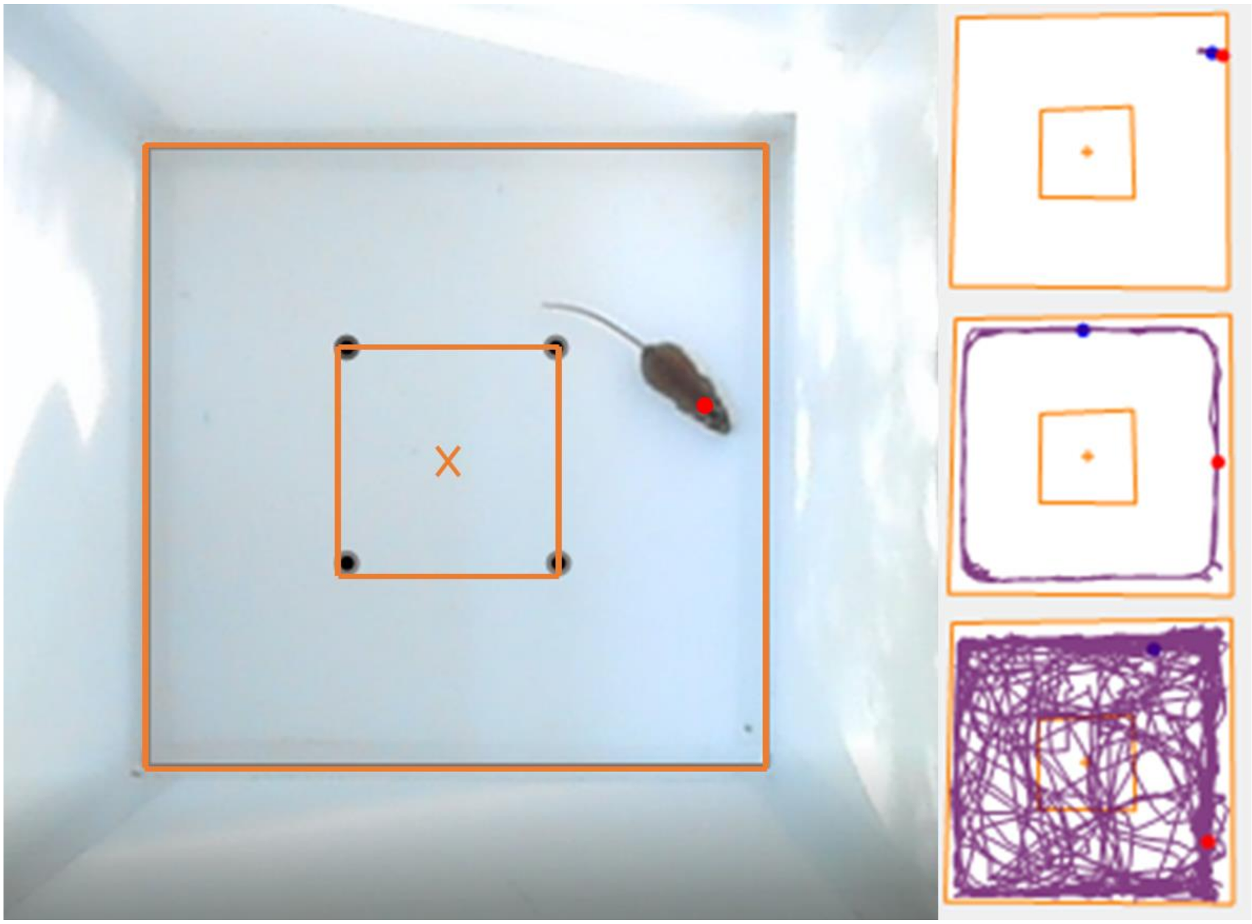

**Figure B2.2 Apparatus in ANY-maze®** behavioral software used to track movements of small mammals. Example trajectories of three different individuals show striking differences in activity.

**Figure B2.3 Seed predation experiment setup.** (**Top left**) A red-backed vole, *M. gapperi,* inspects an artificial seed at an experiment in the field. (**Bottom left**) Artificial seeds of varying sizes were presented in the field. Reflecting tags allowed for easy relocation of dispersed. (**Bottom middle**) a high definition game camera mounted above the experiment recorded seed choices and interactions with seeds by small mammals. (**Right**) An example of the seed experiment setup.

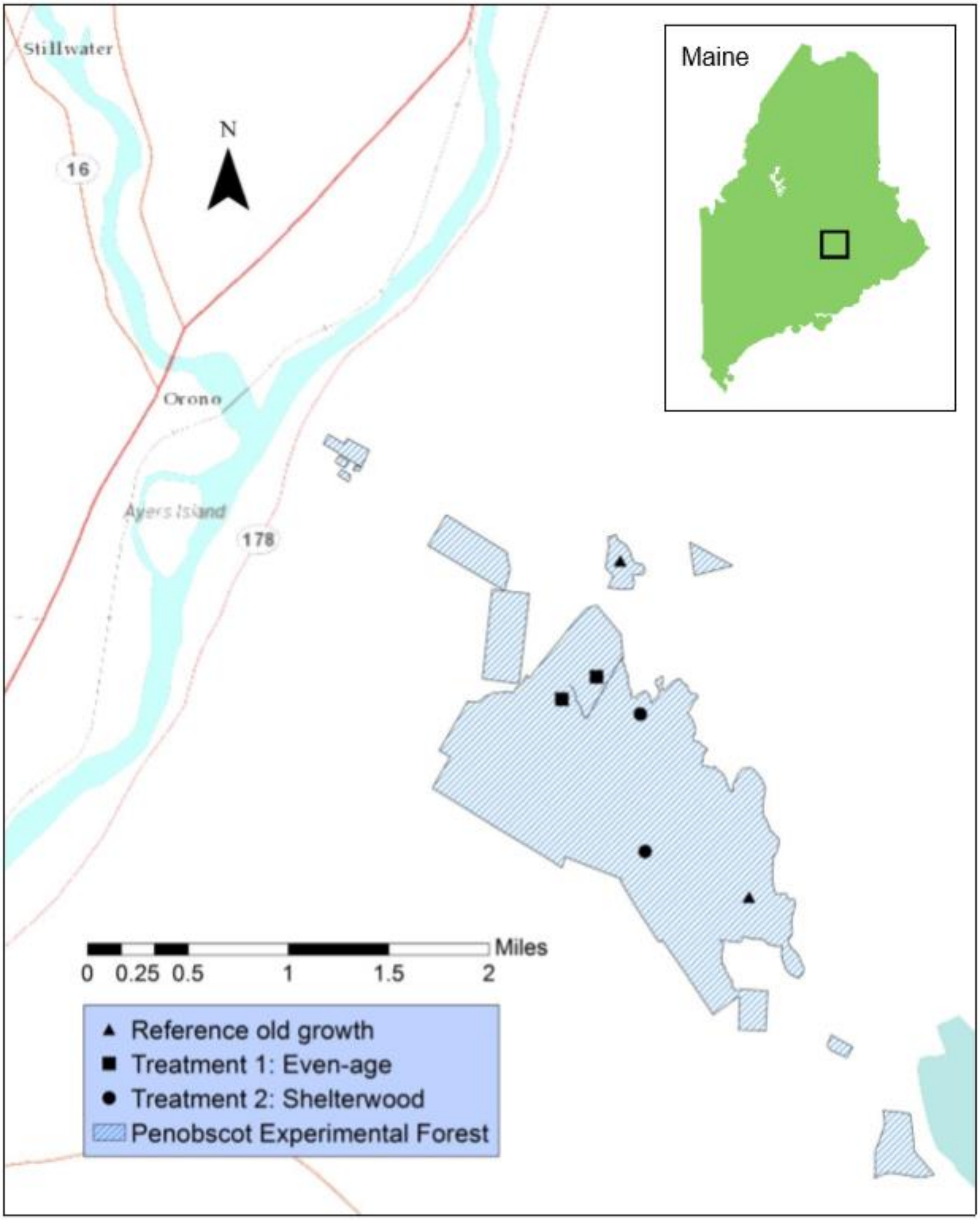

**Figure B2.4** Map of our study area at the Penobscot Experimental Forest, Bradley and Eddington, USA.

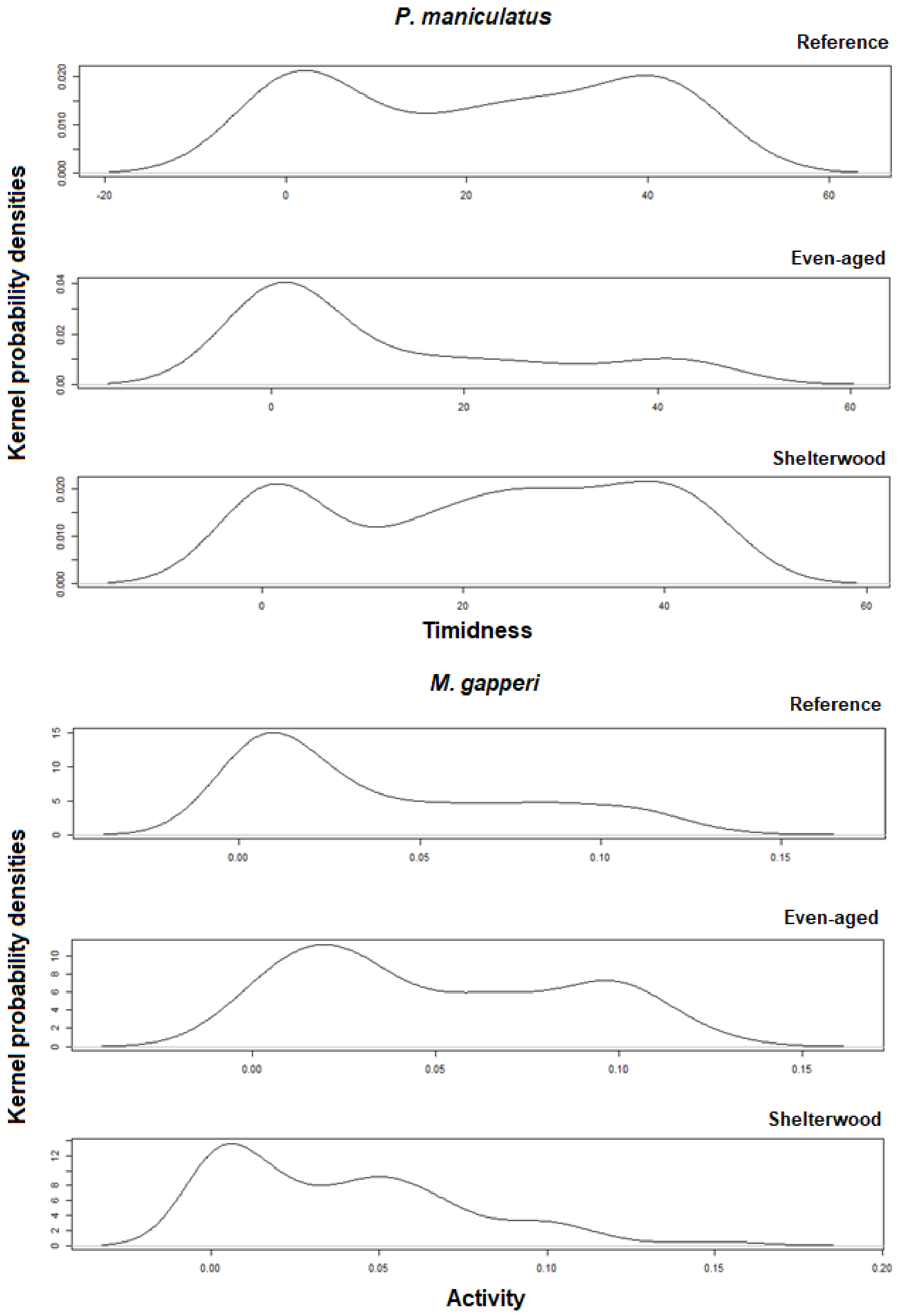

**Figure B2.5 Kernel density plots** showing relative densities of timid and active personality types present in different forestry treatments for *P. maniculatus* and *M. gapperi*.

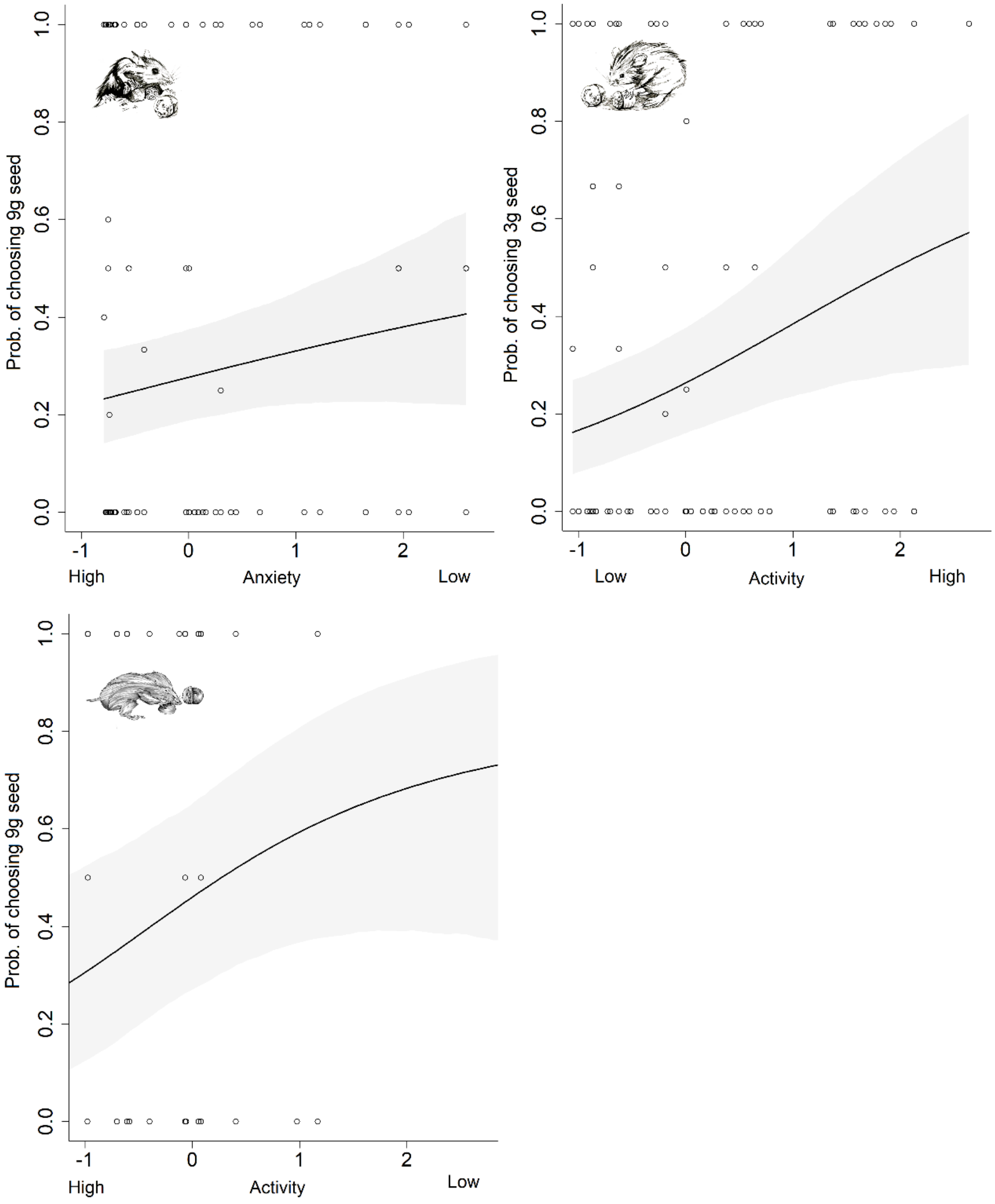

**Figure B2.6 Effects of personality on seed size preference.** Study species included *P. maniculatus* (top left), *M. gapperi* (top right), and *B. brevicauda* (bottom left). Results were obtained from multinomial mixed-effects models with identity included as a random effect. 89% percentile intervals are shown.

**Table B2.1** Key to interpretation of personality variables. Study species included the deer mouse (*Peromyscus maniculatus*), the southern red-backed vole (*Myodes gapperi*), and the northern short-tailed shrew (*Blarina brevicauda*). Provided are: the behavior (as referenced in other tables), description, personality traits it represents, behavioral test it was measured using, notes on interpretation, and a non-exhastive list of references

| **Behavior** | **Behavioral Test** | **Description** | **Personality trait** | **Notes about interpretation** | **Sources** |
|---|---|---|---|---|---|
| Handling | Handling bag | Total number of seconds of inactivity during a 1-minute handling bag test | Docility | An individual's handling score is commonly interpreted as a measure of docility or as a response to stressful confinement. | Montiglio et al. 2012; Boon et al. 2007; Taylor et al. 2012; Taylor et al. 2014; Martin and Reale 2008 |
| Latency.emerge | Emergence | Latency (in seconds) to emerge from trap in the emergence test. An animal was considered to have emerged when all four feet left the trap | Bold/timid | The latency to emerge from a shelter and into a novel or open environment is commonly assessed on a timid/bold continuum where increased latency signals increased timidity. | Gracceva et al. 2014; Carter et al. 2013; Brown and Braithwaite 2004; Lopez et al. 2005 |

## Table B2.1 continued

| | | | | | |
|---|---|---|---|---|---|
| Latency.tunnel | Emergence | Latency to go to the end of the trap tunnel in the emergence test. An animal was considered to have reached the end of the tunnel when the end of the nose protruded from the door | Bold/timid | The latency to emerge from a shelter and into a novel or open environment is commonly assessed on a timid/bold continuum where increased latency signals increased timidity. | Gracceva et al. 2014; Carter et al. 2013; Brown and Braithwaite 2004; Lopez et al. 2005 |
| Time.tunnel | Emergence | Total number of seconds spent at the end of the tunnel before emerging | Bold/timid | See note for Latency.emerge. Since mice who spent more time in the tunnel were less likely to emerge overall (cor = -0.41; p <0.05), this suggests that these individuals had a more timid/fearful behavioral tendency and required time to survey the arena before emergence. Thus, we interpreted an increased time at the end of the tunnel to signal increased timidity. | |

**Table B2.1 continued**

| | | | | | |
|---|---|---|---|---|---|
| Mean.speed | Open field | Mean speed in the open field test in (m/s). Calculated by dividing the total distance traveled in the test by the test duration | Activity | This is a direct measure of locomotion and activity in the open field test. | Russel 1983;<br>Gracceva et al. 2013;<br>Carter et al. 2013 |
| Max.speed | Open field | Maximum speed in the open field test (m/s) | Activity | This is a direct measure of locomotion and activity in the open field test. | |
| Prop.groom | Open field | Proportion of test duration spent grooming | Anxiety/stress | Grooming in small mammals is an indicator of anxiety and stress. Research suggests that in highly aversive environments, self-grooming is a form of de-arousal and the highest levels of grooming may indicate a lower anxiety level and better coping than lower levels of grooming. The open-field test exposes small mammals to several naturally aversive stimuli (i.e. novel, open areas, and bright light). Thus, it is likely that to the deer mouse, a nocturnal species, the open-field | Kalueff et al. 2016;<br>Fernández-Teruel and Estanislau 2016;<br>Choleris et al. 2001 |

**Table B2.1 continued**

| | | | | | |
|---|---|---|---|---|---|
| | | | | test represents an environment of high aversiveness and increased grooming suggests less anxiety. In contrast, for the vole (a more diurnal species) low to moderate grooming seems to signal coping, whereas high amounts of grooming indicate high anxiety. | |
| Rear.rate | Open field | Rate of rearing (rears/s). Rearing is defined as forelegs leaving the arena floor | Activity | Rearing is commonly assessed as correlating positively with activity. | Choleris et al. 2001; Martin & Reale, 2008; Prut & Belzung, 2003 |
| Jump.rate | Open field | Rate of jumping (jumps/s) | Activity | Jumping is commonly assessed as correlating positively with activity. | Boon et al. 2007; Choleris et al. 2001; Boyer et al. 2010 |
| Prop.center | Open field | Proportion of test duration spent in the center portion of the arena | Bold/timid | Thigmotaxis, or the avoidance of open spaces, is a common fear/anxiety reaction in small mammals (*35*) wherein if given the option, individuals will maintain contact with perimeters. Consequently, the act of entering into open, “unsafe” areas | Choleris et al. 2001; Eccard et al. 2013; Gracceva et al. 2013; Ramos et al. 1997; Treit et al. 1989; |

**Table B2.1 continued**

| | | | | | |
|---|---|---|---|---|---|
| | | | | signifies boldness and avoidance of these areas indicates fearfulness. | Barnett et al. 1976 |
| Latency.groom | Open field | Latency (in seconds) before the first grooming event | Anxiety/stress | See notes on grooming above; increasing latency to engage in grooming behavior can be interpreted as suppression of this behavior during moments of high anxiety. | Estanislau et al. 2013 |
| Latency.jump | Open field | Latency (in seconds) before the first jump | Activity | Jumping indicates activity (see notes on Jump.rate above), therefore the latency to do so might signify lower activity levels, and this latency to engage in activity or exploration has been described as behavioral inhibition. Previous research has shown this inhibition to be unrelated to anxiety or fear; so we interpret this latency to engage in activity as a decreased activity level. | Diaz-Moran et al. 2014 |
| Latency.rear | Open field | Latency (in seconds) before the first rear | Activity | Since rearing indicates activity (see notes on Rear.rate above), the latency to do so might signify lower activity levels, and this latency to engage in activity or | Diaz-Moran et al. 2014 |

**Table B2.1 continued**

| | | | | |
|---|---|---|---|---|
| | | | | exploration has been described as behavioral inhibition. Previous research has shown this inhibition to be unrelated to anxiety or fear so we interpret this latency to engage in activity as a decreased activity level. |
| Dist.center | Open field | Mean distance from the exact center of the arena | Bold/timid | See notes on Prop.center above; the mean distance from the center of the open field arena was interpreted as indicating boldness where increasing distance signaled timidness and a shorter distance signaled boldness. |

**Table B2.2** List of microhabitat variables used in models predicting seed predation decisions. Study species included deer mice, *Peromyscus maniculatus*, southern red-backed voles, *Myodes gapperi*, and northern short-tailed shrews, *Blarina brevicauda*

| **Microhabitat variable** | **Description** | **Citations** |
|---|---|---|
| Canopy | Percent canopy cover (calculated using a concave spherical densiometer) | Mortelliti and Boitani 2007 |
| Shrubs | Percent cover of shrubs (includes three height categories: knee height to 1 meter, 1-2 m, and 2-4 m) | Manson & Stiles, 1998; Munoz et al. 2009 |
| CWD | Meters of coarse woody debris (CWD) (includes both small: diameter 10-20 cm, and large: diameter 20+ cm). Defined as dead wood on the ground or at an angle ≤ 45° from the ground and supported by the ground in at least 3 locations. In an instance where a piece of woody debris fell partway out of the site, only the part within the site was counted. | Miller and Getz, 1977; Harmon et al., 1986; McMillan and Kaufman 1995 |
| Moon | Illumination percent (0% indicates a new moon and 100% indicates a full moon) | Perea, González, Miguel, & Gil, 2011; Blair 1943; Kaufman & Kaufman 1982; Kotler 1984; Travers et al. 1988; Diaz 1992; Kotler et al. 2010 |
| Sky | Sky clarity score; based on the weather at the specific time of the visit (0 indicated clear skies and 4 very heavy rain or fog) | Vickery and Bider, 1981; Stokes, Slade, & Blair, 2001 |

**Table B2.2 continued**

| | | |
|---|---|---|
| Cones | An estimate of cone availability (proxy for seed availability). Included a summed abundance of white and red pine, red and white spruce, and balsam fir cones | Lobo, Green, & Millar, 2013; Vander Wall, 2010; Zhang, Cheng, Xiao, & Zhang, 2008 |

**Table B2.3** List of variables selectively imposed in models predicting seed predation decisions. Study species included deer mice, *Peromyscus maniculatus*, southern red-backed voles, *Myodes gapperi*, and northern short-tailed shrews, *Blarina brevicauda*

| **Variable** | **Description** | **Citations** |
|---|---|---|
| Availability | Proportion of each seed size available; must consider when assessing seed choice | Cooper & Millspaugh, 1999; Manly, McDonald, Thomas, McDonald, & Erickson, 2002; Richardson, Lichti, & Swihart, 2013 |
| Degree of uncertainty | A score of 0 indicates that the individual was seen arrive at and leave the seed station; 1 = the individual was either already at the site when the video started, or was still at the site when the video ended, or 2 = the individual was at the site both when the video started and ended | |
| Size of seed | The size of the seed that was chosen; important to consider when predicting the amount of seed consumed, the distance dispersed, and the cache location | Xiao, Zhang, & Wang, 2005; Muñoz & Bonal, 2008; Lichti, Steele, and Swihart, 2015 |
| Distance to barycenter | The distance to the barycenter of the individual's home range | |
| Body weight | The body weight of the individual; important to consider when assessing the size of chosen seeds and dispersal distance | Muñoz & Bonal, 2008 |

**Table B2.4** Repeatability estimates for target behaviors measured in three behavioral tests. Behaviors from handling bag, emergence, and open field tests in deer mice, *Peromyscus maniculatus*, southern red-backed voles, *Myodes gapperi*, and northern short-tailed shrews, *Blarina brevicauda*

| Behavioral Variable | Mean | Range | Repeatability (95% CI) |
|---|---|---|---|
| ***P. maniculatus*** | | | |
| Handling | 19.90 | (0, 60) | 0.273 (0.07, 0.572) |
| Latency.emerge | 50.80 | (1, 94) | **0.49 (0.331, 0.648)** |
| Latency.tunnel | 42.00 | (1, 86) | **0.465 (0.324, 0.625)** |
| Time.tunnel | 19.20 | (1, 43) | **0.596 (0.476, 0.714)** |
| Mean.speed (m/sec) | 0.10 | (0, 0.25) | **0.75 (0.701, 0.8)** |
| Max.speed (m/sec) | 0.60 | (0, 1.97) | **0.562 (0.492, 0.639)** |
| Prop.groom | 0.09 | (0, 0.96) | **0.754 (0.708, 0.804)** |
| Latency.groom (sec) | 72.80 | (0.6, 296.3) | **0.685 (0.621, 0.754)** |
| Jump.rate | 0.10 | (0, 0.55) | **0.601 (0.532, 0.673)** |
| Latency.jump (sec) | 63.80 | (1.1, 299.3) | **0.712 (0.655, 0.771)** |
| Rear.rate | 0.17 | (0, 0.68) | **0.783 (0.74, 0.827)** |
| Latency.rear (sec) | 18.70 | (0.40, 282.8) | **0.745 (0.692, 0.798)** |
| Prop.center | 0.01 | (0, 0.70) | **0.559 (0.48, 0.636)** |
| Dist.center (m) | 0.24 | (0.06, 0.29) | **0.745 (0.694, 0.796)** |
| ***M. gapperi*** | | | |
| Handling | 49.00 | (0, 60) | **0.421 (0.232, 0.638)** |
| Latency.emerge | 57.90 | (1, 94) | **0.593 (0.463, 0.709)** |
| Latency.tunnel | 43.50 | (1, 86) | **0.61 (0.487, 0.721)** |
| Time.tunnel | 21.50 | (1, 43) | **0.7 (0.594, 0.795)** |
| Mean.speed (m/sec) | 0.04 | (0, 0.16) | **0.613 (0.534, 0.684)** |

## Table B2.4 continued

| | | | |
|---|---|---|---|
| Prop.groom | 0.04 | (0, 0.70) | **0.569 (0.49, 0.644)** |
| Latency.groom (sec) | 89.20 | (0.5, 286.9) | **0.736 (0.655, 0.813)** |
| Jump.rate | 0.02 | (0, 0.33) | **0.448 (0.354, 0.537)** |
| Latency.jump (sec) | 105.40 | (1.60, 291.10) | **0.705 (0.614, 0.789)** |
| Rear.rate | 0.07 | (0, 0.56) | **0.504 (0.416, 0.588)** |
| Latency.rear (sec) | 54.90 | (0.20, 294.20) | **0.546 (0.448, 0.64)** |
| Prop.center | 0.04 | (0, 1.0) | **0.608 (0.532, 0.678)** |
| Dist.center (m) | 0.23 | (0.02, 0.29) | **0.584 (0.503, 0.662)** |
| ***B. brevicauda*** | | | |
| Handling | 36.40 | (0, 60) | **0.426 (0.154, 0.717)** |
| Latency.emerge | 48.50 | (1, 94) | **0.549 (0.346, 0.732)** |
| Latency.tunnel | 36.00 | (1, 86) | **0.413 (0.212, 0.624)** |
| Time.tunnel | 24.40 | (1, 43.0) | **0.632 (0.457, 0.778)** |
| Mean.speed (m/sec) | 0.10 | (0, 0.25) | **0.833 (0.771, 0.887)** |
| Max.speed (m/sec) | 0.46 | (0, 2.01) | **0.837 (0.779, 0.889)** |
| Jump.rate | 0.14 | (0, 1.11) | **0.795 (0.721, 0.86)** |
| Latency.jump (sec) | 61.90 | (2.70, 292.30) | **0.749 (0.652, 0.839)** |
| Rear.rate | 0.08 | (0, 0.57) | 0.225 (0.073, 0.414) |
| Latency.rear (sec) | 41.66 | (0.50, 289.90) | **0.824 (0.754, 0.866)** |
| Prop.center | 0.03 | (0, 1) | **0.669 (0.56, 0.775)** |
| Dist.center (m) | 0.23 | (0.03, 0.28) | **0.864 (0.809, 0.908)** |

Repeatability was calculated from univariate mixed-effect models with identity included as a random effect. Parametric bootstrapping was used to calculate 95% confidence intervals. *N* = 705 observations from 295 individual deer mice, *N* = 646 observations from 244 individual voles, and $N$ = 246 observations from 109 individual shrews. See Methods for more information. Significant repeatability estimates are shown in bold.

**Table B2.5** Top ranked models predicting seed predation response variables in the deer mouse, *Peromyscus maniculatus*, southern red backed vole, *Myodes gapperi*, and northern short-tailed shrew, *Blarina brevivauda*

| **Behavior and Species** | **Model**[a] | **ΔAICc**[b] | ***R*$^{2}$** [c] |
|---|---|---|---|
| **Size of seed removed** | | | |
| *P. maniculatus* | Seed_availability + CWD + Time.tunnel | 0.00 | 0.24 |
| | Seed_availability + CWD | 0.70 | 0.23 |
| | Seed_availability + CWD + exp(Dist.center) | 1.47 | 0.23 |
| | Seed_availability + CWD + Latency.em | 1.48 | 0.23 |
| | Seed_availability + CWD + log(Latency.tunnel) | 1.64 | 0.23 |
| *M. gapperi* | Session * Dist.center | 0.00 | 0.08 |
| *B. brevicauda* | Seed_availability + Canopy | 0.00 | 0.34 |
| | Seed_availability | 0.01 | 0.32 |
| | Seed_availability + Shrubs | 1.23 | 0.33 |
| | Seed_availability + exp(Mean.speed) | 1.44 | 0.33 |
| | Seed_availability + Max.speed | 1.49 | 0.33 |
| | Seed_availability + CWD | 1.54 | 0.33 |
| | Seed_availability + exp(Prop.center) | 1.60 | 0.33 |
| | Seed_availability + exp(Latency.jump) | 1.60 | 0.33 |
| | Seed_availability + exp(Latency.rear) | 1.60 | 0.33 |
| | Seed_availability + Cones | 1.91 | 0.32 |
| | Seed_availability + Time.tunnel | 1.93 | 0.32 |
| | Seed_availability + CI | 1.97 | 0.32 |

## Table B2.5 continued

| | | | |
|---|---|---|---|
| **Distance seed is removed** | | | |
| *P. maniculatus* | Sky_condition + Session * Dist.center | 0.00 | 0.41 |
| | Sky_condition + exp(Mean.speed) | 0.17 | 0.33 |
| | Sky_condition + Dist.center | 0.63 | 0.39 |
| | Sky_condition | 1.48 | 0.37 |
| | Sky_condition + Latency.groom | 1.65 | 0.41 |
| | Sky_condition + Latency.rear | 1.65 | 0.41 |
| | Sky_condition + Prop.time.center | 1.73 | 0.41 |
| | Sky_condition + Prop.time.groom | 2.00 | 0.39 |
| *M. gapperi* | Prop.groom + Prop.groom^2 + Latency.rear | 0.00 | 0.38 |
| | Prop.groom + Prop.groom^2 + Latency.rear + log(Handling) | 1.02 | 0.4 |
| | Prop.groom + Prop.groom^2 + Latency.rear + exp(Latency.tunnel) | 1.91 | 0.39 |
| *B. brevicauda* | Session + CWD | 0.00 | 0.88 |
| | Session | 0.27 | 0.59 |
| | Session + Sky_condition | 0.77 | 0.69 |
| | Session + Canopy | 1.61 | 0.9 |
| **Amount of seed consumed** | | | |
| *P. maniculatus* | Size_removed + Sky_condition + Session + exp(Rear.rate) | 0.00 | 0.42 |
| *M. gapperi* | Size_removed + Prop.groom + Prop.groom^2 + exp(Handling) | 0.00 | 0.70 |
| | Size_removed + Prop.groom + Prop.groom^2 | 0.11 | 0.54 |
| | Size_removed + Prop.groom + Prop.groom^2 + exp(Jump.rate) | 0.81 | 0.60 |
| | Size_removed + Prop.groom + Prop.groom^2 + exp(Max.speed) | 1.02 | 0.57 |

**Table B2.5 continued**

| | | | |
|---|---|---|---|
| | Size_removed + Prop.groom + Prop.groom^2 + log(Dist.center) | 1.39 | 0.58 |
| | Size_removed + Max.speed + Max.speed^2 | 1.66 | 0.43 |
| | Size_removed + Prop.groom + Prop.groom^2 + log(Time.tunnel) | 1.71 | 0.54 |
| | Size_removed + Prop.groom + Prop.groom^2 + log(Latency.groom) | 1.82 | 0.53 |
| | Size_removed + Prop.groom + Prop.groom^2 + exp(Rear.rate) | 2.00 | 0.57 |
| *B. brevicauda* | Canopy | 0.00 | 0.29 |
| | ~1 | 1.29 | 0 |
| | Latency.emerge | 1.84 | 0.17 |
| | Rear.rate | 1.94 | 0.15 |
| | exp(Latency.rear) | 1.99 | 0.29 |
| **Probability of removing seed** | | | |
| *P. maniculatus* | Session + Cones + exp(Jump.rate) + Trt * Latency.jump | 0.00 | 0.36 |
| | Session + Cones + exp(Jump.rate) | 0.91 | 0.31 |
| | Session + Cones + exp(Jump.rate) + Trt * Prop.center | 1.89 | 0.34 |
| | Session + Cones + exp(Jump.rate) + Trt * Latency.groom | 1.94 | 0.34 |
| *M. gapperi* | Seed_availability + Repro + exp(Prop.center) + log(Latency.tunnel) | 0.00 | 0.4 |
| | Seed_availability + Repro + exp(Latency.jump) | 0.78 | 0.39 |
| | Seed_availability + Repro + exp(Latency.rear) | 0.94 | 0.39 |
| | Seed_availability + Repro + exp(Prop.center) | 0.96 | 0.39 |
| | Seed_availability + Repro + exp(Latency.groom) | 0.99 | 0.39 |
| | Seed_availability + Repro + exp(Prop.center) + Mean.speed + Mean.speed^2 | 1.27 | 0.38 |
| | Seed_availability + Repro + Prop.center + Prop.center^2 | 1.33 | 0.37 |

## Table B2.5 continued

| | | | |
|---|---|---|---|
| | Seed_availability + Repro + exp(Prop.center) + log(Prop.groom) | 1.39 | 0.38 |
| | Seed_availability + Repro + exp(Prop.center) + log(Latency.groom) | 1.68 | 0.37 |
| | Seed_availability + Repro + exp(Prop.center) + Dist.center + Dist.center^2 | 1.73 | 0.38 |
| | Seed_availability + Repro + exp(Prop.center) + log(Max.speed) | 1.84 | 0.37 |
| | Seed_availability + Repro + exp(Prop.center) + log(Latency.rear) | 1.94 | 0.37 |
| *B. brevicauda* | Session | 0.00 | 0.01 |
| | Session + Moon | 0.22 | 0.01 |
| | Session + CWD | 0.94 | 0.01 |
| | Session + Shrubs | 1.15 | 0.02 |
| | Session + Jump.rate | 1.46 | 0.02 |
| | Session + Dist.center | 1.66 | 0.16 |
| | Session + Max.speed | 1.92 | 0.15 |
| | Session + log(Latency.tunnel) | 1.97 | 0.15 |
| **Size of first choice seed** | | | |
| *P. maniculatus* | Seed_availability + Prop.time.grooming | 0.00 | --- |
| | Seed_availability + Jump.rate | 0.60 | --- |
| | Seed_availability + Latency.tunnel | 0.07 | --- |
| | Seed_availability | 1.90 | --- |
| *M. gapperi* | Seed_availability + Mean.speed | 0.00 | --- |
| *B. brevicauda* | Seed_availability + Latency.jump | 0.00 | --- |
| **Cache site** | | | |

## Table B2.5 continued

| | | | |
|---|---|---|---|
| *M. gapperi* | Handling | 0.00 | --- |

---

[a] *Model structure; see supporting information for description of predictor variables.*

[b] *Delta Akaike information criterion corrected for small sample sizes (difference between each model and the top ranked model). Only models ≤2 Δ AICc are shown.*

[c] *Conditional coefficient of determination - cannot be calculated from multinomial models*

# BIOGRAPHY OF THE AUTHOR

Allison M. Brehm was born in Manchester, New Hampshire on March 17th, 1991 to William and Sara Brehm. She was raised in Pembroke, New Hampshire with her two siblings, and attended and graduated from Pembroke Academy in 2009. She pursued a degree in Zoology from the University of New Hampshire, where she was captain of the Women’s Track and Field team. After completing her Bachelor of Science degree in May of 2014, Allison went on to work as a field technician at the Cambridge-University run Kalahari Meerkat Project in South Africa where she spent her days following meerkats through the Kalahari desert. Her love of animal behavior grew, and she went on to pursue a graduate degree that would merge the fields of Behavioral Ecology and Conservation Biology.

In June of 2016, Allison moved to Maine to pursue a Master’s degree in Wildlife Ecology, and became the first graduate student to work in the lab of Dr. Alessio Mortelliti. During her Master’s work, she was humbled to be recognized as the 2018 Outstanding Graduate Student in the Colleges of Natural Sciences, Forestry, and Agriculture. Allison completed 15 months of fieldwork in the Penobscot Experimental forest in Bradley and Eddington Maine, where she handled thousands of small mammal captures and fed many mosquitos. She served as a mentor to more than 20 undergraduate technicians and acted as a co-advisor on one honors committee. She is a member of the American Society of Mammalogists and has published one peer-reviewed manuscript in the Journal of Animal Behaviour and is currently working on the submission of a second. Allison is a candidate for the Master of Science degree in Wildlife Ecology from the University of Maine in December 2018.