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Predation risk and personality influence seed predation and dispersal by a scatter-hoarding small mammal

Margaret R. Merz[1] ⬤ | **Sara R. Boone**[1] | **Alessio Mortelliti**[1,2] ⬤

[1]Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, Orono, Maine, USA

[2]Department of Life Sciences, University of Trieste, Trieste, Italy

Correspondence
Alessio Mortelliti
Email: alessio.mortelliti@maine.edu;
alessio.mortelliti@units.it

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Abstract

Small mammals are key scatter hoarders in forest ecosystems, acting as both seed predators and dispersers. The outcome of their interactions (i.e., predation vs. dispersal) is determined by a series of decisions made by small mammals, such as the choice of seed, whether the seed is immediately consumed or cached, and where it is cached. These decisions are influenced by a variety of factors, including the intrinsic traits of the seed, the individual personality of the scatter hoarder, and the perceived risk of predation while foraging. Furthermore, these factors may all interact to dictate the fate of the seed, with consequences for forest regeneration. Nevertheless, the ways in which perceived predation risk and personality interact to affect the seed dispersal decisions of scatter hoarders are still poorly understood. To contribute in filling this knowledge gap, we tested the hypotheses that southern red-backed voles (*Myodes gapperi*), an important scatter hoarder in forest ecosystems, would exhibit personality-mediated foraging and that predation risk would alter associations between personality and seed dispersal. We conducted a large-scale field experiment, offering seed trays at stations with altered risk levels and recorded foraging decisions of free-ranging voles with known personalities. We found that personality and perceived predation risk influenced decisions made by foraging voles. Specifically, docility, and boldness predicted foraging site selection, boldness predicted seed species selection and the number of seeds individuals selected, and the tendency to explore of an individual predicted whether voles would remove or consume seeds. Predation risk, mediated by the amount of cover at a site and by moon illumination, affected which foraging site individuals chose, seed species selection, and the probability of removal versus consumption. We did not find support for an interaction between personality and predation risk in predicting foraging decisions. These findings highlight the importance of scatter hoarder personality and perceived predation risk in affecting foraging decisions, with important consequences for seed dispersal and implications for altered patterns of forest regeneration in areas with different small mammal personality distributions or landscapes of fear.

INTRODUCTION

Scatter-hoarding small mammals are the main seed dispersers for many woody plant species, facilitating forest regeneration by dispersing seeds to many undefended caches (Lichti et al., 2017; Steele et al., 2014; Vander Wall, 2001). Small mammals play a dual role in this process, however, acting as both seed dispersers and seed predators (Gómez et al., 2019; Lichti et al., 2017). The outcome of this conditional mutualism depends upon a series of decisions by foraging small mammals, including: (1) whether to consume seeds immediately or to disperse them, (2) how far to disperse seeds, and (3) where to cache dispersed seeds (Gómez et al., 2019). Key decisions associated with this process also include (4) where to forage, (5) which seed species to select, and (6) how many seeds to select (Lichti et al., 2017; Wang et al., 2013) (Figure 1).

The key decisions made by small mammals, and therefore the fate of encountered seeds, are affected by seed traits such as size, perishability, nutrient level, and tannin content, and small mammal's internal energetic state (Hadj-Chikh et al., 1996; Steele et al., 2014; Wang et al., 2013; Wang & Corlett, 2017; Yi & Wang, 2015). Additionally, all of these decisions are mediated by individual personality (Boone et al., 2022; Brehm et al., 2019), that is, consistent individual behavioral differences across contexts (Dingemanse et al., 2012; Réale et al., 2007; Sih et al., 2004), ultimately affecting the outcome of this conditional mutualism (Brehm & Mortelliti, 2022).

Perceived predation risk (and consequent fear) is another important factor influencing small mammal foraging decisions. Indeed, the fear of being predated affects foraging behavior through two mechanisms: directly mediating seed interactions and mediating the selection of foraging site (Boone et al., 2022). Small mammals are common prey for a variety of predators and must forage in a landscape of fear, defined as "peaks and valleys in predation risk across space and time" and determined by predator presence and habitat features (Bleicher, 2017; Laundré et al., 2001; McArthur et al., 2014). Perceived predation risk alters small mammal foraging behavior, resulting in less time spent foraging and less food acquired (Koivisto & Pusenius, 2003; Kotler et al., 1991, 1993). Fear also alters foraging site selection due to small mammals' reliance on microhabitat structure over direct predation cues as an indication of risk (Brown, 1999; Orrock et al., 2004). Specifically, small mammals prefer foraging sites with increased cover to reduce risk (Bleicher, 2014; Brown et al., 1992; Crego et al., 2018), resulting in lower foraging effort and time and faster selection of seeds in more exposed areas (Denny et al., 2021; Eccard et al., 2008; Kotler et al., 1991; Orrock et al., 2004; Perea et al., 2011; Powell & Banks, 2004).

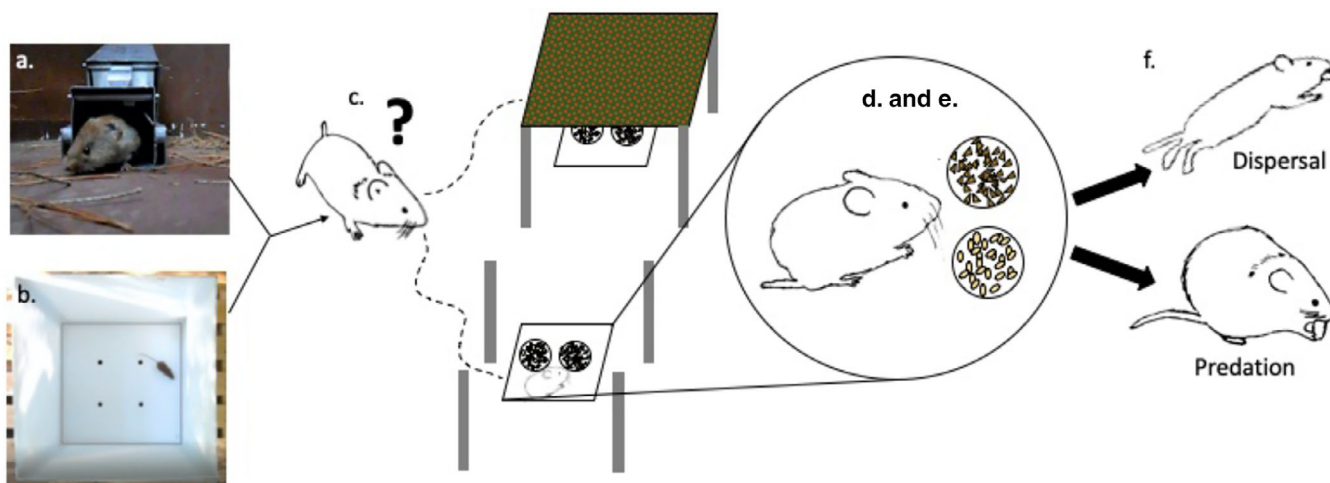**FIGURE 1** An overview of our experimental design to investigate small mammal foraging decisions. We will investigate how personality, measured in (a) an emergence test, (b) an open-field test, and a handling bag test (not shown) mediates decisions including (c) foraging site selection (sheltered vs. unsheltered), (d) seed choice, (e) how many seeds to select, and (f) whether to remove or consume seeds. Photo credit: Allison Brehm.

Microhabitat selection, such as where individuals spend time within their home range (which directly affects foraging site selection), also varies among individuals, with individual personality playing an important role in the selection of features such as cover, refuge, and food resources (Brehm & Mortelliti, 2021; Schirmer et al., 2019). As an example, in our study system, it has been found that more active small mammals select for increased ground cover and more docile individuals avoid areas with more food resources (Brehm & Mortelliti, 2021). Therefore, personality can mediate foraging behavior directly and through selection of foraging site, which in turn affects foraging decisions due to altering perceived predation risk.

In deer mice (*Peromyscus maniculatus*), both personality and predation risk were found to affect seed dispersal decisions (Boone et al., 2022). Specifically, it was found that docility predicts the selection of sheltered versus nonsheltered foraging sites and the consumption versus removal of seeds, activity rate predicts seed choice, and boldness predicts the number of seeds selected, while foraging site (i.e., sheltered vs. nonsheltered) mediates these relationships (Boone et al., 2022). Much remains to be investigated about these processes, however, and studying different species may offer further insight. Previous work conducted in our study system found that some associations between personality and microhabitat selection, such as the relationship between activity and docility and habitat use, were similar between deer mice and southern red-backed voles (*Myodes gapperi*), while other findings were specific to voles (Brehm & Mortelliti, 2021). For example, voles exhibited a correlation between boldness and selection for food resources, which was not seen in mice (Brehm & Mortelliti, 2021). Seed preference is also variable between these two small mammal species, with mice consistently showing strong preference for white pine (*Pinus strobus*) seeds, while voles showed preference for red maple (*Acer rubrum*), and their selection preferences remained largely unchanged as seed availability fluctuated while mice altered their selection (Boone & Mortelliti, 2019). Therefore, relationships between microhabitat selection, seed availability, and personality may vary between these two small mammal species that live and disperse seeds in similar environments.

Overall, empirical evidence shows that personality affects foraging and that predation risk mediates this relationship (Boone et al., 2022; Dammhahn & Almeling, 2012; Mella et al., 2015), but there is still much to understand about the mechanisms behind these relationships. The observed differences between mice and vole seed preference and microhabitat selection suggest that exploring the roles of perceived risk and personality in vole seed dispersal will offer further insight about how small mammals are foraging in a landscape of fear. In this study, we investigated these relationships, pursuing the following objectives: objective 1: determine whether personality predicts foraging site selection in southern red-backed voles; objective 2: assess whether foraging decisions vary with personality and/or microsite selection; and objective 3: investigate whether personality and perceived risk interact to mediate foraging outcomes. Following previous findings showing that individual microhabitat use varies with personality (Bonnot et al., 2018; Schirmer et al., 2019), we predict that personality in southern red-backed voles will mediate foraging site selection, specifically predicting that more active voles will select sheltered sites more often, in line with findings from Brehm and Mortelliti (2021) on vole microhabitat use. Additionally, it has been found that bolder voles select for areas with more food resources, potentially demonstrating a competitive advantage (Brehm & Mortelliti, 2021). Therefore, we predict that bolder voles will preferentially select higher quality seeds. Overall, we expect less foraging and selection of fewer seeds at exposed versus covered sites due to predation risk (Orrock et al., 2004; Powell & Banks, 2004; Verdolin, 2006), but these effects may be stronger for more timid individuals who are less willing to forage at risky sites (Dammhahn & Almeling, 2012). Lastly, we expect the availability of seeds to affect site selection and foraging decisions, as bolder individuals may be willing to forage at risky sites only when high-quality food is available (Mella et al., 2015).

METHODS

To test our hypotheses, we conducted a large-scale field experiment across six small mammal trapping grids in forest stands characterized by differing forest management strategies. We captured and marked southern red-backed voles, collecting data on personality for six years. Then we established paired seed stations, with "risky" and "safe" sites, and recorded vole behavior at each site, noting seed species selection, removal versus immediate consumption, and the number of seeds selected (Figure 1). Pairing foraging behavior with known personality of individuals, we assessed how personality affects foraging decisions and how foraging site selection is influenced by personality and affects foraging behavior.

Study area

Our study was conducted in the Penobscot Experimental Forest (PEF, 44°51′ N, 68°37′ W) in Maine, USA.

The experimental forest is composed of forest units managed with different silvicultural treatments with at least two replicates per treatment (Kenefic & Brissette, 2014). We established small mammal trapping grids within compartments managed with two different silvicultural treatments and within reference units that have not been logged since the late 1800s (Kenefic & Brissette, 2014). Using replicate forest treatment units, we established two trapping grids per forest treatment, totaling six small mammal trapping grids.

Small mammal trapping

We have implemented a large-scale mark–recapture study for six years (2016–2021) in our six selected trapping grids. Each grid is composed of 100 flagged points spaced 10 m apart in a 90 × 90 m grid equaling 0.81 ha (i.e., <10% of the treatment area and placed in the center to minimize edge effects). Longworth traps were placed at every flagged point, bedded with poly-fiber, and baited with oats, freeze-dried mealworms, and sunflower seeds. Traps were set for three consecutive days and nights from June to October of each year and were checked twice daily, shortly after sunrise and shortly before sunset. Personality data for this experiment came from all six years of trapping at all six grids, totaling over 45,000 active trap nights, and seed selection data were collected from July through September of 2018.

Animal behavioral testing and processing

Before handling captured individuals, we use three behavioral tests to measure personality. We conduct an open-field test to measure activity levels and exploration of a novel environment (Carter et al., 2013; Gharnit et al., 2020; Perals et al., 2017), a handling bag test to measure docility and tolerance of handling by a human observer (Martin & Réale, 2008; Mella et al., 2015), and an emergence test to measure boldness (López et al., 2005; Martín & López, 1999). The tests are all run on palettes and under a tarp to ensure consistent light levels and a level surface. Individuals are tested once per month to minimize habituation.

The emergence test is conducted by transferring individuals into a clean Longworth trap and placing it into a 46 × 46 × 60 cm box, which has been painted brown and scattered with leaf litter and pine needles. The trap is then locked in the open position and individuals are left for 3 min and recorded with a camera placed opposite the trap door. Small mammals are then transferred to the center of a clean, white box for the open-field test and recorded

for 5 min from above. Lastly, the observer catches the individual in a clean Ziploc bag and holds it still for 1 min while recording the time the individual is immobile.

After behavioral testing, individuals are weighed using a 100-g Pesola spring scale, sexed, aged, and their reproductive status recorded, and then marked with passive integrated transponders (Biomark PIT tags; MiniHPT8, 134.2 kHz), ear tags, and haircuts for visual identification. Tail and body measurements are taken while individuals are anesthetized with isoflurane. Upon recovery, individuals are released at the site of capture.

Seed experiment

The seed predation experiment was conducted from July through September of 2018. Each month, five to six seed stations were established within each of our trapping grids. At each station, paired foraging sites were created, with a "safe" site covered using a 1 × 1 m tarp and a "risky" site, which had an identical dowel frame but without the tarp for cover (Figure 1). Sites were placed 2–3 m apart and equidistant from potential small mammal refuge or runways. Each site consisted of two small plastic cups on a vinyl floor tile, one containing 5 g of white pine (*P. strobus*) seeds, a highly preferred seed for granivorous small mammals, and the other containing balsam fir (*Abies balsamea*) seeds, a seed of low preference (Boone & Mortelliti, 2019). We offered seeds approximately equal to the number of seeds found in two cones for each species, totaling on average 110.0 white pine seeds (~46–54 seeds per cone; Noland et al., 2006) and 253.7 balsam fir seeds (~134 seeds per cone; Franklin, 1974). These availabilities allowed multiple visits to stations before depletion.

Remote infrared cameras (Reconyx XR6 Ultrafire) were mounted above each site to record foraging behavior and seed selection in 30-s videos (1080P HD) (Video S1). Cameras were set to a 1-s delay between triggers and took one photo (8MP) before each video and once an hour to assist in tracking seed availability in trays. An antenna and a radio frequency identification (RFID) reader were used to scan and record the PIT tags of known visiting individuals. The antennas were situated approximately 3.8 cm above the tile with both seed cups centered within it, recording PIT tags as individuals ran beneath them. Antennas were connected to the RFID reader (Priority1 RFIDLOG dual animal tag data logger), which was powered by a 6-V battery and kept in a dry bag. These paired stations were set up in each trapping grid upon completion of monthly trapping. Sites were visited daily to count seeds, but were left for three to four consecutive nights, or until seeds were depleted.

Behavioral analysis

Recordings of behavioral tests were analyzed back in the laboratory to quantify behavior. Emergence tests were analyzed for the following variables: whether the individual emerged (defined as having all 4 feet outside of the Longworth tunnel), the latency to approach the end of the tunnel, the total time spent at the end of the tunnel before emerging, and the latency to emerge. Open-field tests were analyzed using the behavioral tracking software ANY-maze (version 5.1; Stoelting, CO, USA). ANY-maze records the time spent frozen, the distance traveled, and the number of quadrants in the open-field arena that the individual enters while an observer records the amount of time spent grooming and the number of jumps and rears. We emphasize that the open-field test and emergence test measure different aspects of boldness. The time individuals spend at the end of an emergence tunnel indicates the time individuals require to survey their surroundings before emerging (Brehm & Mortelliti, 2021) and thus a cautiousness, or lack of cautiousness, to initially leave shelter or home refuge. The time individuals spend in the center of an open-field test, on the other hand, indicates an individual's willingness to explore risky areas.

To determine which of the quantified behaviors could be considered personality traits, we calculated the adjusted repeatability, estimated from models including fixed effects (Wilson, 2018), for each trait using data from all six years. We calculated repeatability using our complete dataset in order to increase the accuracy of our calculations and increase confidence in which behaviors are repeatable and can be considered personality traits. Repeatability is defined as the amount of variability in the data that can be attributed to differences among individuals, as opposed to within-individual differences (Dingemanse & Dochtermann, 2013). Mixed models for repeatability were run using the "lme4" package in R (Bates et al., 2015) and included individual identification as a random effect and sex, body condition (using the scaled-mass index; Peig & Green, 2009), silvicultural treatment, and trapping session as fixed effects. Using 1000-permutation bootstrapping in the "rptR" package (Stoffel et al., 2017), we calculated estimates of adjusted repeatability with 95% CI. We used Box–Cox transformations (Box & Cox, 1964) on response variables when necessary to approach normality, assessed by looking at residual plots. Any trait with a repeatability estimate that had a 95% CI excluding zero was considered a personality trait (Nakagawa & Schielzeth, 2010).

To account for variability in the behavioral measurements of each individual, we calculated mean best linear unbiased prediction (BLUP) values over 1000 simulations for each personality trait for each individual (Dingemanse et al., 2020; Gharnit et al., 2020; Villegas-Ríos et al., 2018) using the "arm" package (Gelman & Su, 2018). Subsequent mentions of personality refer to this mean BLUP value.

Analysis of seed videos

Seed predation videos were analyzed to record data on small mammal seed choice, seed availabilities, number of seeds chosen, and whether seeds were removed or consumed at each visit (Video S1). Seed availability was tracked for each selection event so that we could determine true selection, as opposed to use (Lichti et al., 2017; Mortelliti et al., 2019; Richardson et al., 2013). Selection indicates preference by an animal, not just utilization of a resource, because it requires use disproportionate to availability (Manly et al., 2002). Daily seed counts, still pictures, and tracking the number of removed seeds in each video were all used to obtain accurate counts of availability. Moon illumination at the time of selection was also recorded and classified into five categories representing the new, crescent, quarter, gibbous, or full moon.

Statistical analysis

Using the lme4 package in R (Bates et al., 2015), we ran mixed-effects models to explore the four foraging decisions, using seed choice, site choice, number of seeds selected, and removal versus immediate consumption as the dependent variables. Individual identification was included as a random effect and seed availability as a fixed effect in every model to allow us to make inferences about selection. We fit generalized mixed-effects models for the binomial (family = binomial, link = logit) and count (family = poisson, link = log) variables.

We followed a forward model selection approach, starting with a base model including seed availability. We first tested individual variables, including sex and body condition, against the base model. We tested additive effects of any models that had a better fit than the base model and were within 2Δ Akaike information criterion (2ΔAIC) of the top model. The final top model in this model set became the base model for the next set, with covariates in the top model included in all subsequent models.

The second model set we ran included variables describing time- and grid-level conditions, including trapping session, moon illumination, and monthly population abundance in a grid (i.e., number of voles captured

in a trapping grid in one month). Once again, any model ranking above the base model for this set became the base model for the next model set and those covariates were incorporated in subsequent models. The third model set included seed choice, foraging site, removal versus consumption, and/or the number of seeds removed depending on the response variable in question and the hypothesis we were testing based on known behavior (i.e., voles prefer white pine seeds so seed choice may affect the number of seeds selected). We ran these model sets before testing for the effects of personality to account for as much variation as possible before introducing personality (Boone et al., 2022).

Next, we tested seven personality traits including mean speed, rear rate, proportion time spent grooming, and proportion time spent in the center of the open-field test, latency to emerge in the emergence test, time spent at the end of the emergence tunnel, and time spent immobile in the handling test (Table 1). All variables were z-transformed before being included in models. Additive effects of any personality variables within 2ΔAIC of the top model were tested, aside from variables falling above the $R < 0.7$ threshold for collinearity (Dormann et al., 2013), which were not tested in the same model. The last model sets we ran included interactive effects of personality and seed choice, site choice, or seed availability depending on the response variable and whether these interactions were logical. From our last set, we selected final top models and used model averaging for all models within 2ΔAIC of the top model to make inferences (Burnham & Anderson, 2002).

Ethical note

All trapping and experimental research was approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC A2015_11_02 and A2018-11-02);

this research followed procedures designed to ensure the health and safety of all animals and researchers.

RESULTS

We analyzed personality data from 1208 individual voles and found significant repeatability estimates (mean = 0.253, range = 0.17, 0.323) for all personality traits used in this analysis (Table 1).

In our seed selection experiments, we had a total of 603 visits by southern red-backed voles. Of these visits, there were 306 selection events from 16 individuals with known personalities and 297 visits where voles approached seed trays but did not select any seeds.

Microsite choice

The top-ranked models for the selection of foraging site included three personality traits, with handling score (i.e., docility; Table 2), proportion of time spent in the center of an open-field test (i.e., boldness; Table 2), and time spent at the end of an emergence tunnel (i.e., timidity; Table 2) all predicting microsite selection (Table 3). More docile voles, bolder voles (measured from the open-field test), and more timid voles (measured from the emergence test) were all more likely to forage at covered sites (Figure 2). Moon illumination was included in top models, with covered sites more likely to be chosen when moon illumination was higher (Table 3).

Seed choice

The top-ranked model predicting seed choice included an interaction between the proportion of time individuals spent in the center of an open-field test (interpreted as

TABLE 1 Adjusted repeatability estimates for personality traits of southern red-backed voles from 2016 to 2021 from data collected in behavioral tests.

Behavioral variable	Mean	Range	Repeatability	95% CI	Observations	Individuals
Mean speed	0.042	0–0.204	0.323	0.254, 0.400	1694	1069
Rear rate	0.085	0–0.5567	0.266	0.199, 0.336	1693	1064
Proportion grooming	0.116	0–0.8993	0.17	0.099, 0.242	1685	1062
Proportion time center	0.035	0–1	0.254	0.188, 0.333	1698	1069
Handling	51.538	0–60	0.187	0.120, 0.265	1560	955
Time end tunnel	6.386	0–180	0.267	0.187, 0.353	1178	758
Latency to emerge	97.109	0–225	0.302	0.228, 0.378	1450	899

Note: Handling and emergence test variables have fewer observations due to not being conducted during the first year of the experiment. Estimates were calculated using mixed-effects models with individual ID as a random effect and CI were estimated using parametric bootstrapping.

T A B L E 2   Behavioral variables we quantified with our three behavioral tests and their interpretations.

Test	Behavior	Description	Interpretation	Literature
Open field	Mean speed	Total distance traveled during the test divided by duration of the test (in meters per second).	Higher mean speed indicates higher activity levels	Brehm et al. (2019), Choleris et al. (2001), Martin and Réale (2008)
	Rear rate	No. rears per second. A rear is when an individual lifts both forelegs from the floor.	A higher rear rate indicates more highly exploratory individuals	Archer (1973), Brehm et al. (2019), Choleris et al. (2001), Martin and Réale (2008)
	Proportion time grooming	Amount of time an individual spent grooming divided by the duration of the test.	High amounts of grooming indicate high anxiety	Brehm et al. (2019), Choleris et al. (2001), Martin and Réale (2008)
	Proportion time in the center	Amount of time an individual spent in the center portion of the arena divided by the duration of the test.	Longer time in the "risky" portion of the arena signifies boldness[a]	Archer (1973), Brehm et al. (2019), Herde and Eccard (2013)
Handling bag	Handling time	No. seconds spent immobile during the test.	Longer time spent immobile signals more docile individuals	Boon et al. (2007), Brehm et al. (2019), Martin and Réale (2008), Mella et al. (2015)
Emergence	Time at end of emergence tunnel	Total time spent at the end of the emergence tunnel before emerging.	Longer time at the end of the tunnel indicates hesitancy and timidity[a]	Brehm and Mortelliti (2021), Brehm et al. (2019)
	Latency to emerge	No. seconds spent in the emergence trap before emerging, defined as having all 4 feet leave the trap.	A longer latency to emerge signifies timidity	Brehm et al. (2019), Brown and Braithwaite (2004), Carter et al. (2013)

[a]The time spent in the center of an open-field test arena and the time spent at the end of the tunnel in an emergence test measure different aspects of boldness. The open-field test indicates a willingness to explore open, more risky areas, while the emergence test indicates a cautiousness, or lack thereof, to initially leave a refuge.

Source: Table modified from Brehm and Mortelliti (2021).

boldness; Table 2) and the proportion of white pine seeds available (Table 3). Bolder individuals were more likely to choose white pine seeds than balsam fir seeds at moderate seed availability (Figure 3). Interestingly, personality effects on seed choice were important at moderate seed availability, but at high and low availability there was no observed effect of personality (Figure 3). Rear rate, interpreted as an indication of exploration (Table 2), was also included in the top model set for selection of white pine, with more exploratory individuals choosing white pine more often (Table 3). Individuals with a higher body condition index and individuals selecting seeds at exposed sites were both more likely to choose white pine seeds. We found no support for an interaction between personality and risk levels (Table 3).

Number of seeds selected

Our top-ranked model included an interaction between time spent at the end of the emergence tunnel and seed choice as predictors of the number of seeds voles selected (Table 3). More timid voles (measured from the emergence test; Table 2) selected fewer seeds, particularly when selecting white pine seeds, while selection of balsam fir was always lower (Figure 4). Additionally, more exploratory individuals (measured by rear rate; Table 2) selected fewer seeds, individuals having a higher body condition index selected fewer seeds, and voles consuming seeds, rather than removing them, selected fewer seeds (Table 3).

Remove or consume

Exploration (indicated by rear rate; Table 2) was included in the top model, predicting whether voles removed seeds or consumed them immediately (Table 3). More exploratory voles were more likely to remove seeds (Figure 5). Voles were unlikely to remove balsam fir seeds ($n = 11$ observations). Additional variables in the top model included trapping session, with the probability of

TABLE 3 Results from the model selection process for analyses that included running mixed-effects models testing each of our four response variables.

Response variable	Model	K	AIC_c	ΔAIC	AIC mass	R^2
Foraging site	Proportion Balsam Fir ($\beta = -0.149$, SE $= 0.62$) + Proportion White Pine ($\beta = 1.057$, SE $= 0.40$) + Time at End of Tunnel ($\beta = -0.318$, SE $= 0.23$) + Handling ($\beta = -0.535$, SE $= 0.31$) + Proportion Time in Center ($\beta = -0.491$, SE $= 0.24$) + Illumination ($\beta = -0.338$, SE $= 0.21$)	8	401.71	0	0.35	0.34
	Proportion Balsam Fir ($\beta = 0.190$, SE $= 0.59$) + Proportion White Pine ($\beta = 1.047$, SE $= 0.40$) + Proportion Time Center ($\beta = -0.536$, SE $= 0.23$) + Handling ($\beta = -0.598$, SE $= 0.33$) + Illumination ($\beta = -0.362$, SE $= 0.21$)	7	401.81	0.12	0.33	0.30
	Proportion Balsam Fir ($\beta = -0.203$, SE $= 0.64$) + Proportion White Pine ($\beta = 1.049$, SE $= 0.40$) + Handling ($\beta = -0.677$, SE $= 0.377$) + Time at End of Tunnel ($\beta = -0.419$, SE $= 0.26$) + Illumination ($\beta = -0.438$, SE $= 0.21$)	7	402.99	1.28	0.18	0.38
	Proportion Balsam Fir ($\beta = -0.118$, SE $= 0.62$) + Proportion White Pine ($\beta = 1.051$, SE $= 0.40$) + Handling ($\beta = -0.850$, SE $= 0.40$) + Illumination ($\beta = -0.472$, SE $= 0.21$)	6	403.57	1.86	0.14	0.38
Seed choice	Proportion Balsam Fir ($\beta = 6.45$, SE $= 2.05$) + Proportion White Pine $\times$ Proportion Time Center ($\beta = 1.867$, SE $= 1.15$) + Body Condition Index ($\beta = 0.7117$, SE $= 0.32$) + Site (Exposed site, $\beta = 1.22$, SE $= 0.62$)	8	132.53	0	0.46	0.89
	Proportion Balsam Fir ($\beta = 6.903$, SE $= 2.09$) + Proportion White Pine ($\beta = 5.996$, SE $= 1.35$) + Proportion Time Center ($\beta = 1.44$, SE $= 0.521$) + Body Condition Index ($\beta = 0.7191$, SE $= 0.32$) + Site (Exposed site, $\beta = 1.221$, SE $= 0.60$)	7	133.55	1.02	0.28	0.85
	Proportion Balsam Fir ($\beta = 7.139$, SE $= 1.99$) + Proportion White Pine ($\beta = 5.768$, SE $= 1.26$) + Rear Rate ($\beta = 1.62$, SE $= 0.530$) + Body Condition Index ($\beta = 0.852$, SE $= 0.35$) + Site (Exposed site, $\beta = 1.088$, SE $= 0.58$)	7	133.72	1.19	0.26	0.85
No. seeds	Proportion Balsam Fir ($\beta = 0.14$, SE $= 0.21$) + Proportion White Pine ($\beta = -0.007$, SE $= 0.10$) + Time at End of Tunnel $\times$ Seed Choice (White Pine, $\beta = -0.175$, SE $= 0.098$) + Body Condition Index ($\beta = -0.035$, SE $= 0.035$) + Removed ($\beta = 0.618$, SE $= 0.07$)	9	1328.76	0	0.42	0.42
	Proportion Balsam Fir ($\beta = 0.047$, SE $= 0.20$) + Proportion White Pine ($\beta = -0.006$, SE $= 0.10$) + Time at End of Tunnel ($\beta = -0.101$, SE $= 0.058$) + Body Condition Index ($\beta = -0.040$, SE $= 0.035$) + Removed ($\beta = 0.621$, SE $= 0.07$) + Seed Choice (White Pine, $\beta = 0.313$, SE $= 0.12$)	8	1329.99	1.24	0.23	0.4
	Proportion Balsam Fir ($\beta = 0.133$, SE $= 0.21$) + Proportion White Pine ($\beta = -0.009$, SE $= 0.10$) + Rear Rate ($\beta = -0.047$, SE $= 0.063$) + Time at End of Tunnel $\times$ Seed Choice ($\beta = -0.16$, SE $= 0.099$) + Body Condition Index ($\beta = -0.039$, SE $= 0.035$) + Removed ($\beta = 0.620$, SE $= 0.07$) + Seed Choice (White Pine, $\beta = 0.314$, SE $= 0.12$)	10	1330.37	1.61	0.19	0.41
	Proportion Balsam Fir ($\beta = 0.135$, SE $= 0.19$) + Proportion White Pine ($\beta = -0.009$, SE $= 0.10$) + Rear Rate ($\beta = -0.083$, SE $= 0.046$) + Body Condition Index ($\beta = -0.050$, SE $= 0.035$) + Removed ($\beta = 0.622$, SE $= 0.07$) + Seed Choice (White Pine, $\beta = 0.352$, SE $= 0.12$)	8	1330.76	2	0.16	0.35

(Continues)

TABLE 3 (Continued)

Response variable	Model	K	AIC_c	ΔAIC	AIC mass	R^2
Remove or consume	Proportion Balsam Fir ($\beta = 2.40$, SE $= 0.80$) + Proportion White Pine ($\beta = 1.99$, SE $= 0.45$) + Rear Rate ($\beta = 0.638$, SE $= 0.186$) + Session ($\beta = 1.23$, SE $= 0.23$) + Site (Exposed site, $\beta = 1.38$, SE $= 0.32$)	7	312.4	0	0.84	0.48

Note: Final models for each of the response variables included all models within 2ΔAIC of the top-ranked model. Parameter β estimates and standard errors are given.

Abbreviation: AIC_c, corrected Akaike information criterion.

removal increasing from July through September, and foraging site, with a higher likelihood of seed consumption at covered sites (Table 3).

DISCUSSION

Through a large-scale field experiment, we found that personality mediates multiple foraging decisions by southern red-backed voles. These include the selection of foraging site, seed species selection, how many seeds individuals select, and whether they removed seeds or immediately consumed them. Specifically, we found that docility and boldness predicted site selection, boldness predicted selection of high-quality seeds and the number of seeds voles selected, and exploratory tendency predicted the propensity to remove or immediately consume seeds. Furthermore, we found that predation risk, mediated by levels of cover at foraging sites and moon illumination, altered foraging behavior. We found that the probability of seed removal and selection of high-quality seeds by voles was higher at risky sites. High levels of moon illumination increased the probability of choosing a covered foraging site. These findings highlight the influence of personality and predation risk on small mammal seed dispersal decisions.

Effects of personality on seed decisions

Foraging site selection was affected by multiple measures of personality, in line with studies investigating how patterns of space use and spatial distribution are mediated by personality (Boyer et al., 2010; Knotts & Griffen, 2016; Leclerc et al., 2016; Spiegel et al., 2015). Timidity, measured from an emergence test, and docility both predicted a higher probability of foraging at covered sites, which parallels previous findings that more timid individuals select for more cover (Carrete & Tella, 2010; Holtmann et al., 2017). On the contrary, however, boldness (as measured in an open-field test) also correlated with a higher probability of choosing a

covered site. This result is in line with the findings of Schirmer et al. (2019) on bolder bank voles' (*Myodes glareolus*) preference for cover during home range selection. Boldness is a broad behavioral response, known to potentially incorporate multiple different behavioral traits (Carter et al., 2013), and we reiterate that the emergence test and the open-field test measure different aspects of boldness.

Our finding that individuals exhibiting boldness in the open-field test were more likely to select for covered sites could evidence a competitive advantage of individuals willing to explore risky areas outcompeting more timid individuals for better foraging sites. These findings are in line with recent work in our study system, where it was found that bolder voles selected microhabitats with more food resources (Brehm & Mortelliti, 2021). Here, these individuals also had a higher probability of selecting high-quality seeds, lending support for the idea that they may have increased competitive ability over more timid individuals. Overall, these findings provide evidence that individual conspecifics may have differing competitive abilities, use different resources, and occupy functionally different niches (Bolnick et al., 2003), with personality as a driver of interindividual niche differences (Boon et al., 2007; Boyer et al., 2010; Kobler et al., 2009).

The number of seeds voles selected was influenced by boldness, with more timid individuals selecting more seeds. It has been found that under risk small mammals limit the amount of time spent on seed discrimination (Perea et al., 2011). Therefore, highly hesitant voles may be perceiving higher levels of predation risk while foraging and in turn may be selecting more seeds in order to reduce time spent being selective. Additionally, selection for a higher number of seeds suggests that these individuals may be more likely to remove seeds than to consume them, as individuals can only consume one seed at a time. Thus, this may be evidence that more timid individuals are removing more seeds in order to decrease time spent at foraging sites. The probability of removal was predicted by exploratory levels, however, with more exploratory individuals being more likely to remove seeds. Small mammals mediate risk
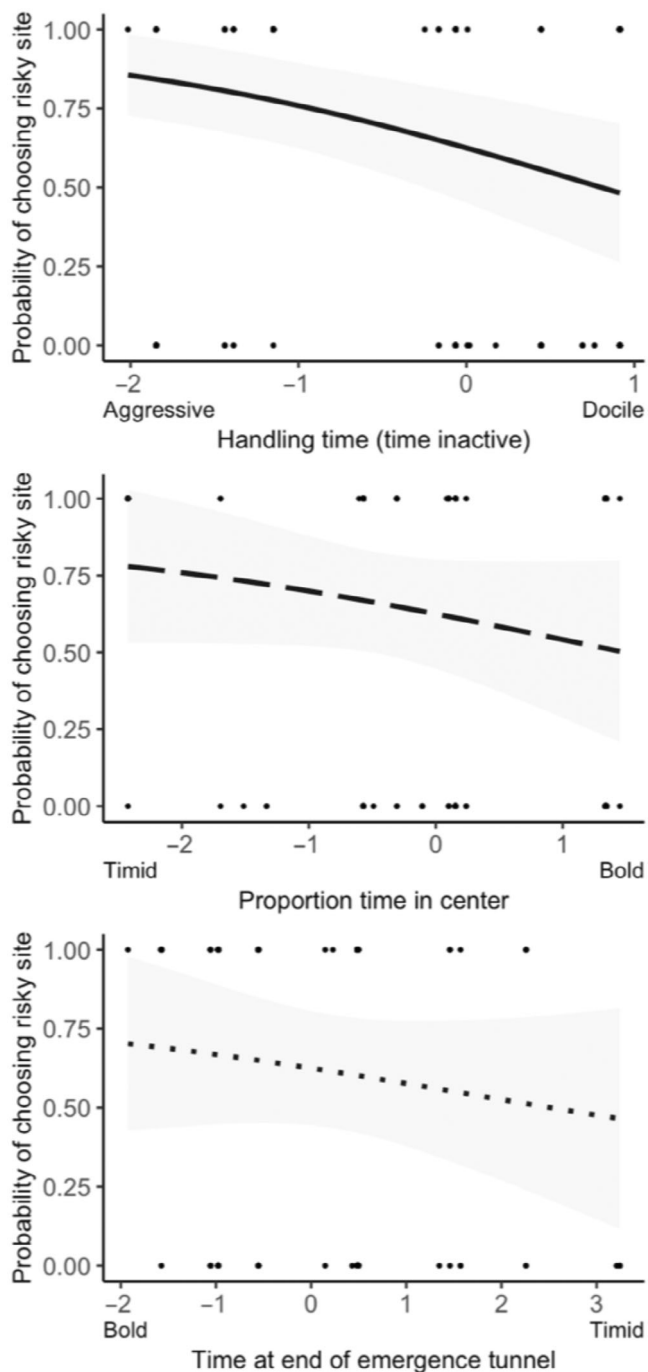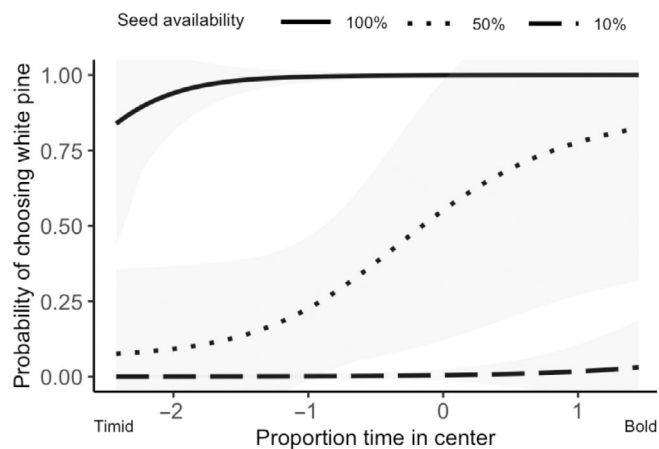
FIGURE 3 At intermediate seed availability, bolder voles (i.e., spending more time in the center of the open-field test arena) were more likely to choose high-quality white pine seeds. There is no observed effect of personality at high and low seed availability. Seed availabilities represent the percent of white pine and balsam fir seeds initially offered that are still present in the seed tray at the time of a visit. Predictions shown were obtained from model averaging the top models for this response variable and 95% CI are shown. Proportion time in the center is a scaled variable.
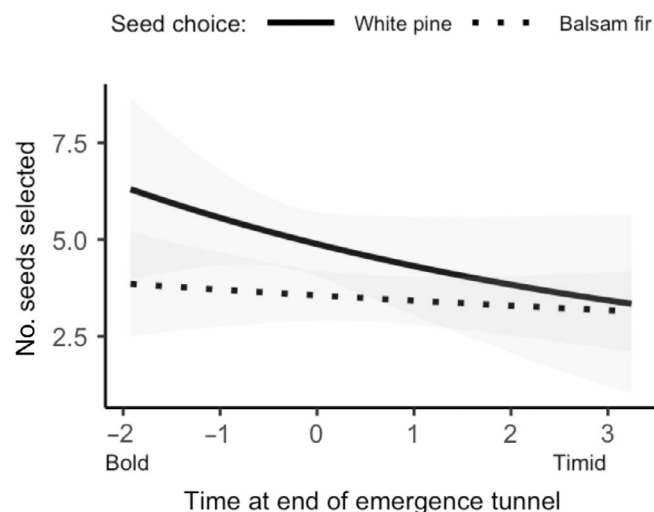

FIGURE 2 More docile voles, bolder voles (i.e., more time spent in the center of an open-field test, more willing to explore risky areas), and more timid voles (i.e., more time spent at the end of an emergence tunnel before emerging, more cautious initially leaving refuge) were more likely to forage at covered sites. Model-averaged predictions are shown, obtained from averaging all models within 2Δ Akaike information criterion of the top-ranked model, and are plotted with 95% CI. All personality traits are scaled. Data points show raw data for individual's selection of covered or uncovered sites.

FIGURE 4 More timid voles (i.e., those spending longer at the end of the tunnel before emerging) selected fewer seeds. This effect was stronger when voles were selecting high-quality white pine seeds. Model-averaged predictions are given with 95% CI. Time spent at the end of an emergence tunnel is a scaled variable.

while foraging by taking seeds away rather than consuming them, as seed removal limits foraging time (Lima et al., 1985). Thus, our findings may illustrate a behavioral

response by exploratory individuals to reduce predation risk while foraging. This result may also conform with findings from Mazza et al. (2019) that faster individuals exploited multiple experimental food patches more than slower ones, gaining access to more food while spending less time at patches. Removal limits time at foraging sites
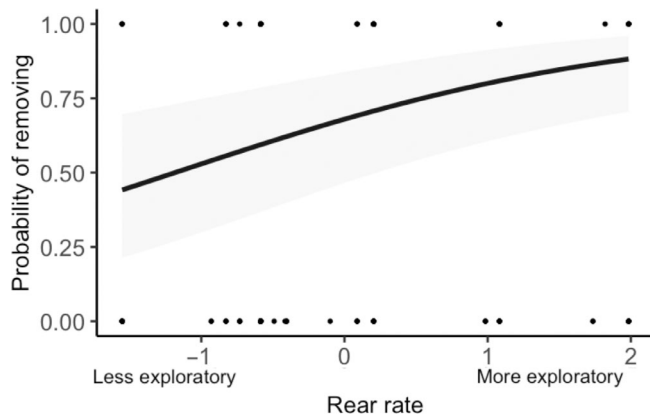
FIGURE 5 More exploratory voles (i.e., having a higher rear rate) were more likely to remove than to immediately consume seeds. Predictions were obtained from the top-ranked model and the 95% CI is shown. Data points depict the raw data. Rear rate is a scaled variable.

and allows for the selection of more seeds, indicating that exploratory individuals may be using this strategy to increase food resources while limiting time spent at a site in order to visit multiple foraging sites.

Foraging site selection and perceived predation risk

Voles were more likely to forage at covered sites when moon illumination was higher, providing evidence for the idea that small mammals use illumination levels as an indirect cue of predation risk (Kotler et al., 1991; Perea et al., 2011). Risk altered foraging behavior as well, with individuals selecting high-quality white pine seeds more often at risky foraging sites. This suggests that foraging small mammals will take risks for high-quality food that they are unwilling to take for lower quality food (McArthur et al., 2012, 2014). Small mammals were also less likely to consume seeds at risky sites, showing a behavioral response to limit foraging time at risky sites (Dammhahn & Almeling, 2012). These results suggest a link between small mammal risk perception and both seed selection and predation rates with implications for forest regeneration. In areas with less cover and higher small mammal predation risk, although foraging may be reduced, selection of high-quality seeds such as white pine may increase with lower rates of immediate consumption, increasing the chances of mutualistic interactions with high-quality seeds that are normally consumed (Boone & Mortelliti, 2019). Therefore, areas lacking microhabitat structure may offer important opportunities for the dispersal of white pine seeds.

Southern red-backed voles as unique seed dispersers

Notably, our results differed from what was seen in deer mice, with no interaction between personality and predation risk influencing vole foraging decisions. Mice and voles do fill different, though complementary, roles in the seed dispersal mutualism, however. Voles are omnivorous and opportunistic feeders, utilizing many sources of food along with nuts and seeds (Merritt, 1981). Therefore, vole foraging decisions in this study, which only offered seeds, may be variable compared with mice due to voles' reliance on other food sources, while mice specialize on seeds. Specifically, perhaps no interaction between personality and risk was observed, as was seen in mice (Boone et al., 2022), because when seed stations were deemed to be too risky to visit, voles utilized other sources of food.

Voles also exhibit both nocturnal and diurnal activity, unlike mice, when different predators are active and light levels are highly contrasted. Previous work has found that time of day and microhabitat interact to influence foraging behavior of common voles (*Microtus arvalis*), with voles preferring different microhabitat depending on the time of day or night (Jacob & Brown, 2000). This offers another mechanism through which voles are modifying their behavior and space use to mediate risk. In our study area, due to predation by a variety of predators that are active at day and night and are most effective in varying habitats, voles are likely using multiple behavioral strategies to reduce risk. Therefore, this study provides some insight into the effects of microhabitat on vole foraging behavior, but other factors mediating risk, such as time of day, may be at play that were not observed in this study and that may merit beneficial future research.

While our overall sample size (1069 voles) was large, the number of marked voles visiting our stations was relatively small (16 individuals). This was inevitable due to the nature of our field study being conducted with free-ranging individuals and is likely reflected in the relatively large CI on our predictions. We emphasize that this number is in line with work from similar field studies (Brehm & Mortelliti, 2022; Martin & Réale, 2008) and includes data from a greater number of seed selection events. Further studies conducted in other settings will contribute to generalize our results.

CONCLUSIONS

Through this field experiment, we have demonstrated that southern red-backed voles, an important seed

predator and disperser in forest ecosystems, display personality-mediated foraging behavior. Overall, these findings may have important implications for forest regeneration. Human disturbance in forests is known to alter the distributions of personality traits in small mammal populations (Brehm et al., 2019). Therefore, in consideration of our findings about the impacts of personality on foraging behavior, altering forest ecosystems may have cascading effects on forest regeneration by shifting the balance of individuals with different personalities participating in seed dispersal processes. Additionally, disturbance that alters microhabitat features also modifies small mammal landscapes of fear, with further consequences for seed dispersal. Our empirical work highlights the importance of considering personality and predation risk in small mammal communities when considering seed dispersal. Future research is warranted focusing on the long-term impacts of microhabitat structure and small mammal personality distributions on forest regeneration in order to make long-term predictions about changing forest structure.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data and code used for analyses (Merz et al., 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.21512436.

ORCID

Margaret R. Merz https://orcid.org/0000-0002-7904-7463
Alessio Mortelliti https://orcid.org/0000-0003-0480-6100

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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