

## ARTICLE

# Navigating novel resources: A field test of the effects of small mammal personality on dispersal of *Quercus* seeds

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**Handling Editor:** Rebecca J. Rowe**Abstract**

Climate change is shifting the habitable ranges of hundreds of species, and a greater understanding of the mechanisms driving migration velocity may make the difference between extinction and persistence for at-risk species. However, predicting migration velocity is particularly complicated for sessile organisms that rely on animals for the dispersal of their propagules. Extrinsic factors (e.g., seed availability, forest structure) and intrinsic factors of propagules and dispersers (e.g., seed mass, disperser species) interact to influence the seed dispersal process at multiple levels, complicating the conditions under which mutualism can occur. Small mammals are important seed predators and dispersers, and thus, their collective actions may modulate the migration velocity of seed-bearing plants. Recent studies have revealed the importance of disperser intraspecific variation, but the role of behavioral variation—animal personality—is infrequently studied and remains poorly understood. Personality may be critical to consider in the context of novel seeds as inexperienced individuals may default to specific behavioral tendencies and foraging strategies when deciding if and how to utilize resources. In a large-scale field experiment in central Maine (USA), we examined seed selection behavior in two species of small mammals (*Peromyscus maniculatus* and *Myodes gapperi*) for eight species of *Quercus* acorns—two of which are native to Maine and six of which are novel to our populations but expected to migrate northward. We found no discernible effects of seed novelty at any stage of the seed dispersal process, but we found evidence of personality-driven patterns in caching behavior. Docility positively predicted removal probability in voles and distance to burrow caches in mice. Lastly, individual antagonism–mutualism scores for voles were influenced by personality, where shy individuals were more antagonistic to acorns and bold individuals were more mutualistic. Put together, our results indicate that behavioral diversity may be important to consider for the maintenance of ecological function and provide a basis from where conservationists can work toward clarifying plant fitness in their novel ranges, species-specific extinction probabilities, and future trends in forest regeneration.

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**KEYWORDS**conditional mutualism, intraspecific variation, *Myodes gapperi*, *Peromyscus maniculatus*, seed dispersal, seed selection**INTRODUCTION**

Plants are expected to respond to warming temperatures in the face of climate change by shifting their ranges to higher latitudes and elevations (Kelly & Goulden, 2008; Rigling et al., 2013; Zhu et al., 2012). However, despite strong theoretical support, less than half of observed range shifts are consistent with these expectations, suggesting that processes beyond temperature are contributing to the global redistribution of biodiversity (Rubenstein et al., 2023). Many studies have investigated the influence of habitat loss, fragmentation, and land-use change on climate change-induced range shifts (Hansen et al., 2001; Honnay et al., 2002), but species interactions can also have strong impacts on climate change responses (Åkesson et al., 2021; Angert et al., 2013; Hille Ris Lambers et al., 2013) and these are seldom, if ever, incorporated in range-shift predictions.

Competitors, consumers, mutualists, and facilitators can alter the distribution and abundance of species at leading and trailing ends, modulating migration velocity (Hille Ris Lambers et al., 2013). Previous investigations have revealed that species interactions can impede (Harley, 2011), accelerate (Bever, 1994; Tilman & Wedin, 1991), and even reverse species' responses to climate change (Suttle et al., 2007); however, the number of studies into this topic is few. This shortage of real-world data coupled with uncertainty in vegetation dynamic models makes it particularly difficult to generalize the conditions under which species interactions will substantially modulate range shifts. Nonetheless, generating ecologically relevant data will lay the groundwork for conservationists to incorporate species interactions when predicting range shifts.

Species interactions can strongly influence plant migration velocity by modulating dispersal capacity, and while some relationships are more straightforward, others can be more nuanced. Scatter-hoarding rodents play the dual role of seed dispersers and predators and have been documented to harvest preferred seeds within home ranges at rates as high as 95% (Jansen et al., 2004; Lobo, 2014; Vander Wall, 2010). Concurrently, the absence of scatter-hoarding rodents has been linked to low plant diversity and limited plant succession (Corlett, 2011). Thus, scatter-hoarding rodents have been previously described as conditional mutualists because outcomes can vary depending on variables such as conspecific

density, seed abundance, availability of other seeds, predator abundance, and lunar cycle (Brehm & Mortelliti, 2022; Bronstein, 1994; Theimer, 2005).

However, within the framework of climate change, it may be crucial to acknowledge the potential that ecological relationships observed in prior contexts may not apply to novel ranges (Gilman et al., 2010; Hille Ris Lambers et al., 2013). Plant species are now encountering populations of granivores with no prior experience with these propagules, potentially leading to altered harvesting and caching behaviors (Mortelliti et al., 2019). Despite several studies delving into the fundamental question of whether food choice in scatter-hoarding rodents is innate or learned, a consensus remains elusive (Lichti et al., 2017). While Muñoz and Bonal (2008) identified learning as a significant factor influencing decision making in *Mus spretus*, Steele et al. (2006) found evidence indicating innate abilities in gray squirrels that influence food choice. Without relevant empirical evidence in novel contexts, outcomes for range-shifting species may be difficult to predict (Urli et al., 2016). Deeper exploration into the role of rodents in modulating migration velocity amidst anticipated climate shifts holds promise in elucidating crucial aspects of plant fitness within novel ranges, species-specific extinction risks, and the prospective trajectory of ecological community dynamics (Barber et al., 2016; Keane & Crawley, 2002; Pearson, 2006; Woodall et al., 2009).

As imperfect foragers, scatter-hoarding rodents ultimately promote seed dispersal by failing to recover cached seeds (Vander Wall, 2010), but the choices they make prior to caching, such as selection, consumption timing, and cache location, can culminate in effects that can hinder or accelerate migration velocity (Dennis, 2007). Research shows that they are sensitive to seed traits such as shell hardness, nutritive content, and perishability (Jansen et al., 2004; Moore et al., 2007; Steele et al., 1996; Wang & Chen, 2009) and will further adjust caching strategies based on season and seed availability (Franzoi Dri et al., 2024; Lichti et al., 2017). For instance, it is well known that eastern gray squirrels differentially cache and consume acorns according to acorn germination patterns, most likely as a strategy to optimize recovery (Steele et al., 2001). In another example, Mortelliti et al. (2019) demonstrated that seed size and shell hardness, rather than “novelty,” positively correlated with selection probability and cache distance. By selectively

harvesting seeds and ignoring others, scatter-hoarding rodent populations have the potential to significantly influence plant dispersal capacity, consequently shaping migration velocity and the future community composition of forest ecosystems (Brown & Vellend, 2014; Gilman et al., 2010; Lobo, 2014; Mortelliti et al., 2019).

Most research on rodent seed dispersal is approached from the population level, chalking individual variation up to noise around an average (Brehm et al., 2019; Feldman et al., 2019; Mortelliti et al., 2019), but personality—defined as consistent behavioral variation over time and across contexts—can have large ecological implications (Sih et al., 2012; Wolf & Weissing, 2012; Zwolak, 2018; Zwolak & Sih, 2020). Personality can affect how thoroughly individuals explore and use their habitat and their neophobic tendencies, as well as how flexible individuals are in response to changes in their environment (Carter, Feeney, et al., 2013; Dingemans et al., 2010; Dyer et al., 2012; Mazza et al., 2019; Sih et al., 2004). In this respect, individuals can drastically differ in their influence on ecological functions. Since scatter-hoarding rodents act as both seed predators and seed dispersers, conspecifics can play disparate roles in seed dispersal (Brehm et al., 2019; Brehm & Mortelliti, 2022; Merz et al., 2023). Some theoretical frameworks exist, but few empirical studies have investigated how personality relates to seed dispersal (Brehm et al., 2019; Brehm & Mortelliti, 2022; Merz et al., 2023). However, Brehm et al. (2019) provide foundational evidence that boldness in *Peromyscus maniculatus* and *Myodes gapperi* positively affects the size of selected (artificial) seed and dispersal distance, respectively, and certain personalities are more mutualistic toward certain seeds than others (Brehm & Mortelliti, 2022). However, to the best of our knowledge, no study has addressed whether personality influences the use of novel seeds.

Within the context of human-induced rapid environmental change, many studies have been conducted to estimate population response to novel resources, highlighting behavioral flexibility and learning as key features (Hendry et al., 2008; Sih et al., 2011). Just as species vary in these traits, so too do individuals, and such variation may be critical to consider in the context of novel seeds. Inexperienced individuals may default to specific personality tendencies and foraging strategies when deciding if and how to utilize the resource. For instance, dominant male carrion crows reliably made first contact with novel food, while low-ranking female Japanese macaques were more likely to interact with novel objects (Arnaud et al., 2017; Chiarati et al., 2012). One field experiment revealed that only when information about the environment was unreliable did personality predict foraging decisions (Carter, Marshall, et al., 2013).

This finding highlights a critical point—even though personality is consistent across contexts, it is not synonymous with personalities acting precisely the same way in all contexts. Thus, it may be critical to capture variance in the behavior of different personalities in novel contexts.

Our goal was to determine the role of personality and seed traits in the selection and dispersal of *Quercus* seeds. Our objectives were to (1) assess whether personalities differentially selected seeds based on traits such as familiarity and size, (2) explore drivers of dispersal distance, (3) and lastly, evaluate whether personality predicted where individuals fall along the continuum of antagonist to mutualist. To address the objectives, we conducted a large-scale capture–mark–recapture study and seed experiment in Maine, USA, a region that has experienced climate shifts of more than 100 km in the 20th century (Zhu et al., 2012). With 64 woody plant species reaching their northern limits within the state, our study area is well-positioned to address how small mammals may affect the range expansion of plant species (Mortelliti et al., 2019). We trapped for two of the most abundant scatter-hoarding small mammal species in the region, deer mice (*P. maniculatus*) and the southern red-backed vole (*M. gapperi*); measured their personality traits using three standardized behavioral assays; and offered novel seeds alongside familiar reference seeds to monitor selection and dispersal decisions.

We expected that shyer individuals, being more thorough and flexible foragers, would more often select and disperse novel seeds (Carere et al., 2010; Carter, Feeney, et al., 2013; Dyer et al., 2012; Koolhaas et al., 1999; Mazza et al., 2019; Sih et al., 2004). Conversely, shy individuals, being more risk averse, may select, predate, and thus disperse novel seeds less often than bold individuals (Cole & Quinn, 2014). Building on previous research, we also anticipated that bolder individuals would cache further (Brehm et al., 2019) potentially because they are trading off the risk of pilferage for the risk of predation (Steele, 2021). Lastly, we predicted that bold individuals, being more competitive, would have a greater probability of harvesting native seeds as well as caching aboveground and therefore have more mutualistic relationships.

## MATERIALS AND METHODS

### Study site and small mammal trapping

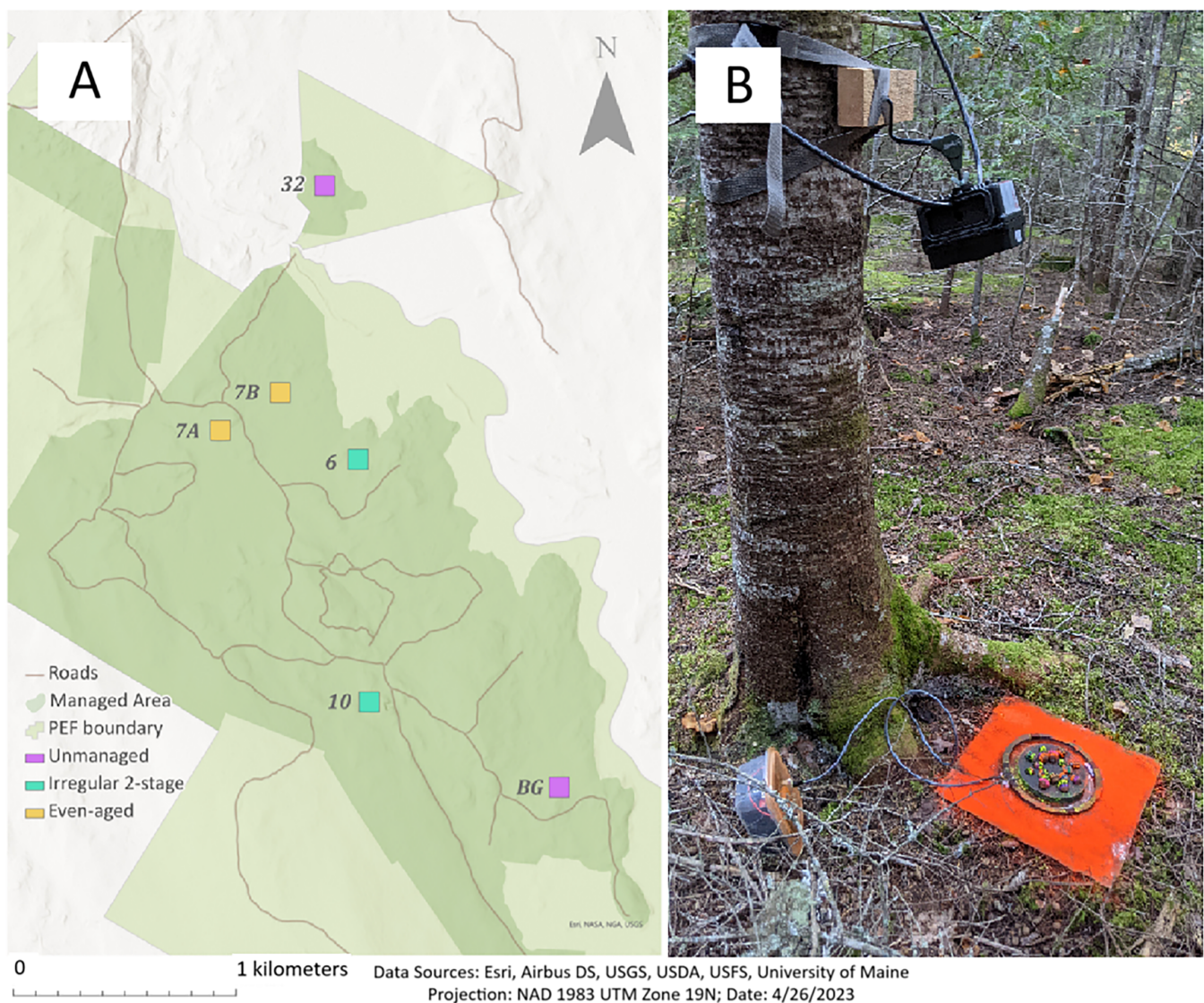
We conducted this study at the Penobscot Experimental Forest (44° 510 N, 68° 370 W) in Maine (USA), a mixed conifer deciduous forest that spans 1578 ha. This study site comprises randomized, replicated forest compartments that

have undergone various silviculture treatments and hosts two reference sites that have been unmanaged since the late 1800s (Kenefic & Brissette, 2014). From June to October (2016–2022), we conducted a large-scale capture–mark–recapture experiment approved by the University of Maine’s Institutional Animal Care and Use Committee (IACUC numbers A2015\_11\_02, A2018\_11\_01, and A2021-12-01) in six areas of the Penobscot Experimental Forest. We centered each trapping grid within treatments to control for edge effects and positioned each at least 1.42 km away from any neighboring grids (Figure 1A). All six trapping grids consisted of 100 flagged points spaced 10 m apart, and each point was set with one Longworth small mammal trap bedded with cotton stuffing and baited with black oil sunflower seeds, oats, and

freeze-dried mealworms. We checked traps twice daily (after sunrise and before sunset) and set at each grid for three consecutive days and nights each month to total ~63,000 trap nights (active traps × nights).

## Behavioral assays and animal processing

Following protocols outlined in previous studies, we conducted three standard behavioral assays to assess boldness, activity and exploration, and docility (Appendix S1: Figure S1 and Table S1; Choleris et al., 2001; Graceva et al., 2014; Martin & Réale, 2008). We performed emergence, open-field, and handling bag tests sequentially at trapping grids before handling and marking, on leveled



**FIGURE 1** (A) Map of the Penobscot Experimental Forest (PEF) in Bradley, Maine, USA, and sites of trapping grids and seed experiment across three forestry treatments. (B) Seed dispersal experimental setup involving trail camera, radio frequency identification reader, and seed tray, on which we offered painted seeds to track dispersal behavior with fluorescent powder. Photo credit: Ivy Yen.

platforms, and under tarps to standardize light levels and canopy cover. We conducted tests on individuals only once per month to prevent habituation.

Upon capture, we transferred individuals from the capture trap to a clean Longworth trap with a 4-liter plastic bag for the emergence test. This trap was then placed within a brown box (46 × 46 × 60 cm) scattered with leaf litter, locked open, and positioned to allow observation via a digital camera (Nikon CoolPix S3700) for a 3-min trial. Following completion of the emergence trial, the focal individual was recaptured in a plastic bag and released in the center of the open-field test arena (46 × 46 × 60 cm) where its behavior was recorded using a mounted digital camera for a 5-min trial. For the last behavioral assay, the individual was recaptured and suspended in the center of the open-field area for a 1-min handling bag trial. After each trial, we sanitized all equipment with 70% isopropyl alcohol and allowed it to air dry.

We later analyzed recorded emergence and open-field trials in the laboratory. For emergence tests, observers recorded latency to reach the end of the tunnel, time spent at the tunnel end, and latency to emerge, defined as all feet exiting the trap. Trials in which individuals did not emerge within 3 min were set to 1.25× the maximum test length for latency to emerge (3.75 min; Brehm & Mortelliti, 2021, 2022; Merz et al., 2023). Open-field trials were analyzed using ANY-maze software (version 5.1; Stoelting CO, USA) to record various behaviors, including mean speed and proportion of time spent in the center of the arena. The number of seconds spent immobile during the 1-min handling bag test was recorded in the field. Following behavioral tests, individuals were anesthetized with isoflurane for subcutaneous PIT tag insertion (passive integrated transponders; Biomark MiniHPT8), ear tagging (National Band, style 1005-1), and biometric measurements before being released at their capture site.

## Seed experiment and seed interaction video analysis

After completion of trapping and around the time of natural seed drop, we deployed seed stations for an average of three nights each month from September to October (2021 and 2022). We offered eight species of *Quercus* acorns (F. W. Schumacher; Appendix S2: Table S1) at each station in duplicate. Two species are native to Central Maine and six are novel but expected to shift their ranges northward into the state in response to climate change (Mortelliti et al., 2019; Schauffler & Jacobson, 2002). We first visually inspected all seeds for rot, weevil-holes, or cracks; then float-tested them; and

rendered non-viable through a brief microwave treatment to control contrived germination. Seeds were then painted with non-toxic fluorescent paint (MidnightGlo, ASTMD-4236 certified) previously determined to have no influence on seed dispersal behavior (Brehm & Mortelliti, 2022) and labeled with permanent marker to aid in tracking and identification. Prior to the field experiment, we offered trays of non-microwaved, labeled seeds with microwaved, labeled seeds in the lab in April 2021 and found no differences in selection behavior ( $n = 14$  [mice], 84 [acorns];  $\chi^2 = 0.034$ ;  $p > 0.99$ ) (I. Yen, unpublished data).

We randomly arranged seeds on a 16-well, plastic tray dusted with fluorescent powder (TechnoGlo) and monitored the tray with a motion-triggered trail camera (Reconyx XR6 Ultrafire) and a radio frequency identification (RFID) reader set to scan and identify PIT-tagged individuals (Figure 1B). We deployed seed stations at sunset to minimize visits by non-target species and visited prior to sunrise to track dispersed seeds in the dark. Fluorescent powder trails were then followed using an ultraviolet flashlight and tracked until the trail led to a seed, a hole, or faded out. Upon visual location of a seed, the identity, state (consumed or intact), distance (direct and path), and location were recorded. For seeds that could not be visually located, we recorded the dispersal distance if there was only one trail leading to a hole; if multiple trails led to multiple holes, we recorded the average distance to all holes. At stations that contained trails that faded out, unlocated seeds were removed from the dispersal and antagonism–mutualism score analysis as we could not confidently determine dispersal distance. Stations were removed at dawn and reset unless all seeds had been removed.

Videos from trail cameras were played back in the laboratory, and interactions, which we defined as deliberate sniffing or manipulation of a seed for more than 1 s, were assigned to individuals based on their unique haircut or time-stamped RFID reads. Time of each interaction was recorded and coded as “removed” if the seed was taken from the station, “rejected” if it was not, and “no interaction” if the individual did not exhibit any of these behaviors. In total, 1544 interactions were recorded, and a representative video is included in Video S1.

## Statistical analyses

First, to discern personality traits from the behavioral variables obtained from the three behavioral assays, species-specific repeatability analyses were performed using package “rptR” (Dingemanse & Dochtermann, 2013; Stoffel et al., 2017). Logit or Box–Cox transformations were used to

normalize response variables when non-normality was detected by visual assessment of Q-Q plots, histograms of residuals, and plots fitted against residual values of linear mixed-effects models and generalized linear mixed-effects models (Box & Cox, 1964; Yang et al., 2011). To determine the proportion of behavioral variance attributable to intraindividual differences, all mixed-effects models included individuals with two or more repeated observations where individual identity (PIT) was included as a random effect and forest treatment, trapping month, and body condition (calculated using the scaled-mass index method) as fixed effects (Dingemanse & Dochtermann, 2013; Peig & Green, 2010). Datasets for each behavioral trait were variable in length as emergence assays were not implemented until 2017, and unreliable tests due to operator error or poor conditions were excluded. We then calculated adjusted repeatability and associated CIs for all models with 1000 parametric bootstraps and 100 permutations and behavioral traits that excluded zero within its 95% CI were considered personality traits (Nakagawa & Schielzeth, 2010).

We calculated an adjusted individual-level mean value by simulating best linear unbiased predictors (BLUPs) for each individual and personality trait 1000 times while controlling for variation due to sex, body condition, forest type, trapping month, and year using the “arm” package (consistent with methods used by Dingemanse et al., 2020; Gharnit et al., 2020; Mortelliti & Brehm, 2020). Resulting individual mean BLUP values for each personality variable were then scaled (z-standardized; Dormann et al., 2013) and screened with body mass and body condition to avoid collinearity during model selection using a correlation threshold of  $r < 0.7$  (Appendix S1: Table S2). Further references of “personality” refer to species-specific individual mean BLUP value.

Following the exclusion of “no interaction” events and unassigned interactions, we conducted weighted logistic regressions to predict removal probability. We assigned weights ranging from 0 to 1 based on an exponential decay function applied to individual encounter numbers and the number of available acorns. This weighting scheme prioritizes earlier interactions when most acorn species are available, offering a more focused assessment of selection dynamics. All models included individual identity as a random effect and the total mass of available seeds as control variables. All continuous variables were scaled (z-standardized; Dormann et al., 2013) and tested for collinearity before inclusion in removal probability, dispersal distance, and antagonism–mutualism score models. We followed a nested hypothesis testing approach where models were run in sets that tested for effects of environmental variables, seed traits, and small mammal traits suspected to influence removal probability (Table 1). Within each set, additive effects were tested when more

than one model scored higher than the null model. Models within 2.0 corrected Akaike information criterion for small sample sizes ( $\Delta AIC_c$ ) of the top model are typically considered to have comparable support (Buckland et al., 1997; Burnham et al., 2002), but we conservatively only carried over the simplest model.

More specifically, the null model was first compared against a set of environmental models, each with a unique environmental variable. We were only able to test for the effect of year in voles as only one mouse visited seed stations in 2021. The best supported model in this set was carried over and tested against five seed trait models. To avoid collinearity during model selection, three components were extracted from six seed traits, that is, seed mass and average lipid, protein, and tannin content, kilocalorie per gram, and shell hardness of each *Quercus* species, using a varimax rotation to maximize the sum of variance of the squared loadings. We referred to the Kaiser–Guttman criterion to select the number of principal components to retain (Kaiser, 1991). From here, the most supported model was tested against three physical trait models and lastly, against five personality models. We elected to narrow our focus to examining five uncorrelated personality traits obtained from the three different behavioral assays to prioritize variables that have exhibited substantial effects in prior experiments and to reduce the complexity of tested models (Brehm et al., 2019; Brehm & Mortelliti, 2021, 2022). Because we were interested in examining the possibility of seed trait interactions with personality, we also tested interactive models with seed traits.

Next, to determine predictors for caching behavior, we ran four sets of linear mixed models predicting direct seed dispersal distance of located seeds. The response variable was  $\log_{10}$  transformed, and all models included individual identity as a random effect. Like the weighted logistic analysis, we first tested the null model against environmental variables and physical trait variables before testing for personality effects. For this specific analysis, we opted to include both species to directly compare dispersal distances by species. Interactive models were included in the third and fourth model sets to test differences in caching tendencies by cache location, species, and personality. Environmental variables included cache location, year, month, forest treatment, and density. Physical trait variables included species, sex, body mass, and body condition.

Lastly, to examine intraspecific variation in the seed dispersal mutualism, we first calculated scores along the antagonism–mutualism continuum for each focal species (Brehm & Mortelliti, 2022). Here, negative events were defined as removed seeds that were cached down a hole, and positive events were defined as removed seeds that

**TABLE 1** Predictor variables used in the weighted logistic regression for removal over rejection probability, cache distance, and antagonism–mutualism analysis in *Peromyscus maniculatus* and *Myodes gapperi*.

Model set	Fixed variable	Variable description
1	Environmental variables	
	Year	Year of interaction event: 2021–2022 (only tested for <i>M. gapperi</i> )
	Month	Month of interaction event: September–November
	Day	Day since start of experiment each year
	Treatment	Silviculture treatment; reference (mature), uniform or irregular two-stage shelter wood
	Density	Total no. small mammals captured per month per grid
	mass.avail	Total mass of available seeds at start of interaction
	Hole	Y/N seed cached in a hole
2	Seed traits	
	PC1	First component extracted from a seed trait PCA interpreted as a measure of energy accessibility
	PC2	Second component extracted from a seed trait PCA interpreted as a measure of digestibility
	PC3	Third component extracted from a seed trait PCA interpreted as mass of seed
	Red/white	Category of seed dormancy and stratification strategy
	Native/novel	Native to central Maine or not
3	Small mammal phenotypic variables	
	Sex	Male or female
	Body mass	Weight of small mammal (g)
4	Small mammal personality variables	
	BCI	Body condition index: calculated scaled mass index using body length and mass
	Mean speed (MS)	Measure of activity (m/s)
	Proportion center (PC)	Proportion of time spent in center of the open-field arena
	Handling time (H)	No. seconds individual spent inactive during handling test
Latency to emerge (LE)	No. seconds before an individual emerges	
Tunnel time (TT)	No. seconds individual spent at end of tunnel	

Abbreviation: PCA, principal components analysis.

were cached on the surface. Individual locations on the continuum were determined by subtracting the proportion of negative events from the proportion of positive events and then used as the response variable in a linear regression analysis. The null model was tested against the total number of observed interactions by an individual, forest treatment, trapping grid, sex, body condition, body mass, and five personality traits (i.e., mean speed, proportion time center, handling time, latency to emerge, tunnel time).

## RESULTS

### Repeatability of behavioral variables

From emergence, handling bag, and open-field tests, we examined 1102 individual *P. maniculatus* and 1357 *M. gapperi* captured from 2016 to 2022. Of these, 409 mice

and 515 voles had repeated observations. All 10 measured behavioral variables were significantly repeatable with a mean of 0.34 (range 0.20–0.41) for *P. maniculatus* and 0.25 (range 0.16–0.31) for *M. gapperi* (Table 2).

### Seed trait principal components analysis

Following dimension reduction of the six continuous seed traits at the species level, we retained three components. The first component (PC1) described a gradient of energy accessibility where high scores reflected high energy seeds that are difficult to access (tannins and hardness) and low scores reflected low energy seeds that are easier to access (Appendix S2: Table S2). The second component (PC2) had high positive loadings for tannin level and high negative loadings for protein level. We therefore interpreted this second component as a measure of

**TABLE 2** Adjusted repeatability estimates for *Peromyscus maniculatus* and *Myodes gapperi* obtained from three standardized behavioral assays (i.e., handling bag, emergence, and open-field).

Species	Behavior trait	Mean	Range	Repeatability	95% CI	No. observations	No. individuals
<i>P. maniculatus</i>	Mean speed	0.09	0–0.29	<b>0.41</b>	<b>0.34, 0.47</b>	1542	955
	Prop center	0.02	0–0.73	<b>0.33</b>	<b>0.26, 0.40</b>	1542	954
	Handling time	15	0–60	<b>0.40</b>	<b>0.33, 0.47</b>	1367	812
	Latency to emerge	56	0–225	<b>0.33</b>	<b>0.26, 0.41</b>	1280	770
	Tunnel time	6	0–180	<b>0.24</b>	<b>0.16, 0.33</b>	1179	719
<i>M. gapperi</i>	Mean speed	0.04	0–0.20	<b>0.31</b>	<b>0.25, 0.38</b>	1849	1179
	Prop center	0.03	0–1	<b>0.25</b>	<b>0.19, 0.32</b>	1854	1184
	Handling time	52	0–60	<b>0.18</b>	<b>0.11, 0.26</b>	1720	1068
	Latency to emerge	103	0–225	<b>0.31</b>	<b>0.24, 0.38</b>	1607	1014
	Tunnel time	6	0–180	<b>0.27</b>	<b>0.19, 0.36</b>	1337	875

Note: Values in boldface designate behavioral variables with CIs that exclude zero.

negative digestibility. The Kaiser–Guttman rule recommended retaining only two components, but we opted to also retain the third component (PC3) because it has high positive loadings for seed mass—a frequently investigated seed trait variable in dispersal literature.

### Effects on probability of removal

Over the course of two autumn seasons, we deployed close to 4800 seeds at over 300 stations. Overall, small mammals removed 36% of deployed seeds, 7% (330) of which were removed by *P. maniculatus* and another 7% (312) by *M. gapperi* (Appendix S3: Figure S2). Other visiting species include *Peromyscus leucopus* and *Glaucomys* spp. squirrels, which removed 2% (79) and 21% (1017), respectively, as well as some visits from American red squirrels (*Tamiasciurus hudsonicus*) and the eastern chipmunks (*Tamias striatus*), although these were not analyzed. Of the 1304 observed focal interactions, 1220 were confidently assigned to an individual. Of these, 50% (616) were scored as removal events, 36% (443) as rejection events, and 13% (161) as “no interaction” events, and virtually no predation events were observed (Appendix S3: Table S2). Throughout the experiment, approximately 40% of focal individuals—14 out of 33 *P. maniculatus* and 12 out of 29 *M. gapperi*—failed to successfully harvest any acorns from the stations during their recorded interactions.

The top model for the weighted logistic regression revealed that the probability of removal for mice was affected by the seed mass principal component (PC3) (Table 3). We found no effect of environmental variables, small mammal trait variables, or seed familiarity. Where the smallest seeds had an approximate 75% chance of removal, the largest seeds had about a 50% chance of removal (Figure 2A;  $n = 532$ ,  $\beta = -0.24$ ,  $SE = 0.12$ ). The

top-ranked model for voles was affected by energy accessibility (PC1; Figure 2B;  $\beta = -0.47$ ,  $SE = 0.12$ ), seed mass (PC3; Figure 2C;  $\beta = -0.41$ ,  $SE = 0.13$ ), day (Figure 2D;  $\beta = 0.28$ ,  $SE = 0.13$ ), and handling time (Figure 2E;  $\beta = 0.36$ ,  $SE = 0.14$ ) (Table 3). Here, again, we observed no effect of seed familiarity. All models within  $2 \Delta AIC_c$  for small sample size are reported in Table 3 and beta estimates are reported in Appendix S3: Table S1.

### Effects on dispersal distance

Of 616 focal seed dispersal (removal) events that were confidently assigned to individuals, 203 were successfully located on the surface of the forest floor and 297 were confidently determined to have been dispersed down a hole (Appendix S3: Figure S2). The top model from the linear mixed model predicting direct dispersal in 30 unique individuals (*P. maniculatus*:  $n = 15$ ; *M. gapperi*:  $n = 15$ ) showed an interaction between cache location ( $\beta = 0.41$ ,  $SE = 0.04$ ), species ( $\beta = 0.27$ ,  $SE = 0.13$ ), and handling time ( $\beta = -0.09$ ,  $SE = 0.09$ ) in *P. maniculatus* (Table 3). Figure 3 illustrates minimum variance in seed dispersal distance by voles and mice with low handling time scores, whereas caches made by mice with high handling time scores tended to be either far burrow caches or close surface caches.

### Antagonism–mutualism scores and effect of personality

No models performed better than the null model for mice; however, the top model for voles showed a positive effect by total number of interactions (Figure 4A;  $\beta = 0.51$ ,  $SE = 0.10$ ) and a negative effect by the

**TABLE 3** Top weighted logistic mixed-models predicting seed removal (*Peromyscus maniculatus*: 532 observations, 22 individuals; *Myodes gapperi*: 526 observations, 21 individuals), linear mixed-models predicting dispersal distance (442 observations, 27 individuals), and linear models predicting individual antagonism–mutualism scores (*P. maniculatus*:  $n = 19$ ; *M. gapperi*:  $n = 17$ ) within 2 delta corrected Akaike information criterion ( $\Delta\text{AIC}_c$ ) for small sample sizes.

Dependent	Species	Model	$K$	$\Delta\text{AIC}_c$
Removal probability	<i>P. maniculatus</i>	(1 PIT) + mass.avail + PC3 + H	5	0
		(1 PIT) + mass.avail + PC3	4	0.21
		(1 PIT) + mass.avail + PC3 + sex	5	0.53
		(1 PIT) + mass.avail + PC3 + BCI	5	0.74
		(1 PIT) + mass.avail + PC3 $\times$ H	6	0.84
		(1 PIT) + mass.avail + PC3 + PC	5	1.81
	<i>M. gapperi</i>	(1 PIT) + mass.avail + PC3 + MS	5	1.82
		(1 PIT) + mass.avail + day + PC1 + PC3 + H	7	0
		(1 PIT) + mass.avail + day + PC1 + PC3 $\times$ H	8	0.82
Dispersal distance	Both	(1 PIT) + mass.avail + day + PC1 $\times$ H + PC3	8	1.60
		(1 PIT) + hole $\times$ species $\times$ H	10	0
Antagonism-mutualism score	<i>P. maniculatus</i>	Body mass	3	0
		Sex	3	0.20
		Null	2	0.46
	<i>M. gapperi</i>	tot.intx + LE	4	0

Abbreviations: BCI, body condition index; H, handling time; LE, latency to emerge; MS, mean speed; PC, proportion time center; PIT, passive integrated transponder.

personality variable latency to emerge (Figure 4B;  $\beta = -0.25$ ,  $\text{SE} = 0.10$ ) on an individual's antagonism–mutualism score (Table 3). Thus, bolder voles and those that interacted more with stations had more positive, mutualistic scores.

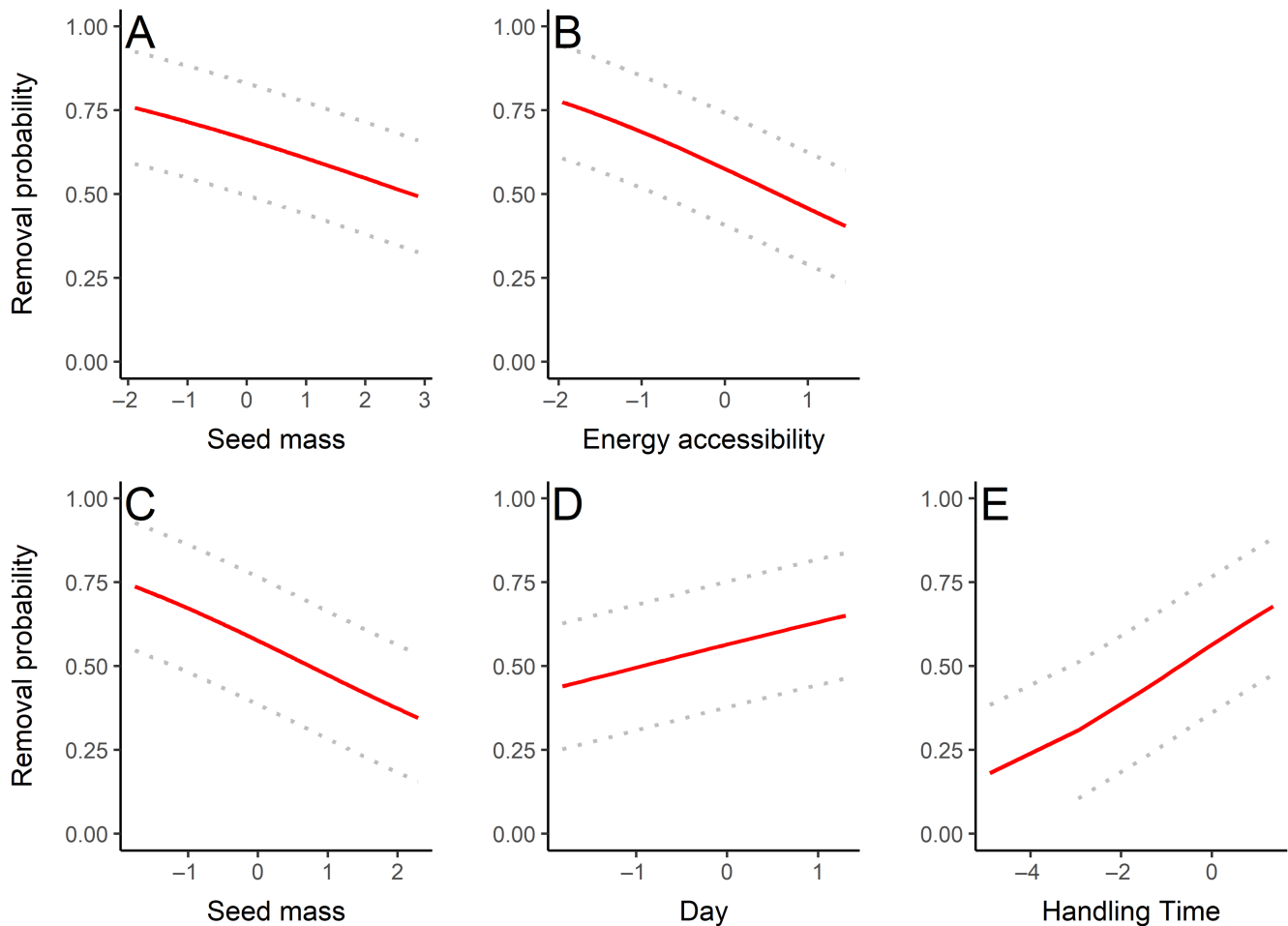
## DISCUSSION

In our field experiment, we found that selection patterns were predominantly driven by seed traits such as mass and energy accessibility and that caching behavior and the degree of mutualism exhibited by individuals toward acorns were notably influenced by small mammal personality traits. Collectively, our findings indicate that acorns are not a favored food source among our focal species while also suggesting that oak species that produce smaller acorns may be facilitated by small mammals for their dispersal. However, the biological and behavioral composition of scatter-hoarding populations plays an important role in shaping the spatial distribution of propagules and thus their overall contribution to seed dispersal dynamics, which in turn can influence colonization patterns. What emerges from our findings is a complex interplay between different steps in the seed dispersal process and associated variables, underscoring the necessity of adopting a holistic approach when

investigating seed dispersal dynamics. To gain a comprehensive understanding of the intricate relationship between small mammals and seed-bearing plants, it is imperative to consider all contributing factors collectively across each step in the seed dispersal process.

In contrast to a previous experiment conducted at the study site in 2020, we observed a substantially lower overall removal of deployed acorns by focal species. Where 68% (261) were removed in 2020, only 14% (642) were removed in this experiment (Brehm & Mortelliti, 2022). This observed disparity is most likely due to differences in availability and population density—fewer acorns and seed species were offered in 2020 to a population that was two times more dense than that of 2021 and three times that of 2022. Interestingly, across both experiments, there were virtually no observations of focal species predated acorns at the experimental stations. This phenomenon could be attributed to the relatively large size of acorns coupled with their hard shells, which render them a risky resource to predate immediately. There may exist a behavioral preference for the immediate consumption of smaller seeds, driven by factors such as nutritional content, ease of handling, or energy requirements (Lichti et al., 2017). Importantly, these potential explanations are not mutually exclusive.

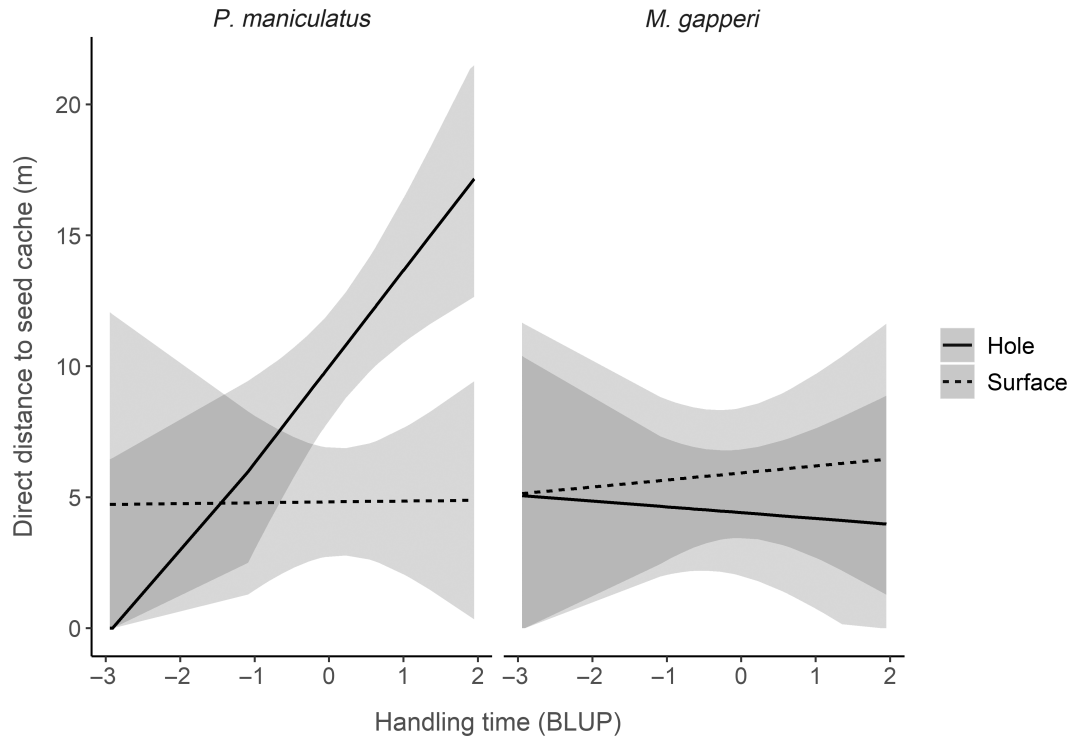
The top model predicting removal probability in mice included only one additional variable alongside the



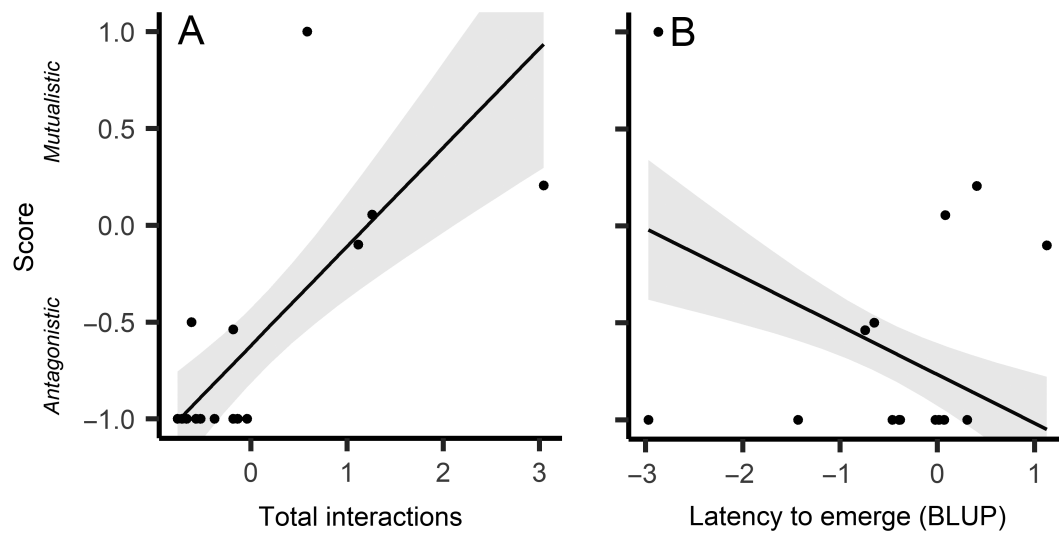
**FIGURE 2** Effect of seed traits on removal probability in (A) *Peromyscus maniculatus* and (B and C) *Myodes gapperi* and the environmental variable of (D) day and (E) handling time in *M. gapperi*. The model predictions were obtained from a weighted logistic mixed model, and the 85% CIs are shown. Predicted probability of removal is shown for mean values of all other included variables.

control variables, namely, a negative effect by seed mass. Seed mass was also included in the top model for voles, with a more pronounced relationship. This preference for smaller seeds contradicts common findings in studies investigating seed size. A global meta-analysis by Dylewski et al. (2020) reported a preference for seeds of intermediate size, with the greatest proportion of removed seeds observed for seeds weighing 5 g. However, these trends may not be mutually exclusive. First, the probability of removal compared to the proportion of removed seeds are two different measures. Although each interaction with a larger seed may be less successful compared to interactions with smaller seeds, the overall proportion of larger seeds removed may end up being greater. Second, the scope of the meta-analysis spanned various ecosystems, while ours is limited to one population in a temperate region. It is possible that although the collective pattern is quadratic, the trend within our specific system is linear.

Beyond seed mass, vole removal probability was also influenced by energy accessibility, day, and handling score. These observed trends align with expectations based on the broader literature. Voles, being omnivorous in nature, exhibit fewer specialized adaptations for seed predation in comparison to the predominantly granivorous *P. maniculatus*. Morphological and behavioral adaptations such as enhanced dentition to process seeds and digestive physiology that impart tannin tolerance may explain why mice are far less responsive to energy accessibility than voles (Lobo & Millar, 2011; Martin et al., 2016). Regarding the temporal variable “day,” as winter approaches and herbaceous resources diminish, foraging pressure for enduring food sources increases (Delgado et al., 2014). The heightened probability of seed removal by voles is likely a reflection of shifting resource availability. The absence of a comparable response in mice could stem from their existing prioritization of seeds, or possibly, an earlier transition to a seed-exclusive diet, which we may have failed to capture within our study



**FIGURE 3** Effect of cache location and the personality variable, handling time, on direct dispersal distance of acorns in *Peromyscus maniculatus* and *Myodes gapperi*. Handling time and cache location interact significantly in *P. maniculatus*, where mice with high handling scores are more likely to disperse seeds farther in holes than on the surface ( $n = 268$ ). *M. gapperi* dispersal distance does not significantly vary by either cache location or handling time ( $n = 232$ ). The model prediction was obtained from a linear mixed model, and the 85% CIs are shown. BLUPs, best linear unbiased predictors.



**FIGURE 4** Effect of (A) total number of interactions and (B) latency to emerge on antagonism–mutualism scores in 17 individual *Myodes gapperi*. Increasing number of interactions predicts more positive, mutualistic scores, while greater scores of latency to emerge predict more negative, antagonistic scores. The model prediction was obtained from a linear mixed model, and the 85% CIs are shown. BLUPs, best linear unbiased predictors.

timeframe. The last result for the selection analysis revealed that voles with higher handling scores were more likely to remove seeds compared to individuals with

low scores. Handling scores reflect the propensity to engage in energetically costly behaviors, or not, under direct threat and are typically interpreted as a measure of

docility (Réale et al., 2000). While this relationship warrants further study, we speculate that docile voles are outcompeted by less docile (more aggressive) voles for safe food resources. However, previous work shows that more docile voles are more likely to forage in enclosed, less risky sites, which may mitigate some of the risk incurred from foraging for risky resources (Merz et al., 2023). It could also be that more docile voles, by engaging in more static behaviors such as freezing, provide themselves with more and/or longer foraging opportunities within the same site. Regardless, it appears that seed traits such as size and energy accessibility, as opposed to novelty, are important contributors in seed selection dynamics for our focal species along with some temporal and small mammal personality effects.

We acknowledge that one of the primary limitations of this study was sample size. While some analyses, particularly those related to harvesting, utilized a large dataset, others—most notably the dispersal distance and antagonism–mutualism analyses—had comparatively smaller samples. Although we did identify some personality-driven patterns, this limitation reduced our ability to detect personality effects in these later stages of caching behavior. While a larger investigation would enable the testing of more complex models and provide a more comprehensive understanding of the role of personality in this context, our results, in conjunction with past studies, suggest that small mammals, at both the species and individual levels, do not differentiate between familiar and novel acorns when harvesting (Mortelliti et al., 2019). In other words, the utility of an acorn for an individual small mammal appears to depend more on its size and accessibility than on familiarity. Overall, while both voles and mice predate seeds, their adaptations seem to be logically reflected in their harvesting patterns.

While personality does not seem to play a significant role during selection in mice, we observed personality-driven trends in caching behavior. Supporting previous findings by Brehm et al. (2019), which identified certain mouse personality types that more frequently cached seeds farther, our results demonstrate an interaction between personality and cache location. Specifically, highly docile mice tended to create the most distant underground caches at approximately 17 m from the seed station. This interaction suggests that highly docile mice are willing to travel farther to and from their burrow to forage and that the distance threshold for less docile mice is much lower. This is consistent with previous research that has revealed personality-driven home range sizes where bolder individuals tend to occupy larger home ranges (Schirmer et al., 2019). However, since seeds stored underground can no longer germinate, such actions ultimately lead to an

unsuccessful seed dispersal event (Vander Wall, 1990). According to the Janzen–Connell hypothesis, the likelihood of propagule exposure to competition, predation, and disease decreases with increased dispersal distance (Connell, 1971; Janzen, 1970). Thus, our results suggest that highly docile mice disperse *Quercus* seeds at comparable distances relative to non-docile mice and even to docile and non-docile voles. Further investigations into whether rates of surface and burrow caches relate to docility may reveal whether this trait can influence the rate of assisted migration.

Incidentally, we found no effect of personality in the mutualism–antagonism analysis for mice. Along with sample size limitations, it may be that other, untested factors drive individual mutualism–antagonism scores. It is also likely that our relatively simplified analysis did not fully capture the complexity of dispersal dynamics. We chose to score interactions on a binary scale rather than on a continuous scale because evidence for which variables and the degree to which they dictate successful germination in this system are not yet fully understood. Even so, our analysis was able to successfully discriminate a personality effect in voles, where bolder voles had more mutualistic relationships with *Quercus* seeds. Several reasons may be driving the effect of latency to emerge on individual mutualism–antagonism scores. First, it may be that timid individuals are more likely to cache in burrows due to smaller realized home ranges (Schirmer et al., 2019). If timid individuals are foraging in smaller areas, their burrows may be relatively closer, and thus, they may be more likely to cache belowground, where the probability of germination is virtually eliminated. It may also be that timid individuals are less likely to cache such large and conspicuous seeds in risky microhabitats (i.e., aboveground). This falls in line with the habitat structure hypothesis, which makes the argument that individuals make a trade-off between higher predation risk with lower pilferage risk when caching in more open microhabitats (Steele, 2021). Along with personality, mutualism scores were also driven by an individual's total number of interactions. While this could be related to an inflated rate of successful location, this relationship might also be explained by the habitat structure hypothesis. Individuals who interact more with the experimental stations presumably have a relatively higher preference for acorns and may thus treat them as higher-value food resources by caching them in more open microhabitats. Put together, these results suggest that not all individuals play equivalent roles in the seed dispersal process and that bold individuals, defined by our behavioral assays, reflect bolder tendencies by caching in riskier sites.

In the context of rapid climate change and shifting habitable ranges, conservation managers planning to use

assisted migration techniques for at-risk plant species will need to consider the timing of seed deployment, the effects of seed traits such as mass and energy accessibility, as well as the biological and behavioral composition of small mammal populations. Our study reveals that of the 40% of mice and voles that use acorns as a food resource, it will be the bold voles who are more likely to facilitate seed dispersal, regardless of whether the seeds are familiar or novel. To ensure successful dispersal of at-risk seeds, further research on the topic will be necessary. Suffice it to say, as these relationships have not been replicated, it would be in the best interests of forest and conservation managers to maintain species as well as behavioral diversity.

### AUTHOR CONTRIBUTIONS

Ivy Yen and Alessio Mortelliti designed the research. Ivy Yen performed fieldwork. Ivy Yen and Alessio Mortelliti wrote the paper. All authors have read, commented, and agreed to the final draft of the manuscript.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

### DATA AVAILABILITY STATEMENT

Data (Yen & Mortelliti, 2024) are available on Figshare: <https://doi.org/10.6084/m9.figshare.27606738.v3>.

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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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