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RESEARCH ARTICLE

Pilfering personalities: Effects of small mammal personality on cache pilferage

Brigit R. Humphreys[1] | Alessio Mortelliti[1,2]

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

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

Correspondence
Alessio Mortelliti
Email: alessio.mortelliti@units.it

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Abstract

1. Small mammals such as mice and voles play a fundamental role in the ecosystem service of seed dispersal by caching seeds in small hoards that germinate under beneficial conditions. Pilferage is a critical step in this process in which animals steal seeds from other individuals' caches. Pilferers often recache stolen seeds, which are often pilfered by new individuals, who may recache again, and so on, potentially leading to compounded increased dispersal distance. However, little research has investigated intraspecific differences in pilfering frequency, despite its importance in better understanding the role of behavioural diversity in the valuable ecosystem service of seed dispersal.
2. We conducted a field experiment in Maine (USA) investigating how intraspecific variation, including personality, influences pilferage effectiveness.
3. Within the context of a long-term capture-mark-recapture study, we measured the unique personality of 3311 individual small mammals of 10 species over a 7-year period. For this experiment, we created artificial caches using eastern white pine (*Pinus strobus*) seeds monitored with trail cameras and buried antennas for individual identification.
4. Of the 436 caches created, 83.5% were pilfered by 10 species, including deer mice ((*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*). We show how individuals differ in their ability to pilfer seeds and that these differences are driven by personality, body condition and sex. More exploratory deer mice and those with lower body condition were more likely to locate a cache, and female southern red-backed voles were more likely than males to locate caches. Also, caches were more likely to be pilfered in areas of higher small mammal abundance.
5. Because the risk of pilferage drives decisions concerning where an animal chooses to store seeds, pilferage pressure is thought to drive the evolution of food-hoarding behaviour. Our study shows that pilferage ability varies between individuals, meaning that some individuals have a disproportionately strong influence on others' caching decisions and disproportionately contribute to compounded longer-distance seed dispersal facilitated by pilferage. Our results

add to a growing body of knowledge showing that the unique personalities of individual small mammals play a critical role in forest regeneration by impacting seed dispersal.

KEYWORDS
animal personality, cache pilferage, forest management, intraspecific variation, land-use change, scatter-hoarding, seed dispersal, small mammals

1 | INTRODUCTION

Small mammals such as mice and voles play a fundamental role in the ecosystem service of seed dispersal by caching seeds in small hoards (Gómez et al., 2019; Vander Wall, 1990). When cached seeds are not retrieved, because the rodent dies or forgets the caching location, these dispersed seeds have an opportunity to germinate, marking a mutualistic benefit to the plant (Sawaya et al., 2018). Pilferage is a key step in this process in which animals locate and steal seeds from other individuals' caches (Dally et al., 2006; Vander Wall, 2000). Pilferers often recache the stolen seeds, which may then be pilfered by new individuals and can be moved to over 30 different caches by pilferers or recaching owners (Jansen et al., 2012; Vander Wall & Joyner, 1998), potentially resulting in compounded increased seed dispersal distance, or alternatively, increased likelihood of seed predation (Brehm & Mortelliti, 2022; Cao et al., 2018; Jansen et al., 2012). Pilferage is prevalent in small mammal communities and is the greatest threat to an individual's cached food reserves (Cao et al., 2018; Dittel et al., 2017). It is estimated that 2%–30% of an individual's caches are pilfered per day, with even just a 2% loss being substantial and unsustainable for a cacher, unless they compensate by pilfering other individuals' caches themselves (Vander Wall & Jenkins, 2003). To evade thieves, cache owners may recache seeds further from the source where there are less concentrated caches and fewer potential onlookers (Vander Wall & Jenkins, 2003), highlighting how pilferage pressure drives the evolution of scatter-hoarding behaviour. Moreover, redistributed seeds are often scatter-hoarded into several smaller caches, likely further benefiting the plant (Hollander & Vander Wall, 2004), though seed predation rates may increase as well.

While a detailed understanding of factors affecting pilferage is emerging, such as the critical role played by soil moisture (Geluso, 2005; Vander Wall, 2000) and small mammal density (Dittel & Vander Wall, 2018), little research has investigated intraspecific differences in pilfering frequency. Determining what characteristics allow an individual to pilfer more often is important for understanding which phenotypes may be disproportionately important in longer-distance seed dispersal, as well as providing critical knowledge on the evolution of this intriguing behaviour. Our goal here is to contribute to filling this knowledge gap by testing key hypotheses on the role played by intraspecific traits in affecting pilferage effectiveness.

1.1 | Intraspecific traits affecting pilferage

Previous work has found preliminary evidence that some individuals of the same species are better pilferers than others (Hollander & Vander Wall, 2004; Vander Wall & Jenkins, 2003); however, limited knowledge exists about what individual traits allow for this discrepancy. While age and olfactory ability have been found to affect pilferage propensity (Donald & Boutin, 2011; Yi et al., 2016), little is known regarding the influence of other individual traits, including sex, social dominance, body condition and personality (Donald & Boutin, 2011; Vander Wall & Jenkins, 2003). Personality, defined as behavioural tendencies that remain consistent across time and context (Dall et al., 2004; Sih et al., 2004), may play an important role in individual pilferage effectiveness, as it can influence decision-making in scatter-hoarding small mammals (Boone et al., 2022; Brehm et al., 2019; Brehm & Mortelliti, 2021). In addition to personality, body condition has been found to influence several aspects of foraging behaviour, including the trade-off between vigilance and foraging (Bachman, 1993), early-life foraging skills acquisition (Thornton, 2008) and seed choice (Merz et al., 2023) in small mammals and may, therefore, be important for individual pilferage effectiveness.

1.2 | Environmental factors affecting pilferage

Environmental characteristics also potentially influence pilferage behaviours. Past research has found that pilferage rates vary with moisture, depth and substrate, with higher pilferage rates at wetter caches (Vander Wall, 2000), shallower caches (Geluso, 2005) and caches in sand compared to ash (Briggs & Vander Wall, 2004) due to increased odour emissions. In addition, higher densities of small mammals increased pilferage (Dittel & Vander Wall, 2018), yet seed abundance was found to have no effect (Yi et al., 2019). Forest structure may also contribute to differing pilferage rates. Unique logging practices produce contrasting silvicultural treatments in forests, which create distinct microhabitats (Mortelliti & Brehm, 2020; Weaver et al., 2009). Because some microhabitats have more conducive physical and chemical conditions for seed germination than others, with these ideal conditions varying by plant species (Hillel & Kozlowski, 2012), it is critical to take into account how silviculture practices and other environmental factors may affect relevant microhabitat features. Additionally, this type of anthropogenic land-use change results in consequent shifts in small mammal communities and scatter-hoarding behaviour (Kellner & Swihart, 2014; Zhang et al., 2016). However, we are not aware of any research determining how anthropogenic land-use change affects pilferage. In a rapidly changing world, it is critical to understand how human-driven activities will influence seed dispersal and forest regeneration at large.

We investigated how pilferage behaviour varies among individuals and different environmental conditions. Specifically, we sought to determine (1) how intraspecific variation in personality and body condition influence the probability of an individual to pilfer a cache and the probability of transporting the pilfered seeds rather than immediately eating them, (2) how microhabitat (cover and moisture) influence pilferage rates and (3) the effects of land-use change on pilferage (Figure 1).

We predict that more exploratory individuals will be more likely to pilfer, as exploratory tendency is associated with fast behavioural types that gather more food with less consideration of risk (Sih & Del Giudice, 2012). In addition, we predict that less docile individuals will be more likely to transport pilfered seeds rather than immediately consume them (Boone et al., 2022) and that individuals with lower body condition will pilfer more (Bachman, 1993). We also predict that caches in more covered locations (Boone et al., 2022; Orrock et al., 2004) and with higher soil moisture (Geluso, 2005; Vander Wall, 2000) will be pilfered more often. Accordingly, we hypothesized that the highest pilferage rates will be areas characterized by dense cover of tightly packed trees, low sunlight penetration and substantial downed woody material, creating moist microhabitat and low risk perception by small mammals.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study was conducted in the Penobscot Experimental Forest (PEF) (44°51′N, 68°37′W, Maine, USA), composed of a mixture of conifer and deciduous trees with management units created through distinct logging practices (Kenefic & Brissette, 2014). In this study, we compared three different silvicultural treatments that provide distinct microhabitats to small mammals, each with two replicates, totalling six trapping grids: (1) uniform shelterwood forest, characterized by small densely packed trees, little understory light and sparse herbaceous cover, (2) irregular shelterwood forest, characterized by a mixture of large and small trees, a mossy understory and abundant woody material and (3) unmanaged forest (since the late 1800s), characterized by large spaced trees, abundant woody debris and large open areas.

2.2 | Small mammal trapping

All activities were approved by the University of Maine's Institutional Animal Care and Use Committee (A2021-12-01, A2018-11-02 and A2015_11_02). This research followed procedures designed to ensure the health and safety of all animals and researchers.

As part of an extensive 7-year (2016–2022) capture-mark-recapture study, we set 100 Longworth traps spaced 10 m apart and 50 Tomahawk traps spaced 20 m apart in each of our six trapping grids measuring 90 × 90 m (0.81 ha). Longworth traps were baited with sunflower seeds, oats and freeze-dried mealworms and contained polyester fibre for bedding. Tomahawks traps were baited with peanut butter. Traps were placed in each grid for three consecutive days in the beginning of each month from June–October each year and checked twice daily. Longworth traps targeted deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*), while Tomahawk traps targeted American red squirrels (*Tamiasciurus hudsonicus*). Personality data for our experiment came from all 7 years, totalling over 60,000 Longworth trap nights and over 30,000 Tomahawk trap days.

2.3 | Behavioural testing and processing

Each individual small mammal captured within the 7 years (excluding *Sorex* spp.) was subject to three behavioural tests in the field a

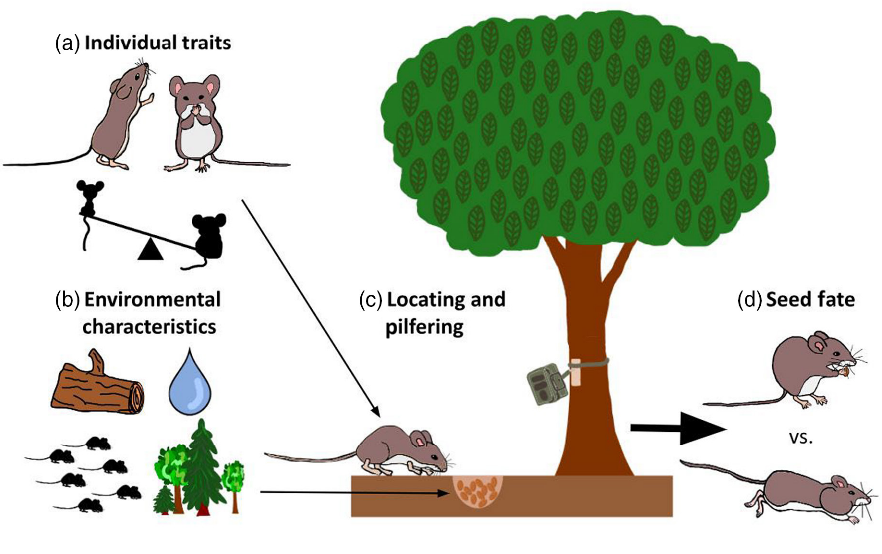

FIGURE 1 Conceptual overview of our pilferage experiment. We investigated how (a) individual traits (personality and body condition) and (b) environmental characteristics (microhabitat, soil moisture, conspecific abundance and silvicultural treatment) influenced (c) how effective an animal is at locating and pilfering a cache, as well as (d) whether a pilferer will eat or transport the stolen seeds, which will affect seed dispersal outcomes. We conducted our experiment by creating artificial caches of buried eastern white pine (*Pinus strobus*) seeds monitored with trail cameras to observe pilferage behaviour.

maximum of once per month to avoid habituation: (1) emergence test, measuring boldness (Carter et al., 2013), (2) open-field test, measuring activity and exploration in a novel context (Perals et al., 2017) and (3) handling bag test, measuring docility and response to being handled by a human (Martin & Réale, 2008). Instead of the emergence test, squirrels and chipmunks went through a mirror test, measuring sociality and aggression. For the emergence test, individuals were transferred from the trap in which they were caught into a clean Longworth trap, which was placed into a 46 × 46 × 60 cm brown box with scattered conifer needles and leaves. The trap door was locked open and a camera faced the opening of the trap for 3 min. For the open-field test, individuals were immediately transferred from the emergence trap to a 46 × 46 × 60 cm white open-field box (larger 79 × 79 × 79 cm for squirrels and chipmunks). A camera pointed downwards into the arena for 5 min. For the handling bag test, individuals were caught in a clean Ziploc bag, ensuring sufficient air for comfortable breathing and held while an observer recorded the time the animal spent immobile for 1 min. All tests were performed on palettes beneath tarps to ensure a level surface and consistent light conditions. During tests, observers left the area (besides the handling bag test) and remained quiet. Open-field boxes, emergence traps and Ziploc bags were cleaned with 70% isopropyl alcohol between individuals.

Following behavioural testing, the following information was collected on each individual: weight, sex, age class and reproductive status. Each individual received a passive integrated transponder (Biomark PIT tags; MiniHPT8, 134.2 kHz) subcutaneously, an alphanumeric ear tag and a distinct haircut for visual identification. For mice and voles, body and tail length were measured. Each individual was subsequently released in the exact location in which they were trapped.

2.4 | Creating artificial caches

We conducted our pilferage experiment in our trapping grids after trapping during each month from July–October 2022, targeting individuals captured within the month. During these time periods ranging from 21 to 28 days each month, we created a total of 436 artificial caches. To create caches, we used eastern white pine (*Pinus strobus*) seeds, as this species is consistently preferred among the small mammals in our study system, likely due to their high protein, fat and caloric value (Boone & Mortelliti, 2019). We buried groups of 30 seeds at a depth of 0.5 cm (Abbott & Quink, 1970; Vander Wall et al., 2001), covered the seeds with a bit of substrate and ensured that the seeds were completely out of view and that the forest floor did not appear disturbed.

In each trapping grid, we placed 10 artificial caches at a time in different microhabitats, spread out to maximize independence and the number of unique individuals encountered. We chose four microhabitats where small mammals typically cache seeds (Brehm et al., 2019): (1) moss, (2) coarse woody debris, (3) base of a big tree and (4) base of a small tree (within approximately 30 cm of tree bases; Figure S1). We measured the volumetric water content (VWC%) of the substrate using a moisture meter upon cache creation and each day of monitoring. Our monitoring scheme allowed us to always measure moisture on the day of or day before a pilferage event. We recognize that the moisture could have changed during this time; however, sites tended to vary consistently, so that a precipitation or drying event would have impacted all caches relatively evenly.

2.5 | Antenna and camera monitoring of caches

We buried circular antennas 2 cm deep around each cache, ensuring it was out of view. A radio frequency identification (RFID) reader board, which was connected to the buried antenna and a motorcycle battery as its power source, was hidden under leaves and debris. The purpose of the antenna and reader board was to log when an individual containing a PIT tag found a cache so that we could link the pilferage event to the personality traits of that individual.

At each cache, we mounted a Reconyx trail camera (UltraFire XR6) on a tree at waist height facing downward at the cache. These cameras were motion-triggered and set to take a photo and 2-min video to capture pilferage behaviour. We analysed each video to collect the following information: date and time of visit, approximate number of seeds taken and whether the seeds were eaten at the cache or transported away (several examples are provided in Video S1). We determined the identity of the pilferer and other visitors primarily using PIT tag identification from the antenna-RFID reader system and secondarily using individuals' unique haircuts observed from camera footage (Video S1).

We checked caches every other day. If the cache was pilfered, we moved the equipment to a new site with new seeds, ensuring an equal distribution of microhabitat sites across time. If there were any seed shells present at the cache, we conservatively classified the seeds as eaten, as determining the exact number of shells was unreliable. If a site was not pilfered, the cache remained in place until the maximum of six nights passed, after which all seeds and equipment were removed from the grid.

2.6 | Home range calculation

To identify which caches were available to which individuals, even if they did not locate the cache, we calculated home ranges for all captured mice and voles during 2022 ($N = 110$ and $N = 114$, respectively). Using the capture locations of each individual across the year, we calculated home ranges using 75% fixed kernel density estimates (Chirima & Owen-Smith, 2017; Dri et al., 2022) for individuals caught five or more times. For individuals caught less than five times, we averaged home range size among single species and placed circular buffers using weighted centrepoints around these individuals to represent estimated home ranges. We generated a list of all artificial cache locations that fell within the estimated home ranges of each individual in order to compare the traits of individuals that located the caches with those that did not locate the caches, but were available in the area. For home range calculations, we used the software R (R Core Team, 2022) packages adehabitatHR and secr (Table S2).

2.7 | Personality analysis

We analysed behavioural test videos to quantify personality traits of each captured individual. For emergence test videos, we recorded latency to emerge and time spent at the end of the tunnel (Table S1). The open-field test was analysed using ANY-maze© behavioural tracking software (version 5.1; Stoelting, CO, USA), which measured rear rate and proportion of time spent grooming (Table S1).

We estimated repeatability, defined as the amount of variation attributed to differences among individuals, rather than differences within individuals (Dingemanse & Dochtermann, 2013), for all measured behavioural variables across all 7 years of our long-term field study in order to determine which traits could be considered repeatable personality. The usage of individuals captured in the previous 6 years was for calculating behavioural trait repeatability, as only individuals from 2022 were expected to be alive to pilfer caches. To do this, we calculated the adjusted repeatability of each trait with individual identity as a random effect, and sex, body condition (scaled mass index; Peig & Green, 2009), silvicultural treatment and trapping session as fixed effects using the lme4 package (Table S2). We conducted Box–Cox transformations (Box & Cox, 1964) on all behavioural variables to approach normality, creating Gaussian error models with an identity link function. All subsequent analyses used these transformed behavioural data. We used the rptR package (Table S2) to calculate adjusted repeatability estimates using a 95% confidence interval (CI) and 1000-permutation bootstrapping. We considered any trait that had a repeatability estimate, with a 95% CI excluding zero, a personality trait (Nakagawa & Schielzeth, 2010).

For each behavioural measurement for each individual, we calculated mean best linear unbiased prediction (BLUP) values across 1000 simulations, which is a method for obtaining a single point estimate of a random effect in a mixed-effects model (Dingemanse et al., 2020), using the arm package (Table S2). The use of BLUP calculations without simulations has been criticized for overlooking uncertainty in estimates (Houslay & Wilson, 2017), so we used simulated BLUP values as a less precise yet unbiased approach that accounts for this uncertainty to obtain a single mean BLUP estimate for each personality trait for each individual (Dingemanse et al., 2020; Villegas-Ríos et al., 2018). Subsequent references to personality refer to this mean BLUP value.

To avoid collinearity, we tested for correlations between each combination of personality traits for each species using all individuals captured within the 7-year period, as well as between all independent variables used in the analyses. All variable combinations had correlation coefficients less than 0.5 (i.e. below the 0.7 threshold suggested by Dormann et al., 2013). Variance inflation factors were evaluated to assess multicollinearity and all were below 2, indicating the absence of multicollinearity.

2.8 | Likelihood ratio tests

We conducted generalized linear mixed-effects modelling using the lme4 package (Table S2) to investigate four aspects of pilferage for deer mice and southern red-backed voles separately, as these two species had the highest number of unique tagged pilferers ($N=29$ and $N=12$, respectively). Our response variables were (1) cache locating, (2) cache pilferage, (3) seed fate and (4) cache fate. We excluded southern red-backed voles from the seed fate analysis, as the sample size of vole transportation events was too small ($N=3$). We used individual identity as a random effect in cache locating, cache pilferage and seed fate analyses, and both cache identity and cache nested within trapping grid as random effects in cache fate analyses, fitting all models for binomial variables.

We performed likelihood ratio testing to compare full model versions with nested models (Table S3) using the lmtest package (Table S2). For each dependent variable of interest, we used a forward model selection technique (Blanchet et al., 2008), beginning by testing if the addition of single explanatory variables improved the nested null model. If the test produced a significant p-value (following the Benjamini-Hochberg correction for multiple testing), the variable was included in subsequent models. First, we explored the effects of individual variables (i.e. sex and body condition) against the null model, followed by time-varying variables (i.e. trapping session and conspecific population abundance, or the number of individuals of a given species captured during the month), followed by environmental characteristics (i.e. silvicultural treatment and microhabitat and moisture when applicable). Finally, we tested the effects of four repeatable personality traits in deer mice and five in southern red-backed voles (i.e. rear rate, proportion of time spent grooming, time spent inactive during the handling bag test, latency to emerge from the emergence test trap, and time spent at the end of the tunnel of the emergence test trap; Table 1; Table S1), which were all z-transformed to make the coefficients comparable and tested biologically relevant interactions between top personality traits and silvicultural treatment. We selected the top model from the final test set for inference (Table 2). We used the Benjamini-Hochberg correction, which controls false discovery rate and reduces Type I errors, to get an adjusted set of p-values corrected for multiple testing (Benjamini & Hochberg, 1995) using the car package (Table S2). QQ-plots and residual plots were used to visualize top models.

3 | RESULTS

We tested and analysed the personality of 989 deer mice and 1210 southern red-backed voles from 2016 to 2022 and found significant adjusted repeatability estimates for all five personality traits used in our analysis (deer mice: mean = 0.336, range = [0.246, 0.397]; southern red-backed voles: mean = 0.239, range = [0.159, 0.305]) (Table 1).

Of the 436 caches, 364 of them, or 83.5%, were pilfered in six nights or less by 10 different species, including 218 pilfers by 51

TABLE 1 Adjusted repeatability estimates (RPT) for personality traits of deer mice and southern red-backed voles calculated from behavioural tests from 2016 to 2022. See Table S1 for descriptions of each personality trait.

Species	Personality trait	Mean	Range	RPT	[95% CI]	No. of observations	No. of individuals
Deer mouse (*Peromyscus maniculatus*)	Rear rate	0.182	0–0.680	0.354	[0.287, 0.423]	1555	954
	Handling	15.138	0–60	0.397	[0.335, 0.467]	1376	812
	Latency to emerge	55.581	0–225	0.346	[0.272, 0.422]	1287	770
	Time at end of tunnel	5.694	0–180	0.246	[0.174, 0.331]	1186	719
Southern red-backed vole (*Myodes gapperi*)	Proportion of time spent grooming	0.121	0–0.899	0.159	[0.098, 0.232]	1848	1165
	Rear rate	0.082	0–0.557	0.283	[0.217, 0.358]	1857	1168
	Handling	51.917	0–60	0.182	[0.120, 0.258]	1728	1072
	Latency to emerge	102.978	0–225	0.305	[0.233, 0.380]	1613	1015
	Time at end of tunnel	6.003	0–180	0.268	[0.192, 0.351]	1341	874

TABLE 2 Top models from the likelihood ratio test analysis for deer mice and southern red-backed voles.

Species	Response variable	Top model	R^2_c (R^2_m)
Deer mouse (*Peromyscus maniculatus*)	Locate	Rear rate (β=0.910, SE=0.330) + conspecific abundance (β=0.507, SE=0.190)	0.808 (*0.074*)
	Pilfer	Body condition index (β=−0.951, SE=0.320)	0.599 (*0.110*)
	Seed fate	Null (intercept: β=−0.394, SE=0.375)	0.313 (*0*)
Southern red-backed vole (*Myodes gapperi*)	Locate	Sex (female: β=−1.241, SE=0.522, male: β=−1.962, SE=0.647)	0.615 (*0.113*)
	Pilfer	Null (intercept: β=−3.732, SE=0.775)	0.480 (*0*)
All pilfering spp	Cache fate	Trapping session (β=0.431, SE=0.164) + total abundance of all pilfering species (β=0.921, SE=0.250)	0.324 (*0.280*)

Note: The response variables are: (1) Locate, including all instances of animals finding the cache location, including pilfers and non-pilfer visits, indicated by digging or intense, directed sniffing of the exact cache location, (2) pilfer, referring to only the instances where animals ate or transported seeds from the cache, (3) seed fate, describing whether pilfered seeds were eaten immediately or transported away from the cache and (4) cache fate, describing whether or not a cache was pilfered within six nights of being set by any small mammal. Seed fate for voles is excluded due sample size constraints. Models for locate, pilfer and seed fate used individual identity as a random effect and models for cache fate used cache identity and cache nested within grid as random effects. For each model, the conditional (R^2_c) and marginal (R^2_m) R^2 values are given.
The italics values are the marginal *R*-squared values, which take into account only the variance of the fixed effects and do not include that of the random effects.

unique PIT-tagged individuals with known personalities. We had a total of 700 visits (including pilfers and post-pilfer visits). Of the 218 pilfers, there were 114 by deer mice (*Peromyscus maniculatus*, 29 individuals), 42 by American red squirrels (*Tamiasciurus hudsonicus*, 4 individuals), 20 by southern red-backed voles (*Myodes gapperi*, 12 individuals), 20 by eastern chipmunks (*Tamias striatus*, 3 individuals), 17 by woodland jumping mice (*Napaeozapus insignis*, 2 individuals) and 5 by white-footed mice (*Peromyscus leucopus*, 1 individual). Deer mice were the most effective pilferers, making up 52.5% of total tagged pilferers. The average number of caches pilfered by pilferers varied by species: deer mouse (mean=3.97, SD=3.51, N=29), southern red-backed vole (mean=1.67, SD=1.37, N=12), white-footed mouse (caches pilfered=5, N=1), woodland jumping mouse (mean=8.5, SD=7.78, N=2), American red squirrel (mean=10.5, SD=4.43, N=4) and eastern chipmunk (mean=6.67, SD=6.03, N=3). Untagged animals (especially *Sorex* spp.) pilfered our caches as well, but from tagged species, untagged pilferers were rare.

3.1 | Cache locating

Our cache-locating analysis included 255 visits and 527 non-visits from 87 unique deer mice, and 73 visits and 171 non-visits from 81 unique southern red-backed voles. The top model predicting whether deer mice will locate a cache included rear rate (a proxy for tendency to explore) and conspecific abundance (Table 2). More exploratory deer mice were more likely to locate caches (Figure 2). When deer mouse abundance was higher, a cache was more likely to be located. For southern red-backed voles, the top model predicting whether an individual will locate a cache included sex (Table 2), with female voles more likely to locate caches (Figure S2).

3.2 | Cache pilferage

Our cache pilfering analysis included 114 pilfers and 668 non-pilfers (including post-pilfer visits and non-visits) from 87 unique deer mice, and 20 pilfers and 224 non-pilfers from 81 unique southern red-backed voles. The top model predicting whether deer mice will pilfer a cache included body condition (Table 2). Deer mice with lower body condition were more likely to pilfer caches (Figure 3). For voles, the top model for pilfering was the null model (Table 2).

3.3 | Seed fate

Our seed fate analysis included 56 transports and 58 eating events (indicated by the presence of any seed shells) from 29 unique deer mice. Voles were excluded due to low sample size of transport events ($N=3$). Seed fate of deer mice pilfers was divided equally, with 49% of pilfers by deer mice resulting in transported seeds and 51% resulting in eaten seeds. In contrast, for southern red-backed voles pilfers, only 15% resulted in transported seeds, while 85% resulted in eaten seeds. The top model predicting seed fate of deer mice pilfers was the null model (Table 2).

3.4 | Cache fate

Our cache fate analysis including pilfers from all species included 322 pilfered caches and 72 non-pilfered caches. The top model predicting cache fate included trapping session and total small mammal abundance (Table 2), calculated by summing unique captures of each pilfering species per grid per session. Caches set in later sessions and in areas with higher total small mammal abundance were more likely to be pilfered (Figure S3).

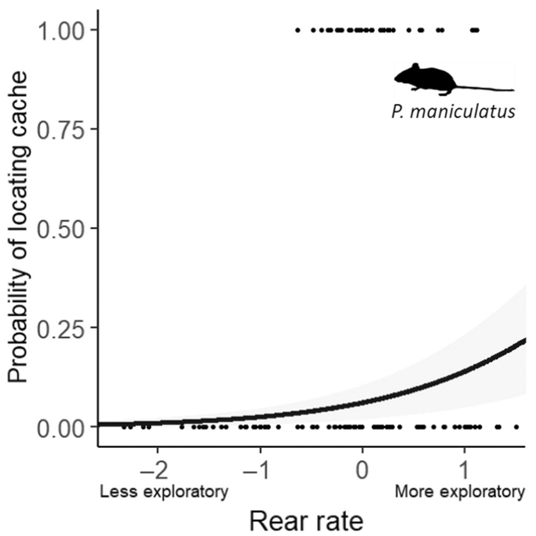

FIGURE 2 More exploratory deer mice (i.e. higher rear rate in the open-field test) were more likely to locate a cache. Predictions were obtained from the top model and the 95% CI is shown. The predicted relationship is shown for the mean deer mouse abundance. Data points depict the raw data and rear rate is a scaled variable.

4 | DISCUSSION

Through our field experiment conducted on small mammal populations in Maine (USA) we found that individuals differ in their ability to pilfer seed caches and that these differences are driven by intraspecific variation in personality, body condition and sex. We also found that pilferage was positively related to small mammal abundance. Our findings reveal the importance of considering intraspecific variation in cache pilferage ability, which has key consequences for the seed dispersal process.

4.1 | Effects of personality on pilferage

Individual personality influenced the likelihood of individuals to locate caches in deer mice. More exploratory deer mice were more likely to locate caches, as we predicted, which is in line with previous research finding that more exploratory individuals find food more frequently through their increased motion (Budaev, 1997), decreased consideration of risk (Sih & Del Giudice, 2012) and higher motivation to feed (David et al., 2012). In contrast, no personality trait significantly influenced voles' frequency of locating caches. We rejected our hypothesis that less docile individuals would be more likely to transport pilfered seeds, despite previous research observing this (Boone et al., 2022).

4.2 | Effects of body condition on pilferage

For deer mice, individuals with lower body condition were more likely to pilfer caches, supporting our prediction and paralleling past studies finding that individuals of lower body condition express a higher motivation to feed (David et al., 2012) and arrive earlier at food sources (Crino et al., 2017). Even a modest decrease in body mass is associated with more time spent foraging and less time spent being vigilant (Bachman, 1993), suggesting that individuals with lower body conditions will spend more time searching for food and, therefore, be more likely to pilfer.

4.3 | Effects of sex on pilferage

For southern red-backed voles, females were more likely to locate caches, supporting past research on sex-dependent foraging strategies in voles (Hovland et al., 1999; Morris, 2023). In addition, past research has found that male southern red-backed voles have larger home ranges than females, yet females shared areas more often with both sexes (Tisell et al., 2019), suggesting that even though females have smaller home ranges, they may be able to more flexibly forage in high-quality areas when available, despite overlapping space with other individuals.

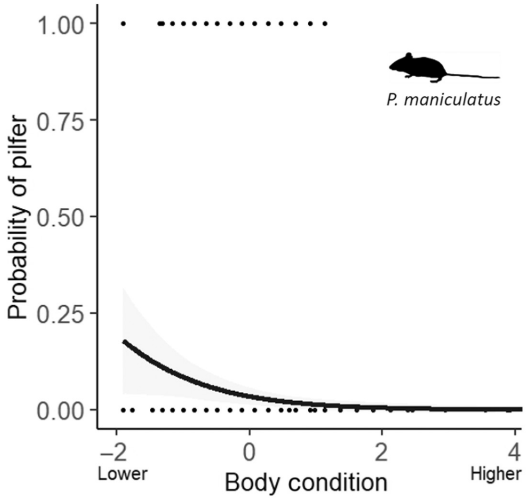

FIGURE 3 Deer mice with lower body condition were more likely to locate a cache first and pilfer it. Predictions were obtained from the top model and the 95% CI. Data points depict the raw data and body condition is a scaled variable.

4.4 | Effects of small mammal abundance on pilferage

Abundance of small mammals predicted cache locating and cache fate. When deer mouse abundance was higher, deer mice were more likely to locate caches, and when total small mammal abundance was higher, pilferage rates were higher across grids and sessions, in line with past research indicating density-dependent competition as a main determinant in pilferage rates (Dittel & Vander Wall, 2018), which may lead to increased immediate consumption of seeds and decreased benefit to the plant (Zwolak et al., 2023). Thus, a variety of pilferage avoidance strategies have evolved, including spatial memory techniques (Ribeiro & Vieira, 2016), active cache surveillance (Hirsch et al., 2013) and recaching seeds to safer locations (Vander Wall & Jenkins, 2003), which can significantly reduce pilferage while bolstering seed recovery by cache owners (Dally et al., 2006).

We found no other environmental factors significantly influencing the likelihood of a cache to be pilfered, including soil moisture, microhabitat and silvicultural treatment, despite our predictions regarding more pilferage in wetter, more covered areas. Past research has found that foraging and pilfering occur more often in wetter (Geluso, 2005; Vander Wall, 2000) and more covered locations (Boone et al., 2022; Orrock et al., 2004), while other work determined mixed effects and no effect of microhabitat on pilferage rate (Dimitri & Longland, 2022; Pansing et al., 2017). We note that several of these were significant prior to the Benjamini-Hochberg correction, suggesting that further analyses with higher statistical power may be needed to verify the role of environmental factors.

4.5 | Differences in pilferage abilities between species

In addition to intraspecific variation in pilferage ability, it was clear that different species differed in their pilferage effectiveness, in line with past research (Dittel et al., 2017; Leaver & Daly, 2001). Deer mice were the most effective pilferers, making up over half of total tagged pilferers, despite being only the second most abundant species in our study area after southern red-backed voles. On average, deer mice pilferers pilfered over twice as many caches as southern red-backed vole pilferers. In regard to seed fate, deer mice pilferers were just as likely to transport the stolen seeds as they were to eat the seeds at the cache. In contrast, southern red-backed vole pilferers were approximately six times more likely to eat the seeds rather than transport them. These behavioural differences may be due to voles' lack of large cheek pouches, making it difficult for them to transport 30 seeds from the cache in a single trip. This suggests that deer mice may be disproportionately more important in seed dispersal than voles, who carried out disproportionately more seed predation. Although deer mice pilfered the most caches as a species, red squirrels on average pilfered the most caches as individuals.

4.6 | Limitations

We acknowledge that limitations exist in our study design. First, our pilfering experiment was conducted during a single year and, therefore, only encapsulated one combination of seed and small mammal abundance, which fluctuate from year to year. While a second year would have strengthened our results, the moderate seed abundance year, indicated by our cone counting and seed trapping, and the moderate-to-high small mammal capture year, allowed for sufficient sample size of cache pilferers to analyse. We predict even higher rates of pilferage than we observed during years with higher small mammal abundance. In addition, increased sample sizes of unique deer mice and voles ($N=29$ and $N=12$, respectively) would have bolstered our results, especially for voles. However, we used personality data from all 110 and 114 individuals captured during the year, respectively, to compare cache visitors and non-visitors, as well as 3311 total individuals across 7 years for calculating repeatability.

4.7 | Broader implications

Trees of the forest and small mammal scatter-hoarding seed dispersers depend on each other for survival (Gómez et al., 2019), and conditional mutualisms like this are fundamental to ecosystems (Bascompte, 2019; Janzen, 1985). Beyond benefiting the plants and animals involved, the seed dispersal mutualism provides vast economic benefits to humans as an ecosystem service (Mortelliti, 2023). However, seed dispersal is threatened by human activities, including habitat fragmentation, overharvesting and climate change, so efforts must be made to conserve this fundamental function in our changing world (McConkey et al., 2012).

Pilferage is a key step in the seed dispersal process, a major evolutionary driver in scatter-hoarding behaviour, a determinant in seed fate (Cao et al., 2018) and may increase dispersal distance (Jansen et al., 2012). Increasing seed dispersal distance is important not only because it allows seeds to avoid density-dependent mortality close to the parent tree (Howe & Miriti, 2004), but it also allows plants to migrate in latitude and elevation with our changing climate (Davis & Shaw, 2001). In addition to body size and migratory movement (Nathan et al., 2008), individual behavioural traits have been found to impact seed dispersal distance (Brehm et al., 2019; Poulsen et al., 2021). Therefore, it is vital that we identify which behavioural traits make individuals more effective at contributing to this critical ecosystem service by potentially increasing seed dispersal distance. Our findings reveal that beyond species variation, individual variation must be taken into account.

Furthermore, our findings provide useful insights into the evolution and maintenance of pilferage in food-hoarding communities. Within a caching system, pilferage is reciprocal, stable, tolerated at high levels, and not necessarily susceptible to cheaters, which are individuals who only steal food and do not cache resources for themselves (Vander Wall & Jenkins, 2003). However, unreciprocated pilferage can occur, which may be damaging to a food-hoarding community's balance and is often attributed to interspecific pilferage since different species often have distinct hoarding behaviours (Leaver & Daly, 2001; Vander Wall & Jenkins, 2003). For example, if one species is pilfering many of another species' caches because they are undefended and shallow, but the pilferage is not reciprocated because the pilfering species larder-hoards in deep defended caches, then the species that cannot reciprocate pilferage is at a disadvantage. Our research has shown that beyond interspecific pilferage, intraspecific pilferage should be considered in identifying unreciprocated pilferage relationships. We show that some individuals are much better pilferers than other individuals of the same species, due to personality, body condition and sex, and therefore, a caching system's reciprocal nature could be thrown off, even focusing on just a single species. Therefore, in these unreciprocated contexts, we predict there is a trade-off between pilfering and caching ability at the individual level, with a strong evolutionary pressure to either be: (1) an effective pilferer or (2) an effective pilferage avoider, with the skilled pilferage avoiders putting pressure on the pilferers to improve their cache-locating abilities and the skilled pilferers putting pressure on cachers to improve their pilferage avoidance strategies. Overall, pilferage by members of the same species may be just as important as pilferage by other species in shaping the hoarding behaviours of animals.

4.8 | Importance of intraspecific variation

Our field experiment provides empirical evidence that individuals of the same species are not equally effective pilferers, and this is partially driven by intraspecific variation in personality and body condition. Intraspecific niche specialization has important ecological, evolutionary and conservation implications and can change ecological dynamics and outcomes (Bolnick et al., 2011). Different personalities have distinct roles in a community and without the whole range of behavioural types, certain ecological functions may be lost. By identifying the traits of the most effective pilferers, we are discovering which individuals may be disproportionately vital in longer-distance seed dispersal, through multiple seed transportation events, or in increasing seed predation rates, as well as highlighting which individuals have a disproportionately strong influence on other animal's caching decisions, who are doing all they can to avoid pilferage of their stashed resources. Our study adds to the growing empirical evidence (Hunter et al., 2022) that beyond conserving biodiversity, we must conserve intraspecific behavioural diversity in order to truly maintain functional ecosystems.

AUTHOR CONTRIBUTIONS

B. R. H. and A. M. conceived the ideas, designed the methodology, collected the data, performed the analysis and wrote the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

None declared.

DATA AVAILABILITY STATEMENT

The data and code are available from the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.25111781 (Humphreys & Mortelliti, 2024).

ORCID

Brigit R. Humphreys https://orcid.org/0009-0001-6335-1356

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SUPPORTING INFORMATION

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

Table S1. Descriptions and interpretations of the behaviors measured in our three behavioral tests.

Figure S1. Four microhabitat types for pilfer stations.

Figure S2. Female southern red-backed voles were more likely to locate caches compared with males of the same species.

Figure S3. When more individuals of pilfering small mammal species were present in the trapping grid, caches were more likely to be pilfered.

Table S2. List of all packages we used in the software R for our analysis along with a description of what we used them for and citations.

Table S3. Top model sets from our likelihood ratio test analysis for deer mice and southern red-backed voles.

Video S1. Compiled examples of pilfering video footage analysed to collect pilferage behaviour data and visually identify individuals from their distinct haircuts. The video includes multiple species of pilferers and is in MP4 format.

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