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Seed predation and dispersal by small mammals in a landscape of fear: effects of personality, predation risk and land-use change

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Scatter-hoarding small mammals act as both seed predators and seed dispersers in forest ecosystems. Their choices regarding consuming or caching seeds must balance the risk of predation with the energy rewards gained from immediate or delayed consumption of seeds. Several factors influence their interaction with seeds, including the individual's personality. Little is known about how personality affects foraging decisions in response to predation risk. This missing information is critical because if foraging decisions differ among individuals in response to perceived risk, then varying combinations of personality types in a population (and varying risks of predation across forest types) may have diverse effects on forest regeneration. Further, land-use change may influence the interplay of personality, risk perception and foraging decisions by altering the distribution of personality types in the landscape and the risk perceived by individuals. To contribute to filling these knowledge gaps, we designed a large-scale field experiment to evaluate how personality, perceived predation risk and land-use change affect the interaction of deer mice *Peromyscus maniculatus* and seeds. Using infrared cameras, we recorded the choices of individuals of known personality at paired experimental sites with high versus low perceived predation risk (n = 2389 observations from 74 individuals). We found that personality influenced multiple foraging decisions, and perceived risk affected how individuals with different personalities responded to those decisions. Specifically, exploration/activity influenced seed choice, boldness affected the number of seeds selected and docility influenced both foraging site selection and whether mice immediately consumed or removed seeds. Since personality only affected foraging microsite selection in unmanaged forests, our results show that land-use change decreased the importance of personality in affecting risk perception. We demonstrate the importance of considering personality on foraging decisions under varying levels of risk, and more generally, underscore the importance of considering individual variation in affecting ecological processes.

Keywords: behavioral syndrome, foraging decisions, individual variation, predation risk, scatter-hoarding, seed selection, silvicultural practices, temperament

Introduction

Ecologists are becoming increasingly aware of the importance of considering individual variation (such as individual variation in behavior) in affecting ecological processes (Bolnick et al. 2011). An example of an area where individual variation is proving to be important, is the key process of animal-mediated seed predation and dispersal (Bolnick et al. 2011, Brehm et al. 2019, Zwolak and Sih 2020). Here, the existence of among-individual variation in certain foraging decisions implies that some individuals may have disproportionate effects on seed dispersal or predation. Consequently, we need to better understand the extent to which individual variation affects and modulates seed predation and dispersal in order to manage this ecological process in a changing world. To contribute to filling this knowledge gap, we here focus on individual variation in scatter-hoarding behavior by small mammals with emphasis on the interplay of land-use change (Brehm et al. 2019) and perceived predation risk (i.e. landscape of fear) (Laundré et al. 2001, Preisser et al. 2005, Gaynor et al. 2019).

Landscapes of fear are defined by Gaynor et al. (2019) as the spatial variation in prey perception of predation risk. Here we are specifically interested in exploring the effects of perceived predation risk on foraging decisions and the role that personality plays in this relationship (Gaynor et al. 2019; Fig. 1). A majority of the existing literature on landscapes of fear focuses on large mammals, invertebrates or birds (Gaynor et al. 2019), and those that focus on small mammals almost exclusively examine giving-up densities (reviewed by Bleicher 2017). Although very few studies address the role of individual variation in perceived predation risk (Eccard et al. 2020, Steinhoff et al. 2020), this is a crucial step towards understanding how the spatial variation in perceived predation risk may influence forest ecosystems via the foraging decisions of scatter-hoarding small mammals.

Factors affecting seed dispersal versus predation

The outcome of the interaction between scatter-hoarding small mammals and seeds plays a key role in forest regeneration (Forget et al. 2005, Vander Wall et al. 2005, Lichti et al.

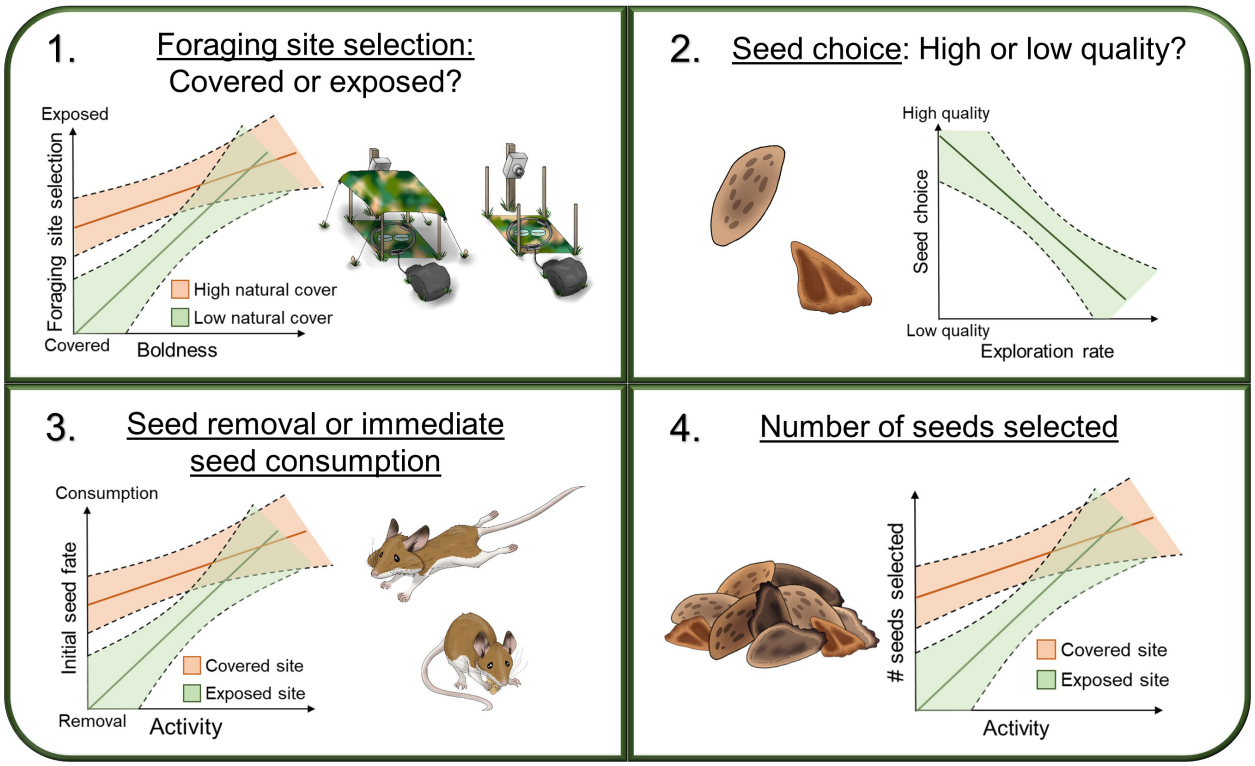

Figure 1. Overview of four major decisions made by small mammals when foraging for seeds and predicted effects of personality, land-use and perceived predation risk. Through a large-scale field experiment conducted in Maine (USA), we assessed how individual personality, perceived predation risk and forest management affected these decisions. Using infrared cameras combined with RFID readers and antennas, we identified individual deer mice *Peromyscus maniculatus* of known personality and monitored their foraging decisions at covered (safe) and exposed (risky) sites in stands treated using different types of forest management. We predicted that: 1) bolder individuals would be more likely to forage at exposed sites, but this relationship would be stronger in areas with less natural ground cover (i.e. mature stands); 2) slower explorers would forage more efficiently and be more likely to choose high-quality pine over lower-quality balsam fir regardless of land-use or perceived predation risk; 3) highly active individuals would immediately consume seeds more often at the site due to increased metabolic needs; and 4) activity rates would correlate positively with the number of seeds initially selected. We predicted that (3–4) would show stronger relationships at exposed sites.

2017, Zwolak 2018), since small mammals often fill both the role of seed predators (i.e. by consuming seeds) and seed dispersers (i.e. when their cached seeds germinate) (Steele et al. 2014, Lichti et al. 2017, Gómez et al. 2019). When a small mammal encounters a seed, it must decide whether to consume it or cache it for later consumption. This decision is often modulated by the perceived risk of predation for the small mammal itself (Orrock et al. 2004). As small mammals have numerous predators, lingering too long while interacting with a seed may increase the likelihood of being detected by a predator. Thus, when interacting with each seed they find, small mammals must balance the risk of predation with the energy rewards gained from the immediate or postponed consumption of the food item (Lima and Dill 1990, Ferrari et al. 2009, McArthur et al. 2014). Decision making in this tradeoff is affected by factors such as seed size and difficulty of handling the seed (Muñoz and Bonal 2008, Wang and Chen 2009, Mortelliti et al. 2019), the seed nutrients/quality and toxin content (Fedriani and Boulay 2006, Ancillotto et al. 2015, Wang and Corlett 2017, Boone and Mortelliti 2019), intra- and inter-specific competition (Halliday and Morris 2013, Roschlau and Scheibler 2016, Serrano-Davies et al. 2017a), the availability of other food resources in their home-range (Ivan and Swihart 2000, Richardson et al. 2013, Boone and Mortelliti 2019) and, importantly, the perceived risk of predation (Brown 1999) and individual variation in behavior (i.e. personality) (Brehm et al. 2019, Feldman et al. 2019, Mazza et al. 2019). While small mammal foraging and perceived predation risk have been studied extensively (Lima and Dill 1990, Kotler et al. 1991, Orrock et al. 2004, Powell and Banks 2004, Apfelbach et al. 2005, Eccard et al. 2008, Ferrari et al. 2009, Fanson 2010, Perea et al. 2011, Ceradini and Chalfoun 2017, Jacob et al. 2017, Carreira et al. 2020, Moll et al. 2020), we are missing a crucial piece of this puzzle – the influence of individual behavior, or personality. Personality is defined as the behavioral variation among individuals of the same species that is consistent over time and across contexts (Sih et al. 2004, Wolf and Weissing 2012, Carter et al. 2013).

Personality and foraging decisions

Quantifying the extent to which personality affects and modulates seed predation and removal (resulting in the potential for dispersal) is critical to manage this ecosystem process in a changing world. Specifically, if foraging decisions (such as the seed preference, quantity of seeds selected or the immediate or delayed consumption of seeds) differ among individuals in response to perceived risk, then varying combinations of personality types in a population (and varying risks of predation across forest types) may scale up to have diverse effects on forest regeneration. While the effects of personality on foraging decisions have been investigated for several species (Bergvall et al. 2011, Dammhahn and Almeling 2012, Kurvers et al. 2012, Mella et al. 2015), the impact of individuality on small mammal foraging decisions is just recently gaining research attention. We found only four studies examining how individual small mammals with varying personalities respond to foraging decisions based on perceived risk (two of which investigate varying levels of risk in a laboratory/enclosure setting (Feldman et al. 2019, Mazza et al. 2019)). In field experiments, Dammhahn and Almeling (2012) examined boldness on risk-sensitive foraging of grey mouse lemurs *Microcebus murinus* under high and low predation risk, and Brehm et al. (2019) demonstrated that personality affected how free-living deer mice *Peromyscus maniculatus* and southern red-backed voles *Myodes gapperi* interacted with and dispersed seeds of varying sizes (a proxy for risky behavior). Further, only a few studies address personality and foraging in the landscape of fear; Steinhoff et al. (2020) examined how personality affected risk-taking and foraging behavior of jumping spiders *Marpissa muscosa*, and Eccard et al. (2020) explored how personality affected the response of common voles *Microtus arvalis* to either a safe or a risky food patch within an enclosure. While the aforementioned studies provide foundational evidence that personality affects the interaction of scatter-hoarders with seeds, three critical knowledge gaps still exist. In particular, it is still unclear: 1) whether personality affects the choice of different seed types, such as high- versus low-quality seeds, and when those seeds are consumed; 2) if and to what extent perceived predation risk mediates the relationship between personality and foraging decisions; and 3) how personality may explain spatial variation in antipredator behavior based on the amount of perceived risk. Filling these knowledge gaps is critical because if personality traits drive contrasting foraging decisions in response to perceived risk, this implies that the composition of personalities in a population may affect the regeneration of forests differently in areas with higher versus lower perceived risk of predation (Chandler et al. 2020 for an example of altered seed removal in response to predator abundance).

Land-use change and seed predation and removal

Furthermore, land-use change and the associated modification of habitat can influence the risk perceived by small mammals (Arthur et al. 2004, Ceradini and Chalfoun 2017, Guiden and Orrock 2017), as well as the distribution of personality types (Miranda et al. 2013, Merrick and Koprowski 2017, Brehm et al. 2019, Gaynor et al. 2019, Mortelliti and Brehm 2020). Consequently, we hypothesize that land-use change, by altering the structure of small mammal habitat, may influence the relationship between risk perception and foraging decisions by individuals with different personalities. In particular, we predict that perceived risk in forests with less understory cover will be greater than perceived risk in dense forest habitat (Kotler et al. 1991, Hinkelman et al. 2012, Loggins et al. 2019), and thus will mediate the observed relationship between personality and the selection of foraging sites (Fig. 1). Specifically, if bolder individuals are more likely to forage at exposed (risky) sites (Dammhahn and Almeling 2012, Schirmer et al. 2019), then we would expect this relationship to be stronger in forests with less natural understory

cover. We anticipate that individuals that are slow explorers are likely more thorough foragers (Montiglio et al. 2018, Mazza et al. 2019, Gharnit et al. 2020) and will choose high-quality seeds, while fast explorers may be less efficient and more likely to choose lower quality seeds (Fig. 1). Finally, since activity rates have been shown to correlate with metabolic needs (Careau et al. 2008, Serrano-Davies et al. 2017b), we expect that active individuals with higher metabolic rates will be more likely to immediately consume seeds at the site rather than remove them (Brehm et al. 2019) and will select more seeds overall than less active individuals. Importantly, we predict that the relationships between activity rates and foraging decisions will be stronger at exposed (risky) foraging sites (Fig. 1), and baseline foraging levels will likely be higher at covered sites, since previous studies have shown that small mammals increase foraging time when the perceived predation risk is low (Orrock et al. 2004, Powell and Banks 2004, Verdolin 2006, Jacob et al. 2017).

We designed a large-scale field experiment focused on evaluating how personality, perceived predation risk and land-use change affect the interaction of small mammals and seeds. Specifically, our objectives were to:

1. Assess how personality affects four key aspects of seed dispersal under varying levels of perceived risk: foraging site selection, seed choice, seed removal versus immediate seed consumption and the number of seeds selected.
2. Examine how land-use change mediates risk perception and foraging decisions of small mammals with varying personalities. Specifically, test for an interaction between personality and the amount of natural cover, and how this affects foraging site selection and seed decisions.

To accomplish our objectives, we designed a controlled and replicated large-scale field experiment in contrasting areas including mature unmanaged forest, and forests subject to intensive silvicultural practices. Here, we captured and marked our target species, deer mice and recorded behavior in standardized tests to determine personality. To examine foraging decisions in response to perceived risk, we provided paired covered and exposed sites where we offered seeds, creating 'safe' and 'risky' sites at each experimental station. Using infrared game cameras, we recorded seed choice and foraging behavior of known individuals at each site, which we paired with each individual's personality data to determine the role of personality in foraging decisions in response to risk (Fig. 1).

Methods

Study area

This study was conducted in the Penobscot Experimental Forest, a 1578-ha forested area located in Penobscot County in south-central Maine, USA (44°51′N, 68°37′W). Trees commonly found in the experimental forest included balsam fir *Abies balsamea*, eastern hemlock *Tsuga canadensis* and red spruce *Picea rubens*, as well as eastern white pine *Pinus strobus*, northern white-cedar *Thuja occidentalis*, red oak *Quercus rubra*, red maple *Acer rubrum*, birches *Betula* spp. and aspen *Populus* spp.

The experimental forest is composed of blocks managed using varying silvicultural treatments. We selected three silvicultural treatment types in which to conduct our experiments: 1) even-aged treatments were characterized by harvesting a majority of the stand at the same time, creating a dense stand of trees mostly within the same-age class and containing a crowded canopy and little understory; 2) two-stage shelterwood treatments retained large trees while the remaining trees were removed, resulting in more vertical structure and varied growth, increased understory patches and multiple-age classes of trees; and 3) reference blocks (i.e. unmanaged mature forest) consisted of large, widely-spaced mature trees and were typically open with abundant coarse woody debris and patchy understory cover (Supporting information). Each treatment type had an independent replicate resulting in six total blocks (Supporting information). Each replicate treatment block used in this study averages 12.84 ha in area (range 8.32–17.49 ha), while the two reference blocks of forest (25 total ha) have remained unmanaged since the late 1800s. The most common small mammal species found in each block included deer mice *Peromyscus maniculatus*, southern red-backed voles *Myodes gapperi*, North American red squirrels *Tamiasciurus hudsonicus* and northern short-tailed shrews *Blarina brevicauda*. For this study, we focused on deer mice due to sample size and their known preferences of certain seed species (Boone and Mortelliti 2019).

Trapping methods

We placed one 90 × 90 m square trapping grid within each of the six blocks, and each grid point was marked with a flag spaced every 10 m. We placed Longworth traps at each flag (total n = 100) for three nights, and traps were bedded with organic cotton and baited with sunflower seeds, oats and dried mealworms. Traps were checked twice a day; in the morning after sunrise and in the evening prior to sunset. Trapping was conducted yearly from June through October in 2016–2019.

Behavioral testing and animal processing

We used three behavioral tests, each designed to measure behaviors representative of an aspect of animal personality (Supporting information). Tests were conducted for each individual at the first capture each month and performed in the same order each time before tagging and processing individuals: 1) the emergence test measures behaviors interpreted as indicators of boldness or risk-taking (Carter et al. 2013, Gracceva et al. 2014); 2) the open-field test measures exploration and activity levels (Walsh and Cummins 1976, Carter et al. 2013); and 3) the handling bag test measures behaviors interpreted as the level of docility of an individual (Martin and Réale 2008, Mella et al. 2015) (Supporting

information). These behavioral tests produced scores that determined where individuals fell on each personality continuum (e.g. an individual score may lay anywhere on the timidness – boldness gradient). More information about these tests is listed in Supporting information. The behaviors were recorded on a digital camera and videos were processed in the laboratory. With the completion of behavioral tests, we recorded the individual's mass using a 100 g-Pesola spring scale and anesthetized the animals using isoflurane. We inserted passive integrated transponders (Biomark PIT tags; MiniHPT8, 134.2 kHz) subcutaneously, and recorded body and tail length measurements while the animal was anesthetized. All animals received a metal ear tag and/or a unique haircut for additional external identification. Individuals were sexed and aged, and reproductive condition recorded.

After adequate time for recovery, we released individuals at their point of capture and reset the trap. Previous work in our study system (Brehm and Mortelliti 2018, Brehm et al. 2020) has showed that personality does not affect the probability of being trapped and that trap confinement does not affect our behavioral measurements, thus suggesting that our sample is unlikely to be biased towards certain personality types and that our methods of sampling are not impacting our behavioral measurements.

Seed experiment

We designed a seed experiment to explore the role that personality plays on seed selection in the presence of risk, conducted from July through September 2018. Five to six experimental stations were placed within each trapping grid each month. We focused on indirect cues of predation risk and manipulated the perceived risk by creating two foraging sites per station; one 'safe' site and one 'risky' site (Fig. 1, Supporting information). A 1 × 1 m tarp supported by a dowel frame was secured above one site, creating a 'safe' location, while the paired 'risky' site had an uncovered dowel frame that left the site exposed from above (Powell and Banks 2004, Dehn et al. 2017, Jacob et al. 2017). Tarp corners were secured with twine and garden staples, and sites were placed 2–3 m apart and equidistant from likely cover or runways. We attached two cups each containing 5 g of one of two seed species to a vinyl floor tile (30.48 cm square) that was centered inside the dowel frame at each site (Supporting information). One seed species, white pine *Pinus strobus*, represented a highly preferred seed for *Peromyscus maniculatus* and the other, balsam fir *Abies balsamea*, represented a seed of low preference (Abbott 1962, Duchesne et al. 2000, Boone and Mortelliti 2019) (Supporting information). With a relatively low handling time, white pine delivers approximately 0.102 kcal/seed, while balsam fir has only 0.046 kcal/seed (Boone and Mortelliti 2019) and unpalatable secondary compounds (resins and terpenes) (Lobo and Millar 2011, Kshatriya et al. 2018). White pine is slightly larger than balsam fir, by approximately 0.01 g (Boone and Mortelliti 2019) (Supporting information). Seeds in each cup were then counted to obtain a starting availability in each seed cup (average starting availabilities: white pine = 110.0 seeds; balsam fir = 253.7 seeds), which was tracked throughout the experiment (see Video processing – seed experiments). These starting availabilities were approximately equal to the average number of seeds found in two cones of each species (white pine: approx. 46–54 seeds per cone (Noland et al. 2006), balsam fir: approx. 134 seeds per cone (Franklin 1974)), and were chosen to allow multiple individuals to visit before seeds were depleted without providing excessive supplemental food.

Using remote infrared cameras (Reconyx XR6 Ultrafire) mounted above the tile with adjustable tree mounts, we recorded seed selection and behavior of visiting individuals (Supporting information). In order to identify individual mice, we employed a system using an antenna and a radio frequency identification (RFID) reader to scan and record the PIT tags of visiting individuals. The antenna (Priority1 RFIDCOIL – 160a, 134.2 kHz operating frequency) was seated approximately 3.8 cm above the tile and connected to the RFID reader (Priority1 RFIDLOG dual animal tag data logger), which was powered by a 6-volt battery and housed in a dry bag. This allowed us to pair the behavior and seed selection recorded in the videos with the individual's personality and information recorded during capture (sex, body condition, etc.).

We placed the experiment stations in each trapping grid after the completion of trapping each month. We left stations out for three to four nights, or until seeds were depleted. We checked and counted seeds daily and removed seed shells to allow for easier tracking of seed availability. Cameras recorded 30 s 1080P HD videos (30 fps) and were set to the shortest delay (approximately 1 s) between triggers. Cameras also took an 8-megapixel picture before each video and once every hour to assist with identifying an animal's position in between videos and to permit zooming in on images of the seed cups.

Video processing – behavioral tests

We processed open-field test videos using ANY-maze software (ver. 5.1), which tracks the individual's movement and speed, and records the time spent in each area of the arena. The software allows observers to record additional behaviors including jumping, grooming and rearing. We processed emergence videos by recording the latency for the individual to approach the end of the tunnel, the time spent in the tunnel opening and the latency to fully emerge from the trap.

Video processing – seed experiments

We collected 2389 observations of deer mice seed selection from 10 831 videos and from 97 experimental sites. A total of 88 individuals with associated personality tests visited the seed experiment stations, with 74 individuals selecting a seed during a visit. Videos from the seed experiment were processed to record seed choice events at each site. From the videos, we recorded data on small mammal species and

individual ID, availability of all seeds at the time of choice, seed species chosen, number of seeds consumed, illumination, rain, and if the seeds were removed or immediately consumed. Consumption results in immediate death of a seed; however, while removal may result in consumption away from the site, it may also result in the caching of a seed. We tracked seed availability using the videos to determine how active seed selection, rather than just use, varied by site (Manly et al. 2004, Lichti et al. 2017, Boone and Mortelliti 2019, Mortelliti et al. 2019). A resource is 'used' if utilized in proportion to its availability and 'selected' if utilized disproportionately to its availability (Manly et al. 2004); therefore, selection reflects the actual preference of an animal whereas use reflects the simple utilization of a resource. Starting with a known number of seeds in each cup, we subtracted the seeds removed or consumed in each video to track seed availability throughout the experiment until seeds were gone or the sites were moved.

Daily seed counts and still pictures captured by the camera before each video assisted with accurate tracking of the availability of seeds. We classified illumination into five night-time values for light levels (new moon, crescent, quarter, gibbous, full moon) and included a sixth day-time value for light from sunrise to sunset. We noted rain events using videos and used a pre-rain value, a during-rain value and a post-rain value to account for changes to seeds after rain and for behavioral changes small mammals may make during rain events.

Additionally, we placed 20 Bushnell trail cameras (Standard 8MP Trophy Cam) for three days after trapping was completed each month to survey for the presence of predators in each grid. We spaced cameras throughout the grid to maximize the likelihood of a predator being captured on camera and aimed cameras toward natural openings or possible paths of travel near the trap locations. We placed cameras at the second and seventh flag on the first line, the fourth and ninth flag on the second line, and alternated as such for each subsequent line. We tagged images by species and compiled predator data in each grid by presence and by total predator species.

Statistical analysis

We ran a repeatability analysis on variables collected from the behavioral tests for each species to determine which variables were repeatable and could be considered personality (Bell et al. 2009, Nakagawa and Schielzeth 2010, Stoffel et al. 2017). Statistically, repeatability refers to the proportion of the total phenotypic (i.e. behavioral) variance that can be attributed to differences among individuals (Wilson 2018). Using the R package lme4 (Bates et al. 2015, <www.r-project.org>), we ran separate mixed effect models for each behavioral variable in which we used individual identity as a random effect and the behavioral variable as the dependent variable. Covariates, including a scaled mass index of body condition (Peig and Green 2009), sex, silvicultural treatment and month, were included as fixed effects in the models; therefore repeatability as calculated here is considered an 'adjusted repeatability' (Nakagawa and Schielzeth 2010). Using the rptR package in R (Stoffel et al. 2017), we ran 1000-iteration bootstrapping and permutation tests to estimate 95% confidence intervals and the significance of the repeatability for each behavior. We did not censor individuals with only one observation from this repeatability analysis, as Martin et al. (2011) has shown censoring individuals to hinder the ability to detect variance in behavioral plasticity.

To assess whether personality and perceived predation risk influenced small mammal foraging choices, we used mixed effects models in the lme4 package in R (<www.r-project.org>). Our dependent variables included: foraging site (i.e. if the visited station was covered versus exposed), seed choice (i.e. the selection of white pine versus balsam fir), seed removal versus consumption and number of seeds selected. We fitted generalized linear mixed effect models for binomial variables (family = binomial, link = logit) and count variables (family = Poisson, link = log). We used individual identification (ID) as a random effect in all models. We also tested grid as a random effect, as well as an additive model using grid and ID. As ID was always 2 ΔAIC below any model including grid as a random effect, we did not include grid in subsequent models.

We followed a forward approach for model selection (Burnham and Anderson 2002). We started with a base model that included seed availability (i.e. proportion of seeds available), as availability changed over time (i.e. as seeds were depleted); this approach allowed us to make inferences on seed selection rather than use (Manly et al. 2004, Richardson et al. 2013, Boone and Mortelliti 2019, Brehm et al. 2019) and allowed us to account for how decision-making may change in response to the depletion of the preferred seed. Our forward selection model testing approach allowed us to account for as much variability as possible before testing our personality variables (Burnham and Anderson 2002, Brehm et al. 2019) (Table 1). To avoid collinearity, all variables were screened for correlation prior to analysis (using $R < 0.7$ as threshold) (Dormann et al. 2013).

Starting with our base model (including seed availability), we tested individual level variables which included sex and body condition index (Table 1). We did not include reproductive status since most individuals were not reproductively active at the time of their visit. If more than one model had a better fit (lower AIC) than the base model and was within 2 ΔAIC of the top model, we ran additional models to test for additive effects (Burnham and Anderson 2002). The top model from this model set became the base model in the next model set. If no variables had a better fit (2 ΔAIC lower) than the base model, this was used in the following stages of analyses.

In the second model set, we tested location and time variables including silvicultural treatment, month of the experiment and the total and species-specific population levels in each grid (Table 1). The top model was again selected and became the base model for the third model set, which included habitat variables. We used a principal component analysis (PCA) on the microhabitat variables measured at

Table 1. Predictor variables used in the analyses of four response variables – i.e. foraging site selection (covered or exposed), seed choice (white pine or balsam fir), seed fate (consumed or removed) and number of seeds selected.

Model set	Fixed variable	Description of variable
0	Base model*	*Seed availability variables were included in all models, regardless of the model set.
	White pine availability	Proportion of white pine seeds left in the seed cup at the time a choice was made
	Balsam fir availability	Proportion of balsam fir seeds left in the seed cup at the time a choice was made
1	Individual variables	
	Sex	Male or female
	CI	Body condition index. Calculated scaled mass index using body length and mass
2	Month and location variables	
	Silvicultural treatment	Forest block type. Mature (reference), even-aged or two-stage shelterwood
	Session	Month of experiment
	Grid population	Population of all small mammal species in each grid each month
	PM population	Population of deer mice *P. maniculatus* in each grid each month
3	Microhabitat variables	
	Site ID	Foraging site- either covered or exposed
	Pine cones	Number of new pine cones in each grid. Used as a proxy for food availability in each grid
	Fir cones	Number of new fir cones in each grid. Used as a proxy for food availability in each grid
	Spruce cones	Number of new spruce cones in each grid. Used as a proxy for food availability in each grid
	Total cones	Number of cones from all tree species in each grid. Used as a proxy for food availability in each grid
	Rain	Used to differentiate before, during and after rain events
	Alt animal	Another small mammal was either present or not present at a station when a choice was being made by a mouse
	Illumination	Levels of ambient light. 0 – new moon, 1 – crescent, 2 – quarter, 3 – gibbous, 4 – full, 5 – daylight
	PC1	Result of a principal component analysis for vegetative microhabitat variables (Supporting information)
	PC2	Result of a principal component analysis for vegetative microhabitat variables (Supporting information)
	PC3	Result of a principal component analysis for vegetative microhabitat variables (Supporting information)
4	Personality variables	
	Latency to emerge	The number of seconds it takes for a test subject to emerge from a trap. Measure of boldness obtained from the emergence test
	Time at end of tunnel	The number of seconds spent looking out from the end of the tunnel. Measure of boldness obtained from the emergence test
	Mean speed	A measure of activity (meters/second) in the open-field test
	Proportion time grooming	The proportion of time spent grooming. A measure of stress in the open-field test
	Rear rate	A measure of activity and exploration (rears/second) in the open-field test
	Proportion time in center	The proportion of time the animal spent moving through the center of the open-field test. Used as a measure of boldness
	Handling time	The number of seconds an animal spent frozen or motionless in a handling bag for one minute. Used as a measure of docility

each site (Supporting information) to simplify many structural habitat components into representative variables, and the PCA components were then used in this third model set (Supporting information). Other variables in this model set included the number of conifer cones (pine, spruce and fir) in each grid, rain variables, illumination and if another individual was present at the same time as the target individual (5.1% of total observations). We did not include predator presence from our camera survey, as we captured mainly larger mammals in images, and may have under-surveyed certain species (i.e. *Mustela* spp. and raptors).

Once a top model was selected using this selection process, we tested personality variables in the models (Table 1). We selected seven personality variables (Supporting information), including: the latency to emerge from an emergence test, time spent at end of the emergence tunnel, the mean speed in an open-field test, proportion of time grooming in an open-field test, proportion of time in the center of an open-field arena, rear rate in the open-field test and the number of seconds of immobility in a handling bag test (handling time) (Brehm et al. 2019). We tested for additive effects between any personality variables from models within 2 ΔAIC of the top model. Additionally, we were interested in testing if the influence of personality on our response variables varied under certain conditions, so we tested interactive effects of personality with other variables including foraging site (i.e. perceived predation risk (Martin and Réale 2008, Luttbeg and Sih 2010, Toscano et al. 2016, Mazza et al. 2019)), seed choice (Bolnick et al. 2003, Toscano et al. 2016, Feldman et al. 2019), seed availability (Dingemanse et al.

2004, Boon et al. 2007) and silvicultural treatment (i.e. habitat use (Boon et al. 2008, Pearish et al. 2013, Brehm et al. 2019)). From these models, we selected the final top models and used model averaging to obtain predicted datasets for model predictions and confidence intervals (Burnham and Anderson 2002).

Ethical note

All trapping and experimental research was approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC A2015_11_02 and A2018-11-02); this research followed procedures designed to ensure the health and safety of all animals and researchers.

Results

From our standardized behavioral tests, we ran 1976 field tests on 671 individual deer mice. The repeatability estimates for all tested behaviors (mean = 0.328, range = 0.189–0.424) were statistically significant (Table 2). Personality traits were included in the top model sets for all four of our foraging dependent variables (i.e. foraging site, seed choice, seed removal versus immediate consumption and number of seeds selected; Table 3). The magnitude of the effect of predictor variables varied, as an example handling time and read rate exerted a relatively strong effect on foraging site and seed choice, whereas session and body condition index exerted a relatively weak effect on the number of seeds selected (as shown by the parameter estimates and their SE, which are reported in Table 2).

Foraging site selection (high versus low perceived predation risk)

The top-ranked model predicting foraging site selection in our mixed effect models included an interaction between silvicultural treatment and the behavioral variable handling time (seconds of inactivity during a handling bag test) (Table 3). We interpreted handling time as a continuous measure of 'docility' where greater handling times correlated with increasing docility (Supporting information). Docile mice were more likely to visit exposed (risky) sites in mature forest stands, while in managed stands (with increased understory cover and tree density), docility had no effect on foraging site selection (Fig. 2). Additional variables in the top-ranked model included seed availability (proportion of white pine and proportion of balsam fir), month, body condition index (BCI) and whether another animal was present at the site (Table 3).

Seed choice (selection of white pine versus balsam fir)

The top-ranked model predicting seed choice in the mixed effect model analysis included the following fixed effects: a three-way interaction between the behavioral variable rear rate, the availability of white pine and foraging site (perceived predation risk) (Table 3). Rear rate affected the probability of choosing white pine at varying availabilities of seeds and varying risk (covered versus exposed sites) (Fig. 3). We interpreted rear rate as a measure of 'activity and exploration' where increasing rates of rearing correlated with increasing activity and exploration (Supporting information). Personality (i.e. the levels of activity and exploration of an individual) was important at intermediate levels of availability; when seeds were reduced to 50% availability, the probability of choosing balsam fir was higher for more exploratory and active individuals. However, regardless of personality, almost all mice chose white pine seeds at high seed availability, while few mice selected white pine at low seed availability. Additional variables in the top-ranked model included seed availability, month, body condition index, total predators in a grid and PC2 (defined as the amount of understory cover, amount of coarse woody debris and diameter of large trees present at the foraging site, Supporting information, Table 3).

Seed removal or immediate seed consumption

The top-ranked model predicting seed removal versus immediate consumption in the mixed effect model analysis included an interaction between the behavioral variable handling time ('docility', Supporting information) and the seed chosen (Table 3). Docile individuals had a higher probability of removing balsam fir seeds and immediately consuming white pine seeds, whereas less docile individuals were more likely to remove white pine seeds and immediately consume

Table 2. Repeatability estimates for behavioral variables collected from standardized behavioral tests for deer mice *Peromyscus maniculatus* from 2016 to 2019. These include an emergence, open-field and handling bag test. The mean number of tests per individual *Peromyscus* was 1.65 ± 1.08 (range: 1–10). Results in bold are significantly repeatable and were calculated using mixed effect models with ID as a random effect. 95% confidence intervals were estimated using parametric bootstrapping. See the Supporting information for a description of the behavioral variables.

Behavioral variable	Mean	Range	RPT	(95% CI)	Observations	Individuals
Latency to emerge	56.20	(0, 225)	**0.419**	**(0.322, 0.527)**	641	394
Time at end of tunnel	7.08	(0, 180)	**0.347**	**(0.241, 0.479)**	578	356
Mean speed	0.09	(0, 0.27)	**0.424**	**(0.340, 0.520)**	891	574
Proportion time grooming	0.13	(0, 0.96)	**0.189**	**(0.101, 0.303)**	889	572
Rear rate	0.20	(0, 0.68)	**0.303**	**(0.212, 0.412)**	891	574
Proportion time in center	0.03	(0, 0.73)	**0.222**	**(0.131, 0.34)**	890	573
Handling time	16.06	(0, 60)	**0.392**	**(0.308, 0.5)**	700	428

Table 3. Mixed effect model results (n = 2389 observations). The top-ranked models from each of the analyses testing our four response variables. Each analysis had only one top model; all other models were above 2 ΔAIC of the top-ranked model. Parameter β estimates and SE are also provided.

Response variable tested	Top-ranked models[1]	AIC	ΔAIC	R^2
Foraging site	Proportion white pine (β = 0.12, SE = 0.18) + Proportion balsam fir (β = 0.22, SE = 0.15) + Handling × Silvicultural treatment (Mature/reference treatment: β = 0.46, SE = 0.22; Two-stage shelterwood: β = 0.05, SE = 0.23) + Extra animal (Extra animal present: β = −0.81, SE = 0.21) + Session (β = 0.21, SE = 0.09) + BCI (β = −0.28, SE = 0.09)	3231.33	0.00	0.21
Seed choice	Proportion balsam fir (β = 3.86, SE = 0.38) + Proportion white pine × Rear rate × Foraging site (Exposed site: β = 1.72, SE = 0.74) + PC2 (β = 0.25, SE = 0.13) + Session (β = −0.36, SE = 0.14) + BCI (β = 0.33, SE = 0.13)	1224.91	0.00	0.71
Seed removal versus consumption	Proportion white pine (β = 0.06, SE = 0.24) + Proportion balsam fir (β = 2.25, SE = 0.22) + Handling × Seed choice (White pine: β = −0.84, SE = 0.14) + Session (β = 0.71, SE = 0.11) + BCI (β = −0.47, SE = 0.11)	2214.98	0.00	0.52
Number of seeds selected	Proportion white pine (β = 0.16, SE = 0.04) + Proportion balsam fir (β = 0.27, SE = 0.03) + Latency to emerge × Seed choice (White pine: β = −0.16, SE = 0.02) + Seed removal (Removed: β = 1.34, SE = 0.02) + Session (β = 0.09, SE = 0.02) + BCI (β = −0.02, SE = 0.02)	13 603.98	0.00	0.51

[1] Proportion white pine = proportion of white pine seeds available; Proportion balsam fir = proportion of balsam fir seeds available; Handling = handling bag test score (personality variable); Silvicultural treatment = forest block type (reference, even-aged, two-stage shelterwood); Extra animal = whether another small mammal was present at the time of choice; Session = month; BCI = body condition index; Rear rate = rate of rearing seen in the OFT (personality variable); Foraging site = covered or exposed site; PC2 = microhabitat variable from PCA analysis (Supporting information); Seed choice = selection of white pine or balsam fir; Latency to emerge = latency to emerge from a trap in the emergence test (personality variable); Seed removal = whether seeds chosen were consumed or removed.

balsam fir seeds (Fig. 4). Additional variables in the top ranked model included seed availability, month and body condition index (Table 3).

Number of seeds selected

The top-ranked model predicting the number of seeds selected in the mixed effect model analysis included an interaction between latency to emerge and the seed species chosen (Table 3). We interpreted latency to emerge as a measure of 'boldness' where mice with shorter latencies to emerge were 'bolder' and mice with longer latencies were more 'timid' (Supporting information). Timid mice took larger quantities of balsam fir seeds and smaller quantities of white pine seeds than bolder mice, while bold mice took seeds from both seed species almost equally. Additional variables in the top ranked model included the consumption or removal of seeds, seed availability, month and body condition index (Table 3).

Discussion

Through a large-scale field experiment, we demonstrated that personality interacts with perceived predation risk to affect multiple aspects of seed dispersal – where an individual decided to forage, which seed they chose, whether the seed was immediately predated or removed, and the number of seeds selected. Specifically, we found that rear rate

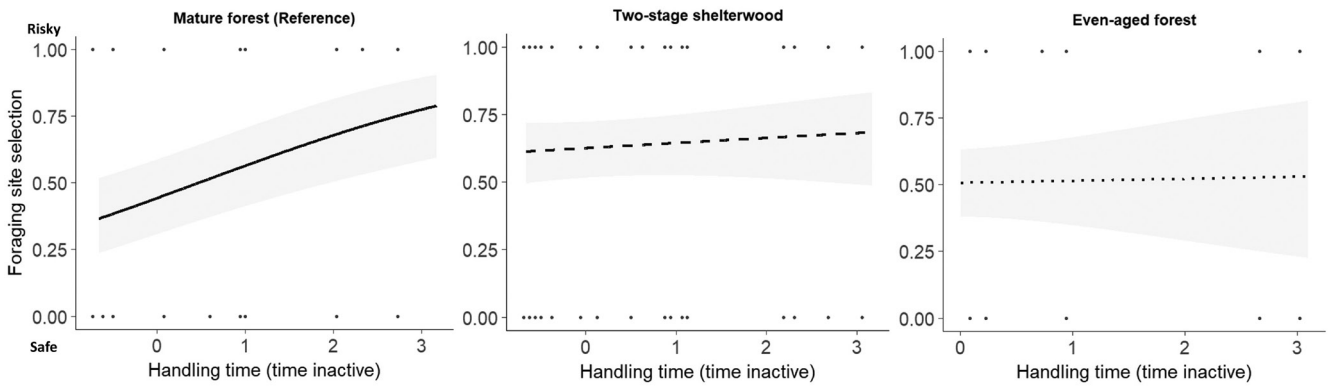

Figure 2. In mature forests only, handling time (interpreted as docility) affects the likelihood that deer mice will forage at riskier sites. More 'docile' individuals (i.e. higher time inactive during the test) were more likely to choose risky sites to forage. However, there is no effect of handling time on foraging site selection in denser and more structured forest, such as the two-stage shelterwood and even-aged stands. Predictions were obtained from the top generalized linear mixed effects model; 95% confidence intervals are shown, and docility is a scaled variable. n = 2389 observations from 74 individuals.

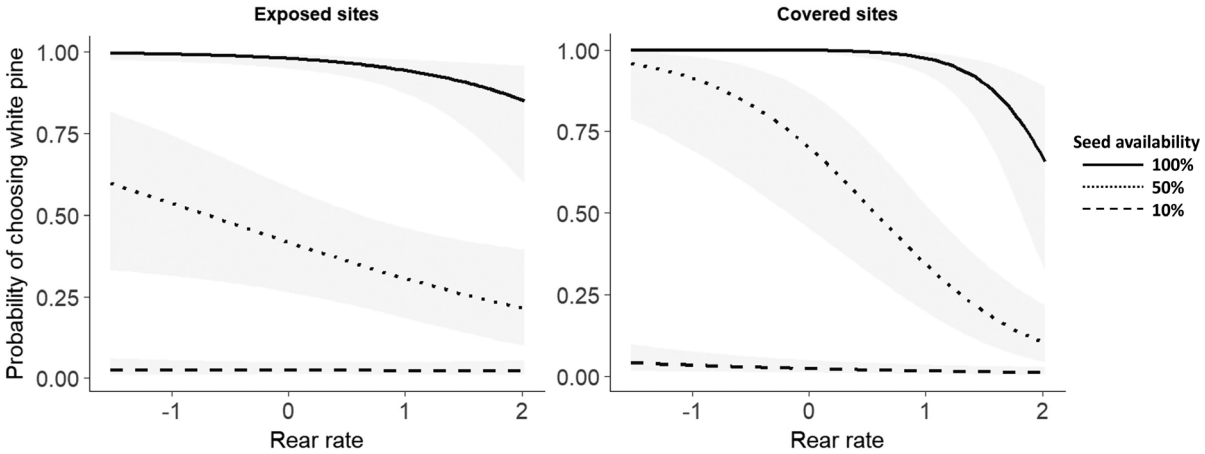

Figure 3. Probability of deer mice choosing the high-quality white pine over balsam fir as a function of the rate of rearing (interpreted as an indicator of exploration/activity), as predicted by mixed effects models. The probability of choosing white pine is higher for individuals with low rates of rearing once seed availability is reduced to intermediate levels (i.e. ~50% for balsam fir and for white pine) and this relationship is amplified at safer (covered) foraging sites. When white pine and balsam fir are highly available (i.e. ~100%), almost all mice choose the high-reward white pine seeds, regardless of their personality. Similarly, when only a few seeds of each species remain (low availability), personality has little effect on the probability of white pine selection, which is low for all mice. Predictions were obtained from the top generalized linear mixed effects model; 95% confidence intervals are shown. n = 2389 observations from 74 individuals.

(interpreted as activity/exploration) influenced the choice of seed species at intermediate levels of availability, that handling time (interpreted as docility) influenced the choice of foraging sites and whether mice consumed or carried seeds away, and that latency to emerge (interpreted as boldness) affected the number of seeds selected. Furthermore, we found that land-use change, in the form of intensive silvicultural practices, influenced seed choice and risk perception; specifically, personality affected the choice of foraging site only in the in the reference forest. This study distinctly demonstrates an interaction between personality and foraging decisions under varying levels of perceived risk, with the added interplay of land-use change.

Personality, predation risk and seed choice

When seed availability was high (e.g. 100%) (Fig. 3), most individuals chose the high-reward white pine seeds regardless of their personality. However, when seed availability was reduced to intermediate levels (e.g. 50%), the most active/exploratory individuals selected for the lower-quality balsam fir seeds, while the least active/exploratory individuals selected

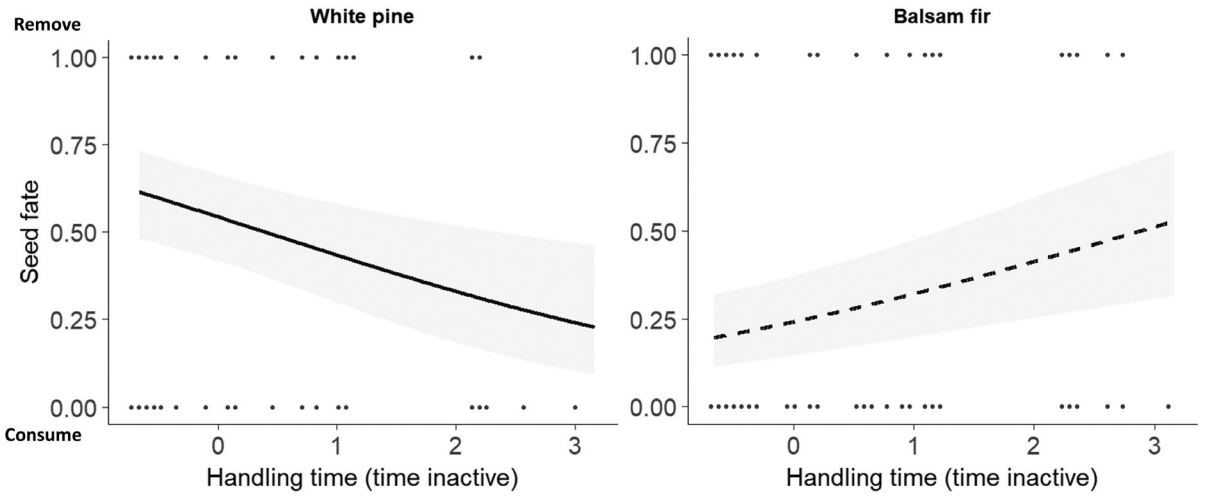

Figure 4. Predictions for the seed removal analysis. Handling time (interpreted as an indicator of boldness) influenced the probability that deer mice either removed or consumed seeds. Mice with higher handling times are more likely to remove balsam fir seeds but consume white pine seeds, while the opposite is true for mice with low handling times. Predictions were obtained from the top generalized linear mixed effects model; 95% confidence intervals are shown.

high-quality white pine seeds. Additionally, the strength of this personality effect changed with foraging sites (i.e. the effect was much stronger in the safer covered sites than in the exposed sites) (Fig. 3). Exploratory and active individuals are known to generally be less neophobic, more apt to use a greater variety of food resources, and have a higher metabolism (Toscano et al. 2016, Merrick and Koprowski 2017); thus, as white pine seed availability decreases, exploratory individuals were likely the first to switch to other food/energy resources such as balsam fir. However, this relationship was less evident at exposed sites. Mice may have been less selective about seeds and more likely to select whatever food item they found, so as to maximize their energy rewards under the perceived increase in risk. White pine is slightly larger than balsam fir; consequently, there were approximately 2–3 times more balsam fir seeds than white pine at any given value of availability. As an example, when availability drops to 50%, the available mass of seeds is the same, but the larger number of balsam fir seeds at this availability means that the balsam fir plate appears fuller. This may explain why the more curious and active individuals switch their choice to the lower quality seeds, since at this point, energy gains per time unit may be higher for balsam fir, as search time is lower in a full plate. Once the availability of both seeds dropped to low levels (e.g. 10%), there was once again no effect of personality or risk at the foraging site. In such circumstances, most mice selected balsam fir regardless of their personality, indicating that the time spent searching for and inspecting remaining white pine seeds was perceived to be a greater risk than the energy rewards obtained by choosing those seeds. Seed shells may have made it harder to find remaining whole seeds at low availability, and any hesitation could cost the life of a mouse. Our results show that the overall change in selection from white pine to balsam fir is initiated by the most curious and active individuals, which start shifting their choice once seed availability decreases (Merrick and Koprowski 2017).

Foraging site selection and seed removal

Personality, risk perception and seed species also affected foraging site and seed removal or immediate consumption; specifically, docility (handling time) influenced whether an animal would choose a covered or exposed site, and whether it would immediately predate or remove a seed by carrying it away in their cheek pouch (Vander Wall and Longland 1999). As docile individuals were more likely to forage in riskier open sites (Fig. 2), they may only have been willing to consume high-quality seeds at the site because of the higher energy reward, while low-quality seeds were removed to be cached or consumed at a safer location (Fig. 4). In contrast, less docile individuals were more likely to consume balsam fir seeds at safe sites (Fig. 2,), but removed white pine seeds (Fig. 4), which increased the chance that a portion of those seeds were cached, rather than immediately consumed. Foraging in exposed areas may mean that docile individuals were at a greater risk of being captured by predators than the individuals foraging in covered areas (Kotler et al. 1991, Longland and Price 1991, Connolly and Orrock 2018), but further research is needed to determine if there is a difference in survival between these personality types.

Notably, the effect of docility on foraging site selection was only observed in the reference blocks (i.e. mature forests) (Fig. 2). There was no effect of personality on foraging sites in the two silvicultural treatment blocks, as more canopy, understory and denser stands of trees likely reduced the perceived risk of predation (Supporting information). Sites in the two-stage shelterwood treatment blocks had high levels of cover and structure (increasing escape routes and cover to stay undetected), thus supporting a higher probability that all mice would forage at both covered and exposed sites (Longland and Price 1991, Perea et al. 2011, Dehn et al. 2017, Loggins et al. 2019). Comparatively, even-aged treatment blocks had much less understory, but a tight canopy and dense stand of trees, which could make maneuvering difficult for aerial predators, such as owls. In these areas, the probability was slightly lower that a mouse would forage at exposed sites than in two-stage shelterwood areas (Fig. 2); still, personality did not affect foraging site in either management area. It should be noted that perceived risk does not necessarily equal actual predation risk. However, this likely did not influence our results, as indirect cues are more influential than direct cues (Merkens et al. 1991, Orrock et al. 2004, Verdolin 2006). Small mammals chose to forage in each treatment block type based on their perceived risk, which again, likely relates to the level of exposure while foraging and dispersing seeds and is thus mainly driven by vegetation cover (Kotler et al. 1991, Dehn et al. 2017).

Seed species, personality and whether the seed was consumed or removed influenced the number of seeds selected (Table 3). Bold individuals removed both seed species at similar rates, while timid individuals selected more balsam fir seeds on average and fewer high-quality white pine seeds than bold mice. As white pine seeds are slightly larger (Supporting information), bolder individuals may have consumed more of these higher energy foods, as several studies suggest that bolder individuals have higher metabolisms (Careau et al. 2008, Toscano et al. 2016, Zwolak 2018).

Ecological implications of our results

Our results have major implications for research related to landscapes of fear. We establish that personality plays an important role in how individuals perceive and respond to risk while foraging. Docile individuals were more likely to forage in riskier open sites, while less docile individuals foraged in safer covered sites (Fig. 2), indicating that personality may be key in determining an individual's perceived landscape of fear. This is crucial to consider in future studies, as accounting for behavioral variation among individuals may help to better understand not only species interactions in the landscape of fear, but also the effects of 'individual landscapes of fear.'

Our results also suggest a relationship exists between personality and seed dispersal effectiveness (Schupp et al. 2010).

We acknowledge that further research is needed to tease out these complex relationships, as our study followed seed removal but not final seed fate. We have shown, however, that when food is readily available, some seed species may be more likely to be removed, or consumed, than others. For example, most mice chose white pine at high availability. Docile mice were more likely to consume white pine at the site while less docile individuals removed white pine to another location. While some of these seeds removed by less docile mice may have been cached, it is likely that many of them were consumed, considering that some long-term survival studies on acorns (*Quercus* sp.) estimate survival of removed seeds is less than 10% (Steele et al. 2004, Cilles et al. 2016, Guiden and Orrock 2017, Lichti et al. 2018, Bartel and Orrock 2020). Comparatively, docile mice, though initially consuming numerous seeds at the site, may be important for seed dispersal, as the few seeds they do remove may be more likely to be cached, rather than consumed at another location. Once overall availability decreased, active and exploratory personality traits began to mediate the choice of seed species. More active and exploratory individuals increased selection of balsam fir seeds (Toscano et al. 2016, Merrick and Koprowski 2017), relieving some of the immediate predation pressure on white pine. Individual mice may be unequal in their contributions to the overall seed dispersal in a system, and personality traits likely influence this variation (Zwolak and Sih 2020). Indeed, these results underscore the importance of considering the effects of individual variation on ecological processes (Bolnick et al. 2011).

Conservation implications of our results

The effects of personality on foraging site selection were seen in mature forests, but to a much lesser degree in the managed areas, indicating that the effects of personality can be mediated by different environmental contexts of anthropogenic origin (Wolf and Weissing 2012). Specifically, docile mice were more likely to visit exposed sites in mature, relatively open forests, but personality had no effect where silvicultural treatments created denser vegetation. While this relationship warrants further study, we speculate that competition for the covered foraging sites was high in this forest characterized by open understory. Docile mice were either displaced from safer, covered areas by less docile individuals, or were forced to forage in exposed sites for access to more food resources, despite the increased risk, due to energetic constraints and high competition (Gaynor et al. 2019, Mazza et al. 2019) (Carreira et al. 2020 for related evidence of competition and predation risk). As vegetative cover was more readily available throughout even-aged and two-stage shelterwood stands, competition for safe foraging sites was lower and individuals of varying docility foraged at both the covered and exposed sites.

Recall that landscapes of fear are the spatial variation in prey perception of predation risk. The spatial variation in the utilization of 'safe' microsites that we observed is spatial variation in antipredator behavior. This indicates that forest management can alter the landscape of fear, and that personality was vital in perceiving and responding to these landscapes of fear. Specifically, our results suggest that land-use change can modify the structure of habitats and, consequently, alter the risk perceived by small mammals (Arthur et al. 2004, Ceradini and Chalfoun 2017, Guiden and Orrock 2017). Therefore, the landscape of fear may be a crucial mechanism driving personality differences in seed dispersal and foraging decisions. Further, land-use change can potentially alter the actual risk of predation; possibly acting as a driver of differences in personality composition observed between populations (Brehm et al. 2019).

Not only does land-use impact the landscape of fear, evidence suggests that land-use can shape the distribution of personalities in a population (Miranda et al. 2013, Merrick and Koprowski 2017, Brehm et al. 2019), which may have the potential to affect the plant recruitment success in a management area. For example, modification of landscapes may alter the selection pressures for certain personality types, resulting in a less diverse population which is not resilient to further change (Wolf and Weissing 2012, Smith and Blumstein 2013, Merrick and Koprowski 2017), as well as a loss of a beneficial personality types that perform specific functions, such as seed dispersal to optimal microsites or over long distances. Brehm et al. (2019) concluded that active mice were more likely to consume seeds, and even-aged forests had higher proportions of active mice, which could result in less recruitment for trees in even-aged stands. Our results indicate that differing personalities make different foraging choices that could potentially regulate the recruitment of certain tree species and influence the composition of the stand (i.e. boldness influenced the number of seeds removed, docility influenced immediate consumption or removal of each seed species, and activity influenced the seed species chosen). Further, high-quality seeds tend to be consumed immediately, while less perishable seeds or those with higher tannin content are more likely to be cached (Wang and Chen 2008, Cilles et al. 2016, Lichti et al. 2018). This is important to understand as white pine is a valuable timber species, while balsam fir is often a lower-value tree (Livingston 2016, Maine Forest Service 2018, Costanza et al. 2019), and illuminating the impacts of varying personalities on these two timber resources can help managers predict the potential impacts of small mammals on tree recruitment. In Maine, white pine trees within the region of our study usually mast every 1–3 years while balsam fir masting is more variable (i.e. every 2–5 years (unpubl., Frank 1990, Wendel and Smith 1990)). We provided seeds in quantities approximately equal to what would be found in two cones of each species, which is comparable to the availability of seeds in a low production year. We speculate that in mast years, where many more seeds are available, the effects of small mammal personalities may occur at an even greater scale.

Conclusions

Through our large-scale field experiment we demonstrated novel interactions among varying personality types, perceived

predation risk and foraging decisions that depend on the availability of seeds and the degree of forest alteration by humans. We established that personality plays an important role in the foraging decisions of individuals in the landscape of fear, and that land-use modified the perceived risk and response of individuals. Our study demonstrates that to promote ecological functions such as seed dispersal, researchers and managers should consider the key role played by individual personality and how the interaction between land-use and perceived predation risk may be involved. Future studies coupling personality measurements and survival rates of cached seeds should expand our knowledge on the extent to which our predictive ability increases by incorporating individual variation.

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

Author contributions

Sara R. Boone: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Software (equal); Writing – original draft (equal); Writing – review and editing (equal). **Allison M. Brehm**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Software (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Alessio Mortelliti**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal).

Data availability statement

Data and scripts are available at Dryad Digital Repository (<https://doi.org/10.5061/dryad.8kprr4xnm>).

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