Small mammal tree seed selection in mixed forests of the Eastern United States

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ABSTRACT

Small mammals play a critical role in forest ecosystems as both seed predators and dispersers; they have been shown to affect tree species composition within forests and may significantly reduce recruitment rates of certain tree species, many of which are commercially valuable. Thus, understanding small mammal seed preference is essential for both animal ecologists and foresters. Although extensive research on small mammal seed choice has been conducted both in North America and Europe, limited knowledge is available on: (1) the effects of silvicultural practices on seed choice; (2) seed *selection* – as most studies focus on seed *use*; and (3) certain understudied seed-small mammals interactions – e.g. few studies have concurrently examined both coniferous and deciduous seeds from North American mixed forests, and the seed selection of some small mammal species is not well-known (e.g. *Napaeozapus*). To contribute to filling these gaps, our study focused on the following objectives: (1) to quantify seed selection of seven forest seed species by small mammal species within the mixed forests of the eastern US; (2) to evaluate the influence of silvicultural practices on seed choice; (3) to explore relationships between seed choice and environmental factors such as weather and microhabitat.

We conducted a series of cafeteria-style experiments in the field and in the laboratory; 2459 seed choice events, mostly by four small mammal species (*Peromyscus maniculatus*, *Myodes gapperi*, *Napaeozapus insignis*, and *Tamiasciurus hudsonicus*) were analyzed using multinomial mixed-effect models, allowing us to determine the probability of selection for each seed species. We identified a consistently high-preference seed (*Pinus strobus*) and one low-preference seed (*Betula papyrifera*). All other species (*Acer rubrum*, *Picea rubens*, *Tsuga canadensis*, *Quercus rubra*, and to some extent, *Abies balsamea*) had intermediate preference levels. Indeed, selection varied also by small mammal species (e.g. *Acer rubrum* was the top choice for *Myodes gapperi* in the field).

Further, we found that the silvicultural practices examined here (even-aged management, two-stage shelterwood, and unmanaged) did not directly influence seed choice, whereas illumination (night- and day-time light levels), rain, and temperature did, and the magnitude of the effects varied by small mammal species. Our results show that in mixed forests, small mammals may impact seeds of economically valuable trees (e.g. *Pinus strobus* and *Acer rubrum*), whereas they may ignore seeds of less valuable trees (e.g. *Betula papyrifera* and *Abies balsamea*). We recommend that forest managers consider small mammal communities when developing forest regeneration plans.

1. Introduction

Small mammals play a crucial role in forest ecosystems as both seed predators and dispersers (Forget et al., 2005; Vander Wall, 2010) and have been shown to affect tree species composition within forests (Côté et al., 2003; Lobo et al., 2009; Peters et al., 2004). For example, squirrels and mice may harvest up to 95% of preferred seed species available in their territory such as white pine (*Pinus* spp.) and white spruce (*Picea glauca*) (Abbott and Quink, 1970; Peters et al., 2004; Radvanyi, 1970; Samano and Tomback, 2003), and thus may significantly reduce recruitment rates of specific tree species (Peters et al., 2003; Siepielski and Benkman, 2008). As many of these species are commercially valuable, seed choice by small mammals is of interest to forest managers as well as ecologists.

Extensive research on small mammal seed choice has been conducted, including research on seeds of North American conifers (Abbott, 1962; Fletcher et al., 2010; Lobo et al., 2009; Martell, 1979), as well as deciduous species (Cramer, 2014; Ostfeld et al., 1997), particularly those with acorns (Greenberg and Zarnoch, 2018; Ivan and Swihart, 2000; Perea et al., 2011b). However, at least three knowledge

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gaps still exist, and these may affect management outcomes. In particular:

(1) *Limited knowledge is available on how silvicultural practices* (Perea et al., 2011a) *may affect seed choice by small mammals* (Kellner et al., 2014; Simard and Fryxell, 2003; Zwolak et al., 2010). Previous studies have shown that silvicultural practices may influence small mammal survival, abundance, and community diversity (Dracup et al., 2015; Kaminski et al., 2007; Le Blanc et al., 2010; Raybuck et al., 2012; Zwolak, 2009). Variation in small mammal abundance resulting from silvicultural practices may affect rates of seed predation/dispersal, but may also affect seed choice itself, as this choice is known to depend on perceived intra- and inter-specific competition (Lichti et al., 2017; Moore et al., 2007; Xiao et al., 2013; Zeng et al., 2019). Further, modifying forest structure through silvicultural practices (e.g. density of shrubs, canopy cover, or other habitat features) may change the perceived risk of predation for small mammals, which may consequently impact seed choice (Jacob et al., 2017; Kotler et al., 1991; Orrock et al., 2004; Sunyer et al., 2013). Understanding how forest management could impact seed predation and dispersal, and therefore tree species composition, is important for the forestry industry, which, as an example, had an economic impact of over $8 billion in 2016 in the state of Maine, USA (Anderson and Crandall, 2016).

(2) *Many previous studies have focused on seed* ***use****, but few have been able to infer active seed* ***selection****.* Seed *use* (i.e. a resource is used by an animal proportionally to its availability) does not imply selection while the seed selection process implies the *preference* of one resource over others, regardless of its availability (Ivan and Swihart, 2000; Manly et al., 2004; Richardson et al., 2013). These preferred resources are typically selected because they maximize fitness (Cooper and Millspaugh, 1999; Johnson, 1980; Lichti et al., 2017). To determine seed selection, the availability of each seed species must be known each time a choice is made (Manly et al., 2004; Richardson et al., 2013). Before the development of high quality infrared cameras, performing true seed selection studies was complicated and, therefore, studies inferring seed selection are uncommon in the literature (Ivan and Swihart, 2000; Jansen and den Ouden, 2009; Perea et al., 2011a). Quantifying selection allows researchers to identify the resources that are most important to an animal and provides valuable information on which tree species are the most likely to be impacted by small mammals.

(3) *The taxonomic scope of previous studies is limited, both in terms of seeds and small mammal species.* Most studies typically reflect local species composition, resulting in certain combinations of small mammals and seeds that are commonly studied and others that have not been explored yet. As an example, a majority of North American seed choice studies have focused on seeds from either coniferous or deciduous species (Abbott and Hart, 1960; Cramer, 2014; Greenberg and Zarnoch, 2018; Lobo et al., 2009) whereas studies including a variety of both are far less common (Ivan and Swihart, 2000; Ostfeld et al., 1997; Plucinski and Hunter, 2001; Simard and Fryxell, 2003). Mixed forests, which are widespread in temperate regions of both North America and Eurasia, generally have both coniferous and deciduous trees, resulting in extreme variation in seed types (such as acorns, small conifer seeds, samaras, and catkins). Conducting experiments with seeds from coniferous and deciduous trees would provide valuable information that would allow us to rank relative preferences of North American small mammals directly.

Further, while the selection of certain seed species, such as eastern white pine (*Pinus strobus*), has been investigated before (Abbott, 1962; Duchesne et al., 2000; Martell, 1979), very little is known for other species such as paper birch (*Betula papyrifera*) (Simard and Fryxell, 2003) or eastern hemlock (*Tsuga canadensis*) (Abbott, 1962), but these seeds are likely used to some extent. For example, Siberian flying squirrels heavily rely on birch catkins during the winter (Selonen and Mäkeläinen, 2017). Likewise, while seed selection has been extensively studied for certain small mammal species, such as for eastern gray squirrels (*Sciurus carolinensis*) (Clay, 2006; Greenberg and Zarnoch, 2018; Steele et al., 1993; Sundaram et al., 2015), and for mice (*Peromyscus* spp.) and southern red-backed voles (*Myodes gapperi*) (Abbott, 1962; Lobo and Millar, 2011; Martell, 1979; Simard and Fryxell, 2003), we still have limited knowledge on other species such as the woodland jumping mouse (*Napaeozapus insignis*) (Vickery, 1979).

To help fill in the aforementioned knowledge gaps we focused on the following objectives:

(Obj. 1) *Quantify seed selection of seven forest seed species by small mammal species within mixed forests.* This will help us to determine potential influences of a small mammal community on tree species composition, as well as determine if specific small mammal species have a greater impact on certain forest trees.

(Obj. 2) *Evaluate the influence of silvicultural practices on seed choice*. We aim to better understand how forestry practices may affect the selection of seeds (influencing forest species composition), which may promote or hinder the outcome of a given management practice. For example, if a specific silvicultural practice increases the predation of a highly valuable species, then alternative management actions may need to be considered.

(Obj. 3) *Explore relationships between seed choice and environmental covariates*. To understand how environmental context may interplay with the choices made by small mammals (Orrock et al., 2004; Perea et al., 2011a, 2011b; Roschlau and Scheibler, 2016), we explored the effects of microhabitat and weather on seed selection.

We conducted our study in six sites maintained using three management types (two-stage shelterwood, even-aged and unmanaged forest) within a mixed forest ecosystem in Maine, USA. We used highly sensitive infrared cameras that allowed us to identify visiting small mammals and record seed choices for each individual. By measuring the availability of all seeds at each point in time, we aimed to infer selection rather than just seed use.

2. Methods

2.1. Study area

This study was conducted in the Penobscot Experimental Forest (PEF), located between Bradley and Eddington, Maine, USA (44°51′N, 68°37′W). The 1578-hectare area is the only experimental forest located in an Acadian forest system, which is characterized as a transitional zone of mixed forest dominated by conifers that represents the transition between the southern deciduous forests of the United States and the northern boreal forests of Canada. The PEF is composed of trees typically found in this mixed forest type; balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and eastern hemlock are the most common, along with eastern white pine, red maple (*Acer rubrum*), birch (*Betula* spp.), aspen (*Populus* spp.), and northern white cedar (*Thuja occidentalis*). The humid, cool climate averages a mean temperature of 6.7 °C with January being the coldest month and July the warmest (−8.1 to 20.3 °C). Annual precipitation averages 1.02 m with 58 percent falling during the winter season (United States Forest Service, 2018). The PEF is sectioned into compartments, each managed using one of several silvicultural treatments. We selected three management types, each of which had a replicate, in which to conduct our seed preference experiments. These included two reference sites (unmanaged, mature forest areas that have not been harvested since the late 1800 s), two even-aged treatment sites, and two treatment sites of two-stage shelterwood (Supp. Table 1), totaling six sites (Fig. 1). Within these sites, composition of tree species somewhat varies – the unmanaged sites are the most variable, although eastern hemlock, pines, and red maple are most abundant; the even-aged sites are characteristically less varied, mainly dominated by balsam fir and pines; and the two-stage shelterwood stands are well-mixed, although eastern

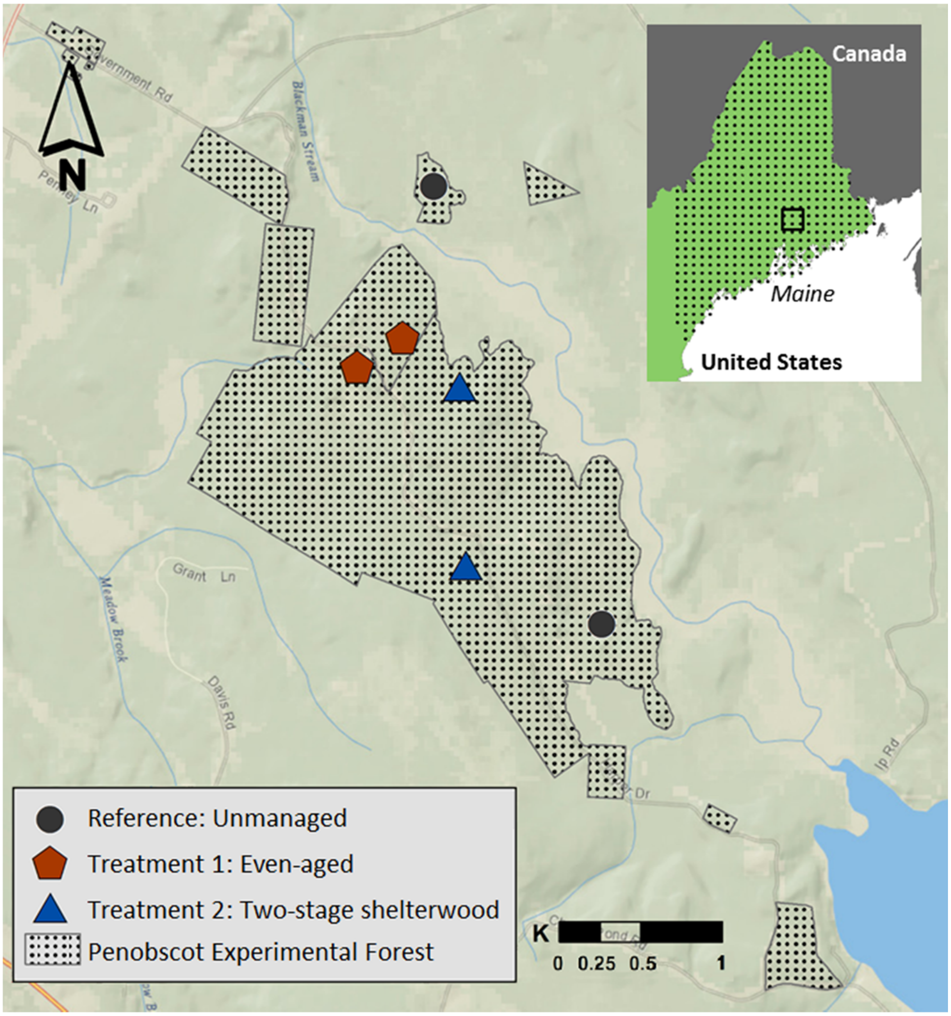

Fig. 1. Treatment sites used within the Penobscot Experimental Forest for seed preference experiments. Even-aged = characterized by a single age class of trees that regenerate from seeds and saplings in the absence of overstory canopy trees; Two-stage shelterwood = characterized by removing the overstory in two stages at different times resulting in canopy retention and at least two age classes; Reference (unmanaged, mature) = characterized when large, individual overstory trees die naturally and are replaced by understory trees.

hemlock, balsam fir, and red spruce are most abundant. The most abundant small mammal species present within all sites include deer mice (*Peromyscus maniculatus*), southern red-backed voles, northern short-tailed shrews (*Blarina brevicauda*), North American red squirrels (*Tamiasciurus hudsonicus*), *Sorex* spp., woodland jumping mice, northern flying squirrels (*Glaucomys sabrinus*), and eastern chipmunks (*Tamias striatus*).

2.2. Experimental design

In order to compare seed selection from the variety of seeds naturally available in mixed forests, we selected seven seed species based on the most common and representative trees in the PEF – balsam fir, eastern hemlock, red spruce, eastern white pine, paper birch, red maple, and northern red oak (*Quercus rubra*) (Supp. Fig. 1) – and purchased them from regional commercial providers. Although some studies hypothesize that small seeds such as eastern hemlock or birch are too small for rodent consumption (Schnurr et al., 2002), other studies have shown they provide an important resource for small mammals (Abbott, 1962; Abbott and Hart, 1960; Selonen and Mäkeläinen, 2017), and thus were included in our study. Seeds were offered in equal quantities (i.e., the total mass of seeds in each plate was the same) to allow us to monitor animals responses to a standardized seed availability (Berl et al., 2017; Lobo et al., 2009; Mortelliti et al., 2019; Simard and Fryxell, 2003). As red oak acorns weighed substantially more than the other seed species (Table 1), we opted to run two trials. The first trial used 2 g of the six smallest seeds (balsam fir, eastern hemlock, red spruce, white pine, paper birch, and red maple) and excluded red oak. The second trial used 5 g of balsam fir, white pine, and red maple (the largest of the small seeds, with removed wings), paper birch (the smallest seed, for comparison), and included red oak. Conifer seeds were presented with the seed coats intact (with removed wings) but seeds were removed from cones to replicate how terrestrial small mammals would naturally retrieve these seeds on the ground.

Seeds were offered in a cafeteria-style experiment (Krebs, 1999) during July and August of 2017 (Supp. Fig. 2). Small seed cups (6.5 cm in diameter) were attached with Velcro© to the floor of a wire cage (31 cm cube) to increase the stability of the cup. Cages were used to discourage visits from non-target species such as birds and larger mammals and were secured in place using three to four small ground stakes. Two square openings (approximately 7 cm wide) on either side of the cage allowed small mammals to enter and increased access to all seed cups (Supp. Fig. 2). To decrease bias, seeds were placed in different cup positions within each cage, reducing the likelihood that one seed would be continually more accessible (closer to a door) or continually placed next to other more/less preferred seeds. Six seed cages were deployed within a treatment and placed at least 50 m (up to 150 m) apart to reduce the possibility of an individual visiting more than one

Table 1

Results of testing for nutritional content (calories, protein, carbohydrates, fat, and moisture) for six tree seed species (balsam fir, red maple, paper birch, red spruce, eastern white pine, and eastern hemlock). *Red oak results are reported from Sundaram et al. (2015). kcal/seed/second (i.e. the estimate of the number of calories ingested by an animal per second) was calculated by dividing kcal/seed by handling time.

Common name	Scientific name	Trial	Handling time (seconds)	Mass (g)	Calories			Protein (%)	Carbohydrates (%)	Fat (%)	Moisture (%)
					kcal/g	kcal/seed	kcal/seed/second				
Balsam fir	*Abies balsamea*	1 & 2	5.936	0.0074	6.16	0.046	0.0077	18.1	23.0	50.2	5.75
Red maple	*Acer rubrum*	1 & 2	7.010	0.0156	4.21	0.066	0.0094	36.6	36.7	14.2	7.93
Paper birch	*Betula papyrifera*	1 & 2	3.046	0.0004	4.70	0.002	0.0007	12.8	56.3	21.5	6.41
Red spruce	*Picea rubens*	1	3.564	0.0031	5.83	0.018	0.0051	27.4	18.8	44.2	4.71
Eastern white pine	*Pinus strobus*	1 & 2	4.331	0.0164	6.22	0.102	0.0236	34.1	4.9	51.7	5.05
Eastern hemlock	*Tsuga canadensis*	1	4.012	0.0037	6.47	0.024	0.0060	27.1	10.4	55.3	3.87
Northern red oak*	*Quercus rubra*	2	10.827	2.3928	5.578	13.347	1.2328	6.05	65.12**	20.13	17.35

** Tannins were reported in a separate column and were not included in the carbohydrate measurement for northern red oak (Sundaram et al., 2015). Tannins were not measured for the other species, and thus any tannins or secondary compounds are included in the carbohydrate value.

seed cage. Cages were left for three nights and were checked and cleaned of empty seed shells daily. Seeds were not replenished within the three-day period to test whether least preferred seeds were selected as a last choice or completely ignored. After the third night, cages were moved to another treatment. New cage sites were selected in each treatment for the second trial, except in the reference grids due to the small size of the compartment areas. In total, 60 sites were deployed over two trials within six compartments and three management types.

Seed selection and availability was monitored with infrared game cameras (Reconyx XR6 Ultrafire), which were mounted to trees above the seed cages using adjustable tree mounts (Supp. Fig. 2). Cameras were positioned between 0.75 and 1 m directly over the cage to balance clarity of the video and ideal triggering of the camera. 1080P HD videos (at 30 fps) recorded for 30 s (the maximum length the cameras allowed), and an 8-megapixel picture was taken prior to the start of the video to allow for zooming in on seed cup images. The cameras were set to the shortest delay between videos (approx. 1 s), thus the image captured before the video assisted with identifying the animal's position and behavior in between videos.

2.3. Laboratory experiments

All sampling protocols were reviewed and approved by the Institutional Animal Care and Use Committee at the University of Maine (protocol number A2015-11-02). We complemented our field experiment with cafeteria experiments conducted in the laboratory to assess whether our field results are comparable to those from a controlled environment. The experiment was conducted on deer mice and red-backed voles, which are the most abundant species in our study system (Brehm and Mortelliti, 2018). Ten deer mice and ten red-backed voles (five males and five females) were captured and transferred into the laboratory setting where they were housed in a plastic laboratory cage (43.25 × 30.50 × 15.25 cm) lined with aspen bedding. A ball of organic cotton was provided for nesting material and water was available through a drip water bottle. A plexiglass tray was cut to fit within the bottom of the cage, to which seven plastic cups were attached in a semicircle to ensure as equal access to each cup as possible (Supp. Fig. 3). All seven seed species from the field experiment were added to the tray in quantities of 2 g, except for the larger red oak, of which two acorns were provided. Although the acorns were much heavier, we provided two acorns to guarantee replication. Seed placement within the cups was randomized for each individual, and trays were placed in the cages for two nights (preliminary trials showed that most seeds were eaten after the second night and thus a third night was not necessary). Seed shells were removed once daily, as in the field experiment, and seeds were counted after each check. Individuals were then fed sunflower seeds and oats for 3–7 additional nights before being released. Animal body mass and sex were recorded at the start of each individual trial and used as predictor covariates.

2.4. Microhabitat

Available habitat and forest structure are key factors affecting seed choice. Canopy cover may provide cover from predators and reduce the impact of moonlight, while lower understory and coarse woody debris may provide a refuge for hiding and escaping from predators (Fauteux et al., 2012; Jacob et al., 2017; Longland and Price, 1991; Roschlau and Scheibler, 2016). We collected microhabitat data within 5 m of each seed cage site, including grass and herbaceous cover (%); shrub and sapling cover (%) at less than 1 m, 1–2 m, and 2–4 m; moss cover (%); coarse woody debris (total m) 10–20 cm in diameter and greater than 20 cm in diameter; canopy cover (%); and the largest tree's DBH (cm).

2.5. Seed traits

Average seed mass was calculated from the number of seeds within a 1-gram sample, except for red oak, for which seed mass was sampled and averaged from 50 acorns. Nutritional traits for a sample of our seeds were obtained from a laboratory analysis (performed by Eurofins Food Integrity and Innovation) (Table 1) including protein, carbohydrate, lipid, and moisture measurements. Acorn traits were obtained from the literature (Sundaram et al., 2015) (Table 1).

2.6. Video processing

Field videos were processed to record seed choice events. Data collected from the videos included the small mammal species, time of day, the seed chosen, the number of seeds consumed, the availability of each seed prior to a choice, illumination, temperature, rain, and the handling time for seeds consumed in the seed cage. Availability of each seed species at the time of seed selection was calculated by subtracting the number of seeds consumed from the availability of that seed before a choice was made. Despite the small size of some seeds, this subtraction method, along with the number of seeds known to be consumed in videos, allowed us to maintain relatively accurate availability estimates. Daily counts of seeds provided a supplementary check to ensure seed availabilities were accurate. Further, cameras were programmed to take a still photo every hour and before each video triggered, which allowed us to track and adjust seed availability if needed. Rain was recorded to determine if selection changed once the seeds became wet and was noted using the videos. Temperature was also recorded using the videos, as the cameras reported temperature in the photo image. Illumination included values for night-time light levels (i.e. phases of the moon recorded by the Reconyx cameras: new, crescent, quarter, gibbous, and full), as well as a value for "daylight". Average handling time for each species of seed was collected from field videos with a stopwatch (measured as the total time elapsed from when an animal first picked up a seed to when it finished consuming the seed). As the videos did not allow us to monitor the fate of seeds removed from the seed cage, we did not determine the handling time for dispersed seeds. The handling time of a consumed seed, which generally accounts for search time, shelling, and consumption, is important to consider as an animal must balance the time spent foraging and handling a seed with the time the animal must be vigilant to avoid predation (Nordell and Valone, 2013; Treves, 2000). Thus, a seed with a high handling time may pose a higher risk of predation and be selected less often. Laboratory videos were processed similarly to field videos to collect data on seed choice events, however, given the constant environment in the lab, temperature, rain, and illumination were not recorded.

2.7. Data analysis of seed choice

We fitted multinomial mixed effect models to our seed choice data, which are commonly used for behavior and food selection (Koster and McElreath, 2017; Manly et al., 2004; Mortelliti et al., 2019; Richardson et al., 2013). The choice of seed made by a visiting individual is the categorical response variable in the models (e.g. *P. strobus*). We used "site" as a random effect to account for the potential dependence between the choices made at the same site, as one individual may have visited that site multiple times (Brehm et al., 2019). Models were fit using the R packages 'rethinking' and 'Rstan' (version 3.5.0) (R Core Team, 2018). Following Koster & McElreath (2017) and McElreath (2015), we provided weakly informative priors for the fixed effect parameters and variance–covariance matrices. The models used 1000 warm-up iterations, as well as three chains each containing 2000 iterations. Traceplots were used to help assess the convergence of the models and ensure suitable mixing, as well as to check the n_eff (n of effective samples) and Rhat (Gelman-Rubin convergence diagnostic).

We first analyzed seed choice including all small mammal species, which included deer mice, red-backed voles, woodland jumping mice, North American red squirrels, eastern chipmunks, northern short-tailed shews, northern flying squirrels, and *Sorex* species. We also analyzed red squirrels, deer mice, red-backed voles, and woodland jumping mice separately to tease out variation in seed preference between species, as these four small mammals were the most abundant visitors to the cages. The availabilities of each seed species were used as fixed effects in each model and were calculated as the proportion of seeds available during a choice (i.e. relative to the 100% available at the first-choice event). We then individually added trial, microhabitat variables, illumination, rain, and temperature as additional fixed effects. Using the Widely Applicable Information Criterion (WAIC) to compare models, inference was made using models within two delta WAIC (dWAIC) of the top model. As multinomial models are difficult to interpret and the coefficients may be misleading (Koster and McElreath, 2017), we inferred selection based on the predicted probability of selection with 89 percentile intervals to quantify uncertainty (see McElreath, 2015 for a discussion on 89 vs 95 percentile intervals).

2.8. Data analysis – Laboratory seed choice

Seed choice within the laboratory experiment was analyzed similarly to the field data. We fitted multinomial mixed effect models to our seed choice data and used "individual" as the random effect (instead of "site") to account for the dependence between the choices made by each individual deer mouse or red-backed vole. Fixed effects included seed availability, sex, and mass.

2.9. Data analysis – Seed traits

Our analyses focused on 7 different seed species, which is a relatively small sample for making inferences on traits affecting choice. Consequently, we elected to use the trait data available (Table 1) in a qualitative way that would enable us to generate hypotheses for future studies.

2.10. Seed fate – Seed predated vs removed

Our video quality made it possible for us to identify whether a seed was immediately eaten or was removed from the cage after it was chosen. While we could not determine in this experiment if the seed was cached for consumption at a later time or consumed just outside of the camera's view, we can still determine if immediate predation was more likely for certain seeds than delayed consumption. We analyzed these data using mixed effect models by fitting a binary logistic response variable (seed was eaten within the seed cage or was removed from seed cage) with the 'glmer' function in Program R. Site was used as a random effect and data were analyzed for each species separately. We only fitted the null model and used the sign of the intercept to interpret results.

3. Results

Over the course of the field experiment, we collected 3686 videos, from which we obtained 2459 choice events: 949 choice events for deer mice, 308 events for red-backed voles, 310 events for North American red squirrels, and 600 events for woodland jumping mice. We also had 292 visits from eastern chipmunks, northern flying squirrels, northern short-tailed shrews, and *Sorex* spp., but visit occasions were too low to analyze those species individually. We collected 8142 laboratory videos, of which 574 were deer mice choice events, and 913 were red-backed vole choice events.

3.1. Seed preference – All small mammal species

Top-ranking models for all combined small mammal species included trial and illumination in addition to the availability of each seed (imposed covariate, see methods for details) (Table 2). Model predictions show that white pine seeds were consistently the most selected

Table 2
Results for the multinomial mixed-effects models with seed choice as categorical response variable. Model ranking according to ΔWAIC (delta Widely Applicable Information Criterion); only models < 2 ΔWAIC are shown. Availability = availability of each type of seeds at any given point in time during the experiment; trial = trial 1 had six seeds (balsam fir, eastern hemlock, red maple, red spruce, white pine, and paper birch), trial 2 had five seeds (balsam fir, eastern red maple, red oak, white pine, and paper birch); temp = temperature in degrees Celsius; illumination = light levels: phases of the moon and daytime (0 – new moon, 1 – crescent, 2 – quarter, 3 – gibbous, 4 – full, 5 – daylight); weight = individual weights of lab-tested animals.

Model	ΔWAIC	Cumulative Akaike weights
Field Experiment		
All species		
Availability + trial + illumination	0.000	0.980
Tamiasciurus hudsonicus		
Availability + trial + rain	0.000	0.333
Availability + trial + temp	0.496	0.260
Availability + trial	0.580	0.249
Peromyscus maniculatus		
Availability + trial + rain	0.000	0.791
Myodes gapperi		
Availability + trial + rain	0.000	0.620
Napaeozapus insignis		
Availability + trial + illumination	0.000	0.868
Laboratory Experiment		
Peromyscus maniculatus		
Availability + weight	0.000	0.961
Myodes gapperi		
Availability + weight	0.000	0.954

seed: their probability of selection was remarkably higher than other seeds in both trials (Fig. 2) (see Section 2 for detailed methods). The probability of selection of red maple and balsam fir was low in trial 1 (similar to other seeds) however it increased for both species in trial 2 (marked increase for red maple). Illumination influenced selection of some seeds: as light level increased, white pine selection increased while red maple selection decreased, whereas the effect of light was negligible on the probability of selection for the other seed species (Supp. Fig. 4).

To evaluate whether the selection probabilities changed with varying availabilities of seeds (e.g. if the probability of selection of white pine was different when the availability of all seeds was lower) we also calculated the probabilities of selection for a scenario in which only 50% of the amount of each seed was available. Thus, when the seed availability was adjusted to 50 percent, we observed an increase in the selection probability of species such as red maple, balsam fir, paper birch, and red oak (Supp. Fig. 5).

3.2. *Seed preference – Deer mice*

The top-ranking model for deer mice included trial and rain as fixed effects, in addition to the availability of each seed (Table 2). White pine had the highest probability of selection among all seeds, however, the probability of selecting balsam fir and red maple increased remarkably in trial 2 (Fig. 3). When seed availability was adjusted to 50 percent, the probability of selecting white pine dropped and was comparable to the probability of selection for red maple and balsam fir (Supp. Fig. 6). The overall effect size of rain was small; the only noticeable differences were a slight increase in the selection probability of balsam fir with rain, and a slight decrease in the selection of white pine (Supp. Fig. 7).

3.3. *Seed preference – Southern red-backed voles*

The top-ranking model for red-backed voles included trial and rain as fixed effects, in addition to the availability of each seed (Table 2). Red maple had the highest probability of selection among all seeds for both trial 1 and trial 2 (Fig. 3). The selection probability for balsam fir, eastern hemlock, and red spruce was consistently low, whereas the selection probability for red oak and white pine was only slightly higher in trial 2. When seed availability was adjusted to 50 percent, the selection probabilities for all seeds were relatively unaffected (Supp. Fig. 6). The overall effect size of rain was small; the only variation was a small increase in paper birch selection with rain (Supp. Fig. 7).

3.4. *Seed preference – Red squirrel*

Top-ranking models for red squirrels included trial, temperature, and rain as fixed effects, in addition to the availability of each seed (Table 2). The most preferred seed by red squirrels was white pine, whereas all other seeds ranked similarly low (Fig. 3). When seed availability was adjusted to 50 percent, the probability of selection of white pine, although dropping by half, still held the highest selection probability, and was followed closely by red oak, balsam fir, red maple, and paper birch (Supp. Fig. 6). Rain had a small effect size on selection, apart from red spruce, which marginally increased with rain (Supp.

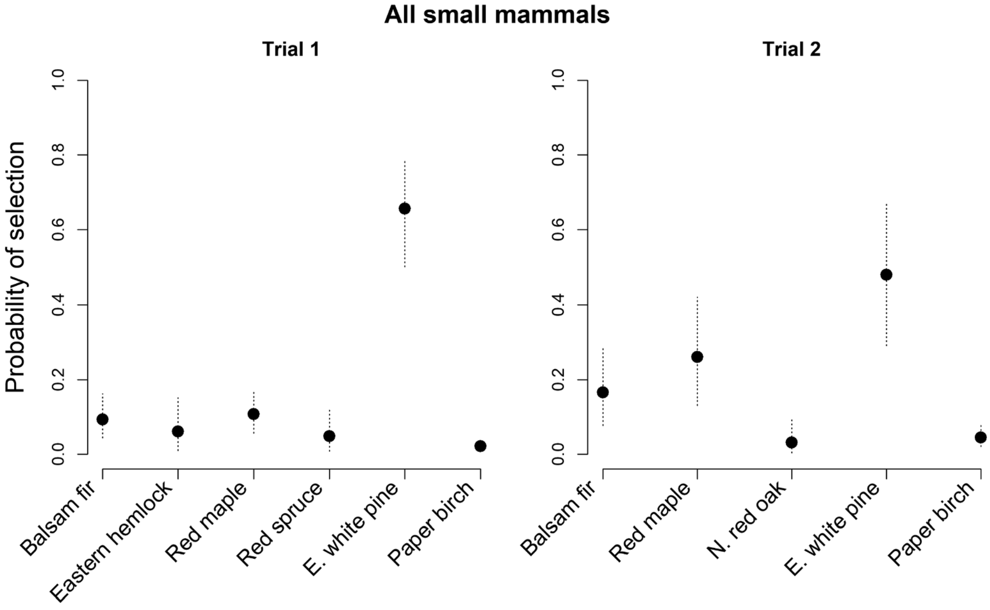

Fig. 2. Relative probability of selection for seven tree seed species by all small mammals during two trials of experiments. Trial 1 offered balsam fir (A. balsamea), eastern hemlock (T. canadensis), red maple (A. rubrum), red spruce (P. rubens), white pine (P. strobus), and paper birch (B. papyrifera). Trial 2 offered balsam fir, red maple, red oak (Q. rubra), white pine, and paper birch. Dashed lines are the 89% percentile intervals (calculated from the posterior samples of the top model).

Fig. 7). Similarly, probability of selection for all seeds remained relatively constant as temperature increased, apart from white pine, which showed a slight decrease as temperature increased (Supp. Fig. 8).

3.5. Seed preference – Woodland jumping mouse

The top-ranking model for woodland jumping mouse included trial and illumination as fixed effects, in addition to the availability of each seed (Table 2). White pine had the highest probability of selection for Trial 1, while all other seed species had similar low probabilities of selection (although red maple was slightly higher than the rest) (Fig. 3). However, for Trial 2, the probability of selection of white pine and red maple was almost equal, followed closely by balsam fir. Similar patterns emerged when seed availability was adjusted to 50 percent (Supp. Fig. 6). No visits by jumping mice occurred during the day, thus only moon-phase illumination was considered. Jumping mice exhibited a pattern of seed selection influenced by moonlight; specifically, the probability of white pine selection decreased as the moon approached full, contrasting balsam fir, eastern hemlock, red spruce, and paper birch for which selection increased (Supp. Fig. 9). Selection for red maple was highest in between new and full moon.

3.6. Laboratory seed preference

Results for deer mice in the laboratory cafeteria experiments partly mirrored results obtained in the field. The most preferred seed for deer mice was white pine (similar to the field), whereas the least preferred was the balsam fir (which in the second field trial had a slightly higher

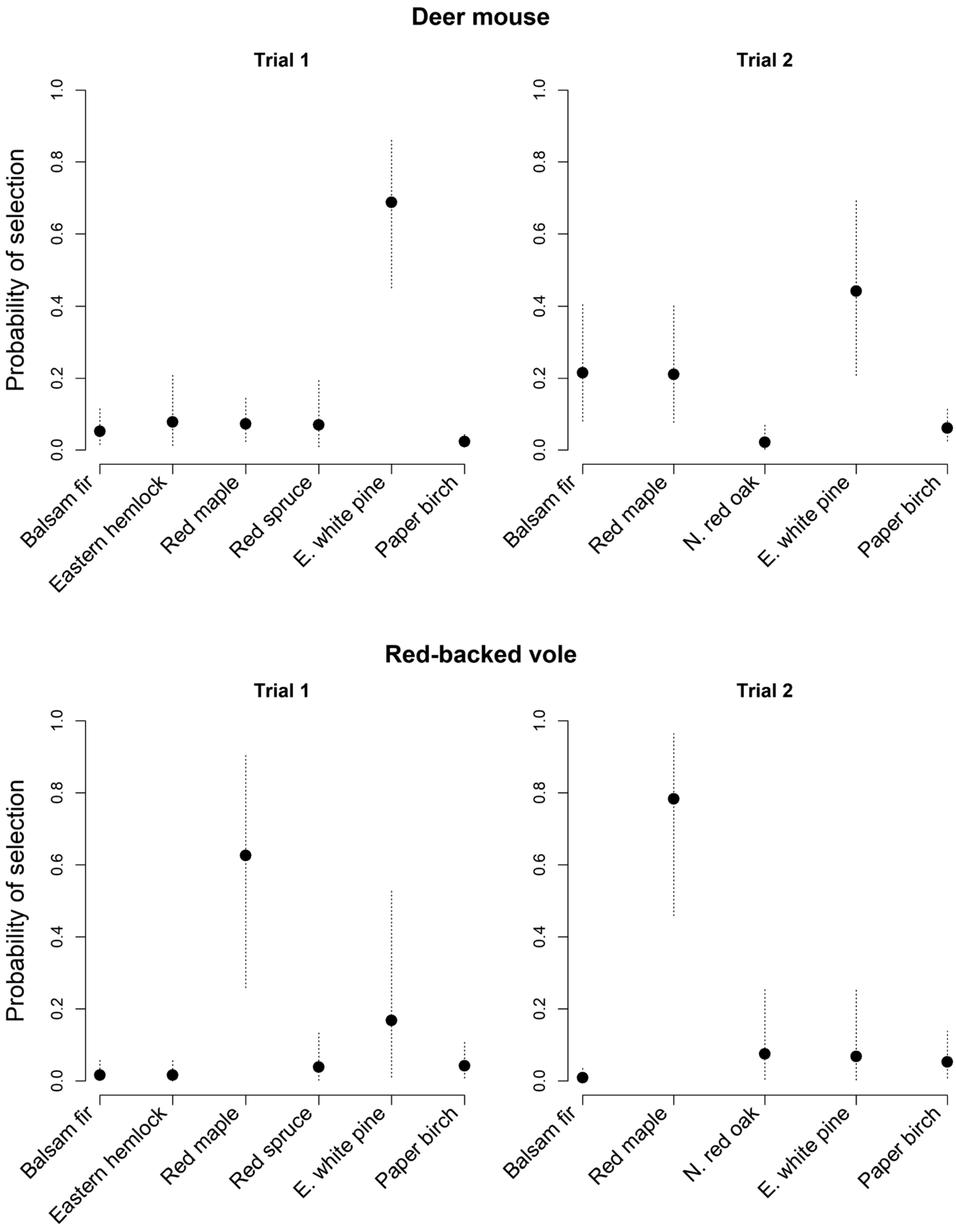

Fig. 3. Relative probability of selection for seven tree seed species by four small mammal species during two trials of experiments. Trial 1 offered balsam fir (A. balsamea), eastern hemlock (T. canadensis), red maple (A. rubrum), red spruce (P. rubens), white pine (P. strobus), and paper birch (B. papyrifera). Trial 2 offered balsam fir, red maple, red oak (Q. rubra), white pine, and paper birch. Dashed lines are the 89% percentile intervals (calculated from the posterior samples of the top model).

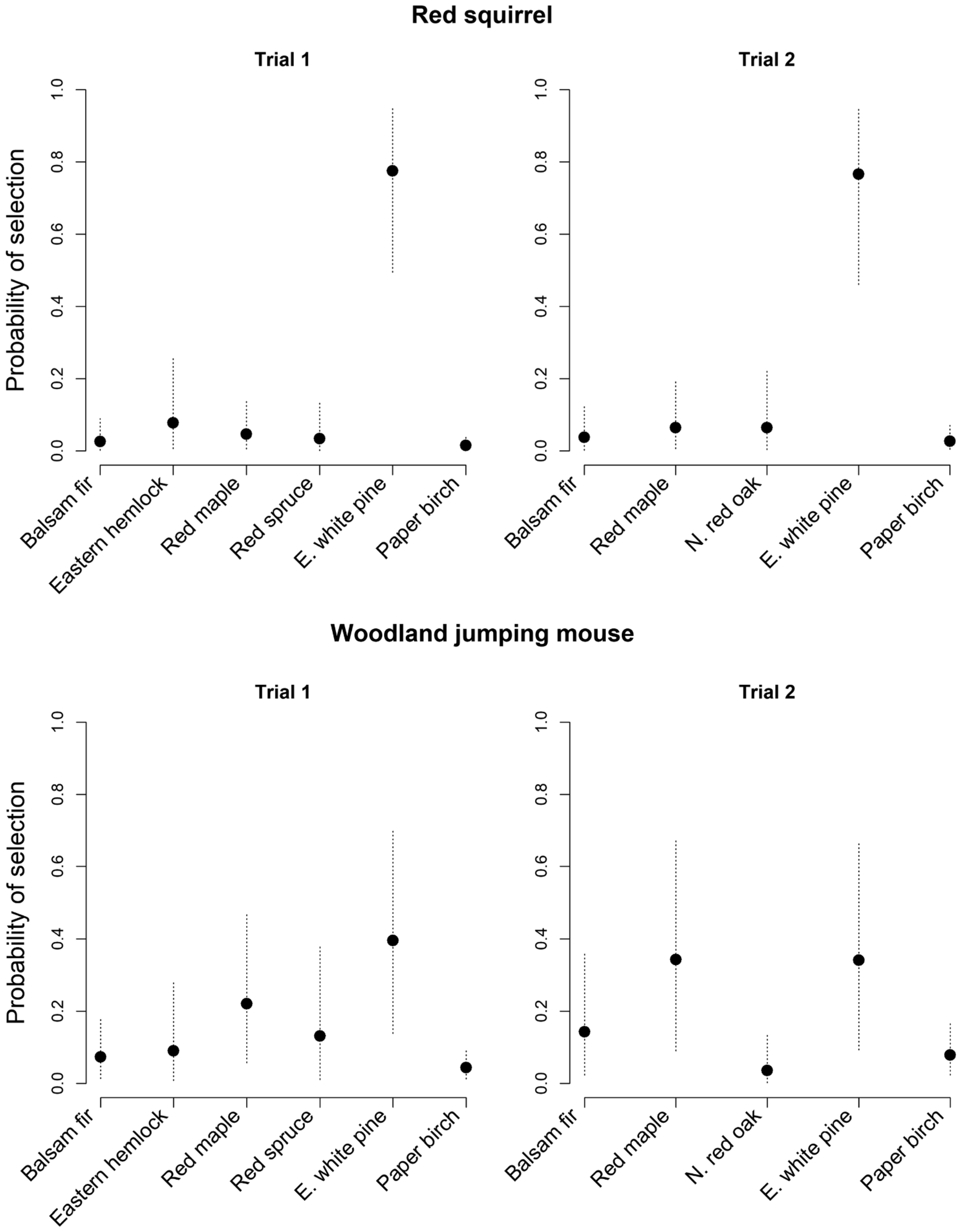

Fig. 3. (*continued*)

probability of selection). All other seeds had similar (relatively low) selection probabilities (Fig. 4). Results for red-backed voles were quite different from field results: white pine had the highest probability of selection, followed closely by eastern hemlock, red spruce, and red oak. Surprisingly and in contrast to field results, red maple had a lower selection probability, followed by paper birch, and balsam fir (Fig. 4). Individual body weight was included as a predictor in the top-ranking models for both species (Table 2), however the effect size of this variable was relatively small.

3.7. Seed fate – Seed predation vs seed removal

Using logistic regression, we found the probability of immediate predation (all small mammal species combined) was significantly higher than the probability of seed removal for all seed species (white pine: $\beta = -3.2$, $p < 0.01$, balsam fir $\beta = -4.6$, $p < 0.01$, eastern hemlock $\beta = -2.9$, $p < 0.01$, red maple = $\beta = -5.1$, $p < 0.01$, red spruce = $\beta = -9.3$, $p < 0.05$). The probability of removal of red oak was significantly lower than the probability of predation ($\beta = -1.05$, $p < 0.01$), however, 41.67% of the total acorns were removed during the course of the experiment. We could not fit mixed effects models to the paper birch data because all 112 observations included predation.

4. Discussion

Through our field and laboratory experiments we were able to identify a consistently high-preference seed (white pine) and one low-preference seed (paper birch). All other species (red maple, red spruce, eastern hemlock, red oak and, to some extent, balsam fir) had intermediate levels of preference. Selection also varied by small mammal species – notably, red maple was the top choice for red-backed voles in the field. Further, through our analyses, we found that the management practices here examined (even aged management, two-stage shelterwood, and unmanaged) did not directly influence seed choice, whereas illumination, rain, and temperature sometimes did, although the magnitude of the effects varied by small mammal species.

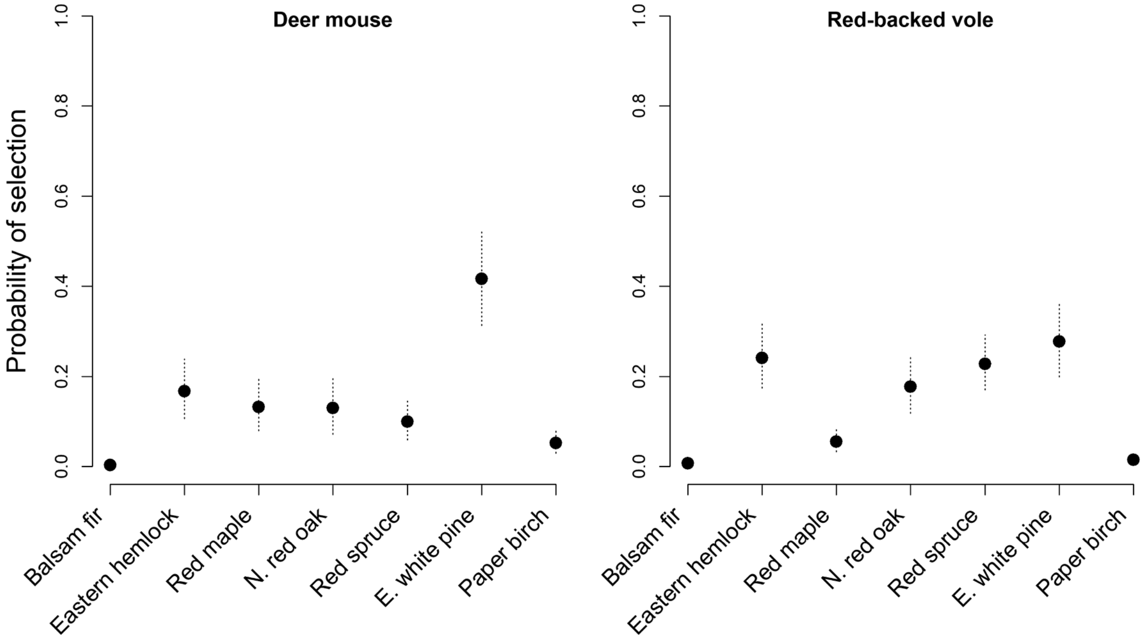

Fig. 4. Relative probability of selection of seven tree seed species by deer mice (*P. maniculatus*) and red-backed voles (*M. gapperi*) in a laboratory experiment. Predictions were made from the top-ranked model which included weight calculated from the average mass of individuals from each species tested. The average mass of deer mice was 17.5 g and the average mass of red-backed voles was 18.5 g.

4.1. Treatment

We did not find any direct effect of treatment on seed choice. This does not imply, however, that seed predation does not vary by treatment. For example, both deer mice and jumping mice visited seed cages at higher rates (not considering population abundances) than other small mammal species in the unmanaged and two-stage shelterwood sites, which generally had a greater mix of tree species. Conversely, in the less varied even-aged stands, red squirrels and northern flying squirrels made up the greatest number of visits, while mice and voles visited at relatively similar lower rates. Additionally, the total number of seeds consumed varies by treatment, as well as some proportions of each seed species eaten (e.g. eastern hemlock was consumed in lower proportions in the mature stands than in the managed stands) (Supp. Table 3). While we found no differences in the preferences of each small mammal species between treatments, the differences in small mammal populations resulting from varying management practices could change the selection pressure on certain seed species, as forest management practices can alter the abundance and density of small mammals (Gasperini et al., 2016). This complex relationship between the type of forest management, small mammal populations, and seed choice will be the object of future work.

4.2. Seed choice – Eastern white pine

Through our field cafeteria experiments, we found that white pine had the highest selection probability for the whole small mammal community (Fig. 2) and in all the single-species analyses, except for red-backed voles (Fig. 3). These results are in line with existing knowledge indicating white pine seeds are highly utilized and consumed in large quantities (Abbott, 1962; Abbott and Quink, 1970; Duchesne et al., 2000; Plucinski and Hunter, 2001), and that their abundance may affect small mammal population dynamics (Ogawa et al., 2017). White pine was also among the most preferred seed in our laboratory experiments. Specifically, it was the top choice for deer mice and in the top group for red-backed voles, which is consistent with previous laboratory experiments (Abbott, 1962; Martell, 1979). White pine had the second highest caloric value per seed and very high protein and fat content, making it a highly profitable seed for its size (Table 1).

Our results show that the probability of white pine selection decreased as the seed availability decreased (small mammal community-level analyses), and for both deer mice and woodland jumping mice, (Figs. 2 and 3; Supp. Fig. 5 and 6). These results show that despite preferring white pine, individuals will choose other seeds as the white pine seed cup empties. The high preference for this seed, and the fact that almost two-thirds of seeds were immediately predated rather than removed, may suggest that small mammal communities could potentially hinder white pine recruitment, particularly in years with a low seed crop. Consequently, this has important implications for forest management, as white pine is a common and valuable species, especially for sawtimber (Costanza et al., 2019; Maine Forest Service, 2018; Northeast Timber Exchange, 2019).

4.3. Seed choice – Red maple

As red maple seeds were high in protein, relatively high in calories, and relatively low in fat, we would expect them to be an intermediate choice, which was consistent with our results. Despite intermediate selection by most small mammals in our study, selection of red maple by red-backed voles was very high, even over white pine in the field experiment. Schnurr et al. (2002) found a positive correlation between the removal of red maple seeds and the density of red-backed voles, which is in line with our findings. However, it appears that despite being a highly selected seed, red maple seed abundance does not affect vole density (Elias et al., 2006; McCracken et al., 1999; Ogawa et al., 2017).

Red maple seeds often had the second highest selection probability for deer mice and for woodland jumping mice (Fig. 3). In particular, selection of red maple by jumping mice was comparable to white pine, especially during Trial 2 when red spruce and eastern hemlock were absent. We are not aware of any previous studies exploring red maple seed choice by jumping mice and only a few studies for *Peromyscus*; Cramer (2014) found deer mice prefer red maple over sugar maple seeds, and at a population scale, McCracken et al. (1999) reported seasonal correlations of red maple seed crops with white-footed mice populations. We could find no research examining selection or consumption of red maple by squirrels and, based on our findings, it appears as if these are not a highly used resource.

Surprisingly, we found red-backed voles changed their selection preferences in laboratory experiments (red maple selection dropped, and white pine selection was highest), while selection preferences of deer mice remained relatively consistent (Fig. 4). Reasons for this selection-shift could include an absence of competition for food resources (Ostfeld et al., 1997; Schnurr et al., 2012) or that certain seeds were already depleted by the time voles arrived. However, we note that voles still chose red maple when they were the first arrival at a cage, despite the high availability of other seeds. The most likely explanation is that the laboratory environment may have altered the perceived risk, as individuals were close to their nests, thus affecting the vole's decision-making process (Lichti et al., 2017). These differences in preference demonstrate the value of testing experiments in both a field and a controlled laboratory setting. Dual-testing allowed us to confirm a majority of seed preferences, including the high preference for white pine, but allowed us to identify more complex relationships that may have been missed in a dynamic natural environment.

The observed high preference for red maple by red-backed voles could influence the regeneration success of the tree, especially during peaks in vole populations. Considering red maple seed fall occurs in the spring, whereas most of the other tree species in our experiment drop seeds in autumn or winter, selection of red maple may vary seasonally (i.e. higher selection probability overall in the spring), although this may be somewhat offset by the availability of alternative, non-seed foods. Red maple is a frequently harvested species (Irland et al., 2001; Northeast Timber Exchange, 2019; NYSDEC, 2018; Ward et al., 2013), so management practices that foster the expansion of red-backed vole populations could impact the success of red maple in a stand.

4.4. *Seed choice – Balsam fir*

Our results show that balsam fir seeds are used as a resource (Supp. Table 2) but its probability of selection is low, especially when other seeds are available. However, we found that as the availability of preferred seeds decrease, the selection of balsam fir increases for both squirrels and deer mice (Fig. 3; Supp. Fig. 6). This was especially apparent in trial 2, when red spruce and eastern hemlock were absent. Interestingly, balsam fir had relatively high caloric and fat content per gram, making them relatively nutritious seeds for their size. Yet, the seeds also contain secondary compounds (such as phenols or sticky resin) and volatile components (terpenes) that act as unpalatable deterrents to small mammals (Kshatriya et al., 2018; Langley, 2017; Lobo and Millar, 2011; Smith, 1970), and likely reduce the probability of selection. Likewise, we observed in our trials that seed shells removed from the balsam fir cup had a strong odor compared to the other seeds (personal observation). Abbott (1962) found deer mice and red-backed voles rejected balsam fir seeds, occasionally choosing to ignore it even when no other food was available. This is consistent with our findings, as balsam fir consistently had the lowest selection probability for both voles and deer mice in the laboratory experiment, and was generally only consumed on the second night or when almost all other seeds were depleted.

Our results demonstrate balsam fir is used as a food resource, but is a lower preference seed that is often selected secondarily (Abbott, 1962; Abbott and Hart, 1960; Duchesne et al., 2000). As such, economic resources provided by balsam fir are unlikely to be affected by small mammal communities. The value of balsam fir can vary (Maine Forest Service, 2018; NYSDEC, 2018), but the lower quality of the wood and shorter lifespan make it less desirable for timber. It is used for pulpwood in some regions and has some non-timber value as well (e.g. Christmas wreaths and trees) (Fuller, 2015).

4.5. *Seed choice – Red oak*

Selection of red oak was higher in the laboratory experiment than the field experiment, presumably because the seeds were closer to the nest in the artificial environment, therefore animals did not have to carry these large seeds far when caching (Muñoz and Bonal, 2008; Perea et al., 2011b). Surprisingly, selection was lower than expected in our field experiment, especially for mice. Many studies illustrate the importance of red oak acorns as a resource for *Peromyscus* species (Greenberg and Zarnoch, 2018; McCracken et al., 1999; Plucinski and Hunter, 2001; Schnurr et al., 2012, 2002) and squirrels (Clay, 2006; Greenberg and Zarnoch, 2018; Lichti et al., 2017; Steele et al., 2004, 1993; Xiao et al., 2010). Red oak had the highest caloric value per seed (Table 1), however, selection of acorns is likely affected by other factors such as the size of the acorn, thickness of the shell (handling time), and the high concentration of tannins (Ancillotto et al., 2015; Kirkpatrick and Pekins, 2002; Vander Wall, 2010; Wang and Chen, 2009), all of which make red oak a riskier and less palatable choice. While red oak selection was not as high as expected for red squirrels in our trials, it did increase as availability decreased (Fig. 3; Supp. Fig. 6); likely for squirrels, the size, shell hardness, and tannin content was less of a hindrance than for the smaller rodents, and the nutritional value made it a more profitable choice than the small seeds (paper birch, red spruce, and eastern hemlock) for the larger seed predator.

As the overall selection probability of red oak was intermediate, acorns may experience increased predation pressure during years when alternative seed crops are low, impacting red oak regeneration success. Red oak is frequently harvested and is one of the most valuable tree species in the northeast United States (Irland et al., 2001; Maine Forest Service, 2018; NYSDEC, 2018; Ward et al., 2013). Yet, even though "predation" of acorns in our study was significantly higher than removal, this may be due in part to the coding of the data which was specific to acorns due to their large size: partial consumption was recorded as a predation event. However, we emphasize that removal by small mammals was fairly frequent, in fact 41.67% of the total acorns were removed during the course of the experiment. Thus, the regular removal of acorns may consequently indicate small mammals are important facilitators of acorn dispersal and regeneration. Further research is needed to investigate cache frequency by small mammals and germination success of acorns in different forest types, to determine the conditions that change which small mammal species hinder regeneration success or facilitate acorn dispersal and germination (Morán-López et al., 2016).

4.6. *Seed choice – Red spruce, eastern hemlock, and paper birch*

Selection preferences of red spruce and eastern hemlock were very similar and had intermediate to low probabilities of selection. In trial 1, when availability of all seeds was high, selection of red spruce and eastern hemlock was generally greater than paper birch, and sometimes greater than balsam fir. However, when availability of all seeds was lower, selection probabilities often dropped below balsam fir and paper birch (Figs. 2 and 3; Supp Fig. 5, 6). Relatively few studies exist that examine seed predation of either red spruce or eastern hemlock. Schnurr et al. (2002) hypothesized that their size is too small for rodent consumption, however we found the use of these species can be high (Supp. Table 2), which is consistent with several other studies using small seeds (Abbott, 1962; Abbott and Hart, 1960; Côté et al., 2003; Fletcher et al., 2010; Peters et al., 2003; Selonen and Mäkeläinen, 2017). Both eastern hemlock and red spruce were high in calories, fat, and protein, but their small size likely only made them profitable when a larger quantity of seeds was present to consume at once (the number of calories ingested per second is relatively low, Table 1).

Conversely, selection of paper birch was consistently low for all small mammal species. However, we did note that its selection marginally increased above white pine in red-backed voles when the availability of other seeds was low (Fig. 3; Supp. Fig. 6), indicating that paper birch may be utilized as a last resort. These results are in line with the findings of Ogawa et al. (2017) who suggested that paper birch was not an optimal resource for red-backed voles but may be an important resource when the population density is high and other seed resources are depleted. Paper birch seeds are characterized by a very small size and low nutritional content (the number of calories per second was the lowest observed in our sample); therefore, they have a low profitability for small mammals. Additionally, selection by deer mice and woodland jumping mice marginally increased above red spruce and eastern hemlock when availability was low (especially in trial 2 when those small seeds were absent). This suggests that when other seed quantities were reduced, paper birch selection increased as the large quantity, small size, and very low handling time made it easy to consume a large number all at once.

As preference for paper birch was so low, its regeneration success is unlikely to be affected by small mammals. Similarly, eastern hemlock seed selection is unlikely to have a major economic impact for foresters, despite the intermediate preference, as the tree has a low value for harvest (Maine Forest Service, 2018; NYSDEC, 2018). Conversely, red spruce is commercially significant and frequently harvested in the northeast (Huff and McWilliams, 2016; Irland et al., 2001; Northeast Timber Exchange, 2019; NYSDEC, 2018). Commonly grown in spruce-fir forests (Ward et al., 2013), red spruce would likely incur higher seed losses than balsam fir, as spruce seeds are often selected over balsam fir (Abbott and Hart, 1960).

4.7. *Environmental effects on seed choice*

Although the covariates for rain and temperature were included in top-ranked models for several small mammal species, the effect sizes of rain and temperature on seed choice were small (except for temperature on red squirrel selection of white pine, for which selection slightly decreased as temperature increased (Supp. Fig. 8)). We could find very little information about how these environmental factors impact seed choice or predation by seed predators (see a few examples regarding desert rodents (Fuller and Hay, 1983; Roschlau and Scheibler, 2016)) and thus, additional research is needed to further investigate the extent that environmental factors impact small mammal seed choice, particularly in temperate forested ecosystems.

Illumination, however, did have an effect for the overall small mammal community and woodland jumping mice. As the amount of light increased, white pine selection increased, and red maple selection marginally decreased. These patterns are likely influenced by the temporal patterns of certain seed predators. A majority of the diurnal visits (when light levels were very high) were made by red squirrels and chipmunks, and red squirrels heavily selected for white pine. For the generally nocturnal jumping mouse, only light levels from moon phases were considered, as they were not active in our cages during the day. Jumping mice exhibited a distinct pattern of seed selection involving seed size and moonlight factors (Supp. Fig. 9); as the phase of the moon increased, they selected for smaller seeds such as paper birch, red spruce, and eastern hemlock, while red maple selection was slightly higher between full and new moons. This pattern suggests that light levels may be an important factor influencing the seeds selected based on perceived risk versus seed profitability, which is supported by other studies (Orrock et al., 2004; Perea et al., 2011a).

4.8. *Conclusions*

Identifying the seed preferences of small mammals is beneficial for better understanding predation pressure on managed trees in mixed forests. Small mammals may influence forest composition by facilitating the regeneration of seeds that are less preferred and hindering the regeneration of preferred seeds. Eastern white pine and red maple are most likely to be impacted by small mammal populations as they, overall, had the highest selection. Northern red oak, red spruce, and eastern hemlock may experience impacts on regeneration by small mammals, especially in areas where white pine or red maple is absent; however, the strength of the impacts may vary based on the abundance of seeds, and the availability of other seed species, and the small mammal species present. Although balsam fir selection may occasionally be high, the presence of other seed species will likely reduce the probability of selection; thus, regeneration of balsam fir is unlikely to be heavily impacted by small mammals. Similarly, selection of paper birch was consistently low, and the regeneration of this species is unlikely to be affected.

Although forest treatment did not directly influence seed selection, silvicultural practices can alter small mammal abundance and diversity, which can have cascading effects on seed predation. Consequently, the type of silvicultural management should be carefully selected, not only considering the trees in the stand, but considering other biotic factors as well; forest managers should incorporate the impact of small mammals into regeneration models (used to forecast and predict stand conditions and outcomes using various silvicultural techniques), at least for the most preferred species (Weiskittel et al., 2011). Currently, forest prediction models concentrate on abiotic factors and stand structure but including quantitative information about the effects of small mammals can help forest managers improve the accuracy of the forest prediction models and make more informed management decisions.

Declaration of Competing Interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117487.

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