

Research Article

Patterns of acorn selection in *Peromyscus* mice and possible implications in a changing climate

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Abstract

Rodents play a key role in forest regeneration by dispersing seeds and interspecific differences in seed preferences could have important consequences for forest growth. The White-footed Mouse (*Peromyscus leucopus*) and Deer Mouse (*Peromyscus maniculatus gracilis*) are 2 closely related species that can exploit Red Oak (*Quercus rubra*) acorns but may display different preference levels due to the high tannin concentration present in these acorns. Here we investigated how White-footed Mice and Deer Mice differ in their ability to exploit Red Oak acorns. We conducted a cafeteria-style experiment where we offered mice ($n = 61$) acorns of Red Oak and Bur Oak (*Q. macrocarpa*; control seed with lower tannin levels) and video-recorded their preference and the acorn fate (consumed or cached). Using mixed-effects models, we found that both mouse species selected and consumed Bur Oak acorns at a high rate; however, White-footed Mice were 6.67 times more likely to select and consume Red Oak acorns than Deer Mice. Furthermore, White-footed Mice tended to cache Red Oak acorns near the surface where there is a higher chance of germination, while they usually consumed Bur Oak acorns. Our results suggest that Red Oaks have a better strategy for avoiding predation than Bur Oaks (i.e., high tannin levels leading to caching), and the strong interaction between the White-footed Mouse and Red Oak might be an important mechanism behind the current range expansion of both species in response to climate change.

Key words: foraging behavior, *Quercus rubra*, seed dispersal, tannins, White-footed Mouse.

Small mammals are important seed dispersers because of their scatter-hoarding behavior, storing seeds in caches away from the parent tree for later consumption (Jensen and Nielsen 1986). Although most of these caches are predated before germination (Jensen and Nielsen 1986; Steele et al. 2001; Yang and Yi 2012), seeds that do survive represent successful dispersal events at a local scale (Steele and Smallwood 2002; Feng et al. 2021). Seed dispersal is a crucial life-history stage of most tree species as it increases the likelihood of seed germination and seedling survival (Howe and Miriti 2004). Many nut-bearing trees, which rely on scatter-hoarding animals to disperse their seeds, produce large acorns that are attractive food for such granivores (Steele and Smallwood 2002). This mutualistic association between small mammals and oak trees is highly context-dependent as it is influenced by small mammal density (Boone et al. 2021; Brehm and Mortelliti 2022) and by seed traits such as nutritional content that can directly affect the behavior of seed predators (Steele et al. 1993; Chung-MacCoubrey et al. 1997; Wang and Chen 2008).

The White-footed Mouse (*Peromyscus leucopus*) and the Deer Mouse (*P. maniculatus*) are 2 important scatter-hoarding rodents in North American forests. They are morphometrically very similar and have a widely overlapping geographic range, but the Deer

Mouse is better adapted to cold, conifer forests (Choate 1973; Wolff 1996) where it rarely encounters Red Oaks (*Quercus rubra*), whereas the White-footed Mouse is usually found in deciduous forests where Red Oaks are abundant (Vessey and Vessey 2007). Although presumably ecologically similar, this small difference in habitat requirements may reflect distinct food preferences. Indeed, Red Oak acorns were least preferred by the Deer Mouse compared to 7 other species of seeds in a cafeteria-style experiment (Boone and Mortelliti 2019). In contrast, Red Oak acorns are highly selected by White-footed Mice (Briggs and Smith 1989) and play a key role in White-footed Mouse population dynamics. Multiple studies have documented that White-footed Mouse density increases following Red Oak masting due to the positive effects of this added food source (Hansen and Batzli 1979; Elias et al. 2004; Dri et al. 2022). In short, closely related species that seem ecologically similar may have different food preferences and display different foraging behavior. Because mice are important seed dispersers, interspecific differences in their interactions with acorns could have important consequences for forest regeneration (Cramer 2014).

Potential differences in the interactions between these 2 species of mice and Red Oak acorns may be related to chemical composition of the acorn. Oak species differ significantly in the chemical

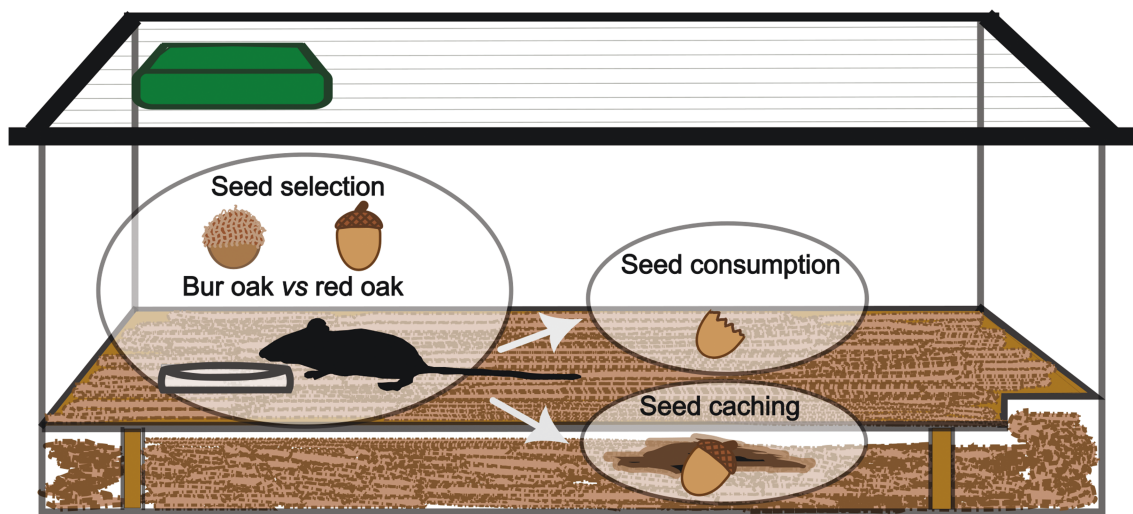


Fig. 1. Conceptual framework of the laboratory experiment conducted in Maine, United States, during September and October of 2021 and 2022. Individuals of White-footed Mouse (*Peromyscus leucopus*) and Deer Mouse (*P. maniculatus*) were housed in glass tanks where we monitored with a camera their foraging decisions regarding Red Oak (*Quercus rubra*) and Bur Oak (*Q. macrocarpa*) acorns: seed selection and seed fate (cached or consumed).

and nutritional content of their acorns, influencing many traits from germination phenology to seed palatability. The “Red Oak” group (*Q. rubra* and its close relatives including *Q. velutina* and *Q. phellos*) is known to have high levels of tannin—a defensive phenolic compound that affects seed palatability and thus influences seed selection, predation, and dispersal by animals (Wang and Chen 2008; Zhang et al. 2013; Ancillotto et al. 2015). Tannins are in the apical region of the acorn, protecting the embryo against predation and harsh weather conditions, and increasing its odds of surviving winter to germinate in spring. Species in the “White Oak” group (*Q. alba* and relatives such as *Q. macrocarpa* and *Q. muehlenbergii*) have a lower tannin content making them a preferred choice for consumers. Because White Oak acorns have lower tannin levels and germinate soon after falling, they tend to be predated more, rather than dispersed and cached (Fox 1982; Wang and Chen 2008).

Currently, there is a knowledge gap regarding how 2 similar *Peromyscus* species interact with oak species differing in tannin content and phenology (earlier or later germination). Understanding these differences is important because it has potential implications for the ongoing range expansion of northern Red Oaks and White-footed Mice. Due to climate and land-use change, some *Quercus* species—including Red Oak—are suffering a population decline in their current geographic range in the eastern United States (McEwan et al. 2011) and are predicted to move to more northern latitudes because of increased regeneration success (Woodall et al. 2009; Duveneck et al. 2014; Etersson et al. 2020). More specifically, the Northern Red Oak (*Q. rubra*)—an important food source for small mammals and the most common oak species in the north-eastern United States—is predicted to gain a large area of suitable habitat due to climate change (Stern et al. 2020). The current trends of climate change—especially shorter winters—are expanding the distribution of White-footed Mice northward, and are projected to continue this range expansion into the future (Myers et al. 2009; Roy-Dufresne et al. 2013). A strong interaction among species can drive or facilitate simultaneous range expansion (Clark et al. 2020), and this may be the case for White-footed Mice and Red Oak acorns.

Here we aim to investigate how 2 species of *Peromyscus* mouse differ in their ability to exploit Northern Red Oak acorns—the most common oak species in our study area. By conducting a laboratory experiment simulating the natural environment and offering acorns of Red Oak (*Q. rubra*) and Bur Oak (*Q. macrocarpa*, a type of white oak

and our control seed) that differ in their tannin concentration we asked whether (Fig. 1): (1) *P. leucopus* and *P. maniculatus* have different preferences between Red and Bur Oak acorns; (2) the mice species have different strategies for how they cache these acorn species; and (3) the final fate (cached or consumed) of these acorn species. We expected the White-footed Mouse to have a higher preference for Red Oak acorns than the Deer Mouse, and that this difference would be manifested in different probabilities to cache versus consume. Because of differences in acorn palatability associated with tannins, we expected Red Oak acorns to be primarily cached and Bur Oak acorns to be primarily consumed.

Materials and methods.

Study area and trapping methods.

The study was conducted at 3 sites in Maine, United States, to ensure the capture of both species given that *P. leucopus* is more common in southern Maine while *P. maniculatus* is more abundant in the central/northern regions of the state. Our southern Maine site was the Holt Research Forest, located in Arrowsic, and our central Maine sites were the University Forest located in Orono, and the Penobscot Experimental Forest located in Bradley (Fig. 2). Forests cover almost 90% of the state, mostly consisting of a mixture of conifers and hardwood species such as Red Oak, Red Maple (*Acer rubrum*), American Beech (*Fagus grandifolia*), White pine (*Pinus strobus*), and Eastern Hemlock (*Tsuga canadensis*).

Trapping occurred during September 2021 and 2022 when seeds were naturally available. In 2021, we trapped between 1 September and 5 October and in 2022 between 1 and 20 September. We conducted our experiment simultaneously with trapping, housing up to 7 individuals at a time in our experiment stations. Because the 2 sites in central Maine were very near each other (3 km apart), we only set up 2 experiment stations: one at the University Forest and the other at the Holt Research Forest. For all captured individuals we recorded age, sex, and weight, and collected ear tissue to use species-specific primers in qPCR and SYBR green reactions to distinguish between *Peromyscus* species (Rounsville et al. 2021)—in Maine, the *P. maniculatus* subspecies is *P. m. gracilis*. We caught a total of 100 individuals but only kept 72 adult mice in the experiment as juveniles and lactating or pregnant females were immediately released. Individuals were kept for the tank experiment and then released at

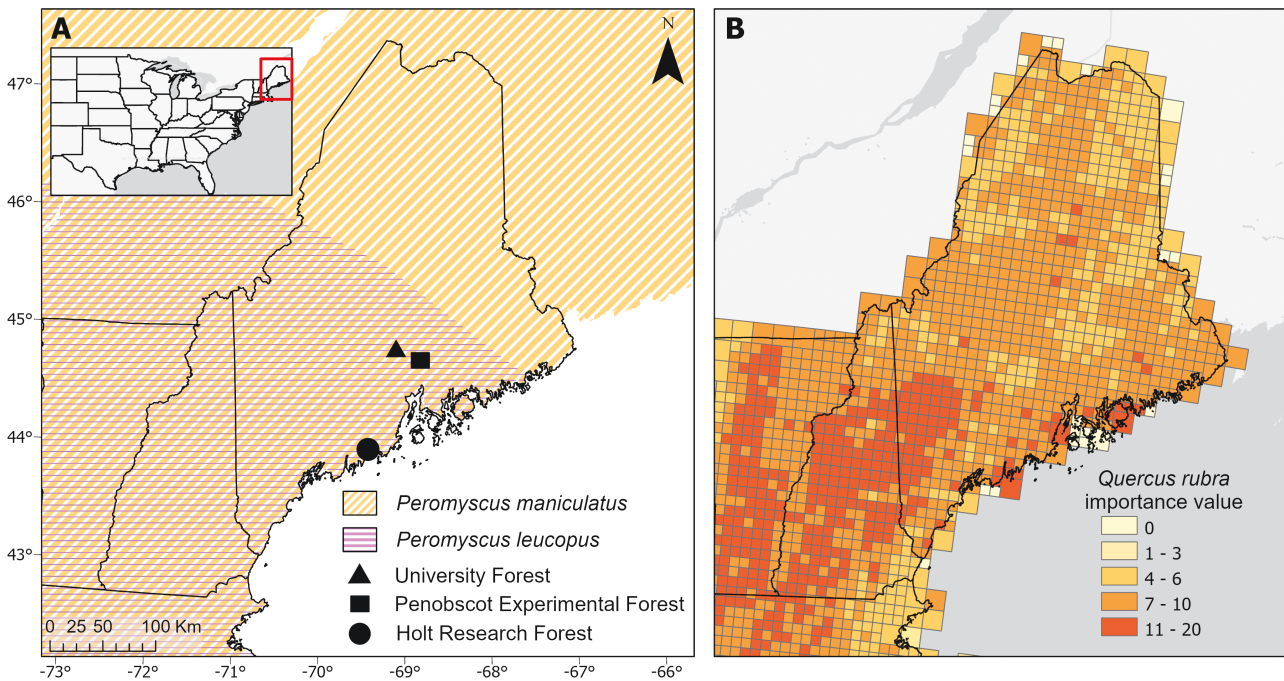


Fig. 2. Study area in Maine, United States. (A) The distribution range of the White-footed Mouse (*Peromyscus leucopus*) and the Deer Mouse (*P. maniculatus*) according to the IUCN red list, and the 3 trapping locations. (B) Predictions for the Northern Red Oak (*Quercus rubra*) distribution range according to the USDA Forest Service using the average of 3 GCMs (general circulation models) under a moderate emissions scenario (representative concentration pathways [RCP] 4.5). Importance values are based on relative density and basal area for overstory and understory at a 20 × 20 km grid scale.

the location of capture. Body mass did not differ significantly before and after the experiment (*P. maniculatus*, average body mass capture = 15.65 g and release = 16.79 g; *P. leucopus*, average body mass capture = 18.23 g and release = 18.12 g).

All trapping and experimental research followed the American Society of Mammalogists guidelines (Sikes et al. 2016) and were approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC A2018-11-01 and A2021-12-01).

Seed experimental design.

To investigate differences in the foraging behavior between *P. leucopus* and *P. maniculatus* regarding Red Oak acorns, we kept wild-caught individuals of both species in captivity briefly to analyze their foraging behavior in a controlled environment. We performed a cafeteria-style experiment to collect data on seed selection (preference) and seed fate (consumed or cached) for 72 individuals for 2 consecutive nights.

We housed individuals separately in glass tanks (51 × 32 × 27 cm) to easily observe the experiment without disturbing the mouse inside the tank. Tanks were kept outside to simulate the natural environment (i.e., natural sounds and environmental temperature fluctuations) under a roof to protect against the weather and to secure mice against predators. Temperature was approximately 20 °C during the day and 7 °C at night, with similar conditions between sites and years. There was 4 cm of soil in the bottom of the tank and then a wooden platform 5 cm high with 2 cm of soil to create a 2-level setup (Fig. 1). An opening in 1 corner of the platform allowed individuals to move between levels. This 2-level setup created more room for individuals and provided diverse opportunities to cache acorns, and the lower level simulated a tunnel system. We provided polyester fiber bedding for nesting material, and water was available ad libitum through a drip water bottle. Tanks had a mesh lid to allow ventilation. We housed individuals for a total of 4 nights: 1 night of acclimatization in the tank with sunflower seeds, oats,

and apple slices; 2 nights of the experiment with acorns; and 1 final night of sunflower seeds, oats, and apples before release. To avoid starvation and dehydration, we added a few sunflower seeds and apple slices on the second night of the experiment as some individuals did not consume the acorns.

To assess acorn selection and fate, we offered 3 Red Oak (*Q. rubra*) and 3 Bur Oak (*Q. macrocarpa*) acorns (6 acorns total per mouse) purchased from local vendors (F. W. Schumacher Co., Inc. and Sheffield's Seed Co., Inc.). Total number of acorns used in the experiment was 366 (6 acorns × 61 individuals; see below) and we did not reuse any acorns (i.e., if a mouse did not eat an acorn, we did not present this acorn to another mouse). Acorns were placed in a small tray on the wood platform for 2 nights (Fig. 1). We conducted the experiment for only 2 nights in order to avoid starvation. Besides different tannin concentrations, these acorns also differ in other traits including size, calories, and lipids (Table 1; Supplementary Data SD1).

Acorn selection was monitored with infrared cameras (Reconyx XR6) positioned on the tank lid facing downwards at the seed tray (Fig. 1). Cameras were motion-triggered and set to take 30-s videos (the maximum length) to record mouse–acorn interactions. Interaction consisted of the mouse touching or sniffing the acorn for at least 1 s, and it might or might not result in a selection event. A selection event was defined as the mouse either consuming the acorn in situ or taking it away from the camera view. Finally, we counted the number of acorns available in situ when a mouse interacted with/selected an acorn to determine availability.

Acorn fate was determined by checking the tanks once a day in the morning, and recording whether acorns were intact, consumed, or cached. Acorns were considered intact if they remained on the seed tray throughout the night (i.e., the individual did not select the acorn), consumed if they were clearly eaten by the individual and could be located either in the seed tray (i.e., the acorn was consumed inside the tray) or elsewhere in the tank (i.e., the individual moved the acorn before consuming it). Because individuals varied

Table 1. Nutritional content of Red and Bur Oak acorns (*Quercus rubra* and *Q. macrocarpa*, respectively). This analysis was performed by Eurofins Food Integrity and Innovation with 100 g per species of crushed acorns without caps and shells.

Seed	Mass (g)	Kcal (kcal/100 g)	Tannins (%)	Lipids (%)	Carbohydrates (%)	Proteins (%)	Moisture (%)
Red Oak	3.93	346	9.84	7.61	52.27	4.63	33.78
Bur Oak	2.11	271	4.69	2.21	50.30	5.44	40.34

in how they consumed acorns, we quantified acorn consumption as the proportion that was consumed (25%, 50%, 75%, 100% consumed) and recorded which end was consumed (base or apex). Cached acorns were acorns that a mouse selected and moved elsewhere in the tank but were not consumed. Importantly, we cannot infer that these acorns were indeed cached by the mouse under the conditions of our experiment because they could have been rejected seeds after the in situ selection (Zhang et al. 2013). Nonetheless, because ultimately such acorns were selected, moved away, and not consumed, we refer to them as “cached” (with quotation marks). For these acorns, we recorded if they were on the surface (i.e., completely above the soil) or buried in the soil (i.e., completely or partially hidden under the soil).

Statistical analysis.

We conducted the experiment with 72 individuals, a sample size consistent with most analogous behavior studies (DeMots et al. 2010; Lobo and Millar 2011); however, we removed 11 from the analyses due to video issues (e.g., camera did not trigger). Therefore, our final sample was 61 individuals (23 *P. maniculatus* and 38 *P. leucopus*) with a balanced number of males and females within each species (*P. maniculatus* = 11 females and 12 males; *P. leucopus* = 20 females and 18 males).

To assess differences in acorn selection between the 2 *Peromyscus* species, we performed 3 sets of logistic regressions. We estimated: (1) probability of selecting Bur Oak instead of Red Oak; (2) overall probability of selecting Red Oak; and (3) overall probability of selecting Bur Oak. For the first model, we subset the data to only have selection events of either acorn species ($n = 384$). This data set had 138 Red Oak selections and 246 Bur Oak selections between both mouse species, and 54 individuals (16 *P. maniculatus* and 38 *P. leucopus*). For the other models (overall probabilities of selecting Red Oak and Bur Oak), we used the full data set with all interaction events for any acorn species ($n = 734$). The Red Oak model had 138 Red Oak selections and 596 nonselections, and the Bur Oak model had 246 Bur Oak selections and 488 nonselections. For these 2 models, we included 61 individuals (23 *P. maniculatus* and 38 *P. leucopus*). For all 3 models, we used generalized mixed-effect models with a binary distribution and mouse ID as a random effect. The response variable was acorn selection and the predictor variable was mouse species (*P. maniculatus* or *P. leucopus*) controlled by acorn availability. In the Bur Oak model, we also added a quadratic effect of acorn availability to ensure the goodness-of-fit.

For the differences in acorn fate, we performed logistic regressions separately for each acorn species. The Red Oak model ($n = 211$) had 143 acorns consumed, 68 “cached,” and 46 individuals (9 *P. maniculatus* and 37 *P. leucopus*). The Bur Oak model ($n = 276$) had 251 acorns consumed, 25 “cached,” and 54 individuals (16 *P. maniculatus* and 38 *P. leucopus*). We again used generalized mixed-effect models with a binary distribution and mouse ID as a random effect. The response variable was acorn fate (consumed or nonconsumed) and the predictor variable was mouse species (*P. maniculatus* or *P. leucopus*).

To determine if the 2 *Peromyscus* species consumed different proportions of the acorn, we performed linear regressions separately

for each acorn species. The Red Oak model ($n = 143$) had 40 individuals (3 *P. maniculatus* and 37 *P. leucopus*), whereas the Bur Oak model ($n = 251$) had 53 individuals (16 *P. maniculatus* and 37 *P. leucopus*). We used linear mixed-effect models with Gaussian distribution and mouse ID as a random effect. The response variable was the proportion of the acorn that was consumed (ranging from 25% to 100% consumed) and the predictor variable was mouse species (*P. maniculatus* or *P. leucopus*).

Finally, to evaluate if the 2 species of acorn were “cached” in different ways (i.e., on the surface or buried in soil), we performed a logistic regression. Here we combined the 2 *Peromyscus* species because of limited sample size since most acorns were consumed (see Results). This data set contained 93 caching events (68 Red Oak and 25 Bur Oak) and 34 individual mice (9 *P. maniculatus* and 25 *P. leucopus*). We used a generalized model with a binary distribution. The response variable was the probability of “caching” the acorn on the surface rather than burying it in soil, and the predictor variable was acorn species (Red Oak or Bur Oak).

All analyses were performed in R version 4.0.3 (R Development Core Team; 2020). We used “lme4” (Bates 2015), “lmerTest” (Kuznetsova et al. 2017), “bootpredictlme4” (Duursma 2022), and “MuMin” (Barton 2020) packages to run the analyses. We assessed the goodness-of-fit by performing a Hosmer–Lemeshow test using the “ResourceSelection” (Lele et al. 2023) package and by calculating the model R^2 .

Results

Data summary.

We collected 734 observations of mice–acorn interactions. Of the 366 acorns, 281 (76%) were selected and 85 (24%) remained intact throughout the experiment (i.e., not selected, consumed, or “cached”). Among the selected acorns, 253 (90%) were consumed (102 Red Oaks and 151 Bur Oaks) and 28 (10%) were “cached” (22 Red Oaks and 6 Bur Oaks) by the end of the experiment. Among mice, 55 (90%) individuals selected at least 1 acorn (38 *P. leucopus* and 17 *P. maniculatus*). An example of a selection is provided in Supplementary Data SD2.

Seed selection.

Through our mixed-effects models, we found that both mouse species preferred Bur Oak acorns over Red Oak acorns, but *P. maniculatus* had a stronger preference for Bur Oak acorns ($\beta_{\text{maniculatus}} = 1.51$, $SE = 0.36$, $R^2_{\text{marginal}} = 0.30$, $P < 0.05$; Fig. 3). This pattern was corroborated when comparing the selection of each acorn species separately. The overall probability of Red Oak selection was higher for *P. leucopus* than for *P. maniculatus* ($\beta_{\text{maniculatus}} = -1.91$, $SE = 0.04$, $R^2_{\text{marginal}} = 0.26$, $P < 0.05$; Supplementary Data SD1). The Hosmer–Lemeshow test results indicated an overall goodness-of-fit for all models (Supplementary Data SD1).

Seed fate.

Both mouse species consumed Bur Oak acorns more often than cached them ($\beta_{\text{maniculatus}} = 1.20$, $SE = 1.28$, $R^2_{\text{marginal}} = 0.01$, $P = 0.34$), but *P. leucopus* had a significantly higher probability of consuming Red

Oak acorns than *P. maniculatus* ($\beta_{\text{maniculatus}} = -2.93$, $SE = 0.90$, $R^2_{\text{marginal}} = 0.15$, $P < 0.05$; Fig. 4). Among the consumed acorns, Red Oak tended to be around 50% consumed by *P. leucopus* and around 25% consumed by *P. maniculatus* ($\beta_{\text{maniculatus}} = -0.23$, $SE = 0.08$, $R^2_{\text{marginal}} = 0.08$, $P < 0.05$). Bur Oak acorns were consumed almost fully (75%) by both mouse species but *P. leucopus* tended to consume a slightly higher proportion of the acorn ($\beta_{\text{maniculatus}} = -0.19$, $SE = 0.03$, $R^2_{\text{marginal}} = 0.12$, $P < 0.05$; Fig. 5). In all cases, the acorn was consumed in the basal area (i.e., the area with less tannin content). Among the “cached” acorns, Red Oak was more likely to be cached near the surface than Bur Oak ($\beta_{\text{Red Oak}} = -1.79$, $SE = 0.51$, $R^2_{\text{marginal}} = 0.11$, $P < 0.05$; Fig. 6).

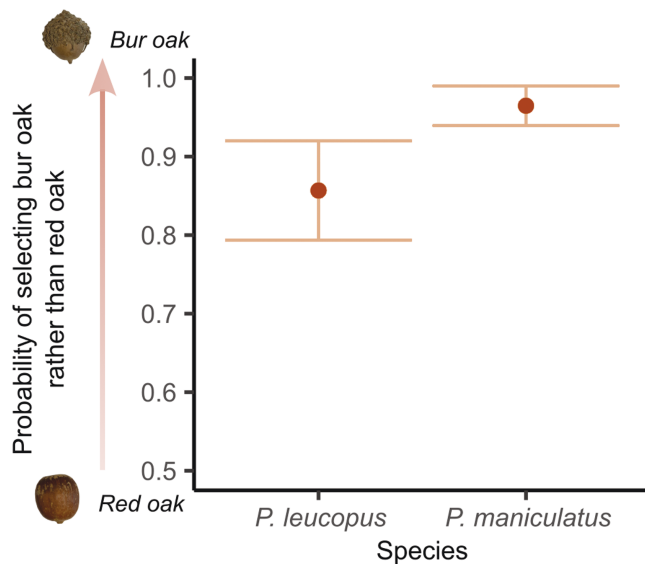


Fig. 3. Probability of *Peromyscus leucopus* and *P. maniculatus* choosing Bur Oak (*Quercus macrocarpa*) over Red Oak (*Q. rubra*) predicted by mixed-effect models (prediction for full availability of acorns). *Peromyscus maniculatus* has a higher preference for Bur Oak than *P. leucopus*. Data were collected in Maine, United States, during September and October of 2021 and 2022.

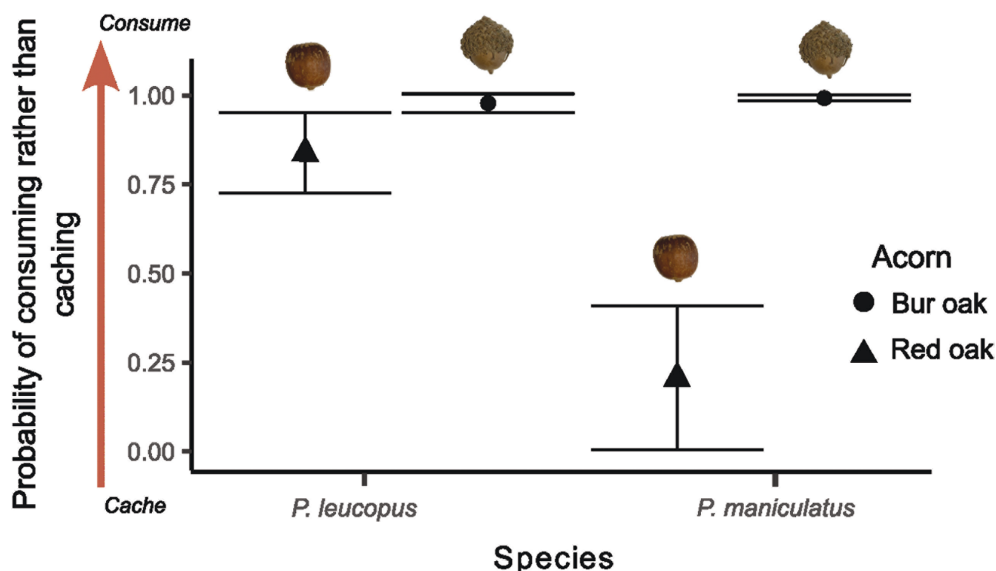


Fig. 4. Probability of *Peromyscus leucopus* and *P. maniculatus* consuming acorns over caching them as predicted by mixed-effect models. Both species were very likely to consume Bur Oak acorns (*Quercus macrocarpa*), but for Red Oak (*Q. rubra*) acorns *P. maniculatus* tended to cache them while *P. leucopus* tended to both consume and cache them. Data were collected in Maine, United States, during September and October of 2021 and 2022.

Discussion

We conducted a cafeteria-style experiment in a controlled environment to investigate how the White-footed Mouse and the Deer Mouse, 2 abundant seed dispersers in North America, interact with acorns with distinct life-history strategies (e.g., low and high palatability; late and early germination). We found key differences in their foraging behavior. First, White-footed Mice were 6.67 times more likely than Deer Mice to select and consume Red Oak acorns. Second, Red Oak acorns “cached” by White-footed Mice were more often placed on the surface where they have a higher chance of germinating (Vander Wall 1990, 1993). Finally, Bur Oak acorns tended to be selected and consumed at a high rate by both mouse species. These results highlight a potential consequence of the trade-off between tannin level and palatability in acorns. On the one hand, Red Oak acorns have higher tannin levels and thus are less selected by mice, although when selected, there is a higher opportunity for a successful dispersal event. On the other hand, Bur Oak acorns have lower tannin levels, so they are selected more frequently, but they are usually fully consumed and thus not dispersed.

Bur Oak acorns were highly preferred by both mouse species, and although the preference for Red Oak acorns was much lower, White-footed Mice selected Red Oak acorns significantly more than Deer Mice (Fig. 3). This pattern corroborates our predictions and the close association between White-footed Mice and Red Oak acorns (Hansen and Batzli 1979; Elias et al. 2004; Dri et al. 2022). Acorns are a stable food source for many rodents because they are high in lipids, but some species also have high levels of tannins creating a trade-off between palatability and energy content that influences seed selection (Wang and Chen 2012). Nonetheless, our results may indicate that White-footed Mice can overcome high tannin levels and exploit the energy present in Red Oak acorns while Deer Mice cannot. Besides tannins, another important difference between Red Oak and Bur Oak acorns that could be influencing selection is their size: Red Oak acorns are almost twice the size of Bur Oak acorns (Table 1). Most seed predators prefer larger over smaller seeds (Vander Wall 2010; Bartlow et al. 2018) but high tannin levels in addition to high handling time may be limiting the suitability of Red Oak acorns for *Peromyscus* species, especially Deer Mice.

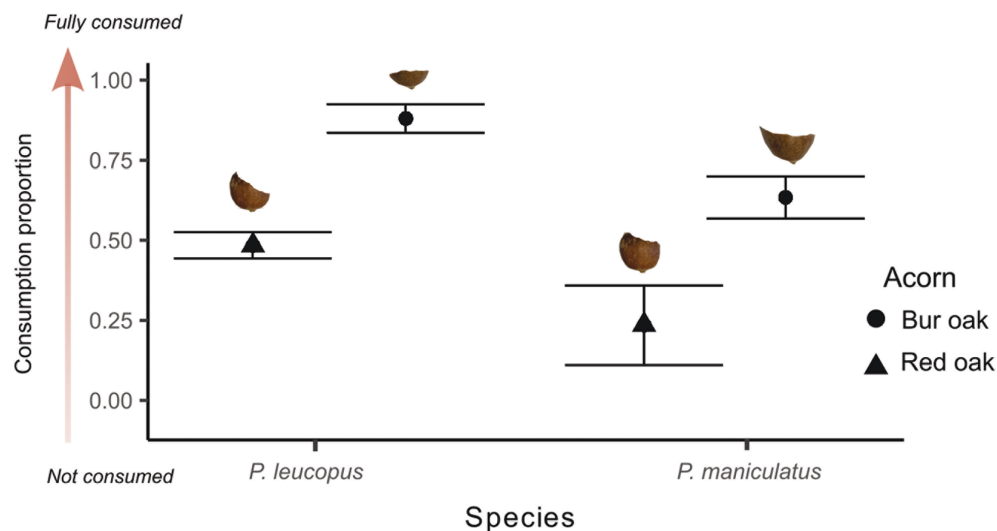


Fig. 5. Consumption proportion of Red Oak (*Quercus rubra*) and Bur Oak (*Q. macrocarpa*) acorns by *Peromyscus leucopus* and *P. maniculatus* as predicted by mixed-effect models. Both species tended to consume high proportions of Bur Oak acorns (around 75% of the acorn), whereas Red Oak acorns were usually partially consumed (around 50%), and this pattern was stronger for *P. leucopus*. Acorn icons on the top of the box plot visually show the proportion of consumed acorns. Data were collected in Maine, United States, during September and October of 2021 and 2022.

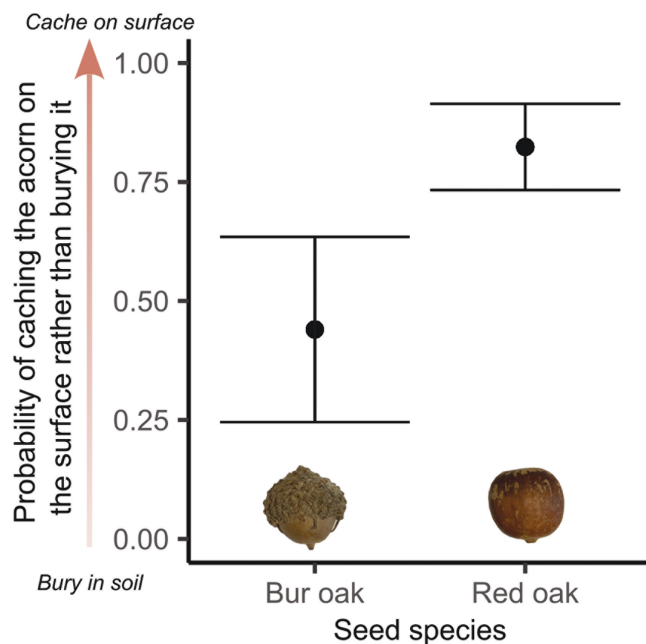


Fig. 6. Probability of Red Oak (*Quercus rubra*) and Bur Oak (*Q. macrocarpa*) acorns to be cached on the surface rather than being buried in soil by both *Peromyscus leucopus* and *P. maniculatus* as predicted by mixed-effect models. Red Oak acorns tend to be cached near the surface while Bur Oak acorns tend to be cached either near the surface or underground. Data were collected in Maine, United States, during September and October of 2021 and 2022.

Differences in food preference among seed predators can have large impacts on seed fate and ultimately forest regeneration. A previous study found that White-footed Mice and Deer Mice also differ in their preference regarding maple seeds (*Acer* spp.), and this difference led to lower concentrations of maple trees in areas dominated by Deer Mice (Cramer 2014). Similar patterns may arise in our system since ongoing range expansion of the White-footed Mouse in areas dominated by the Deer Mouse could shift the relative abundances of these *Peromyscus* species via competition (Myers et al. 2009; Roy-Dufresne et al. 2013; Gaitan and Millien 2016) influencing

forest composition due to their differences in seed selectivity. This is particularly important because expansion of oak-dominated stands can result in an ecological shift with implications for forestry, hunting, vectors, and their pathogens (Rustad et al. 2012).

Both mouse species had a high probability of consuming Bur Oak acorns rather than “caching” them. However, only White-footed Mice were also willing to consume Red Oak acorns while Deer Mice would usually “cache” them (Fig. 4). This result is consistent with the “high-tannin hypothesis” which states that Red Oak acorns are more likely to be cached by rodents due to their low palatability and late germination and thus they have a higher likelihood of being dispersed and established in a new location away from the parent tree (Steele et al. 1996; Chang and Zhang 2014; but see Zhang et al. 2013). Importantly, our definition of cache was “selected but non-consumed,” and although these seeds may have been rejected after in situ selection (Zhang et al. 2013), mice had still chosen to carry them away from the seed tray (analog to the parent tree). Furthermore, acorn movement by mice also changes overall distribution of acorns in the environment by spreading them over a larger area and thus making them harder to locate and consume by other animal species. Therefore, we believe that this action of selecting and then dropping the acorn could be considered a dispersal event in the context of our study.

Additionally, we found that Red Oak acorns had a higher chance of being “cached” on the surface rather than being buried in soil (Fig. 6). Cache placement (surface or under soil) and microhabitat (shrubs or open areas) strongly influence ultimate seed fate and eventual seedling establishment (Vander Wall 2010; Wang and Corlett 2017). Specifically, seeds cached near the surface under a pile of litter or moss have a higher likelihood of germination than seeds cached deep in burrows (Vander Wall 1990, 1993). Therefore, our experiment showed that the few Red Oak acorns that were “cached” were usually placed in good conditions for a successful dispersal event, indicating that Red Oak acorns may have a better strategy to escape predation than Bur Oaks.

Our experiment also showed that both mouse species consumed Bur Oak acorns almost entirely, whereas they partially consumed Red Oak acorns (Fig. 5), indicating that tannins may be a limiting factor for seed consumption (Smallwood et al. 2001; Shimada and Saitoh 2003; Xiao et al. 2008). We also found that mice consumed

acorns through the basal portion regardless of acorn species. This preference for the base has been found in other animals including Gray Squirrels (*Sciurus carolinensis*), Common Grackles (*Quiscalus quiscula*), Wood Mice (*Apodemus sylvaticus*), Blue Jays (*Cyanocitta cristata*), and Acorn Weevil larvae (*Curculio* spp.)—and is probably a strategy of animals to avoid tannins, which are concentrated in the apical portion of the acorn where the embryo is located (Steele et al. 1993; Perea et al. 2011). Interestingly, studies that monitored seeds after dispersal found that acorns can still germinate and grow as seedlings even with part of the embryo removed, suggesting that animals are getting nutrients while still contributing to successful seed dispersal (Steele et al. 1993; Wang and Chen 2012; Yang and Yi 2012; Bartlow et al. 2018).

This was a laboratory study in which we assessed mice foraging behavior in a controlled environment. Although animals may behave differently when confined to a small enclosure (Xiao et al. 2008), many studies have found similar results between captive and free-living small mammals (Zhang et al. 2013, 2018; Boone and Mortelliti 2019), suggesting that our results may hold for individuals in the wild. Our experiment was a first step in investigating foraging differences between White-footed Mice and Deer Mice, 2 morphologically and ecologically very similar species, regarding Red Oak acorns and future studies should test our hypothesis in the field and with other white oak species. We used Bur Oak acorns to represent other low-tannin oak species common in Maine such as *Q. alba*. We acknowledge that Red Oak and Bur Oak acorns differ in traits other than tannins such as mass, calories, and lipids (Table 1), which also influence caching decisions for a rodent (Wang and Corlett 2017; Mortelliti et al. 2019). Although we could have included more seed species in our cafeteria experiment to control for some confounding variables, we chose to use oaks within the distribution range of both of our trapping locations (southern and central Maine).

Altogether, our results and previous literature (Steele et al. 1993, 2001; Bartlow et al. 2018) indicate that Red Oak acorns that were selected and subsequently “cached” on the surface or that were partially consumed (around 50% of the seed consumed) may be considered as a dispersal event. Interestingly, White-footed Mice were the main species responsible for this process, suggesting that they might have evolved a tolerance to tannins in order to exploit Red Oak acorns (Onodera et al. 2017) as has been found in many *Apodemus* species (Shimada et al. 2011; Zhang et al. 2018). Similar ecosystems worldwide may have similar dynamics of competition, coexistence, and resource preferences among scatter-hoarding rodents and the seeds they consume. For example, in Europe, 2 *Apodemus* mice species (*A. flavicollis* and *A. sylvaticus*) are morphologically and ecologically similar but may also differ in terms of acorn preference (Gasperini et al. 2016), and the same may be true of other *Apodemus* species in Asia (Zhang et al. 2018). We hypothesize that mice interactions and foraging behaviors in response to acorns with different traits (e.g., size and tannins) might be important mechanisms behind the range expansion of the White-footed Mouse and Northern Red Oak in response to climate change. Climate change is creating more suitable habitats for oaks, but ultimately oaks, and other nut-bearing trees, still rely on mice and other dispersers; thus, range expansion of *P. leucopus* may be facilitating (i.e., accelerating) Red Oak dispersion northward.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Figures comparing Bur Oak and Red Oak acorns in terms of their weight and selectivity by *Peromyscus* species, and a table showing the goodness-of-fit results.

Supplementary Data SD2.—Video showing an example of acorn selection. White-footed Mouse (*Peromyscus leucopus*) selecting a Bur Oak acorn.

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Author contributions

GFD, MH, and AM conceived and designed the experiments. GFD performed the experiments, analyzed the data, and wrote the original draft. MH and AM reviewed and edited the manuscript.

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Conflict of interest

None declared.

Data availability

Data and code to replicate our results are available in the Figshare repository (<https://doi.org/10.6084/m9.figshare.22439002>).

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