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Deciphering the effects of disperser assemblages and seed mass on patterns of seed dispersal in a rodent community

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Abstract

The sizes of both seed dispersers and seeds are traits that are likely to interact to influence seed fate in many synzoochoric plant species. Here, we examined whether members of a granivorous rodent community consisting of species of different body size vary in their effectiveness as seed dispersers, and how this relationship may be altered by seed size. We marked northern red oak (*Quercus rubra*) acorns with plastic tags and placed them in size-selective rodent exclosures. The exclosures allowed differential access of rodent groups based on different body size: (i) small (e.g. *Peromyscus* spp.); (ii) small and medium (e.g. *Tamias striatus*); and (iii) small, medium and large (e.g. *Sciurus carolinensis*) species of rodents. Acorn removal did not differ among exclosure types, but more seeds were missing when removed by small rodents, probably because of larderhoarding. The treatments did not influence the relative frequency of acorn consumption. However, small rodents cached considerably fewer and partially ate more acorns than the other 2 groups. The mean dispersal distance was the longest for cages with medium openings, intermediate for cages with large openings and the shortest for cages with small openings. Acorn mass positively affected the probability of caching and this relationship was unaffected by exclosure type. In conclusion, granivorous rodents of different body sizes strongly differed in their interactions with acorns, with small rodents acting primarily as acorn predators and medium and large species contributing significantly more to dispersal of red oaks.

Key words: acorn dispersal, initial seed fate, plant–animal interactions, rodent community, scatterhoarding

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INTRODUCTION

Most zoochoric plants rely on multiple species of seed dispersers (Vander Wall 1990; Schupp & Fuentes 1995; Cheng *et al.* 2005; Forget *et al.* 2005; Beck & Vander Wall 2010). However, animal species often use seeds differently with respect to quantity (i.e. number of seeds dispersed) and quality (e.g. relative proportion of seeds cached) (Schupp 1993; Hollander & Vander Wall

2004; Bellocq *et al.* 2005; Cheng *et al.* 2005; Muñoz & Bonal 2008; Beck & Vander Wall 2010; Galetti *et al.* 2013; Pesendorfer & Koeing 2016; Pesendorfer *et al.* 2016). Both of these factors affect seed dispersal effectiveness (*sensu* Schupp *et al.* 2010). Such interspecific differences between seed dispersers in response to various seed characteristics often result in dramatically different patterns of seed dispersal. For example, frugivores often have species-specific seed deposition sites, which might promote or hinder seed survival and reproduction (Wenny 2001; Jordano *et al.* 2007), and individuals of some granivore species scatterhoard single seeds in shallow caches, while other dispersers larderhoard seeds too deep for successful germination (Lu & Zhang 2008; Beck & Vander Wall 2010; Pesendorfer & Koeing 2016). In addition, different species of granivores vary in the proportion of seeds cached versus consumed (Hollander & Vander Wall 2004; Cheng *et al.* 2005). In the case of scatterhoarders, these variable responses often determine whether their interaction with plants is mutualistic or antagonistic (Theimer 2005; Jorge & Howe 2009; Zwolak & Crone 2012).

Among granivorous rodents, body size is a key functional trait that affects seed dispersal (e.g. Díaz 1994; Muñoz & Bonal 2008; Yi & Wang 2015). As a general rule, larger species are able to remove larger seeds and use a wider spectrum of seed sizes than smaller species (Díaz 1994; Westcott & Graham 2000; Jordano *et al.* 2007; Galetti *et al.* 2008; Muñoz & Bonal 2008). Moreover, larger species usually have greater home ranges and transport seeds greater distances than smaller species (Fragoso 1997; Sun *et al.* 1997; Jansen *et al.* 2004, 2012; Spiegel & Nathan 2007; Muñoz & Bonal 2008; Galetti *et al.* 2008, 2013). Thus, body size of seed dispersers is often correlated with dispersal effectiveness (Spiegel & Nathan 2007; Galetti *et al.* 2013).

In addition, seed size often determines seed fate in rodent-dispersed plant species. In both intraspecific and interspecific comparisons, larger seeds are often cached more frequently (Jansen *et al.* 2002, 2004; Vander Wall 2003; Xiao *et al.* 2004; Zhang *et al.* 2008; Wang *et al.* 2014), and dispersed farther than smaller seeds (Jansen *et al.* 2002; Xiao *et al.* 2004; Steele *et al.* 2015; Yi & Wang 2015). However, the opposite has also been observed (Brewer 2001; Moles *et al.* 2003). The probability that seeds will be removed may decrease when the ratio of seed size to rodent size is too high and transporting seeds becomes too costly for the disperser (Muñoz & Bonal 2008; Galetti *et al.* 2013). Moreover, the impact of seed size on effectiveness of dispersal might change with dispersal stage. For example, larger acorns of Liaodong oaks (*Quercus liaotungensis*) were harvested more frequently and dispersed farther by rodents, but had lower survival after caching in comparison to smaller acorns (e.g. Zhang *et al.* 2008). Thus, although researchers agree that disperser decisions often constitute a selective force in shaping seed size (Gómez 2004; Xiao *et al.* 2004; Galetti *et al.* 2013; Wang *et al.* 2013; Yi & Wang 2015), the relationship between seed mass and dispersal efficiency of granivores remains unclear.

The link between seed mass and dispersal efficiency becomes even more complex when a plant is dispersed by a guild of seed consumers. Thus, it can be argued that understanding these interactions requires a community-level perspective rather than focusing on the effectiveness of a single dispersal agent (Strauss & Irwin 2004).

We examined how rodents of various body size influence seed dispersal of the northern red oak (*Quercus rubra*) by presenting acorns to rodents inside size-selective rodent exclosures. We hypothesized that dispersal quantity (the number of removed acorns) will be highest when all members of the granivore rodent community have access to acorns, but larger species will provide higher quality of dispersal (measured here as the proportion of cached acorns). Small and medium-sized dispersers of the northern red oak (mice [*Peromyscus* spp.] and eastern chipmunks [*Tamias striatus* Linnaeus, 1758]) are thought to consume or larderhoard acorns, whereas larger rodents, such as eastern grey squirrels (*Sciurus carolinensis* Gmelin, 1788), are known as avid scatterhoarders (Hadj-Chikh *et al.* 1996; Steele *et al.* 1996). Furthermore, we expected that larger species would disperse seeds at greater distances than smaller species. This prediction is based on the general relationship between body mass, home range and distances traveled in mammals (Lindstedt *et al.* 1986). Finally, we expected that all species will preferentially choose larger acorns for caching and smaller acorns for consumption based on the evidence from numerous studies on seed dispersal by rodents (Jansen *et al.* 2004; Moore *et al.* 2007; Steele *et al.* 2014) as well as the optimality prediction that caching requires effort that should be reserved for the most profitable food items (Gerber *et al.* 2004; Wang *et al.* 2014).

MATERIALS AND METHODS

Study site and rodent species

The study was conducted in Harvard Forest, located in the town of Petersham in north-central Massachusetts, USA (42.5°N, 72°W). This region is characterized by a cool, moist temperate climate. The average air temperature is 20 °C in July and −7 °C in January. The annual precipitation averages 1100 mm, and is distributed fairly evenly throughout the year.

Four experimental sites, 1–9 km apart, were established in transition hardwood forests dominated by northern red oak and red maple (*Acer rubrum*). The ground flora and the understory layer were poorly developed at our stands. In 2014, the acorn crop at Harvard Forest was characterized by a moderate crop of northern red oak acorns, with 3.4 ± 1.2 (mean ± SE) acorns per m^2 (unpublished data).

At our study sites, there are at least 5 rodent species that consume acorns: mice from genus *Peromyscus* (white-footed mice [*P. leucopus* Rafinesque, 1818], deer mice [*P. maniculatus* Wagner, 1845], or both: these species were not distinguished in this study), red-backed voles (*Myodes gapperi* Vigors, 1830), eastern chipmunks (*Tamias striatus* Linnaeus, 1758), southern flying squirrels (*Glaucomys volans* Linnaeus, 1758) and eastern grey squirrels (*Sciurus carolinensis* Gmelin, 1788). These rodents differ widely in body size and mass: deer mouse weighs from 10 to 24 g, white-footed mouse from 20 to 30 g, red-backed vole from 14 to 42 g, southern flying squirrel from 45 to 82 g, eastern chipmunk from 66 to 150 g, and eastern grey squirrel from 400 to 600 g.

Seed preparation

We collected mature, fresh red oak acorns near the study sites and made one composite sample of acorns for the experiment. This was done to minimize the effect of seed characteristics that may be associated with a single tree source. All acorns were floated in water to exclude those that were non-viable (i.e. moldy, broken or infested by *Curculio* sp. larvae). We randomly chose 600 sound acorns for the seed tracking experiment. The average mass of experimental acorns was 4.620 ± 1.440 g (mean ± SD; minimum = 1.08 g, maximum = 8.17 g). We pierced a 1-mm diameter hole through the husk at the basal end of each acorn without damaging the cotyledon and the embryo, and then inserted and tied a steel wire (100-mm length, 0.2-mm diameter) to the acorn and attached a red plastic tag (20 × 40 mm) to the opposite end of the wire (Xiao *et al.* 2006; Yi *et al.* 2008). The set comprised of wire and tag weighed approximately 0.14 g. Each acorn was weighed (± 0.01g) and

its tag individually numbered. Seed tagging (and most other methods of seed marking) could influence rodent behavior (Wróbel & Zwolak 2013), but in this study we evaluated relative differences in dispersal of identically-marked seeds.

Selective rodent exclusions

Rodent exclosures were constructed of wooden frames (1 × 1 × 0.5 m) covered with 1.25-cm mesh hardware cloth for the sides, roof and floor (Moore *et al.* 2007). To test the proposed hypotheses we cut holes on sides of exclosures that either allowed access by: (i) small rodents (mice and red-backed voles only); (ii) small and medium-sized rodents (mice, red-backed voles, eastern chipmunks and southern flying squirrels); or (iii) all rodents, including eastern gray squirrels. All 3 of these treatments excluded large consumers such as white-tailed deer (*Odocoileus viriginanus* Zimmermann, 1780) or wild turkey (*Meleagris gallopavo* Linnaeus, 1758). The access holes in the exclosure were the following sizes: 2.5 × 2.5 cm for the "small" treatment (1); 5 × 5 cm for the "medium" treatment (2); and 10 × 10 cm for the "large" treatment (3). At each study site, we placed 3 exclosures (1 per treatment). Cages within each site were located ≥70 m from one another, and filled with 50 randomly chosen experimental acorns (50 acorns × 3 exclosures × 4 study sites). We deployed the experiments in October 2014, and monitored acorn removal and fate each morning during the first 10 days, and then conducted checks 14, 28, 227 and 360 days after placement of the acorns. If marked acorns were removed, the area around the cage (20-m radius) was searched. For all recovered acorns or tags, we measured the distance from the cage of origin and divided their post-dispersal fates into 5 categories: (i) "eaten" (i.e. only a tag and seed fragments remained); (ii) "partially eaten" (i.e. only basal area of the acorn was consumed, but the apical part that contains embryo was left undamaged); (iii) "cached" (i.e. buried in the soil); (iv) "left on surface" (i.e. deposited intact on the surface); and (v) "missing" (i.e. not recovered within the search area).

Seed disperser identification

To verify whether the exclusion treatments effectively separated small, medium and large rodents, we used camera traps (Reconyx HyperFire PC800 Professional; Reconyx, Inc., Holmen, Wisconsin, USA). The cameras were set up during the first 13 days of this study at 20–30-cm distance in front of cages. Because there were more cages than cameras, we monitored all study cages

sequentially. Pictures were taken in sets of 5 with 1-min pauses between series. Each set of pictures was treated as an independent arrival of a seed disperser. Pictures of animals outside the cages were not counted as visits.

Statistical analysis

We analyzed whether exclosure treatment and acorn mass influenced: (i) the proportion of seeds removed; (ii) the proportion of seeds removed and found; (iii) the proportion of removed seeds that were found and consumed; (iv) the proportion of removed seeds that were not consumed and cached; (v) the proportion of removed seeds that were not consumed entirely but partially eaten; and (vi) removal distance. In analyses (i)–(v), we used binomial error distribution (logit link), and in analysis (vi) Gaussian error distribution (identity link) with removal distances log-transformed. The analysis was conducted in R using lme4 package (Bates *et al.* 2011; R Development Core Team 2013), with mixed models fitted by maximum likelihood using a Laplace approximation. In each model, we entered cage treatment, acorn mass, and their interaction (only if significant) as fixed effects, whereas site and exclosure (nested within site) were included as random effects. Testing for statistical significance was conducted with Wald c^2-tests (package "car" [Fox & Weisberg 2011]).

RESULTS

Seed disperser identification

We obtained 431 recordings of rodents from all cages. The most frequently occurring removal agents were individuals of *Peromyscus* spp. which accounted for 91% of all rodent visits in cages with small openings, 73% in cages with medium openings and 76% in cages with large openings (Table 1). Red-backed voles were not recorded in cages with small openings and only rarely in cages with medium and large holes (2% and 5% of rodent visits, respectively). Eastern chipmunks visited mostly cages with medium openings, where they accounted for 21% of recorded visits (versus only 6% in cages with small openings and 1% in cages with large openings). Southern flying squirrels mostly entered cages with large openings (13% of all visits in this treatment), with rare appearance also in cages with medium (4% of visits) and even small openings (1% of all rodent visits in this type of cage). Eastern grey squirrels were the rarest seed removal agents: they were not recorded in cages with small openings, and accounted for 1% of rodent visits in cages with medium openings and 4% in cages with large openings.

Seed removal and retrieval

Rodents removed 94% (48% within first 10 days) of acorns from cages with small openings, 96% (54% within first 10 days) from cages with medium openings, and 99% (57% within first 10 days) from cages with large openings ($\chi^2 = 5.746$, df = 2, $P = 0.06$; Fig. 1; Table 2). Moreover, the probability of removal tended to increase with acorn mass ($\chi^2 = 3.498$, df = 1, $P = 0.06$ for combined data). This tendency was pronounced over the first 2 weeks after the experiments were deployed (after 10 days: $\chi^2 = 16.737$, df = 1, $P < 0.001$; after 14 days: $\chi^2 = 10.283$, df = 1, $P = 0.001$), but not over longer timeframes (results non-significant after 28, 227 and 360 days). Adding quadratic effects of acorn mass did not improve the fit of the models.

In total, we retrieved 71% of acorns removed from cages. The treatments significantly differed in the proportion of acorns found after removal ($\chi^2 = 14.687$, df = 2, $P < 0.001$). This proportion was the lowest for cages with small openings (56%), intermediate for cages with large openings (72%), and the highest for medium openings (85% of acorns found after removal: Fig. 1). In ad-

Table 1 Numbers of rodent visits at different exclusion treatments (small, medium and large openings in exclusion cages)

Rodent species	Size group	Exclosure treatment			
		Small	Medium	Large	Total
Mice *Peromyscus* sp.	Small	64 (91%)	144 (73%)	125 (76%)	333
Red-backed vole	Small	0 (0%)	4 (2%)	9 (5%)	13
Eastern chipmunk	Medium	4 (6%)	41 (21%)	2 (1%)	47
Southern flying squirrel	Medium	2 (3%)	7 (4%)	21 (13%)	30
Eastern grey squirrel	Large	0 (0%)	1 (1%)	7 (4%)	8
Total	All	70 (100%)	197 (100%)	164 (100%)	431

Percentages in parentheses are calculated from the number of total records in particular exclosure treatments.

dition to this effect, heavier seeds were significantly less likely to be found, regardless of cage type (χ^2 = 17.413, df =1, P < 0.001).

Seed fate

The exclosure treatments did not differ in the propor-

Acorns offered
S: 100% (N = 200)
M: 100% (N = 200)
L: 100% (N = 200)

Removed
S: 94% (N = 187)
M: 96% (N = 192)
L: 99% (N = 197)

Not removed
S: 6% (N = 13)
M: 4% (N = 8)
L: 1% (N = 3)

Found
S: 56% (N = 104)
M: 85% (N = 164)
L: 72% (N = 141)

Not found
S: 44% (N = 83)
M: 15% (N = 28)
L: 28% (N = 56)

Not eaten
S: 44% (N = 46)
M: 60% (N = 98)
L: 46% (N = 65)

Eaten (entirely)
S: 56% (N = 58)
M: 40% (N = 66)
L: 54% (N = 76)

Partially eaten
S: 93% (N = 43)
M: 42% (N = 41)
L: 43% (N = 28)

Cached
S: 4% (N = 2)
M: 47% (N = 46)
L: 38% (N = 25)

Left on surface
S: 2% (N = 1)
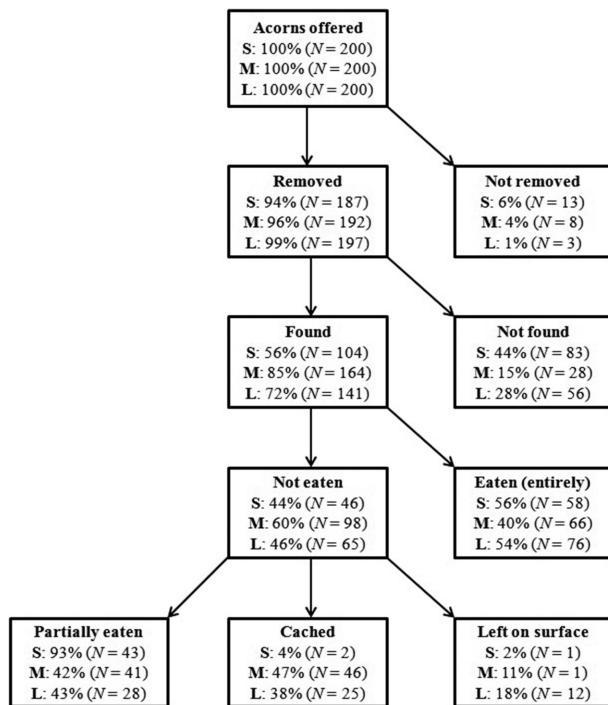M: 11% (N = 1)
L: 18% (N = 12)

Figure 1 Diagram of initial acorn fate, showing the percentages and numbers of acorns for each fate category. At each step, percentages are calculated from the number of acorns at the previous level. S, "small" treatment; M, "medium" treatment; L, "large" treatment; N, number of acorns.

tion of acorns that were consumed after removal (χ^2 = 2.583, df = 2, P = 0.28; Fig. 1). In comparison to other treatments, uneaten acorns from cages with small openings were rarely found cached (4% *vs* 47% for acorns from cages with medium openings and 38% for acorns from cages with large openings; χ^2 = 6.800, df = 2, P = 0.03; Fig. 1), but were often partially eaten (93% *vs* 42% for medium-sized and 43% for large-sized cages; χ^2 = 18.007, df = 2, P < 0.001; Fig. 1). Regardless of rodent exclusion treatment, heavier seeds had significantly higher probability to be cached (χ^2 = 8.213, df = 1, P = 0.004). In addition, heavier seeds had lower probability of being partially eaten (χ^2 = 23.924, df = 1, P < 0.001). However, the negative effect of seed mass on the probability of partial consumption was significantly stronger in cages with large opening than in cages with medium and small openings (interaction treatment × weight: χ^2 = 53.967, df = 2, P < 0.001).

When considering the total numbers of seeds offered (N = 200 for each treatment), rodents cached 1% and completely consumed 29% of acorns from cages with small openings. In the treatment with medium-sized openings, rodents cached 23% and completely consumed 33% of acorns. For acorns from cages with large openings, these proportions equaled 13% for caching and 38% for complete consumption.

Removal distance

The mean acorn dispersal distance was significantly greater at exclosures with medium openings (253.1 ± 11.9 cm, mean ± SE, N = 76) than for cages with large openings (184.5 ± 13.7 cm, mean ± SE, N = 28), and for cages with small openings (179.0 ± 14.3 cm, mean ± SE, N = 28) (χ^2 = 18.647, df = 2, P < 0.001; Fig. 2a. Seeds eaten *in situ* were excluded from the analysis of removal distance, but most seed consumption took place

Table 2 Summary of main generalized linear mixed models testing effects of exclosure treatments on seed fate

Seed fate	Exclosure treatments			Exclosure treatments × Weight		
	df	χ^2	P-value	df	χ^2	P-value
Removal	2	5.746	0.06	2	0.809	0.67
Retrieval	2	14.687	<0.001[†]	2	0.325	0.85
Consumption	2	2.583	0.28	2	1.668	0.43
Caching	2	6.800	0.03[†]	2	1.567	0.46
Partial consumption	2	18.007	<0.001[†]	2	53.967	<0.001[†]
Removal distance	2	18.647	<0.001[†]	2	0.608	0.74

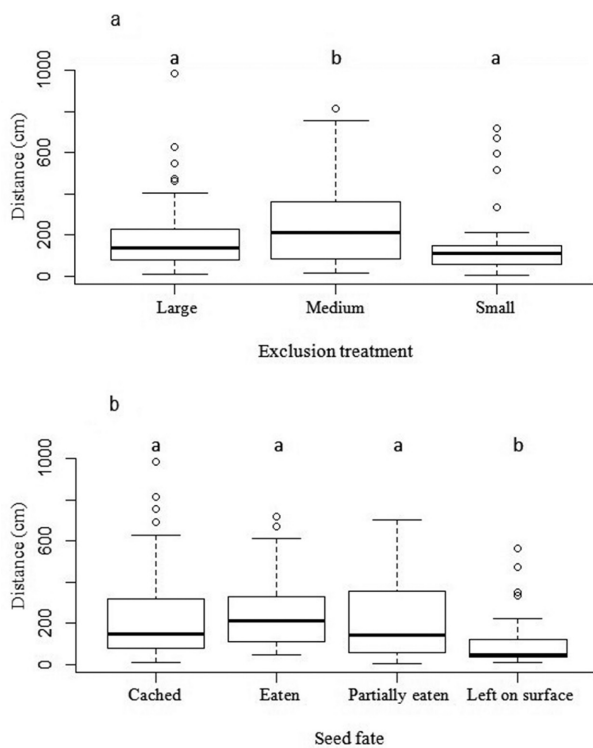[†]Significant effects. N = 600 acorns. df, degrees of freedom.

Figure 2 Distance of acorn dispersal in relation to (a) exclusion treatments (cages with openings of different size) and (b) overall fate of removed seeds. Boxes denote 25th, 50th and 75th percentiles; whiskers denote the farthest data points within 1.5 interquartile range; and the open circles denote data points beyond the 1.5 interquartile range. Different letters indicate difference at $P < 0.05$.

inside experimental cages for all treatments (66%, 82% and 75% of all eaten seeds were eaten *in situ* from cages with small, medium and large openings, respectively; $\chi^2 = 0.002$, df = 2, $P = 0.97$). Seeds consumed (excluding those that were eaten inside the cages) were moved farthest on average (238.8 ± 10.9 cm, mean ± SE), while seeds left uneaten on the surface were moved the shortest distance (123.67 ± 13.4 cm, mean ± SE; Fig. 2b). The mean removal distances of acorns across fates (regardless of treatment) were significantly different ($\chi^2 = 30.312$, df = 3, $P < 0.001$; Fig. 2b). Acorn mass had no influence on removal distance ($\chi^2 = 0.502$, df = 1, $P = 0.48$).

DISCUSSION

The separation of species by size was not perfect in our experiment. Cages with small openings were visited mostly by mice, cages with medium openings by mice and chipmunks, and cages with large openings by mice and squirrels: the southern flying squirrel (medium-sized species) and the eastern grey squirrel (large-sized species). Therefore, to highlight species-specific differences, we will refer to cages with small openings as "mice" treatment, to cages with medium openings as "mice–chipmunks" treatment, and to cages with large openings as "mice–squirrels" treatment.

This study allowed us to draw conclusions about the efficiency of seed dispersal by nested granivore communities. Acorn dispersal by the entire rodent community was characterized by a high proportion of acorns cached that were also moved the greatest distances. However, contrary to one of our hypotheses, exclusion of large species (eastern grey squirrels) had little influence on acorn dispersal. This may be due to the fact that the relative abundance of eastern grey squirrels at our study sites was low and, hence, their role as acorn dispersers was constrained by low densities. In turn, medium-sized rodents (represented mostly by the eastern chipmunk) significantly enhanced seed dispersal effectiveness in terms of caching rates, which went from 1% in "mice" treatment to 23% in "mice–chipmunks" treatment. Acorns offered in cages with small openings ("mice" treatment) were dispersed with markedly lower efficiency: consumption was frequent, caching was rare and dispersal distances were short. Thus, relatively modest experimental changes in the assemblage of seed dispersers strongly affected acorn dispersal. These results support the notion that understanding of plant recruitment patterns requires integrating seed dispersal services provided by the community of dispersers rather than focusing on single species (see e.g. Schupp *et al.* 2010; González-Castro *et al.* 2015).

Almost all acorns were removed from the cages. As we predicted, the proportion of removed acorns increased with the size of cage openings, but the magnitude of this increase was surprisingly small. This result, along with results from camera traps, suggests that mice were responsible for the majority of acorn removal at our study sites. These findings contrast with results of a similar study conducted in Ontario, Canada (Bellocq *et al.* 2005), where the entire rodent community (including mice) removed 2.5 times more northern red oak acorns than did only mice. This discrepancy might be caused by differences in the small mammal community composition (higher abundance of eastern grey squirrels and lack of chipmunks and flying squirrels in Bellocq *et al.*

2005). Alternatively, higher acorn production during experiments described in Bellocq *et al.* (2005) could satiate mice.

Similar proportions of seeds were found eaten in all treatments, suggesting that red oak acorn consumption is either independent of composition of rodent community or that this pattern was driven by high activity of mice at all exclosures. However, scatterhoarding was extremely rare in the "mice" treatment. This type of caching usually improves chances of seed germination by reducing the probability of consumption by strict seed predators and protects seeds from desiccation and other abiotic factors (Vander Wall 1990, 2001; Haas & Heske 2005). The rarity of scatterhoarding in the "mice" treatment is in agreement with results of previous studies, which indicate that *Peromyscus* spp. often larderhoard seeds (Sullivan 1978; Vander Wall 1990; Vander Wall *et al.* 2001), and only rarely cache them in topsoil (see Vander Wall *et al.* [2001] and Beck & Vander Wall [2010] for documented examples of scatterhoarding by *Peromyscus* mice). In line with this reasoning, we retrieved considerably fewer acorns removed from cages of "mice" treatment than from the 2 other exclosure treatments. The missing acorns were probably larderhoarded by mice. It is unlikely that acorns were dispersed beyond our search area because dispersal distances were the lowest for acorns at "mice" exclosures. Thus, if our interpretation of the fate of missing seeds is correct, the missing acorns represent mostly losses for the northern red oak because larderhoarded seeds are placed too deep for successful germination (Vander Wall 1990). In the "mice" treatment, missing acorns were almost 3 times as frequent as when eastern chipmunks were included (44% *vs* 15%).

The highest proportion of seeds scatterhoarded occurred in the "mice–chipmunks" treatment (cages with medium openings). These results were surprising because adult eastern chipmunks are thought to usually larderhoard (Vander Wall & Jenkins 2011), with less common cases of caching at shallow depths performed mostly by juveniles and females with litters (Clarke & Kramer 1994). However, it is also possible that some of the cached seeds represented initial scatterhoarding by chipmunks and mice, performed as a means of rapid sequestration of acorns, which are later larderhoarded. In contrast to mice and chipmunks, eastern grey squirrels are known as typical scatterhoarders (Hadj-Chikh *et al.* 1996; Steele *et al.* 1996), yet acorns were cached as often in the "mice–chipmunks" treatment as in the "mice–squirrels" treatment (cages with large openings). The

lack of difference between treatments probably reflects relatively low visitation rates of grey squirrels (and high by flying squirrels) in the "mice–squirrels" treatment.

Rodents often partially consume large seeds such as acorns (Steele *et al.* 1993; Perea *et al.* 2010). Partial consumption often leads to desiccation and exposes the seed to predators and pathogens (Perea *et al.* 2010). However, as a defense mechanism, many seeds respond to partial consumption through accelerated germination and production of longer roots. Thus, partial consumption is not always equivalent to seed predation (Steele *et al.* 1993; Pérez *et al.* 2008; Perea *et al.* 2010). In this study, partial consumption of acorns was particularly frequent in "mice" treatment. Smaller (e.g. mouse-sized) granivores are more likely to eat only a part of large seeds and abandon the remainder (e.g. Perea *et al.* 2010; Yang & Yi 2012). Thus, despite relatively low caching rates by *Peromyscus* spp., mice might contribute to oak dispersal and recruitment to a larger degree than was recognized previously. Future studies evaluating the impact of partial seed consumption on post-dispersal seed survival will improve the understanding of the role of *Peromyscus* spp. mice in acorn dispersal.

Seeds placed in "mice–chipmunks" treatment were characterized by the longest dispersal distances. This result is counterintuitive because eastern grey squirrels are thought to have the highest dispersal capabilities among the tested species, and generally larger rodents are expected to move seeds further. This pattern may be explained by the fact that grey squirrels visited the cages at rather low numbers. Indeed, all dispersal distances were relatively short compared to those reported elsewhere for grey squirrels (Steele *et al.* 2001, 2014; Moore *et al.* 2007). If a higher proportion of seeds had been dispersed by grey squirrels (and lower by mice), the mean seed dispersal distance would probably have been greater.

In all exclosure treatments, rodents preferentially removed heavier acorns, but this pattern disappeared after the first 2 weeks, probably because the largest acorns were already gone. This finding is in agreement with results of most studies on scatterhoarding rodents (reviewed in Lichti *et al.* 2016): when conspecific seeds are considered, rodents usually prefer larger seeds because they provide more energy. However, acorn mass did not affect acorn consumption at our sites. In general, the influence of acorn mass on predation probability varies considerably among studies (Lichti *et al.* 2015), with positive (e.g. Janzen 1971; Brewer 2001; Gómez 2004), negative (e.g. Jansen *et al.* 2002, 2004; Gómez

et al. 2008) and no associations reported (Zhang *et al.* 2008).

There was no association between dispersal distance and the mass of acorns. This pattern contrasts with results of several other studies on scatterhoarding rodents, which showed greater distances for heavier seeds (Jansen *et al.* 2004; Xiao *et al.* 2005; Steele *et al.* 2014, but see Brewer 2001). In our study, most acorns were dispersed by mice: perhaps the higher food value of large acorns was counterbalanced by higher travel costs (small-sized rodents have restrictions for acorn handling: Muñoz & Bonal 2008); thus, there was no effect of acorn mass on dispersal distance. Nevertheless, our results have to be treated with caution because heavier acorns were less likely to be found than small acorns (see below). Moreover, the relationship between acorn mass and dispersal could be altered by the presence of wires and tags. We note, however, that the mass of the tags represented only a small fraction of the acorn weight (see "Methods").

In addition, heavier seeds were less likely to be found after removal, regardless of the exclosure type. Because we did not find an effect of acorn mass on removal distance, we suppose that heavier seeds were preferentially larderhoarded rather than dispersed beyond our search area. This pattern may be explained by the high contribution of mice to seed removal in all exclosure treatments (see Bellocq *et al.* [2005] for a situation where grey squirrels were responsible for the majority of removal events), and it might reduce fitness of large acorns relative to smaller acorns.

As a final caveat, seed removal (including both dispersal and predation) is extremely dynamic both spatially and temporally. Seed removal by rodents varies both among species and within a species (and even temporally within an individual: e.g. Clarke & Kramer 1994), depending upon many environmental conditions, such as food availability (Vander Wall 2002b; Zhang *et al.* 2008; Zwolak *et al.* 2016), shrub density (Gómez *et al.* 2008) and presence of other herbivores (e.g. ungulates [Muñoz & Bonal 2007]), which makes understanding of seed removal systems more complicated. Our study focused on a small part of this phenomenon because we evaluated only initial seed fate. We did not take into account potential species-specific differences in seed deposition sites and their post-deposition fate: rodents often remove seeds from their own caches and either consume them or recache elsewhere (Vander Wall & Joyner 1998; Vander Wall 2002a). Moreover, cached seeds may be pilfered by conspecifics or heterospecifics (Vander Wall 2002a; Muñoz & Bonal 2011; Jansen *et al.*

2012). The propensity for recaching and pilferage might differ among species. Thus, future studies should aim to evaluate final seed fate and quantify the probability that seeds harvested by different species survive and establish.

CONCLUSIONS

We observed at least 5 rodent species harvesting, consuming and dispersing northern red oak acorns. We demonstrated that the rodents studied here, which vary significantly in body size, also differ in their impact on seed fate. In partial support of our hypothesis, especially medium-sized species (represented by eastern chipmunks and southern flying squirrels) and, to a lesser extent, large (represented by eastern grey squirrels) species provided more effective acorn dispersal than smaller species represented by *Peromyscus* mice. These conclusions are probably conservative because our experimental methods did not allow us to separate the effect of each rodent species. Instead, our experiments simulated a situation in which various rodent species were sequentially removed from the community to evaluate the impact of different assemblages of rodents on dispersal success. Even when *Peromyscus* spp. were the most abundant cage visitors in all treatments, a decrease in their visitation rates significantly improved dispersal services. When other species were allowed to remove seeds, seed caching rates and removal distances were dramatically enhanced. This suggests that slight differences in rodent communities can lead to drastic differences in seed dispersal effectiveness.

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