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ORIGINAL ARTICLE

Does multiple seed loading in Blue Jays result in selective dispersal of smaller acorns?

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Abstract

Studies from both tropical and temperate systems show that scatter-hoarding rodents selectively disperse larger seeds farther from their source than smaller seeds, potentially increasing seedling establishment in larger-seeded plants. Size-biased dispersal is evident in many oaks (*Quercus*) and is true both across and within species. Here, we predict that intraspecifc variation in seed size also influences acorn dispersal by the Blue Jay (*Cyanocitta cristata* Linnaeus), but in an opposite manner. Blue Jays are gape-limited and selectively disperse smaller acorn species (e.g. pin oaks [*Quercus palustris* Münchh]), but often carry several acorns in their crop during a single dispersal event. We predict that jays foraging on smaller acorns will load more seeds per trip and disperse seeds to greater distances than when single acorns are carried in the bill. To test this, we presented free-ranging Blue Jays with pin oak acorns of different sizes over a 2-year period. In each of 16 experimental trials, we monitored the birds at a feeding station with remote cameras and determined the number of acorns removed and the distance acorns were dispersed when cached. Jays were significantly more likely to engage in multiple seed loading with smaller seeds in both years of the study. During the second year, these smaller acorns were dispersed farther than larger acorns, and during the first year, larger acorns were dispersed farther, revealing an inconsistent response to seed size during our study. We suggest that in some circumstances, multiple seed loading by Blue Jays may favor dispersal in some plant species.

Key words: acorn dispersal, Blue Jays, *Cyanocitta cristata*, *Quercus*, seed size.

INTRODUCTION

Scatter-hoarding rodents and birds store seeds and nuts just below the ground surface in individual, widely-spaced cache sites to reduce pilferage and to increase the probability of cache recovery (Smith & Reichman 1984; Vander Wall 1990). Although scatter hoarding is a critical strategy that allows these animals to overcome the seasonal food shortages (Vander Wall 1990), in many systems, this behavior also contributes significantly to dispersal, germination and establishment of seeds when scatter hoarders fail to recover caches (Vander Wall 1990; Steele & Smallwood 2002; Steele *et al*. 2005).

Numerous studies have shown how seed or nut traits, such as germination schedules (Hadj-Chikh *et al*. 1996), handling time (Jacobs 1992), seed chemistry (Smallwood &

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Peters 1986) and seed size (Jansen *et al*. 2004; Xiao *et al*. 2005b; Chang *et al*. 2009; Wang & Chen 2009) each influence the decision to eat or cache seeds, which, in turn, affects the potential for seedling establishment. Seed size correlates with both energy content and handling time, and appears to have a dramatic effect on dispersal distance and the spacing of scatter hoards by rodents. Numerous studies across temperate, subtropical and tropical systems show that larger nuts (both larger-seeded species and larger seeds of the same species) are harvested more quickly (Xiao *et al*. 2004, 2005b, 2006; Perez-Ramos *et al*. 2008), cached more often (Xiao *et al*. 2005b; Wang & Chen 2009) and dispersed greater distances (Jansen *et al*. 2002, 2004; Xiao *et al*. 2004; Moore *et al*. 2007) than smaller nuts. In most of these studies it is also argued that these larger seeds are more likely to germinate and establish (Jansen *et al*. 2004; Xiao *et al*. 2004; Steele *et al*. 2005; Moore *et al*. 2007).

The dispersal advantage of larger nuts is most widely studied in oak (*Quercus*) ecosystems of North America and Asia, where larger acorns appear to have a consistent dispersal advantage over small acorns (both within and between species), at least with respect to rodent dispersal distance (Xiao *et al*. 2004, 2005b; Steele *et al*. 2005, 2006; Moore *et al*. 2007; Wang & Chen 2009; but see Gomez [2004] and Muñoz & Bonal [2008]). These observations strongly suggest that scatter-hoarding rodents exert strong directional selection on acorn size. However, acorn species in both North America and Asia show considerable variation in nut size (from 2 to 8 g), suggesting that smaller-seeded oaks are somehow able to overcome this apparent disadvantage.

In many oak ecosystems of Europe (Bossema 1979; Gomez *et al*. 2003; Den Ouden *et al*. 2005; Pons & Pausas 2007a,b), eastern North America (Johnson & Adkisson 1985; Johnson & Webb 1989; Johnson *et al*. 1997; Steele *et al*. 2010), south-eastern USA (DeGange *et al*. 1989), and western USA (Fleck 1994), jays are as important as rodents in the dispersal of oaks. Yet, these 2 groups of vertebrates appear to influence oak regeneration in different ways. Rodents such as tree squirrels (e.g. *Sciurus*) generally contribute to short distance dispersal (<100 m) within forest interiors (Steele & Smallwood 2002; Moore *et al*. 2007), whereas jays often disperse acorns over longer distances (frequently >0.5 km), potentially between forest patches, along forest edges and into open, disturbed or successional habitats (Johnson *et al*. 1997, Steele *et al*. 2010). Blue Jays (*Cyanocitta cristata* Linnaeus, 1758), however, are constrained by the size of acorns they can handle with the bill, and are widely reported to selectively disperse smaller-seeded oaks due to this gape limitation (Darley-Hill & Johnson 1981; Scarlett & Smith 1991; Moore & Swihart 2006; Steele *et al*. 2010). Moreover, Blue Jays are multiple seed loaders and can disperse several smaller acorns simultaneously by swallowing and carrying them in a distensible esophagus.

We suggest that smaller acorns might experience a dispersal advantage over larger acorns when dispersed and cached by jays because of the ability of the birds to carry several smaller acorns and, therefore, a heavier load during a single dispersal event. We further suggest that if and when jays can carry heavier loads of several small seeds, they should disperse these loads farther to more preferred sites than they would a single acorn much the way rodents disperse larger acorns farther. Thus, we would expect jays to disperse smaller acorns farther than larger acorns because of their ability to carry heavier loads with smaller acorns. We specifically hypothesized that smaller acorns of the same species would result in higher seed loading and greater dispersal distances than larger acorns. We tested this hypothesis by presenting pin oak (*Quercus palustris* Münchh) acorns of different sizes to free-ranging jays and determining the size of seed loads (either the number or the total mass of acorns carried) and the dispersal distances for the resulting caches.

MATERIALS AND METHODS

Study site

The study was conducted from September through late November 2008 and from late December 2009 to early March 2010. All behavioral observations were carried out on the edge of a middle-age, deciduous stand dominated by red oak (*Quercus rubra* Linnaeus), white oak (*Quercus alba* Linnaeus), and sugar maple (*Acer saccharinum* Linnaeus), located in Dorrance Township, north-eastern Pennsylvania, USA (41°08'N, 75°59'W). All observations were made from the southern edge of a 1.5 ha lawn and successional stand bordering a continuous forest of approximately 12 ha to the east, west and north, and a 2.5 ha wetland and pond on the south-western edge of forest. Observations began later in 2009 than 2008 because jays did not come to the artificial feeding station as early as in 2008.

Acorn collection and preparation

Observations on the dispersal of acorns by Blue Jays indicated a strong preference of pin oak acorns over other native oak species (Moore & Swihart 2006). Preliminary observations also suggested that Blue Jays carry multiple pin oak, black oak and smaller white oak acorns, but carry only single acorns of larger species. Therefore, we used pin oak acorns for all experimental trials, but varied the size of the pin oak acorns to determine how size influenced acorn number or total acorn mass and dispersal distance.

We collected acorns from a minimum of 5 trees in the early autumn of each year of the study and stored them in the lab at 3 °C until needed. Sound acorns were distinguished by coloration, durability and visual inspection over flotation, which often fails to distinguish partially damaged acorns. Experimental samples were prepared by mixing all of the sound acorns collected in a year and selecting 2 groups: 1 with the largest acorns (>2.0 g) and another with smaller acorns (<1.5 g). From these 2 groups, we then selected a random sample of 100 acorns for each experimental trial, 50 of which were weighed (±0.01 g) prior to their presentation on the feeder.

Presentation and observation

During each experimental trial, we presented jays with 100 acorns on a 1 m^2 feeding tray positioned atop a 2.5 m wooden post. The tray consisted of a 13 × 13 grid of 1.0 cm diameter, 0.5 cm deep depressions, separated by approximately 1 cm. The depressions each held a single acorn so that it was securely positioned but also easily removed by jays. The 100 acorns were distributed arbitrarily among the 169 positions on the tray. To verify the number of acorns taken, remote cameras (Reconyx RM45 RapidFire Mono IR) were positioned a short distance from the feeding platform. In 2008–2009, 2 cameras, each mounted on tripods, were positioned at right angles approximately 1 m from the feeding tray. In 2009–2010, we used 2 cameras positioned 0.75 m above and facing down onto the tray. This eliminated a small number of blind spots that were evident in the first year of study. We set the cameras to record 1 image every second for 10 s, beginning when a jay visited the tray. This allowed us to confirm the number of acorns removed by each jay as it visited the feeding tray. We calculated the total acorn mass of a load as the number of acorns removed × the mean mass of the acorns in the trial.

To begin each trial, we presented jays with either 100 large or 100 small acorns and then moved to an observation area approximately 50 m from the feeding station, which allowed us to view both the feeding tray and most of the landscape across which the jays dispersed the acorns. The specific treatment (large or small acorns) for each trial was determined randomly. In each year, 8 trials were carried out: there were a total of 7 trials with small acorns and 9 with large acorns. Between 1 and 5 Blue Jays visited the feeder during each trial (mean ± SD = 2.9 ± 1.3). Following acorn placement, 2 or more observers remained at the viewing station until jays visited the feeding tray. If jays did not visit the feeding tray within 2 h, the trial was terminated and then repeated at a later date. When jays arrived at the feeder, each observer selected a focal animal to observe and recorded the number of acorns removed from the tray on each visit, whether the acorns were consumed or cached, and the general location where the jays moved to consume or cache the acorns. Because jays were not marked and jays returned to the feeder rapidly after caching, it was not possible to follow individuals through the course of an entire experimental trial. During the trials, jays rarely consumed acorns but instead carried them to preferred cache sites used in previous experiments.

Jays in this study relied on 7 primary caching sites for the majority of the dispersal events in both years of the study and approximately 15 additional secondary locations closer to the feeder where they sometimes dispersed acorns. Although each of these locations was visible from the observation area, jays were often obscured from view by vegetation when they moved to the ground. However, jays rarely consume food while on the ground (N. Lichti & A. Bartlow, pers. observ.) and spent only a few seconds at a time out of sight, so we assumed that they were caching acorns in these locations rather than eating them. We rarely observed jays to consume acorns, which they did in elevated perches in higher vegetation close to the feeding station.

The location of all primary cache areas (n = 7) was recorded with a differential Global Positioning System unit and the distances from the feeder to the cache sites (±1 m) were determined using a geographic information system and an aerial photograph of the study site. Shorter distances were determined using a hand-held laser distance meter (SONIN Multi-Measure Combo Pro).

Data analysis

We used a truncated Poisson regression to determine whether the number of acorns removed from the feeder differed between years and acorn size (small *vs* large). We observed no significant year-by-size interaction or year effect; therefore, these terms were dropped from the final model, which contained just the effect of acorn size on the number of acorns dispersed. Data were then aggregated at the trial level and a Spearman rank correlation was used to evaluate the relationship between mean acorn number and mean acorn mass across all trials in a year. A Wilcoxon rank sum test was used to evaluate the total

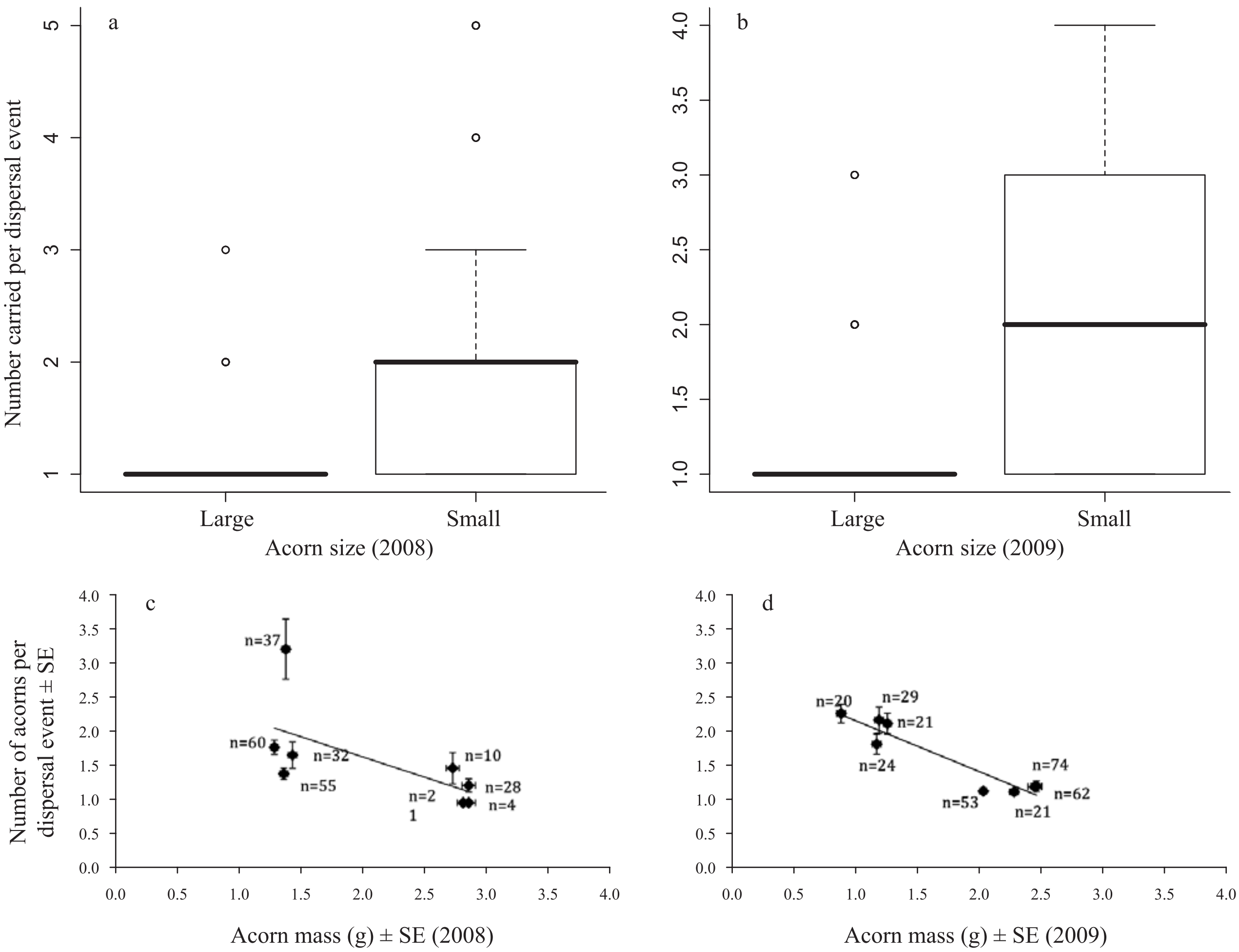

Figure 1 Box plots showing the distribution of the seed loads (number of acorns carried per dispersal event) for large and small acorns in (a) 2008 and (b) 2009. Seed loads were significantly larger for smaller acorns in both years of the study (see text). The relationship between seed mass (g) and seed load (see text) across all trials in (c) 2008 (d) and 2009. Shown are the means per trial (± SE); number of dispersal events is shown for each experimental trial.

load mass in relationship to size (large *vs* small) of the acorns. Regression was used to evaluate the relationship between acorn size and the natural log of dispersal distance, acorn number and the natural log of dispersal distance, and the total acorn mass per load and natural log of dispersal distance. There were significant year interactions, so these data were analyzed separately by year.

In addition, we compared pairs of trials to more closely examine how changes in acorn size affect Blue Jay seed handling behavior. For each unique pair of trials in a given year, we calculated the ratio of mean acorn mass per trial, the ratio of the mean number of acorns transported per load, and the ratio of the mean distances to which acorns were dispersed. We then analyzed the effect of difference in mean acorn mass on mean number of acorns per load and the effect of differences in mass and load number on mean distance using linear regression on the log-ratios. All analyses were carried out with R (R Development Core Team 2010).

RESULTS AND DISCUSSION

Across both years of the study, load sizes varied from 1–3 acorns for large acorns (mean masses >2.0 g) and 1–5 acorns for small acorns (mean masses <1.5 g), although multiple seed loads were more common for smaller acorns (Fig. 1a,b). The number of acorns carried per load was significantly greater for smaller acorns (Poisson regression, n = 547, P = < 0.001). Likewise, the mean

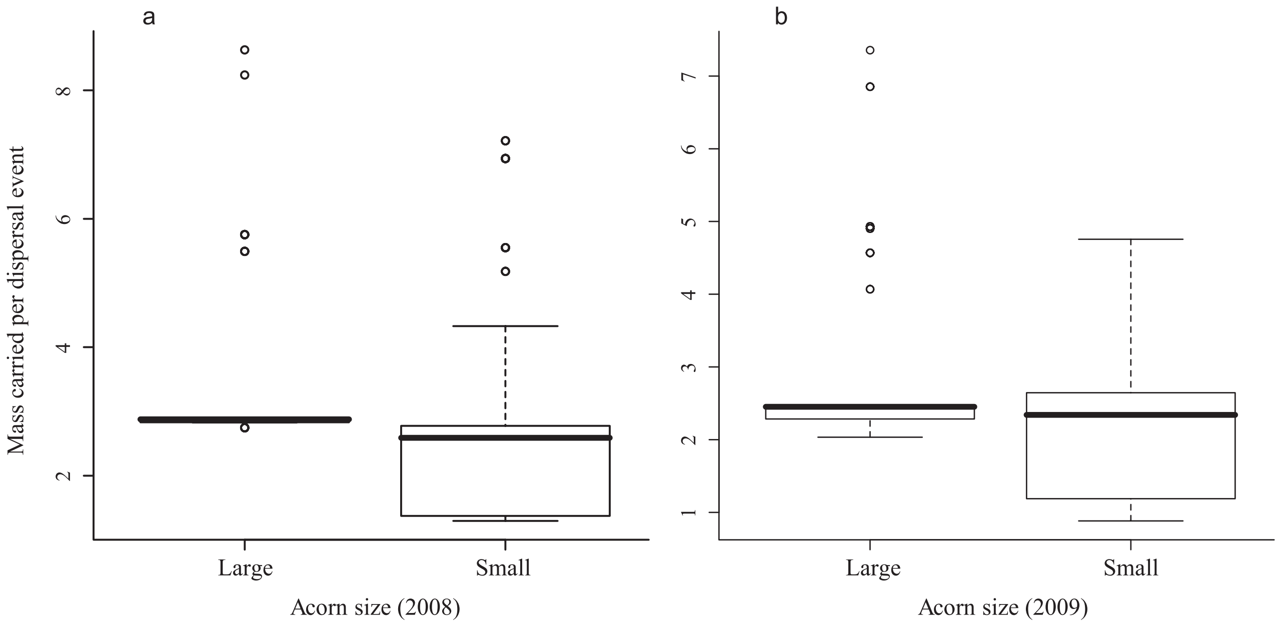

Figure 2 Distribution (box plots) of load sizes (total acorn mass [g] per load) carried per dispersal event for large and small acorns in (a) 2008 and (b) 2009. Although median load sizes were similar for the 2 size classes of acorns, the distribution of load size is skewed toward larger loads (i.e. lighter loads do not exist for larger acorns) and is therefore, significantly larger for larger acorns (see text).

number of acorns per load was negatively correlated with mean acorn mass across experimental trials in 2008 (r_s = –0.75, n = 8, P = 0.031; Fig. 1c). A similar, but slightly weaker pattern was observed in 2009 (r_s = –0.71, n = 8, P = 0.057; Fig. 1d). The total acorn mass carried per load for small and large acorns is shown in Figure 2a and b, respectively.

Although the number of acorns carried was greater for smaller acorns, the total mass per load was significantly greater for larger acorns in both the first (Wilcoxon rank sum, W = 9055, P < 0.001; Fig. 3a) and the second year of the study (Wilcoxon rank sum, W = 11584, P <0.001; Fig. 3b). This appears to be due largely to the fact that lighter loads cannot be carried with larger acorns. As a result, the median mass per dispersal event was similar for small and large acorns in both years of the study (Fig. 2). In pairwise comparisons, the ratio of the mean number of acorns per load had a strong, negative log–log relationship to the ratio of mean acorn mass (Table 1). Load number declined more steeply as a function of mass in 2009 than in 2008, but the 2 years were qualitatively similar. Blue Jays in 2008 did not appear to transport enough smaller acorns to compensate for the mass that they would sacrifice by foraging on smaller seeds, despite the fact that smaller acorns were consistently carried in multiple seed loads (Fig. 4). Based on the load numbers and acorn masses observed in 2009, they would have compensated only if the smaller acorns weighed no more than 26.4% of the larger acorns.

Larger acorns were dispersed significantly farther than smaller acorns in the first year of the study (R^2 = 0.041, N = 244, P < 0.001), whereas the opposite was true in the second year (R^2 = 0.16, N = 303, P < 0.001). In addition, in the second year of the study, the number of acorns carried per load was significantly correlated with the distance that these acorns were dispersed (R^2 = 0.13, N = 303, P < 0.001). Interestingly, however, the estimate of total load mass per dispersal event was not correlated with dispersal distance (R^2 = 0.00038, N = 303, P = 0.348). In contrast, in the first year of the study, total load mass (R^2 = 0.056, N = 244, P < 0.001) and not acorn number were correlated with dispersal distance (R^2 = 0.012, N = 244, P = 0.052). In the pair-wise regression analysis, we found that the ratio of mean dispersal distances increased with the ratios of both acorn number and mean acorn mass, but that both effects varied by year (Table 1; see also Fig. 3). Our pair-wise analyses indicate that Blue Jays dispersed acorns to greater distances in trials where they carried more acorns, heavier acorns, or both.

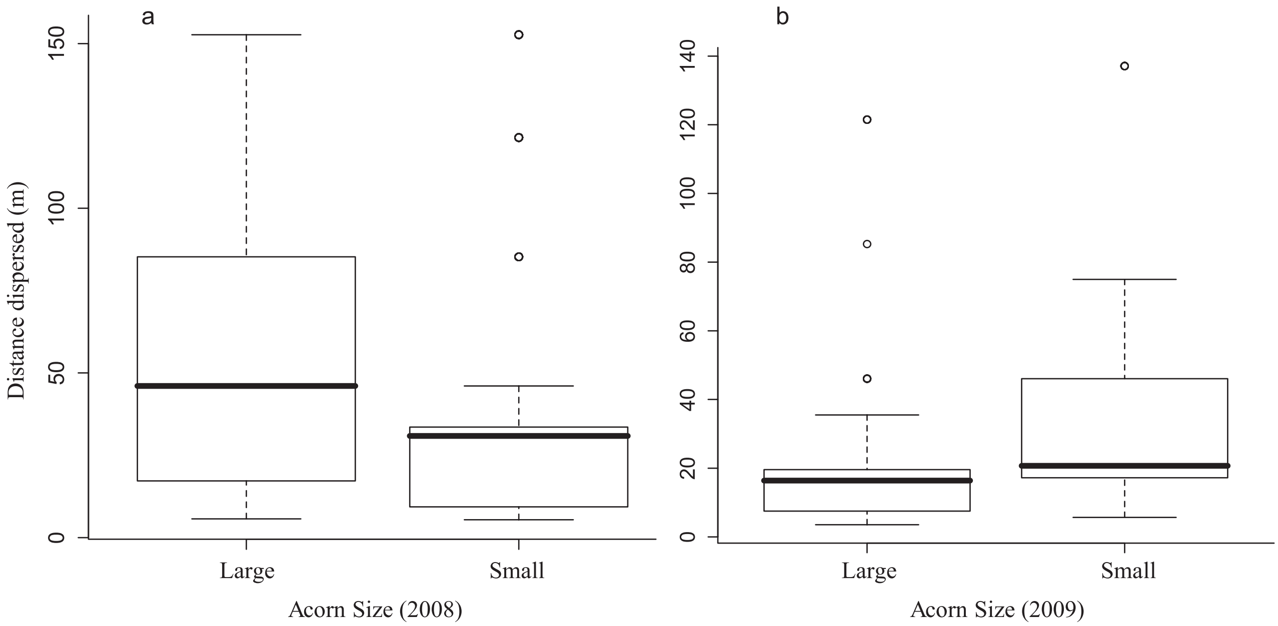

Figure 3 Box plots showing the distribution of dispersal distances for small and large acorns in (a) 2008 and (b) 2009. Dispersal distances were significantly greater in 2008 for larger acorns and significantly greater for smaller acorns in 2009 (see text).

It has been shown previously that jays selectively disperse smaller acorn species (Darley-Hill & Johnson 1981; Scarlett & Smith 1991; Moore & Swihart 2006), and further argued that such preferences might have contributed to both the rapid northward range expansion of some oaks following the last glacial retreat (Johnson & Webb 1989) and the negative latitudinal gradient in acorn size reported for several North American oak species (Aizen & Woodcock 2004). This latter geographic pattern of intraspecifc variation in acorn size, however, has since been attributed to environmental constraints (e.g. temperature and rainfall), rather than jay dispersal (Koenig *et al*. 2009).

In many parts of the eastern deciduous forest, jays regularly disperse large quantities of acorns from oak species that produce small acorns (e.g. black oaks, *Quercus velutina* Lambert, pin oaks, and willow oaks, *Quercus phellos* Linnaeus) compared with those with larger acorns (e.g. red oaks and white oaks; Darley-Hill & Johnson 1981; Scarlet & Smith 1991; Johnson *et al*. 1997; Steele *et al*. 2010). For example, Darley-Hill and Johnson (1981) estimate that jays harvested and dispersed >54% (as many as 133 000) of the acorn crop from a single pin oak tree, and Steele *et al*. (2010) estimate seed removal rates as high as 2675 acorns per day. Moore and Swihart (2006) show a preference for smaller acorn species (e.g. black and pin oaks) over larger species (red and white oak) in experiments with captive jays, but also find that larger acorns (e.g. white oaks) are sometimes eaten by jays when

Table 1 Linear regressions of the log-ratios of mean acorn number per load (*N*) versus mean acorn mass per trial (M) and mean dispersal distance per trial (D) versus mean acorn number and mean mass per trial. Both models include effects of year (2009 *vs*. 2008) as well. Coefficients are point estimates (standard errors).

	Intercept	M	*N*	2009	M × 2009	N × 2009	Adjusted R^2	*F*	*P*
N	0.221 (0.035)	–0.485 (0.064)	—	–0.281 (0.048)	–0.311 (0.086)	—	0.839	96.53 (df = 3, 52)	<0.001
D	–0.590 (0.181)	1.672 (0.371)	3.063 (0.597)	0.520 (0.222)	–1.482 (0.812)	–1.873 (1.047)	0.411	8.66 (df = 5, 50)	<0.001

smaller, more preferred acorns are not available. However, these less preferred acorns are often dropped before being completely consumed. Although the inability of jays to efficiently handle larger acorns might result in accidental dropping, partial consumption, and even dispersal of these damaged acorns (Steele *et al*. 2007), gape-size limitations appear to favor smaller acorn species for dispersal.

Our results extend this argument by suggesting that because jays can carry multiple acorn loads, smaller seeded oak trees might have a dispersal advantage under some circumstances. These results are consistent with those of other studies that suggest that under specific circumstances both rodents (Muñoz & Bonal 2008) and European Jays (Gomez 2004; Pons & Pausas 2007b) might prefer smaller seeds because of the cost/benefit of moving and handling them. In both years of our study, jays were more likely to disperse larger acorn loads (based on acorn number) with smaller pin oak acorns. Based on our regression results (Table 1), blue jays in 2009 would have transported more total mass per load with small acorns, provided that the small acorns weighed no more than 26.4% of the mass of the large acorns. Smaller acorns were also dispersed significantly farther than larger acorns in 2009. Pin oak acorns vary from <1 to >3.5 g in mass (N. Lichti, unpubl. data), and seed size is consistent across years within individual trees (N. Lichti, pers. observ.). Therefore, to the extent that our trials can be considered to be resource patches, similar to individual trees, it is plausible that smaller-seeded trees would experience a selective advantage in some circumstances. It should be emphasized, however, that the dispersal advantage of the smaller acorns was only observed in the second year of the study. The opposite pattern was observed in the first year; larger acorns were dispersed farther. In addition, the fact that jays might receive an advantage by utilizing smaller acorns does not necessarily translate into a selective advantage for small seeded trees; for example, if jays cache all acorns from a single load in closer proximity to each other, this could result in greater pilferage due to higher seed densities or greater crowding of seedlings. Further studies should consider the effect of seed size on post-hoarding survival and establishment of the seeds and the possibility that jays exert stabilizing selection on acorn size.

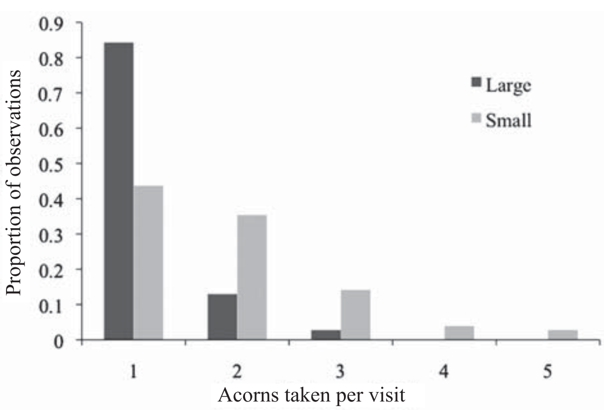

Figure 4 Proportion of acorns taken per visit for small and large acorns for both years of the study.

Several explanations might account for the differences in Blue Jay behavior between years, including lack of precise inter-annual replication, time of year when trials were conducted (see Scarlett & Smith 1991), small differences in seed size during the 2 years of the study (larger acorns were, on average, approximately 20% greater in mass in the first year; Fig. 1), jay densities, and differences in unmeasured, external variables between years, including the abundance of alternative food sources. Regardless of the reason for the differences, our results suggest the possibility of alternate strategies of acorn dispersal by jays based on either acorn mass or acorn number per seed load. We initially expected that the ability of jays to disperse more acorns (i.e. multiple seed loading) would result in greater dispersal distances and that dispersal distances would not vary with acorn number if load masses were equal. In other words, we expected that the mass–dispersal relationship would be effectively the same regardless of the number of acorns dispersed. However, this appeared not to be the case.

We propose that jays might shift strategies with season and acorn availability (see Scarlett & Smith 1991); in particular, we suggest that jays might show a preference for caching greater numbers of smaller acorns versus fewer large ones when acorn abundance is lower or pilfering rates are higher. Such a bet-hedging approach in the face of higher pilferage rates is consistent with a scatter hoarder's general food-hoarding strategy (Smith & Reichman 1984) and might allow jays to reduce losses to competitors (Scarlett & Smith 1991). When pilfering is common, it might be more advantageous to have larger numbers of discrete caches, rather than a larger total mass of stored food. Unfortunately, our data do not allow us to determine whether the jays in this study would have actually chosen smaller acorns over larger ones. Additional research is needed to understand how jays cope with high pilferage rates and whether seed size selection plays a role in these behavioral strategies. We are now exploring these trade-offs.

In conclusion, we show that intraspecifc variation in acorn size can influence dispersal decisions by jays, and that under some circumstances small acorns might have a dispersal advantage over larger conspecifics, although this response appears to be context dependent. Further study is needed to explore how the behavioral decisions of corvids influence seed size selection in oaks and other plant species.

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