

## DETERMINANTS OF SEED REMOVAL DISTANCE BY SCATTER-HOARDING RODENTS IN DECIDUOUS FORESTS

JEFFREY E. MOORE,<sup>1,3</sup> AMY B. MCEUEN,<sup>2</sup> ROBERT K. SWIHART,<sup>1</sup> THOMAS A. CONTRERAS,<sup>2</sup> AND MICHAEL A. STEELE<sup>2</sup>

<sup>1</sup>*Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907 USA*

<sup>2</sup>*Department of Biology, Wilkes University, Wilkes-Barre, Pennsylvania 18766 USA*

**Abstract.** Scatter-hoarding rodents should space food caches to maximize cache recovery rate (to minimize loss to pilferers) relative to the energetic cost of carrying food items greater distances. Optimization models of cache spacing make two predictions. First, spacing of caches should be greater for food items with greater energy content. Second, the mean distance between caches should increase with food abundance. However, the latter prediction fails to account for the effect of food abundance on the behavior of potential pilferers or on the ability of caching individuals to acquire food by means other than recovering their own caches. When considering these factors, shorter cache distances may be predicted in conditions of higher food abundance. We predicted that seed caching distances would be greater for food items of higher energy content and during lower ambient food abundance and that the effect of seed type on cache distance variation would be lower during higher food abundance. We recorded distances moved for 8636 seeds of five seed types at 15 locations in three forested sites in Pennsylvania, USA, and 29 forest fragments in Indiana, USA, across five different years. Seed production was poor in three years and high in two years. Consistent with previous studies, seeds with greater energy content were moved farther than less profitable food items. Seeds were dispersed less far in seed-rich years than in seed-poor years, contrary to predictions of conventional models. Interactions were important, with seed type effects more evident in seed-poor years. These results suggest that, when food is superabundant, optimal cache distances are more strongly determined by minimizing energy cost of caching than by minimizing pilfering rates and that cache loss rates may be more strongly density-dependent in times of low seed abundance.

*Key words:* caching behavior; *Carya*; deciduous forest; forest rodents; *Juglans*; *Quercus*; scatter-hoarding; seed dispersal; seed removal distance.

### INTRODUCTION

Animals manipulate resource availability over space and time by hoarding foods for later consumption (Vander Wall 1990), thereby enabling survival during periods of food scarcity in the surrounding environment and safeguarding food from competitors. Scatter-hoarding rodents store food in a dispersed fashion (e.g., burying one or a few seeds in many locations within the soil), which make individual caches inconspicuous and relatively unattractive to pilferers (compared to larger stores) but also difficult to defend (Vander Wall 1990). Greater seed spacing by scatter-hoarders serves to reduce cache pilfering by conspecifics (Stapanian and Smith 1978, Sherry et al. 1982, Clarkson et al. 1986, Waite 1988, Daly et al. 1992, Tamura et al. 1999). Naïve individuals who incidentally discover another's cache will subsequently search for additional caches within the immediately surrounding area, so the farther apart caches are spaced, the less likely the naïve individual is

to find a second cache before it abandons the search (Stapanian and Smith 1978). However, caching seeds at lower densities requires more travel time and effort, so a scatter-hoarder should not space caches so far apart that the cost of hoarding exceeds the benefit of retrieving more of its own caches. Based on these principles, two models have been proposed to predict how cache-spacing patterns should be optimized by scatter-hoarding animals (Stapanian and Smith 1978, Clarkson et al. 1986). Predictions vary for these models (reviewed by Vander Wall 1995), but both are based on a trade-off between minimizing pilfering rates and minimizing energy costs associated with longer-distance caching, and both predict that individual caches should be sequentially placed farther from the food source in order to maintain optimal cache densities.

A corollary of the last prediction, that caches are sequentially moved greater distances, is that mean cache distance should be greater when food is more abundant because greater distances are required to maintain optimal cache densities as more seeds are cached (Stapanian and Smith 1978, Vander Wall 2002). The "animal-mediated seed dispersal" hypothesis of tree-masting, which suggests that abundant food crops help to attract seed dispersers, also predicts greater dispersal

Manuscript received 13 February 2007; accepted 23 February 2007. Corresponding Editor: B. J. Danielson.

<sup>3</sup> Present address: Duke Center for Marine Conservation, Duke University, Beaufort, North Carolina 28516 USA.  
E-mail: jemoore@duke.edu

distances during large seed crops (Kelly 1994, Vander Wall 2002). However, support for these predictions has been equivocal. With respect to successive cache distances, most studies have not found seeds to be sequentially cached at increasing distances from their source (Stapanian and Smith 1978, Cowie et al. 1981, Sherry et al. 1982, Vander Wall 1995), but Clarkson et al. (1986) did observe this result. With respect to mean cache distance, a few studies have found seeds to be moved less far in seed-rich years than in seed-poor years (Theimer 2001, Jansen et al. 2004), whereas data by Vander Wall (2002, 2003) and Xiao et al. (2005a) were largely consistent with the above predictions.

There are several possible reasons for these conflicting results. First, food abundance should influence mean cache distance not just by affecting the number of seeds cached at some optimal density, but by also affecting optimal cache spacing itself. Rates of cache loss to pilferers have been said to be density-dependent if the rates depend on inter-cache spacing (Clarkson et al. 1986). Strong density dependence should increase with risk of pilferage, with higher pilferage likely in times of food shortage. When risk is low, cache spacing should have a relatively small influence on cache loss (weak density dependence), so animals should minimize cache management costs by dispersing seeds to relatively short distances (and hence high densities). Alternatively, when risk of pilferage is high, cache spacing may have an important effect on rates of cache loss (strong density dependence), and so animals should increase their management costs and increase cache spacing (cache at low densities).

Second, other factors besides food abundance influence risk of cache pilferage and hence cache density. These include the relative profitability of different food items and abundance of potential pilferers at a site. Higher-value food items tend to be cached at lower densities (Hurly and Robertson 1987, Jansen et al. 2004), probably because pilferers are willing to expend more effort (i.e., search a greater area) to find additional high-value items (Stapanian and Smith 1984). With respect to pilferer abundance, Clarkson et al. (1986) found that theft of caches by magpies (*Pica pica*) was uniformly low for all experimental cache densities where conspecifics were rare, whereas pilfering rates were more strongly dependent on cache density in areas with more conspecifics.

Interactions between factors affecting the risk of pilferage (and hence cache spacing) may also be important for understanding variation in caching densities, but have received little attention. Vander Wall (2002) and Jansen et al. (2004) found that the relationship between food abundance and dispersal distance of seeds by rodents depended on seed type or seed size, respectively. Results of these studies were not entirely consistent, however, and they provided different insights. We are not aware of other studies that have investigated interacting effects on cache distances.

Therefore, work is required to elucidate interacting factors affecting caching behavior and implications of these interactions for tree dispersal.

We present results from two studies conducted in widely separated areas (~500 km) of the eastern deciduous forest, USA, in which seed removal distances by granivore communities were quantified for several hard-mast seed types. One study was conducted in eastern Pennsylvania (hereafter, PA) and the other in northern Indiana (hereafter, IN). Our studies collectively include five years of data, including data from three seed-poor years and two seed-rich years. Each study represents part of a larger investigation to determine factors affecting dispersal and establishment of various tree species under varying conditions of mast availability and forest fragmentation. Here we report on the effects of seed type, seed size, and seed abundance on movement of hard mast seeds by communities of scatter-hoarding mammals. We predicted that seed removal distance would be greater (1) for higher-energy food items and (2) when ambient food abundance was lower. Additionally, we predicted (3) that during high food abundance when risk (or cost) of pilferage should be low, variation in dispersal distances across seed size or type also should be low (uniformly short dispersal distances across seed types). In contrast, in years of low food abundance, variation in dispersal among seed types or size is predicted to be high, with high-value food items dispersed farther to decrease risk of pilferage. Prediction 1 has been supported previously in several studies (e.g., Stapanian and Smith 1984, Hurly and Robertson 1987, Jansen et al. 2004, Xiao et al. 2004, 2005b, but see Brewer 2001 and Vander Wall 2003). Relatively few studies have investigated the second prediction, and findings are equivocal (Theimer 2001, Vander Wall 2002, Jansen et al. 2004, Xiao et al. 2005a). Fewer studies still have addressed the third prediction, which is consistent with findings by Jansen et al. (2004) but not findings by Vander Wall (2002).

## METHODS

### *Pennsylvania study*

The first experiment was conducted over three years at three study areas in eastern PA: two in Luzerne County (Mountain Top and Venesky sites) and a third in Skhuykill County on the property of the Hawk Mountain Sanctuary. The forests at all sites were relatively continuous, showing only minor fragmentation due to rural residential homes and small family farms. All forests (PA and IN) were dominated by oak (primarily *Quercus rubra*, *Q. velutina*, *Q. prinus*, and *Q. alba*), hickory (*Carya* spp.), and maple (*Acer* spp.). Acorns and hickory nuts are preferred by seed-hoarding rodents, especially tree squirrels (Ivan and Swihart 2000). Maple seeds are also utilized, but appear less important for most rodent species in our study when larger nuts are available. *Sciurus* and *Peromyscus* densities have both been shown to correlate more

strongly with autumn abundance of oak acorns than maple seeds (Riege 1991, McCracken et al. 1999, Schnurr et al. 2002, Moore and Swihart 2005), and Schnurr et al. (2002) observed higher removal rates of red oak acorns, but not red maple (*A. rubrum*) seeds, when *P. leucopus* densities were higher.

We monitored acorn production for three years (2000–2002) at the Hawk Mountain and Venesky sites and for two years (2001–2002) at the Mountain Top site. At each of the study sites, we monitored acorn production of 15 mature trees for each of the three most dominant oak species at each site (45 trees/site). Two seed traps were positioned beneath each oak tree crown (collecting area/tree = 0.28 m<sup>2</sup>) and monitored every 10–14 days between early September and mid-November. Seed traps consisted of a round laundry basket (internal diameter = 42 cm) attached to a wooden platform and nailed to the top of a 1-m wooden post that was driven 10 cm into the ground. Traps were lined with window screening and equipped with wire mesh tops that allowed acorns to enter but prevented access by squirrels and birds.

We selectively provisioned small mammals with acorns via exclosures consisting of a wooden-frame box (1 × 1 × 0.5 m) with 1.25-cm mesh hardware cloth for the sides, roof, and floor and black garden cloth lining the floor to prevent seeds from falling through. At the base of each side of the exclosures, we cut 10 × 5-cm openings to allow access by all small mammals (e.g., *Peromyscus leucopus*, *Tamias striatus*, *Sciurus carolinensis*). Five exclosures were placed at each of the three study areas, with a minimum distance of 75 m between exclosures (although for many exclosures this distance exceeded 150 m).

During each year of the study we monitored the movement and fate of four acorn types: large red oak acorns (*Q. rubra*, LRO), small red oak acorns (SRO), pin oak acorns (*Q. palustris*, PIO), and white oak acorns (*Q. alba*, WHO). Acorns were tagged with a uniquely colored metal brad, with color corresponding to acorn type. In mid-November of each year, we placed 150 acorns of each type in each of the 15 exclosures (9000 per year). We then followed the removal rates and acorn fates. Recovery of metal tags (using metal detectors; Sork 1984, Steele et al. 2001) involved a systematic, comprehensive search of the area defined by a 30-m radius around each exclosure. Recovery was initiated in late December after small mammals removed all acorns; it continued until May of the following year as allowed by snow cover. For each recovered nail or intact acorn we recorded the acorn species, its fate (buried uneaten, buried partially eaten, eaten [only metal brad is recovered], or unburied partially eaten), the distance and compass coordinate from the exclosure, and the microhabitat in which it was found.

The response variable for statistical analysis was distance (in meters) from the initial release site that a nail or cached acorn was recovered. We included

distances for all tags removed from the source (both cached acorns and the metal tags that remain after seeds are consumed) because previous results showed little difference between distances for cached and eaten acorns of nonperishable seed types (i.e., all seeds in this study except *Q. alba* [WHO] acorns; Steele et al. 2001). Few WHO acorns were retrieved intact, and so movement data for this type may primarily reflect consumption rather than caching patterns (Steele et al. 2001; M. A. Steele, *personal observation*). Distance was natural-log-transformed for analyses because of strong departures from normality in the nontransformed variable. Our analysis excluded acorns that were never removed from exclosures. Analyses were done independently for each forest. Each forest's data were analyzed with a three-way design (ANOVA) using exclosure (exclosure 1–5), acorn type (LRO, SRO, PIO, WHO), and year (2000, 2001, 2002) as factors. Acorn type and year were treated as fixed factors and exclosure location as a random factor in the model. Interactions were included. Tukey hsd post hoc multiple-comparison tests were performed for significant main effects. Sizes of seed types used in PA, based on random samples of ~150 of each type (50 per year), were: LRO, 6.36 ± 1.56 g; SRO, 4.10 ± 0.51 g; WHO, 4.54 ± 1.56 g; PIO, 1.60 ± 0.32 g (mean ± SD). The energetic rankings of seed types, in terms of kilojoules per seed, were LRO > SRO > WHO > PIO (Smith and Follmer 1972, Ivan and Swihart 2000, Moore and Swihart 2006). Therefore, we predicted movement distances would follow this same order.

#### Indiana study

We conducted the second experiment across 29 forest patches (11 in fall 2002, 10 in fall 2003, and 8 in fall 2004) in Tippecanoe and Warren counties, north-central Indiana. This area is predominantly agricultural (corn and soybean), with upland forest habitats distributed across small isolated fragments and some larger contiguous areas along major riparian zones (Moore and Swihart 2005). Forest patches containing our plots varied from 0.8 to 284 ha in size.

Annual autumn surveys of mast abundance for many nut-bearing taxa (including oaks, hickories, and black walnut) were conducted throughout Indiana in each year of our study (P. O'Conner, *unpublished data*). Based on these surveys and our perceptions of annual mast abundance at our study sites, total seed crops were very low (mast failure for most taxa) in autumn 2002 and 2004 and very high (bumper crop) in 2003. Even though annual mast production was likely to be highly autocorrelated across sites within our study area (Koenig and Knops 2000, 2005), across-site variation in mast/tree size and density could alter availability of mast across sites within a year. Thus, we indexed mast variation across the sites (SMAST) by conducting six variable prism plots within each site (Husch et al. 1982). Each prism plot gives an estimate of basal area for tree species of interest, which correlates with seed production

(Greene and Johnson 1994, Greenberg 2000). We estimated the basal area of nut-bearing trees (*Juglans*, *Quercus*, *Carya*) and averaged values from the six plots to obtain a single value for each study grid.

Study plots at each forest patch consisted of a  $25 \times 17$  grid of wire-pin flags spaced at 5 m (i.e., grid size =  $120 \times 80$  m). Flags in the grid were labeled according to a Cartesian coordinate system. At eight evenly spaced locations within a grid, we placed a semipermeable enclosure filled with seeds. The eight enclosures comprised four treatments (two boxes per treatment) that allowed access by nested subsets of the seed consumer community: (1) white-footed mice (*Peromyscus leucopus*) only; (2) mice, eastern chipmunks (*Tamias striatus*), southern flying squirrels (*Glaucomys volans*), and red squirrels (*Tamiasciurus hudsonicus*); (3) all forest rodents, including eastern gray squirrels (*Sciurus carolinensis*) and fox squirrels (*S. niger*); (4) all rodents and similar-sized avian consumers such as Blue Jays (*Cyanocitta cristata*), but not large consumers such as white-tailed deer (*Odocoileus virginianus*) or Wild Turkey (*Meleagris gallopavo*). Enclosures for treatments 1–3 were constructed as in the PA study, except that we cut hole sizes specific to each treatment (sizes in 2003, 2004: 2.5, 5, and 10 cm diameter holes for treatments 1, 2, and 3, respectively; sizes in 2002 were  $\sim 1$  cm larger in diameter for treatments 1 and 2). For treatment 4, the enclosure consisted of a  $1 \times 1$  m tray with the same flooring as box enclosures, surrounded by chicken-wire fencing raised from  $\sim 20$  cm above the ground to a height of  $\sim 1.5$  m. Enclosures were  $\geq 20$  m from one another (45 m apart for the same treatment), and each was 30 m from the nearest edge of the study grid. Laser-triggered cameras placed near a number of enclosures confirmed that only small mammals accessed experimental seeds and that treatments were effective at targeting different subsets of the rodent community (Moore and Swihart 2007).

In late October of each year, we filled each enclosure with 65 (2002) or 50 (2003, 2004) of the following: black walnuts (BLW, *Juglans nigra*, except for treatment 1, because mice do not use these), shagbark hickory nuts (SHH, *C. ovata*), red oak acorns (NRO), pin oak acorns (PIO), and white oak acorns (WHO, except in 2004, because the crop was too small in this year to collect useable samples). Seeds were tagged similarly to the PA study except that color and type coding of brads was used to distinguish not just seed type but also enclosure location.

We used metal detectors to search in spring (April–June) for seeds removed from enclosures during the previous autumn. For the first study year, we conducted half of our search effort in the same autumn as seeds were presented, and we only searched about half of each study grid in total, such that seeds from only half of the enclosures were searched in that year. Thus, the total number of seeds susceptible to search was reduced to  $\sim 42,400$ . The  $25 \times 17$  grid flags at each study plot

created a  $24 \times 16$  grid of  $5 \times 5$  m quadrats. We searched every other quadrat throughout the grid in a checkerboard fashion, except that all quadrats surrounding an enclosure were searched, and some quadrats were not searched due to presence of thick brush or high prevalence of scrap metal. Upon finding a tag, the seed type, treatment, fate (buried uneaten, unburied uneaten, eaten), and nearest flag location were recorded. We calculated movement distance as that from the source enclosure to the flag location.

Because we sampled each grid for metal tags (rather than fully censusing) and because detectability varied for different tag types and states (buried or not), it was necessary to employ correction factors (Appendix; Moore and Swihart 2007) to estimate the number of tags actually occurring near each flag in a grid. Data for each flag were weighted by this correction factor in subsequent analyses.

We used a hierarchical generalized linear model (HGLM; Raudenbush and Bryk 2002) in program HLM 6.0 (Raudenbush et al. 2005) to model seed removal distance as a function of predictor variables. We specified a Poisson (log-linear) error distribution (since distances were  $\geq 0$ ) with overdispersion (since  $SD > \text{mean}$ ). Strictly speaking, Poisson models are used to model count data, not continuous random variables such as distance. However, we considered it practical to model mean distance as a Poisson variable (with overdispersion to deal with non-Poisson variance) because of the large numbers of zeros and short distances in our data, which were not possible to normalize using data transformations (i.e., the data were not log-normally distributed). We expected distances moved for all seeds within a given study plot to be correlated, so we modeled year and site variables (and interactions with these terms) as level 2 random effects. These included dummy variables for year (Y03, Y04, intercept = 2002), the basal area of nut trees for each site (SMAST), and the interaction of year and nut tree basal area (Y03SMAST, Y04SMAST). Level 1 predictor variables included dummy variables for seed type (BLW, SHH, NRO, PIO, intercept = WHO). Energetic rankings for seeds used, in terms of kilojoules per seed, were:  $BLW > NRO > SHH > WHO > PIO$  (Smith and Follmer 1972, Ivan and Swihart 2000, Moore and Swihart 2006), so we predicted distances to follow this order. The correction factor for each found tag was used as a weighting variable. Additionally, we included level 1 variables CACHE and TSCI. The variable CACHE was a binary variable, indicating whether the metal tag we found in spring was from a nut that was still intact (CACHE = 1) or eaten. This was to control for the possibility that seeds that were immediately eaten upon discovery (never cached) might be moved less far than cached seeds, although previous results suggested these differences would not be great (Steele et al. 2001). As with the PA study, we only used seeds that were removed from the enclosures. The variable TSCI was a

TABLE 1. Distances (mean ± SE) moved from exclosures by four seed types following three autumn years, and seed rain estimates for red oak (NRO) and white oak (WHO) at three forested sites in eastern Pennsylvania, USA.

Year, by study site	Distances acorns were moved (mean ± SE)				No. acorns/m <sup>2</sup>		Differences
	LRO	SRO	WHO	PIO	NRO	WHO	
<b>Hawk Mountain</b>							
2000	20.40 ± 2.70	11.58 ± 1.57	11.34 ± 2.20	6.22 ± 1.46	0.4 ± 0.3	0.7 ± 0.2	LRO > SRO, PIO
2001	5.91 ± 0.63	5.50 ± 0.57	3.10 ± 0.29	5.43 ± 0.78	1.9 ± 0.7	1.5 ± 0.6	All > WHO
2002	8.39 ± 0.80	7.96 ± 0.95	10.67 ± 0.82	8.09 ± 0.73	9.0 ± 1.3	1.5 ± 0.4	
<b>Mountain Top</b>							
2000	18.78 ± 1.66	12.19 ± 2.50	7.29 ± 1.78	1.84 ± 0.50	low mast†	low mast†	LRO > WHO, PIO All > PIO
2001	4.10 ± 0.89	2.32 ± 0.43	2.40 ± 0.69	3.75 ± 0.60	12.9 ± 2.4	7.9 ± 2.6	
2002	18.88 ± 2.33	9.85 ± 1.61	7.98 ± 0.90	6.00 ± 1.11	4.4 ± 0.8	0.2 ± 0.1	LRO > All
<b>Venesky</b>							
2000	11.43 ± 1.34	6.50 ± 0.63	7.83 ± 0.94	4.46 ± 0.55	1.0 ± 0.5	2.9 ± 1.1	LRO > SRO, PIO WHO > PIO
2001	8.23 ± 0.95	6.82 ± 0.79	5.42 ± 0.66	9.90 ± 1.05	7.4 ± 2.0	5.9 ± 1.6	PIO > WHO
2002	10.59 ± 1.24	9.18 ± 1.63	7.24 ± 0.60	9.52 ± 0.93	0.9 ± 0.4	0.1 ± 0.1	

Notes: Abbreviations are: PIO, pin oak; SRO and LRO, small and large red oak, respectively. “Differences” reflect nonoverlapping 95% confidence intervals, based on means and SEs.

† No acorn data were collected in 2000 at Mountain Top, but scouting suggested a low mast year.

binary variable indicating whether the found tag came from a treatment in which *Sciurus* species could access seeds (treatments 3 and 4; TSCI = 1). We expected that *Sciurus* would move seeds farther on average than smaller rodents, so that mean movement distances from these treatments would be greater. We first ran a model that included all two-way interaction terms and a three-way interaction for seed type × year × SMAST. Nonsignificant interactions were dropped and the model was refit with constituent main effects only. Finally, any nonsignificant main effects were dropped. Results are presented for the final model.

RESULTS

*Pennsylvania study*

Seed fates were determined for a total of 2670 seeds in the PA sites across the three years. At two of three sites (Hawk Mountain [HM] and Mountain Top [MT]), there were significant differences in the distances that seeds were moved as a function of seed type/size (HM,  $F_{3,14} = 7.19, P = 0.004$ ; MT,  $F_{3,15} = 13.72, P < 0.0005$ ) and as a function of year (HM,  $F_{2,8} = 4.70, P = 0.043$ ; MT,  $F_{2,8} = 12.55, P = 0.003$ ; Venesky,  $F_{2,9} = 1.88, P = 0.210$ ). With respect to seed type/size, large red oak acorns were moved significantly farther than pin oak and white oak acorns at HM and MT ( $P < 0.0005$  for all comparisons) and farther than small red oak acorns at MT ( $P < 0.0005$ ; Table 1). Large red oak acorns were moved farther than other seed types at Venesky as well ( $F_{3,17} = 3.03, P = 0.06$ ).

In terms of annual variation, shortest mean distances at HM and MT were observed during the second year of study (autumn–spring 2001–2002), which was a high- or intermediate-mast year at all three sites (Table 1). For the MT forest, year differences correlated particularly well with acorn masting; acorns were moved greater

distances in years of low acorn production (2000, 2002) than in a year of high acorn production (2001,  $P < 0.0005$  for all post hoc comparisons). At HM, the greatest mean distances were during the season of lowest seed production (2000).

For all three sites, significant interactions between year and the type/size of acorns revealed that effects of acorn characteristics on movement varied between years (HM,  $F_{6,28} = 3.77, P = 0.007$ ; MT,  $F_{6,42} = 8.96, P < 0.0005$ ; Venesky,  $F_{6,39} = 4.33, P = 0.002$ ). Examining mean movement distance for acorn types across years (Table 1) is instructive for interpreting the interactions. At HM in 2001 and 2002 (moderate and high seed crops, respectively), there were no strong differences in movement distances between acorn types, although white oak acorns generally were moved shorter distances than all other seed types in 2001. In autumn 2000, the year with the lowest oak mast, large red oak acorns were moved farther than other seed types. At MT, there were no differences between seed types in 2001, the high-mast year, whereas in 2000 and 2002 (low-mast years), large red oak acorns were moved farther than other types; pin oak acorns also were moved less far than all other types in 2000. At Venesky, differences between seed types were apparent in one of the two seed-poor years (2000); large red oak acorns were moved farther than small red oak or pin oak acorns, and white oak acorns also were moved farther than pin oak acorns. In the high-seed year (2001), pin oak acorns were moved farther than white oak acorns.

Thus at the PA sites, movement differences due to acorn type were most pronounced in low mast years (i.e., stronger density-dependent rates of caching in seed-poor years). In 2000 (low seed crop at all sites), large acorns of red oak were moved the farthest and pin oak moved the shortest distances at all sites. Large acorns of

red oak also were moved the farthest at MT in 2002, another low-mast year at that site. In years during which seed crops were highest (2001 at MT and Venesky, 2002 at HM), there were few or no differences between seed types or sizes in movement distances. Where differences occurred in any year or site, large acorns of red oak typically were moved the farthest and white oak or pin oak acorns were moved the least far. These findings generally were consistent with our predictions based on energy content per seed, except where pin oaks were moved significantly farther than white oaks (at HM and Venesky in 2001).

#### Indiana study

We obtained distance data for 5966 nuts (Table 2). The sum of weights (correction factors) for these was 11 439, which estimates the number of seeds that were removed from exclosures and would have been found had we searched all study grids in entirety and if all eaten or scatter-hoarded nuts on the study grid had a detection probability of 1. An additional 9039 tags were found inside of the exclosures (not used in this analysis), bringing the total number of seeds for whose fates we accounted to 20 478, which is ~48% of the seeds for which we searched in this study. Most of the remaining nuts were presumably larder-hoarded in trees or in burrows (Sork 1984, Steele et al. 2001), and a small number probably were dispersed outside of the study grid, beyond the radius of our search efforts.

As with the PA study, seed movement distances in IN varied with year and acorn type, and we found similar evidence of interactions between these two factors. Cumulative frequency histograms (Fig. 1) depicting the proportion of metal tags recovered at distances from 0 to >95 m from the exclosures (using 5-m distance classes) show that seeds were moved farther on average in 2002–2003 and 2004–2005 (seed-poor years), than in 2003–2004 (seed-rich year). The median removal distances for most seed types in all years ranged from 5 to 15 m, but was as high as 20 and 25 m for red oak and black walnut, respectively, in 2004–2005. Seventy-fifth percentiles were more variable and thus more informative, ranging from only 10–20 m in 2003–2004 (minimum = red oak and pin oak; maximum = black walnut and shagbark hickory) to 15–40 m in 2002–2003 (minimum = white oak and pin oak; maximum = black walnut) and 25–35 m in 2004–2005 (minimum = pin oak and shagbark hickory; maximum = black walnut and red oak).

In all years, black walnuts had the fattest tail or second fattest tail distribution (Fig. 1), suggesting greater mean seed removal distance for this species. Shagbark hickories had the second longest removal distances overall in two of the three years (2002–2003, 2003–2004). Histograms appear visually similar for red oak, pin oak, and white oak; but median, maximum, and 75th percentile distances suggest red oak acorns were moved farther than the other oak species in 2002–

TABLE 2. Number of nuts (those moved by granivores) for which fates were recorded in the Indiana, USA, study sites, by species and year.

Species	Autumn year						Totals	
	2002		2003		2004		Intact	Eaten
	Intact†	Eaten	Intact	Eaten	Intact	Eaten		
BLW	40	320	316	137	24	114	380	571
SHH	65	299	151	213	18	326	234	838
NRO	39	482	61	787	18	348	118	1617
PIO	30	336	41	514	10	357	81	1207
WHO	26	268	18	608			44	876
Totals	200	1705	587	2259	70	1145	857	5109

Notes: Metal-tagged seeds were placed in experimental exclosures in autumn and located the following spring with metal detectors. Intact seeds are those that had not yet been eaten upon their discovery. Abbreviations are: BLW, black walnut; SHH, shagbark hickory; NRO, northern red oak; PIO, pin oak; WHO, white oak.

† For the first year of study, half of the search effort was in autumn shortly after all seeds were removed from boxes. Most intact seeds found in this year were from the autumn search effort.

2003 and 2004–2005 (seed-poor years) and farther than shagbark hickory in 2004–2005 as well. In contrast with expectation, but consistent with results for some site/year combinations in the PA study, white oak acorns were not moved farther than pin oak acorns in the two years for which we had white oak data.

Because of complex interaction terms in the final hierarchical generalized linear model (Table 3), HGLM results are best interpreted graphically (Fig. 2). Variation in distance data was high for all seed types and years. The HGLM estimates were influenced heavily by tags from eaten seeds, which swamped the sample size of seeds found intact and cached (Fig. 2, Table 2). Consequently, models generally fit eaten-seed data better than cached-seed data, and the following description is for eaten-seed results (cached-seed data generally appeared to conform to eaten-seed patterns, Fig. 2). For black walnut, shagbark hickory, and red oak acorns, estimates of seed removal distance were lower overall in 2003–2004 (seed-rich year) than the other two years (Fig. 2a–d). For pin oak (Fig. 2c), movement distances were highest in 2004–2005 (a low-seed year), but there was no apparent difference in movement distances between the other low-seed year (2002–2003) and the seed-rich year (2003–2004). For white oak acorns (Fig. 2e), there were no differences in distance between the two years in which they were studied. At nearly all sites, black walnut had the highest predicted seed removal distance (Fig. 2f). Shagbark hickory had the second farthest predicted distances at most sites in 2002–2003 and 2003–2004. In 2004–2005, red oak was moved the farthest or second farthest. Consistent with the results from the PA study, fitted distance for red oak was greater than white oak and greater than pin oak in low-seed years of 2002–2003 and 2004–2005, but these three species all were moved similarly short distances on

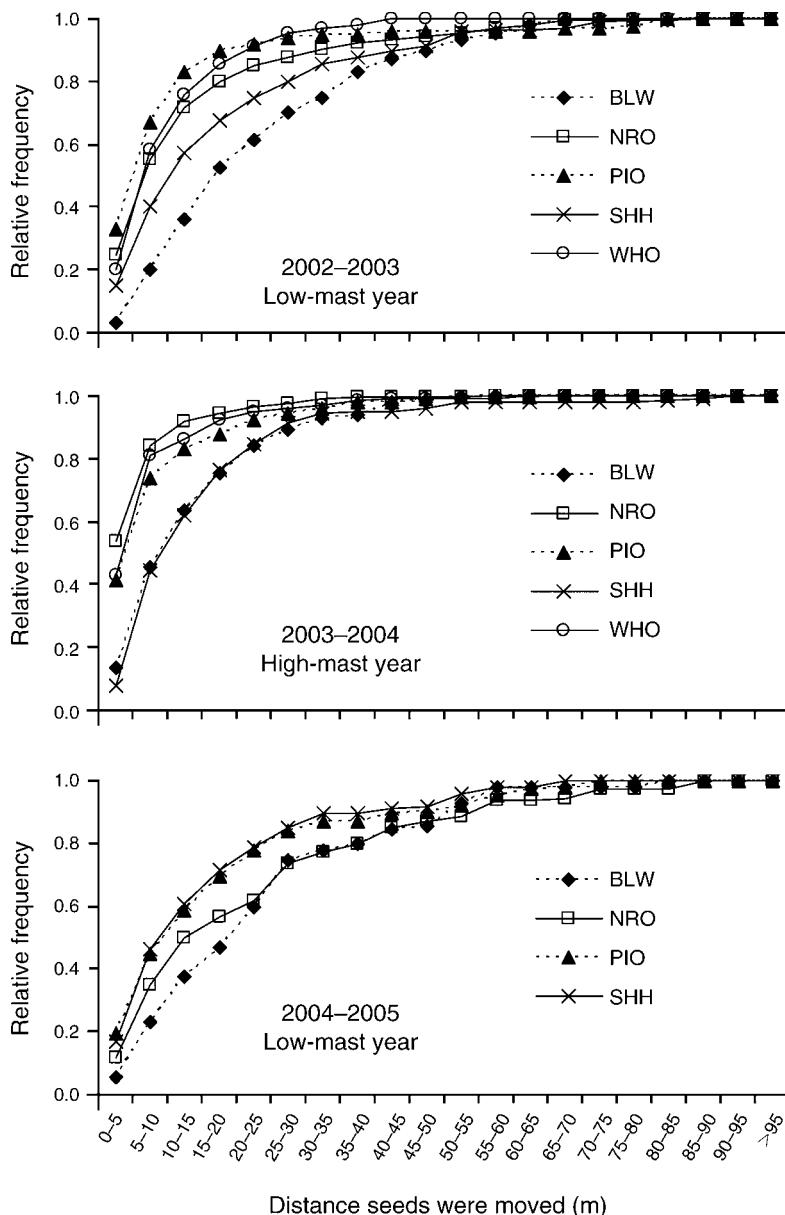


FIG. 1. Cumulative relative frequency distribution of distances that seeds were moved by granivores during three different years in forest fragments of north-central Indiana, USA. Distributions reflect corrected tag totals found at each 5-m distance class (see *Methods*). Abbreviations are: BLW, black walnut; NRO, northern red oak; PIO, pin oak; SHH, shagbark hickory; WHO, white oak.

average (<10 m) in the bumper-crop year (2003–2004). The effect of nut tree basal area at a site (SMAST) was equivocal (Fig. 2). Model estimates suggest that distances actually increased slightly with SMAST in 2002–2003 (contrary to expectation). Distances decreased with SMAST in 2003–2004 for walnut and hickory and in 2004–2005 for hickory and red oak (consistent with expectation).

For shagbark hickory and pin oak in 2002–2003 and 2003–2004, cached seeds (CACHE = 1) were usually found farther from their source than eaten seeds (Fig.

2c, d). Limited data suggested this for red oak in 2004–2005 as well (Fig. 2b). Model estimates also suggested a positive cache effect on distance for red oak in 2002–2003 and pin oak in 2004–2005, but these estimates were driven by data from other years and seed types (since we did not include three-way interaction terms) and they did not appear to fit the limited amount of data actually available for these two seed types in these years. Finally, estimates of cached-seed distances were not greater than eaten-seed distances for black walnuts, red oak acorns in 2003–2004, shagbark hickory in 2004–2005, or white

TABLE 3. Coefficient estimates for hierarchical generalized linear model fit to seed removal distance data from 29 forest fragments in north-central Indiana.

Level 1 effect ( $\beta_{ij}$ ) Level 2 effect ( $\gamma_{ij}$ )	Estimate	SE	<i>T</i>	df	<i>P</i>
<b>Intercept (<math>\beta_{0j}</math>)</b>					
Intercept ( $\gamma_{00}$ )	1.45	0.37	3.91	23	0.001
SMAST ( $\gamma_{01}$ )	0.06	0.02	2.69	23	0.014
Y03 ( $\gamma_{02}$ )	0.55	0.35	1.55	23	0.135
Y04 ( $\gamma_{03}$ )	1.56	0.34	4.56	23	<0.001
Y03SMAST ( $\gamma_{04}$ )	-0.07	0.02	-4.44	23	<0.001
Y04SMAST ( $\gamma_{05}$ )	-0.05	0.02	-3.10	23	0.005
<b>CACHE (<math>\beta_{1j}</math>)</b>					
Intercept ( $\gamma_{10}$ )	0.43	0.20	2.21	5937	0.027
SMAST ( $\gamma_{11}$ )	-0.01	0.01	-1.80	5937	0.072
Y03 ( $\gamma_{12}$ )	-0.19	0.09	-2.05	5937	0.040
Y04 ( $\gamma_{13}$ )	-0.43	0.11	-4.10	5937	<0.001
<b>BLW (<math>\beta_{2j}</math>)</b>					
Intercept ( $\gamma_{20}$ )	1.23	0.35	3.49	25	0.002
SMAST ( $\gamma_{21}$ )	-0.02	0.02	-0.87	25	0.390
Y03 ( $\gamma_{22}$ )	-0.47	0.33	-1.44	25	0.163
Y04 ( $\gamma_{23}$ )	-0.85	0.26	-3.23	25	0.004
<b>NRO (<math>\beta_{3j}</math>)</b>					
Intercept ( $\gamma_{30}$ )	0.48	0.39	1.22	25	0.235
SMAST ( $\gamma_{31}$ )	-0.01	0.02	-0.57	25	0.574
Y03 ( $\gamma_{32}$ )	-0.87	0.37	-2.38	25	0.026
Y04 ( $\gamma_{33}$ )	-0.23	0.29	-0.79	25	0.436
<b>PIO (<math>\beta_{4j}</math>)</b>					
Intercept ( $\gamma_{40}$ )	-0.30	0.42	-0.71	26	0.482
SMAST ( $\gamma_{41}$ )	0.00	0.02	-0.02	26	0.988
Y03 ( $\gamma_{42}$ )	0.34	0.39	0.87	26	0.394
<b>SHH (<math>\beta_{5j}</math>)</b>					
Intercept ( $\gamma_{50}$ )	1.07	0.41	2.61	25	0.015
SMAST ( $\gamma_{51}$ )	-0.04	0.02	-1.69	25	0.103
Y03 ( $\gamma_{52}$ )	-0.39	0.38	-1.03	25	0.312
Y04 ( $\gamma_{53}$ )	-0.83	0.26	-3.14	25	0.005
<b>CACHE <math>\times</math> BLW (<math>\beta_{6j}</math>)</b>					
Intercept ( $\gamma_{60}$ )	-0.31	0.19	-1.66	5937	0.097
<b>CACHE <math>\times</math> NRO (<math>\gamma_{7j}</math>)</b>					
Intercept ( $\gamma_{70}$ )	0.39	0.20	1.96	5937	0.050
<b>CACHE <math>\times</math> PIO (<math>\gamma_{8j}</math>)</b>					
Intercept ( $\gamma_{80}$ )	0.64	0.19	3.29	5937	0.001
<b>CACHE <math>\times</math> SHH (<math>\beta_{9j}</math>)</b>					
Intercept ( $\gamma_{90}$ )	0.12	0.18	0.68	5937	0.496

Notes: Level 1 parameters ( $\beta$ ) are functions of level 2 (site) parameters ( $\gamma$ ), such that  $\gamma_{ij}$  ( $i, j > 0$ ) represent interactions between level 2 and level 1 effects. The intercept model ( $\beta_{0j}$ ) describes white oak in 2002–2003. The linear model predicts log(distance moved). See *Methods* for variable codes.

oak acorns. The treatment type in which seeds were originally placed (TSCI) did not affect seed removal distance ( $P = 0.73$ ), indicating that seeds removed from boxes accessible to *Sciurus* were ultimately moved similar distances to seeds in boxes inaccessible to *Sciurus*.

#### DISCUSSION

Our results provided varying degrees of support for all our predictions concerning factors affecting seed-caching distance. Our first prediction was that seeds of greater energy value would be moved greater distances, to reduce success of pilferers that are expending greater effort (search area) to find such items. In the PA study

sites, large red oak acorns, the most energy-rich seed type at those sites, were moved farther than other seed types. In the IN study areas, black walnuts and shagbark hickory nuts, two items known to be preferred by rodents (walnuts only by squirrels; Ivan and Swihart 2000), were moved greater distances than other seeds in most years. Consistent with PA results, red oak acorns in IN were moved farther than pin oak and white oak in 2002–2003 and farther than all seed types except walnut in 2004–2005.

Although results from both study regions generally are consistent with our first prediction, the correlation between energetic and distance rankings across seed types was imperfect. As a rule, white oak acorns were

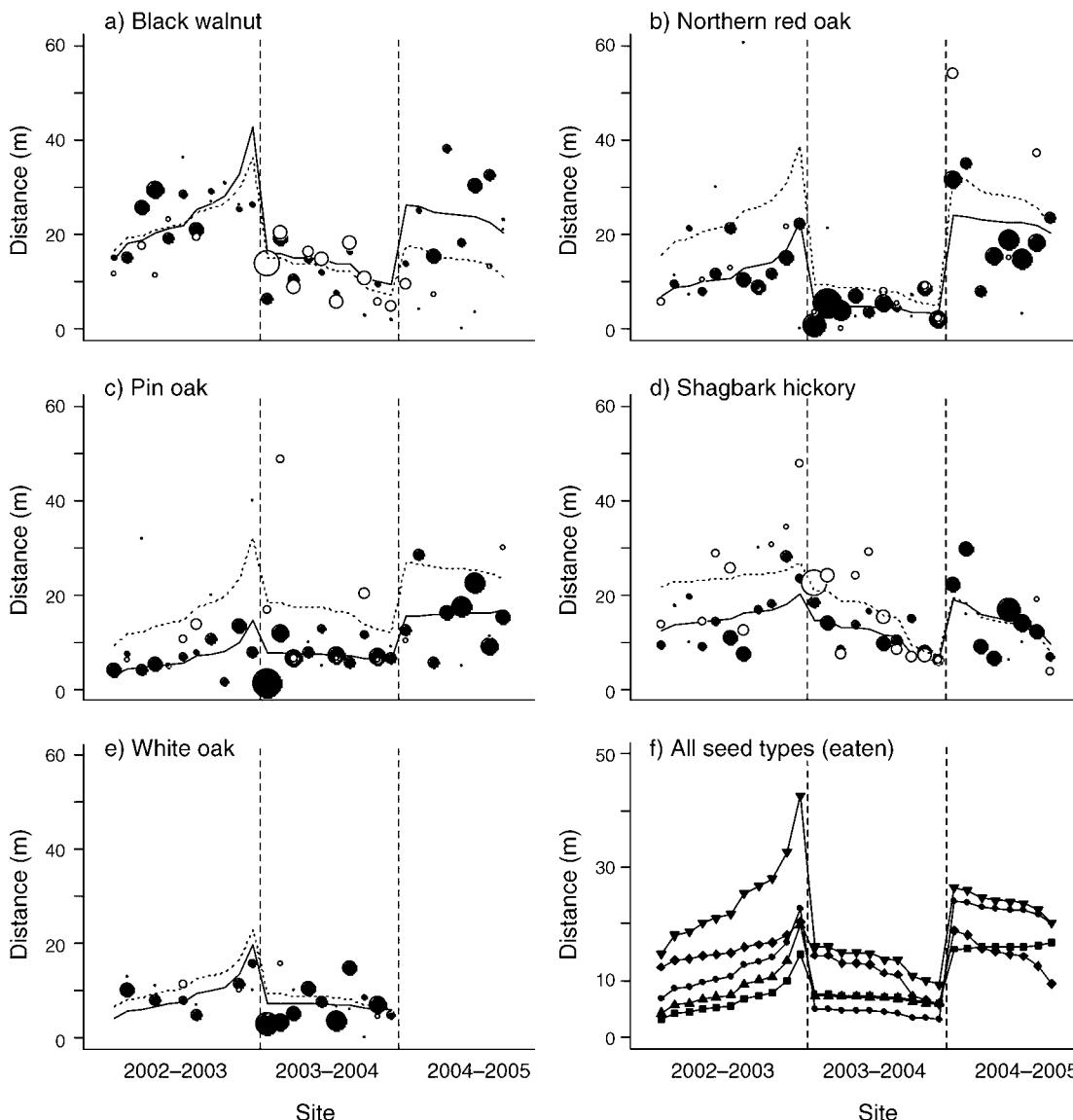


FIG. 2. Distances that five seed types were moved from exclosures by granivores in 29 different forest fragments in north-central Indiana. Study sites are on the x-axis, arranged from lowest to highest SMAST (indexed mast variation across sites) value within each year; years are divided by vertical dashed lines: high-mast year, 2003–2004; low-mast years, 2002–2003 and 2004–2005. In panels (a)–(e), circles depict mean distances for seeds found eaten (solid circles) and cached (open circles), with circle sizes scaled to the square-root of sample size for each point (adjusted by correction factors; see Appendix). Solid and dotted lines depict predicted mean distances for eaten and cached seeds, respectively, based on estimated coefficients from a hierarchical generalized linear model (Table 3). In panel (f), fitted lines for eaten seeds of each seed type (same as solid lines in panels a–e) are plotted together to facilitate comparison; in order of energetic rank (i.e., expected distance rank), species are: black walnut (▼), northern red oak (●), shagbark hickory (◆), white oak (▲), pin oak (■).

not dispersed farther than pin oak acorns, and in IN, red oak acorns were not always dispersed farther than shagbark hickory nuts. This indicates that optimal cache densities for different seed types do not simply depend on energetic value, but probably also depend on other seed characteristics. For example, white oak acorns are unique among seed types used in this study in that they germinate in autumn, immediately after seed drop (rather than after winter dormancy). Acorns become less valuable as a food item once their energy stores

become transferred to their taproots (Smith and Follmer 1972, Fox 1982), so white oak acorns are effectively more perishable as a food item for rodents. Several studies have shown that seed perishability affects foraging behavior and cache management decisions (Post and Reichman 1991, Gendron and Reichman 1995, Kotler et al. 1999, Goheen et al. 2003) and that white oak acorns in particular are selectively eaten (rather than cached) over those of red oak species due to their perishability (Hadj-Chikh et al. 1996, Smallwood et

al. 2001). If white oaks are less valuable as a cached resource or if cached white oaks are retrieved early and not re-cached multiple times (pilferage risk is low), this could explain why we did not find white oak acorns moved farther than pin oak acorns in spite of higher energy values for the former. Similarly, greater dispersal distances of shagbark hickory nuts compared to red oak acorns in two of the years at IN sites may have been influenced by the higher protein : tannin or lipid : tannin ratios found in hickory nuts (Moore and Swihart 2006).

Our second prediction, that seeds would be moved farther when ambient food abundance was lower, was strongly supported by data for annual variation in mast abundance but less so by data for across-site (within-year) variation in seed crop. In PA, the overall trend for red oak (both sizes) and white oak was toward shorter movement distances following autumn 2001, which was the best mast year overall. However, the Hawk Mountain site had its greatest measured mast abundance in 2002, yet seed movement distances were still shortest following the 2001 crop. Thus, seed movement distances at Hawk Mountain seemed more consistent with the regional mast pattern (average annual effect across sites) than the site-specific effect. In IN, seed movement distances were shortest in the high-mast year and greatest in the two seed-poor years, but the relationship between seed removal distance and basal area of nut-bearing trees (a proxy for mast abundance) at different sites was inconsistent. Model-fitted movement distances for some seed types were inversely related to nut tree basal area in 2003–2004 (BLW, SHH) or 2004–2005 (SHH, NRO), but in 2002–2003, the effect appeared to be opposite. Lack of consistent support may be due to unmeasured factors such as abundance and diversity of granivores or other food types (e.g., maple seeds, soft mast) during the caching period or simply because of inaccuracies in local nut production estimates (seed traps in PA and variable-plot indices in IN). For example, relationships between mast abundance and tree basal area may be weak and vary across species (Greene and Johnson 1994, Greenberg 2000). Taken with the highly variable nature of seed distance data (Fig. 2), which will make subtle effects difficult to detect, this underscores the need to collect accurate and precise information on local seed abundance and to examine all food types of possible importance (not just preferred types) in future studies that compare results across sites.

Interactions between annual seed crop and seed type were important factors in our study, with the strongest seed type effects occurring during years of low food abundance. In situations when risk of pilferage is low or inconsequential (e.g., during high food abundance), cache loss rates should be more density independent and low in general; thus, cache management costs should be minimized (by moving seeds less far), and they should probably be more similar across food types. This seemed the case in our study, as evidenced by similar (and lower) seed movement distances for

different acorn types in seed-rich years in both IN and PA. However, in IN, black walnuts and shagbark hickory nuts were moved farther than acorns even in the seed-rich year, suggesting a particularly high importance of these food types, whereby extra effort was expended to reduce pilferage of these items even in years when food was not limiting.

Our study designs did not permit us to determine the manner in which factors affecting seed caching distance differed among granivorous rodent species in the study communities because cachers and consumers of each recovered tag were not identified. In IN, we attempted to identify species-specific effects with different enclosure treatments but found no differences in removal distances between treatments. Only *Sciurus* species typically are viewed as scatter-hoarders in this system; however, all seed-consuming rodents in our study are known to scatter-hoard nuts to some degree (Abbott and Quink 1970, Shaffer 1980, Hurly and Robertson 1987, Vander Wall 1990, Clarke and Kramer 1994, Hurly and Lourie 1997, Goheen and Swihart 2003). Therefore we may conservatively view our results as average effects for the entire seed-caching community. However, we believe that our results, at least for seeds found buried and uneaten, were most strongly affected by *Sciurus* behavior. Black walnuts would have been utilized only by tree squirrels. Red squirrels were not present at the PA sites. For IN, Goheen and Swihart (2003) found that red squirrels in the same study region larder hoarded almost 90% of the items that they cached (red oak acorns, black walnuts, and bur oak [*Q. macrocarpa*] acorns), and most seeds hoarded by eastern chipmunks in autumn are cached in their nest burrows in preparation for winter hibernation (Yahner 1975, Vander Wall 1990). Southern flying squirrels are area-sensitive and would not have occurred in most study patches in IN (Nupp and Swihart 2000, Moore and Swihart 2005). Little is known about hoarding strategies by white-footed mice in deciduous forests, but a substantial proportion of seeds moved by mice were probably larder-hoarded (Vander Wall 1990), and we assume that most tags found at greater distances (e.g.,  $\gg 30$  m) from their source were probably not moved there by mice (Abbott and Quink 1970). However, we did find several surface caches containing  $>10$ – $20$  partially eaten shagbark hickory nuts (typically under a shrub) that we usually attributed to white-footed mice. If *Sciurus* was primarily responsible for the observed dispersal patterns, this implies that many seeds initially cached by other species (e.g., seeds from treatments 1 and 2) were subsequently found and eaten or recached by *Sciurus*.

In summary, we have provided additional evidence that energy content is an important factor affecting cache spacing by the community of scatter-hoarding rodents in eastern deciduous forests. However, we found that the importance of this factor depends on food availability in a given year and that other food

characteristics (e.g., those affecting seed perishability) also may affect cache spacing. Contrary to traditional optimization models and the animal-mediated seed dispersal hypothesis, our results are most consistent with studies that have found that rodents expended less effort in moving and caching seeds (in terms of mean seed-carrying distances) in a year of high food availability than in years of low food availability (Theimer 2001, Jansen et al. 2004). This result may be explained as a minimization of energy costs in times when high cache retrieval rates are less threatened or less important, and it suggests that cache loss rates may be more strongly density-dependent in times of low seed abundance.

Finally, we emphasize the large amount of variability inherent in data in seed dispersal studies and the implications of this variability for identifying general dispersal or behavioral patterns that hold true for multiple systems and taxa. Ours is one of few studies to investigate multiple factors affecting seed dispersal distance at a large number of study sites and in more than one region. Our results were based on a large number of tagged seeds, yet we found substantial variation in the effects of year and seed type on dispersal distances across sites. Had we only conducted our experiments at two to three study sites, our inferences may have been quite different. This could explain some inconsistencies between previous studies that have addressed similar questions. We therefore stress the value of using large sample sizes, multiple study sites, investigating interactive effects, and attempting to model novel sources of variation in seed dispersal distance (e.g., the role of different disperser species) when possible.

#### ACKNOWLEDGMENTS

We thank J. Goheen, D. Jacobs, P. Waser, and two anonymous reviewers for helpful comments on early manuscript drafts or study design. We are grateful to A. Houston, P. Kennedy, J. Griggs, S. Armstrong, A. Castaneda, L. Kriehn, L. Connolly, M. Black, S. Lawyer, S. Reed, M. Sherick, R. From, S. Duncan, A. Berger, J. Orthman, A. Bear, S. Carrow, N. Veldhuizen, K. Neyland, J. Taraschke, S. Pearson, L. Gizza, T. Genna, and B. Beehler for their data collection efforts. We thank T. Vanesky, Hawk Mountain Sanctuary, and many landowners in Indiana for permission to work on their properties. P. O'Conner provided mast index data for Indiana. Support for this project was provided by the Cooperative State Research, Education, and Extension Service, U.S. Department of Agriculture, under Agreement Number 2000-04649, by the John S. Wright Fund, Department of Forestry and Natural Resources, Purdue University, and by the National Science Foundation (DBI-9978807).

#### LITERATURE CITED

- Abbott, H. G., and T. F. Quink. 1970. Ecology of eastern white pine seed caches made by small forest mammals. *Ecology* 51:271–278.
- Brewer, S. W. 2001. Predation and dispersal of large and small seeds of a tropical palm. *Oikos* 92:245–255.
- Clarke, M. F., and D. L. Kramer. 1994. Scatter-hoarding by a larder-hoarding rodent: intraspecific variation in the hoarding behavior of the eastern chipmunk, *Tamias striatus*. *Animal Behaviour* 48:299–308.
- Clarkson, K., S. F. Eden, W. J. Sutherland, and A. I. Houston. 1986. Density dependence and magpie food hoarding. *Journal of Animal Ecology* 55:111–121.
- Cowie, R. J., J. R. Krebs, and D. F. Sherry. 1981. Food storing by marsh tits. *Animal Behaviour* 29:1252–1259.
- Daly, M., L. F. Jacobs, M. I. Wilson, and P. R. Behrends. 1992. Scatter hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. *Behavioral Ecology* 3:102–111.
- Fox, J. F. 1982. Adaptation of gray squirrel behavior to autumn germination by white oak acorns. *Evolution* 36:800–809.
- Gendron, R. P., and O. J. Reichman. 1995. Food perishability and inventory management: a comparison of three caching strategies. *American Naturalist* 145:948–968.
- Goheen, J. R., and R. K. Swihart. 2003. Food-hoarding behavior of gray squirrels and North American red squirrels in the central hardwoods region: implications for forest regeneration. *Canadian Journal of Zoology* 81:1636–1639.
- Goheen, J. R., R. K. Swihart, and J. H. Robins. 2003. The anatomy of a range expansion: changes in cranial morphology and rates of energy extraction of North American red squirrels from different latitudes. *Oikos* 102:33–44.
- Greenberg, C. H. 2000. Individual variation in acorn production by five species of southern Appalachian oaks. *Forest Ecology and Management* 132:199–210.
- Greene, D. F., and E. A. Johnson. 1994. Estimating the mean annual seed production of trees. *Ecology* 75:642–647.
- Hadj-Chikh, L. Z., M. A. Steele, and P. D. Smallwood. 1996. Caching decisions by grey squirrels: a test of the handling time and perishability hypotheses. *Animal Behaviour* 52:941–948.
- Hurly, T. A., and S. A. Lourie. 1997. Scatterhoarding and larderhoarding by red squirrels: size, dispersion, and allocation of hoards. *Journal of Mammalogy* 78:529–537.
- Hurly, T. A., and R. J. Robertson. 1987. Scatterhoarding by territorial red squirrels: a test of the optimal density model. *Canadian Journal of Zoology* 65:1247–1252.
- Husch, B., C. I. Miller, and T. W. Beers. 1982. *Forest mensuration*. Third edition. Krieger, Malabar, Florida, USA.
- Ivan, J. S., and R. K. Swihart. 2000. Selection of mast by granivorous rodents of the central hardwood forest region. *Journal of Mammalogy* 81:549–562.
- Jansen, P. A., F. Bongers, and L. Hemerik. 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs* 74:569–589.
- Kelly, D. 1994. The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution* 9:465–470.
- Koenig, W. D., and J. M. H. Knops. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. *American Naturalist* 155:59–69.
- Koenig, W. D., and J. M. H. Knops. 2005. The mystery of masting in trees. *American Scientist* 93:340–347.
- Kotler, B. P., J. S. Brown, and M. Hickey. 1999. Food storability and the foraging behavior of fox squirrels (*Sciurus niger*). *American Midland Naturalist* 142:77–86.
- McCracken, K. E., J. W. Witham, and M. L. Hunter. 1999. Relationships between seed fall of all three tree species and *Peromyscus leucopus* and *Clethrionomys gapperi* during 10 years in an oak–pine forest. *Journal of Mammalogy* 80:1288–1296.
- Moore, J. E., and R. K. Swihart. 2005. Modeling patch occupancy by forest rodents: incorporating detectability and spatial autocorrelation with hierarchically structured data. *Journal of Wildlife Management* 69:933–949.
- Moore, J. E., and R. K. Swihart. 2006. Nut selection by captive blue jays: importance of availability and implications for seed dispersal. *Condor* 108:377–388.
- Moore, J. E., and R. K. Swihart. 2007. Importance of fragmentation-tolerant species as seed dispersers in disturbed landscapes. *Oecologia* 151:663–674.

- Nupp, T. E., and R. K. Swihart. 2000. Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy* 81:512–526.
- Post, D., and O. J. Reichman. 1991. Effects of food perishability, distance, and competitors of caching behavior by eastern woodrats. *Journal of Mammalogy* 72:513–517.
- Raudenbush, S. W., and A. S. Bryk. 2002. Hierarchical linear models: applications and data analysis methods. Second edition. Sage, Thousand Oaks, California, USA.
- Raudenbush, S., A. Bryk, and R. Congdon. 2005. HLM for Windows. Version 6.0. Scientific Software International, Lincolnwood, Illinois, USA.
- Riege, D. A. 1991. Habitat specialization and social factors in distribution of red and gray squirrels. *Journal of Mammalogy* 72:152–162.
- Schnurr, J. L., R. S. Ostfeld, and C. D. Canham. 2002. Direct and indirect effects of mast on rodent populations and tree seed survival. *Oikos* 96:402–410.
- Shaffer, L. 1980. Use of scatterhoards by eastern chipmunks to replace stolen food. *Journal of Mammalogy* 61:733–734.
- Sherry, D. M. Avery, and A. Stevens. 1982. The spacing of stored food by marsh tits. *Zeitschrift für Tierpsychologie* 58: 153–162.
- Smallwood, P. D., M. A. Steele, and S. H. Faeth. 2001. The ultimate basis of the caching preferences of rodents, and the oak-dispersal syndrome: tannins, insects, and seed germination. *American Zoologist* 41:840–851.
- Smith, C. C., and D. Follmer. 1972. Food preferences of squirrels. *Ecology* 53:83–91.
- Sork, V. L. 1984. Examination of seed dispersal and survival in red oak, *Quercus rubra* (Fagaceae), using metal-tagged acorns. *Ecology* 65:1020–1022.
- Stapanian, M. A., and C. C. Smith. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. *Ecology* 59:884–896.
- Stapanian, M. A., and C. C. Smith. 1984. Density-dependent survival of scatterhoarded nuts: an experimental approach. *Ecology* 65:1387–1396.
- Steele, M. A., G. Turner, P. D. Smallwood, J. O. Wolff, and J. Radillo. 2001. Cache management by small mammals: experimental evidence for the significance of acorn-embryo excision. *Journal of Mammalogy* 82:35–42.
- Tamura, N., Y. Hashimoto, and F. Hayashi. 1999. Optimal distances for squirrels to transport and hoard walnuts. *Animal Behaviour* 58:635–642.
- Theimer, T. C. 2001. Seed scatterhoarding by white-tailed rats: consequences for seedling recruitment by an Australian forest tree. *Journal of Tropical Ecology* 17:177–189.
- Vander Wall, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, Illinois, USA.
- Vander Wall, S. B. 1995. Sequential patterns of scatter hoarding by yellow pine chipmunks (*Tamias amoenus*). *American Midland Naturalist* 133:312–321.
- Vander Wall, S. B. 2002. Mast in animal-dispersed pines facilitates seed dispersal. *Ecology* 83:3508–3516.
- Vander Wall, S. B. 2003. Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. *Oikos* 100:25–34.
- Waite, T. A. 1988. A field test of density-dependent survival of simulated gray jay caches. *Condor* 90:247–249.
- Xiao, Z., Z. Zhang, and Y. Wang. 2004. Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. *Forest Ecology and Management* 195:141–150.
- Xiao, Z., Z. Zhang, and Y. Wang. 2005a. The effects of seed abundance on seed predation and dispersal by rodents in *Castanopsis fargesii*. *Plant Ecology* 177:249–257.
- Xiao, Z., Z. Zhang, and Y. Wang. 2005b. Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. *Acta Oecologia* 28:221–229.
- Yahner, R. H. 1975. Adaptive significance of scatter hoarding in the eastern chipmunk. *Ohio Journal of Science* 75:176–177.

#### APPENDIX

A description of correction factors used to estimate the number of tagged seeds moved to various distances at Indiana study sites (*Ecological Archives* E088-152-A1).