



Original article

Cache placement, pilfering, and a recovery advantage in a seed-dispersing rodent: Could predation of scatter hoarders contribute to seedling establishment?

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ARTICLE INFO

Article history:

Received 14 October 2010

Accepted 3 May 2011

Available online 31 May 2011

Keywords:

Scatter hoarding

Pilfering

Seed dispersal

Cache recovery

Eastern gray squirrel

Sciurus

Quercus

ABSTRACT

Scatter-hoarding mammals are thought to rely on spatial memory to relocate food caches. Yet, we know little about how long these granivores (primarily rodents) recall specific cache locations or whether individual hoarders have an advantage when recovering their own caches. Indeed, a few recent studies suggest that high rates of pilferage are common and that individual hoarders may not have a retriever's advantage. We tested this hypothesis in a high-density (>7 animals/ha) population of eastern gray squirrels (*Sciurus carolinensis*) by presenting individually marked animals (>20) with tagged acorns, mapping cache sites, and following the fate of seed caches. PIT tags allowed us to monitor individual seeds without disturbing cache sites. Acorns only remained in the caches for 12–119 h (0.5–5 d). However, when we live-trapped and removed some animals from the site immediately after they stored seeds (thus simulating predation), their seed caches remained intact for significantly longer periods (16–27 d). Cache duration corresponded roughly to the time at which squirrels were returned to the study area. These results suggest that squirrels have a retriever's advantage and may remember specific cache sites longer than previously thought. We further suggest that predation of scatter hoarders who store seeds for long periods and also possess a recovery advantage may be one important mechanism by which seed establishment is achieved.

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1. Introduction

Seed dispersal is a key trophic interaction that influences a range of ecological processes such as plant recruitment and demography, community assembly, and even maintenance of plant species diversity (Herrera et al., 1994; Schupp and Fuentes, 1995; Terborgh et al., 2002, 2008). Despite its significance, however, the study of seed dispersal still awaits a comprehensive theoretical framework because so little is understood about the specific mechanisms by which seeds are moved and seedlings are established (Schupp, 2007). Seed dispersal processes in some systems involve complex arrays of diffuse plant–animal interactions that are difficult to evaluate collectively, although recent advances using network theory provide a promising framework for modeling these interactions (e.g., Bascompte and Jordano, 2007).

In many temperate and some subtropical and tropical ecosystems, numerous plant species (e.g., *Quercus* spp.) depend heavily on just a few species of scatter-hoarding mammals and birds for

dispersal, establishment, and recruitment (Smith and Reichman, 1984; Steele et al., 2005, 2007; Theimer, 2005; Vander Wall, 1990). Scatter hoarders and plants in these systems often share a long history of direct mutualism, but the animal acts as a seed predator as well as a dispersal agent. Hence, the process of seed dispersal is closely tied to the animals' fine-scale behavioral decisions (Vander Wall, 2010), and an understanding of seed dispersal and survival requires an intimate awareness of the factors that influence seed placement and recovery, as well as the failure of cache recovery. Specifically, seedling establishment depends critically on decisions regarding what to eat, what to store, and how long to store it.

From the perspective of the scatter hoarder, patterns of cache placement are determined by the costs and benefits of cache establishment, weighted by the probability of cache recovery. For scatter hoarding to evolve, the animal must recover enough of its stored food to survive and reproduce (Andersson and Krebs, 1978; Smith and Reichman, 1984; Vander Wall and Jenkins, 2003). Yet, unlike larder hoarders, which store food in a central location and then vigorously defend it, scatter hoarders cache individual food items in widely dispersed cache sites and rely on little if any direct protection of caches (but see Steele et al., 2008). The result for

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scatter-hoarding animals is that the dispersion of caches, especially as it relates to pilfering risks likely influences the fitness of many scatter-hoarding species.

Despite the ability of scatter-hoarding birds and mammals to recover some of their own food stores (see review by Clayton and Lee, 1998), there exists considerable evidence that pilferage by conspecifics (Dally et al., 2006; Gerhardt, 2005; Guimaraes et al., 2005; Murray et al., 2006; Preston and Jacobs, 2001; Vander Wall and Jenkins, 2003), and perhaps other species as well (e.g., Wauters et al., 2002; Schmidt and Ostfeld, 2008; Thayer and Vander Wall, 2005), may be common in nature and can account for considerable losses for food-hoarding species, especially those that scatter hoard (Clarke and Kramer, 1994; Daly et al., 1992; Kraus, 1983; Sherry et al., 1982; Stapanian and Smith, 1978). Vander Wall and Jenkins (2003), for example, report pilferage rates of artificially made caches as high as 30% per day, and argue that such rates exert strong selective pressure on scatter hoarders. They further argue that reciprocal pilfering between conspecifics may represent an evolutionary stable strategy that allows scatter hoarders to both engage in the behavior and at the same time overcome the negative effects of high pilferage rates.

The work of Vander Wall and Jenkins (2003) supports the widely held assumption that pilferage is one of the key selective pressures that has shaped the evolution of scatter-hoarding behavior. However, despite wide agreement on this point, pilfering behavior has been studied in relatively few systems, especially in free-ranging scatter hoarders (but see Murray et al., 2006; Vander Wall et al., 2006; Vander Wall, 2010; for examples).

In this study we examine scatter hoarding and pilfering behavior in a high-density population of eastern gray squirrels (*Sciurus carolinensis*). Previous observations in this population (Steele et al., submitted for publication, 2001a) suggested extremely high rates of pilferage. Gray squirrels in this system regularly scatter hoard throughout the year, and preliminary observations suggest that hoarded items usually are removed within 48 h (personal observations, M. A. Steele and associates). However, these observations do not make clear whether caches are pilfered or are recovered by their owners. Hence, our goal was to determine the true rates of pilferage and to establish precise recovery rates of cache owners. We hypothesized that in this system, high rates of reciprocal pilfering allowed scatter-hoarding behavior to exist as predicted by Vander Wall and Jenkins (2003).

2. Materials and methods

2.1. Study site

We conducted the field experiments in June to September of 2007 and June to October 2008 in Kirby Park, a >45-ha urban park in Wilkes-Barre, Pennsylvania, USA (41°15'N, 75°53'W). All behavioral experiments were conducted in the north end of the park in a semi-natural stand of mature deciduous trees dominated by pin oak (*Quercus palustris*), red oak (*Quercus rubra*) and silver maples (*Acer saccharinum*), with an open mowed ground cover. The site is bordered by an urban area to the west and a heavily forested riparian flood plain of the Susquehanna River to the east. Squirrels frequently move between the park and riparian forest, but often reside in the numerous tree cavities in the park. Raptors (e.g., red-tailed hawks [*Buteo jamaicensis*] and Coopers hawks [*Accipiter cooperii*]) and unleashed dogs were common in the park and often attempted to prey on the squirrels (M. Steele, personal observation).

The park's proximity to a larger riparian forest ensures a natural population of squirrels with behavior typical of wild squirrels, except that the majority of squirrels are well habituated to human

activity, making them ideal for detailed behavioral experiments. Densities on the site vary seasonally, but previous mark-recapture efforts indicated densities between 5 and 15 animals per ha (Steele, unpublished data), far greater than is typically observed in more rural populations (usually <5 per ha; Steele and Koprowski, 2001).

2.2. Marking and handling of animals

To ensure proper identification of individual squirrels during experimental trials, we live-trapped and marked a significant number (>60) of the gray squirrels residing in the north end of the park during both years of the study. Beginning in early June, we live-trapped squirrels and immediately tagged and released them at the site of capture. Traps were placed and set twice daily just after sunrise and a few hours before dusk, baited with peanut butter, and then observed from a distance (>30 m) until animals were captured.

Captured squirrels were immediately removed from the trap and restrained in a cloth cone for measuring and tagging. Squirrels were ear tagged with uniquely numbered #1 Monel ear tags (National Band and Tag Inc., Newport, KY), sexed, weighed, and then individually marked on the fur with both Nyanzol dye (Greenville Colorants Inc., Clifton NJ) and a small freeze brand (Quick-freeze, Miller Stephenson, Sylmar, CA) that allowed individual identification from 40 m or more. In previous studies we found that this combination of techniques helped to ensure proper identification for both behavioral observations and subsequent live-trapping surveys. Although the Nyanzol fur dye allows a concise mark for behavioral observations, it is lost upon molting. Alternatively, freeze branding results in a permanent mark that is often not distinctive, except for its location on the body. The combination of techniques allowed positive identification during each field encounter, which was necessary to ensure consistent identification through the study.

2.3. Acorn preparation

We conducted all feeding trials with acorns of red oak. Acorns were collected the previous autumn and packaged in storage bags according to the tree from which they were collected, and stored at 3 °C until the experiments the following spring and summer. At the time of the experiments, we mixed three or more tree samples into a composite sample from which acorns were then randomly chosen for the experiments. We prepared experimental acorns by drilling a small hole (<2 mm) in the basal half of the acorn, inserting a single uniquely numbered PIT (passive integrated transponder; Biomark Inc., Boise ID), and sealing the hole with wood glue and sanding dust from the acorn shell. After the glue dried, we then concealed the hole with an odorless furniture wax to further reduce the probability that the animals would perceive the nut as uncompromised and storable.

2.4. Feeding trials

Feeding trials were conducted from June to mid-August in 2007 and 2008. All experiments were conducted a few months before the natural period of autumn caching for several reasons: (1) We knew from previous preliminary trials (1999–2001, Steele unpublished data) that animals regularly scatter hoarded during the summer if experimental food was made available. (2) General patterns of scatter hoarding and cache recovery (i.e., recovery or pilfering of nuts within approximately 48 h) did not differ between autumn and summer. (3) Animals were far more difficult to trap or observe in autumn when food was abundant. And, (4) during the summer

other foods were not available for scatter hoarding; hence it was possible to know the entire contents of each animal's caches during our experiments.

Daily feeding trials were conducted a few hours after sunrise and a few hours before sunset. These trial periods were selected because they corresponded closely with peaks in activity and times during the day when the animals were most likely to be satiated. Feeding trials were performed with 2–4 observers who worked collectively to complete a feeding trial on a single focal animal. To begin a feeding trial, one observer approached a marked squirrel first tossing either a peanut or an untagged red oak acorn to the animal, allowing the animal to eat or cache the nut. If the animal ate the nut, this procedure was repeated with the same focal animal until it cached its first nut. This preliminary feeding sequence was performed to ensure satiation of the focal animal and increase the chances of subsequent caching.

Upon satiation, the focal animal was presented a single PIT-tagged acorn, tossed from a distance of 5 m or more. Observers then continued to observe the focal animal until the nut was eaten or cached. The animal was then presented with another tagged nut and again observed by two or more observers. If the first nut was cached a single observer made note of the precise location of the cache, and, after the animal moved away from the cache site (>10 m), marked the cache site with a pin flag. This procedure was repeated with as many tagged acorns as the animal would cache until it moved away or retreated to a tree. Following each caching event, we recorded the acorn tag number and a detailed description of its location.

Immediately following a sequence of caching events with an individual focal animal, we verified the identity and precise location of each cached nut with a PIT-tag reader without disturbing the cache. Although nuts were usually stored just below the soil surface, they were detectable >6.0 cm below ground. We then measured and recorded the distance (± 0.10 m) and the compass bearing from the nearest permanent object (e.g., tree) to the cache, and removed each pin flag.

2.5. Monitoring of caches

Because previous observations using these feeding techniques indicated that caches typically were recovered within a few days, we revisited and verified each cache every 12 h, usually once in early morning and again before dusk. We used the compass bearing and distance to determine the approximate location of the caches and then swept the ground with the PIT-tag reader to verify the presence or absence of the cached acorn. A positive reading of the same pit tag verified the presence of the cached acorn, and an obvious shallow pit, often with the presence of acorn shells, verified that the nut was removed. Failure to detect either of these after repeated visits to the cache resulted in elimination of the caching event from the data set. This occurred in about 10% of the cached acorns.

2.6. Simulated predation of cache owners

Immediately following a feeding trial in which any acorns were cached, we attempted to capture the focal animal before acorns were pilfered by a conspecific or retrieved by the cache owner by setting live traps in the vicinity of the caching area and the squirrel's nest

tree if its identity was known. In the vast majority of instances, we were unable to live trap the focal animal before tagged acorns were removed from the caches. However over the course of two years, we successfully trapped six animals before caches were removed. Although small, this sample size was more than sufficient to evaluate our hypotheses and accurately estimate actual pilferage rates.

Immediately upon capture, we verified that caches were still intact. We transferred the squirrel to an outdoor holding facility 20 km from the study area. Each squirrel removed from the study area was housed individually in a holding cage (2 m \times 1 m \times 1 m) inside a larger common outdoor holding facility (10 m \times 2.5 m \times 2.5 m). During captivity, squirrels were provided with a wooden nest box (30 \times 15 \times 15 cm) with bedding and an ample supply of water, fruit, nuts, sunflower seeds and rodent chow. We varied the time squirrels were held in captivity (21–44 days) to test whether the holding time was related to cache removal time. Following captivity, all squirrels were transferred back to the study area and released at their sites of capture.

2.7. Data analysis

We used a two-way factorial ANOVA to evaluate the effects of year and squirrel removal on time that cached acorns remained in the ground. Because sample sizes for individual squirrels were sometimes small, a nested design by individual squirrel was not possible. We therefore calculated mean time in the cache for each individual squirrel and also compared the means of squirrels that were temporarily removed from the site with those that were not using an ANOVA. For two individual animals, data was available both before and after the squirrel was removed from the site. For these data, a Mann-Whitney *U*-test was used for comparing time in the cache before and after removal.

We further estimated long-range cache recovery and pilferage rates using two alternative models. In both models, we assumed that the amount of time from when an acorn is cached until it is removed, *y*, is exponentially distributed, and that cache recovery and pilferage rates are additive. Model 1 contained two parameters: the rate of recovery by cache owners (λ_r) and the pilfering rate (λ_p). Model 2 split λ_r into separate rates, λ_{r0} , which applies before a cache owner was captured, and λ_{r1} , after the owner was returned to the study area. The model parameters estimate the number of caches recovered or pilfered per hour. When the owner is present, the likelihood of recovery or pilfering *y* hours after cache establishment in Model 1 is,

$$P(y/\lambda, \text{owner present}) = (\lambda_r + \lambda_p)e^{-(\lambda_r + \lambda_p)y}$$

For Model 2, λ_r is replaced by either λ_{r0} or λ_{r1} , as appropriate. The likelihood that the cache will be pilfered at time *y* if the owner was removed immediately after making the cache is,

$$P(y/\lambda, \text{owner removed}) = \lambda_p e^{-\lambda_p y}$$

Because the exponential distribution has no memory (i.e., $P[\text{cache } y \text{ survives to } t + s | y \text{ survives to } t] = P[y \text{ survives to } s]$), we can classify the likelihoods of individual cache histories into three categories depending on when the cache was removed, relative to the time of the owner's removal (t_1) and return (t_2) (eqn. (1)):

$$P(y = t) = \begin{cases} P(y = t | I = 1) & y < t_1 \\ P(y \geq t_1 | I = 1) P(y = t - t_1 | I = 0) & t_1 \leq y < t_2 \\ P(y \geq t_1 | I = 1) P(y \geq t_2 - t_1 | I = 0) P(y = t - t_2 | I = 1) & y \geq t_2 \end{cases} \quad (1)$$

Here, $I = 1$ if the cache owner is present on the site and 0 otherwise. We fitted eqn. (1) by minimizing the negative log-likelihood and estimated the covariance of λ as the inverse of the observed Fisher information matrix. Because λ are constrained to be >0 , we also estimated 95% confidence intervals using the likelihood profile. We compared the alternative models using the difference in Akaike's information criterion (ΔAIC , Burnham and Anderson, 2002).

3. Results

In 2007 we successfully mapped and followed the fate of 80 caches of 21 squirrels. The caches tracked per squirrel ranged from 1 to 15 (mean \pm SE, 3.33 ± 0.87). Three of these squirrels were successfully removed from their home range within 24 h of preparing caches and prior to the removal of 10 of their caches. In 2008, we followed the fate of 101 caches of 18 squirrels. Caches per squirrel ranged between 1 and 18 per animal (5.07 ± 1.28). Three additional squirrels were removed in 2008 prior to the removal of 20 of their caches.

In 2007, mean cache longevity (i.e., time acorns remained in the cache), for caches belonging to squirrels not removed from the study area, ranged from 2 h to 170 h but averaged 25 h (± 7.7) for all caches (Fig. 1a). A similar, but marginally longer pattern of cache longevity was observed in 2008 for caches belonging to squirrels not removed from the study area ($F = 3.91$, $DF = 1, 173$, $P = 0.049$); cache longevity for these 17 squirrels ranged from 1 to 240 h and averaged 39 h (± 9.51 ; Fig. 1bs).

Cache longevity for the 6 squirrels successfully live-trapped and removed was significantly longer than for caches of animals that remained on their home ranges ($F = 144.52$, $DF = 1, 173$, $P < 0.0001$; Fig. 1C, D). Likewise, comparisons of the mean cache longevity for these two groups of squirrels were notably different ($F = 214$, $DF = 1, 40$, $P < 0.0002$). Mean cache longevity for squirrels temporarily removed from their home ranges was greater than 443 h in both years of the study, more than 10 fold that of caches for animals not removed from the study site (Fig. 1).

For one animal in 2007, a small sample of caches was monitored both before ($n = 4$) and after its removal ($n = 7$). The longevity of caches prior to removal of this animal (57.5 ± 110) was 8-fold lower than after removal (490 ± 105 ; Mann Whitney- U , $U' = 23$, $P = 0.018$). Likewise, for a second animal in 2008, a similar pattern was observed: (before removal, 10 ± 150 [$n = 4$]; after removal, 330 ± 160 [$n = 3$]; MWU, $U' = 12$, $P = 0.034$). A third animal (2008) for which data was collected before and after removal also showed the same pattern (before removal, 45 ± 12 [$n = 9$]; after removal, 630 [$n = 1$]), but small sample sizes prevented statistical comparisons of these data. Regardless, mean cache longevity increased by >14 fold for this animal.

By comparing the elapsed time over which a squirrel was removed to time that caches remained in the ground, it was possible to distinguish which caches were removed during the animal's removal (i.e., pilfered) and which caches were removed after the animal was returned to the study area (i.e., pilfered or recovered). This comparison indicated that although cache longevity increased significantly when squirrels were removed, cache pilferage still occurred while the cache owner was in captivity. However, these actual pilferage rates, although 30% lower than the overall measures of cache longevity, are still considerably higher than removal rates when animals remained on their home ranges (Fig. 2).

Model 2, which included separate cache-owner-recovery rates for before and after the owner was held in captivity, substantially improved the fit relative to Model 1 (Table 1). In both models cache recovery rates when owners remained on site were more than $10\times$ pilferage rates (compare l_p with l_r in Model 1 and l_{r0} in Model 2, Fig. 3). However, after the live-trapped cache owners were returned to the site, they recovered their caches at a rate similar to the pilfering rate (l_{r1} does not differ from l_p in Model 2). Fig. 3A shows the predicted cache-survival curve after cache owners have been removed (dashed line). Assuming that recovery and pilfering rates remain unchanged, the model predicts that 5% of caches whose owners are removed from the site will survive ≥ 93 days, and 1% will survive 143 days. In contrast, only 0.8% of caches whose owners remain on site are predicted to survive beyond 1 week (Fig. 3B).

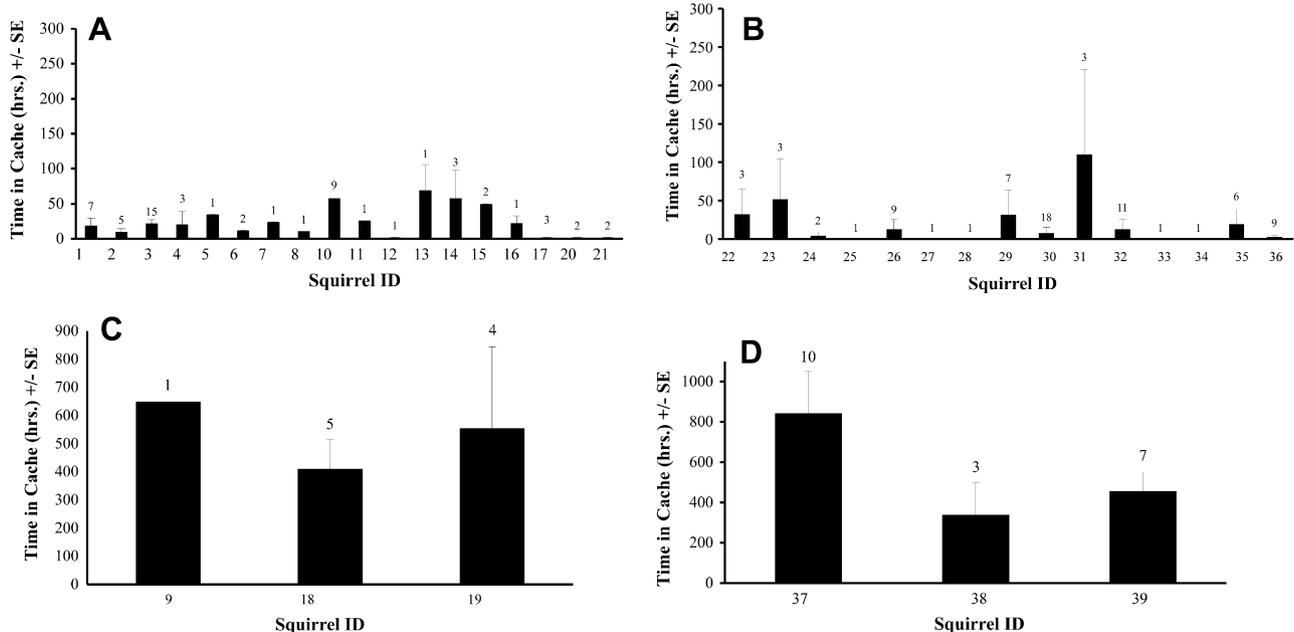


Fig. 1. Mean cache longevity (i.e., time acorns remained in the cache \pm SE), for squirrels not removed from the study area in 2007 (A) and 2008 (B), and, in comparison, mean longevity for caches of squirrels temporarily removed from the study area in 2007 (C) and 2008 (D). Note the differences in the x-axis.

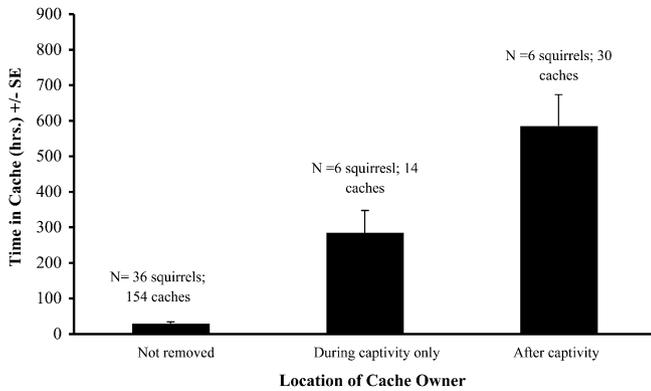


Fig. 2. Time that acorns remained in the cache (1) when cache owners were not removed, (2) when owners were temporarily removed from home ranges (i.e., actual pilferage), and (3) during and after removal combined.

4. Discussion

Our results show clear evidence of a recovery advantage among eastern gray squirrels when caching red oak acorns, even in a high-density population. During our experiment, it was not unusual to observe 10 or more animals foraging in the immediate vicinity of the focal animal. Yet, despite this abundance of potential pilferers, when squirrels were removed from their home ranges immediately after caching, rates of cache removal dropped by >500%. Given the high densities of squirrels at the site compared with that of more natural forests (Steele and Koprowski, 2001), we contend that individual squirrels should have domain over their own caches, especially when competitor densities are lower as they are in more natural woodland environments. However, despite lower densities of conspecifics in forested environments, scatter-hoarding squirrels also have to contend with the risk of pilferage by other rodent species (*Tamias striatus* and *Peromyscus* spp.). Although details on pilfering among these species are not known, we suggest that because they predominantly larder hoard, they are unlikely to be a major factor in cache losses for gray squirrels.

Vander Wall et al. (2006) reported observations similar to ours for yellow pine chipmunks (*Tamias amoenus*) storing pine seeds. They compared cache removal rates of chipmunk-prepared caches with artificial caches prepared by observers and estimated that chipmunks recovered 56–74% of the seeds they cached. When Vander Wall et al. (2006) removed chipmunks from some of their sites, cache retrieval from natural caches at the sites was 3.4–6.5 times lower than for caches at sites where animals were not removed. Interestingly, where chipmunks were not removed there were no differences between removal rates of artificial and natural caches indicating high pilferage rates.

Observations and results in this study are consistent with those of previous research that indicates that tree squirrels rely on spatial memory for relocating caches or concealed food (Lavenex et al., 1998; MacDonald, 1997) in a manner similar to that

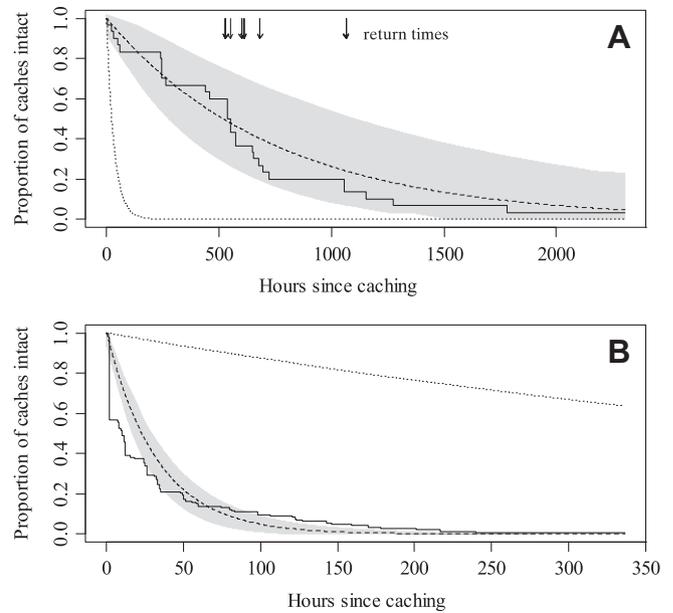


Fig. 3. Model of cache survivorship with (A, $N = 30$ caches, 6 squirrels) and without (B, 147 caches, 36 squirrels) removal of the cache owner. Notice that the x-axis scales differ in A and B. Solid lines show the actual proportion of intact caches over time and dashed lines indicate the fitted survival curve with owner-recovery rate of $\lambda_{r0} = 0.695 \pm 0.060$ caches/day (estimate \pm SE) and pilfering rate $\lambda_p = 0.032 \pm 0.007$ caches/day. Shaded gray areas show 95% prediction envelopes from 10,000 bootstrap samples of the fitted covariance matrix for the parameters. For reference, the dotted line in A shows the predicted survivorship for B, and vice versa. Arrows in A indicate times at which captured squirrels were returned to the site, relative to cache establishment.

reported for food-hoarding corvids (Balda and Kamil, 1998; Bednekoff et al., 1997; Brodin and Bolhuis, 2008; Clayton and Dickinson, 1999; Gibson and Kamil, 2005). Lavenex et al. (1998), for example, showed that fox squirrels (*Sciurus niger*) relied on stationary objects in the environment surrounding a hidden food item to learn and relocate the precise location of the food. They concluded that fox squirrels relied on more permanent spatial information over other temporary cues (e.g., colored or 3-dimensional objects placed near the hidden food), and were effectively triangulating on the location from stationary objects in the environment (e.g., trees). We suggest that spatial memory allows individual squirrels in our study site to recall specific cache locations and provide cache owners with a higher recovery rate from caches than pilfering conspecifics. Interestingly, in our study, recovery rates when squirrels were returned to the site did not differ from pilferage rates. That implies that either the cache owners lost their recovery advantage during captivity, perhaps because they could not refresh their memory.

Despite evidence of a retriever's advantage in our study, pilfering of caches was still evident. During this and other studies (Steele et al., unpublished results, 2008), we observed numerous occasions of pilfering attempts at the time nuts were cached. Focal animals in our study, for example, were often observed by neighboring squirrels, sometimes from considerable distances (e.g., >20 m). Following cache placement, these neighbors would move to the precise location of the cache, sometimes successfully pilfering it even after being displaced by conspecifics along their path to the cache site. During this and other studies (Steele et al., unpublished results, 2008) we also noted conspecifics observing scatter-hoarding squirrels from treetops. Following the hoarder's departure, the observing squirrels immediately moved to the ground and attempted pilfering from these caches.

Table 1

Fitted estimates and likelihood profile confidence intervals for eastern gray squirrel cache recovery and pilferage rates, in caches per day.

Model	AIC	Δ AIC	Parameter	Estimate	S.E.	95% C.I.
1	1871.8	104.2	λ_r	0.410	0.036	(0.343, 0.484)
			λ_p	0.032	0.007	(0.020, 0.049)
2	1767.6	0	λ_{r0}	0.695	0.060	(0.583, 0.820)
			λ_{r1}	0.039	0.023	(0.001, 0.091)
			λ_p	0.032	0.007	(0.020, 0.049)

These observations underscore the importance of spatial information in locating caches but also suggest that because of their use of spatial information, gray squirrels are most likely to attempt pilfering when they observe conspecifics scatter hoarding. This assertion is consistent with the results of Steele et al. (2008), who found that eastern gray squirrels at this same study area frequently engage in behavioral deception at the time of scatter hoarding nuts and that such behavior reduces the probability of cache pilferage by conspecifics. We submit that deceptive caching behavior most likely evolved in response to intensive pilferage at the time of hoarding (Steele et al., 2008). Other research from this study area shows that animals selectively cache more profitable food nuts in the open outside canopy cover, and effectively trade-off an increased risk of predation for a more secure cache site with reduced risk of pilferage (Steele et al., unpublished results). This strategy may further enable squirrels to reduce pilferage and increase the probability of recovery of their own caches.

Vander Wall and Jenkins (2003) argue based on a review of studies on artificially placed caches that pilferage rates range from 2 to 30% per day for many scatter hoarders. They contend that these high rates of pilferage can be catastrophic for an individual hoarder unless it is also regularly engaging in pilferage behavior. They further propose a model of reciprocal scatter hoarding and suggest that for many scatter-hoarding rodents high levels of mutual pilferage should be the norm. Although our original hypothesis that gray squirrels engage in high rates of reciprocal pilfering is not supported, our results demonstrate that pilfering does occur, but on a far lesser scale than we originally expected. Moreover, other studies in our system indicate adaptations by eastern gray squirrels to reduce the risk of pilferage (e.g., deceptive caching behavior, placement of profitable foods in areas of higher predation risks; Steele et al., submitted for publication, 2008), and artificially placed caches at our sites suggest a rate of cache pilferage much lower than that reported by Vander Wall and Jenkins (2003). Regardless, our results do not negate the possibility of reciprocal pilfering at a level lower than that predicted by Vander Wall and Jenkins (2003).

Finally we recognize the unusually short caching times in this study compared with estimates for tree squirrels from more natural settings (up to 6–7 months; Wauters et al., 1995; Wauters and Casale, 1996; Steele et al., 2001b; Zong et al., 2010). We have observed these short caching times during both summer and autumn and therefore do not attribute them to seasonal differences. Instead, we suggest that because of the experimental approach we used, in which individual squirrels were presented with single food items, squirrels were often recovering and re-caching acorns within a few days to secure a better cache site. Such secondary dispersal is reported for other rodents (Vander Wall, 2002) as well as the eastern gray squirrel in more natural forest ecosystems (M. Steele, personal observations). In fact we suggest that frequent recovery and reaching during long hoarding periods may allow scatter hoarders to frequently monitor their caches, reduce pilfering losses, and even recharge their spatial memory. Indeed, the observed survivorship curve for caches whose owners remained on site initially falls more sharply and then levels out more than predicted by the model (Fig. 3B). This systematic lack of fit and sharper-than-expected inflection at ~50 h indicates that the owner-recovery rate is not stable over time, but declines after a cache is approximately 2 days old. This observation is consistent with the idea that squirrels create both short- and long-term caches, but also could be explained by heterogeneity in cache recovery behavior among individual squirrels.

We conclude that gray squirrels indeed possess a notable recovery advantage but also point to an understudied ecological factor that may greatly influence seed dispersal: predation of the scatter hoarder. If individuals that prepare scatter hoards show

a higher potential for cache recovery, then predation of the scatter hoarder soon after cache placement may increase rates of seedling establishment. Depending on the number of acorns cached before predation, the 1% survival to 143 days (4.7 months) predicted in our model could create substantial opportunity for recruitment. Although previously suggested in the literature (Harrington et al., 1997), we are unaware of any experimental studies that have considered predation of the scatter hoarder in the process of seed establishment. We note, however, the ongoing research by R. Kays and M. Wilkelski (U.S. National Science Foundation, 2010) on scatter-hoarding agoutis (*Dasyprocta punctata*) and their predator the ocelot (*Leopardus pardalis*), which suggests such an effect in a tropical system of Panama. Future studies should consider this a potential ecological process that could influence seedling establishment in many systems, especially those in which seed dispersal is directed largely by scatter-hoarding birds and mammals.

Acknowledgments

We thank J. Balint, P. Dombroski, A. Otis, and T. Steele for assistance in the field and T. Steele and S. Marino for assisting with the maintenance of the captive animals. Funding for this project was supported directly by the Wilkes University Mentoring Initiative, and indirectly from the National Science Foundation (DEB-0642434, DEB-0642504) and the Howard Hughes Medical Institute. The project was reviewed and approved by the Institutional Animal Care and Use Committee of Wilkes University (proposal no. 174-08).

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