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Re-caching of acorns by rodents: Cache management in eastern deciduous forests of North America

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ABSTRACT

Scatter-hoarding rodents such as tree squirrels selectively cache seeds for subsequent use in widely-spaced caches placed below the ground surface. This behavior has important implications for seed dispersal, seedling establishment, and tree regeneration. Hoarders manage these caches by recovering and eating some seeds, and moving and re-caching others. This process of re-caching, however, is poorly understood. Here, we use radio-telemetry to evaluate re-caching behavior for the management of acorn caches by rodents in eastern deciduous forests. We also test the hypothesis that as seeds are re-cached, the distance from the source increases. Radio transmitters were implanted in Northern red oak (*Quercus rubra*) acorns and presented to rodents in a natural setting over 3 seasons. We used radio-telemetry to track and document evidence of recovery and re-caching. We tracked a total of 102 acorns. Of the 39 radio-tagged acorns initially cached, 19 (49%) were cached on two or more occasions; one acorn was cached four times. The hypothesis that rodents move seeds to progressively greater distances from the source is not well-supported, suggesting that acorns are being moved within an individual's home range. Given the species of rodents in the study area, gray squirrels (*Sciurus carolinensis*) are the most likely to be responsible for the caching and re-caching events. Gray squirrels appear to engage in extensive re-caching during periods of long-term food storage, which has important implications for understanding how caching behavior influences acorn dispersal and oak regeneration.

1. Introduction

Scatter-hoarding, the process by which mammals and birds store seeds for subsequent use in discrete, widely-spaced cache sites (Smith and Reichman, 1984; Vander Wall, 1990), is considered a primary mechanism of animal-mediated dispersal for many plant species. Scatter-hoarding allows hoarders to minimize food loss to potential pilferers by spacing caches instead of storing food in a single location. This hoarding strategy also results in seedling establishment when scatter-hoarding animals fail to recover their own caches (Cao et al., 2011; Steele et al., 2011). Dispersal of seeds by scatter-hoarding rodents is thus a critical step in the reproduction of many nut-bearing trees and a key process underlying ecosystem function in many terrestrial ecosystems (Steele and Smallwood, 2002). Dispersal of seeds away from parent trees decreases the incidence of density-dependent predation (Janzen, 1970), decreases competition with parents (Janzen, 1970), and often moves seeds to sites more suitable for establishment and recruitment (Wenny and Levey, 1998).

Regardless of how well protected caches may be, cache loss is inevitable. Cache loss can occur because of pilfering by conspecifics and heterospecifics, seed perishability (i.e. germination schedules), insect infestation, or forgetting the cache location (Vander Wall and Smith, 1987). To compensate for these losses, scatter-hoarding animals may over-provision their stores and subsequently fail to recover a portion of cached seeds, thereby contributing to seedling establishment (Vander Wall, 1990). Numerous studies across a variety of temperate, subtropical, and tropical systems show that mammalian scatter-hoarders are highly selective with respect to a variety of seed characteristics (e.g., seed perishability and seed size; Lichti et al., 2014), maintain an advantage at recovering their own caches (Steele et al., 2011; but see Vander Wall and Jenkins, 2003), and may continually manage seed stores during the hoarding period, through a process of cache recovery and re-caching (Vander Wall and Joyner, 1998; Vander Wall, 2002; Jansen et al., 2006).

Re-caching, whereby seeds are retrieved from one cache site and moved to a new cache site as a hoarder manages caches, is practiced by both mammals (Vander Wall and Joyner, 1998; Vander Wall, 2002; Jansen et al., 2006; Perea et al., 2011a) and birds (Hutchins and Lanner,

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1982; Waite and Reeve, 1992, 1995; Stotz and Balda, 1995; Burns and van Horik, 2007). Although re-caching has been observed in many instances, we know little about the relative frequency with which the behavior occurs and whether it is a part of ongoing cache management strategies in some seed dispersal systems. Re-caching may affect the probability of seedling establishment by influencing how far seeds are dispersed from the parent tree on subsequent re-caching events (Vander Wall and Joyner, 1998; Jansen et al., 2004).

During redistribution of caches in some systems, the distance from the parent tree increases as seeds are re-cached by cache owners (Perea et al., 2011a; Zhang et al., 2014). The distance from the parent tree can influence germination and survival of seeds and seedlings by decreasing competition for resources with parents and siblings as well as reducing density-dependent predation (Janzen, 1970; Nathan and Muller-Landau, 2000; Hirsch et al., 2012). Shortly after seed fall, seeds may be harvested quickly and cached near the parent tree in an attempt to stop other individuals from collecting seeds (Jenkins and Peters, 1992). Recovery of seeds from the initial caches and placement in new cache sites may result in seeds being taken farther from the parent tree to sites that are more favorable (Hirsch et al., 2012). These new cache locations may be favorable for seeds because of a higher probability of germination and for seed dispersers because they may reduce pilfering and cache loss. This pattern of increasing distance has been attributed to pilferage by conspecifics in other systems (e.g., Jansen et al., 2012).

Acorns of Northern red oaks (*Quercus rubra* L.) are an essential food resource for many animals in eastern deciduous forests. These acorns germinate in the spring, unlike white oak (*Quercus alba* L.) acorns, and are an important resource throughout the winter. In autumn, red oak acorns are cached preferentially over the more perishable white oak acorns (Smallwood et al., 2001). Rodents (e.g. squirrels, chipmunks, and mice) and birds (e.g. jays) are important predators and dispersal agents of acorns and influence seedling establishment and oak forest regeneration when seeds are cached (Steele and Smallwood, 2002; Kellner and Swihart, 2017) or partially consumed (Perea et al., 2011b; Bartlow et al., 2018). Re-caching of acorns is documented for birds, such as Florida Scrub Jays (*Aphelocoma coerulescens*) (Kulahci and Bowman, 2011). However, it is not known whether rodents in eastern deciduous forests engage in re-caching behavior during periods of food storage. If re-caching is a common cache management strategy, it is unclear whether the distance from the parent tree increases as acorns are re-cached or whether acorns are redistributed within an individual's home range.

Here, we sought to determine if re-caching occurs in the oak-dispersal system of eastern deciduous forests. Recent studies suggest that this is a highly dynamic dispersal process (Yi et al., 2012; Lichti et al., 2014; Sundaram et al., 2017). For example, dispersal patterns of acorns are dependent on oak species composition, seed size, and seed abundance (Moore et al., 2007; Bartlow et al., 2011; Lichti et al., 2014). The predominant dispersal agent, the eastern gray squirrel (*Sciurus carolinensis,* Gmelin), appears to rely on memory to relocate caches (Jacobs and Liman, 1991; Lavenex et al., 2000) and may potentially manage caches through the food-storing period. In addition to our primary objective of documenting re-caching, we tested the prediction that if acorns are re-cached, they will be moved farther from the source following cache recovery and re-caching. Behavior resulting in increased net dispersal distance may have implications for oak regeneration and design of future seed dispersal studies in these forests. We used radio-telemetry to determine if cached Northern red oak acorns were recovered and immediately consumed or recovered and re-cached. We chose radio-telemetry for this study because it allowed us to track the movement of individual acorns between cache sites without marking the cache sites with flags or tags.

2. Materials and methods

This study was conducted in late fall and winter of 2007-08, 2008-09, and 2010-11. Although also attempted in 2009, frequent equipment failure caused us to abandon the project during that field season. In 2007 and 2008, the study was conducted from mid-November until mid-March of the following year in a mature, deciduous forest dominated by Northern red oak, white oak, chestnut oak (*Quercus prinus* L.) and sugar maple (*Acer saccharum* Marsh.), located 3 km south of Mountaintop, Pennsylvania, USA (41°05′N, 75°55′W). The start time in each year of the study coincided with the period when most red oak acorns were being consumed or scatter-hoarded, thereby increasing the probability that our presented seeds would be found and dispersed. During the last field season, the study was conducted from mid-December 2010 until late-April 2011 in a similar stand a few kilometers west of the Mountaintop site (41°08′N, 75°59′W). These two locations are within the same forest and have the same forest structure and the same dispersal agents. A second location was added to increase independence of observations and generality of results. In all 3 seasons, we initiated the study in late fall when there was no evidence of eastern chipmunk (*Tamias striatus* L.) activity to ensure that caching was performed only by gray squirrels.

Red oak acorns were collected beneath 5–10 individual trees near the study area in October of each year of the study and subsequently stored at 3 °C until fitted with radio transmitters. In preparation for experiments, we created a composite acorn sample from at least 5 trees, sorted the acorns to remove insect-damaged or rotted acorns, and pseudo-randomly selected acorns to fit with transmitters. Selected acorns were generally > 7 g because of the minimum size needed to fit the transmitters. Each radio transmitter (A2450, 2.2 g, Advanced Telemetry Systems, Inc.) was prepared by wrapping the antenna in a single layer of Parafilm (Bemis Company, Inc.), which was then wrapped in a tight coil around the body of the transmitter, without crossing the antenna over itself. The transmitter was then wrapped with an additional layer of Parafilm to protect the transmitter and prevent the antenna from unraveling. Each radio tag emitted a unique frequency, allowing acorns to be identified remotely.

To fit an acorn with a transmitter, a hole (0.5 cm) was drilled through the basal end (the basal scar) of the acorn using a Dremel drill (Model 200-1/21) to remove much of the cotyledon. A wrapped transmitter was then carefully inserted into the acorn, and pieces of cotyledon were packed tightly into the remaining space to secure the transmitter. The opening in the basal end of the acorn was then filled with a mixture of shell debris and wood filler (Elmer's Wood Filler, E860, Red Oak). The surface was then carefully smoothed over, and after the wood putty dried, sanded lightly to ensure the acorn appeared sound. Rodents selectively consume nuts that appear unsound and preferentially cache those perceived to be sound and less perishable (Hadj-Chikh et al., 1996; Steele et al., 2002). The transmitter in each acorn was switched off by attaching a magnet to the acorn until the acorn was dispersed by rodents. In 2007 and 2010, a sample of the acorns was weighed (± 0.01 g) prior to placing the transmitter inside the acorn, and again after the transmitter was inserted and the wood putty had dried.

Acorns were presented to rodents in semi-permeable enclosures (1 m × 1 m x 0.33 m) composed of 5 cm × 5 cm wooden frames covered on all sides with 0.5-cm mesh hardware cloth. A small hole (5 cm × 5 cm) at the center and base of each vertical side of the hardware cloth allowed access to only small mammals (i.e. gray squirrels, flying squirrels [*Glaucomys volans* L.], chipmunks, and mice [*Peromyscus leucopus* Rafinesque and *P. maniculatus* Wagner]). Radio-tagged acorns were positioned on a 3-x-3 array of magnets that were recessed in a wooden block (5 cm × 5 cm x 2.5 cm) and positioned in the center of the enclosure. Each acorn was carefully positioned over a magnet on the wood block to inactivate the transmitter and save battery life until dispersed. A maximum of 5 radio-tagged acorns were presented at a time, at a single location, along with approximately 100 additional sound red oak and 100 white oak acorns. The additional acorns served to reduce the probability that rodents would associate the