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# Acorn dispersal by rodents: The importance of re-dispersal and distance to shelter

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## Abstract

Factors affecting the ecological balance between seed predation and effective seed dispersal remain unclear. We studied the contribution of scatter-hoarding rodents to effective acorn dispersal by labeling acorns and tracking their fates. Seventy percent of the seeds were re-dispersed from their initial fates with up to five successive dispersal movements, revealing that acorn fate is dynamic along time. Dispersal distances were not affected by the slope and acorns were dispersed farther when heavier. However, we found that successive dispersal movements (re-dispersal of seeds) and distance to rodent shelter (shrub cover) are more important factors than acorn weight to determine dispersal distances and acorn survival. Dispersal distances increased with the number of successive dispersal movements, attaining a total of up to 132 m. Seed re-dispersal enhances the redistribution of seeds, moving the seeds farther from the mother plants and increasing the ability of oaks to colonize. However, high numbers of dispersal movements decreased the probability of seed survival. Surprisingly, open microhabitat was found to increase dispersal distances and seed survival (higher when farther from shelter). More seeds were dispersed to shelter but had shorter dispersal distances and higher predation rates. Despite this, shelter is needed to ensure rodent presence and seed caching, so that structurally complex habitats with open microhabitats and shrub cover will favour oak regeneration. This study also underlines the contribution of rodents to effective seed dispersal (with 36.4% of surviving acorns in favourable caches at the end of autumn and 3.4% in next spring). Both the repeated movement of seeds and distance to shelter are two main factors determining seed dispersal by rodents and should be taken into account in further studies.

## Zusammenfassung

Die Faktoren, die das ökologische Gleichgewicht zwischen Samenprädation und effektiver Samenausbreitung beeinflussen, sind nicht gut bekannt. Wir untersuchten den Beitrag, den Vorräte anlegende Kleinsäuger zur Ausbreitung von Eicheln leisten, indem wir Eicheln markierten und ihr weiteres Schicksal verfolgten.

Siebzig Prozent der Eicheln wurden aus ihren ursprünglichen Mikrohabitaten weiterverbreitet, bei bis zu fünf aufeinander folgenden Transportbewegungen. Die Ausbreitungsentfernungen wurden nicht vom Gefälle beeinflusst, und größere Eicheln wurden weiter transportiert. Wir fanden, dass sukzessive Ausbreitungsbewegungen (mehrfache Verlagerung einer Eichel) und die Entfernung zur Deckung für die Kleinsäuger (Strauchdichte) wichtigere Faktoren für die Ausbreitungsdistanz und das Überleben der Eicheln sind als das Eichelgewicht. Die Ausbreitungdistanz nahm mit der Anzahl der Verlagerungen zu und erreichte in der Summe bis zu 132 m.

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Indessen nahm mit der Anzahl der Verlagerungen die Überlebenswahrscheinlichkeit der Samen ab. Ein offenes Mikrohabitat erhöhte die Ausbreitungsdistanzen und mehr Samen überlebten entfernt von der Deckung. Eine höhere Anzahl von Samen wurden in die Deckung getragen, aber ihre Ausbreitungsdistanzen waren geringer und die Prädationsraten höher. Dennoch ist Deckung notwendig, um die Anwesenheit der Kleinsäuger und das caching sicherzustellen, so dass strukturell komplexe Habitate mit offenen Bereichen und Strauchbeständen die Fortpflanzung der Eichen begünstigen.

Diese Untersuchung unterstreicht den Beitrag der Kleinsäuger zur effektiven Samenausbreitung (mit 36.4% der überlebenden Eicheln in günstigen Verstecken am Ende des Herbstes und 3.4% im nächsten Frühjahr).

Die wiederholte Verlagerung der Samen und die Entfernung zur Deckung sind zwei Hauptfaktoren, die die Samenausbreitung durch Kleinsäuger bestimmen, und ihnen sollte in zukünftigen Untersuchungen Rechnung getragen werden.


***Keywords:*** Acorn weight; *Apodemus sylvaticus*; Dispersal distance; Re-caching; Shrub cover; Scatter-hoarding

## Introduction

Oak trees are major components of forests and woodlands in the Northern Hemisphere. Persistence of oak ecosystems relies on successful natural regeneration where seed dispersal is an important step, frequently mediated by biotic agents (Vander Wall 2001). Among biotic agents, rodents are considered one of the main guilds of acorn removers worldwide (Den Ouden, Jansen, & Smit 2005; Pulido & Díaz 2005; Xiao, Zhang, & Whang 2005; Steele et al. 2007). Some rodents prey on the acorns leading to seed predation, whereas others (mainly scatter-hoarders) can also act as effective dispersers (Xiao et al. 2005; Den Ouden et al. 2005; Steele et al. 2007; Gómez, Puerta-Piñeiro, & Schupp 2008). In fact, scatter-hoarding rodents increase the probability of seedling establishment by storing acorns in suitable sites (Vander Wall 2001; Steele et al. 2007). Though many studies still assume that seeds removed by hoarding rodents are eventually consumed, few investigations have indeed tackled the real final fate of acorns because of the complexity it entails (but see Xiao et al. 2005; Gómez et al. 2008). Thus, the ecological balance between seed predation and effective dispersal is largely unknown. This lack of knowledge leads to misinterpretation oak ecosystem dynamics.

Seed viability, dispersal distance and microhabitat conditions are three main aspects of acorn dispersal that will determine a successful oak regeneration. First, seed viability is an essential requirement to achieve effective dispersal. Second, dispersal distance reduces density-dependent mortality and determines demographic and genetic structure (Vander Wall 2001; Valbuena-Carabaña et al. 2005). And finally, microhabitat of origin and destination are main factors of seed encounter (Hulme 1994) and dispersal quality (Schupp 1993) since the microsite where seeds are deposited determines seed survival and seedling recruitment (Vander Wall 2001).

Most dispersal studies examine acorn fate at a certain time without considering successive fates along time. Though there is growing evidence suggesting that rodents move seeds repeatedly (Vander Wall & Joyner 1998; Vander Wall 2002; Vander Wall 2003; Jansen, Bongers, & Hemerik 2004), including acorns (Den Ouden et al. 2005; Xiao et al. 2005; Xiao, Jansen, & Zhang 2006), very few studies have addressed specifically the repeated movement of acorns and its ecological consequences in acorn dispersal and survival. However, it is crucial to understand whether seeds are moved from their initial fate, and whether subsequent movements of seeds may affect the probability of seedling establishment. In addition, rodent behavior may be affected by the provision of shelter where rodents can safely forage and feed (Díaz 1992; Hulme 1994; Den Ouden et al. 2005). In that way, shrub cover, a common shelter for rodents (Muñoz, Bonal, & Díaz 2009), has been found to increase rodent activity. Thus, distance to safe sites (shelter) may affect the re-dispersing behavior of rodents and, consequently, acorn dispersal patterns and oak regeneration. In the present study, we specifically test whether both re-dispersing behavior of rodents and distance to shelter interact and affect: (1) seed encounter (2) acorn dispersal distances, (3) acorn deposition and (4) acorn survival.

## Material and methods

### Study area

The study area is located in the Ayllon mountain range in central Spain (3°30′W, 41°07′N, Madrid province), at 1400 m a.s.l., with 958 mm annual rainfall and a two-month summer dry season. This study was conducted in a mixed oak stand of *Quercus pyrenaica* Willd. and *Quercus petraea* (Matt.) Liebl. (380 stems per ha; basal area 22.21 $m^2$ per ha) with scattered European beech-trees (*Fagus sylvatica* L.) at 83 stems per ha and 0.79 $m^2$ per ha. The understory is formed mainly by a few shrub species (*Erica arborea* L., *Ilex aquifolium* L., *Genista florida* L., *Crataegus monogyna* Jacq., *Rubus ulmifolius* Schott and *Rosa* sp.). Wood mouse (*Apodemus sylvaticus*) is the main acorn remover in the study area with an estimated density of $9.6 \pm 2.3$ individuals/ha in autumn 2008 (unpublished data). Estimated acorn crop size for both *Quercus* species was: 16.7 acorns/$m^2$ for autumn 2008 and 23.2 acorns/$m^2$ for autumn 2009 (unpublished data).