Forest Ecology and Management 379 (2016) 226–231

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Small rodents trading off forest gaps for scatter-hoarding differs between seed species

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ARTICLE INFO

Article history:
Received 15 April 2016
Received in revised form 2 August 2016
Accepted 2 August 2016
Available online 21 August 2016

Keywords:
Seed dispersal
Forest gap
Tradeoff
Predation risk
Pilferage risk
Seed profitability

ABSTRACT

Cache site selection by scatter-hoarding animals can be affected by habitat structure; however, cache establishment by animals in response to habitats with different predation risks have rarely been investigated. Gap formation significantly alters habitat structures and the distribution and abundance of scatter-hoarding animals. To date, little is known whether and how scatter-hoarding animals tradeoff forest gaps for scatter-hoarding. In this study, we released seeds of three tree species (*Juglans mandshurica*, *Quercus mongolica*, and *Q. aliena*) at the edges of forest gaps, to explore spatial seed dispersal and cache placement by small rodents in northeastern China. Our results showed that 18.5% of scatter-hoards of *Juglans mandshurica* were established in gaps by small rodents, while only 5.3% and 3.7% of scatter-hoards of *Q. mongolica* and *Q. aliena* were found in gaps, indicating that trading off gaps with high predation risks for distributing caches by small rodents appears to be seed species dependent. Camera trapping and GUD measurements showed that predation risks in gaps were much higher than those in the associated closed canopy forest. Moreover, seed pilferage rates were lower in gaps compared to those in the closed canopy forest. Our one-year results potentially indicate that gap formation significantly influences the placement of scatter-hoarded seeds by small rodents. Higher predation risks but lower pilferage rates in forest gaps appear to influence scatter-hoarding decisions. Caching seeds in gaps by food hoarding animals is expected to benefit natural regeneration of forest gaps.

1. Introduction

Scatter-hoarding animals significantly contribute to seed dispersal and seedling establishment through burying relatively small quantities of seeds in shallow, inconspicuous pits (Vander Wall, 1990; Lai et al., 2014; Wang et al., 2014). The hypothesis of directed seed dispersal highlights the importance of cache site selection for seedling recruitment (Hirsch et al., 2012; Salazar et al., 2013; Carlo et al., 2014; Moose and Vander Wall, 2015). However, cache site selection by scatter-hoarding animals is usually context-dependent (Yi et al., 2013; Steele et al., 2015; D. Zhang et al., 2016). Previous studies have found that the spatial distribution of the scatter hoards made by scatter-hoarding animals represents a trade-off between energy investment in establishing caches and the increased risk of pilferage (Kraus, 1983; Hurly and Robertson, 1987; Steele et al., 2014), which has been regarded to be most important among various factors affecting cache loss (Jenkins and Peters, 1992; Jenkins et al., 1995; Steele et al., 2014). Although placing food items across a wide area prevents some caches from being retrieved, scatter-hoarding animals are inevitably at the risk of predation by predators during cache establishment. Safer places for scatter-hoarded food are usually at higher predation risks (Steele et al., 2015). From an evolutionary standpoint, scatter-hoarding animals may have adopted behavioral strategies to trade-off cache site selection against the risk of predation. Previous studies have extensively investigated cache site selection strategies of scatter-hoarding animals (Vander Wall, 1993; Hampton and Sherry, 1994; Lorenz et al., 2011); however, few studies have directly addressed the tradeoffs between cache site selection and predation risks. A pioneering study by Steele et al. (2014) proposed the habitat structure hypothesis that typically holds that food items are more likely to be stored by scatter-hoarding animals in open habitats where there is higher predation risk but potentially lower risk of cache pilferage. Recently, Steele et al. (2015) presented further evidence that scatter-hoarding rodents tradeoff higher risks of predation for more secure cache sites. Therefore, understanding how scatter-hoarding animals tradeoff between

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http://dx.doi.org/10.1016/j.foreco.2016.08.005

predation risk and cache site selection appears to be an important question in ecology.

Previous studies have indicated that predation risk appears to be linked to landscape attributes (Lone et al., 2014; Hernandez and Laundré, 2005; Blanchard et al., 2016; Donadio and Buskirk, 2016). An increasing body of literature has suggested that the perception of predation risks by animals varies considerably across the landscape and habitat structures (López-Barrera et al., 2005; Guzmán-Guzmán and Williams-Linera, 2006; Arias-Del Razo et al., 2012; Laundré et al., 2014; San-José et al., 2014; Leonard et al., 2015). Further evidence shows that animals are able to modify their foraging decisions and the way of habitat use in response to potential predation risks (Brown and Kotler, 2004; Orrock et al., 2004; Laundré et al., 2014; Wheeler and Hik, 2014). However, scatter-hoarding behavior and cache establishment by animals in response to habitats with different predation risks have been rarely investigated (Steele et al., 2014, 2015).

Gaps are commonly found in various forest ecosystems and have been shown to alter the distribution and abundance of small mammals due to the increased predation risks (Levey, 1988). Previous studies have indicated that forest specialists are generally more reluctant to enter gaps (Rail et al., 1997; Rodriguez et al., 2001; Bakker and Van Vuren, 2004). This apparent reluctance to occupy forest gaps could be explained by higher perceived predation risk in open habitats (Lima and Dill, 1990). Higher predation risk in the open habitats may represent lower pilferage rates of caches made by hoarding animals (Steele et al., 2015); however, little is known about the changes of scatter-hoarding behaviors of small rodents in response to forest gaps. Although small rodents prefer open habitats for cache site selection (Steele et al., 2014); whether they tradeoff forest gaps for scatter-hoarding remains unknown. Possibly, dispersal agents are trading off higher predation risk in gaps for lower risk of cache pilferage and thus access to more food later. Moreover, seeds with contrasting physical or chemical traits may attract scatter-hoarding animals in different ways (Z. Zhang et al., 2016). More information is needed on the role of seed traits in affecting seed dispersal in response to predation risk, though large acorns of are more likely to be cached in open habitats by scatter-hoarding animals (Steele et al., 2014). Therefore, it is important to elucidate how scatter-hoarding animals handle tree seeds with different traits in response to predation risks, which is of great importance for natural regeneration of forest gaps because more seeds are expected to be dispersed into gaps where they have a higher probability of germination.

In this study, we released tagged seeds of three tree species (*Juglans mandshurica*, *Quercus mongolica* and *Q. aliena*, see Table 1) differing in seed size and profitability (value to the dispersal agent as a food source) at the edges of artificial forest gaps, to investigate spatial seed dispersal and cache placement by small rodents in a temperate forest in northeastern China. We tracked seed dispersal and cache site selection by small rodents both in the forest gaps and associated closed canopy forest. Our aim was to test whether small rodents prefer forest gaps with high predation risk for cache placement. Moreover, we sought to know whether small rodents tradeoff highly profitable seeds for scatter-hoarding in forest gaps where there potentially is higher predation risk but lower probability of cache pilferage.

2. Materials and methods

2.1. Study site

Our experiments were conducted in Daxicha, Qingyuan county, Fushun, Liaoning, China (41°50′N, 124°47′E). The climate of the region is a continental monsoon type with a humid and rainy summer and a cold and snowy winter. Mean annual air temperature varies between 3.9 °C and 5.4 °C with the minimum of −37.6 °C in January and the maximum of 36.5 °C in July. The mean annual precipitation ranges between 700 mm and 850 mm, 80% of which falls from June to August. The frost-free period lasts for 130 days on average, with an early frost in October and late frost in April (Zhu et al., 2007).

Table 1
Seed traits of *Juglans mandshurica*, *Qurecus mongolica* and *Qurecus aliena* in this study. Data are expressed as mean ± SD.

Seed traits	*J. mandshurica*[a]	*Q. mongolica*[a]	*Q. aliena*
Seed mass (g)	13.61 ± 1.28	2.86 ± 0.21	1.84 ± 0.25
Seed coat thickness (cm)	0.32 ± 0.65	0.05 ± 0.01	0.14 ± 0.01
Proportion of kernel mass (%)	21.10 ± 0.86	85.75 ± 1.66	76.33 ± 2.26
Tannin concentration (%)	0.07 ± 0.01	4.33 ± 0.34	7.15 ± 0.01
Protein (%)	27.02 ± 0.71	7.4 ± 0.21	5.49 ± 0.03
Fat (%)	61.11 ± 0.25	1.76 ± 0.14	1.76 ± 0.14
Starch (%)	0.07 ± 0.07	38.27 ± 1.97	31.03 ± 0.09
Caloric value per seed (kJ)	81.61 ± 0.21	20.96 ± 0.97	8.54 ± 0.55

[a] Data are cited from Yi et al. (2015).

2.2. Seed release and cache placement

In October 2015, seeds of *J. mandshurica*, *Q. mongolica*, and *Q. aliena* were independently released at the edge of each of six gaps with different sizes (range 260–984 m^2) for three consecutive bouts within 25 days. These gaps were created in March 2015 by the Qingyuan Forest Ecosystem Research Station of Chinese Ecosystem Research Network by harvesting trees in a naturally regenerating broadleaved mature forest dominated by *Q. mongolica*, *J. mandshurica*, *Fraxinus rhynchophylla*, and *Acer mono*. All trees including saplings and shrubs were harvested to experimentally create gaps. All logging materials were removed out of the gaps to create a uniform forest floor only with grasses. Until the seed release experiment, grasses and resprouted branches (0.3–2.0 m high) have occupied the ground of each gap. For each tree species, we released 50 tagged seeds in each of four seed stations evenly scattered at the east, west, north and south edges of each gap (see Fig. 1). Seed stations were established 2 m outside far from the trunks of gap border trees to imitate their naturally occurring seed shadow and investigate whether these seeds can be transported into the gaps by small rodents. We, therefore, defined the belt zone (2 m wide) formed between seed stations and gap border tree as gap edge area (see Fig. 1), to distinguish canopy gap and the closed canopy forest. Each seed was labeled by attaching onto a small plastic tag and numbered consecutively, to facilitate seed relocation and identification (Yi et al., 2012). The plastic tag (2.5 cm × 3.5 cm) was less than 0.3 g and did not change seed weight significantly. When the tagged seed was buried by scatter-hoarding animals, the attached tag was often left on the ground, which facilitates recovery of the buried seed by researchers. After release, seed removal was checked every day for six days until most seeds in the seed stations were removed by small rodents. We then searched around each station to locate seeds scatter-hoarded by small rodents within the expanded gaps, gap edges and the associated closed canopy forest with the aid of the plastic tags attached on the seeds. Approximately a 30 m-radius area surrounding each seed station was checked for 3 persons × 2 h. Seed fates were recorded as: intact in situ (IIS), eaten in situ (EIS), eaten after removal (EAR), intact but not buried after removal (IAR), missing (M), scatter-hoarded (SH), scatter-hoarded in gaps (Gap-SH), scatter-hoarded in gap edges (Edge-SH), and scatter-hoarded in closed canopy forest (C-SH), respectively. Seed fates of IIS, EIS, EAR, IAR, M, and SH were mutually exclusive, while SH included Gap-SH, Edge-SH, and C-SH.