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Flying vs. climbing: Factors controlling arboreal seed removal in oak–beech forests

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Nuts are heavy and nutritious seeds that need animals to be successfully dispersed. Most studies address nut removal by a single animal species once seeds fall onto the ground. However, nuts are also accessible before the seed drop and usually to a wide guild of seed foragers. This study examines the factors controlling arboreal seed removal in oak–beech forests within the whole guild of nut foragers. We found that seed-dispersing rodents (*Apodemus sylvaticus*) were the main acorn removers in the oaks (up to 3.75 m height), with a rapid seed encounter and a high removal rate. However, rodents did not climb the beech trees, probably due to their smoother bark in comparison to oak bark and/or the lower nutritional value of beechnuts with regard to acorns. Jays (*Garrulus glandarius*) were more abundant in oak stands (both dense and scattered) and clearly preferred acorns to beechnuts whereas nuthatches (*Sitta europaea*) were more abundant in beech stands and preferred beechnuts to acorns. Non-storing birds such as great tits (*Parus major*) also removed acorns and beechnuts, especially in the stands where oaks are dominant. Jays and rodents preferred sound seeds over insect-infested seeds but such a preference was not found for nuthatches. This study highlights that pure beech stands showed a reduced guild of arboreal nut foragers in comparison to oak stands. This different guild could probably affect the spatial patterns of seed dispersal, with a proportionally higher number of long dispersal events for acorns (mostly jay-dispersed) than for beechnuts (mostly nuthatch-dispersed). Long-distance dispersal of beechnuts (by jays) is determined by the presence of other preferred species (oaks) and their frequency of non-mast years. Seed location in different habitats strongly determines the contribution of different arboreal removers (including climbing rodents) and their removal speed, leading to a differential seed fate that will eventually affect tree regeneration. As nuthatches are sedentary birds, it is important to maintain old and dead trees where they can breed (crevices), forage (arthropods) and store seeds in order to favor beechnut dispersal and gene flow. By maintaining or favoring oak trees within beech stands we will ensure a wider guild of arboreal nut dispersers.

1. Introduction

Seed dispersal is an important component of the tree regeneration process and is the principal ways by which trees move across landscapes (Vander Wall et al., 2005). Nut-producing trees (e.g. Fagaceae) produce abundant and highly nutritious seeds, which are an important food source for many forest vertebrates (Jensen and Nielsen, 1986; Ouden et al., 2005). Nuts are also heavy seeds that need biotic agents (animals) to be dispersed, and, thus, have developed certain traits to attract seed-dispersing animals (Vander Wall, 2001). Genetic parentage analysis also revealed that seedling recruitment in nut-producing trees, such as oaks, occurred at long distances from their mother trees (usually over 50 m) as a result of animal seed dispersal (Valbuena-Carabaña et al., 2005). However, some other animals (seed predators) will only consume and destroy the seeds, reducing tree reproduction efficiency (Herrera, 2002).

Seeds can be removed from the trees (before seed drop) or from the ground (after seed drop or primary dispersal). Many studies have addressed the removal of nuts from the ground (Steele et al., 1993; Gómez et al., 2003; Muñoz et al., 2009; Xiao et al., 2010; Pulido et al., 2010; Perea et al., 2011). However, nuts are also accesible to many foragers when they are still on the mother tree. Following this, a traditional distinction has been made between aerial and terrestrial nut foragers. Among aerial seed foragers, birds are the most prominent guild of nut foragers, which include important scatter-hoarders (e.g. jays) that strongly contribute to seed dispersal (Darley-Hill and Johnson, 1981; Gómez, 2003; Pons and Pausas, 2007a). Among terrestrial, mammals are the main guild of nut foragers with both important seed predators (e.g. ungulates) and potential dispersers (hoarding rodents). However, the contribution of different guilds of animals may differ not only on their foraging ecology (predation vs. dispersal) but on the temporal and spatial scales of their effects and their seed preferences (Hulme and Borelli, 1999). In that way, seed removal has been demonstrated to be determined by the structure of the dominant

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vegetation (Vander Wall, 2001; Hulme and Kollmann, 2005; Perea et al., 2011) due to the fact that some habitats are more suitable for certain foragers (Janzen, 1971; Hulme, 1994). Habitat selection may also determine the proximity of certain seed removers to nut sources, which could eventually affect the probability of nut encounter and the speed at which nuts are removed (Perea et al., unpublished results). In addition, some species of seed foragers are able to discriminate among seeds from different plant species or among intrinsic seed characteristics. Consequently, many seed foragers show preference for certain species over others (Steele et al., 1996; Pons and Pausas, 2007b), mostly in relation to nutritional properties (Wang and Chen, 2008).

Seed quality has shown to be an important trait for many guilds of foragers (e.g. rodents), which clearly preferred large and sound seeds over small and infested seeds (Steele et al., 1996; Muñoz and Bonal, 2008a,b). However, not all foragers show the same preferences for species or have the ability to discriminate some intrinsic seed properties (Cheng and Zhang, 2011; Dixon et al., 1997; Pons and Pausas, 2007b). Thus, different guilds of foragers may contribute differentially to the final seed removal due to dissimilarities in body size, habitat selection, seed preferences or foraging behavior. However, nut removal from the trees have not been fully explored and such factors may be important for seed survival and spatial patterns of dispersal, which will eventually affect tree regeneration.

Although it is widely recognized that small mammals are able to climb the trees (Holisova, 1969; Montgomery, 1980; Štěpánková and Vohralík, 2009), few studies have explored the relative contribution of small mammals to nut removal from the trees (but see Santos and Tellería, 1991; Ida et al., 2004). Seed removal by birds has been demonstrated to play an important role in long distance dispersal (Gómez, 2003; Pons and Pausas, 2007a) whereas small mammals have been considered to be short to medium-distance dispersers (Ouden et al., 2005; Gómez et al., 2008). However, little is known about the role of small mammals as nut removers from the trees, which could compete with avian nut foragers, determining dispersal distances and the eventual seed fate. In addition, no study has yet addressed the foraging decisions of nut-dispersing rodents during the predispersal phase. As a result, it is completely necessary to study the whole guild of nut foragers, including both aerial and climbers, to fully understand the factors controlling the arboreal nut removal and their possible consequences for seed fate and tree recruitment.

The aim of this experimental study was to examine the factors controlling arboreal seed removal in oak–beech forests within the whole guild of nut foragers. We selected oak–beech forest because they are important components of temperate forests in the Northern Hemisphere whose nuts strongly rely on the removal by animals to be effectively dispersed. More specifically, the study goals are: (1) to estimate the relative contribution of different seed foragers to the removal of beechnuts and acorns in the trees; (2) to examine whether seed characteristics (tree-species, seed size and seed infestation) affect seed removal (choice and speed) in the trees; (3) to analyze the influence of different habitats on the relative abundance of each nut forager; (4) to examine whether seed location in different habitats affect the arboreal nut removal along time. Finally, we aim to integrate all these aspects to analyze the consequences of arboreal seed removal (choice and speed) by different nut foragers for the regeneration of oak–beech forests.

2. Material and methods

2.1. Study area

This study was conducted in a mixed forest with three tree-species: a sub-mediterranean oak (*Quercus pyrenaica* Willd.), a temperate oak (*Quercus petraea* Matt. (Liebl.)) and the European beech (*Fagus sylvatica* L.). 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., under a submediterranean climate with 958 mm annual rainfall and a 2-month dry summer. The understory is formed mainly by a few species of evergreen shrubs (*Erica arborea*, *Juniperus communis*, *Ilex aquifolium*, *Genista florida* and *Adenocarpus hispanicus*). Different habitats and microhabitats can be found according to plant composition and vegetation structure resulting in a heterogeneous forest (Pardo et al., 2004). Genetic studies in the study area (parentage analysis) revealed that seedling recruitment occurred at long distances from their mother trees (usually over 50 m) as a result of animal seed dispersal (Valbuena-Carabaña et al., 2005).

Inside the study area we distinguished three main habitats: (1) Mixed oak stand of *Q. pyrenaica* and *Q. petraea* (380 stems ha^{-1}; basal area of 22.21 $m^2\ ha^{-1}$) with scattered beech-trees (83 stems ha^{-1}; 0.79 $m^2\ ha^{-1}$), containing several shrub species in the understorey (mostly *E. arborea* and *G. florida*) (2) scattered oak forest of *Q. pyrenaica* and *Q. petraea* (74 stems ha^{-1}; 2.35 $m^2\ ha^{-1}$) inserted in a matrix of evergreen shrubs (mainly *A. hispanicus* and *J. communis*) and (3) pure stand of *F. sylvatica* (848 stems ha^{-1}; 18.02 $m^2\ ha^{-1}$) and the surface covered by mostly litter and isolated or small groups of holly trees (*I. aquifolium*). The tree inventory for each habitat was performed in 2005 (García, 2006). Each habitat was selected in the tree inventory according to their homogeneity in tree composition and structure. In autumn 2008 seed production (including sound and infested seeds) was an average of 74.1 beechnuts m^{-2} inside the beech forest habitat and 16.7 acorns m^{-2} (both oak-species included) in the mixed oak habitat. Autumn 2009 showed higher seed production with 105.6 beechnuts m^{-2} in the beech forest and 67.7 acorns m^{-2} in the mixed oak habitat (unpublished data).

2.2. Identification of seed removers

In order to identify the seed removers, three motion-detection digital video cameras with night vision were used (one for each habitat). Cameras were placed at approximately 2.5–4.0 m height on a branch of a tree, pointing at a supply tray. The supply tray contained both acorns and beechnuts and was also used for the seed removal experiment (see below). Cameras were rotated every 13–16 days within each habitat and were used in October, November and December, coinciding with the acorn and beechnut ripening period, in 2 years (2008 and 2009).

2.3. Estimation of seed forager densities

To estimate rodent abundance we conducted live trapping of small mammals in each habitat on four consecutive days. The trapping period was middle of October 2008 and 2009. Trapping stations were located in each habitat according to a rectangular 5×4 grid, with 15 m between stations. Each station had one trap, so that sampling effort was 80 trap-nights per habitat and year. Traps dimensions were $27 \times 7.5 \times 7.5$ cm. Bedding was provided (dry leaves) and changed every time an animal was captured. Traps were baited with acorns and sunflower seeds. Captured individuals were identified to species, marked with fur-clipping method and then released at the point of capture (Gurnell and Flowerdew, 2006) in the year 2008. Ear-tagging method was used in the year 2009 (National Band and Tag CO. Newport, KY, USA; type 1005-1 for small mammals; approximately 7 mm length). Permits for live trapping were obtained from the Department of Environment, Regional Government of Madrid (Spain).

To estimate bird abundance we designed a permanent linear transect in each habitat. Transects were 500 m in length and approximately 50 m in width (25 m at each side). Transects were