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SELECTION AND DISPLACEMENT OF ACORNS AND BEECH NUTS BY FAUNA IN AN ANCIENT OAK AND BEECH WOOD-PASTURE

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SUMMARY

The selection and transport of acorns and beech nuts by vertebrate fauna, according to seed quality (size and damage status) and locality (habitat and microhabitat) were analyzed in an ancient mixed oak and beech 'dehesa', or wood-pasture. Video recordings demonstrated that the Wood mouse (*Apodemus sylvaticus*) was the principal animal engaged in discovery and transport of seeds, followed by birds and ungulates. These vertebrates preferred acorns over beech nuts, large seeds over small seeds, and seeds that were undamaged over those attacked by insects. The seeds that were less-favoured by rodents remained on the ground for a longer duration, and were more vulnerable to biotic and abiotic factors. Differences in dispersal rate were primarily associated with the specific microhabitats in which the seeds were located, and less attributable to the type of woodland habitat in general. Consequently, greater dispersal rates were evident in zones characterized by the presence of shrubs, or clearings with dead wood. Conversely, a reduced transport rate was found beneath the canopy of trees, owing to the lack of refuge for rodents. Acorns and beech nuts, formerly appropriated for use as livestock feed, have come to be consumed and dispersed by the vertebrate fauna, with the Wood mouse in particular being their most important transporter, at least in the microhabitats which can provide adequate refuge for mice.

Key words: seed size, infestation, *Quercus*, *Fagus sylvatica*, Wood mouse

INTRODUCTION

Oak and beech nuts present a high calorific content and are highly sought after by both invertebrate (e.g. insect larvae) and vertebrate (ungulates, rodents and birds) fauna. They exhibit a significant cotyledon mass, producing heavy nuts which are difficult to disperse by wind, water, or other abiotic agents. Consequently, the facilitation provided by biotic agents, that are capable of enabling nut dispersal, has become essential. Dispersion of seeds reduces competition between seedlings beneath the crown of a tree, and is a determining factor on the genetic and demographic structure of the plant formation (Vander Wall, 2001), representing a key process in natural regeneration. Although some vertebrates will simply consume each nut and so completely destroy seeds (i.e. 'predators'), others will also contribute to their effective dispersal (i.e., 'dispersers').

Transport of seeds by animals is dependent upon many factors, including both the characteristics of the seed itself, and environmental variables. Animals exhibit greater preference for larger seeds, with higher calorific content, the very same seed type associated with greater success in seedling

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establishment (Bonal *et al.*, 2007; Perea *et al.*, 2011). Furthermore, seeds of larger size exhibit greater dispersion distance (Xiao *et al.*, 2005; Perea *et al.*, 2011). Accordingly, seed size is considered a determining factor in seed dispersion for many arboreal species, including those of the Fagaceae family (Xiao *et al.*, 2005). However, other less well-studied factors can cause important variations in the selection and displacement of seeds. Herbivorous insect attack is a very common phenomenon within the genera *Quercus* and *Fagus*, affecting a considerable proportion of their nuts (Crawley & Long, 1995; Branco *et al.*, 2002), reaching more than 70% in the area of the current study (unpublished data). The consumption of seed reserves on the part of insect larvae reduces not only the calorific resources available to the seed, but also its palatability (Muñoz & Bonal, 2008). Consequently, infested seeds tend to be rejected by vertebrate seed consumers (Crawley & Long, 1995). Similarly, nuts infested with insect larvae exhibit lower germination rates, therefore reducing the efficiency of their contribution to the reproductive success of a tree, relative to undamaged seeds (Bonal *et al.*, 2007). Nevertheless, a notable proportion of infested seeds do come to germinate (Branco *et al.*, 2002), and secondary dispersion by vertebrates can still contribute to the natural regeneration of these arboreal species. However, transport of seeds will depend on the spatial scale and structure of the dominant vegetation (Hulme & Kollman, 2005), and different groups of vertebrates can exhibit elevated dispersive or consumptive activity in particular habitats or microhabitats.

The present study examines the consequences of seed quality in oaks (*Quercus pyrenaica* Will. and *Quercus petraea* Matt (Liebl.)) and beech (*Fagus sylvatica* L.) for their selection and displacement by animals, in an ancient mixed oak and beech 'dehesa', or wood-pasture, in which pastoralism has been prohibited since 1961. The objectives of this study are: (1) estimating the importance of different vertebrate groups (rodents, birds, ungulates) in the consumption or transport of the seeds; (2) determining the degree to which seed characteristics (species, size and damage status) affect selection and transport of seeds by animals; (3) examining the influence of seed location (in terms of habitat and microhabitat) upon the selection and transport of acorns and beechnuts by animals.

MATERIALS AND METHODS

Study area

The study was carried out in the Sierra de Ayllón, in the north east of Madrid province (3°30'W, 41°07'N), at around 1400m above sea level, in a mixed forest of oak (*Quercus petraea* and *Quercus pyrenaica*) and beech (*Fagus sylvatica*). As a consequence of abandonment of pastoralism during the 1960s, the current system comprises a mosaic of mixed and pure stands of variable density, in which a considerable proportion of stems are less than 30cm in diameter. Within the study area, three principal habitats could be identified, established from a survey performed in the year 2000 (Alonso, 2001): (1) mixed forest of *Quercus pyrenaica* and *Quercus petraea* (380 stems/ha: basal area of 22.2 m^2/ha) with scattered beech (83 stems/ha: basal area of 0.8 m^2/ha) and an understory composed primarily of *Erica arborea* L., *Rubus ulmilifolius* Schott, *Rosa* sp. and *Genista florida* L.; (2) open forest of *Quercus pyrenaica* and *Quercus petraea* (74 stems/ha: basal area of 2.4 m^2/ha) set in a matrix of evergreen shrubs (principally *Adenocarpus hispanicus* (Lam.) DC and *Juniperus communis* L.); (3) pure beechwood (848 stems/ha: basal area of 18.0 m^2/ha) with a sparse understory consisting of only small groups of holly (*Ilex aquifolium* L.).

Identification of seed consumers

To identify the seed disperser/predator fauna, two motion detector cameras with night-vision were used. The cameras were each positioned on a tree trunk at a height of 1.5m above the ground, and at a distance of 3-4m from a small wooden board (60cm x 7cm) holding 10 *Quercus pyrenaica* acorns. The cameras were deployed within each habitat (at three locations per habitat), and were rotated between positions every 13-16 days. The cameras were between 150-350m away from any of the other seed

feeding stations (as described below), to avoid attracting potential consumers to the ongoing seed transport monitoring experiments. The cameras were deployed during the months of October, November and December of 2007, and November of 2008, to coincide with the natural fall of acorns and beechnuts.

Seed selection and transport

Three replicate study sites were established at random locations for each habitat. The distance between replicate sites within each habitat was 200-250m. Three microhabitats were considered: (i) beneath the crown of a tree, with fallen leaves providing the only ground coverage, the shrub layer being absent; (ii) beneath dense evergreen shrub coverage; (iii) in a forest clearing, without canopy coverage, the ground coverage consisting only of deadwood and a herb layer —a total of 27 locations (3 habitats x 3 replicates x 3 microhabitats per replicate). Each location contained two seed feeding stations raised 3cm above the ground: one station, protected by a 0.5m x 0.5m mesh, would allow entry only to micromammals (rodents); the other was not covered by any such protection, and so could be accessed by any animals. The stations at each location were 3-5m apart. Each station contained 27 seeds (arranged adjacently together at random). The seeds comprised the three study species (*Quercus pyrenaica*, *Quercus petraea* and *Fagus sylvatica*), with nine seeds per species. In each set of nine seeds, three were of good quality (large, undamaged seeds), three of medium quality (small, undamaged seeds), and three of low quality (small, larval-infested seeds). The infested seeds were acorns attacked by weevils (*Curculio* sp., Coleoptera: Curculionidae) and beechnuts attacked by the Beech moth *Cydia fagiglandana* Zeller (Lepidoptera: Tortricidae), all of which exhibited the larval exit aperture. The undamaged seeds were intact, showing neither a larval exit aperture, nor an aperture from oviposition by an adult, and furthermore, the damage status of each chosen seed was verified by ensuring that it did not float when placed in water. The size of each seed was determined from its length (L) and maximum width (A). Acorns were categorized as 'large' when $375mm^2 < (L \times A) < 450mm^2$, and 'small' when $120mm^2 < (L \times A) < 150mm^2$. Beech nuts were categorized as 'large' when $120mm^2 < (L \times A) < 150mm^2$, and 'small' when $70mm^2 < (L \times A) < 100mm^2$. The experiments were carried out in October and November of 2008, with daily audits of seed disappearance from each station throughout a period of 20 days after the deployment of the seeds at each location.

Data analysis

Generalized linear mixed models (GLMM) with the software R 2.8.1 were used to analyze seed transport. Two models were produced, one for the first day on which vertebrates discovered the seed feeding stations (model M1), and the other for the final day of the experiment (model M2 on day 20). The response variable was binary (seed selected, or not selected). Seeds were considered 'selected' when they were consumed *in situ* or when they disappeared from the station. The random factors were expressed in a nested structure (microhabitat within replicate, and replicate within habitat). The fixed factors were seed quality, species, habitat, microhabitat, and station type (i.e., with or without mesh). Interactions and least significant terms were eliminated to obtain the minimum adequate model.

RESULTS AND DISCUSSION

82 videos were obtained, in which the Wood mouse (*Apodemus sylvaticus* L.) was the principal transporter of seeds, constituting 76% of the recordings, followed by the Eurasian Jay (*Garrulus glandarius* L.) in 8%, the Great tit (*Parus major* L.) and the Eurasian Nuthatch (*Sitta europaea* L.) each in 6%, and finally the European roe deer (*Capreolus capreolus* L.) in 4% of the recordings.

The feeding stations for each location, with and without mesh, were both discovered on the same day in 92% of cases. The proportion of seeds that remained was reduced during the first day to 0.21 in the mesh-protected stations, and 0.29 in stations without protection. There were no significant differences between protected and unprotected stations on the first day, but there were significant

differences by the end of the experiment (Table 1), with 8% higher seed transport from unprotected stations. Rodents rapidly discovered and transported the seeds that they were selecting, whilst the progress of other vertebrates was slower, tending to consume or transport only the seeds that the rodents had already rejected.

The rodents preferentially selected the acorns of *Q. pyrenaica*, followed by those of *Q. petraea*, and then lastly the beechnuts, and preferentially selected intact seeds over infested seeds (Table 1). Furthermore, the large, intact, high quality seeds were preferred over those of medium and low quality. However, at the end of the 20-day experiment, there was no significant difference in preference between large, intact seeds and small, intact seeds (Table 1). The seeds selected by the rodents are dispersed and buried individually (Perea *et al.*, 2011), protecting them from desiccation and potential attack from ungulates and birds. The seeds that the rodents did not prefer remained in the ground-feeders for longer, and therefore were more vulnerable to both biotic agents (ungulates, livestock, bacteria, fungi) and abiotic factors (desiccation and frost). The occurrence of seed masting could be a determining factor as to whether the acorns, as the preferred seeds, subsequently benefit relative to the less-favoured beechnuts. In a year of low production, the acorns will be recovered by rodents from their repository to be consumed, whilst less-favoured beechnuts will remain buried, and so will be able to make a more efficient contribution to beech recruitment.

The pure beechwood demonstrated the least number of seed transportations, a reduction that was significantly different to the frequencies found for the other two habitats (Table 1). Fewer seeds were displaced from beneath a tree crown in comparison to the other two microhabitats (Table 1). Rodents did not transport any seeds from beneath the beech canopy, but did do so from beneath the oak canopy. Beneath the beech canopy, no shrubby vegetation is present that could offer protection to rodents, and therefore their activities in such locations, including feeding, are very limited, or even non-existent. However, other groups of animals were found to take seeds from beneath the beech canopy, although they did so to a lesser degree than for other habitats and microhabitats. There were no significant differences between the shrubby microhabitat, and that of the forest clearings with deadwood, with both providing sufficient refuge to allow the rodents, as principal transporters, to be able to pursue their feeding activities, thereby dispersing seeds in greater quantities, and at a faster rate.

CONCLUSIONS

This study shows that the quality of a seed (species, size and damage status) and its locality (in different habitats and microhabitats) influence how acorns and beechnuts are transported or consumed by different groups of vertebrates (potential dispersers or predators), and the different durations over which dispersal occurs (transport speed). These factors have implications for the survival of seeds, and on the natural regeneration of oak and beech, the heavy seeds of which require dispersal by animals to evade competition with the canopy, and ensure gene flow and colonization of new environments. Acorns and beechnuts formerly appropriated for feeding livestock have come to be consumed and dispersed by vertebrate fauna, with the Wood mouse (*Apodemus sylvaticus*) being the most important transporter of the seeds, provided that appropriate microhabitats are available, to offer sufficient refuge for these rodents, through the presence of shrubs or deadwood remains.

Table 1. Summary of factors affecting the mobilization of acorns and beech nuts, on the first day they were encountered by vertebrates (mixed model M1), and after 20 days of experimental sampling (mixed model M2)

The values of Z and P were obtained relative to the first level of the factor under consideration.

		M1. First day		M2. Last day	
		Z	*P*	*Z*	*P*
Species	*Q. petraea*	-	-	-	-
	Q. pyrenaica	**3.22**	**0.001**	**3.29**	**<0.001**
	F. sylvatica	**-6.21**	**<0.001**	**-5.69**	**<0.001**
Seed quality	High (large, intact)	-	-	-	-
	Medium (small, intact)	**-2.66**	**0.007**	-1.84	0.065
	Low (small, infested)	**-10.81**	**<0.001**	**-10.11**	**<0.001**
Habitat	Mixed oak forest	-	-	-	-
	Pure beechwood	**-2.59**	**0.009**	**-10.71**	**<0.001**
	Open oak forest	0.25	0.800	-1.87	0.166
Microhabitat	Beneath canopy	-	-	-	-
	Beneath shrubs	**3.26**	**0.001**	**3.23**	**0.001**
	Forest clearing	**2.07**	**0.038**	**2.06**	**0.039**
Feeding station type	Without mesh (accessible to all fauna)	-	-	-	-
	With mesh (accessible to rodents only)	1.20	0.230	**-3.28**	**0.001**
Interactions	Medium quality: with mesh	-	-	Not applicable-	
	Medium quality: without mesh	**-2.03**	**0.042**		
	Beneath canopy: mixed oak	-	-	-	-
	Beneath canopy: open oak	-2.59	0.800	-1.87	0.062
	Beneath canopy: pure beechwood	**-2.59**	**0.009**	**-10.71**	**<0.001**

M1: AIC = 520.4; Deviance = 482.8. M2: AIC = 484.1; Deviance = 450.1

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