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Preference of granivorous rodents for seeds of 12 temperate tree and shrub species used in direct sowing

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ABSTRACT

Direct seeding is potentially a cost-effective method for creating woodland and is particularly suited to establishing mixtures of species. Seed predation can cause poor establishment, and information on granivore preference for seed of different species is essential to evaluate relative risk and the need for control measures. We investigated consistencies in the preference of small mammals for removing seeds of 12 tree and shrub species at three sites in southern England using freely available seeds presented as single or mixed species plots. Seed preferences were modelled as preference for removal of seeds of a particular species in relation to others present in a given time period. Across-site comparison of seed preference ranks showed significant agreement, especially at each extreme of the ranks. *Quercus robur* and *Fagus sylvatica* were always ranked first or second, followed by *Corylus avellana* and *Acer pseudoplatanus*, while *Crataegus monogyna* and *Fraxinus excelsior* were ranked last; the relative position of middle ranking species varied between tests. Removal of seeds of highly preferred species was usually absolute, whereas seeds of lower ranked species were more likely to be partially removed. For most species, preference coefficients were positively related to two explanatory variates: the logarithms of whole seed and coat dry mass. The exception was *Fraxinus excelsior*, where preference was lower than predicted, possibly because of chemical defences. Presentation of seeds as either single or mixed species plots had no overall effect on preference ranking. The results suggest that species that produce large nuts, are more vulnerable to predation-loss and might require additional measures, such as treatment with repellents, to reduce predation risk, or might, as in the case of *Q. robur*, be so attractive to rodents that it is unrealistic to direct sow them. The majority of the other species with smaller seed size, however, were much less susceptible to removal by predators. Any losses that do occur with these species are likely to be relatively small and tolerable, and localised.

1. Introduction

There are three ways to establish new woodland: planting seedlings raised in nurseries, colonisation or regeneration from naturally dispersed seeds, and direct seeding where tree and shrub seeds are sown onto the woodland site (Harmer and Kerr, 1995). Although written practical advice dates back to the late 15th century (Harmer and Kerr, 1995; James, 1981), direct seeding has not been extensively practised in the UK as it is considered to be less reliable than planting (Stevens et al., 1990), principally because mortality of seed and seedlings can be caused by a range of factors, often unmeasured, that vary from place-to-place and year-to-year (Harper, 1977). Nevertheless, there has been a revival of interest in the technique because it is potentially cheaper than conventional planting, and is particularly suited to establishing mixtures of species (Willoughby et al., 2004a). Recent studies have reported some success using direct seeding to establish a range of broadleaved species on amenity sites (La Dell, 1988), and for aforestation of reclaimed and former-agricultural land (Bullard et al., 1992; Dey et al., 2008; Jinks et al., 2006; Johnson, 1981; Lockhart et al., 2003; Löf et al., 2004; Madsen and Löf, 2005; Willoughby et al., 2004b).

Seed predation by granivorous rodents is a frequent cause of poor establishment by direct seeding, particularly in forest and woodland situations (Nilsson et al., 1996), and potential control measures have been investigated (Birkedal et al., 2009; Madsen and Löf, 2005; Nilson and Hjältén, 2003; Nolte and Barnett, 2000; Sullivan, 1979). Although predation of naturally dispersed seeds has been widely investigated, fewer studies have focused on direct sown seed where differences in seed characteristics, timing, and disposition from naturally dispersed seed might influence predation risk. Processing procedures such as removal of outer fruit layers, and the application of seed pretreatments to break dormancy (Gordon and Rowe, 1982), might modify the chemical and

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physical properties that influence food recognition and nutritional value. Direct sown seed might be particularly vulnerable to predation because sown areas are high value, relatively high density, patches of food that are available at times when alternative foods may be scarce. Sown areas can consist of a single or a mixture of species; typical seed mixes for new broadleaved woodland might contain up to 12 tree and shrub species (Willoughby et al., 2004a).

Many studies on post-dispersal seed predation have shown that granivores exhibit distinct preferences for the seeds of certain species over others (e.g. Kollmann et al., 1998), although consequences of selectivity on plant demography are variable (Hulme and Benkman, 2002). In direct sowing, more information is needed on the relative preferences of predators for seed of different species. Consistent preferences might restrict direct seeding to a subset of less-preferred species, or additional protection, such as the use of repellents, might be required before highly preferred species can be used reliably.

As well as deriving empirical measures of relative preference for seeds of different tree and shrub species, an understanding of the relationship between preference and seed traits would help improve explanation of measured differences and enable prediction of likely predation risk for other species. Optimal foraging theory predicts that when alternative food items that differ in profitability (energy per attack, divided by handling time per attack) are intimately mixed, a predator will include the profitable items in its diet that maximise net energy intake, and will ignore alternative foods that do not (MacArthur and Pianka, 1966; Stephens and Krebs, 1986). Consequently, granivores should prefer larger, easily handled seeds over smaller, less profitable ones. Although several studies have shown positive relationships between seed weight and seed removal (Boman and Casper, 1995; Hulme, 1998; Kiviniemi, 2001; Reader, 1997), others have found no significant relationship (e.g. Kollmann et al., 1998; Meiners and Stiles, 1997), or even negative relationships (e.g. Blate et al., 1998; Osunkoya, 1994); larger direct species comparisons, and analysis of the literature suggest that positive correlations are weak at best (Moles et al., 2003a,b). As well as size, predation rate can depend on other factors such as nutritional content (Kerley and Erasmus, 1991; Kollmann et al., 1998; Xiao et al., 2006), seed coat composition and thickness (Hulme, 1997; Moles et al., 2003a; Rey et al., 2002), and chemical defences (Kollmann et al., 1998).

The objective of this study was to determine the preference of small mammals for seeds (strictly diaspores) of 12 species that are typical components of mixes for direct sowing in the UK. Seeds varied in size and structure and included nuts with large reserves, e.g. *Quercus robur* L. and *Corylus avellana* L., that are well established as important food for rodents (Jensen, 1985), pyrenes with hard endocarps (e.g. *Prunus avium* L.), and wind dispersed fruits like *Fraxinus excelsior* L. that have been reported to be less predated (Hulme and Borelli, 1999; Hulme and Hunt, 1999).

Despite the range of seed structures, and the inconsistencies in the literature, we hypothesized that species with larger seeds would have higher predation risk than those with smaller seeds. More specifically, we tested (1) for consistency in the relative preference for seed of different species presented on the ground surface as single-species plots across three sites in southern England; (2) that preferences would be unaffected by presenting seed in single- or mixed-species plots; and (3) that preference ranking for seed of different species is related to seed size.

It was assumed that, in any given period, all seeds present had the same chance of being encountered and were accessible for foraging granivores to either remove or reject. Seed preferences were modelled as the preference for removal of seeds of a particular species in relation to others present in a given time period.

2. Materials and methods

2.1. Species

Seeds of 12 species (Table 1) were obtained from a commercial supplier in two batches: January, for the study on three sites, and November 2003 for the comparison of single- and mixed-species plots. According to the supplier's certificates, viability of seedlots exceeded 85% with the exception of the first batch of *Acer campestre* L. where viability was 72%. The structures of nuts (*C. avellana*, *Cornus sanguinea* L., *Fagus sylvatica* L., and *Q. robur*), samaras (*F. excelsior*), and samara-like mericarps (*A. campestre*, *A. pseudoplatanus* L.) were unchanged from naturally dispersed fruits; however, drupes (*Crataegus monogyna* Jacq., *Prunus avium*, *P. spinosa* L., *Viburnum lantana* L., *V. opulus* L.) had been processed to remove fleshy pericarps, hence cleaned pyrenes (pits) were the structures tested. At the time of receipt, all seeds were undergoing appropriate dormancy breakage treatments to ensure spring germination, and were stored moist at 4 °C until used.

For each species, dry mass of the whole seed, the embryo + endosperm fraction, and the outer coat were determined on samples of 30 seeds.

2.2. Consistency of predator preference for seed of 12 species across three sites

Preferences for seed of the 12 species were tested at three sites in southern England: Site 1, a forest nursery (Headley Nursery, 51:08:02 N 0:50:42 W) with established populations of *Apodemus sylvaticus* and *A. flavicollis*; Site 2, a *F. sylvatica* woodland at Micheldever Woods (51:08:29 N 1:14:22 W), and Site 3, a forest restocking site (Chawton Park Woods, 51:07:22 N 1:01:57 W) where the previous crop of *Pseudotsuga menziesii* (Mirb. Franco) had recently been clear-felled. Prior to each experiment, the number of small mammals accessing each experimental area was assessed by live trapping using Longworth traps (Gurnell and Flowerdew, 1989) set out for four trap-nights as a grid of 25 paired traps spaced at 5 m apart (Site 1), 20 m apart (Site 3), and 40 m apart (Site 2).

Seeds were exposed to predation as randomised single-species plots that were set out on 18, 22, and 28 February 2003 for each site respectively. A plot consisted of 20 seeds of a given species laid out in a 5 × 4 grid on a square of plastic-mesh fabric (Rokolene Protection Netting); 20 × 20-cm squares were used for the larger nuts, and 10 × 10-cm squares for the smaller-seeded species. Each seed was attached to the mesh using a small drop of glue (Loctite 454 (Gel) Instant Adhesive, Loctite 7455 Activator) to prevent seeds from being moved by the wind, but not inhibit detachment of seed by foraging small mammals (Alcantara et al., 2000; Herrera et al., 1994; Rey et al., 2002). The mesh squares were fixed to the ground surface with wire staples. Four replicates of each species plot were set out at each site, giving a total of 80 seeds for each species at each site. At Site 1, the plots were set out at a single location on bare soil alongside a hedge where *A. sylvaticus* were nesting and actively foraging. To account for variation in predation with distance from the nesting area, the species plots were laid out as a Trojan semi-Latin square design generated by the AGSEMILATIN procedure of GenStat (Payne and Lane, 2006), with three plots set out contiguously at each cell of the row × column grid, and 2-m separating cells. The locations of nesting sites were unknown at Sites 2 and 3; consequently to increase the chances that plots would be encountered, sets of 12 species plots were laid out at four locations within each site, separated by 50–75 m. At each location, the 12 species plots were randomly laid out 1.5 m apart in a 4 × 3 grid.