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Spatial-scale dependencies in the predation of seeds by rodents

A dissertation submitted in partial fulfilment of the degree of
Masters of Science

by

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1995

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28 MAR 1996

SUMMARY

1. Previous studies have shown rates of seed predation in deciduous woodland to be high (on average 60%) and extremely variable in space and time.
2. Post-dispersal seed predation by forest rodents was examined simultaneously in five areas of deciduous woodland surrounding Durham City, Co. Durham.
3. This study investigated the influence of seed density, seed burial and seed species in determining the rates of seed encounter and exploitation by rodents of both native and exotic seed. The effect of within- and between-sites differences were also examined.
4. Live-trapping studies and the use of exclosure treatments revealed that *Apodemus sylvaticus* and *Clethrionomys glareolus* were the major seed predators. Together, they were responsible for removing between 55-80% of the experimental seed supply.
5. Seed burial accounted for a high proportion of the variation and significantly reduced the frequency of rodent encounter compared to surface seeds at both seed densities. Furthermore, it increased the variation in encounter due to density, species and site effects. It had no significant influence, however, on the extent to which groups of ten seeds were exploited once encountered.
6. Variations in the frequency of seed encounter and exploitation were both strongly affected by changes in seed density, with high densities increasing the chance of seed detection and removal. Significant species effects were also detected for seed encounter and exploitation.
7. Seed predation was spatially patchy, between and within experimental sites, possibly reflecting variation in the spatial distribution of seed predators.
8. The selective nature of the seed predators, plus the relative patchiness of predation intensity in space, suggest that post-dispersal seed predation may play an important role in determining the distribution and/or abundance of deciduous woodland plants.

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3. INTRODUCTION

The literature concerning the impact of seed predators and their role following seed dispersal by plants is voluminous (Watt 1919, 1923; Gashwiler 1970; Marshall & Jain 1970; Radvanyi 1970; Brown *et al.* 1975 Borchert & Jain 1978; Reichman 1979; Mares & Rosenzweig 1978; Hay & Fuller 1981; Heithaus 1981; Abramsky 1983; Mittlebach & Gross 1984; Jensen 1985; Price & Jenkins 1986; Klinkhammer 1988; Schupp 1988; Hulme 1994; Boman & Casper 1995).

Previous studies on the subject have shown rates of seed predation to be high and extremely variable in space and time. So far, at least six major sources of variation have been identified in the field: the effect of habitat and micro-habitat, season, seed species and the impact of density and burial. Identifying these sources is fundamental, since post-dispersal seed predation, defined as the consumption and killing of seeds in the field (Crawley, 1992), can be a potentially strong agent of selection on plant dispersal patterns (Willson & Whelan, 1990), influencing plant recruitment (Borchert & Jain 1978; Brown *et al.* 1975; Mittlebach & Gross 1984), plant-species diversity (Janzen 1971; Hubbell 1980) and plant community structure (Inouye *et al.* 1980).

In both tropical and arid environments seed predators have been shown to remove substantial numbers of seeds and to affect the distribution and abundance of plants. Janzen (1971) stresses the importance of seed predation as an explanation for high diversity in tropical forests, and in deserts rates of seed loss recorded have been in the order of 70-100% of available seeds removed per day (Brown *et al.* 1975; Reichman 1979; Abramsky 1983). Hulme (1994), studying post-dispersal seed predation in grassland, reports losses of approximately 70-80 %.

Not only do granivores gather large numbers of seeds, but they also collect from specific locations, thus affecting the distribution of the remaining seeds. Harper (1977) notes that selective foraging by granivores "has a great effect on seed populations

remaining to germinate" and that selective granivory may cause changes in the density of certain species. The demography of four species of Californian annual grasses, for instance, was significantly affected by rodent granivory (Brochert & Jain, 1978). Seed removal rates of 37-75% in these grasses reduced adult density in two species by selectively decreasing the densities of the preferred seed species, thus influencing inter- and intra-specific interactions among plants. In British oak and beech woodlands the failure of natural regeneration of trees has been attributed to the destruction of seeds by small mammals (Watt, 1919, 1923; Ashby, 1959).

Previous studies have shown rates of seed predation in deciduous woodland to be high (on average 60%). Rodents can become significant seed eaters in European forests, which often exhibit periodic fluctuations in the production of seed crops. Jensen (1985) showed that in years of major seed production ("mast" years), a large number of beech (*Fagus sylvatica*) nuts survive and retain the potential to germinate. In contrast, between mast years rodents alone may consume large percentages of the seeds produced, thus potentially affecting the regeneration patterns of many plant species (Telleria et al., 1991).

Many rodents have shown a response to small-scale differences in micro-habitat (Hay & Fuller 1981; Price & Waser 1985; Hulme 1994). It is believed that the spatial heterogeneity of the vegetation cover in a particular habitat may influence small mammal abundance and subsequent patterns of seed predation (Price & Jenkins 1986; Hulme 1994). Coexisting species may differ in their affinities for foraging micro-habitats to the extent that some species will avoid open areas and limit their use of open space in response to increased levels of predation (Mittlebach & Gross 1984) or to avoid intra-specific hostility by reducing direct encounters (Smal & Fairley, 1982). The degree of responsiveness expressed, however, should involve trade-offs between the value of specific food items and the costs associated with foraging in different micro-habitats.

Between-habitat differences in the degree of vegetation cover may also cause variation in seed predation. Habitat differences in seed predation have been reported

within grasslands and old-fields (Mittlebach & Gross 1984), between forests and grassland (Janzen 1982) and between wooded habitats and tree-fall gaps (Webb & Willson 1985; Schupp 1988; Boman & Casper 1995). Generally fewer seeds are removed in open habitats than in those with substantial vegetation cover.

Studies on the effect of seed species on rates of seed predation have brought to light distinct predator preferences linked to differences in seed size (Smigel & Rosenzweig 1974; Gadekar 1975; Inouye *et al.* 1980; Abramsky 1983; Mittlebach & Gross 1984; Jensen 1985; Hulme 1994; Boman & Casper 1995), handling time (Kaufman & Collier 1981; Price 1983, 1984) and nutritional content (Partridge & Maclean 1981; Kelrich *et al.* 1986; Jenkins 1988). One of the predictions of optimal foraging theory is that the optimal diet should always include the food type of the highest rank, and that food types should be added to the diet in rank order as food density decreases (Pyke *et al.* 1977). Following the predictions, seed predators have mostly been shown to harvest larger seeds first when presented with a range of seed sizes (Jensen 1985). As the range of seed sizes decreases, so does selectivity and other characteristics take precedence in influencing seed choice (Reichman 1977; Hulme 1993).

The reported effects of density on post-dispersal seed predation vary considerably in time and space due to habitat (possibly related to local food abundance) and micro-habitat effects, seed species present (Willson & Whelan 1990), nature and density of the seed predators (Reichman 1979). In their studies Mittlebach and Gross (1984) report that seed density has only a minor effect on predation rates, while others have found that a smaller proportion of seeds survive at high density, with rates of removal rising with increasing seed density (Webb & Willson 1985; Hulme 1994). Rodents, which are thought to locate their food by olfaction (Jennings 1976; Howard *et al.* 1968; Lockard & Lockard 1971) are, in fact, most efficient at detecting and exploiting larger seed clumps, which may incidentally attract rodents from their usual foraging areas (Brown *et al.* 1975).

Seed burial has also been shown to influence seed predation rates. In previous studies rates of seed loss for buried seeds have been substantially lower than those for seeds exposed on the surface (Reichman 1879; Hulme 1994). For buried seeds the probability of encounter increases rapidly with seed size. Once buried, in fact, small seeds are relatively safe from small mammal predation, but rodents have no difficulty in detecting larger seeds that are buried at considerable depths (Crawley 1992). Furthermore, burial has been found to reduce seed losses of low-density seeds proportionately more than those at higher density. The nature of the soil in which the seeds are buried is also important, and seed recovery rates by rodents have been shown to depend on the texture of the soil and the particle size distribution relative to the size of the seeds in question (Price & Waser 1985).

These studies suggest that the relative contribution of seed predation to seed occurrence and plant dynamics varies over several orders of magnitude among plant species and among communities. The magnitude and importance of each of these sources of variation is largely unknown. With the exception of Hulme (1994), most studies on seed predation, so far, have considered each of these sources separately and experimental data needed to determine the general contribution of seed predation to the dynamics and evolution of plant regeneration are lacking (Louda 1989). In an attempt to improve the understanding of seed-seed predator interactions, this paper presents the results of a field study on rodent granivory designed to :

1. examine the influence of between and within-habitat variation in determining rates of seed removal by rodents;
2. assess the magnitude of individual effects on levels of post-dispersal seed predation by examining the influence of seed density, seed burial, seed species, and within- and between-habitat variation on the rates of removal of four seed species
3. determine whether the patterns of seed predation highlighted by Hulme (1994) in his study on rodent granivory in grasslands also apply to woodland species.

The seed predators under investigation are two of the commonest murid rodents: the wood mouse (*Apodemus sylvaticus*, L.), and the bank vole (*Clethrionomys glareolus*, Schreber). The two species are widely distributed throughout Europe and their ecology has been extensively studied (Ashby 1976; Flowerdew *et al.* 1985; Alibhai & Gipps 1991; Flowerdew 1991; Gipps & Alibhai 1991). Both species rely heavily on seeds as a major food source (Hansson, 1985).

4. MATERIALS AND METHODS

4.1 STUDY SITES

The experiments were undertaken simultaneously in five areas of deciduous woodland surrounding Durham City, Co. Durham (Fig. 4.1). In all the sites the parent rock is boulder clay of sub-glacial origin, containing a substantial sandy fraction that varies in proportion between sites. Habitat characteristics for the different sites obtained using the point-centered quarter method are summarised in Table 4.1.

The Houghall Wood, Hollingside Wood and Mountjoy sites all lie approximately one mile south of the city centre and are found on sloping ground of varying degrees immediately west of the floodplain of the river Wear (Ashby, 1976). The steepest of the sites, Mountjoy (45%), faces east and has the highest density of trees/ha. It contains a substantial canopy, composed of silver birch (*Betula pendula*), mountain ash (*Sorbus aucuparia*), oak (*Quercus petraea*), beech (*Fagus sylvatica*), sweet chestnut (*Castanea sativa*), and sycamore (*Acer pseudoplatanus*). The understorey vegetation consists predominantly of holly (*Ilex aquifolium*) and locally occurring hazel (*Corylus avellana*). An incomplete cover of bramble and ferns occurs at ground level.

The Houghall Wood site faces SE and is situated on sloping ground varying between 10-30%. The transect, which runs from west to east, crosses a variety of vegetational habitats in which *Q. petraea* is largely the dominant tree. Also present in the canopy, however, are *F. sylvatica*, *A. pseudoplatanus* and *B. pendula*. The understorey vegetation at the western end of the transect is composed of a mixture of elder (*Sambucus nigra*), young mountain ash (*S. aucuparia*) and locally abundant Wych elm (*Ulmus glabra*), while a contiguous stand of holly (*I. aquifolium*) runs parallel to the northern edge of the transect; in the latter's eastern end the understorey vegetation is mostly absent and is replaced, at ground level, by an incomplete cover of ferns (*Dryopteris spp.*), mosses and a dense carpet of *Vaccinium myrtillus*.

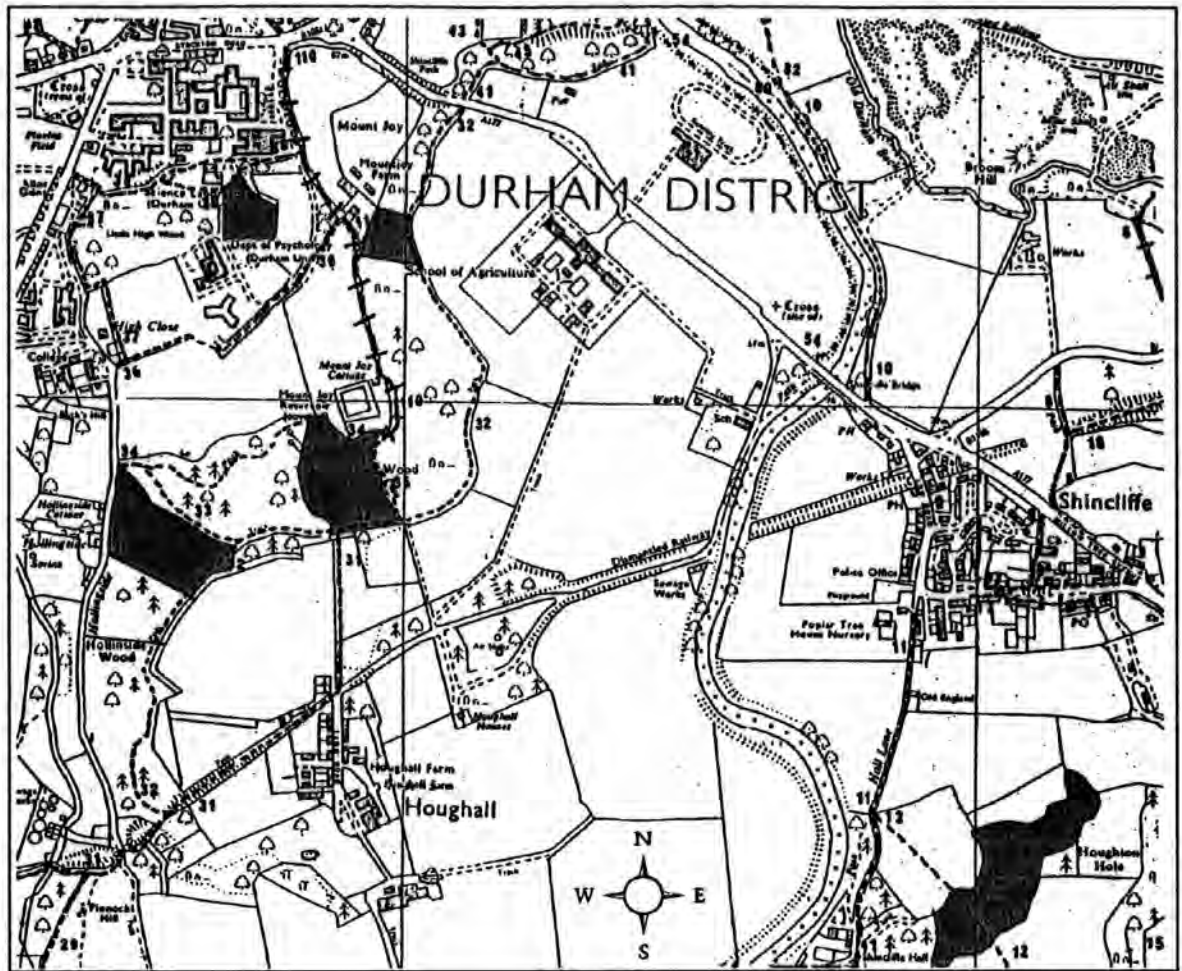


Fig 4.1. The five study sites (shaded grey) surrounding Durham City where field trials were carried out.

The Hollingside Wood site faces east and is the second steepest with a slope of approximately 40%. It is largely a beech woodland, characterised by the presence of an abundant leaf litter and humus layer at ground level. Sycamore, oak and mountain ash are also present in the canopy, as are *C. sativa*, *S. nigra* and *B. pendula*, which are locally abundant. Holly trees are present towards the southern end of the transect, whereas ferns offer partial cover at ground level throughout the transect.

Table 4.1. Species densities (De) and basal areas (Ba) estimated for individual species at each of the five sites using the point-centered quarter method. Canopy basal areas (m²/ha) and total tree densities (trees/ha) are also estimated.

	Shincliffe Wood		Great High Wood		Science Site		Mountjoy Wood		Hollingside	
	De	Ba	De	Ba	De	Ba	De	Ba	De	Ba
<i>Acer pseudoplatanus</i>	130.94	18.20	134.72	31.03	248.49	3.05	205.39	38.03	50.43	6.82
<i>Betula pendula</i>	-	-	-	-	16.57	0.42	88.02	2.52	7.20	0.15
<i>Castanea sativa</i>	-	-	-	-	265.05	16.80	117.36	0.95	7.20	1.60
<i>Corylus avellana</i>	-	-	-	-	-	-	58.60	0.59	-	-
<i>Fagus sylvatica</i>	202.37	35.25	22.45	0.22	16.57	0.38	352.09	2.45	122.48	25.87
<i>Ilex aquifolium</i>	59.52	0.21	89.82	1.92	33.13	0.06	88.02	1.39	21.61	0.90
<i>Lonicera periclymenum</i>	-	-	-	-	-	-	29.34	0.05	-	-
<i>Quercus petraea</i>	-	-	538.89	35.82	82.83	29.58	88.02	0.27	36.02	2.85
<i>Sambucus nigra</i>	83.33	0.80	22.45	0.14	-	-	-	-	7.20	0.13
<i>Sorbus aucuparia</i>	-	-	22.45	0.03	-	-	146.70	7.58	36.02	4.40
<i>Ulmus glabra</i>	-	-	22.45	0	-	-	-	-	-	-
Canopy basal area	476.15	54.47	898.16	70.24	662.63	50.30	1173.63	53.86	288.177	42.72
Total tree density										

The Science Site transect runs from east to west on NE-facing ground (slope 35%) within Durham University's Science Site. It is largely dominated by sycamore and sweet chestnut, but also present in the canopy are silver birch, beech and oak. The understorey layer is dominated by holly, which tends to be present locally throughout the transect. At ground level vegetation cover is sparse with localised clumps of ferns and bramble and an abundance of leaf litter. A gap in the canopy of approximately 10m lies at midpoint in the course of the transect, where pipe-laying was conducted before the commencement of the experiment.

Approximately 2 miles from the centre of Durham, and west of the river Wear, lies the fifth site, situated on a west-facing slope (20-30%) within Shincliffe Wood. The wood runs parallel to the river's course and is dominated by beech, with sycamore also present at relatively high densities. *Ilex aquifolium* and *Sambucus nigra* are the main constituents of the understorey vegetation, while ferns and bramble largely dominate at ground level.

4.2 SEED EXPERIMENTS

Seed predation trials were conducted using replicate sets of feeding stations. In each of the five sites 10 feeding stations were set up at 10 m intervals along a 100 m transect.

Seeds were presented in the field in plastic petri-dishes 9cm in diameter and 1cm in depth, filled with soil and secured to the ground using 5" nails. Three petri-dishes, set equidistantly apart (1m) in a triangular array, were used at each feeding station. Taxon-specific exclosures were utilised around 2 of the 3 feeding depots (Fig.4.2) to quantify the relative impact of invertebrates and granivorous rodents on rates of seed removal and exploitation. In the invertebrate treatments seeds were protected from rodents and other seed-eating animals by a 30 x 30 x30 cm³ 1.2 cm wire-mesh cage, buried 3-4 cm within

the soil to prevent dislodgement. Larger mammals and seed-eating birds (e.g wood pigeons) were excluded from the rodent treatment using cages constructed from 3 cm wire-mesh. Cages were 40 cm high, 10 cm wide and closed at the top with a wire-mesh lid. An open petri-dish was used as the control treatment to assess background seed losses.

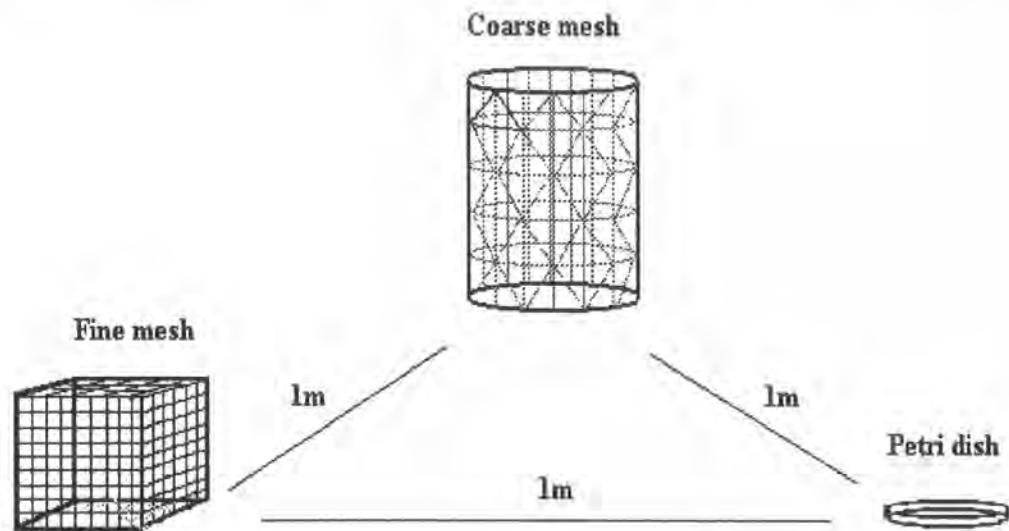


Fig.4.2 Triangular positioning of the taxon-specific exclosures surrounding feeding depots at each of the experimental feeding stations.

Seeds of *Taxus baccata*, *Fraxinus excelsior* and *Ulmus glabra* and commercially available mung beans were used in the seed predation trials. Seeds were placed inside the petri-dishes at densities of either 1 or 10 seeds per species, and the effect of burial on seed encounter and removal tested by either burying the seeds or by placing them on the soil surface. Seed species, density and burial treatments were assigned to each feeding station

in a unique, randomised order and presented so that the invertebrate, vertebrate and open petri-dish trials at each feeding station exhibited the same seed/density/burial treatment at any one time. The randomised sequence was replicated in each of the study sites.

Petri-dishes were exposed in the field for three consecutive days, after which remaining seeds were collected and counted. Assessments were made of seed damage (more than 50% of each seed remaining) and seed consumption *in situ* (less than 50% remaining), and seed removal.

In an attempt to assess the identity of the seed predators, the presence of slugs or faeces within the dishes, the nature of seed damage and evidence of seed caches or rodent burrows lying in the immediate vicinity of the sampling stations was also recorded. After each trial petri-dishes were supplied with a new set of randomly chosen seeds, at different densities and burial regimes, until, by the end of the experiment, all feeding stations had received the complete sequence of seed treatments.

4.3 RODENT TRAPPING

Density estimates and distribution of woodland rodents were obtained from capture-mark-recapture studies on the small mammal populations at each of the study sites. Live-trapping was conducted over three consecutive nights in mid-June, mid-July and mid-August using a line of 10 Longworth traps set 10 m apart. Traps were laid along the transects at each study site, within a 1m radius of each feeding station. They were covered with leaf litter to minimise extremes of heat and cold and to conceal the traps from passers-by. Traps were checked twice-daily, in the early morning and late afternoon, and captured animals were individually marked using the fur-clip marking procedure (Gurnell & Flowerdew, 1982). Date of capture or recapture, species, sex age and weight were also recorded for each animal and estimates were drawn of the individual and

combined numbers of *Apodemus sylvaticus* and *Clethrionomis glareolus* present at each station, as well as overall number of rodents present at each site.

The seed exposure experiments were designed to fit between these monthly samples so that seed predation could be related to rodent abundance.

4.4 DATA ANALYSIS

Data analysis followed Hulme (1994) and examined two components of seed predation: seed encounter, considered as the probability of at least one seed being removed; and seed exploitation, i.e. the proportion of seeds being removed once they were encountered. Seed encounter was a binary variable (encountered or not encountered) and enabled direct comparisons of density treatments. Seed exploitation was only applicable to high densities and was described as the proportion of seeds being removed.

ANOVA was used to analyse the arc-transformed data of both seed encounter and exploitation, and to detect between- and within-site variations due to differences in cage treatment, burial, seed density and seed species utilised during the course of the experiment. *A posteriori* multiple range tests (Tukey's Honestly Significant Difference test) were used to compare treatment effects. Statistical significance and consistency of trends among the data sets were used to explore the data in more detail. Correlation analysis was used to compare percentage removal and encounter with rodent abundance and habitat characteristics.

5. RESULTS

5.1 ENCOUNTER OF SEEDS BY RODENTS

Significant variation in seed encounter occurred between treatments ($F=22.386$; $p<0.01$) in the five sites (Table 5.1.). Seed detection in the fine mesh was low compared to the coarse-mesh and petri-dish treatments to which rodents had access (Fig. 5.1). In the coarse cage and open petri-dish treatments, in fact, seeds experienced a two- to three-fold increase in the frequency of detection. No differences in the rate of seed encounter were detected between the latter two.

Table 5.1 The percentage of total variation for encounter of seeds by rodents estimated using ANOVA. The main effects of burial [bu], cages [ca], density [de], species [sp] and site [si] are shown as well as all higher order interactions found to be significant at the 0.05% (*) and the 0.01% level (**).

Terms	d.f	Mean squares	F Value
Burial	1	31.30	94.55 (**)
Cages	2	71.93	218.49 (**)
Density	1	18.46	56.07 (**)
Species	3	4.86	14.76 (**)
Site	4	10.79	32.78 (**)
Bu.Ca.	2	4.16	12.63 (**)
Bu.De.	1	7.96	24.18 (**)
Bu.Sp.	3	2.94	8.92 (**)
Bu.Si.	4	1.04	3.15 (*)
Ca.De.	2	2.18	6.61 (**)
Ca.Si.	8	3.04	9.22 (**)
De.Sp.	3	1.35	4.10 (**)
Sp.Si.	12	0.9	2.76 (**)
Bu.Ca.De.	2	1.10	3.35 (*)
Bu.Ca.Sp.	3	3.12	3.12 (*)
Residual	2160	0.329	
Total	2399	0.454	

Burial of seeds in all cage treatments, at both densities, significantly reduced the frequency of rodent encounter ($F=69.36$; $p>0.01$) compared to surface seeds. In

other words it was more likely for a seed species to be encountered when present on the surface of the petri-dish than when it was buried.

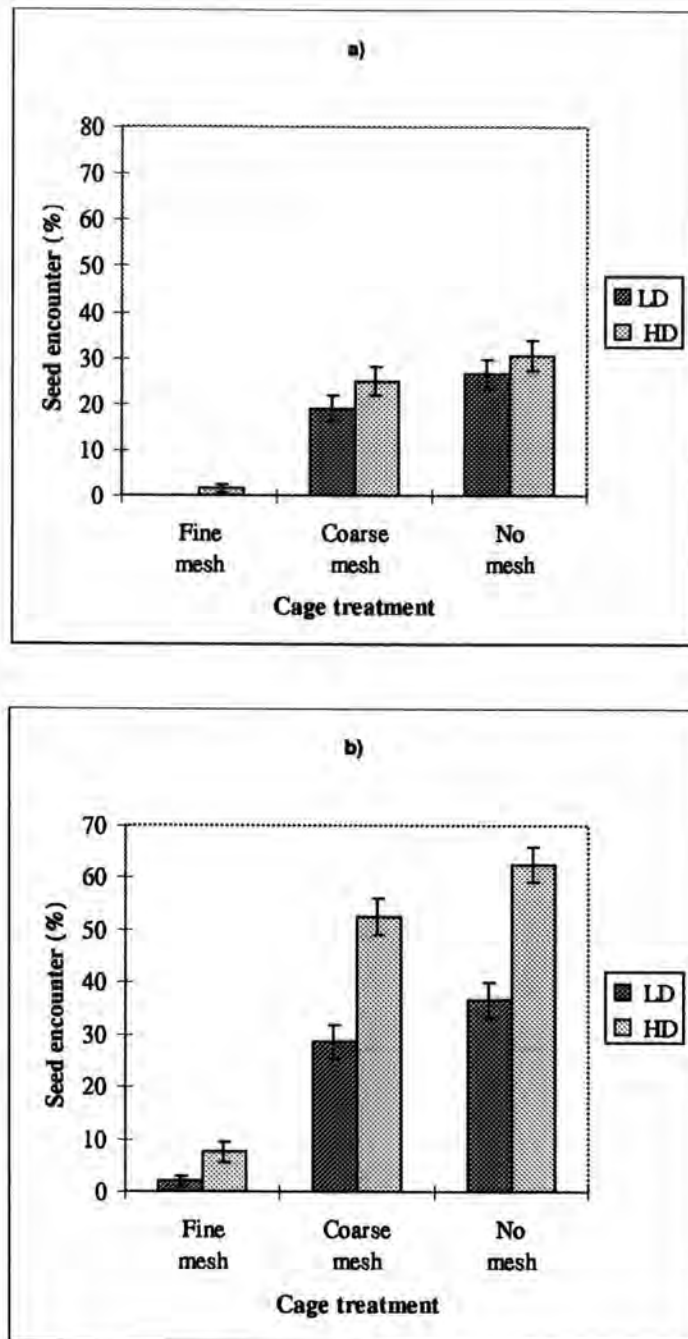


Fig 5.1 Observed variation in the rates of seed encounter by rodents in the fine mesh, coarse mesh and open petri-dish treatments. Encounter is expressed as the mean percentage (± 1 S.E.) for seeds at high and low densities either a) buried or b) exposed.

Variations in the frequency of seed encounter were strongly affected by changes in seed density. High seed densities increased the chance of seed depots being detected, such that depots containing ten seeds (high density) were significantly more likely to be detected ($F=56.047$; $p>0.01$) than depots containing only one seed (low density) (Figs. 5.1, 5.2 and 5.3). Burial of seeds at the higher and lower seed densities significantly reduced the frequency of seed encounter in all the enclosure treatments in each of the five sites.

The frequency of seed encounter by rodents varied considerably from site to site ($F=32.785$; $p>0.01$), ranging between 20.6% in Shincliffe Wood to 51.6% in Great High Wood. Patterns of seed encounter were similar in the Shincliffe (20.6%), Science (24.4%) and Mountjoy (30.3%) sites, but shifted considerably in magnitude in Great High Wood and Hollingside, where rates of encounter were significantly higher at 51.6% and 49.4% respectively (Fig. 5.2.). Trapping confirmed that both *Apodemus sylvaticus* and *Clethrionomys glareolus* were present in all sites, but that they differed in relative abundance within each. (Table 5.2.).

Table 5.2 *Apodemus sylvaticus* (AS) and *Clethrionomys glareolus* (CG) captures obtained in the five study sites using small mammal trapping techniques. Individual and total number of rodents are presented for each site.

	Sh	GHW	Ss	Mo	Ho
<i>Species</i>	n	n	n	n	n
AS	0	4	6	4	3
CG	13	2	2	9	9
Total	13	6	8	13	12

In Shincliffe Wood, for example, where no wood mice were caught bank vole captures were high. *Apodemus* numbers in the Science Site, on the other hand, were significantly greater than recorded numbers of bank voles found on that site. Overall, total rodent numbers were greater in the Shincliffe Wood and Mountjoy sites, where 13 rodents were caught over the three trapping periods. The lowest catches were recorded in Great High Wood (6 rodents).

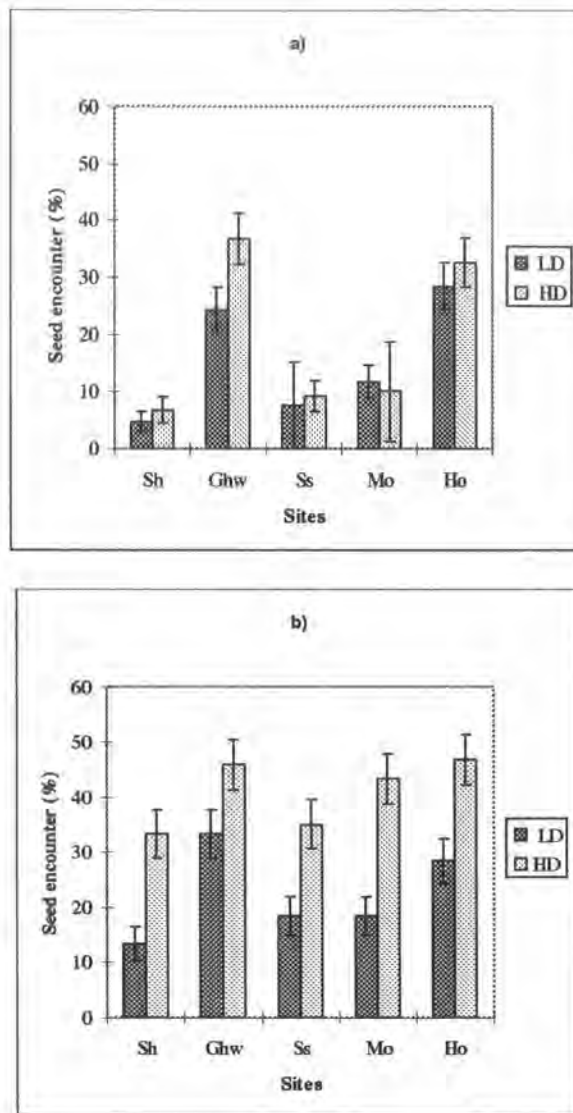


Fig 5.2. The observed variation in the rates of seed encounter by rodents expressed as a function of site. Overall mean percentage seed encounter (± 1 S.E.) is shown for seeds at high and low densities in the a) buried and b) surface treatment.

Despite these differences, however, no correlation was found among variations in the frequency of seed encounter registered between sites and the individual and total number of rodents present in each. Similarly, differences in habitat characteristics between the five sites (Table 4.1.) did not appear to influence rates of seed encounter. A significant proportion of the variation in seed encounter was also attributable to seed species effects ($F=4.101$; $p<0.05$), which differed significantly between sites ($F=2.760$; $p=0.01$) (Fig.5.3). Detection of ash seeds mostly occurred in Hollingside Wood, whereas yew, elm and mung were most frequently encountered in Great High Wood,

where percentage encounter approximated 50% for all seed species. A drop in seed density reduced encounter of ash seeds significantly more than other seed species. No interactions were found at the cage treatment level, i.e. the presence of exclosures did not influence the rate at which seeds of individual species were encountered by rodents.

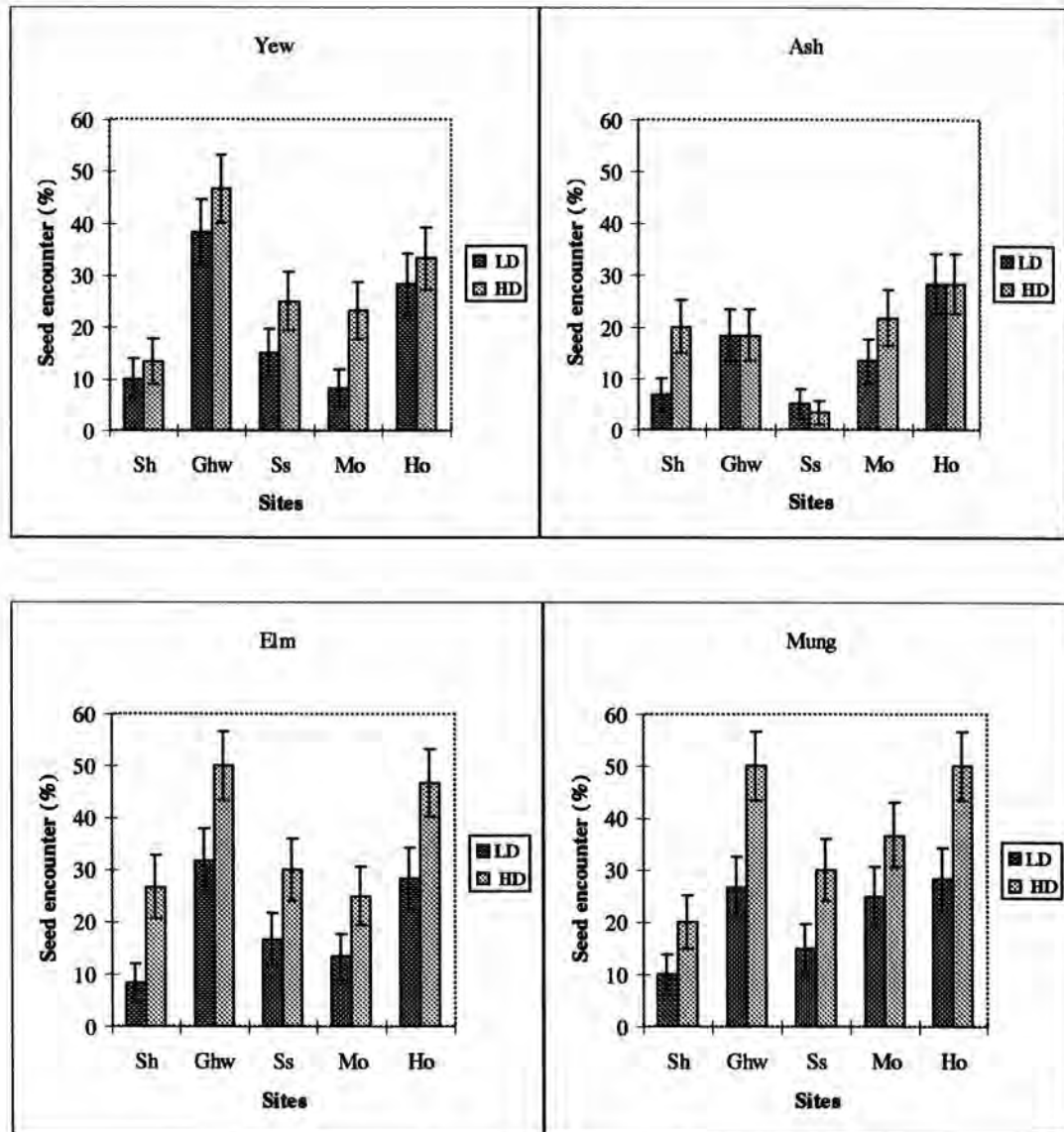


Fig.5.3. The observed variation in the rates of seed encounter by rodents for a) yew, b) ash, c) elm and d) mung. Encounter is expressed as the mean percentage (± 1 S.E.) for seeds exposed at high and low densities.

5.2 SEED EXPLOITATION BY RODENTS

Recorded seed exploitation by woodland predators was high (between 55-80%) and extremely variable. Analysis of variance (Table 5.3.) revealed significant variation in the rates of seed removal due to the effect of cages, site and species examined. Total seed removal from the fine mesh was low, and although slugs were sometimes observed causing damage to samaras, losses attributable to invertebrates were negligible

Table 5.3. The percentage of total variation for exploitation of seeds by rodents divided into its main effects of burial, cages, species and site. No higher order interactions were found. (**) indicates significance at the 0.01 level.

<i>Terms</i>	<i>d.f.</i>	<i>Mean square</i>	<i>F Value</i>
Burial	1	0.151	0.706 (ns)
Cages	2	1.901	8.887 (**)
Species	3	1.974	4.534 (**)
Sites	4	0.970	9.233 (**)
Residual	342	0.214	-
Total	352	0.251	-

Seed removal was greatest from the coarse mesh treatment and the open petri-dish treatment to which rodents had access (Fig 5.4.).

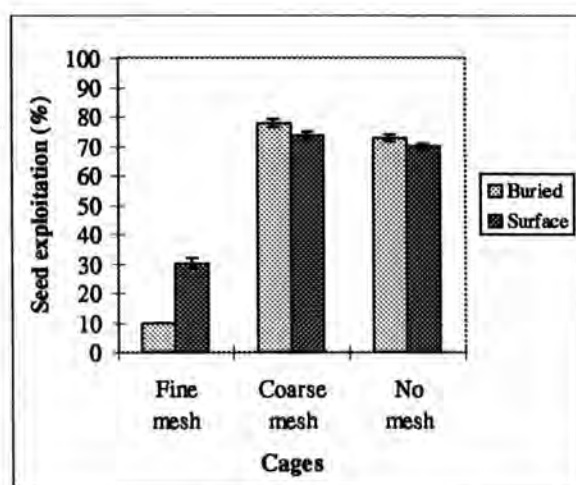


Fig. 5.4. Observed variation in rates of seed removal by rodents in the fine-mesh, coarse-mesh and open petri-dish treatments. Exploitation is expressed as the mean percentage (± 1 S.E.) for buried or surface seeds at high seed densities.

During predation trials seeds were either removed from the feeding station, consumed *in situ*, damaged or left untouched. The highest proportion of seeds was consumed *in situ* (as testified by the presence of seed remains). A negligible proportion was damaged or completely removed from the petri-dishes.

In none of the comparisons did burial significantly alter the extent to which groups of ten seeds were exploited once they had been encountered. Buried seeds in the coarse and open-cage treatments were equally attractive to the major seed predators and were removed in slightly greater proportion compared to surface seeds.

Examination of overall variation in the rates of seed exploitation revealed a strong species effect ($F=9.233$; $p>0.01$), linking differences in removal rates by predators to variations in seed species. Tukey's HSD test detected significant differences in the removal rates of ash and elm, which were harvested considerably less frequently than yew and mung. The magnitude of exploitation of the latter two species was approximately the same (Fig.5.5).

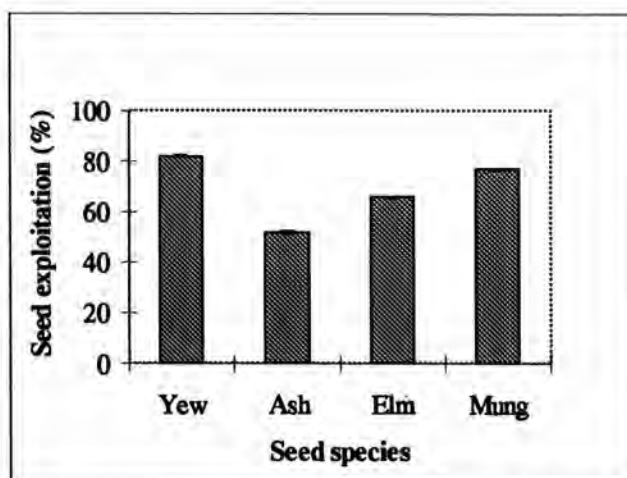


Fig.5.5. The relative proportion of seeds exploited during predation trials for each seed species. Exploitation is presented only for the high seed densities and is expressed as the mean (± 1 S.E.).

Seed predation was relatively intense throughout the five sites, ranging from 54.4% in Shincliffe Wood to a maximum of 79.8% in Hollingside Wood, in which percentage removal was considerably greater (Fig. 5.6.). Even though information

drawn from trap-line indices of rodent abundance revealed a significant variation in the numbers of *Apodemus* and *Clethrionomys* present at each site, no correlation was found between varying rates of seed predation recorded in each site and relative rodent abundance. Furthermore, differences in the canopy and species composition detected using the point-centered quarter method were found to have no effect in determining spatial use by the resident rodent populations.

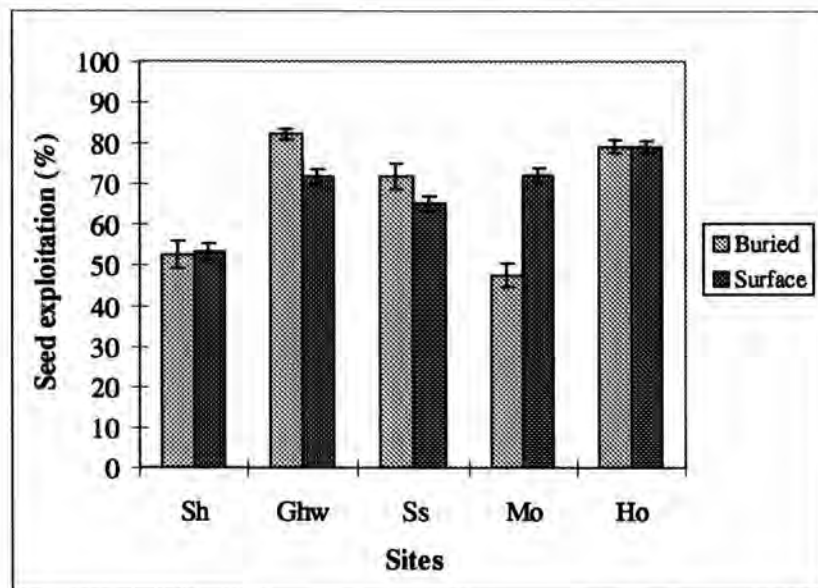


Fig. 5.6. Observed variation in the rates of seed exploitation by rodents expressed as a function of site. Overall mean percentage seed exploitation (± 1 S.E.) is shown for buried and surface seeds at the high seed density.

Although ANOVA detected no high order interactions, it was found that variation between sites increased the differences due to species effects. Fig.5.7.. illustrates the mean number of seeds of each species that were consumed in the five sites over the 16 predation trials. Yew was consumed in relatively large proportions throughout the five sites and was totally removed in Great High Wood. Removal rates of mung beans were also high and consistent throughout the sites with a maximum exploitation of circa 80%. Elm was harvested considerably less frequently in Shincliffe than it was in Great High Wood, Hollingside or Mountjoy, where rates of removal

when seeds were buried were comparable to percentage removal calculated for yew and mung. Ash seed consumption was also greater in Hollingside Wood, where rates of seed removal approximated 100%, but was overall considerably lower compared to other seed species, with low rates of seed removal recorded throughout the sites.

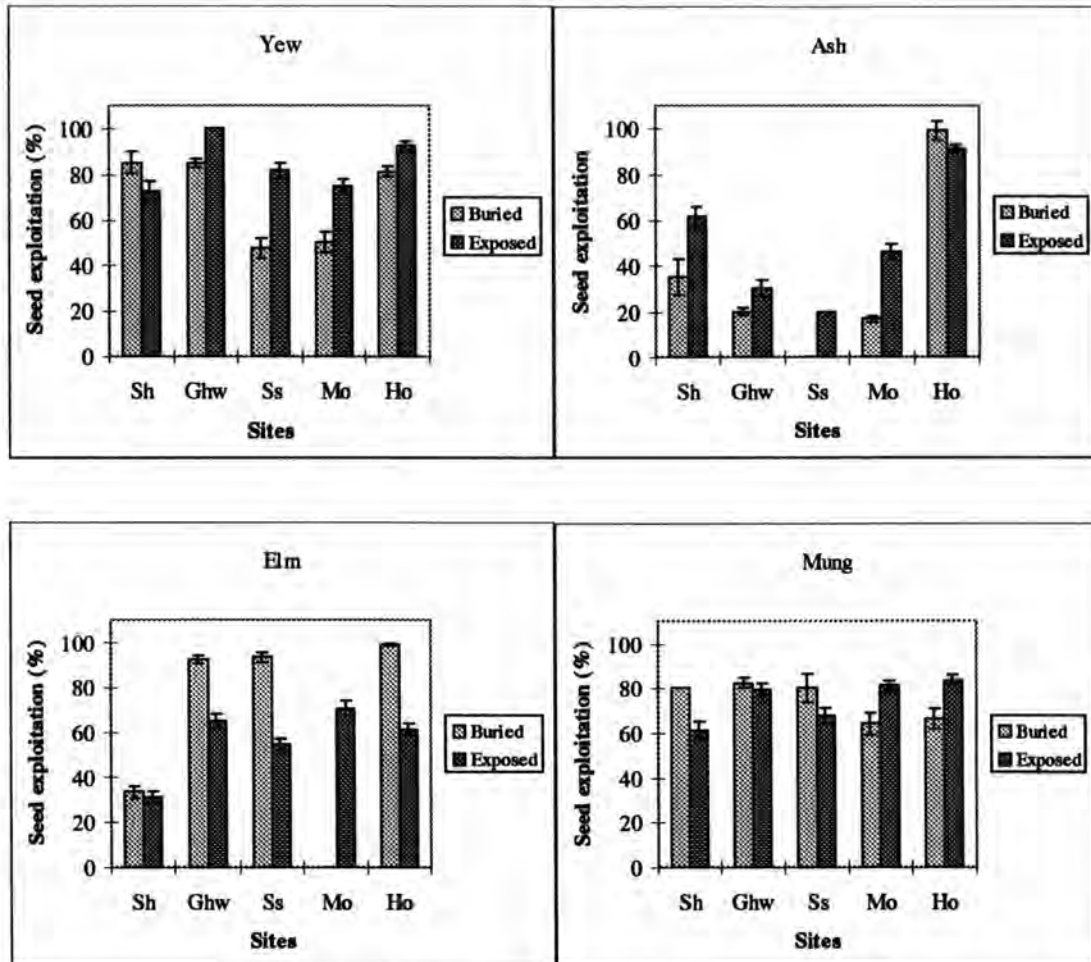


Fig. 5.7. The observed variation in the rates of seed exploitation by rodents for yew, ash, elm and mung. Exploitation is expressed as the mean percentage (\pm S.E.) for buried and surface seeds at the highest seed density.

6. DISCUSSION

6.1 EFFICIENCY OF RODENT SEED PREDATION

Previous studies have shown that small mammals may play an important role in woodland ecosystems by dispersing, burying and consuming large quantities of seeds (Watt 1919, 1923 ; Ashby 1976; Price and Jenkins, 1986). High seed losses are common in the case of forest trees (Shaw 1968) and are thought to influence forest regeneration. The destruction of acorn and beechmast by small woodland rodents is considered, in fact, to be responsible for the failure of natural regeneration in British oak and beech woodland (Watt 1919, 1923; Ashby, 1976).

During the present study there was abundant evidence of small mammal activity. The high level of seed removal from the enclosure treatments to which rodents had access, the appearance of rodent trails close to the feeding stations, characteristic seed damage observed in seed remains and the abundance of rodent droppings in or around the feeding depots, all seem to suggest that rodents were indeed the major seed predators. Seed predation by invertebrates, on the other hand, was negligible and no evidence was found of feeding by other granivorous rodents and birds (i.e. squirrels, wood pigeons). Catches of *Apodemus sylvaticus* and *Clethrionomys glareolus*, on the other hand, were consistent throughout the trapping period, supporting previous field studies which have shown rodents to be the main seed consumers in woodland ecosystems.

Results from the present study have shown that rodents were efficient at locating and exploiting the experimental seed supply. A number of seed attributes and environmental factors, however, have been shown to determine the probability of seed detection and exploitation. Most rodents locate their prey by olfaction (Howard *et al.* 1968, Lockard & Lockard

1971, Jennings 1976, Johnson & Jorgensen, 1981). Emission of volatile chemicals by the seed are thought to provide cues as to the location, identity and density of the food supply (Jennings 1976) as well as its suitability as a food source. The detection of the food item and the recognition of the food item as prey will depend, therefore, on a number of factors, i.e. the olfactory acuity and foraging efficiency of the rodent predators (Price, 1978) and the olfactory conspicuousness of the seed (Reichman, 1981).

Wood mice are predominantly nocturnal (Greenwood 1978, Montgomery & Gurnell 1985) and rely heavily on olfaction as a means of habitat exploration. Studies on *Apodemus* (Jennings 1976) suggest, in fact, that wood mice use olfaction in the detection of food items as prey. The olfactory biology of the bank vole, on the other hand, has been relatively ignored, perhaps due to the fact that this species is crepuscular in its activity, and is therefore thought to rely predominantly on visual rather than olfactory cues when foraging. Bank voles, however, have an extremely varied diet (Hansson 1985) and are obliged to make complex choices between different food types. It is fair to assume, therefore, that olfaction may play a role in food detection, complementing visual and gustatory cues.

6.2 THE EFFECT OF BURIAL

Environmental factors such as seed burial have been found to influence the predation sequence and to affect the ability of rodents in seed detection (Lockard & Lockard 1971, Hulme 1994). Buried seeds are effectively concealed from predators which rely exclusively on visual acuity as a means of detecting a food source. Encounter and retrieval of

buried seed by rodents which rely on olfactory cues in a number of studies was largely a function of burial (Reichman 1979) and burial depth (Lockard & Lockard 1971, Reynolds 1958). A recent study conducted by Hulme (1994) on mesic grasslands revealed that encounter of seeds by rodents was significantly reduced when seeds were buried. Burial in the experimental sites was also found to be a significant determinant in the rates of seed predation by forest rodents.

The depth at which the seed or seeds are buried may affect odour concentrations to the extent that olfactory conspicuousness decreases with increasing depth of burial. As volatile molecules diffuse, their concentration decreases at a rate directly proportional to the distance from the seed (Reichman & Oberstein 1977; Reichman 1981). Furthermore, soil characteristics, such as soil particle size, moisture content or temperature, may influence odour diffusion and adversely affect subsequent seed detectability (Reichman 1981; Johnson & Jorgensen 1981).

Results from the present experiment support these findings and burial was found to significantly reduce the frequency of rodent encounter for all seed species. This was found to be particularly true for the smaller seeds, ash and elm. Reichman (1981) suggests that seeds emanate volatile chemicals at a rate inversely proportional to seed size. Given this assumption, one could explain why burial is a more effective means of escape for smaller seeds than for larger ones. By burying smaller seeds the effect of seed size is augmented and olfactory conspicuousness is further reduced, thus explaining why smaller seeds in the experiment were encountered less frequently than larger ones. Similarly, patches of higher seed densities were found to be more vulnerable to predation than low-density seed treatments. It is not clear, to what an extent this is a function of clumped seeds being more conspicuous and therefore affecting rates of seed detection (Price & Jenkins 1986), yet the probability of rodent

encounter during the predation trials appeared to be significantly affected by patch size.

Depth of burial and soil attributes have also been shown to affect the probability of a buried seed being harvested once it has been encountered (Lockard & Lockard 1971; Price & Heinz 1984). Although the willingness to dig up buried seeds has been shown to be species-specific in rodents (Johnson & Jorgensen 1981), all rodents will generally avoid deeply buried seeds, presumably as a result of the higher energetic costs involved (Lockard & Lockard 1971; Reichman & Oberstein 1977; Reichman 1979; Heithaus 1981; Abramsky 1983) and the higher predation risks associated with foraging in any one patch for an extended period of time. Seeds in previous studies have been retrieved from considerable depths (Lockard & Lockard 1971; Reichman & Oberstein 1977) and *Apodemus sylvaticus* had no difficulty in detecting and removing seeds buried underneath a 3cm layer of peat moss (Jennings 1976). Seeds in the current experiment were buried 1 cm below the soil and burial was found to have no significant effect on the rate at which seeds were exploited once they had been encountered.

6.3 THE EFFECT OF DENSITY

As previously stated, results in this study have shown a pronounced effect of density on the rates of seed encounter, with single seeds being encountered approximately half as frequently as seeds present in groups of ten. Tests on the rates of seed exploitation, on the other hand, did not enable direct comparisons of density treatments, although previous studies using artificial and/or natural seed clumps have shown removal rates to increase with increasing seed density (Brown *et al.* 1975; Price 1978;

Reichman 1979; Heithaus 1981; Price & Waser 1985). Presumably, the value of clumped seeds (even less profitable ones) is higher than the value of individual seeds, and certainly in energetic terms foraging in high-density patches should be more cost-effective than foraging for dispersed seeds.

6.4 THE EFFECT OF SEED SPECIES

It has been mentioned that smaller seeds were encountered less frequently than larger ones during predation trials and that seed size may have affected odour conspicuousness and subsequent seed detectability by rodents. Once a seed has been encountered, however, it can either be harvested or ignored. Previous studies, which have examined rodent seed predation on two or more species, have almost always found significant variation in the rates of seed removal of different seed types (Inouye *et al.* 1980; Abramsky 1983; Mittlebach & Gross 1984; Jensen 1985; Kelrich *et al.* 1986; Willson & Whelan 1990; Boman & Casper 1995). In all the studies one obvious and potentially relevant trait is seed size. Results from the present investigation have shown that, out of the four seed species, the larger seeds, yew and mung (Table 5), were consistently preferred to seeds of *Fraxinus excelsior* and *Ulmus glabra*.

Table 5 Characteristics of the experimental deciduous tree and exotic seed species. Seeds of *Fraxinus excelsior* and *Ulmus glabra* were husked prior to analysis. Weight is expressed in (g/dwt); energetic content in (kcal/dwt).

Seed species	Weight	Energy content
<i>Taxus baccata</i>	0.075	8
<i>Mung beans</i>	0.058	0.16
<i>Fraxinus excelsior</i>	0.045	0.21
<i>Ulmus glabra</i>	0.035	0.01

The results are in accordance with field and laboratory experiments conducted by Jensen (1985) on seed preference of forest rodents in Denmark, in which the larger seeds of *Quercus*, *Fagus* and *Corylus* were harvested preferentially with respect to ash and elm, which showed low preference ratings. In Jensen's study (1985) rodents were also found to harvest seeds with the highest energetic value. The optimal foraging theory predicts, in fact, that foragers should maximise net energy intake per unit time spent foraging (Schoener 1971; Pyke *et al.* 1977). Testing this prediction, however, demands measurements of individual foraging efforts which unfortunately, due to temporal constraints, were not obtained. Data from Jensen (1985), Reichman (1976) and Hulme (personal communication) have shown that large seeds generally contain more energy than smaller seeds. Moreover, in their experiments Kelrich *et al.* (1986) found that total calories per seed were highly correlated with seed weight. This prediction was borne out in yew, which ranked highest on the rodents preference hierarchy, but not in mung, which in terms of energy content, ranks lower than ash (Table 5) and yet was harvested in greater proportion.

Size, however, is not the only attribute which determines a seed's energetic value. The cost of seed processing, i.e. the seed's handling time, has also been found to affect rates of seed selectivity (Price 1983; Kelrich *et al.* 1986). One of the major components affecting handling time is the period required for a forager to remove the husk (Rosenzweig & Sterner 1970). Rodents are sensitive to this cost and have been found to prefer husked over unhusked seeds (Kaufman & Collier 1981). It is possible, therefore, that the avoidance in this study of *Fraxinus excelsior* in favour of mung beans, is a result of the presence in the latter species of a comparatively thick husk. Mung, by contrast, possesses a very thin seed coating. Arguably, however, the use of commercially available mung

beans, which are unfamiliar to the local seed predator populations, might have suffered untypically high rates of predation if the seeds were especially attractive.

6.5 SPATIAL EFFECTS

Rodents have shown species-specific microhabitat and habitat preferences (Brown *et al.* 1975; Hay & Fuller 1981; Heithaus 1981; Mittlebach & Gross 1984; Webb & Willson 1985; Klinkhamer 1988; Hulme 1994; Boman & Casper 1995). Studies on the behaviour of *Apodemus sylvaticus* (Brown 1956; Montgomery & Gurnell 1985; Flowerdew 1991) have shown this species to be highly adaptable and therefore present in a wide variety of habitats. *Clethrionomys glareolus*, on the other hand, is limited in its spatial distribution by the presence of heavy vegetation cover (Watts 1968; Corbet & Southern 1977; Smal & Fairley 1982; Gipps 1985; Alibhai & Gipps 1991).

The differential use of space by these two species is thought to be the result of distinct predator avoidance strategies. *Apodemus* is mainly nocturnal and is therefore little affected by the presence of substantial vegetation cover (Ashby 1976). The bank vole, by comparison, is partly diurnal and relies more heavily on ground cover for protection (King 1985). It was assumed, therefore, that differences in the density as well as the macro- and micro-habitat use of rodent predators might reflect spatial variation in the rates of seed encounter and exploitation. In other words, that the vulnerability of seeds within and between sites may have depended on the structure of the existing vegetation and on the relative abundance of *Apodemus* and *Clethrionomys*.

Results, however, have shown no correlation between total tree density and rodent abundance. It can be argued that if rodents, particularly bank voles, are responding to heterogeneous levels of ground cover, total tree density estimates obtained for the five sites, are not an adequate term of comparison. Canopy density, in fact, may have no effect on the distributions of rodents. Unfortunately, ground cover estimates were not obtained. In addition, although rates of seed removal were high, no correlation was found between rodent abundance and frequency of seed encounter or exploitation by rodents. Arguably, the deployment of a single trap per feeding station might lead to competition for traps among rodents and consequent failure to determine reliable estimates of population densities. Southern (1973), however, states that reasonably consistent population estimates will be extrapolated if at least 20% of the traps remain unoccupied throughout each trapping period, a condition which was always fulfilled during the course of this study.

Differences in the behavioural response to traps may also distort population estimates. Using live-traps, Tew and co-workers (1994) have shown that residual odours within the traps, may selectively attract different rodent species and different age and sex classes within the rodent populations. *Apodemus* and *Clethrionomys*, in fact, have shown marked preferences for traps previously occupied by conspecifics and in wood mice by members of the opposite sex. Furthermore, wood mice avoided traps which had previously held bank voles. If rodents species show differential response to heterospecific and conspecific residual odours, then the assumption of equal trappability throughout the sampling population, which underlies capture-mark-recapture studies and trap-based descriptions of space use, would be questionable. Traps utilised in the current study, however, were diligently washed prior to each trapping session. Moreover, the effect of odour has been shown to be particularly

important when catches are high relative to the number of traps deployed. Catches being low, it is highly unlikely that residual odours played a significant role in trap avoidance or attraction in the two rodent species. More simply the deployment of only ten traps per site was insufficient to provide reliable population estimates when population densities were low and only managed to provide an insight into the site's species composition. Higher trap numbers would have been needed to carry out systematic sampling and obtain reliable quantitative data (Gurnell & Flowerdew 1982). The number of traps deployed in this study were a compromise between the researcher's ability to operate trap-lines during time of high catches and the need to trap in several sites simultaneously. Only by reducing the number of sites, would it have been possible to increase trap numbers and therefore obtain reliable population estimates.

6.6 SEED PREDATION IN DECIDUOUS WOODLAND COMPARED TO PREDATION IN GRASSLANDS

Hulme (1994) investigated seed predation by *Apodemus sylvaticus* and *Microtus agrestis* in two grassland sites (dry grassland and meadow) on a wide variety of herbaceous seed species, which varied in size between 0.37 mg (*Poa pratensis*) to 2.53 mg (*Festuca pratensis*). The study, which simultaneously examined the effects of seed species, seed burial, seed density, season, habitat and microhabitat differences on the rates of seed encounter and exploitation, revealed marked variation in predation rates. Experimental seed burial reduced predation rates in both sites, by 98% and 40-90% respectively. The larger the buried seed, the more likely it was to be eaten by small mammals. Seed density effects accounted for a significant percentage of the variation, with single seeds encountered less

frequently than seeds at high densities. Species effects were significant for seed exploitation, but not for encounter. Most of the spatial variation was attributed to within- rather than between-habitat effects, with strong emphasis on small-scale spatial differences occurring within each site.

Results from the present study have shown some similarities with Hulme's findings. Experimental seed burial, seed density and seed species all showed marked effects on the variation in seed encounter and exploitation experienced by the native and exotic seed species. In contrast to Hulme's work (1994), a significant amount of the variation was due to differences between the sites rather than to variation within the sites themselves. The failure to detect within-site differences, however, was most probably due to lack of information concerning ground cover vegetation and subsequent patterns of rodent abundance. Differences between-habitat, however, were highly expected due to the distance between the sites and their contrasting plant species and vegetation structure.

7. CONCLUSIONS

Seed predation trials in this study have shown that rodents are important seed harvesters in deciduous forest ecosystems, removing between 60-70% of the experimental seed supply. As in other studies investigating small mammal predation (Brown *et al.* 1975; Ashby, 1976; Borchert & Jain 1978; Heithaus 1981; Abramsky 1983; Hulme 1994; Boman & Casper, 1995), there was enormous spatial variation in predation rates.

The probability of a seed being encountered is dependent on seed burial, seed density and seed species, as well as between-site variations most probably linked to differences in rodent abundance. The extent to which seeds are exploited is slightly less variable and has been shown to be largely a function of seed species effects. The role of seed size and relative energy values on determining rates of seed consumption requires further investigation.

In conclusion, the selective nature of the seed predators, plus the relative spatial patchiness of predation rates, suggest that post-dispersal seed predation may play an important role in determining the distribution and/or abundance of deciduous woodland plants.

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