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FORAGING BEHAVIOUR OF SMALL MAMMALS FOR SESSILE PREY

A dissertation submitted in partial fulfilment of the requirements for the degree of
Master of Science in Advanced Ecology.

by

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SUMMARY

1. The foraging behaviour of two rodents (*Apodemus sylvaticus* and *Cleothrionomys glareolus*) was studied in respect to their response to variations in seed characteristics and experimental manipulations of seed handling time, seed abundance and seed distribution in a woodland site. Results were evaluated under an optimal foraging approach.
2. Two exotic seed species differing in handling constraints and in the amount of secondary compounds, respectively, where used as experimental food items in feeding trials. Seeds were offered either exposed or buried. Rates of consumption were examined along three different microhabitats composing the study area. A detailed vegetation assessment together with a small mammal trapping program was undertaken in order to identify the roles of vegetation cover and rodent density in rates of seed predation.
3. Handling constraints imposed by seed coats did not influence significantly rates of consumption. Seed burial, however, decreased exploitation both for hulled and coated seeds. Although not significant, a gradient in the degree of exploitation was found between the seed types/burial levels combinations, with hulled/exposed and coated/buried as extremes of preference.
4. Toxic secondary compounds were found to induce an overall decrease in the rates of consumption of three varieties of Kidney beans differing in values of toxicity. No ranking of preference was detected. However, a slight preference for the less toxic seed was observed. Partial consumption was observed, as predicted by the "nutrient/toxins constraints" model.
5. A consistent spatial pattern of seed exploitation was observed, related to vegetation cover. Open patches were strongly avoided, with the increase in seed handling times restricting even more the utilisation of the food patches to areas with high vegetation cover and density. This was attributed to a risk sensitivity response, rodents having decreased both rates of food intake and patch exploitation to avoid the risk of being preyed upon.
6. Rodents exhibited frequency-dependent selectivity, preferring rarer food items between two syntopic prey types differing in profitability (amount of secondary compounds). A slight preference for the less toxic form was observed, although not statistically supported.

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1 GENERAL INTRODUCTION

As a result of evolutionary selective pressures, animals tend to hunt for their food efficiently - assuming that an individual's fitness depends largely on its behaviour while foraging (Pyke *et al.* 1977; Krebs *et al.* 1981; Pyke 1984; Stephens and Krebs 1986). Thus, foraging animals must continuously make decisions, at each step of the feeding process, starting from the search for the food item until its actual consumption - for instance, where to forage, which prey to eat, and when to move to a new patch (Krebs and Davies 1978; Collier and Rovee-Collier 1981, Krebs and Houston 1988; Krebs and Kacelnik 1991). The 'optimal foraging theory' assumes that these decisions involve maximising benefit, using some optimality criterion to assess the trade-off between alternative courses of action.

The optimality approach in foraging behaviour has been often criticized for being too simplistic, including a number of unrealistic assumptions in the analysis of decision-making, facing the complexity of factors acting on animal's behaviour in their natural environments (*e.g.* Gray 1987; see also reviews by Pyke 1984, Stephens and Krebs 1986, and Schoener 1987). However, optimality models are a valuable tool for analysing decision-making in foraging animals in terms of their costs and benefits, making explicit the currencies and constraints for hypothesis-testing (Krebs and Davies 1993), allowing therefore quantitative predictions on the animal's behaviour as a response to environmental conditions (Pulliam 1974).

The study of foraging for seeds by rodents provides suitable models to evaluate optimal foraging predictions since seeds, as discrete units, can be easily perceived and quantified in the environment and in the animals' diet

(Reichman 1981). Rodents, in addition, are know,to be selective in their diets; therefore seed selectivity can be considered as the behavioural manifestation of preference (Kelrick *et al.* 1986). According to Hulme (1993), by breaking down the constituent steps of seed predation by rodents (seed detection, identification, acquisition, manipulation and consumption), it is possible to identify parameters which determine foraging success. Such foraging parameters are linked to seed attributes, rodent traits and to environmental factors. Considering the parameters involved in each step of the foraging process in terms of trade-offs between costs and benefits, therefore, it is possible to infer the sources of behavioural decisions taken by rodents in their feeding strategies.

Being mainly seed eaters (Hansson 1985), woodland rodents are responsible for the removal of large number of seeds, their action being considered important as a regulating factor in temperate woodland systems, where rodent seed predation is known to interfere with natural regeneration processes (Watt 1919, 1923; Abbot and Quink 1970; Gashwiler 1970; Radvanyi 1970; Heithaus 1981). Since seed preferences by important seed predators such as rodents may influence the composition of the plant community, it is important to understand the processes involved in their foraging behaviour in order to be able to evaluate the potential effect of their predation.

In this study, the foraging patterns presented by woodland rodents (wood mice - *Apodemus sylvaticus,* L. and bank voles - *Clethrionomys glareolus,* Schreber) were examined under an optimal foraging approach, in terms of their response to variation of seed characteristics, seed burial, seed abundance and distribution, which have previously been identified as important sources of variation in seed predation (Hulme 1993). This paper presents the results of three field experiments designed to

a) examine rodent selectivity on seeds presenting different energetic rewards, determined by different handling constraints;

b) examine rodent selectivity on seeds presenting similar morphological and nutritional attributes, but differing in toxicity values;

c) determine whether frequency-dependent selectivity occurs under natural conditions, by rodents feeding on seeds differing in toxicity and handling constraints;

d) measure the extent of spatial variation in seed predation, determining if the patterns are predictable with respect to rodent abundance and selected vegetative characteristcs related to risk sensitivity.

2 STUDY AREA AND GENERAL EXPERIMENTAL DESIGN

2.1. Study Site Description

Experiments on seed predation were undertaken from May to July 1995, at the University of Durham Field Centre (National Ordnance Survey Grid NZ 274 406) (Fig. 2.1), a mixed-deciduous woodland with distinct spatial heterogeneity in ground cover density and tree composition.

An area of approximately 0.4 ha was chosen within the woodland, on a Southwest facing slope. The study area comprised at least three distinct patches of dominant vegetation - reflecting discrete microhabitats (Fig. 2.2):

- *Bramble Site*: Approximately 300 m^2. The sparse canopy in this patch is composed of *Betula pendula*, *Fraxinus excelsior*, *Prunus avium* and *Sambucus nigra*. The shrubby ground vegetation is mainly composed by *Rubus fruticosus*, which covers most of the area. *Carduus acanthoides*, *Crataegus monogyna*, *Epilobium angustifolium*, *Galium aparine* and *Urtica dioica* are frequent ground species (Plate 2.1).
- *Beech Site*: An area of approximately 600 m^2 dominated by beech trees. The shade formed by the dense canopy cover has prevented a significant undergrowth from forming on the woodland floor. Thus, open ground covered with leaf litter constitutes great part of this area (Plate 2.2).
- *Mixed Vegetation Site*: Comprising approximately 2100 m^2, this area is composed by dense clusters of trees and ground and understory vegetation. *Acer pseudoplatanus*, *Betula pendula*, *Fraxinus excelsior*, *Larix decidua*, *Prunus avium*, *Quercus petraea*, *Q. robur*, *Sambucus nigra* and *Sorbus aucuparia* are the main components of the tree canopy. The understory

vegetation is dominated by *Ilex aquifolium*, which grows in dense shrubby patches. The ground vegetation is mainly composed by grass species and *Lonicera periclymenum*, with the presence of *Crataegus monogyna*, *Pteridium aquilinum*, *Rubus fruticosus*, *Trifolium repens* and *Urtica dioica* (Plate 2.3).

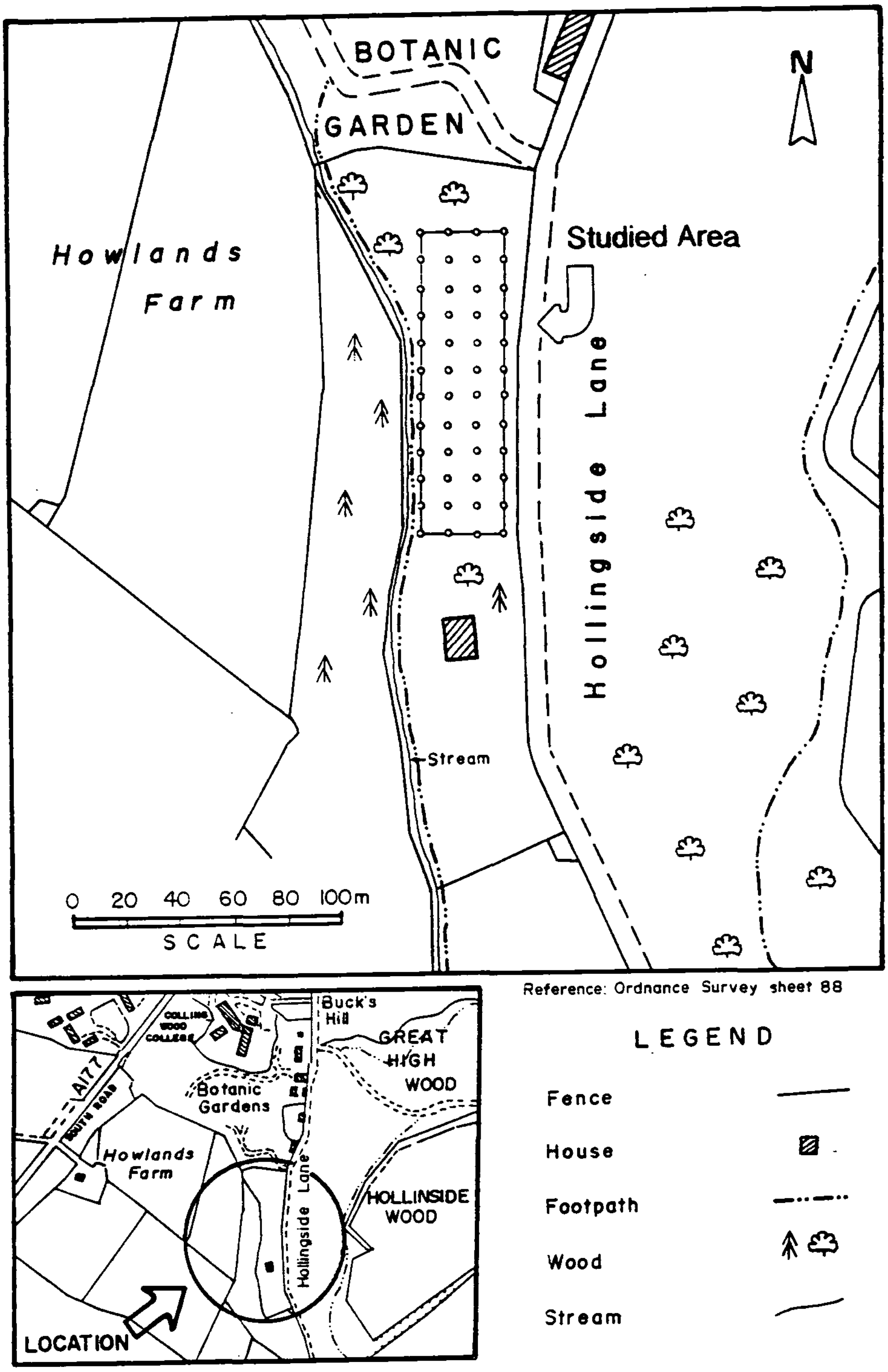

Figure 2.1. Location of the study area.

Plate 2.1. Bramble Site

Plate 2.2. Beech Site

Plate 2.3. Mixed Vegetation Site

2.2. General Experimental Design

Field experiments on seed predation were undertaken using 48 replicated sets of feeding stations deployed in a 12 x 4 grid of points spaced at 10 m intervals (Fig. 2.2). The grid was deliberately set out to sample all the three main woodland microhabitats described above.

The basic experimental unit consisted of a 9 cm Petri plastic dish fixed to the ground by a 5" nail, in which experimental seeds were presented. Three units were installed at each grid point (Plate 2.4). So that the effects of different groups of seed predators (Invertebrates; Rodents; and Squirrels, Rabbits and Birds) could be inferred, three exclosure treatments were used:

- Invertebrate Treatment (*Fine Mesh*) - to prevent entry to animals other than invertebrates, a 14.5 x 14.5 cm fine mesh cage (1.2 cm wire mesh) surrounded one of the experimental units;

- Small Mammal Treatment (*Coarse Mesh*) - to quantify seed exploitation and removal by rodents and invertebrates, a 15 cm Ø, 30 cm height exclosure was made with 3 cm wire mesh surrounded a second experimental unit;
- Open Treatment (*Open*) - this unit had no exclosure, allowing predation by birds and larger mammals, as well as rodents and invertebrates.

Using the same main experimental design, three different experiments on seed predation were undertaken, using artificial seeds presented in 'cafeteria' trials. The harvesting or consumption rates were estimated by the monitoring rates at which the seeds were removed or damaged, which were measured by examining the seeds at different time intervals over a period of three days. The presence of faeces and the characteristics of the seed remains were recorded, in an attempt to identify seed predators.

Two assumptions underlined the experiments: a) The disappearance of seeds from the Petri dishes was a consequence of removal by seed predators; that is, no losses by wind or rainfall occurred; b) Observed selectivity at seed dishes resulted from preferences which also govern selectivity in the natural foraging habits of these predators.

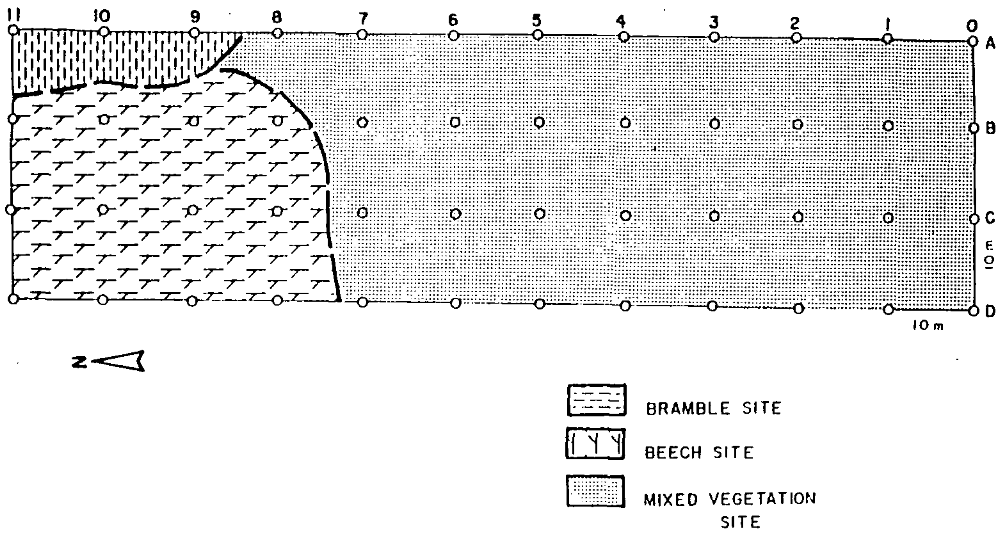

Figure 2.2. Graphic representation of the study site, showing the grid of experimental depots (O) and the three main microhabitats composing the area.

Plate 2.4. Experimental depot, showing the three experimental exclosures.

3 SEED PREFERENCE

3.1. Introduction

According to classical optimal foraging theory, foraging animals should select, from the available food items, those that maximize net benefit (Emlen 1966; MacArthur and Pianka 1966; Pulliam 1974; Emlen and Emlen 1975). The currency adopted to evaluate this benefit has generally been the rate of energy intake, that is, the energy yielded by the animal per unit time spent foraging.

The profitability of a food item is considered, in this way, to be directly related to the time required for its processing by the animal - its handling time, which includes aspects concerned with searching for the food item, its manipulation/capture and final consumption.

Hence, the optimal foraging approach assumes that different food items can be ranked by desirability, with those requiring the least amount of processing time (h) per nutritional gain (E), - higher E/h value - being preferred over those ones with lower E/h value. According to this, if food items of higher value are available, lower-value items should be rejected, regardless of their abundance - determining that foragers should increase specialization as the abundance of more desirable food items increase. As a corollary, food items should be either completely accepted or rejected - no partial consumption should occur (Pyke *et al.* 1977; Krebs 1978).

Later developments of the classical model of diet optimization have included alternative currencies, such as amino acids and other nutrient requirements (reviewed by Pyke 1984), allowing a better fit of the theory's predictions to the observed feeding patterns. If fitness is maximised when the rate of food gain is maximised, but subject to the constraint of the rate of gain of some nutrient, partial preferences should be expected. In this case, the preference of a particular food type may depend not only on the abundances of the more preferred food type, but also on its own abundance (Pulliam 1975).

Following the classical optimal prediction, seeds preyed upon by rodents should be selected for their energy rewards. Supporting this, studies on dietary preferences have indeed shown that rodents select seeds with higher energetic values, which are considered to be correlated with lipid content (Price 1983; Henderson 1990), and size (Reichman 1977; Abramski 1983; Mittelbach and Gross 1984; Jensen 1985).

Rodent selectivity, however, seems to be determined not only by the currency of energy reward. Seed intrinsic characteristics such as protein (Henderson 1990), soluble carbohydrate (Kelrick *et al.* 1986: but see Jenkins 1988), moisture (Frank 1988), and toxin (Sherbroke 1974) contents were also observed to influence rodent dietary preferences.

In an attempt to evaluate these currencies under natural conditions, the relationships between rodent seed preferences and seed characteristics were investigated, in what is concerned to seed's handling time constraints and toxic composition.

3.2. Seed Preference According to Handling Time Constraints

Models of optimal foraging strategy predict that food items requiring the least amount of processing time - that is, for its capturing, subduing and consumption, would provide the predator with greater energetic rewards, having a high E/h rate. Hence, these food items would be preferred over those with lower E/h rate (Pyke *et al.* 1977).

As mentioned before, energetic intake rate is an important component in rodent dietary selectivity. In this way, for rodents - as granivore predators, the energetic value of a food item (seed) is correlated with its processing time in terms of finding, harvesting and final consumption.

According to Price and Jenkins (1986), rodent preferences are influenced by processing constraints which are both intrinsic and extrinsic to the seeds' attributes. Extrinsic factors that have been found to influence processing time are rodent morphology, seed density and burial level (Rosenzweig and Sterner 1970; Smigel and Rosenzweig 1974; Reichman and Oberstein 1977; Price and Heinz 1984). The major intrinsic components of a seed's processing costs are those related to its properties, such as size, shape, surface texture and tissue anatomy, since they can impose constraints in terms of the seed's identification (possibly reducing odour escape), manipulation, and subsequent consumption by rodents (Lawhon and Hafner 1981; Kelrick *et al.* 1986; Henderson 1990).

Between these possible sources of handling constraints, the presence of protective tissues such as seed coats are known to reduce the seed's profitability in terms of energy intake, since they possess little or no nutritional value, and increase handling time costs by forcing the rodent to husk the seed in order to reach the nutritive endosperm (Emlen and Emlen 1975). Laboratory studies on rodent dietary selectivity focusing on handling constraints have demonstrated a significant preference for hulled over coated sunflower seeds (Ebersole and Wilson 1980; Collier and Rovee-Collier 1981; Kaufman and Collier 1981; Phelan and Baker 1992), the same being observed for other seed species (*e.g.* Kerley and Erasmus 1991). This preference was attributed to a difference in handling between hulled and coated seeds. Kaufman and Collier (1981) observed that rodents consumed hulled seeds about 1.6 times faster than coated seeds), indicating that in their preference for hulled seeds, rodents were minimising handling time, supporting in this way the optimal foraging theory predictions.

Seed burial has been mainly discussed in terms of its influence on detection (Howard *et al.* 1968; Lockard and Lockard 1971; Jennings 1976;

Reichman and Oberstein 1977; Abramsky 1983; Hulme 1994), where it has been demonstrated that rodents employ primarily olfactory cues for seed encounter. However, as mentioned by Price and Heinz (1984), it would be reasonable to consider that the retrieval of buried seeds could also decrease the net rate of energy intake, since the seed extraction implies in metabolic costs due to the digging effort.

In this study, the response of rodent foraging patterns to an increase in handling time in field conditions was tested, assuming that any significant effect of handling cost on feeding behaviour should be reflected in differences in the patterns of seed consumption. Handling time was manipulated by offering coated and hulled sunflower seeds (*Helianthus annuus*), and by burial level. Following Kaufman and Collier 1981), we assumed that the nutritive and caloric values of the seed kernels of the two seed types were constant; therefore only handling costs varied between them.

3.2.1. Methodology

Feeding trials were performed following the general experimental design described in Chapter 2. At each feeding station, 10 sunflower seeds, either hulled or with seed coats, were offered in the experimental exclosures.

Since rodents generally locate food using visual and olfactory cues, being able to detect food buried as deep as 10 cm (Howard *et al.* 1968; Lockard and Lockard 1971; Jennings 1976; Lawhon and Hafner 1981), burial of 1 cm depth was not considered as a constraint in terms of searching ability. Thus, both hulled and coated seeds were offered at two burial levels, *exposed* on the Petri dishes or *buried* (under a layer of 1 cm of soil, in the Petri dish), in an attempt to increase handling time due to the mechanical act of seed retrieval. The presentation of the seed type/burial combinations was randomised, under the constraint that each of the 4 combinations was used once, at each feeding station.

Seeds were exposed for three days. The remaining seeds were counted in the morning of the fourth day, collected, and replaced by a new randomly chosen feeding trial.

3.2.2. Results

As a result of granivore's action, seeds were either completely removed from the feeding station, consumed "in situ", damaged, or left untouched. Consumers may drop or cache some of the removed seeds, assessment of which was impossible. Therefore, 'predation' was implied from the seed's disappearance, that is, the seeds were considered destroyed (Janzen 1970). The characterisation of consumption "in situ" was given by the presence of seed coats on the Petri dish or surrounding area, and "damage" by the presence of small chewing marks. The extent of the latter type of consumption was not considered enough to prohibit further seed germination.

Due to the characteristics of seed consumption and the presence of urine and faecal pellets, the exploitation of the seeds presented in the "coarse mesh" and "open" treatments were attributed mainly to rodents. Seed removal occurred only in the treatments to which rodents had access. Slugs (*Arion sp.*, *Agriolimax sp.*) were responsible for almost all the consumption attributed to invertebrates, although beetles were also observed feeding on the experimental seeds.

Birds (*e.g. Turdus merula*) were observed foraging on the woodland floor, mainly in open areas. Seeds presented in "open" treatments, in these areas, were often found scattered immediately around the Petri dish. These spillages were not considered as losses, since the spilled seeds were always collected, and the source dish of these seeds was always identified. Although the spillages were attributed to birds, no signs of actual consumption were found. Predation by birds was therefore considered negligible.

The considerably high rates of predation by rodents in this experiment have shown that sunflower seeds are preferred food items. In some cases, rodent predation was observed even in the invertebrates exclosures*, indicating the high profitability of these seeds. As invertebrates played an insignificant role in seed consumption, data analysis focused only on the "coarse mesh" and "open" experimental treatments, accessible to rodent exploitation.

As can be seen in Fig. 3.1, there was no significant difference in the consumption of hulled or coated seeds at any burial level. The figure suggests, however, that burial decreased the rates of consumption in approximately 30%. To evaluate this trend statistically, we conducted a three-way ANOVA, comparing the influences of seed type, burial level and exclosure (Table 3.1). The results indicate that husking seeds apparently did not increase the difficulty in seed exploitation up to the point of effectively reducing the consumption. Burial, however, similarly decreased the rates of consumption for hulled and coated seeds, as can be seen in Fig. 3.1, suggesting that retrieval of buried seeds implied in significant constraints.

Interactions between seed type and burial level were not found significant. A slight gradient of preference did exist, however, amongst the different seed type/burial level combinations (Table 3.2). "Hulled exposed" seemed to be more frequently exploited than "coated buried", and "hulled buried" and "coated exposed" lay in between. Although this gradient was more apparent in the "open" treatment (Fig. 3.1.*b*), no significant interactions were found between exclosure and seed type, neither between exclosure and burial level. Higher order interactions (*i.e.* between seed type, exclosure and burial level) were also not found significant.

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* In face of this, invertebrates exclosures were double checked, with any possible gap corrected in order to avoid further entrance of rodents.

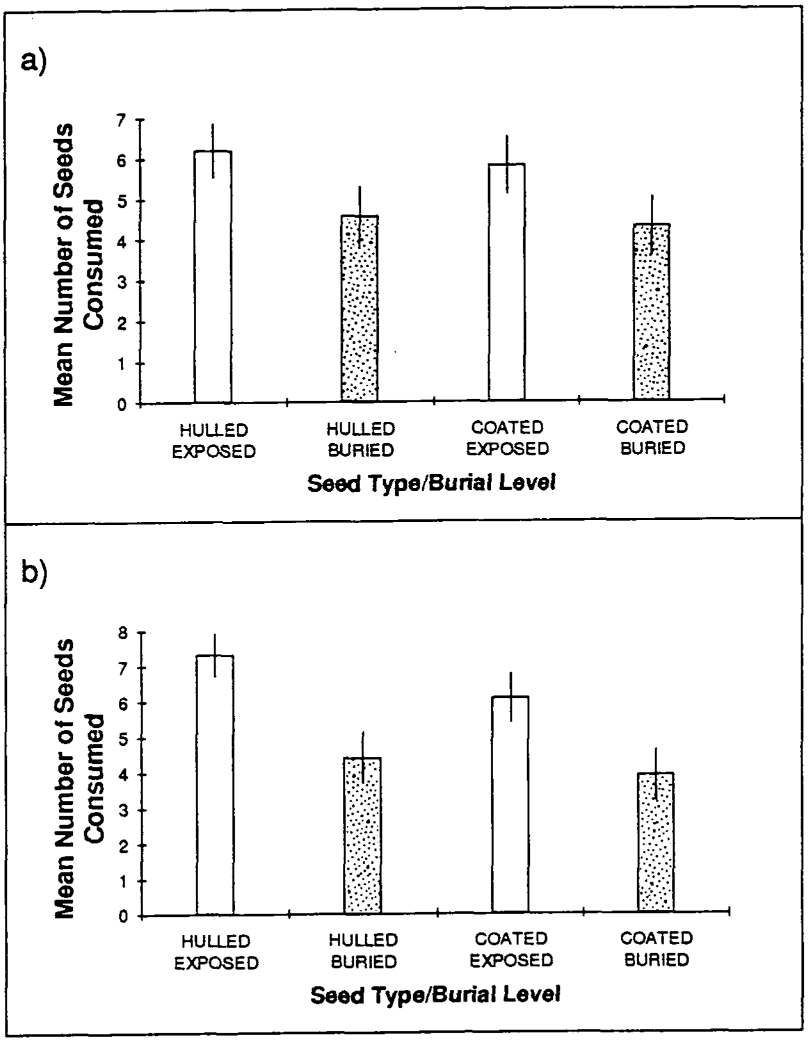

Figure 3.1. Observed variation in the numbers of seeds consumed, categorized by the presence/absence of seed coat and by burial level. (S. E. bars presented). a) "Coarse Mesh", b) "Open" treatments.

Source	*DF*	*SS*	*MS*	*F*
Seed Type (S)	1	0.768	0.768	1.377 (P>0.05)
Exclosure (E)	1	0.117	0.117	0.210 (P>0.05)
Burial (B)	1	10.077	10.077	18.080 (P<0.01)
S x E	1	0.198	0.198	0.355 (P>0.05)
S x B	1	0.093	0.093	0.166 (P>0.05)
E x B	1	0.605	0.605	1.085 (P>0.05)
S x E x B	1	0.056	0.056	0.100 (P>0.05)
Residual	376	209.561	0.227	
Total	383	221.473	0.578	

Table 3.1. The three-way ANOVA on arcsine transformed square root values indicates only a significant influence of burial level in the rates of consumption, with no interaction between the main possible sources of variation.

Seed Type /	*Total Consumption*	
Burial Level	***Coarse Mesh***	***Open***
HE	6.21 (0.66)	7.33 (0.60)
HB	4.58 (0.73)	4.42 (0.72)
CE	5.83 (0.70)	6.10 (0.69)
CB	4.33 (0.71)	3.92 (0.70)

Table 3.2. Mean values of the proportion of seeds consumed for each seed type/burial level combination, in the two cages accessible to rodents. "HE" - Hulled/Exposed, "HB" - Hulled/Buried, "CE" - Coated/Exposed, "CB" - Coated/Buried. (S.E.)

3.2.3. Discussion

Rodent selectivity between hulled and coated seeds was not detected in this experiment. This suggests that the presence of seed coats, alone, did not impose a significant handling constraint for the consumption of sunflower seeds, under field conditions, up to the point of severely restricting exploitation. Such results do not coincide with previous studies undertaken in laboratory conditions (*e.g.* Kaufman and Collier 1981; Phelan and Baker 1992), where it was found that rodents preferred the lower-cost hulled seeds, therefore maximising efficiency by increasing the E/h values. Although a decrease of approximately 4 seconds in the handling times provided by hulled sunflower seeds may constitute a significant increase in energetic profitability under controlled situations, it may not be so in natural conditions, where environmental aspects may act together with seed intrinsic characteristics, altering rodent selectivity (Lawhon and Hafner 1981).

Seed burial, however, was found to interfere in rodent selectivity, confirming previous studies (*e.g.* Heithaus 1981; Price and Heinz 1984; Hulme 1994). Burial has been normally reported to hinder seed detection due to concealing of the seed's odour (Reichman 1981). However, our previous assumption that the burial treatment would not impose restrictions in terms of searching abilities was confirmed by the fact that seeds were detected as long as the patch where the experimental units were deployed was exploited by rodents. Differential exploitation of buried seeds followed therefore a spatial variation (to be discussed in Chapter 4). The mechanical effort of seed retrieval was found to consistently reduce the rates of seed harvesting, suggesting an increase of handling constraints, hence being likely to decrease rates of energy intake.

The gradient of preference observed between the exploitation of the different combinations of seed type and burial level may reflect the interaction between intrinsic and extrinsic seed handling constraints, provided respectively by seed coat and burial. The extremes of handling constraint of "hulled/exposed" and "coated/buried" seeds could be categorised as "least preferred" and "most preferred", according to the optimal foraging theory, and would be expected to be ranked in terms of rodents preference. This was observed in this experiment, although not supported statistically. Seed coats and burial acting together, however, may contribute to determine rodent selectivity, in terms of energy expenditure, and are likely to constitute an efficient mechanism of seed escape from rodent predation. On the other hand, seed coats and burial, by themselves, proved to be important deterrents of invertebrate predation, since no consumption was observed for either coated or buried seeds in the invertebrates exclosures. These results agree with Abramski (1983), who also found differences in the abilities of rodents and invertebrates to exploit buried seeds, highlighting seed burial as a factor that could allow coexistence between ants and rodents, potential competitors in desert environments.

3.3. Seed Preference According to Seed Toxicity

Herbivore-defensive secondary compounds present in seeds have been credited to strongly interfere in rodent diet selection (Freeland and Janzen 1974;

Sherbroke 1976; Henderson 1990). The potential for dietary choice to be influenced by seed defenses is underscored by the variety of compounds known to occur in seeds, with properties ranging from haemagglutinins and enzyme inhibitors to cyanogenic glucosides, which, among others, are known to be severely detrimental to small mammals (Freeland and Janzen 1974).

The potential interplay between energetic, nutritional and defensive components of the food items in rodent's diet have been investigated, so far, comparing the rates of predation on different seed species that presented different characteristics (*e.g.* Kerley and Erasmus 1991). It would be interesting to examine toxicity as a source of selectivity between seeds of the same plant species, which present similar energetic constraints and nutritional values, but differ mainly in toxic contents.

This being so, an experiment was designed to verify if woodland granivores forage differentially on seeds of similar size, morphology and consequently handling constraints, but differing in their digestibility and toxic composition.

Kidney beans (*Phaseolus vulgaris* - Leguminosae) seeds are known to contain secondary compounds such as lectins, trypsin inhibitors and polyphenols, which are potentially toxic to rodents. Results of feeding laboratory rats with such seeds were described by Jaffé (1977) and Pusztai (1991) as causing mainly loss of body weight followed by renal and respiratory complications, with death of the animals due to inhibition of protein digestion and erythroagglutination. In this study three varieties of Kidney beans ("red", "black" and "white") were chosen to be used as experimental food items: these varieties present different amounts of secondary compounds (Table 3.3), but are similar in their morphology (Table 3.4).

Hence, the assumptions underlying this experiment were: a) the three types of Kidney beans, having the same size and weight, would promote the same handling constraints for their harvest; b) there is no evidence in the literature for difference in the nutritious values between the three varieties; and

c) "black" and "red" are more toxic than "white" Kidney beans. Therefore, a differential rate of seed consumption given by the toxic composition would be expected.

Seed Variety	*Digestibility*	*Protease Inhibitors (U/g)*	
		Trypsin Inh.	*Quimotrypsin Inh.*
Black	55	65	17
Red	56	39	22
White	52	0	11

Table 3.3. Values for digestibility and some secondary compounds present in the three varieties of Kidney beans utilized in this study (data from Jaffé (1977)).

Seed Variety	*Length (mm)*	*Width (mm)*	*Weight (gr.)*
Black (n=30)	15.95	7.33	0.60
Red (n=30)	15.81	6.95	0.54
White (n=30)	16.42	6.79	0.59

Table 3.4. Average morphological dimensions of three Kidney Bean varieties used in this study. A one-way ANOVA for comparison of means has shown no significant variation between the length of the three varieties ($F(2,89)=2.4547$, $P>0.05$). The significant variation found in width ($F(2,89)=9.7552$, $P<0.01$) and weight ($F(2,89)=3.2008$; $P<0.05$) was attributable to the "red" variety, which was smaller than the other varieties.

3.3.1. Methodology

The experimental procedure followed the general experimental design described in Chapter 2. Ten seeds of one bean variety were distributed in the experimental treatments of each feeding station in a randomly assigned order, so that at the end of the experiment, each feeding station was tested for all three bean varieties. The depots were checked daily in the mornings, over a 3-day period. In the last day of each trial, the remaining seeds dish contents were removed and replaced by a different randomly chosen bean variety.

3.3.2. Results

The overall consumption of Kidney beans in this experiment, around 15%, was considerably lower than the previous trials with sunflower seeds, and very variable. Invertebrate predation was almost negligible, compared with rodent's action, being limited to seed damage (Figs. 3.2.*a* and 3.3.*a*). Although rodents were the main seed predators, their actual consumption was also very low. On average, less than two seeds were removed from each dish (as can be seen in Figures 3.2.*b* and *c*), with the rates of seed damage being even lower (Fig. 3.3.*b* and *c*).

A two-way ANOVA (undertaken on arcsine square root transformed values), detected significant variation due to the effect of exclosure treatments on rates of removal (Table 3.6). Seeds were only removed from the "open" and "coarse mesh" treatments (Fig. 3.2). Seed variety, however, exerted very little influence on removal (Table 3.6), indicating that there was no selectivity for any type of seed. No interactions between the seed varieties and exclosure treatment were observed.

The patterns exhibited in seed damage where slightly different from the described above for seed removal, in terms of exploitation by vertebrates and invertebrates. A two-way ANOVA (on arcsine square root transformed values) detected no influence of exclosure treatment in rates of damage (Table 3.7). Again, seed variety was not an influent factor. Although being not statistical significant, the number of "white" seeds damaged was higher than the numbers for "red" and "black" seeds damaged, for the three experimental exclosures.

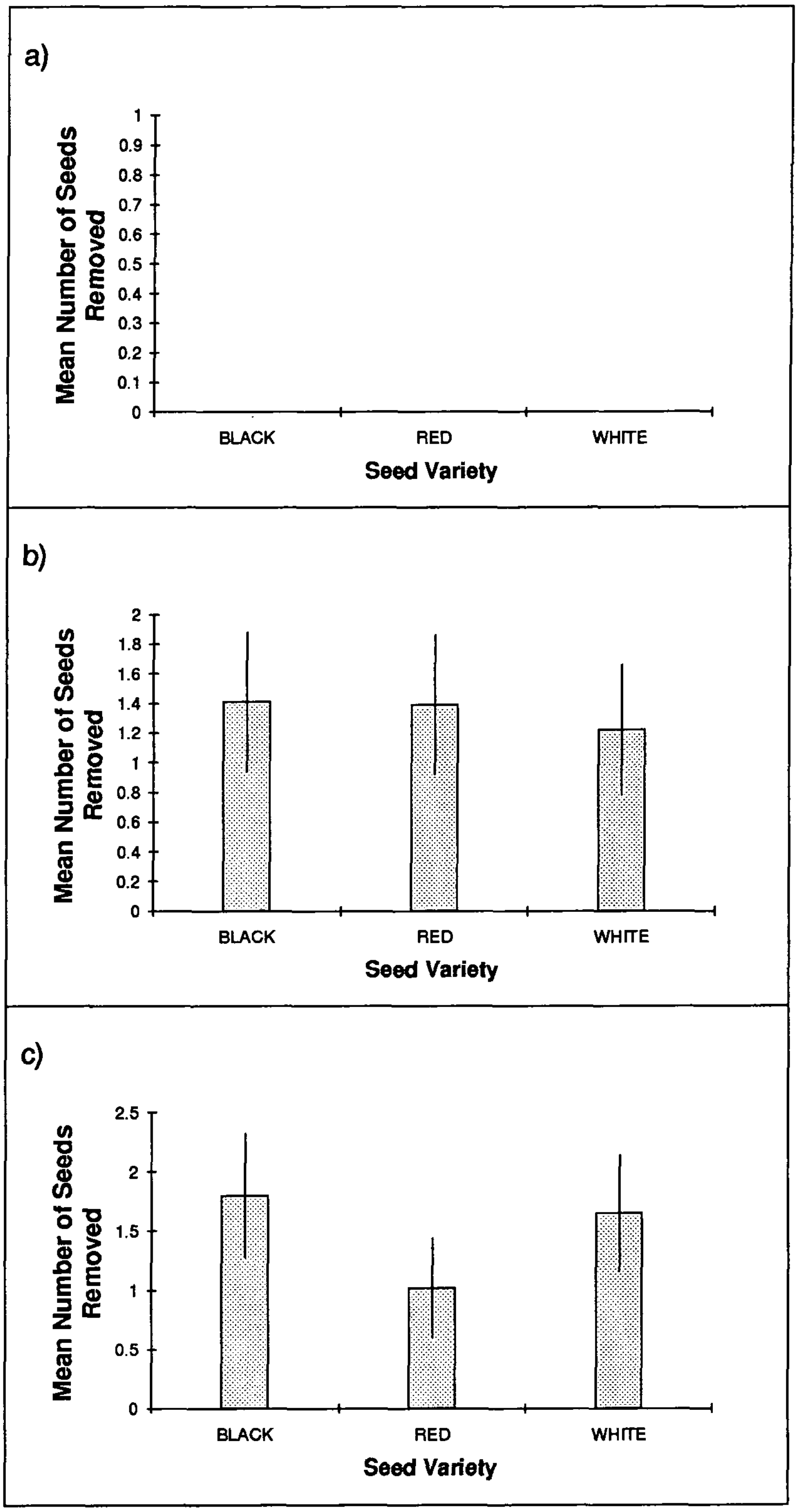

Figure 3.2. Observed variation in the numbers of seeds of each variety removed from each experimental exclosure (S.E. bars presented): a) "Fine Mesh", b) "Coarse Mesh", c) "Open".

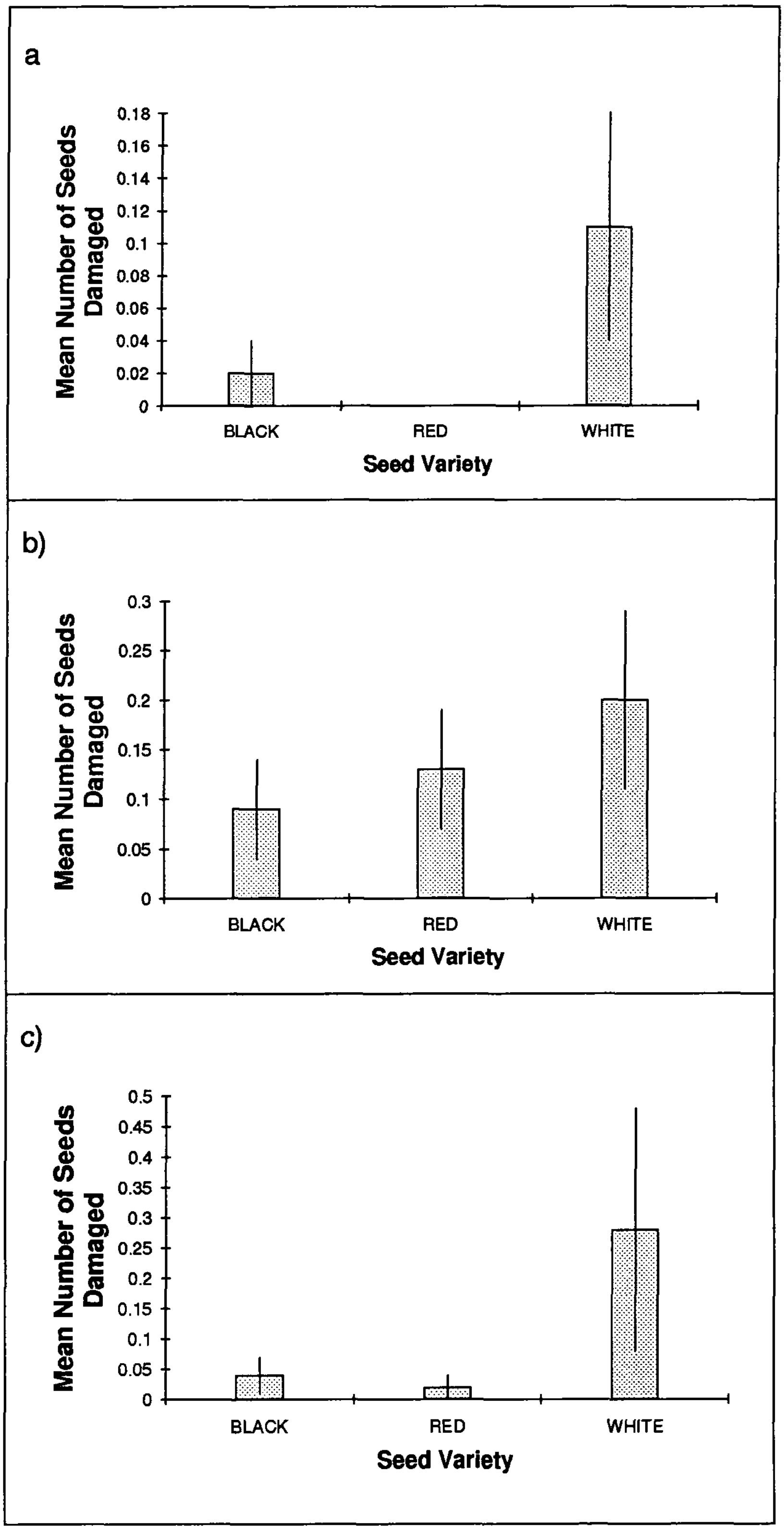

Figure 3.3. Observed variation in the numbers of seeds of each variety damaged, in each experimental exclosure (S.E. bars presented): a) "Fine Mesh", b) "Coarse Mesh", c) "Open".

Seed Variety	***Exclosure***	***Removal***	***Damage***
Black	Fine Mesh	0 (0)	0.0022 (0.0147)
	Coarse Mesh	0.1413 (0.0470)	0.0087 (0.0354)
	Open	0.1804 (0.0521)	0.0043 (0.0206)
Red	Fine Mesh	0 (0)	0 (0)
	Coarse Mesh	0.1391 (0.0470)	0.0130 (0.0400)
	Open	0.1022 (0.0421)	0.0022 (0.0147)
White	Fine Mesh	0 (0)	0.1909 (0.0482)
	Coarse Mesh	0.1217 (0.0436)	0.0196 (0.0619)
	Open	0.1652 (0.0489)	0.0283 (0.1361)

Table 3.5. Mean values of the proportions of "black", "red" and "white" seeds consumed (S.E.), according to the exclosure treatment.

Source	***DF***	***SS***	***MS***	***F***
Seed Variety(S)	2	0.129	0.064	0.397 (P>0.05)
Exclosure (E)	2	5.322	2.661	16.412 (P<0.01)
S x E	4	0.413	0.103	0.637 (P>0.05)
Residual	405	65.668	0.162	
Total	413	71.532	0.173	

Table 3.6. Two-way ANOVA on the arcsine transformed squared root of the proportions of seeds removed. Only "Exclosure" exerts a significant effect, which is justified since removal occurred only in the exclosures accessible to rodents.

Source	***DF***	***SS***	***MS***	***F***
Seed Variety(S)	2	0.065	0.032	2.843 (P>0.05)
Exclosure (E)	2	0.043	0.022	1.912 (P>0.05)
S x E	4	0.017	0.004	0.372 (P>0.05)
Residual	405	4.603	0.011	
Total	413	4.728	0.413	

Table 3.7. Two-way ANOVA on the arcsine transformed squared root of the proportions of seeds damaged. Again no significant variation was found, in any of the possible sources.

3.3.3. Discussion

The presence of secondary compounds of different types and in different concentrations is a well known defensive mechanism of plants against herbivory (Janzen 1969). Rodents, as generalists, have evolved detoxification mechanisms that allow them to feed on a broader diet, including plants with some degree of toxicity (Hansson 1985). However, as consuming secondary compounds is potentially hazardous and metabolically expensive, animals should prefer food items that are not toxic, or at least those that contain only small amounts of secondary compounds. Doing so, rodents would reduce danger and metabolic costs (Freeland and Janzen 1974).

According to optimal foraging principles, food items should be ranked in order of preference, which is dictated by the net benefit they provide. Extrapolating this to the consumption of toxic seeds by rodents, the exhibition of a ranking according to the level of toxicity should be expected.

The present experiment provided woodland granivores with seeds that could be ranked in profitability by the amount of present toxic compounds. Our results, however, demonstrated no apparent selectivity for any type of bean variety, and no pattern of consumption indicates a consistent trend in terms of ranking of preference. Rodents seemed to have reacted to the overall presence of toxins by reducing the rate of predation of all the varieties, not having differentiated between small changes in the amount of toxins. Such lack of ranking contradicts the prediction of classical optimal foraging theory mentioned above.

The evidence of partial consumption given by seed damage violates another basic classical prediction, which is that preys should always be consumed, when encountered, or not consumed at all. However, our latter finding supports Pulliam (1975), in his “nutrients as constraints” model, which can be adapted to the needing of toxin’s avoidance. Partial consumption is predicted, in this model, since toxins are tolerated at most in a fixed amount by animals (Stephens and Krebs 1986).

The occurrence of partial consumption of food items by rodents has already been reported as "sampling" (Barnett, cited in Freeland and Janzen 1974; Ebersole and Wilson 1980; Partridge 1981). Such behaviour occurs when rodents are presented with a new food - they will often avoid it, at the beginning, subsequently taking small samples, and after a few days they will either accept the food or completely reject it. Sampling is expected in generalists such as rodents, since this behaviour allows them to learn about the profitability of new food items, while minimising the chance of ingesting a lethal dose, if encountering a toxic aliment. This is especially important, since the nature of the food available in their environment changes with time, and sampling the food supply continuously may allow the animals to be aware of the arrival of new foods, adjusting their food choice according to the prevailing situation (Partridge 1981). Therefore, having a mixed diet, rodents have to ingest a number of different food types over a short period of time and sampling simultaneously, neither maximising the number of types of foods that are potentially available, nor maximizing the total amount of food eaten, but rather maintaining a compromise between both (Freeland and Janzen 1974).

The absence of selectivity between the three seed types may therefore be explained by the rodent's generalist feeding habits. However, rodents should be particularly sensitive to the chemical variations in their diet. Therefore, although not supported statistically, the tendency to consume "white" Kidney beans, as can be seen in the numbers of seeds damaged by both rodents and invertebrates, may be related to their smaller toxicity.

4 *RISK SENSITIVITY*

Classical optimal models consider an animal exploiting a food patch as exclusively engaged in foraging activity, assuming the energy maximization or other currency related to feeding as the major criterion determining its foraging decisions (MacArthur and Pianka 1966; Charnov 1976; Pyke *et al.* 1977). Hence, there is an assumption that an animal's foraging strategy is affected only by factors that determine fitness through foraging efficiency, that is, feeding rate maximisation. Fitness, however, must be considered as an *n*-attribute phenomenon, in which foraging is only an aspect, together with others such as reproductive needs and predator avoidance (Lima *et al.* 1985; MacNamara and Houston 1986). In this chapter, rodent strategies referring to the latter aspect will be discussed.

Optimal foraging theory predicts that animals should preferentially exploit patches with the highest harvesting rates. However, it has been shown that the risk of predation has a special importance in the animal's decisions related to the choice of which patch to exploit, since a conflict may arise between maximising rates of energy intake and minimising exposure time to possible predators. This conflict can be illustrated, for example, by the need of scanning for predators and food handling (*e.g.* Caraco 1979; Lima 1985). A strategic trade-off between these two conflicting demands is therefore expected, in order to maximising fitness. Sih (1980), Werner *et al.* (1983), Kotler (1984) and others (reviewed in Sih 1982 and Lima and Dill 1990) have shown that areas of high foraging efficiency may be partially or completely avoided if their exploitation implies a danger. Foragers may also shift to an area with a lower feeding rate, if that area is less dangerous (*e.g.* Phelan and Baker 1992).

Vegetation cover has been attributed as an important subcomponent of risk escape, being a determinant factor in feeding-site selection for birds and mammals (Lima and Dill 1990). Rodents show pronounced microhabitat preferences, concentrating their foraging activity in particular patches, suggesting that they perceive these microhabitats as differing in quality (Price and Jenkins 1986). Although the importance of the predation risk in governing habitat use is debated (*e.g.* Price 1984), there is evidence that rodents may limit their use of open space in response to increased predation risk in such areas; open patches are therefore generally avoided, with the more exploited patches normally being those with the densest vegetation cover (Rosenzweig and Winakur 1969; Rosenzweig 1973; Stamp and Ohmart 1978; O'Dowd and Hay 1980; Hay and Fuller 1981; Mittelbach and Gross 1984; Webb and Willson 1985; Anderson 1986; Simonetti 1989; Hulme 1994).

The decision of where to feed, however, is just one in the hierarchy of decisions made by a feeding animal (Pyke *et al.* 1977). The risk of predation may also influence lower-level decisions in the hierarchy, such as those dealing with how to feed and on what to feed, and with what intensity. Animals may decrease their vulnerability to predators also by altering their food preferences, particularly those that require significant handling time (Lima 1985). Models of feeding behaviour have typically treated handling times as a fixed time constraint, although a few studies (*e.g.* Lima 1985; Lima and Valone 1986) have reported an energy-predation risk trade-off. Handling times were found to be 'distance from cover' responsive, that is, animals exhibit shorter handling times when in the open than in protective cover.

In the present study, the trade-off between energy maximisation and the predation pressures was tested for woodland rodents, in an attempt to verify how risk of predation may influence food selectivity. Predation risk was assumed to be related to vegetation cover, that is, patches with low cover were considered hazardous areas. Hence, assuming the previous results on differential handling time constraints provided by hulled/coated sunflower seeds offered exposed or buried (Chapter 3), we tested if seed predation would be reflected in a spatial pattern, associated with the vegetation characteristics. Rodent distribution and density were also verified, complementing the evaluation of the patterns of seed predation. Considering the trade-off between the value or attractability of the seeds (less in the case of buried seeds), and the probability of predator attack on foraging animals, the results were evaluated in terms of risk-sensitivity .

5.2. Methodology

In order to determine the influence of vegetation cover on the rates of seed predation, a detailed vegetation assessment was conducted, based on the grid of feeding stations. A tree survey was carried out by the point-centered quarter method, at each feeding station. From the measurements, the estimates of the total tree density and the canopy basal area were obtained for each location. Estimates of the structure and architecture of the understory and ground vegetation at each feeding station were also performed, using point-quadrats. A 1.90m scaled bamboo cane, used as a pin, was lowered vertically 10 times through the vegetation around each experiment treatment. The plant species and the number of touches on the pin at 5cm intervals were recorded. The median height and the density of the vegetation were obtained for each location. All the measurements took place after the herb layer was fully developed.

A trapping program was carried out in order to relate rates of seed predation to the taxonomic composition and the abundance of small mammals, as well as to spatial variation in foraging intensity. Live-trapping was performed 3 times (May, June and July), between the periods when seed experiments where conducted, in order to avoid interference. A grid of 48 Longworth live-traps was set, overlaying the grid of seed depots. A standard trapping procedure was adopted (Grunell and Flowerdew 1982, 1994); traps were baited with wheat grains and set for three consecutive nights, without pre-baiting. The traps were checked in the mornings and afternoons of each day. Captured animals were individually marked by fur-clipping, and the species, sex, weight and position of capture were recorded.

4.3. Results

Figures 4.1.*a, b,* and 4.2.*a, b* graphically illustrates the vegetation characteristics of the study area, in relation to tree density, canopy basal area, ground/understory vegetation density and ground/understory vegetation median height, respectively.

The vegetation assessment showed marked within-site differences in vegetation physiognomy, reflecting three distinct microhabitats (Table 4.1). Tree density and ground vegetation density differed significantly between the three microhabitats, tree density being about five times higher in the "mixed vegetation" site than in "bramble" and "beech" sites, and ground/understory vegetation density being almost 6 times lower in the "beech" site, compared with the other two patches. Canopy basal area and median height of ground/understory vegetation did not vary significantly within the study area.

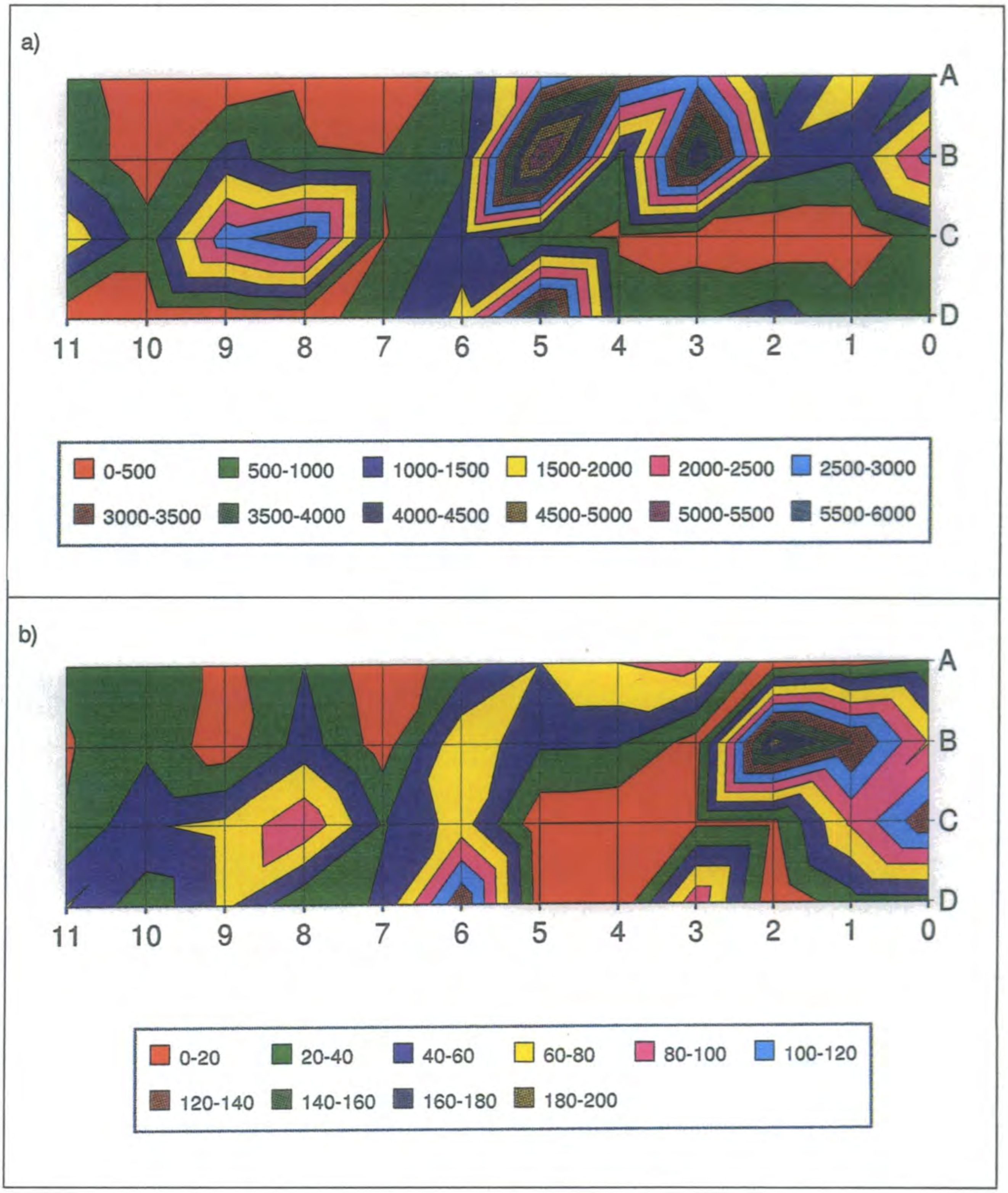

Figure 4.1. Graphic representation of (a) Tree density (tree/ha) and (b) canopy basal area (m^2/ha), along the study site. Please refer to Fig.2.2 for the location of the "bramble", "beech" and "mixed vegetation" microhabitats.

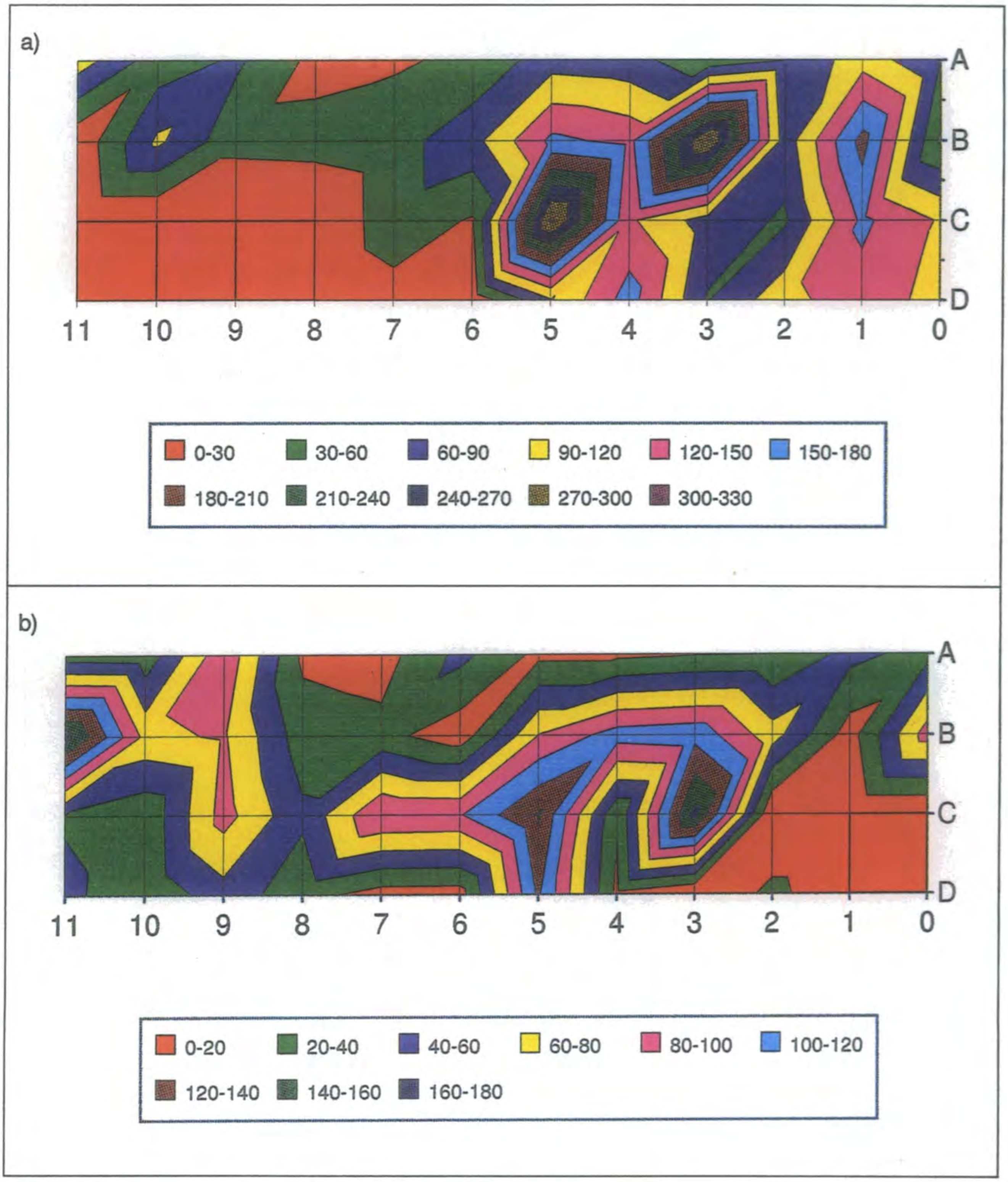

Figure 4.2. Graphic representation of (a) ground/understory vegetation density and (b) ground/understory median height (cm) along the study site. Please refer to Fig.2.2 for the location of the "bramble", "beech" and "mixed vegetation" microhabitats.

	Bramble Site	***Beech Site***	***Mixed Vegetation Site***
Tree Density (tree/ha)	337.68 (198.38,3)	392.16 (109.22, 12)	1618.72 (241.17, 33)
Canopy Basal Area (m^2/ha)	24.24 (6.45, 3)	43.77 (7.54, 12)	50.20 (8.34, 33)
Ground/Understory Density	70.67 (18.41, 3)	15.42 (8.46, 12)	94.51 (12.55, 33)
Ground/Understory Median Height (cm)	51.47 (22.02, 3)	46.01 (18.4, 12)	48.55 (6.79, 33)

Table 4.1. Mean values for the vegetation measurements of each microhabitat. (S.E., n). A one-way ANOVA detected significant variation in tree density and ground-understory density between the three sites ($F_{(2,45)}=5.6215$, $P<0.01$ and $F_{(2,45)}=6.9771$, $P<0.01$, respectively). No significant difference was found between the three microhabitats in terms of canopy basal area ($F_{(2,45)}=0.5582$, $P>0.05$) and median height of ground/understory vegetation ($F_{(2,45)}=0.020$, $P>0.05$). (please see Appendix 1 for a detailed description of the three sites in terms of canopy composition).

Seeds consumed by rodents were either removed or consumed "in situ", revealed by the presence of seed coats on the Petri dishes or surrounding area. The proportions of seeds removed and consumed "in situ" were evaluated together as total consumption. The values of consumption "in situ" were given by the proportions of seed coats found at each experimental treatment, therefore considered only the consumption of coated seeds.

Rodents harvested the experimental seeds differentially across the three habitats (Fig. 4.3.). Considering both hulled and coated seeds offered in the exposed treatment, the exploitation of experimental depots had similar proportions in the "bramble" site and in the "mixed vegetation" site, but was reduced in nearly 50% in the "beech" site. The exploitation of the depots with buried seeds was high at the "bramble" site (around 90%), being less at the "mixed vegetation" site (60%) and drastically reduced at the "beech" site, where only 4% of the depots were visited.

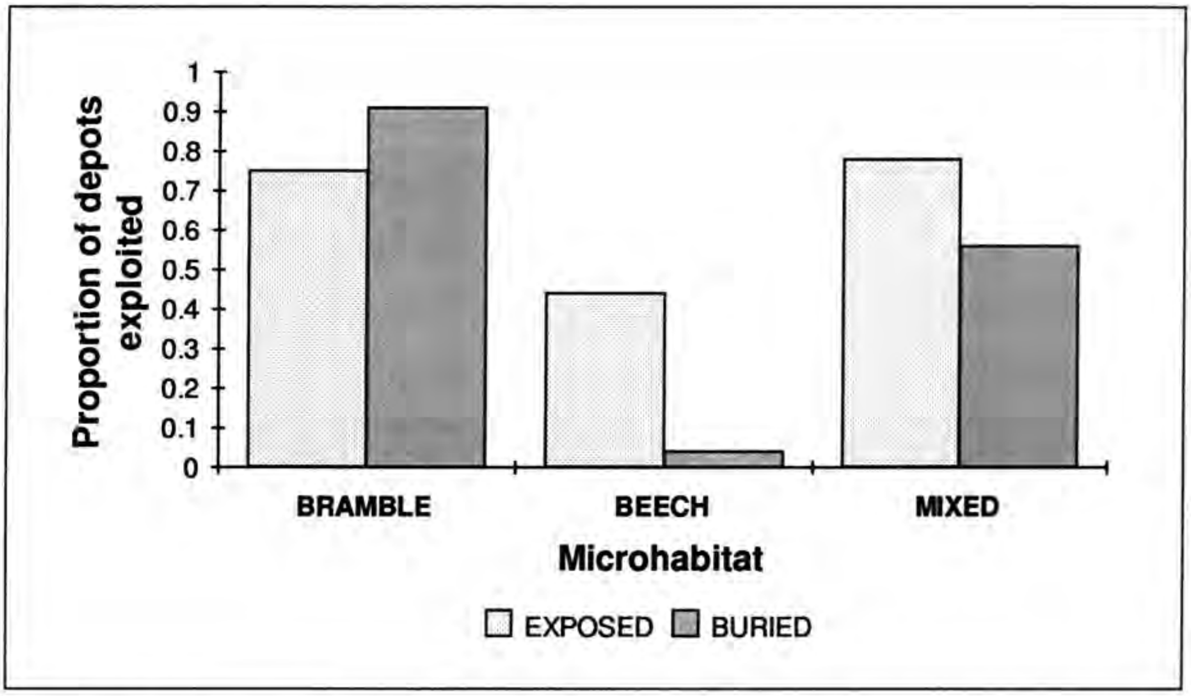

Figure 4.3. Proportion of experimental depots exploited by rodents at each microhabitat, according to the burial level.

Figures 4.4 and 4.5 illustrates the spatial patterns of total consumption of hulled and coated seeds, respectively, across the three microhabitats. Only results of "coarse mesh" are represented. Exposed seeds were taken by rodents in all three microhabitats (Fig. 4.4.*a*). Consumption from the buried presentations, however, were restricted to the "bramble" and "mixed vegetation" sites (Fig. 4.4.*b*). Coated seeds were avoided at the "beech" site in both burial level presentations, as can be seen in Figs. 4.5.*a* and *b*, their exploitation being limited to the "bramble" and "mixed vegetation" sites. The exploitation of coated/buried seeds, however, was even more restricted to areas of higher vegetation density in the two microhabitats (Fig. 4.5.*b*). Comparing visually the spatial patterns of predation of both hulled and coated seeds, it is possible to observe an overall reduction in the exploitation of patches in the case of coated seeds, this being more evidenciated in the buried treatments.

Consumption of seeds "in situ" was extremely restricted to patches of high density and median height of vegetation cover, as can be seen in Fig. 4.6.

Again, burial limited exploitation, reducing consumption even in the "bramble" site.

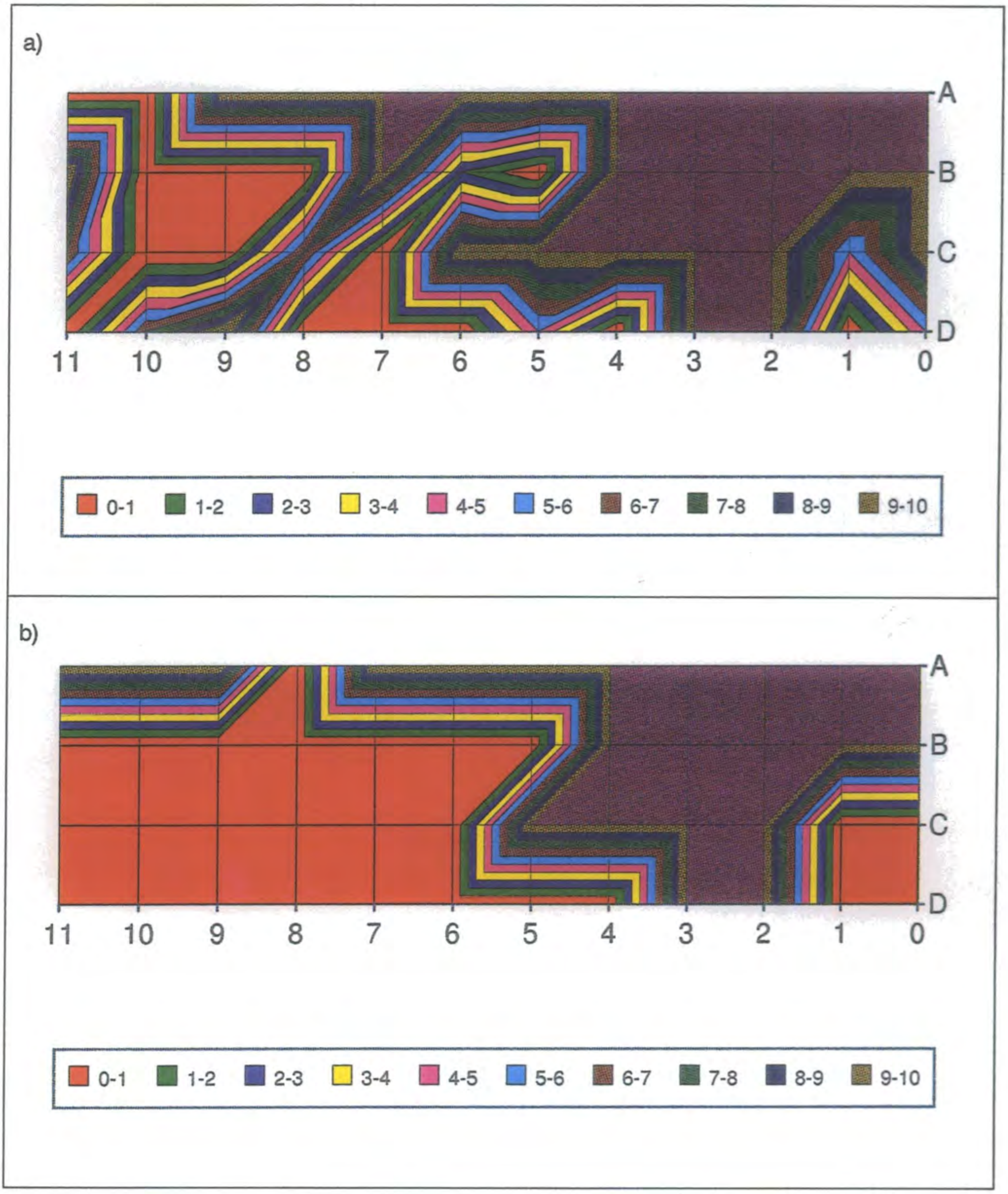

Figure 4.4. Spatial variation in the numbers of hulled seeds predated in the "coarse mesh" exclosures, at each depot. a) Exposed and b) buried treatments. Please refer to Figs. 4.1 and 4.2 for the identification of vegetation characteristics.

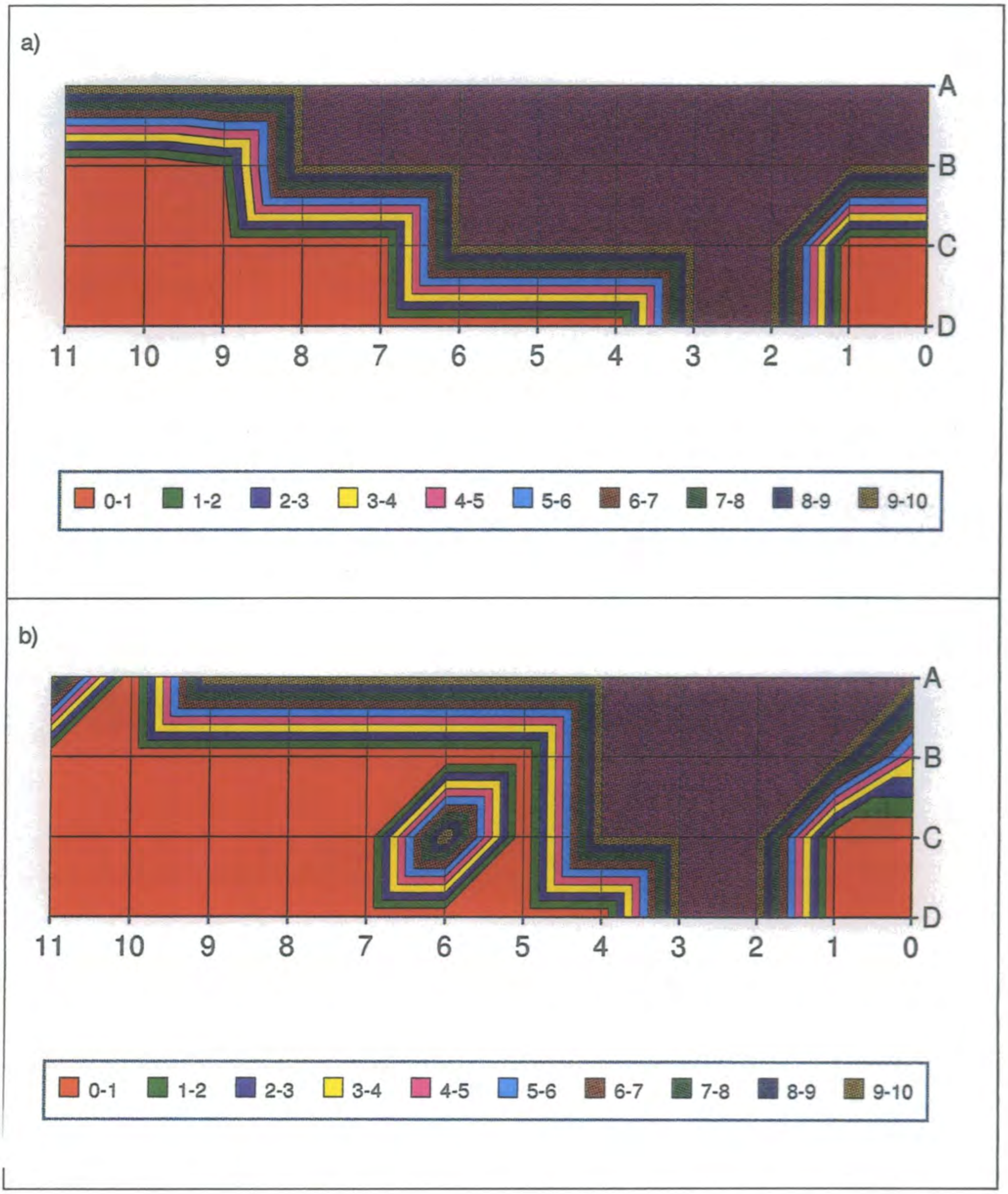

Figure 4.5. Spatial variation in the numbers of coated seeds predated in the "coarse mesh" exclosures, at each depot. a) Exposed and b) buried treatments. Please refer to Figs. 4.1 and 4.2 for the identification of vegetation characteristics.

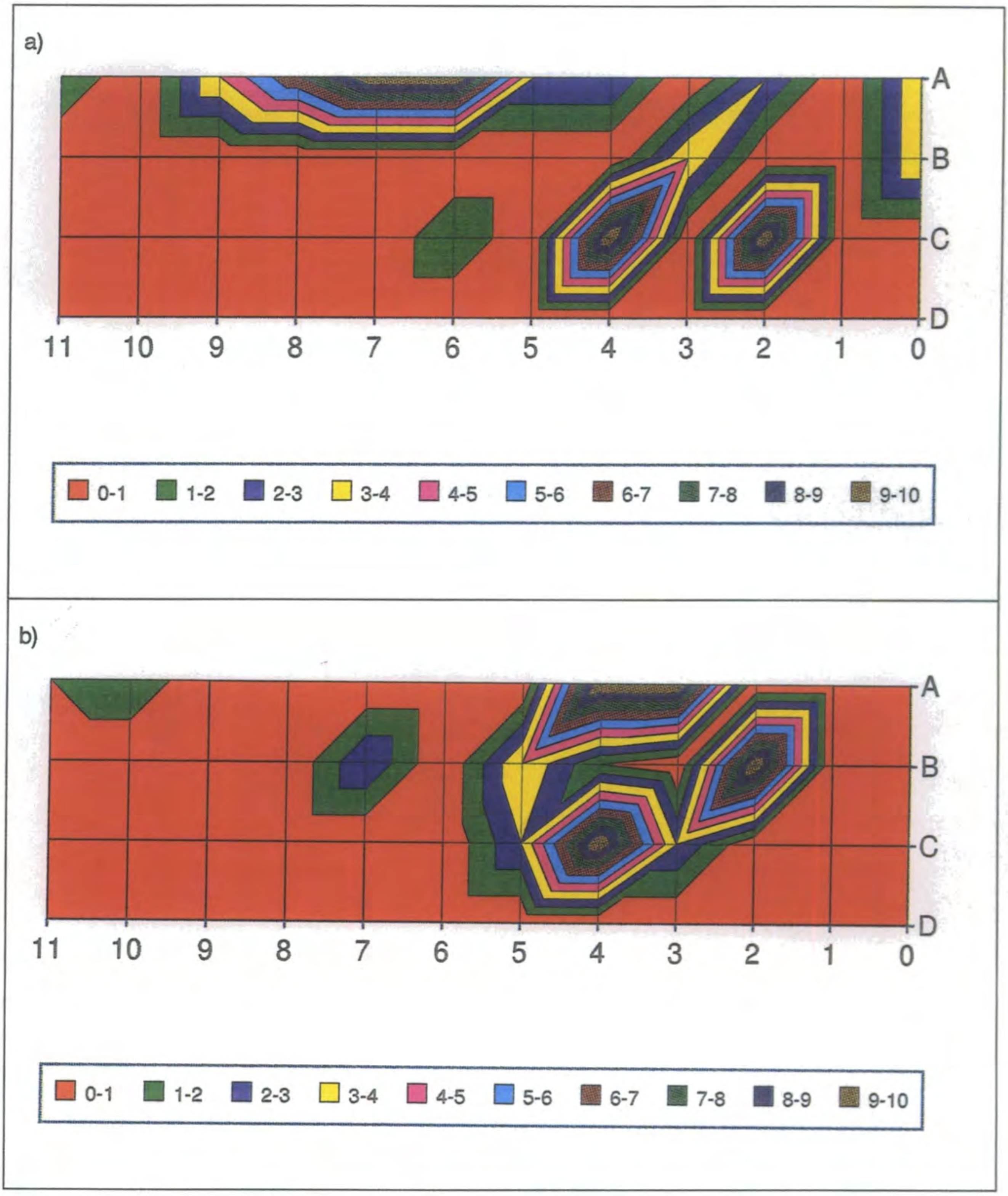

Figure 4.6. Spatial variation in the numbers of coated seeds consumed "in situ", in the "coarse mesh" exclosures at each depot. a) Exposed and b) buried treatments. Please refer to Figs. 4.1 and 4.2 for the identification of vegetation characteristics.

In order to evaluate the above patterns in terms of small scale variations in the vegetation characteristics along the microhabitats, correlations were undertaken on the rates of total consumption and consumption "in situ" and the aspects of vegetation cover at each experimental depot.

The correlation coefficients obtained for the proportions of total seed consumption are displayed on Table 4.2. Correlations between the proportions of seeds consumed and vegetation density tended to be positive for all seed type/burial level combinations. Significant positive correlations were found between the rates of consumption of "hulled/buried" seeds and the ground/understory vegetation density for both "coarse mesh" and "open" experimental treatments. "Coated/exposed" seeds offered in the "coarse mesh" were significantly positively correlated to tree density. Although not being statistically significant, a trend for negative correlation between the proportions of seeds consumed in both burial levels and canopy basal area was observed.

Seed Type/ Burial Level		***Ground/ Understory Vegetation Density***	***Ground/ Understory Median Height (cm)***	***Tree Density (tree/ha)***	***Canopy Basal Area (m^2/ha)***
HE	*C*	0.1685	0.2539	0.1882	0.0383
	O	0.1144	0.1946	-0.0747	-0.0405
HB	*C*	0.3244 (*)	0.0986	0.2387	-0.0605
	O	0.3610 (*)	0.0681	0.1814	-0.0965
CE	*C*	0.2695	0.0990	0.2784 (*)	-0.0653
	O	0.1301	0.0261	0.1895	0.0087
CB	*C*	0.1535	0.1189	0.2109	0.0034
	O	0.0742	0.2193	0.1555	-0.1629

Table 4.2. Correlation coefficients indicating the degree of association total consumption and the vegetation characteristics at each feeding station. Values for the proportions were arcsine square root transformed. "HE" - Hulled/Exposed, "HB" - Hulled/Buried, "CE" - Coated/Exposed, "CB"- Coated/Buried. "C" - "coarse mesh", "O" - "open" treatments (*,**,*** denote significance at the 0.05, 0.01 and 0.001 levels respectively).

Table 4.3 shows the correlation coefficients of the proportions of seeds consumed “in situ” and the vegetation characteristics for each burial level. Consumption “in situ” of exposed seeds was correlated positively with all the evaluated vegetation characteristics. Consumption was significantly correlated with tree density for both experimental exclosures, and with canopy basal area for the “open” treatment. The consumption “in situ” of buried seeds was positively correlated with ground/understory vegetation median height and with tree density for both experimental exclosures, and with ground/understory vegetation density, for the “open” treatment. Negative correlations were observed between consumption from “coarse mesh” and ground/understory density, and from both experimental exclosures and canopy basal area. Significance in negative correlations, however, was found only for the consumption “in situ” from the “open” exclosure and canopy basal area.

Burial Level		***Ground/ Understory Vegetation Density***	***Ground/ Understory Median Height (cm)***	***Tree Density (tree/ha)***	***Canopy Basal Area (m^2/ha)***
Exposed	*C*	0.1242	0.0639	0.3045 (*)	0.2148
	O	0.0992	0.1004	0.3280 (*)	0.3118 (*)
Buried	*C*	-0.2013	0.1268	0.0401	-0.2754
	O	0.1164	0.1184	0.1010	-0.3330 (*)

Table 4.3. Correlation coefficients indicating the degree of association between the proportions of seeds consumed "in situ" (given by the number of seed coats left in the Petri dishes or surrounding area) and the vegetation characteristics at each feeding station. Proportions were arcsine square root transformed. "HE" - Hulled/Exposed, "HB" - Hulled/Buried, "CE" - Coated/Exposed, "CB" - Coated/Buried. “C” - “coarse mesh”, “O” - “open” treatments. (*,**,*** denote significance at the 0.05, 0.01 and 0.001 levels).

The results of the small mammal trapping program are summarised in Table 4.4, for each microhabitat. Rodents trapped included 2 species - *Apodemus sylvaticus* and *Cleothronomys glareolus*. Trapping success was very low, with an average of 23%. Clear spatial patterns were observed in the trapping program, caughts being limited to the "bramble" and "mixed vegetation" sites, and with no captures in the "beech" site.

Unfortunately, no rodent species were captured frequently enough to calculate statistically reliable density estimates. The basic spatial patterns of captures, however, were correlated with the observed spatial patterns and intensity of seed predation during the feeding trials (Fig. 4.7).

Species	***Bramble Site***	***Beech Site***	***Mixed Vegetation site***
Apodemus sylvaticus	2	0	18
Chleothronomys glareolus	4	0	8
Total	6	0	26

Table 4.4. Total number of rodents captured at each microhabitat.

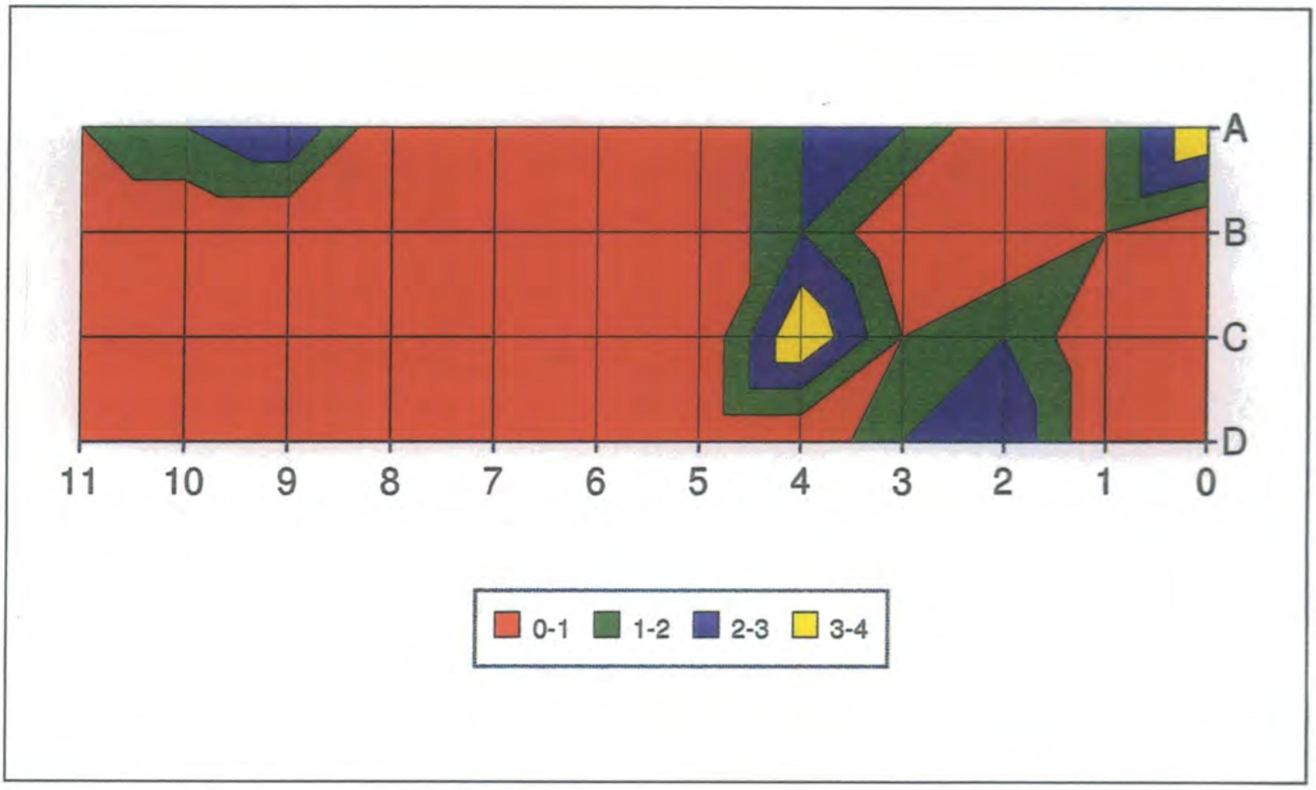

Figure 4.7. Spatial variation in the number of rodents caught along the study area. Please refer to Figs. 4.1 and 4.2 for identification of the vegetation characteristics.

4.4. Discussion

A great variation in the rates of seed predation was observed along the study area, suggesting that rodents followed spatial patterns in seed foraging. Such patterns were related to the spatial heterogeneity of vegetation cover within the study site, both in large scale, (microhabitats) and fine scale (vegetation characteristics at specific locations).

Differential microhabitat use by rodents has already been reported for woodland (Anderson 1985; Webb and Willson 1985; Whelan *et al.* 1990), shrubland (Simonetti 1989), cereal crops (Diaz 1992), old fields (Mittelbach and Gross 1984), grassland (Hulme 1994), and deserts systems (Rosenzweig and Winakur 1969; Stamp and Ohmart 1978; O'Dowd and Hay 1980; Hay and Fuller 1981), usually related to vegetation cover.

Although vegetation cover and food abundance may be correlated, therefore influencing rodent abundance and distribution in terms of rates of food intake (Price 1984), differential predation risk is normally attributed as the main factor for the preferential use of areas with dense vegetation cover (Rosenzweig and Winakur 1969; Rosenzweig 1973, 1974; Stamp and Ohmart 1978; Kotler 1984). One of the reasons may be the increase efficiency in aerial predators such as owls, which have been shown to be much more dangerous in open places (King 1985) therefore increasing considerably the risk in such areas, although the role of vegetation cover on mammalian predators is not clear.

In the present study, rodents consistently avoided open patches in their exploitation of the feeding depots, consuming preferentially seeds in depots near vegetation cover. This corresponds with the general pattern found for foraging rodents, in that less seed predation is often observed in open patches (Hulme 1993).

The avoidance of open patches was absolute in the consumption of food items imposing greater handling constraints. The removal of either buried or coated seeds was limited to areas with vegetation cover, being even more restricted in the case of buried/coated seeds. Consumption "in situ" was observed only in locations with high vegetation density and cover, with the exploitation of buried/coated seeds being extremely restricted.

Such patterns in seed exploitation may be explained by higher predation risks associated with foraging in open patches for an extended period of time, imposed by increased handling constraints. Mice and voles can be considered as central-place foragers (Pyke 1984; Stephens and Krebs 1986), since they often travel outward from and returning to their burrows, caching the food items, in the course of their foraging activity. As the experimental seeds could be considered as excessive for total consumption in the site at one time (Hulme, *pers. comm.*), it is reasonable to think that rodents would have to visit the experimental depots more than once, in order to completely exploit the food supply. This would increase risk, since they would be more frequently exposed in open patches. In the case of the exploitation of coated seeds, Rosenzweig and Sterner (1970) states that above ground seed husking should occur whenever the space saved by husking yields enough of a saving in trips to an from the burrow to increase the net harvest rate. It may also be expected when the risk of exposure to predation while husking is not great as the risk undertaking by extra trips. Therefore, the value of seeds with coats or buried may decrease considerably under the risk of predation, indicating that vulnerability to predation may interfere in rodent selectivity in terms of the food type that will be harvested. This may have important implications in terms of seed escape for less-preferred seeds, and thus influence in plant community structure (Hay and Fuller 1981).

Rodents were sacrificing the rates of energy intake in order to avoid the risk of predation, since even the consumption of more profitable seeds in terms of energy gained per unit of handling time (hulled/exposed) decreased considerably in open patches. Such behaviour is contrary to the expectations of classical diet theory, in that preferred foods should always be taken, but is consistent with a foraging-predation risk trade-off. The results of Phelan and Baker (1992) on foraging mice subjected to predation risk in enclosures have shown that animals would shift preference for less profitable, but safer food, if given a chance, in order to avoid being preyed upon. The shift in seed preference was also accompanied by predation-risk-reducing changes in spatial foraging patterns, with which our results agree.

Some of the fine-scale vegetative characteristics at each experimental depot were found to be correlated with the rates of seed consumption, and may be responsible for the above described patterns. The positive correlations between seed consumption and ground/understory vegetation density and median height is likely to be due to the protection provided by dense cover. This was significant in the case of the retrieval of hulled seeds, perhaps because hulled seeds were more likely to be consumed "in situ", even if limited by the constraint of burial retrieval. Consumption "in situ" of exposed seeds were highly correlated with tree density, higher in the "mixed vegetation" site. This indicates that tree density may be important in terms of rodent escape from predators, but can also reflect the distribution of burrow locations, often found between tree's roots. Negative correlations of seed predation with canopy basal area may be an artifact caused by the great canopy basal area recorded for the "beech" site, where seed predation was very low, since it is unlikely that this attribute of the vegetation have great influences over rodent foraging behaviour.

Trapping results, although few, reflected at some extent our findings in the feeding trials, in terms of foraging activity. However, although higher rodent abundance is normally associated with greater vegetation cover (Hulme 1993), our few captures do not allow any inference in the role of vegetation cover in rodent distribution in this area.

5 FREQUENCY-DEPENDENT SEED SELECTION

5.1. Introduction

One of the basic assumptions of classical optimal foraging theory is that food items are encountered sequentially, the rates of encounter with different food types being constant and independent of each other (Pyke 1984). The decision to consume a food type, according to this model, is independent of its abundance, depending only on the absolute abundances of food types of higher rank (Hubbard *et al.* 1982; and see Chapters 3).

In many situations, however, a predator may be faced with several syntopic prey species, *e.g.*, occurring together in the same place. In such cases, it has been shown that the predator's selective response can be determined by the frequency with which it encounters the alternative prey (Greenwood and Elton 1979). Frequency-dependent selection occurs when predators exhibit preferences for the commoner or the rarer type of prey, consuming it disproportionately in relation to its occurrence.

Visually oriented predators have often been reported to exhibit the first type of preference, denominated by Clarke (cited in Ayala and Campbell 1974) as *pro-apostatic selection*, since such preference favours the survival of the rarer forms (apostates). This kind of frequency-dependent selection has been previously denominated as "switching", for the predators attention on the prey types may change according to the change in their relative abundances (Greenwood 1985). The initial proximate explanation to pro-apostatic selection was that predators would form "search images" (Timbergen 1960), due to repeated encounters with the more common species (Clarke, cited in Ayala and Campbell 1974). Nowadays, however, pro-apostatic selection is expected to result also from any proximate mechanism that causes the risk for a prey type to increase disproportionately with increasing frequency, such as its distribution in space, the constraints it may impose in terms of capture and handling and so on (Greenwood 1984, 1985; Allen 1988).

When the rarer forms are taken in a disproportionate manner in relation to their availability, a*nti-apostatic selection* is said to occur. In this case, the commoner forms are at a selective advantage (Ayala and Campbell 1974). This kind of selection is attributed to the rarer forms contrasting against the background set by the commoner forms, as may occur at high prey densities (Greenwood 1985). In the case of non-contiguous prey, the explanation for anti-apostatic selection is that animals tend to be confused by the presence of more than one prey object in their sensory field at once, thus slowing down the hunting reaction. In order to maintain efficiency, animals would tend to get the prey that differs from all the others (Greenwood 1985).

Frequency-dependent prey selection has important evolutionary implications. In the case of pro-apostatic selection, it may contribute to the maintenance of a stable equilibrium of morph frequencies, generating polymorphism in natural populations; in the case of anti-apostatic selection, it may promote uniformity in prey populations (Ayala and Campbell 1974; Greenwood 1985; Allen 1988). The importance of evaluating such preferences in granivores species is therefore clear, since frequency-dependent seed-predation could affect vegetational diversity (Greenwood 1985).

Studies on frequency-dependent selection by granivores have generally investigated the characteristics of predator's perception and discrimination, using artificial baits of different colours or scents as prey types (Allen 1976; Fullick and Greenwood 1979; Horsley *et al.* 1979; Greenwood *et al.* 1984*a*, *b*; Allen 1988). Studies on visually-oriented granivores, such as birds, have found a general trend for pro-apostatic selection (see review in Allen 1988). At high prey densities, however, this tendency changes direction, becoming anti-apostatic. In the few works on olfactory-oriented granivores such as rodents, diverging results were described. Soane and Clarke (1973) found pro-apostatic selectivity in trained mice feeding on coloured/flavoured baits. Greenwood *et al.* (1984*a, b*), however, reported anti-apostatic selection by naïve mice feeding on the similar baits used by Soane and Clarke.

Ultimate causes of frequency-dependence are still not very well understood. Pro-apostatic selection may be argued to be an optimal foraging strategy, since by concentrating on common forms, predators may maximise fitness by maximising net energy consumption. It might be an advantage neglecting rare prey types, if an animal is less efficient when foraging on two types of prey - even if the rarer form is more profitable than the commoner (*Hubbard et al.* 1982). Greenwood (1984) pointed out that if there are costs to the consumption of mixed diets, animals should select pro-apostatically, and anti-apostatically if there are benefits in mixed diets. Anti-apostatic selection should also favour animals if the rarer preys are easier to detect and pick up.

The interpretation of the results obtained by experiments on animals feeding on artificial baits, however, gives little insight in terms of optimal foraging theory, since it is difficult to assess the relative profitability of different colours or flavours (*Hubbard et al.* 1982). It would therefore be interesting to evaluate frequency-dependent selection by animals foraging on food items that varies in terms of nutrient contents, energetic rewards, or other currency (Greenwood 1985).

In this study, frequency-dependent selectivity was evaluated for rodents foraging on seeds differing in toxicity values and handling constraints, in field conditions, in an attempt to understand frequency-dependent predation under an optimality approach.

5.2. Methodology

In order to evaluate the effect of relative seed abundance on predator selectivity, two varieties of Kidney Beans were chosen: "black" and "white". The two varieties were chosen since their morphological measures were most similar (see Table 3.4), differed most in the toxic values (see Table 3.3), and because they differed most in the rates of consumption attributed to rodents, in the experiment on seed preferences (see Chapter 3).

The methodology followed the main experimental design described in Chapter 2. Each experimental treatment at each feeding station was supplied with the same total seed density of Kidney Beans (10 seeds), but with the assignment of 5 different proportions of the two varieties for each feeding trial (Table 5.1). The influence of seed burial in the consumption was also tested, each proportion of exposed seeds having a buried replicate**. The specific seed proportions to be deployed at each feeding station were chosen randomly, so that each feeding station received all 5 frequency combinations for both surface and buried seeds. Again, the counting of the remaining seeds and the assessment of seed damage at the end of each trial was performed every three days, followed by its replacement with a new trial.

Experiment Classification	*White Seeds*	*Black Seeds*
A	1	9
B	3	7
C	5	5
D	7	3
E	9	1

Table 5.1. Number of seeds of "black" and "white" Kidney Beans assigned for each feeding trial. A buried replicate was also undertaken for each proportion.

** Burial replicates were undertaken following the same methodology described in pag. 13, Chapter 3.

5.3. Data Analysis

Analysis of frequency-dependent selection was undertaken following the model proposed by Elton and Greenwood (1970), Greenwood and Elton (1979). The model refers to any number of prey types, though parameters are easier to estimate if only two types are considered:

If $\boldsymbol{A}_1$, $\boldsymbol{A}_2$ are the numbers of the two prey types available, and $\boldsymbol{e}_1$, $\boldsymbol{e}_2$ are the numbers eaten respectively, the model can be expressed as:

$$\frac{e_1}{e_2}=\left(V\frac{A_1}{A_2}\right)^b$$

where ***b*** is a constant that measures the degree of frequency-dependent selection; if ***b***>1, selection is pro-apostatic; if ***b***<1, selection is anti-apostatic; if ***b***=1, selection is frequency-independent. The constant ***V*** is a measure of basic relative preference or visibility (frequency-independent selection); if ***V***>1, there is a preference for prey-type 1; if ***V***<1, there is a preference for prey type 2; if ***V***=1, there is no preference.

According to Greenwood and Elton (1979), the sampling distribution of ***V*** is not normal. As this has implications in hypothesis testing, in such situations it is advisable to employ $\log V$. The null hypothesis of no frequency-dependence, therefore, will be $\log V=0$. The values of ***b*** and $\log V$ can be estimated from the sample data by linear regression of log-transformed ratios, using the equation $\log(e_1/e_2)=b\log V+b\log A$, where $A=A_1/A_2$. The intercept of the line of the best least-squares fit is given by $b\log V$, and its slope is given by ***b***.

In this study, on several occasions preys of one type were not consumed in any trial. This made the use of log values impossible, since the values tend to plus or minus infinity. In these cases, Greenwood and Elton (1979) suggest the use of a relationship between ***A***, which is the ratio of frequencies offered $(A_1/A_1 + A_2)$, an ***p***, which is the proportion of the first prey taken $(e_1/e_1 + e_2)$:

$$p = \frac{(VA)^b}{\left[1 + (VA)^b\right]}$$

As the range of the possible values of ***p*** is between 0 and 1, the problem of values tending to infinity is eliminated. However, as the relationship of ***p*** to ***A*** in this model is not linear, the parameters ***V*** and ***b*** must be estimated from the sample data by non-linear least squares techniques.

Seed consumption was given by the sum of seeds damaged and removed. Transformations of the values were undertaken, for homogeneity. The absolute numbers of seeds consumed were log-transformed, and the proportions of seeds consumed according to each frequency were arcsine square root transformed.

5.4. Results

A two-way ANOVA reveals a significant influence of the experimental exclosure ($F_{(2,1410)}$=58.092; P<0.01) and seed variety ($F_{(1,1410)}$=27.590; P<0.01) on the proportions of seeds consumed. The interaction between the two factors was significant ($F_{(2,1410)}$=4.290; P<0.05), indicating that seed preference was taxon-specific.

Burial prevented seed consumption by invertebrates, and largely reduced seed consumption from the experimental treatments accessible to rodents (Table 5.2). A one-way ANOVA on the number of seeds consumed showed a high influence of burial level on the consumption in the "coarse mesh" ($F_{(1,478)}$=8.321; P<0.01) and "open" ($F_{(1,478)}$=13.470; P<0.01) treatments.

The parameter estimates obtained for frequency-dependence are displayed in Table 5.3. No preference was found in the consumption of exposed seeds, for any experimental exclosure. Nonetheless, a tendency for greater consumption of "white" seeds was observed (*V*>1), especially in the treatments accessible to rodents. Although considering the overall data a significant influence of seed variety was found (see ANOVA results above), the preference for "white" seeds was not confirmed as statistically significant for the data for each experimental frequency. These results support those observed in the first experiment, in which we compared rates of seed removal (see Chapter 3), in terms of no significant preference for any type of seed, but with a slight tendency for greater consumption of "white" seeds .

The estimates of ***b*** for consumption of exposed seeds shown that rodents tended to exhibit frequency-dependent selection against rare forms (***b***<1), and invertebrates frequency-dependent selection against commoner forms (***b***>1). Such tendencies, however, were only confirmed statistically for the cages where rodents had access (Fig. 5.1).

Little data were obtained from the buried presentations, since few buried seeds were consumed in the vertebrate exclosures, and none consumed in the invertebrate exclosures. The trends, however, where similar to the exposed seeds, in that there was no evidence for seed preference.

The estimates of ***b*** again indicate anti-apostatic selectivity for rodents. Nonetheless, the data present substantial heterogeneity, and this trend was not proved to be statistically significant

Experiment Classification		1			2			3			4			5		
Seed Variety/ Burial Level		F	C	O	F	C	O	F	C	O	F	C	O	F	C	O
White	*ex*	0	0.13	0.21	0.08	0.06	0.33	0.08	0.27	0.83	0.02	0.19	0.46	0.02	0.33	0.60
		(0)	(0.05)	(0.06)	(0.05)	(0.04)	(0.11)	(0.07)	(0.11)	(0.20)	(0.02)	(0.07)	(0.15)	(0.02)	(0.17)	(0.21)
	bu	0	0.04	0.13	0	0.06	0.17	0	0	0.29	0	0.17	0.31	0	0.19	0.31
		(0)	(0.03)	(0.05)	(0)	(0.06)	(0.7)	(0)	(0)	(0.13)	(0)	(0.15)	(0.15)	(0)	(0.19)	(0.21)
Black	*ex*	0.10	0.19	0.79	0.08	0.06	0.56	0.04	0.10	0.56	0	0.06	0.19	0	0	0.13
		(0.07)	(0.08)	(0.30)	(0.07)	(0.04)	(0.21)	(0.03)	(0.04)	(0.16)	(0)	(0.04)	(0.08)	(0)	(0)	(0.05)
	bu	0	0.21	0.73	0	0.02	0.17	0	0.06	0.17	0	0.08	0.13	0	0.02	0
		(0)	(0.11)	(0.28)	(0)	(0.02)	(0.08)	(0)	(0.05)	(0.08)	(0)	(0.07)	(0.06)	(0)	(0.02)	(0)

Table 5.2. Mean values of number of seeds consumed at each frequency, according to the seed variety and experimental treatment. "F" - Fine Mesh; "C" - Coarse Mesh; "O" - Open; "*ex*" - exposed; "*bu*" - buried. (S.E.)

Treatment		*V*	*S.E.$_V$*	*b*	*S.E.$_b$*
F	ex	1.646	0.745 (P>0.05)	1.384	1.102 (P>0.05)
	bu	-	-	-	-
C	ex	7.516	8.867 (P>0.05)	0.401	0.245 (P<0.05)
	bu	0.466	0.386 (P>0.05)	0.774	0.563 (P>0.05)
O	ex	2.633	1.578 (P>0.05)	0.389	0.162 (P<0.01)
	bu	1.928	0.611 (P>0.05)	0.859	0.255 (P>0.05)

Table 5.3. Parameter estimates from the model of Greenwood and Elton (1979) applied to the data, obtained by non-linear least-squares method. "F" - Fine Mesh; "C" - Coarse Mesh; "O" - Open; "*ex*" - exposed; "*bu*" - buried.

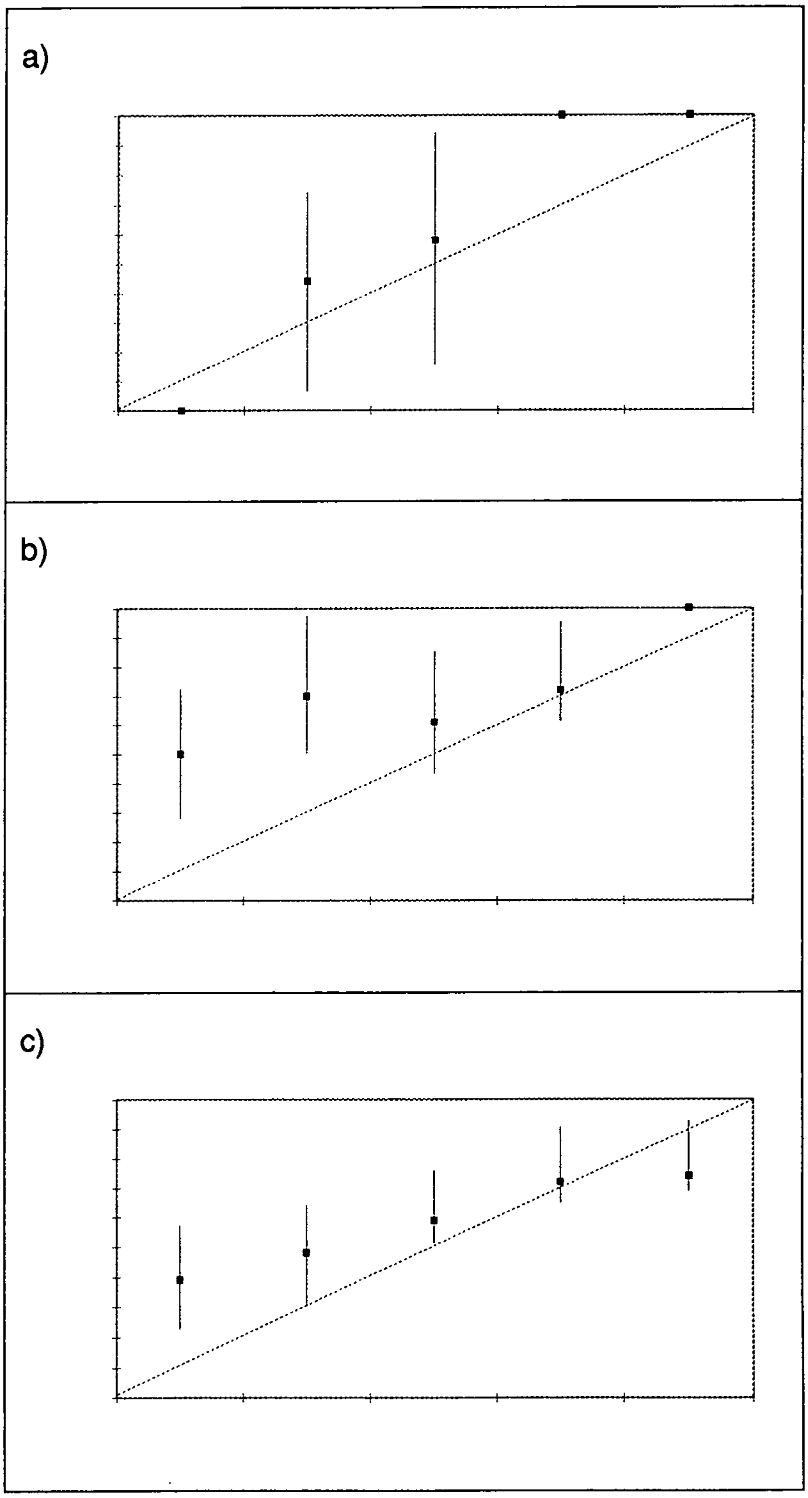

Figure 5.1. Mean values for the proportions of "white" seeds eaten in relation to the proportion offered, for exposed seeds, in each experimental treatment. a) "Fine Mesh"; b) "Coarse Mesh"; c) "Open". The broken line represents the line of no selection, at which the ratio eaten equals the ratio available (*b*=1, *V*=1). (S.E. bars included).

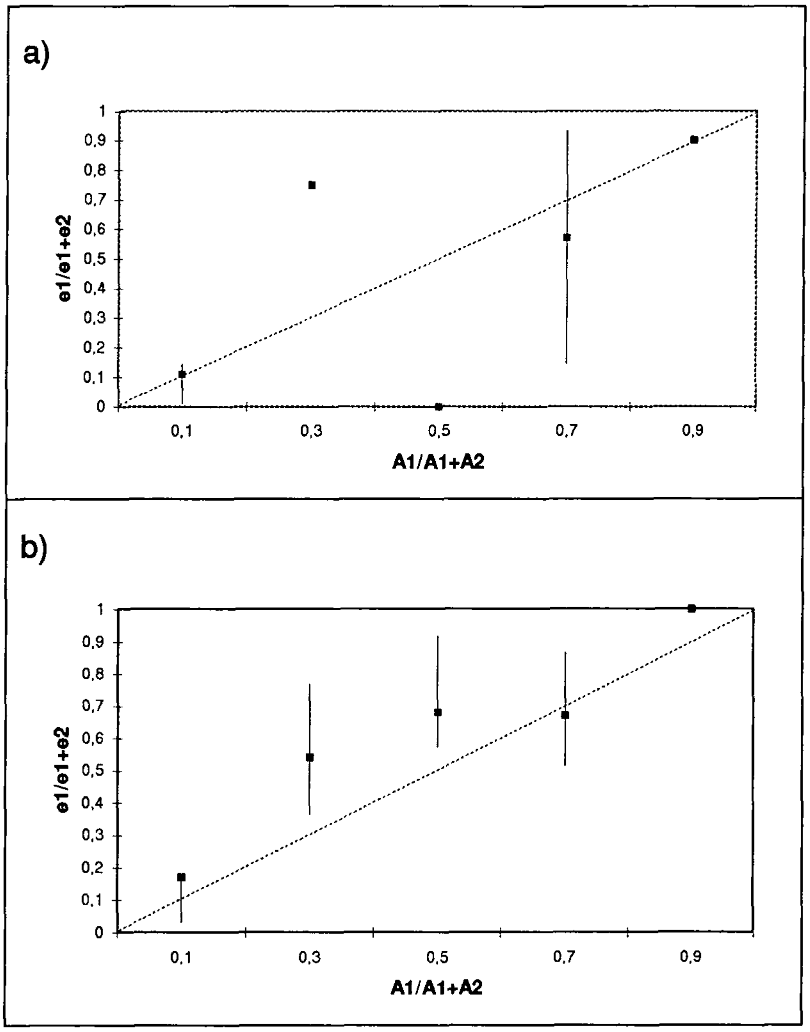

Figure 5.2. Mean values for the proportions of "white" seeds eaten in relation to the proportion offered, for buried seeds, in each exclosure treatment. a) "Coarse Mesh"; b) "Open". "Fine Mesh", not presented, had null rate of consumption. The broken line represents the line of no selection, at which the ratio eaten equals the ratio available (*b*=1, *V*=1). (S.E. bars included).

5.5. Discussion

The results of this experiment confirm the previous findings from the seed preference and handling time experiments (Chapters 3). No preference for any type of seed was found, and the retrieval of buried seeds increased handling time, this being reflected by the decrease in the rates of consumption on the buried replicates.

In this experiment, rodents concentrated their attention consistently more on rare seeds (*e.g.* anti-apostatic selectivity). This kind of food selection has been previously reported for visual predators foraging on high prey density

(Horsley *et al.* 1979; Allen and Anderson 1984), where it was attributed to the greater detectability of the apostates against the common forms. Rodents, as olfactory-oriented animals, have also been observed to forage anti-apostatically at high prey densities (Greenwood *et. al.* 1985*a, b*). According to these authors, such selectivity may arise from factors correlated with the identification of the rare form's odour, more conspicuous against the contiguous background provided by the commoner form's odour.

Taking into account the low availability of natural seeds during the foraging trials in this study, it would be possible to consider the experimental depots as patches of high food density for rodents (Hulme, *pers. comm.*). Our results, therefore, confirm the evidence of anti-apostatic selection at high prey densities. Under an optimality view, concentrating on rare individuals when the prey form a contiguous mass is probably the more efficient strategy, in terms of searching time, since animals may be confused by the presence of more than one prey object in their sensory field at once (Greenwood 1984, 1985).

Identification mechanisms may be related to learning processes, and rodents are known to prefer familiar prey (Soane and Clarke 1973; Partridge 1981; Partridge and Maclean 1981). Therefore, changes in preference would be expected with experience, altering the frequency-dependence trend towards pro-apostatic selection. In this study, the rodents had previous experience with the experimental seeds, therefore our results may reflect the already established patterns of selectivity. However, although not examined statistically, a general decrease in consumption of both "white" and "black" seeds was observed as the feeding trials were performed. Such decrease in the exploitation of the experimentals seeds may have been related to the increase in the natural food availability towards the end of the Spring and beggining of the Summer. The evaluation of the consumption rates throughout the experiment, however, would have been interesting, in order to examine the above patterns in more detail.

As discussed in Chapter 3, being generalists, there is a great possibility of encounter of noxious food items in natural conditions. Rodents may therefore benefit from mixed diets, for this would reduce the amount of toxins ingested. Greenwood (1985) points out the consumption of mixed diets as one of the factors leading to frequency-dependent selectivity. According to him, mixed diets would lead to pro-apostatic selectivity if the prey's density and handling constraints are small, i.e. '*if the benefit of a mixed diet is small or if a large proportion of the predator's time is taken up in searching for prey rather than handling it*'. If there is benefit in a mixed diet and the prey's density and handling time is large, a predator may maximise consumption if it concentrates its attention on rarer forms.

In this study, the degree of frequency-dependence varied according to the burial level, therefore in handling time. The values for *b* where significantly less than one only for the exposed treatments, where in the buried treatments the values approached the unity. Although there is no statistical significance in these results, the trend contradicts Greenwood (1984) of that maximisation of feeding rate by pro-apostatic selectivity would be expected, if handling time is small, and anti-apostatic selectivity, if large. However, it would be necessary to gather more data on the consumption of buried seeds at several frequency/density combinations, in order to establish this relationship in a more accurate way.

According to Greenwood (1985), frequency-dependent selection will maximise feeding rates if the food types differ in profitability: if the more profitable prey is less easily found than the less profitable, pro-apostatic selectivity may occur; if the more profitable type is more easily found, the more profitable type will always be taken in excess, but the extent of this excess will be less when it is rare than when it is common. Although not significant, the slight larger values of vertebrate and invertebrate consumption of "white" seeds may reflect their profitability in terms of less toxicity, if compared with "black" seeds, as discussed in Chapter 3. This may explain the patterns found in this experiment, where the rodent consumption of "white" seeds increased as their frequency increased (Figs. 5.1 and 5.2). This implies, however, in differential detectability for the two seed types, perhaps in terms of olfactory stimulus, since the same pattern was observed in both exposed and buried treatments (with the exception of the high variation found at frequency 0.7, at the "Coarse Mesh/ Buried" treatment).

Our results may be attributed to more than one ultimate causes that are referred as leading to anti-apostatic selection, and further experiments would be necessary to evaluate separately each aspect discussed above, in order to weight their interaction. It would be also interesting to evaluate, between them, the possible influence of sampling in determining the outcome of the frequency-dependence, since its importance in terms of rodent foraging behaviour as a mechanism of assessment of food profitability.

6 *GENERAL DISCUSSION*

Our study suggests that rodent preferences may be affected by various factors related to seed attributes and environmental characteristics, throughout the steps of the foraging sequence described by Hulme (1993).

Although being attributed as an important determinant in seed predation by rodents in previous studies (*e.g.* Hulme 1994), burial was not considered to have hindered seed encounter in this study. Burial has been ascribed as decreasing seed detectability by concealing seed's odour, in a direct relation to depth and seed size (Reichman 1981). The diffusion of odour molecules may be reduced with the distance from the seed, therefore becoming less perceptible, as occurs with increasing burial depth. However, odour may be emanated more strongly as the seed size increases. The combination of both factors may be responsible, therefore, for the decrease of detectability in small buried grass seeds, as found by Hulme *op. cit.* Our observations may be related to the fact that Kidney beans and sunflower seeds, used in this study, were fairly big compared with the seeds used in his experiment.

Density has been also attributed to influence detectability of buried seeds (Price and Jenkins 1986). As already mentioned, our seed depots could be considered as dense food patches, and therefore very likely to constitute conspicuous olfactory stimuli.

Although it is not easy to distinguish occasions when rodents detect buried seeds but do not exploit them from those when seeds go undetected (Hulme 1993), we have no reasons to attribute the differentiated rates of exploitation of our buried experimental seeds to variations in olfactory conspicuousness, as exposed above. Our results may be rather related to seed qualitative attributes, as well as factors concerned to environmental characteristics, as will be discussed later on.

Olfactory cues may have not interfered in terms of seed detectability, but may have influenced seed identification and posterior selection. In the experimental manipulation of frequencies of two types of seeds presented, rodents exhibited preference for the rarer seeds. An increased perception of rarer forms against the contiguous odour background set by the commoner forms is accounted for anti-apostatic selection, as discussed in Chapter 5.

Rodents are known to prefer familiar foods (Partridge 1981; Partridge and Maclean 1981), since their benefits have already been identified. New foods are reported to be carefully sampled, and exploited completely only if they prove to be profitable. The very low rates of consumption observed for the Kidney beans may be related to an initial sampling and posterior decrease in exploitation, with the recognition of toxic compounds in the seeds.

The profitability identified for sunflower seeds, on the other hand, may have been determinant to the high levels of exploitation observed for these seeds, comparing with the toxic Kidney Beans. This was evident also by the appearance of burrows near the experimental depots during the feeding trials using sunflower seeds, suggesting that rodents were relying not only on olfactory cues for seed location, but also on learning processes (Lockard and Lockard 1971; Armstrong *et al.* 1987; Baum 1987).

The presence of seed coats, expected to increase the manipulation constraints and therefore reduce energetic rewards, did not prove to be a determinant factor in rodent selectivity under natural conditions. Seed burial, however, was an important handling constraint, consistently reducing seed acquisition. Burial increased selectivity in the case of Kidney beans, demonstrated by the very little exploitation of buried seeds. This indicates that the expenditure of energy for the retrieval of low-ranked food items such as toxic seeds may be not considered worthy, by rodents.

However, rodent selectivity did not seem to be highly correlated with maximisation of energy intake as it has been often reported (Reichman 1977; Abramski 1983; Price 1983; Mittelbach and Gross 1984; Jensen 1985; Henderson 1990), as could be inferred by the lack of selectivity between hulled and coated seeds. Although burial has been considered as imposing significant handling constraints, differential rates of seed exploitation were observed to follow rather a spatial pattern. This can be affirmed because at some experimental depots sunflower seeds were always exploited, in both burial levels, and at others these seeds were only exploited in the exposed presentations. This indicates that seed value was modified by its spatial distribution.

Our results suggest that rodents were highly selective in the use of space, in their foraging activities. The spatial patterns in seed exploitation found in this study consistently followed vegetation characteristics, mainly vegetation density and cover. Even dense clumps of highly profitable food items such as hulled/exposed sunflower seeds were not exploited in open areas, indicating that other currencies rather than rate of energy intake operates in rodent selectivity. This may be attributed to a decrease in risk of being preyed upon given by the possibility of escaping to the protective vegetation cover, what agrees with previous studies on energetic rewards-predation risks trade-offs (Lima *et al.* 1985; Anderson 1985; Lima and Valone 1986; Phelan and Baker 1992). Therefore, rodents have shown to be highly selective in their diets, under the risk of predation, reducing both rates of energy intake, in the case of profitable seeds buried in areas of "medium risk", and completely avoiding profitable but dangerous patches.

Hulme (1993) suggested that the foraging steps involved in the detection, identification and acquisition of seeds are less influential in the determination of selectivity than the ones involved in manipulation and consumption, under natural conditions. Our results support this, in the case of the experiment undertaken with the highly profitable sunflower seeds. However, the exploitation of toxic seeds was found to be limited in the identification stage, suggesting that for these woodland rodents foraging choices may be severely constrained by toxic substances. Therefore, the presence of secondary compounds may be an important factor in terms of seed escape from rodent consumption, as well as the combination of seed coats, burial and spatial variation, for non-toxic seeds.

Our results did not support basic predictions of the classical optimal foraging theory, for instance that the optimal diet depends only on the values of the food gains and handling times for each food type, with food types being ranked by the average energy gain to average handling time ratio, or that a food type is either completely included in the diet or completely excluded from it (Pyke 1984). However, our findings may be predicted by developments of the classical models, as in the case of the "nutrient/toxins as constraints" model (Pulliam 1975) or the "rate-maximising predator-avoidance trade-off" model (Lima *et al.* 1985). The optimality approach, therefore, may be considered as an useful tool to understand the decision-making of foraging woodland rodents.

Optimal foraging theory does not assume any particular mechanism that leads to maximisation of rates of intake, while frequency-dependent theory highlights the importance of learning and preferences as causal mechanisms of foraging choices (Hubbard *et al.* 1982). The two approaches are not exclusive, however, and further studies on frequency-dependent selectivity using natural food items instead artificial baits may improve the understanding of optimal choices of animals facing simultaneously more than one prey types differing in profitability.

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APPENDIX 1. Estimates of species densities (SD) and basal areas (BA) for individual species at each of the three microhabitats in the study area, using the point-centered quarter method.

	Bramble Site		***Beech Site***		***Mixed Vegetation Site***	
	SD	***BA***	***SD***	***BA***	***SD***	***BA***
Acer pseudoplatanus	-	-	-	-	40.434	0.555
Betula pendula	-	-	98.129	2.775	823.135	10.19
Crataegus monogyna	-	-	-	-	20.468	0.371
Fagus sylvatica	-	-	131.207	31.448	35.779	0.102
Fraxinus excelsior	22.534	4.111	2.988	0.127	-	-
Ilex aquifolium	-	-	39.93	0.089	164.403	1.163
Larix decidua	-	-	-	-	24.327	4.590
Quercus robur	11.267	0.367	57.633	5.436	288.248	31.378
Sambucus nigra	-	-	62.209	0.3954	-	-
Sorbus aucuparia	-	-	-	-	194.605	1.657
Prunus avium	11.267	0.033				