The functional response does not predict the local distribution of European Rabbits (*Oryctolagus cuniculus*) on grass swards: experimental evidence

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Summary

1. The relationship between available biomass and short-term rate of intake (functional response) of herbivores is expected to provide a link between their food supply, and their distribution.

2. The functional response of captive wild rabbits (*Oryctolagus cuniculus* L.) on artificially produced broad-leaved (*Lolium perenne* L.) and narrow-leaved (*Festuca ovina* L.) grass swards was quantified.

3. The general prediction that habitat selection varied with biomass, and reflected the potential rate of intake defined by the functional response, was also tested. The main alternative predictions, that both intake rate and habitat selection increased asymptotically with biomass, or were biased towards intermediate habitat standing crop biomasses, were distinguished.

4. There was no relationship between biomass and short-term rate of intake on the narrow-leaved *Festuca* swards, but on the broad-leaved *Lolium* sward the short-term rate of intake increased asymptotically with biomass.

5. In a field experiment on *Lolium* swards, a population of free-living wild rabbits selected the shortest swards with the lowest biomasses, and which provided the lowest potential rates of intake.

6. Results demonstrate that free-living wild rabbits do not select habitats that provide the maximum potential rate of intake, nor did they select foraging habitat with intermediate standing crops. It is suggested that their selection of foraging areas in these grasslands which typify rabbit foraging habitat, is dominated by antipredator considerations rather than purely by rate of intake.

Key-words: Foraging, functional response, habitat selection, rabbits

Introduction

The relationship between the rate of food intake by a herbivore, and the biomass of available food (the functional response) is of ecological significance because it provides a mechanism linking the animal’s distribution to its food supply (Holling 1959; Fryxell 1991, 1992; Sutherland 1996; Illius & Gordon 1999). The ideal free distribution predicts that animals in a population distribute themselves in direct proportion to, or according to some increasing function of their attainable intake rate (Fretwell & Lucas 1970; Farnsworth & Beecham 1997). Because the functional response is expected to map directly onto the distribution of the animals, its precise form is crucial to the prediction of animal distribution.

In general, the rate of food intake of vertebrate herbivores is an asymptotic function of bite mass, a relationship that holds for grazing and browsing animals, regardless of the biomass of available forage (Spalinger & Hobbs 1992). However, for herbivores grazing simple grassy swards there is a close relationship between sward biomass and bite mass, and despite some compensation because of greater rates of biting on low sward biomasses, the functional response relationship of intake rate with biomass is also asymptotic (Laca et al. 1994). This arises because on short swards, the mouth is not filled at each bite, but as sward height increases, bite sizes increase until a point is reached, above which further increases in sward biomass result in no further increase in bite dimensions or short-term intake rate. Although the relationships between bite mass and intake rate of lagomorphs have been established (Gross et al. 1993), there is surprisingly little
published empirical evidence on the relationship between intake rate and biomass on grass-dominated swards, the main habitat of the European Rabbit (Oryctolagus cuniculus L.). Attempts have been made to measure daily intake rate of rabbits by sampling vegetation biomass before and after grazing periods lasting several days (Short 1985; Armstrong 1988). Short (1985) fitted an asymptotic functional response relationship. However, the fit of the asymptotic model was poor at high biomasses, the fitted asymptote lying between the alternative extremes of the intake rate continuing to increase at high biomasses or declining at high biomasses to give a unimodal form to the functional response. If the functional response of rabbits follows the asymptotic form, then we would expect their distribution also to increase monotonically with biomass. Alternatively, it has been suggested for several intermediate-sized herbivores, including rabbits, that foraging efficiency is impaired both at low standing crops, by limited food availability, but also at high standing crops, by the requirement for selection among the structurally more complex food environment (Van de Koppel et al. 1996). Under these circumstances, the postulated resultant unimodal functional responses were hypothesized to underlie the observed patterns of habitat selection, which were biased towards intermediate standing crops (Van de Koppel et al. 1996).

We adopt an experimental approach with captive European Rabbits to quantify their functional response on simple Ryegrass (Lolium perenne L.) swards. We also test the extent to which the observed functional response predicts the habitat selection by foraging, free-living wild rabbits, on similar swards in the field situation.

It is apposite to investigate the generality of the rabbit’s functional response and therefore assess its applicability to prediction of distribution in contrasting situations. There is considerable evidence that the morphology of plants and the structure of the sward also influence vertebrate herbivores’ intake rate and therefore their functional response (Gross et al. 1993; Rowcliffe, Sutherland & Watkinson 1999; Bergman, Fryxell & Gates 2000). Greater sward complexity at high biomass was the hypothesized cause of reduced foraging efficiency, and the reduced selection of high standing crop communities by intermediate-sized herbivores (Van de Koppel et al. 1996). But this effect is likely to be more profound in selectively foraging, small and medium-sized herbivores, than in larger grazing herbivores, whose biting characteristics are determined by whole-sward characteristics, rather than the morphology of individually prehended plants or plant parts. Therefore we also compare the functional response of rabbits on the relatively simple broad-leaved Ryegrass swards, with that on a Sheep’s Fescue (Festuca ovina L.) sward. Sheep’s Fescue is a narrow-leaved grass with lower biomass per leaf length than Ryegrass (Illius et al. 1995; Tallowin, Brookman & Santos 1995), and greater leaf and tiller-densities than the broader-leaved grasses (Illius et al. 1995). We test the prediction that greater overall rates of intake can be achieved by rabbits on the broader-leaved grass.

**Methods**

**EXPERIMENT 1: THE FUNCTIONAL RESPONSE OF RABBITS**

**Preparation of swards**

Pure grass seed of either the broad-leaved grass Lolium perenne or the narrow-leaved grass Festuca ovina were sown at a rate of 16 600 and 33 200 seeds per m², respectively, into seed trays (0·21×0·35×0·05 m³) in a 5 : 1 mixture of compost (B & Q, Aberdeen) to perlite, to which a nutrient mixture containing trace elements was added (Chem-pack; LBS, Warrington). Sowing took place in May after mixing the appropriate mass of seed per tray with silver sand. The trays were maintained in an outdoor covered area under natural lighting conditions, until September; they were watered regularly and liquid fertilizer added weekly. The swards were initially mown weekly to 3 cm above the soil surface. Prior to the experiments, they were trimmed to less than their target heights using battery-powered hand shears, and allowed to grow to their target heights for the experiments. This permitted presentation to the animals of a realistically heterogeneous sward surface profile.

**Experimental animals and procedure**

Five captive, individually penned, non-breeding adult rabbits were used (three males and two females). Their mean body mass was 1·55±0·031 kg. The rabbits were housed in adjacent pens (3 m × 5 m), each containing a shelter and an ad libitum supply of water and a complete, pelleted rabbit food. All rabbits were accustomed to grazing experimental swards prior to experimental measurements.

Swards were prepared so that approximately equal numbers, within each of five approximate height categories, spanning the desired range (2–14 cm), could be presented to each rabbit. Each experimental evening, each rabbit was offered between two and four swards (depending on the time taken to feed on each in relation to available daylight) in only one of the five height categories. The height category offered to each rabbit on each day was stratified across the five rabbits. The sward trays were presented on an exterior plywood board in which a slot was cut which held the soil surface flush with the surface of the board. Each trial lasted for 15–60 min, the termination being judged to coincide with sufficient depletion to give accurately measurable mass differences, but no more than 50% of the sward area being grazed. During that time, a video camera mounted on a tower recorded all grazing activity.
Immediately prior to the trials, any grass growing in the pens was cut short and removed, and the pelleted ration was withdrawn. The time since withdrawal of pelleted food was recorded. Trials were conducted to coincide with the animals’ peak of activity around sunset, and for no more than two consecutive nights each week.

Sward measurements

Prior to the trials, the height of each sward offered to rabbits was measured at 25 points with a sward stick (Barthram 1986). Swards in seed trays were weighed accurately to the nearest 0.01 g prior to being offered to the rabbits and again immediately after removal from the pens. The postgrazing height of each sward was measured with a ruler, at 25 points on leaves or stems, which were actually grazed. All grazed trays were harvested level with the soil, with electric shears and the cut grass was oven-dried at 50 °C. Samples of ungrazed grass swards (ungrazed controls) distributed across the approximate height categories (Lolium, \( N = 30 \); Festuca, \( N = 25 \)) were similarly measured, harvested and oven dried. They were milled prior to chemical analysis for nitrogen following a kjeldahl digestion, and neutral detergent fibre (NDF: Van Soest & Wine 1967), both quoted as percentage of dry matter (%DM). For 5 of the 25 Festuca samples insufficient material was available for NDF analysis. Six mass-loss control trays of similar height to the experimental swards were placed adjacent to the rabbit pens, and weighed before and after the trials, to correct for any non-grazing mass changes in the experimental swards.

The amount of grass eaten was calculated by difference, corrected for other sources of mass change using the controls, and converted to dry matter (DM) grazing offtake. The biomass of forage offered in each tray (g DM m\(^{-2}\)) was calculated as DM eaten plus DM remaining in the tray. The rate of intake during each trial was determined by dividing total amount of grazing offtake by the time of active foraging, extracted from the video recordings.

Statistical analysis

The functional response curves for rabbits grazing Lolium were described using the asymptotic curve of the form:

\[
\text{Intake rate} (g \text{ DM min}^{-1}) = A + \frac{B(1 + Dx)}{1 + Dx}, \quad \text{eqn 1}
\]

where \( x \) = biomass (g m\(^{-2}\)) or sward height (cm).

Curves were fitted to individual rabbits using the ‘fit non-linear’ procedure available on the Genstat statistical package (Genstat Committee 1993), weighting points by the reciprocal of the fitted values squared. Other comparisons were made using either ANOVA, or alternatively where sample sizes or designs were unbalanced, Residual Maximum Likelihood (REML) analysis, converting Wald statistics to \( F \)-values for probability testing (Elston 1998). Relationships among physical and chemical sward measurements were investigated using linear or curvilinear regression analysis.

**EXPERIMENT 2: HABITAT SELECTION BY WILD RABBITS**

A 4 \times 4 matrix of 16 plots, each 7.5 \times 7.5 m was created and maintained by mowing a re-seeded pasture at the MLURI Glensaugh research station, Kincardineshire, Scotland (Fig. 1). The pasture was dominated by Lolium perenne and also contained a low cover of Poa trivialis, Trifolium repens and Ranunculus repens. The treatments were the four target sward heights of 2, 4, 7 and 12 cm, each replicated four times (Fig. 1). The matrix was a modified latin-square design containing one plot of each treatment in each row and column, and equal numbers of treatments at the periphery and interior of the matrix. The modification ensured that the areas closest to the known rabbit warrens were not spatially biased towards any of the treatments. The sward preparation protocol was the same as for Experiment 1. Following an initial 2-week period during which all plots were mown to 3 cm, from 7 July to 9 August 1997, the swards were prepared on three occasions, for three experimental sampling periods, each lasting 6 days. Each plot was mown to slightly below its target height and rabbits were excluded using a temporary electric fence for a period of a few days to allow the sward to grow naturally to reach target height. On the third day of each sampling period (i.e. the

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Rabbit foraging and habitat selection

mid-point), a sample of vegetation was clipped using rechargeable hand shears, from a 100 × 20 cm quadrat randomly placed in each plot. After oven drying at 50 °C the mass of these samples was determined, and a subsample was milled prior to chemical analysis for nitrogen and NDF. Prior to clipping, the sward height in each quadrat was measured at 20 points using a sward stick (Barthram 1986). The distribution of free-living wild rabbits, and their activity on each plot, was recorded on a total of 18 days, using a video camera (JAI 733 SIT, JAI, Copenhagen, Denmark) mounted on a 10-m tower, and a time lapse video recorder (Sanyo TLS1000P, Sanyo Commercial Video, Hemel Hempstead), recording every 0.96 s. Recordings were made for each day between approximately 1 h before sunrise and 1 h after sunset. The field of view of the camera was alternated daily, between the eight easterly and the eight westerly plots. These two halves of the matrix of treatments are referred to as Blocks. For each rabbit observed in the experimentally mown matrix, a Foraging Session number was assigned, its initial plot number, and both total time and feeding time in that plot, and in subsequent plots was recorded. Its group number, and both total time and feeding time in that plot, and in subsequent plots was recorded. Its group size was defined as the total number of rabbits within a 10-m radius, plus itself.

The time spent foraging by rabbits in each plot, by Sward Height and Group size, was analysed using REML, and treating Plots within Blocks, and individual Foraging Sessions, as random factors. Although individual rabbits were not marked, this design makes effective use of the data, comparing the time spent in different parts of the experimental grid. The number of feeding rabbits observed on each treatment was analysed using REML after summing feeding observations on each plot on each day, treating days within plots as random variables. Counts were transformed by log(y + 1).

Results

EXPERIMENT 1: THE FUNCTIONAL RESPONSE OF RABBITS

For both the Lolium and the Festuca swards the relationship between the sward height and the biomass was approximately linear, although in both cases the mass per height declined at the tallest sward heights (Fig. 2). We henceforth describe swards in terms of their height (cm) from which mass can be calculated from the following polynomial relationships:

Lolium:
\[
\text{mass (g DM m}^{-2}\) = -20.5 + 34.7 Sward Height
- 1.2 Sward Height^2,
\]

Festuca:
\[
\text{mass (g DM m}^{-2}\) = -119.6 + 52.7 Sward Height
- 1.9 Sward Height^2,
\]

The addition of the quadratic term significantly improved the fit of the relationship for both species (additional \(r^2\) due to added quadratic term: \(Lolium = 13.7\%\), \(F_{1,133} = 21.1\), \(P < 0.001\); \(Festuca = 16.4\%\), \(F_{1,116} = 22.8\), \(P < 0.001\)).

The mean NDF concentration in the ungrazed control samples was 60.45% DM (SE 0.456) and did not vary significantly between the two grass species (\(F_{1,46} = 0.6\), NS). The NDF concentration declined as the overall height increased (cm) in the Lolium control swards (slope = -0.487, SE 0.185, \(F_{1,28} = 6.9\), \(P < 0.05\), \(r^2 = 17\%\)), but did not vary with height in the Festuca controls (\(F_{1,19} = 1.49\), NS). The nitrogen concentration in the control swards did not vary significantly with changing sward height (\(F_{1,51} = 1.06\), NS) but was significantly higher in the Festuca than the Lolium swards (Festuca: mean 3.143% DM; Lolium: mean 1.975% DM, SED 0.159, \(F_{1,51} = 53.4\), \(P < 0.001\)).

The mean wet mass eaten by rabbits was 7.5 g trial\(^{-1}\) (SE 0.56), which did not differ between the two grass species (\(F_{1,395} = 3.8\), NS). Rabbits spent less time foraging during the trials with Festuca swards than with Lolium (Festuca: 578.5 s, Lolium: 828.5 s; \(F_{1,395} = 29.5\), \(P < 0.001\)) and they ate correspondingly less dry plant material (Festuca: 1.68 g DM/trial, Lolium: 2.32 g DM/trial, \(F_{1,195} = 16.6\), \(P < 0.001\)), but the rate of intake did not differ between the two grass species (\(F_{1,195} = 3.8\), NS).

The functional responses of the five individual rabbits grazing Lolium swards were typically asymptotic in form (Fig. 3a, Table 1). Those on the Festuca swards

![Fig. 2. The relationship between sward height and standing crop biomass of mini-swards of (a) Lolium perenne and (b) Festuca ovina, offered to captive rabbits to determine functional responses.](image-url)
were variable but definitely not described by an asymptotically increasing relationship; they tended to be negatively relationships (see Fig. 3b).

After fitting functional response curves for each rabbit on *Lolium* swards, and fitting the overall mean rates of intake for each individual on the *Festuca* swards, the residuals about these fitted relationships were found to be weakly negatively correlated with the number of hours elapsed since removal of pelleted food ($F_{1,199} = 4.18$, $P < 0.05$, $r^2 = 1.6\%$). The height of the areas of grazed swards remaining after each trial, was unrelated to the time since removal of pelleted food ($F_{1,194} = 0.17$, NS) but was positively related to the initial height of the sward ($F_{1,197} = 795.45$, $P < 0.001$, $r^2 = 91.3\%$), the slope of the relationship being significantly greater in *Festuca* ($b = 0.351$, SE 0.0167) than in *Lolium* ($b = 0.24$, SE 0.0131: grass species $\times$ initial sward height, interaction $F_{1,195} = 26.7$, $P < 0.001$).

After adjusting for these effects, the height remaining after grazing was significantly greater on the *Festuca* than the *Lolium* swards (*Festuca*: 2.70 cm, *Lolium*: 2.31 cm, SED 0.064, $F_{1,195} = 14.08$, $P < 0.001$).

### Table 1. Estimates of the parameters and their standard errors of the asymptotic curves $y = A + B/(1 + Dx)$, fitted to the functional responses of intake (g DM min$^{-1}$) against the height (cm) of *Lolium* swards for individual rabbits

<table>
<thead>
<tr>
<th>Rabbit no.</th>
<th>Parameter estimates (standard errors)</th>
<th>$r^2$</th>
<th>$F$ (df)</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.491 (0.647) -0.471 (0.189) 0.328 (0.075)</td>
<td>72.2</td>
<td>28.23</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2</td>
<td>0.006 (0.064) 0.132 (0.007) 0.132 (0.008)</td>
<td>34.8</td>
<td>6.08</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>3</td>
<td>3.49 (7.69) 1.12 (0.007) 0.286 (0.008)</td>
<td>76.5</td>
<td>33.52</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>4</td>
<td>-0.423 (0.022) 0.019 (0.010) 0.225 (0.019)</td>
<td>67.3</td>
<td>22.64</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>5</td>
<td>12.0 (362.0) -2.8 (81.2) 0.217 (0.046)</td>
<td>37.0</td>
<td>6.87</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

**Discussion**

**RABBIT FORAGING BEHAVIOUR**

In general, higher fibre content of a food source due to twig diameter eaten by browsers, or greater proportions of stem in the grassy swards eaten by grazers, is expected to lead to a greater prehension and chewing effort (Shipley & Spalinger 1992; Penning et al. 1994). However, this is unlikely to explain the asymptotic functional responses of rabbits grazing *Lolium*. Although the shorter artificially produced swards were slightly more fibrous, the NDF concentrations changed very little with height, and all were relatively
The slight decline of NDF with increasing height of the *Lolium* swards may be due to the stem and pseudostem material forming a smaller proportion of the taller swards. We suggest that the increasing phase of the asymptotic functional response curve of the rabbits grazing on the *Lolium* swards is due mainly to a decrease in the time needed to select and prehend individual leaf blades with increasing sward height. The upper asymptote, corresponding to a biomass of about 140 g m\(^{-2}\), could be the result of a maximum rate at which the longer blades can be passed over the molars prior to swallowing. Contrary to expectation, the mean rates of dry matter intake were similar on *Festuca* and *Lolium* swards, but the absence of a functional response by rabbits grazing the *Festuca* is probably due to the complexity of the sward structure. *Festuca* swards had many intertwined narrow leaves, precluding ready selection and prehension of large individual blades. The taller grazed grass heights remaining in the *Festuca* swards after grazing, as compared to the *Lolium* swards, support this hypothesis, as rabbits were either unable or unwilling to graze at the lower horizons within the *Festuca* swards, foraging instead on the upper layers. Additionally, even when long individual leaves of *Festuca* are prehended by a foraging rabbit, their low ratio of mass to length (Illius *et al.* 1995) might not be conducive to as high a rate of dry matter intake as could be obtained by sequential faster cropping of smaller fragments from the upper horizons. This interpretation of the observed functional responses of rabbits grazing on grassy swards is based on the known highly selective nature of rabbit grazing (Gillham 1955) and could be tested using high-speed video recording. The results suggest that rate of intake by rabbits on structurally complex plant communities, such as those containing narrow-leaved grasses or those consisting of mixed species, would be compromised. This observation provides qualitative support for the mechanism proposed by Van de Koppel *et al.* (1996), that sward complexity reduces foraging efficiency. On the broad-leaved sward, our results verified the low foraging efficiency at low sward biomasses, but not at high sward biomasses. However, in natural grasslands, there is an expected decline in vegetation quality, owing to higher proportions of senescent material at higher standing crops (Gordon 1989). Although in our experiments we have effectively standardized for this effect of lower vegetation quality with higher standing crop, in other circumstances this effect may lead to even lower foraging efficiencies, because of the need to forage selectively (Van de Koppel *et al.* 1996). The generally high foraging efficiency on structurally simple swards may be one of the factors underlying the success of rabbits as colonizers of simple grass-dominated swards such as agricultural pastures or cereal crops (Trout 2002).
DISTRIBUTION OF GRAZING RABBITS IN RELATION TO POTENTIAL RATE OF INTAKE

It was hypothesized that a rabbit's selection of foraging habitat in relation to standing crop biomass would reflect the potential rate of intake attainable and would either (i) increase asymptotically with biomass or (ii) be biased towards intermediate standing crop biomasses. Contrary to both these predictions we found that foraging rabbits strongly selected the shorter swards, which had been shown to provide the lowest rates of food intake.

The mowing of the matrix of swards in the habitat selection experiment (Experiment 2) achieved sward heights that approximated the target heights, and spanned the range of heights of *Lolium* swards over which functional responses were measured in Experiment 1. The height–mass relationships of the mown swards in the habitat selection experiment were very similar to those of the artificial swards used in the functional response experiment, but the mass at tall sward heights, was slightly less in the natural swards. NDF concentrations did not vary between the mown sward height treatments, and although the nitrogen concentrations varied little, they followed an inverted U distribution from the shortest through to the tallest swards. This pattern of nitrogen concentration corresponded to the probable distribution of actively growing and unsenesced leaf in the intermediate heights, a pattern of change that would be expected to lead to selection of the intermediate biomasses by rabbits as predicted by Van de Koppel et al. (1996). However, rabbits' digestive systems are highly efficient at processing fibrous, poor-quality forage. Rabbits are able to retain microbial and soluble protein in the gastro-intestinal tract via caecotrophy and colonic separation mechanisms, and they can recycle urea, a catabolic product, back to the gastro-intestinal tract for further assimilation by microbes (Iason & Van Wieren 1999). This means that rabbits are expected to maintain high levels of intake at low forage qualities and not be unduly nutritionally challenged by the very minor variation in the diet qualities they ingested on the different sward height treatments offered in these experiments. Overall, neither the slight variation in quality, nor its pattern of change between the sward height treatments can explain the selection of the shorter swards by rabbits.

Food depletion in the vicinity of rabbit warrens is commonly observed (Thompson 1953). However because the habitat choice experiment was conducted some distance from burrow entrances, and because treatments were located without bias towards the entrances, the distribution of rabbits on the experimental plots cannot be attributed to proximity to their burrows. The experiment was conducted during the summer, when depletion of food during the course of the observations is unlikely, as the patches were continuously replenishing due to new plant growth, and treatments were only imposed for a single week of grazing.

The functional response of predators to their prey density, or of herbivores to their food supply, is expected to form a key link in the quantification of limitation of animal numbers by their food resources (Fryxell 1999; Illius & Gordon 1999). This link is expected to be closest in cases such as rabbits grazing simple grassy swards, which are of uniformly high quality. This study has shown that far from selecting grass habitats that maximize their rates of intake, foraging rabbits selected short grass swards in spite of their low potential maximum rates of intake, which is possibly reduced further by greater interference from other rabbits. The rates of intake observed on the *Lolium* swards presented to captive rabbits in Experiment 1 can be assumed to represent a maximum attainable in the absence of predation or interference. The Ideal Free Distribution (Fretwell & Lucas 1970) predicts that animals distribute themselves among food patches in relation to their rate of intake in the patches. Under this prediction we would have expected more wild rabbits to be observed foraging on the taller swards in Experiment 2, whereas in fact the opposite was observed. Despite the observation that the individual rabbits that occupied the two tallest sward heights foraged for longer bouts than those that used the shorter swards, there were overall greater numbers and greater overall total duration of occupancy by foraging rabbits on the shorter swards. The observed longer duration of foraging bouts in the taller swards also suggests that interactions between foraging rabbits may have been less on the taller swards. Foraging rabbits are frequently seen to displace other rabbits and although small-scale feeding sites or feeding stations may be defended, it is most unlikely that they can defend and exclude other animals from patches as large as 7 × 7 m in this experiment. So it seems likely that interference is greatest on the short swards, which would further diminish their value as feeding patches.

It appears that the factors that determine habitat selection in the field are sufficiently powerful to override the negative effect of lower rates of foraging on the short, most preferred swards. Other determinants of animal distribution include consideration of the effects of predation risk (Newman 1991), travel costs between patches and failures to perceive differences between patches (see Rowcliffe et al. 1999). Neither of the last two is likely for rabbits in the habitat selection experiment, given the juxtaposition of patches and the rabbit's familiarity with their foraging ranges centred on their burrows (Fig. 1). The role of predation risk as a modifier of foraging efficiency and a determinant of rabbit distributions, however, requires further investigation. High standing crops can alter predation risk for an animal, by either providing cover and protection in the event of an attack, or conversely by obstructing its view of approaching predators (see Lazarus & Symonds 1992). The former would decrease the need to scan for predators in higher biomass habitats and therefore increase time spent foraging.
or the efficiency of foraging, and the latter would increase predation risk in high-biomass habitats, resulting in compensation by greater vigilance and lower foraging efficiency (Lima 1987). In an ecologically similar pasture environment, surrounded by burrows, the rate of scanning by rabbits increased, and the duration of feeding without interruption decreased, with increasing length of grass (Roberts 1988), suggesting that tall grass decreases foraging efficiency. For a range of intermediate-sized herbivores including rabbits, selection of intermediate levels of standing crop for foraging was hypothesized to result from low foraging efficiency at both low and high standing crops (Van de Koppel et al. 1996). Although predation risk was considered to be a further moderator of foraging efficiency, the hypothesis was tested and supported in the absence of predators (Van de Koppel et al. 1996). In contrast, we found a clear preference of rabbits for short swards, which we attribute to lower predation risk during foraging. However, it seems unlikely that consideration simply of foraging efficiency or predation risk determines distribution of herbivores that are usually subject to predation, such as rabbits. In many invertebrates and smaller vertebrates including fish, small mammals and birds, the selection of foraging habitats represents a trade-off between nutritional gain and minimization of predation risk (Lima & Dill 1990). As mechanistic determinants of habitat selection, both factors should be considered, along with interaction effects between them. For example, low rates of intake may impose longer daily foraging times, and therefore greater risk of predation, or conversely high rates of short-term intake of taller swards, may be reduced in the longer term by the need for greater anti-predator vigilance, where predators are less detectable.

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