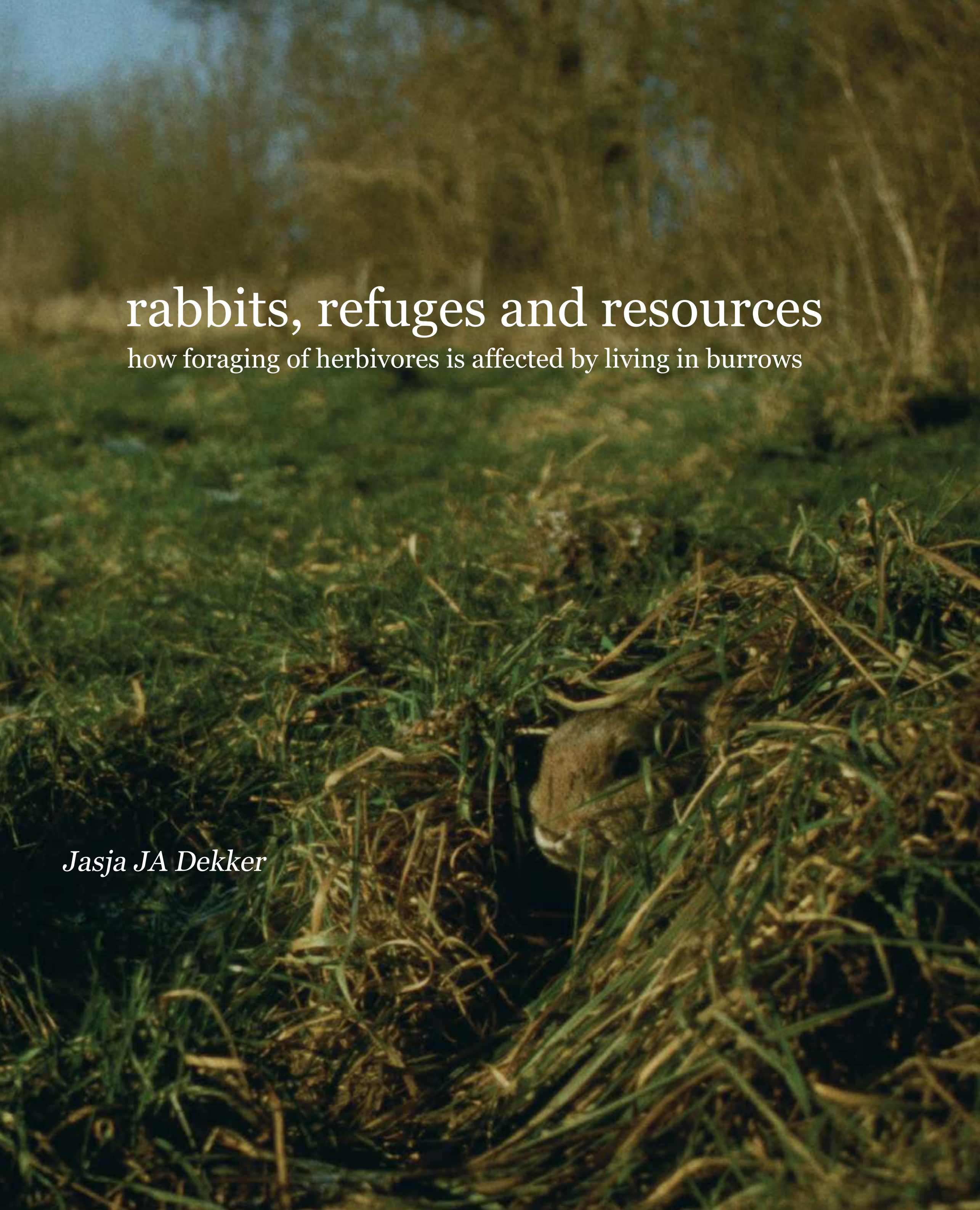

rabbits, refuges and resources

how foraging of herbivores is affected by living in burrows

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Jasja Johannes Antonius Dekker

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How foraging of herbivores is affected by living in burrows

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Chapter 1

Introduction

Burrows and spatial patterns in grazing and vegetation

Many small herbivores live in burrows, to shelter from predators and weather or to provide a safe place for their offspring. Living in burrows affects the interaction between these animals and their environment: it is associated with spatial patterns in foraging intensity, which in turn creates patterns in the surrounding vegetation. Patterns in foraging intensity and their effect on the vegetation around burrows of small herbivores were described by naturalists as early as 1917. E. Pickworth Farrow noted in a paper on the ecology of the vegetation of the Breckland in the UK that "the different intensities of biotic attack at varying distances around the burrows (of European rabbits *Oryctolagus cuniculus* L., JD) produce a characteristic zonation of the vegetation around the burrows on the otherwise uniform sandy plains of Breckland" (Farrow 1917, page 17).

Since this observation was made, patterns in species composition around burrows or refuges, plant biomass and/or intensity in grazing (Figure 1) in relation to distance to the burrow or refuge have been described for European rabbit *Oryctolagus cuniculus* (Tansley & Adamson 1925, Gillham 1955, Monclus & DeMiguel 2003, Bakker *et al.* 2005), American pika *Ochotona princeps* (Huntly 1987, Holmes 1991), Daurian pika *Ochotona daurica* (Komonen, Komonen & Otgonsuren 2003), hoary marmot *Marmota caligata* (Karels, Koppel & Hik 2004), rock hyrax *Procavia capensis* (Kotler, Brown & Knigh 1999) and black-tailed prairie dog *Cynomys ludovicianus* (King 1955, Cincota, Uresk & Hansen 1989). All these species forage on herbacious vegetation and grasses, are small herbivores and show a negative relation between foraging intensity and distance to the refuge.

What shapes spatial patterns in foraging activity?

Several causes have been put forward explaining grazing patterns and zonation in vegetation around burrows: travel costs, existing patterns in the forage and predation risk. Travel costs are the explanatory spatial factor in central place foraging theory. In central place foraging theory (Schoener 1971, Orians & Pearson 1979), costs and benefits of obtaining, handling and transporting or eating a food item are optimised. More energy is required to travel to a food item when the distance between food item and refuge is large. Because foraging on more distant food is less profitable, it will occur less, unless the nutritive value of the food item is larger. Although central

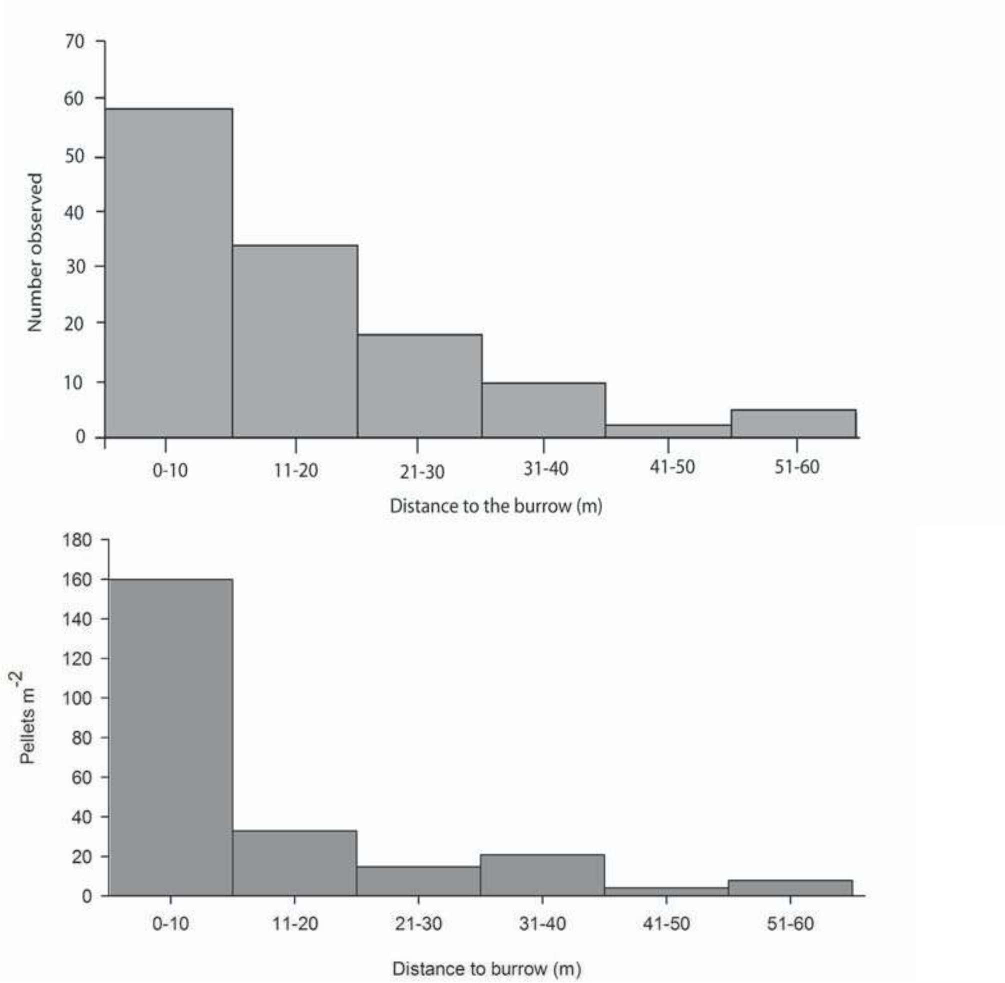

Figure 1. Foraging intensity in relation to distance to the burrow of European rabbits in two different areas. Top graph: number of faecal pellets decreased with distance to the burrow at el Monte de Valdelatas, Madrid, Spain (reproduced from Monclús & DeMiguel 2003).
Bottom graph: faecal pellet densities decreased with distance to the burrow at an enclosed wild rabbit population in Wageningen, the Netherlands. Faecal pellet density is related to foraging intensity (Bakker 2005). Pellets were counted 4 times with 3 week intervals, in 4 m^{-2} plots along a transect between two burrows. Displayed is the total number of pellets counted. Data were gathered by Marjolein van Adrichem.

place foraging theory makes correct prediction for a range of animals foraging from central points (for example, Kacelnik & Cuthill 1990, Fryxell & Doucet 1991), it is unsuitable for refuging grazers. Grazing herbivores make long foraging bouts before returning to the refuge. The costs of travelling to the food are negligible in relation to the food intake in these long bouts. Additionally, for terrestrial herbivores travel costs are negligible when compared to basal metabolic rate (Prins & Van Langevelde in press).

A second explanation is that the foraging patterns of refuge-living herbivores result from existing patterns in vegetation quality. If forage quality is highest close to the burrow, foraging intensity is highest close to the burrow (Bakker *et al.* 2005). While this is true, and localised grazing in turn can amplify this variation in the vegetation (Bakker, De Leeuw & Van Wieren 1984), this hypothesis does not explain how the existing pattern in vegetation quality was initially formed.

A third explanation is that these patterns are caused by predation risk (Holmes 1991). Predation risk increases with distance to the refuge: when the distance to the refuge becomes larger, the animal must detect the predator sooner to reach the refuge in time. Vigilance is known to lower intake rate in mammalian herbivores (Underwood 1992, Fortin *et al.* 2004) and declines with distance from the refuge or other cover in a number of species (for instance, Trouilloud, Delisle & Kramer 2004, Carrascal & César 2006). European rabbits respond to predator scent with an increase in vigilance and a decrease in food intake rate (Monclús *et al.* 2006). Removal of foxes Vulpes vulpes, an important mammalian predator of rabbits, caused an increase in distance to cover during night-time foraging (Banks *et al.*, 1999). So, vigilance requires time that could have been used for foraging, and vigilance seems to increase with distance to the refuge. If this is the case, the intake rate at a location is not only a function of the food density at that location, but also of its distance to the refuge (Figure 2). It follows from optimal foraging theory, that locations that are near the refuge will be preferred for foraging when food is distributed evenly. As the animal forages, it depletes these nearest locations, and areas further from the refuge will become the ones yielding the highest relative intake. This process would result in the grazing and vegetation patterns found in the field. Plant characteristics, such as productivity will affect these patterns. Assuming that the small herbivore has a type II functional response (Figure 2, Holling 1959), it will take will take longer before depletion results in a lower intake rate, and so grazing should occur mostly close to the refuge. Also, when growth rate is high, vegetation that is eaten will (partly) regrow, diminishing the effect of depletion. The intake rate of herbivores can also diminish at high densities of vegetation, due to increasing complexity or decreasing palatability (Prins & Olff 1998, Drescher *et al.* 2006a). If the intake rate of small refuge-living herbivores follows such a unimodal ‘type IV’ functional response, different patterns should result at different plant productivities. Depletion of patches close to the refuge will result in foraging to farther patches at sites of low productivity. At sites of high plant productivity, the animals will graze the vegetation to a density at which intake is higher than at the initial density: the animals facilitate themselves. At high plant growth rate, this could result in the formation of grazing lawns (Vesey-FitzGerald 1960). If central place foragers follow

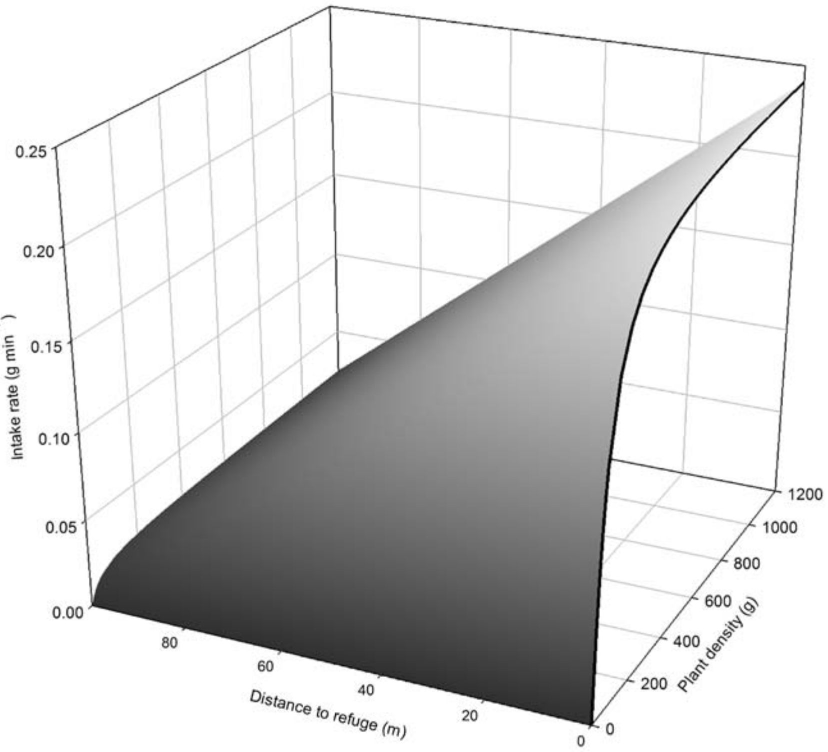

Figure 2. Hypothesized functional response of refuge-living herbivores. Foraging on larger distances from the refuge will result in more time needed for vigilance, and less time left for foraging. This will result in an intake rate that is not only a function of vegetation density (black line; type II functional response,), but also of distance to the refuge (surface).

a unimodal functional response curve, then this will lead to an even stronger pattern formation than if they show an asymptotic functional response.

The present study is dedicated to refuge-living herbivores and their resources, and to the processes that result in the formation of patterns around refuges of small herbivores described above. I focused on the following questions:

- Can avoidance of predation explain gradients in grazing around refuges?
- How do characteristics of the forage, such as nutrient content, digestibility, density, productivity and growth rate influence grazing patterning?

With this thesis I aim to answer these questions, by using ecological experiments and mathematical modelling.

Optimal foraging theory

Throughout this thesis, a mechanistic approach is followed, that is based on optimal foraging theory (Charnov 1976, Stephens & Krebs 1986). In brief, optimal foraging theory states that foraging decisions of animals are based on optimising the trade-off of food intake and feeding costs under certain constraints. In simple situations, this means striving for maximum intake, by choosing locations in which intake rate is highest. As the relation between instantaneous food intake rate and food density is linear or asymptotic (Holling 1959, but see Prins & Olff 1996 and Drescher *et al.* 2006a), animals will generally choose locations where food density is highest. However, by foraging, the animal depletes the food and lowers the intake rate at that location. For this reason, the animal must also find an optimal moment for quitting foraging at a location (Charnov 1976).

Of course, other factors such as social interactions, memory constraints, unpredictability of the forage can also affect foraging behaviour. The greater part of this thesis considers foraging and predation risk within the framework of optimal foraging only, but effects of social interactions on foraging spacing are discussed in chapter 6 of this thesis.

Outline of the thesis

In this thesis wild and domesticated European rabbits are used as a model of refuge-living small herbivores. The European rabbit is well suited for this: it is a small herbivore, lives in a burrow and it is extensively studied (Thompson & King 1994), as it is an important prey species for many animals (Delibes & Hiraldo 1981), popular game and an influential invasive species with a large impact on agriculture and nature (Cook 1987, Moseby *et al.* 2005). Using domesticated rabbits allowed me to do more controlled experiments that would have been impossible to perform with neophobic wild caught European rabbits that are easily stressed.

The conceptual mechanistic model of foraging under predation risk that was outlined above is tested in Chapter 2 by staging domesticated rabbits of different sizes on strips of static (i.e., non-growing) vegetation for 5 weeks.

In Chapter 3 the foraging of refuge-living herbivores is studied on a small timescale: that of instantaneous choices and daytime choices. I wanted to determine in what way quality and quantity of the resource affects spatial patterns in foraging intensity and resulting depletion patterns in the resource. Because quality and quantity of plants are correlated in natural resources, I did experiments in an indoor facility and offered trays of artificial grass pellets that differed in quality and quantity, instead of natural forage. This allowed me to test predictions based on classical optimal foraging theory.

In Chapter 4 I focus on long term interactions between food and forager. On these longer time scales, herbivore grazing can affect biomass, but also digestibility and structure of the vegetation. Also, at these larger time scales plants show variation in growth rate. Free ranging herbivores react to an increase in growth rate by concentrating foraging efforts in small areas when growth rate is high (Vesey-Fitzgerald 1960; Prins, Ydenberg & Drent 1979; Fryxell 1999; Bos, Van De Koppel & Weissing 2004) and move to other locations or switch diet when growth rate decreases. Refuge-living herbivores are forced to stay with their burrow. To determine how refuge-living herbivores deal with this variation in growth of vegetation, I staged pairs or rabbits in sward strips during a full growing season, from April to November. Grazing distribution, vegetation biomass and vegetation growth were measured over this period.

Does foraging from a burrow, and thus being 'stuck' to one area affect population dynamics? To answer this question I use mathematical modelling. In Chapter 5 the conceptual mechanistic model presented in Chapter 2 is implemented in a simulation model. First, the grazing distribution around the refuge and the resulting patterning in the vegetation of a non-reproducing herbivore population are modelled. Apart from a 'normal', type II functional response (Holling 1959), I also implement an unimodal intake rate or type IV functional response, as seen in herbivores foraging on vegetation that increases in complexity and decreases in nutritional value as it is taller (Drescher *et al.* 2006a, Drescher *et al.* 2006b). Additionally, a free ranging large herbivore was added to the model, to study the potential for facilitative interactions in this system.

Space use of animals is not only affected by interspecific, but also intraspecific interactions: food, and other limited resources such as mates or good breeding facilities must be defended (Cowan & Bell 1986, Von Holst *et al.* 2002), which would result in different size home ranges depending on sex and rank of an animal. In Chapter 6 I report of the spatial behaviour of a low density, confined population of wild rabbits.

The risk of being predated upon is expected to be different with different distances to the refuge, but can also differ between habitats. For example, European rabbits prefer the cover of vegetation in the daytime, but open areas at night (Moreno, Villafuerte & Delibes 1996). So, apart from influencing spatial aspects of foraging, predation risk can also influence temporal aspects of foraging. In Chapter 7 I formulate predictions on the temporal distribution of foraging, based on the temporal changes in this habitat preference, and test these by comparing two enclosed European rabbit populations living in different habitats. The differences in habitat are brought about by grazing by cattle: one rabbit population is living in an ungrazed field with tall vegetation; one is living in a grazed field with short vegetation.

In the final chapter, Chapter 8, I give a general discussion of the effects the use of a refuge has on foraging. I also discus the effect that herbivores living in refuges can have on their surroundings: how does the presence of refuge-living herbivores affect an ecosystem, and is this influence different than that of free ranging herbivores?

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Chapter 2

Grazing gradients around refuges of small herbivores are caused by spatial variation in vigilance

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Frank Van Langevelde, Sipke E Van Wieren & Herbert HT Prins

Abstract

Small refuge-living herbivores forage under a spatial constraint: they must return to their refuge after foraging. This results in spatial patterns of vegetation biomass around the refuges of these herbivores. Various theories deal with foraging by refuge or nest living animals, such as central place foraging theory or models that optimise fitness by trading off forage intake and predation, but here we present and test a more parsimonious, mechanistic model that explains the formation of the grazing gradients shown by small refuge-living herbivores. First, we postulate that time spent on vigilance during foraging increases with distance from the refuge. Looking up and scanning for predators requires time that could have been attributed to foraging. As its distance from the refuge increases, the small herbivore will increase its vigilance levels during foraging. Forage intake rate should then decrease with distance. For a maximisation of forage intake, the animal should then concentrate its foraging efforts close to its refuge.

We tested this conceptual model with an experiment with domesticated rabbits and found that vigilance indeed can explain gradients in foraging: on a homogeneous sward, time used for vigilance per time used foraging increased with distance. Following depletion of locations closest to the refuge, the animals shifted to their foraging locations farther out from the refuge. Under an artificially increased predation risk, the animals remained foraging in the same locations, but increased total foraging time and time spent on vigilance.

Introduction

Small refuge-living herbivores must deal with a spatial constraint when foraging: they must return to their refuge after their foraging activities. This means that they can only forage up to a certain distance from that central place. This results in a spatial pattern in grazing pressure and vegetation structure around refuges of small mammalian herbivores, for example in European rabbit (*Oryctolagus cuniculus*; (Farrow 1917; Tansley and Adamson 1925), pika (*Ochotona princeps*; Huntly 1987; Komonen, Komonen & Otgonsuren 2003), hoary marmot (*Marmota caligata*; Karels, Koppel & Hik 2004) and black-tailed prairie dog (*Cynomys ludovicianus*; King 1955). Often, these patterns are described by entering distance from the refuge as a factor in statistical analyses of grazing pressure or biomass measurements. This approach, however does not give insight in the mechanisms that create and shape grazing pressure or vegetation patters around refuges.

Central place foraging theory (Schoener 1971; Orians & Pearson 1979) is a useful concept to explain foraging behaviour of animals from a central point, as shown in starlings (*Sturnus vulgaris*) feeding their chicks (Kacelnik & Cuthill 1990) or beavers (*Castor canadensis*) foraging on trees (Fryxell & Doucet 1991). However, for grazers the resource, grasses and forbs, generally has a continuous distribution, whereas central place foraging theories were developed for animals foraging on discrete food items that are eaten singly, such as seeds, insects or trees. Also, central place theory is based on the assumption that that long travel times or handling times associated with distant food items can outweigh the energetic benefits of obtaining that forage. Travel costs of terrestrial animals are now argued to be negligible when compared to basal metabolic rate (Prins & Van Langevelde, in press). For these two reasons, we argue that central place foraging theory is not suitable for predicting foraging patterns by small refuge-living herbivores.

More recent models of central place foraging assume a maximisation of fitness by trading off forage benefit and predation risk (Brown, 1988), or trading off cost of escape and risk of damage (Ydenberg & Dill 1986). Although the general predictions of these models have been tested in the field with good results (for example Kotler, Brown & Knight 1995), they are based on mechanisms and relations, such as predation rates as a function of distance, that are hard to test or parameterise in the field.

For free ranging herbivores, foraging behaviour has been successfully analysed using optimal foraging theory (Stephens & Krebs 1986): the animal is assumed to maximise its fitness by maximising its harvest rate, selecting patches that yield the highest intake rates.

In this paper, we investigate if this approach can be adapted to refuge-living herbivores by making it spatially explicit. In this way, we want to produce a more parsimonious, mechanistic model to explain the formation of the grazing gradients formed by small refuge-living herbivores.

We predict that the time spent vigilant during foraging increases with the distance from the refuge. As distance from the refuge increases, the small herbivore will need more time to reach its refuge in case of danger. Therefore, the small herbivore must detect the source of danger sooner when venturing farther from safety, so the animal should increase the rate of looking for predators, be it during or between feeding bouts. If this is indeed the case, the ratio of the time that is spent on vigilance to the time that is spent on foraging should increase with its distance from the refuge. Vigilance can influence food intake directly and hence energy gain too, as shown for free ranging large herbivores (Underwood 1982; Fortin, Boyce, Merrill & Fryxell 2004; Illius & Fitzgibbon 1994) and postulated for rabbits (Iason *et al.* 2002): looking up and scanning for predators takes time that could have been attributed to foraging. So, combining vigilance and the functional response, we postulate that the realisable intake rate of a refuge-living herbivore becomes a function of both the vegetation's density and its distance to the refuge. This, of course, will have consequences for the animal's patch choice.

In a situation with a homogeneous resource, animals will stay close to the refuge: the location with lowest vigilance and thus the highest realisable intake. However, because of the grazing of the animal, these locations will become depleted and a resource gradient is formed, with forage density increasing with distance. As foraging on the locations closest to the refuge continues, the intake rate at these locations declines, and eventually the intake rate (per time foraging plus vigilance) will become smaller than that further from the refuge, where more time is needed for vigilance but where intake rate is higher, as vegetation is denser. Consequently, the animal will shift to locations farther away. As both intake rate and energy demand scale with body weight (Shipley, Gross, Spaldinger, Hobbs & Wunder 1994), the costs of vigilance time, expressed in intake rate per body weight, will be the same for animals of difference body size, so small and large animals initially should prefer to forage on the same distances from their refuge. As daily food intake increases with body mass (Shipley *et al.* 1994), depletion and an associated shift to locations farther from the refuge should occur sooner with larger animals.

How do the animals respond to an increase in predation risk in this environment with a resource gradient? The animals can follow two possible strategies to optimise their foraging under such an increase in predation risk: shifting to safer locations or staying where it is and increasing time that is spent on vigilance. The safer locations near the refuge however have a lower grass height, and as intake rate increases with sward height (Iason *et al.* 2002), instantaneous intake rate will be lower closer to the refuge. Staying on the more distant locations will result in a higher intake rate within feeding bouts, but spending more time on vigilance. So, will the refuge-living foraging small herbivores maximise their intake rate within feeding bouts, or minimise the total time that is spent on eating, i.e. foraging plus vigilance? Are small refuge-living herbivores rate-maximisers or time-minimisers? If they maximise their intake rate, an increase in predation risk will not affect the distance on which the animals forage will and will increase feeding time. If they minimise their feeding time, an increase in predation risk will result in foraging closer to the refuge, and a similar feeding time.

Thus, we predict the following for refuge-living herbivores:

1. The vigilance to foraging ratio increases with distance of the animal to the refuge.
2. The animals forage on locations with low vigilance to foraging ratios.
3. Small and large animals do not differ in the distance from the refuge at which they forage when foraging on a homogeneously distributed resource.
4. The distance at which animals are active increases in time and with body size, as resources close to the central place are depleted.

To test these predictions, we performed an experiment with three breeds of domesticated rabbits *Oryctolagus cuniculus*, a refuge-living small herbivore, by staging them on a homogeneous sward with an artificial refuge. We manipulated perceived predation risk by playing recorded calls of buzzard (*Buteo buteo*), an indigenous rabbit predator. Calls of birds of prey are known to alter the perceived predation risk of small mammals (Hendrie *et al.* 1998).

Methods

In a *Lolium perenne* pasture at Achterberg, The Netherlands (51°59’36” N, 5°34’53” E), twelve strips of 3x50 meters were fenced off. Wooden crates, to which the animals were habituated before the experiment, were placed on one side of the strips to serve as refuge. To avoid effects of layout direction, the strips were located back-to-back in two groups of six (Figure 1). Each strip, apart from the first meter, was fenced with mesh wire, to keep the view open and the rabbits feeling “vulnerable”. The first meter and back of each strip was lined with cloth. Average ± SD grass height at the start of the experiment was 8.4 ± 1.9 centimetres.

Twelve adult female rabbits of three breeds, four Polish rabbits (1.2 kg), four Dutch rabbits (2.2 kg) and four Checkered Giants (5 kg) were used. They were placed individually in the fenced-off strips from 7:00 hours until 18:00 hours for four days a week, for five weeks. Every fourth day, increased perceived predation risk was

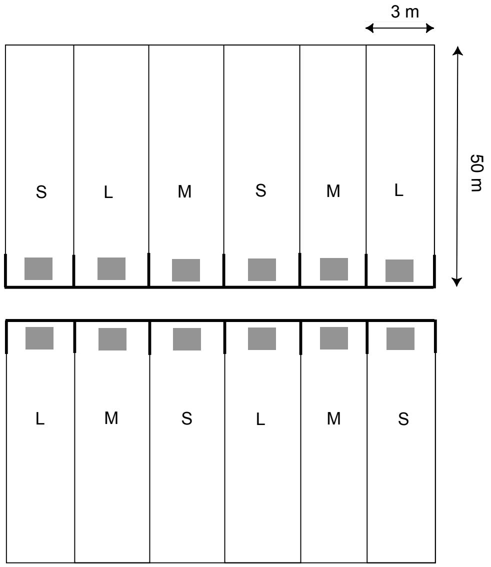

Figure 1. Setup of the experiment. Thin lines represent fences, thick lines cloth. The blocks stand for the artificial refuges. S: small rabbits (Polish), M: medium rabbits (Dutch), L: large rabbits (Checkered Giant).

simulated by playing recorded buzzard sounds for 15 minutes per half hour.

Behaviour was recorded using focal sampling: every 30 minutes each animal was observed for 60 seconds and location and behaviour logged on a handheld computer (Psion with Observer 3.0, Noldus Information Technology bv., Wageningen, The Netherlands). We collected the behaviour as mutually exclusive states feeding, vigilance, moving, resting and other (grooming, digging, etc). In the analysis, foraging, vigilance, moving, and other are considered as active behaviour and resting as inactive. Location of the animals was logged in 2 meter intervals. If an animal moved from one distance interval to another during the scan, the observation was split into two observations.

Before the start of the experiment and after every four-day-block, we measured grass height every 2 meters in each sward strip and in four control strips using the drop disc method (Stewart *et al.* 2001). The experiment ran from the 13th of October until the 17th of November 2003. In this time, grass does not grow.

As behavioural data and changes in grass height were not normally distributed, they were analysed using generalised linear models with log linear link functions and Poisson distributed error terms (McCullagh & Nelder 1983) with generalized estimating equations (Liang & Zeger 1986) as the data consist of repeated measurements of the same animals or sward strips.

The ratio between vigilance-foraging ratio was calculated per observation and only those observations in which the animal was foraging (i.e., foraging time was not zero), were used. Sampling units for these tests were the scans. For the analyses of daily time budget, fractions of time were used, as the number of observations was not equal over the days.

A possible but unwanted effect could have been caused by the transparency of fence: the animals could see each other when foraging, and could share predation avoidance by foraging close together and sharing the time scanning for predator between them. To test for this effect we calculated the Spearman's correlation coefficient of locations between 6 pairs of neighbouring rabbits and 6 pairs of rabbits that could not see each other. The correlations between locations of neighbouring pairs were not significant for all but one pairs ($\alpha = 0.05$). There was no difference in correlation coefficients between pairs of rabbits that could and that could not see each other (Mann-Witney U Test, $U_{12} = 14$, $p = 0.589$). All analyses were done in SAS release 8.2 (SAS Institute Inc, Cary, NC, USA).

The experiment was evaluated and permitted by the Institutional Animal Care and Use Committee of Wageningen University (entry number 2003173c, experiment code 2003136).

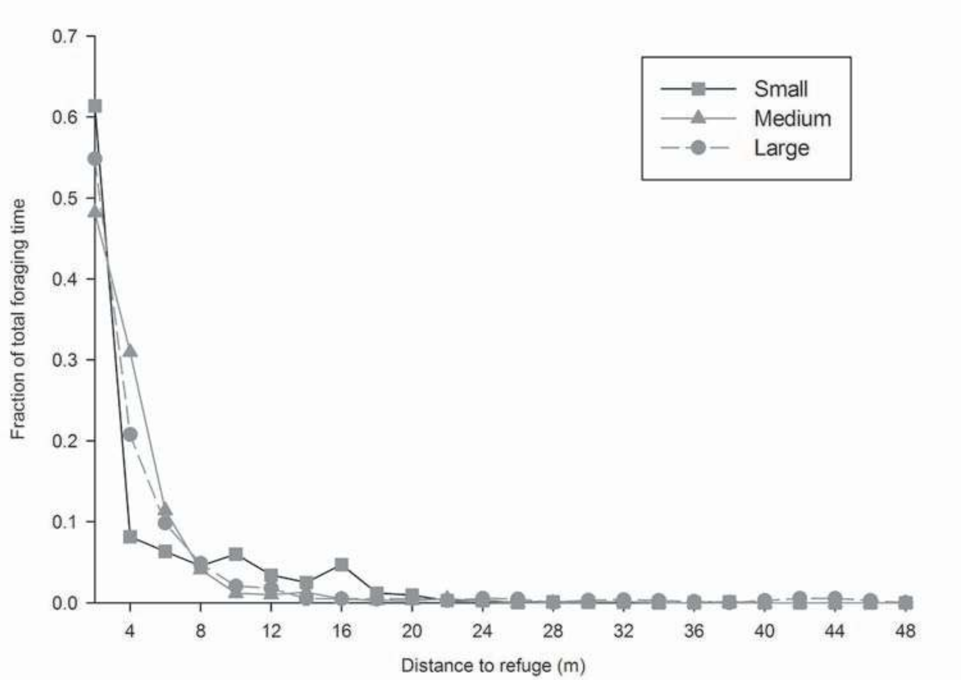

Figure 2. Proportion of time spent foraging (all observations added per individual) against distance from the artificial refuges for small (black solid line, cubes), medium (grey solid line, triangles) and large (grey dashed line, circles) sized rabbits during the behaviour scans. Foraging is almost exclusively done close to the refuge.

Results

The animals behaved as central place foragers: locations showed a strong decline in time being grazed as their distance from the refuge increased (Figure 2). Vigilance-foraging ratio increased with distance from refuge ($Z_{1, 1855} = 3.54$, $p<0.01$), being between on average 0.2 and 1 from 2 to 20 meters from the refuge, and rising up to 4 beyond that distance. Neither size nor increased perceived predation risk resulted in an elevation of the vigilance-foraging ratio. The animals spent less time on locations as the vigilance-foraging ratio corresponding with that location increased ($Z_{1, 931} = -5.05$, $p < 0.01$).

During the experiment, grass height in the strips increased with distance from the refuge, but decreased as the experiment ran (Figure 3; week: $Z_{1, 1872} = -9.83$, $p < 0.01$; distance: $Z_{1, 1872} = 7.41$, $p < 0.01$). The size of the rabbits did not influence the effect they had on the grass height in the grass strips at the end of the experiment; grass was not depleted more if the animal grazing the sward strip was larger.

The distance from the refuge at which the rabbits were active increased during the experiment ($Z_{1, 2710} = 5.56$, $p<0.01$): the rabbits selected locations farther from the refuge as the experiment ran, staying on a median distance of 3 meters from

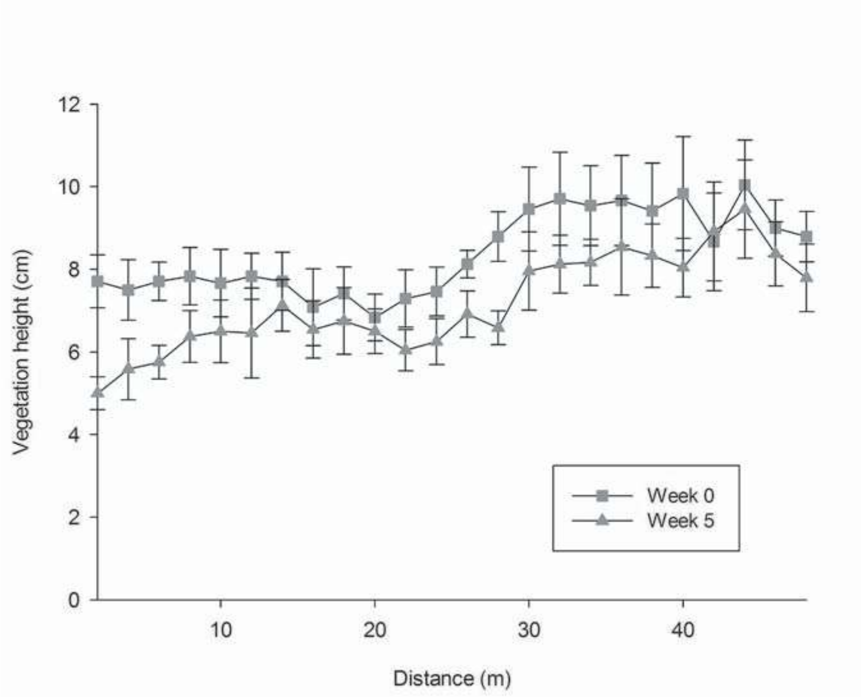

Figure 3. Average ± 95% CI of grass height as a function of distance from the refuge, at the start of the experiment and after week 5, at the end of the experiment. Depletion of grass is strongest close to the refuge.

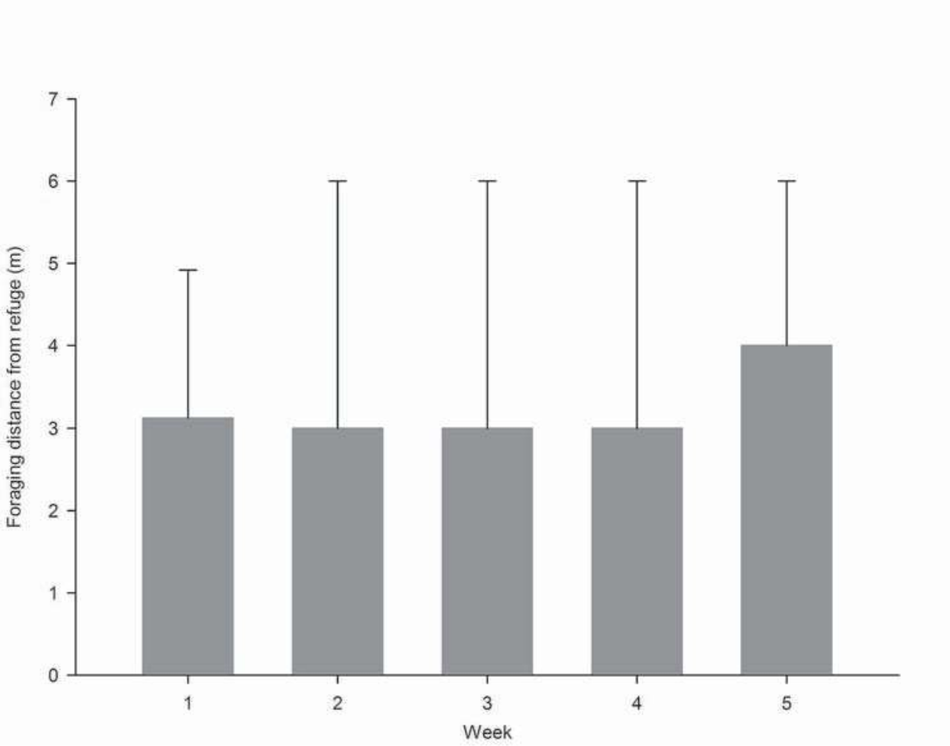

Figure 4. Median and third quartile of the distance from the refuge on which active behaviour was shown, per week. The distance from the refuge at which the rabbits were active increased over the weeks (GLM, p<0.01, n=2710).

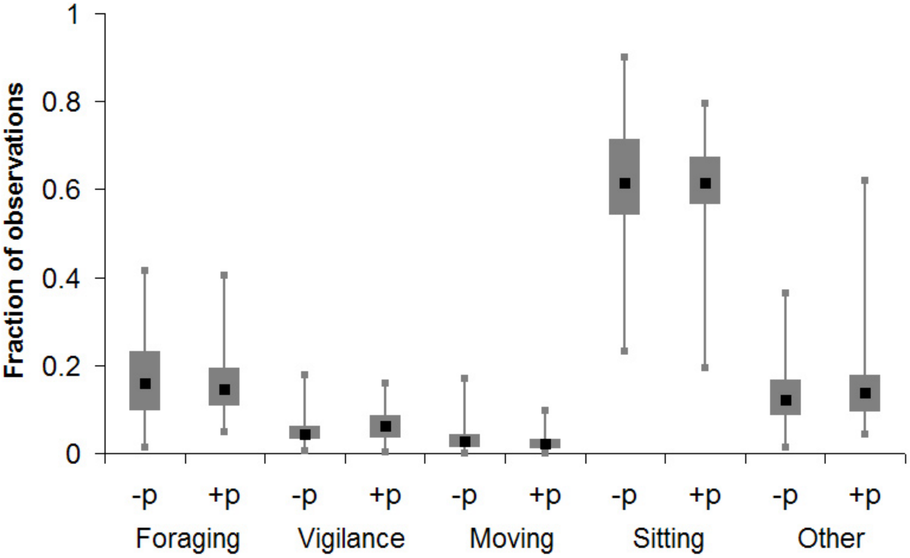

Figure 5. Box plot of the proportion of time of each day that was spent on the different behaviour types. Data from the whole experiment and all animals were lumped for this Figure. p-: no increased predation risk, p+: increased predation risk. An increase in perceived predation risk increased the fraction of time spent on vigilance (GLM, p<0.01, n=228).

the refuge at the start of the experiment, and on 4 meters in the 5th week (Figure 4). Neither rabbit size nor increased perceived predation risk affected this distance.

Over the whole experiment, the animals spent 17% of the total time they were observed foraging, 5% on vigilance, 13% moving, 61% resting, and 13% on other behaviour. The percentage of time spent on vigilance over the total active time (any behaviour but resting) was 25%. The fraction of the day that was spent foraging ($Z_{1, 228} = 0.73$, $p=0.08$) increased with animal size. The fraction of the day used for foraging and being active was not affected by increased perceived predation risk, but under increased predation risk, the fraction of time spent on vigilance was larger ($Z_{1, 228} = -2.81$, $p<0.01$) (Figure 5).

Discussion

We showed that the ratio of time that is spent on vigilance to the time spent foraging increases with an increasing distance from the refuge (prediction 1). This means that with increasing distance, vigilance time per foraging time increased and thus the intake rate, when calculated over the total act of eating, i.e. foraging interspaced with vigilance, became smaller. The rabbits behaved as central place foragers and attribute most of their foraging time close to their refuge, on sites with low vigilance (prediction 2). So, vigilance acts as a modifier of forage intake, a parsimonious mechanistic model explaining gradients of foraging pressure around refuges of small herbivores.

Body size of the rabbits did not affect the change in distance from the refuge on which the animals foraged (prediction 3). Also, the differences in body size did not result in differences in sward height at week 5, in contrast to prediction 4: there was no difference in the degree of depletion between swards grazed by larger and smaller animals. A likely explanation for this is that the range of body sizes (the maximum we could attain within this species) was not wide enough to result in very different intake rates and thus in difference in depletion. If the depletion is not very different between the different sized animals, no differentiation in foraging locations will occur, or the difference will be too small to be detected after 20 days of grazing. Still, grass height decreased as the experiment ran, and all animals shifted their grazing to locations farther away as the experiment ran.

Under an overall artificial increase in predation risk, the animals kept foraging at the same distances from the refuge and did not sacrifice time needed for foraging. They spent the same fraction of the day foraging, and the same fraction of time on active behaviour with or without increased perceived predation risk, but spent more time on vigilance. So, it seems that the animals base their choice for foraging locations solely on instantaneous intake rate within feeding bouts. This is in line with Bakker, Reiffers, Olff & Gleichman (2005), who showed that wild rabbits visited locations near their burrow more than distant locations, that plots treated with mink pellets and control plots were visited equally, but the animals increased their visits when nitrogen content of the vegetation was artificial increased. This indicates that rabbits are rate-maximisers.

Our animals attributed lower percentages of daily time budget for vigilance than in other studies of free-living rabbits; the rabbits in our experiment spent 25% of their active time on vigilance, while (Roberts 1988) reported around 40% vigilance in active rabbits. This may be because our animals were domesticated, as domestication can lead to a decrease in vigilance (McPhee 2004; Price 1999). However, we expected that the effect of domestication on the outcome of experiment would be smaller than the effects of neophobia and confinement that would have occurred had we used wild rabbits in our experimental setup.

Our experiment showed that for small refuge-living herbivores such as the rabbit, the profitability of a location for foraging depends not only on the grass height or biomass on that location, but also on its distance to the refuge. In a situation with an initially homogeneous distribution of the resource, the animals prefer to forage on locations with a low vigilance-foraging ratio, and therefore a high intake, i.e. close to the refuge. When these locations are depleted, it will move outward. This should result in the formation of circle with short grasses or barren ground around the refuge, followed by a ring of grasses and then an area of hardly grazed vegetation. Such patterns are described for rabbit burrows (Farrow 1917).

When the resource quality is distributed heterogeneously, the system will be more complex, as profitability of a location becomes a function of not only distance and resource quantity but also of resource quality. A good quality location far from safety may still be preferred over a location of low quality closer to the refuge, or the two locations may even be perceived equal in profitability. Assuming that the animals distribute their foraging efforts according intake rate and vigilance costs, exact hypotheses on preferred grazing locations and grazing pressure distributions around the refuge can be formulated and tested using the mechanistic model presented in the present study.

In this paper, we have shown that vigilance determines space use of the rabbit, a refuge-living small herbivore: a more parsimonious alternative to the existing models for central place foraging herbivores. Foraging decisions and distributions of grazing pressure are not only affected by forage biomass, but also by distance from the refuge, as a proxy for vigilance modulating intake rate. Foraging farther from the refuge resulted in more vigilance time per foraging time, resulting in less foraging efficiency. This decrease is of great influence on the distribution of grazing effort around the refuge and thus on spatial structure of the grazed resource.

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Chapter 3

Resource quality and quantity shape the spatial distribution of foraging of herbivores living in refuges

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Abstract

Small refuge-living herbivores must optimise costs and benefits of foraging under spatially variable predation risk. We determined how the short term and long term foraging patterns of these herbivores are affected by the quantity and quality of their food, using predictions from optimal foraging theory.

We tested our predictions by offering trays of food pellets at various distances to rabbits, in treatments ranging from low quality and small quantity to high quality and large quantity pellets. Rabbits were allowed to forage freely on these trays for 7 hours.

In the first hour of the trial, the rabbits foraged almost exclusively on the optimal tray, where intake rate was highest, with the other trays being sampled in a few trials.

In the long term, depletion of the nearest patches and subsequent foraging in farther patches resulted in a foraging gradient. This in turn resulted in the formation of spatial patterns in food density. These spatial patterns were affected by food quality and quantity: they were more skewed towards the refuge as the initial food quantity in the trays was larger and the quality of the forage was higher. Long term foraging choices followed our predictions even though there was no functional response to the amount of food. We suggest that the animals did not base their decisions on the experienced intake rate itself, but used the amount of pellets in the tray as a proxy for intake rate.

Introduction

Small herbivores living in refuges must, like all foraging animals, optimise the benefits and costs of foraging (Stephens & Krebs 1986). For these animals, an important and spatially variable cost of foraging is predation risk. Even when actual predation does not occur, the perceived threat of it can influence behaviour (Lima & Dill 1990), causing the animals to become more vigilant for predators. This helps to avoid predation, but results in loss of foraging time (Fortin 2004). In refuge-living herbivores, vigilance increases with distance to the refuge (Chapter 2 of this thesis). So, even without actual predation, there is a spatially explicit cost of foraging for these refuge-living animals.

Optimal foraging theory (Stephens & Krebs 1986) postulates that animals increase their fitness by maximising food intake while minimising the costs of obtaining this food. Using optimal foraging theory to formulate predictions, we test how refuge-living small herbivores distribute their foraging effort over space. Also, the effects of forage quality and quantity on the maximisation of food intake, and thus foraging patterns, are studied.

Instantaneous choice

A simple approach to optimal foraging by refuge-living herbivores in the short term is to view this situation as an optimisation of diet, using the optimal diet model (Schoener 1971) . The optimal diet model predicts that a food item is either neglected or taken, the so called zero-one rule. Diet items are ranked by the ratio of energy gain per forage activity to handling time, and inclusion of an item of rank x in the diet depends on the profitability of the patches with higher ranks (Stephens & Krebs 1986). In a homogeneous distribution of resources, i.e., when every item consists of the same quality and quantity of the resource, the only difference in food quality is expected to be the costs of vigilance or the risk of being predated: the closer the food item is to the refuge, the more profitable. The model predicts that the animals will forage only on the most optimal food item, in this case the food items closest to the refuge.

However, a strict binary use-non use pattern of food type or types is seldom observed: in many studies, partial preferences are found (for example Rechten, Avery & Stevens 1983; Jones 1990; Hassall & Lane 2005). Various explanations for this have been put forward. Firstly, it is suggested that researchers have measured on the wrong temporal scale: for example, while the zero-one rules apply to short term optimisation of foraging, they may need to be tested on a long(er) term diet. A second explanation is that the assumption that animals are optimal (i.e., have perfect knowledge of food value and distribution) is flawed: animals may need to sample food in their surroundings to be able to construct an optimal diet, because of low memory capacity (Belisle & Cresswell 1997). In this situation, however, the food type must be so rare that is it is forgotten before it is encountered again. One of the characteristics of refuge-living herbivores is that they stay in the same, relatively small area for a long time. Therefore, it is not likely that these animals forget the spatial distribution of the food in their environment. A third explanation is that animals sample food items in order to track changes in their value. Sheep, for example, sample more during foraging when spatial variation of food distribution increases (Hewitson *et al.* 2005). If sampling indeed takes place and patches are stable, the suboptimal food items should be sampled once: this should provide ample information on how valuable they are, which is a prediction that is easy to test.

Long term foraging patterns

In non-instantaneous foraging choices, like decisions made over a day, depletion starts playing a role. For predicting foraging choices on this time scale, the marginal value theorem (Charnov 1976) is more suitable. This theorem focuses on food patches and takes into account that the intake rate in a patch usually declines as the remaining food abundance declines: the functional response (Shipley *et al.* 1994). An animal should forage on the patch of highest intake rate, but depart to another patch when the intake rate in the patch under use becomes lower than the intake rate at any other patch minus the loss of intake due to travel to reach this patch. Brown (1988) adapted the marginal value theorem for the prediction of foraging patterns by risk prone foragers, such as central place foraging herbivores. The animal leaves a patch when the rate of intake at this patch is lower than the sum of energetic costs, predation costs and missed opportunity costs at this patch. The approach of Dekker (Chapter 2 of this thesis) is more mechanistic and could be seen as an adaptation of the Marginal Value Theorem. Dekker (Chapter 2 of this thesis) found that the time needed for vigilance during foraging increases with the distance of the central place foraging herbivore to its refuge. The total intake rate, be it expressed as food or energy, is then a function of the forage density at a patch and the distance of that patch to the refuge. The animal should leave the patch under use when the product of intake rate and the fraction of time used for vigilance is lower than that of any other patch. Travel costs are assumed to be negligible in the spatial scale on which central place foraging herbivores forage. So, both Brown's (1988) and Dekker (Chapter 2 of this thesis) approaches predict that foraging by a central place foraging herbivore will result in a spatial pattern of forage that is depleted to so called giving up densities (GUDs, Brown 1988). When vigilance, or costs of predation, increases with distance to the refuge, a gradient of increasing densities of food with distance to the refuge should be the result. It is important to note that GUDs are not constants: they depend on the resource abundance in surrounding patches.

On larger time scales, quality and quantity of the resource in a patch become factors in patch choice patterning. As instantaneous intake rate on a single foodstuff declines when the amount of food in the patch becomes lower (Searle *et al.* 2005), the GUD will be reached sooner when patches contain smaller quantities of forage. In Brown's (1988) approach, a lower quality resource means that the intake rate of energy will be lower than the energetic costs, costs of predation and costs of missed opportunities sooner, resulting in higher GUDs (Brown, Morgan & Dow 1992). In Dekker's (unpublished) mechanistic approach, lower resource quality will also result in higher GUDs. When food quality is lower, the difference in attainable energy due to vigilance between patches becomes relatively smaller. So, when foraging on lower quality resources, the differences between GUDs among neighbouring patches should be smaller. When the animal forages on lower quality resources, it will also need larger amounts, and will therefore deplete patches to lower GUDs.

Our predictions are that refuge-living small herbivores foraging on homogeneously distributed resources [P1] will initially forage only on the nearest patch(es) to the refuge, [P2] will sample the distant patches maximally once, and [P3] will only forage on more distant patches when the patch closest to the refuge is depleted. [P4] Longer foraging will result in an increasing density of resource with increasing distance to the refuge. [P5] This gradient in density will be less skewed towards the refuge when initial resource quantity is smaller, and [P6] this gradient will be less skewed towards the refuge when resource quality is lower.

To test these predictions we set up an experiment using the domesticated rabbit *Oryctolagus cuniculus* L. as a model for small central place foraging herbivores. We created an environment of less and less profitable patches by offering these animals a homogeneous distribution of resource quality and quantity in five trays at different distances from the refuge. To avoid problems with the correlation between quality and quantity that are usually present in vegetation, we used food pellets of two different qualities. This way, we set up an experiment offering forage of the same quantity, but different quality, and vice versa.

Methods

Four domesticated adult female rabbits of the Dutch breed, each weighing 1.5 kg, were staged individually in indoor enclosures of 3 m x 15 m. On one side of each arena an artificial burrow was placed, consisting of a 1.5m x 1.5 m wooden box. To avoid the effects of preference for the direction of the rabbits, the side on which the refuges were placed were different. Five feeding trays with 3 meters between each were fixed to the floor, the closest being 1.5 meters from the refuge. The animals could not see each other. Light was provided from 9:00 to 18:00. Water was offered ad libitum. The animals were habituated to the enclosures for 3 weeks before the start of the experiment.

Food pellets of high quality and low quality were made of respectively 96% ground *Lolium perenne* and 4% molasses and 66% ground *Lolium perenne*, 30% wood cellulose and 4% molasses (Research Diet Services BV, Wijk bij Duurstede, The Netherlands). These two pellet types were checked for a difference in digestibility using percentage neutral detergent fibre (%NDF) as an indicator. The pellets were ground and %NDF of dry matter was determined using the ANKOM filter bag procedure (ANKOM Technology, Macedon, NY, USA) with omission of the sodium sulphite and the heat resistant α-amylase, and with Neutral Detergent Solution prepared following Goering & Van Soest (1970). Digestible energy content of the two food types was calculated using data from Fernandez-Carmona, Cervera & Blas (1996): DE (MJ kg DM^{-1}) = 18.5 – 0.18 % NDF ($F_{21,1} = 43.10$, $p < 0.001$, $R^2 = 0.67$).

Daily requirements for both resource types were determined by offering the animals pellets ad libitum, in the tray closest to the refuge. The animals ate 100.9 ± 33.5 SD grams of high quality pellets and 129.4 ± 15.9 SD grams of the low quality pellets. These amounts were used to ensure the animals could gather their required food intake during the experiments.

The rabbits were offered a homogeneous distribution of pellets in the trays: 30 grams (small quantity) or 70 grams (large quantity) of either high quality or low quality pellets was offered. The amount of pellets offered in the entire enclosure was always enough to fulfil the daily requirements.

The animals were habituated to a new treatment for two days. On the third day, the position and behaviour of the animals were logged continuously on a handheld computer with observation logging software (The Observer 1.0, Noldus BV, Wageningen, the Netherlands) during the light period, from 9:30 to 17:30. The amount of time being vigilant during a foraging bout was measured at each tray where the animal ate, for two minutes. Vigilance was defined as stopping eating and looking up, or flexing ears. Every hour, the amount of pellets remaining in each tray was weighed. The animals were kept in their enclosures for 24 hours a day.

The experiment was evaluated and granted permission by the Institutional Animal Care and Use Committee of Wageningen University (entry number 2004099b, experiment code 2004123).

Data analysis

Time used for vigilance and amounts eaten after one and eight hours were not normally distributed. For this reason, we used a Kruskall-Wallis test followed by Scheffe's post hoc test, to test for differences between trays in the time used for vigilance the amounts eaten. To obtain an objective measure of the shape of distribution of median amounts eaten after eight hours at the trays, skewness of this distribution was calculated for each treatment. Distributions with positive skewness have long right tails; distributions with negative skewness have long left tails. Skewness of more than twice the size of its standard error indicates deviations from symmetric distributions.

To test for a functional response in food intake rate to food quantity present in the tray, intake rates for both types of pellets in the tray were calculated from the observed foraging times and the measured amounts eaten. The average of food present before and after the hour of foraging was taken as food quantity present. We tested for the presence of a linearly increasing (type I) or a logistic (type II) functional response to this food quantity using regression on square-root transformed intake rates. We also tested whether intake rate increased or decreased with increasing distance to the refuge using linear regression on square-root transformed intake rates. Differences in intake rate between treatments were tested using a median test.

Results

The two types of food pellets were different in quality: high quality pellets contained 53 % NDF; low quality pellets contained 66 % NDF. These values are equivalent to digestible energy contents of respectively 9.0 kJ per g dry high quality pellets and 6.5 kJ per g dry low quality pellets. The animals could differentiate between the pellets: when offered both types in abundance, the animals ate the high quality pellets and neglected the low quality pellets. This was probably by taste: the first author could taste differences between the two types, with the low quality pellets having a more woody and dusty taste. Also, the high quality pellets were darker in colour than the low quality pellets.

Animals used more time for vigilance during a feeding bout when foraging at the trays farther from the refuge than when foraging from the nearer trays (Figure 1, $\chi^2_{4,26} = 16.75$, $P = 0.002$). Intake rate decreased with distance to the refuge ($R^2 = 0.12$, $F_{1,118} = 15.55$, $P < 0.001$), but there was no significant linear or logistic relation between amount of pellets in the tray and the intake rate in any of the treatments. Intake rate was similar in the different quality-quantity treatments. Average intake rate ± 95% C.I. was 0.9 ± 0.26 g min^{-1}.

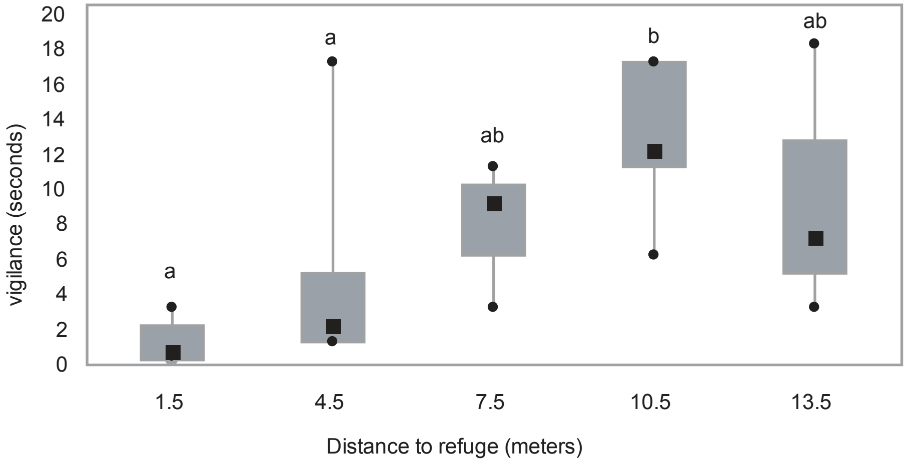

Figure 1. Box plot of the time used for vigilance in 120 seconds of feeding per tray. Differences in letters indicate significant difference in time used for vigilance during foraging (p<0.05).

Short term choices

In the first hour, pellets were almost exclusively taken from the tray closest to the refuge in all treatments (Figure 2). Amounts eaten from the trays were significantly different within the high quality – small quantity treatment ($\chi^2_{4,20}$ = 16.00, P = 0.03), the low amount – low quality treatment ($\chi^2_{4,20}$=9.14, P = 0.058) and the low quality – large quantity treatment ($\chi^2_{4,20}$ = 12.05, P = 0.02). In 4 of the 20 trails, the animals foraged for one bout at other trays than the optimal first one. In 1 of the 20 trails, the animal visited a non-optimal tray twice.

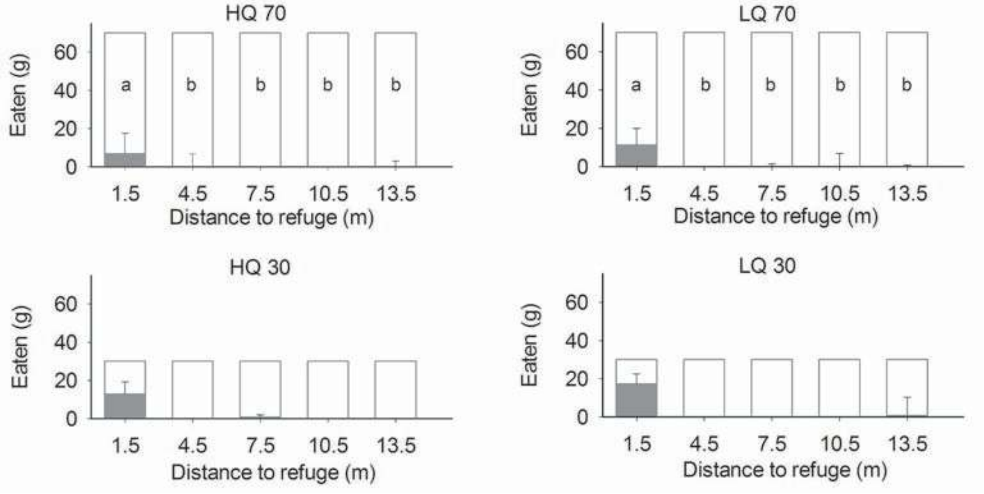

Figure 2. Median + 75% percentile of amounts of pellets eaten after 1 hour of ad libitum foraging in experiment 1. White bars are the amounts offered, grey bars the amounts eaten. Different letters stand for significantly different amounts of pellets eaten (p<0.05). LQ: low quality pellets, HQ: high quality pellets offered. 30: 30 g pellets offered per tray. 70: 70g pellets offered per tray.

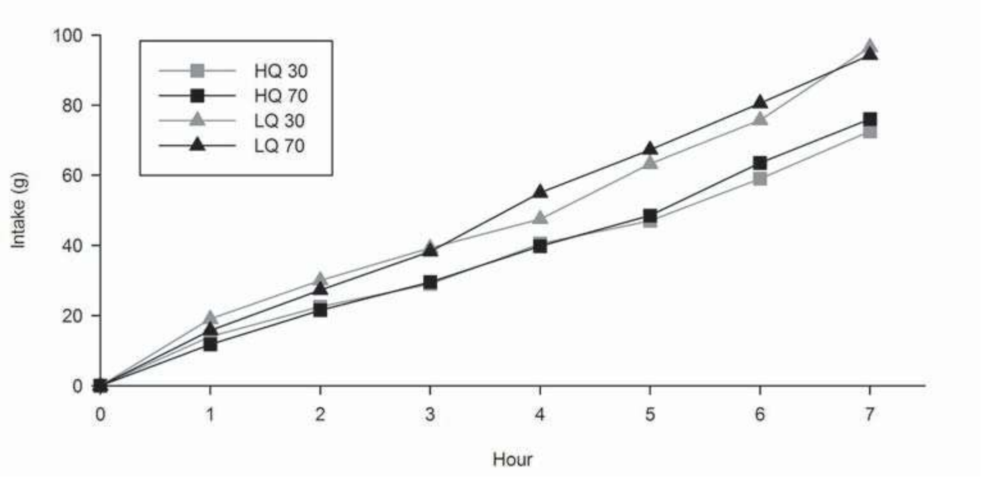

Figure 3. Cumulative mean amount of pellets eaten by the animals, per hour. LQ: low quality pellets, HQ: high quality pellets offered. 30: small quantity of 30 g pellets offered per tray. 70: large quantity of 70g pellets offered per tray.

Long term foraging patterns

After 7 hours of foraging, there were significant differences in the amount of pellets eaten between low quality and high quality treatments (mean ± SD of 74.3 ± 11.2 gram versus 95.4 ± 18.5 gram, $F_{1,12} = 6.60$, $P = 0.03$). However, the animals ate at the same rates and the same amounts from all trays, whether a large or a small quantity of pellets per tray was offered (Figure 3).

After 7 hours, the amounts eaten showed a grazing gradient skewed to the burrow for large quantity offered (Figure 4). This skew was more pronounced as the treatment consisted of both higher quality and larger quantity. GUDs, the amounts left in the trays were significantly different between trays in the high quality-small quantity treatment ($\chi^2_{4,20} = 10.51$, $P = 0.03$) and the high quality-large quantity treatment ($\chi^2_{4,20} = 10.60$, $P = 0.03$): in the treatment with high quality-large quantity treatment, the majority was eaten from the closest tray, while this division was less pronounced in the low quality-large quantity treatment. In the high quality-small quantity and the low quality- small quantity treatments, the amount the animals left in the trays was not significantly different. Skewness of the division amount left in the trays after 7 hours of foraging was skewness = -2.15 for high quality-large quantity, skewness = -2.16 for low quality- large quantity, skewness = -.71 for high quality- small quantity and skewness = 1.17 for low quality - small quantity offered. In all cases, standard error of skewness was 0.91, so only the first two treatments showed a significant departure from symmetry.

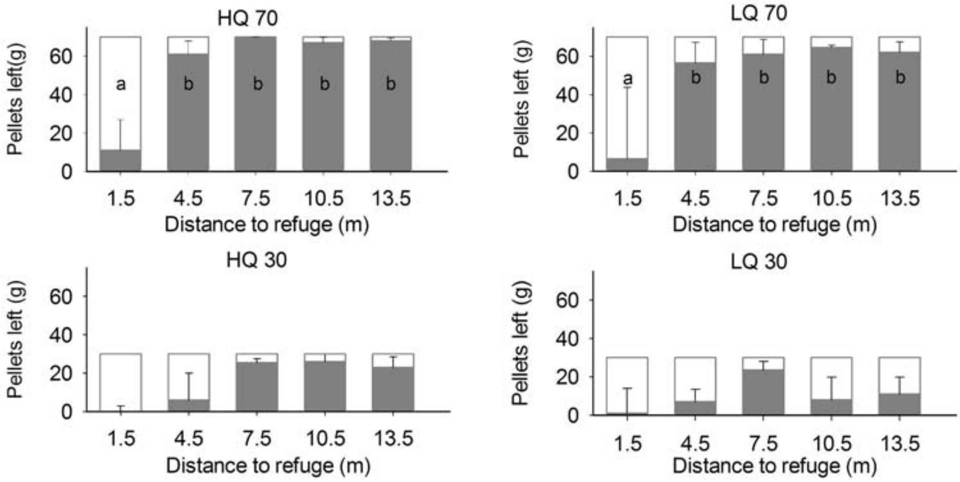

Figure 4. Median + 75 percentile of amounts of pellets left in the trays after 7 hours of ad libitum foraging in experiment 1. White bars are the total quantities offered in each tray, grey bars the amounts eaten: therefore the white area above the grey area in each bar is the giving up density. Different letters stand for significantly different amounts of pellets left ($P<0.05$). LQ: low quality pellets, HQ: high quality pellets offered. 30:30 g pellets offered per tray. 70: 70g pellets offered per tray.

During each trial, all animals switched from the nearest, most optimal tray sooner or later (Figure 5). This switch from the optimal closest tray to suboptimal food trays was made more quickly when the quantity and quality offered was lower: in the 2nd hour in low quality-small quantity treatment, in the 4th hour in high quality - small quantity treatment and the low quality -large quantity treatment, and only in the 6th hour at the high quality - large quantity treatment (Figure 5). The amount of pellets left in the nearest tray also was larger at the moment of departure to another tray when quality and quantity offered is lower (Figure 5).

Discussion

The time that was spent on vigilance during a foraging bout increased with distance to the artificial refuge, which suggests that the animals felt less safe when they were farther from the refuge. This resulted in an intake rate (including time used for vigilance) that declined with distance to the refuge. However, the method used (observations of behaviour as states) may have been too crude to detect large differences in intake rate. The increased time for vigilance with greater distance to the refuge resulted in decreased intake rates the further away the animals were to the refuge. So, our aim of offering a gradient of less profitable patches with distance to the refuge was met. The animals showed an intake rate that was independent of the

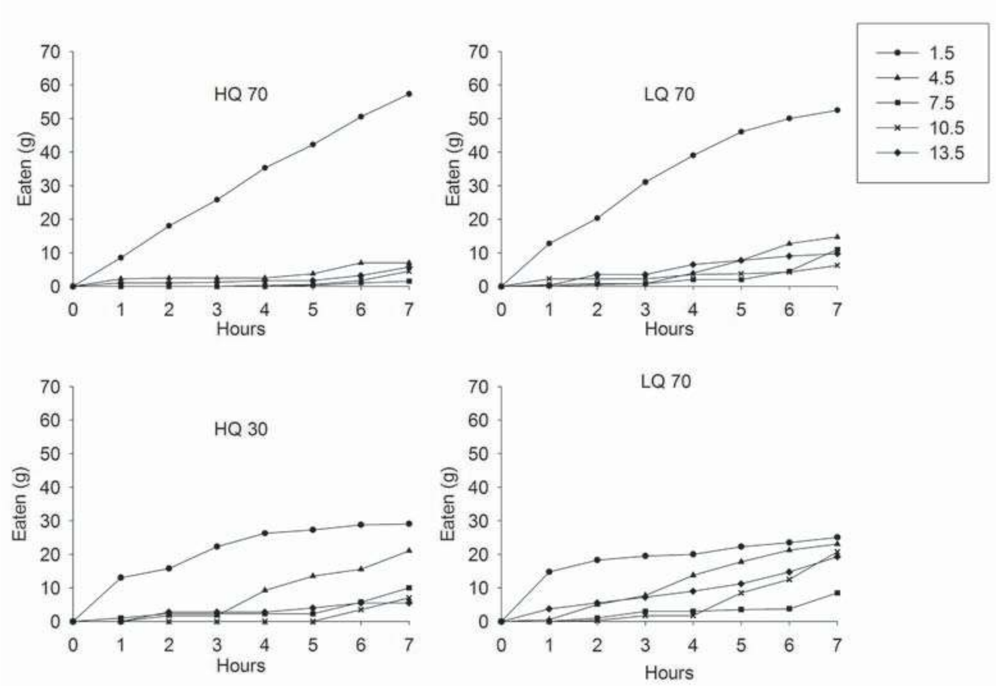

Figure 5. Average cumulative amount of pellets eaten per tray per hour. Numbers in the legend refer to distance from tray to the refuge in meters. LQ: low quality pellets, HQ: high quality pellets offered. 30: 30 g pellets offered per tray. 70: 70g pellets offered per tray.

amount of food offered.

In the short term, in the first hour of foraging, the animals followed a zero-one rule, constructing an optimal diet consisting of the closest tray (P1), with additional sampling of one or more patches in some of the trials (P2). In one of the 16 trials, a tray was visited twice by the animal during the first hour: this animal 'over sampled'.

The animals switched to suboptimal trays before the optimal tray was fully depleted, in contrast to prediction P3. This switch happened sooner as the quality offered was lower or quantity offered was smaller. A forager should leave a patch when the rate of intake at this patch is lower than the sum of energetic costs, predation costs and missed opportunity costs of foraging (Brown 1988) or when the product of vigilance time costs and harvest rate are lower than at surrounding patches. However, these predictions should only apply when there is a saturating functional response of resource intake relative to resource density. On the food type used in our study, the functional response was a constant; independent of the amount of pellets in the tray. Therefore the GUD is zero and the animals should have foraged on the patch with lowest vigilance costs until it was totally depleted. Still, the animals left patches before they totally depleted them and left it sooner when the amount of food offered was lower. We therefore propose that these animals do not base their decisions on the experienced intake rate itself, but use available biomass as a proxy for intake rate.

On natural resources, instantaneous intake rate does indeed increase with food density for rabbits and many other grazers (Iason *et al.* 2002), Shipley *et al.* 1994) and one can imagine that when foraging on a natural resource, the use of biomass as a proxy for intake rate is an efficient way of estimating profitability of a patch, rather than measuring the instantaneous intake rate for that patch by foraging on it for some time. In our experiment, the animals did sample, but apparently sampled food quality and did not calibrate the intake rate expected from the available amount of food with the actual intake rate. So, by offering a foodstuff of which the intake rate does not decline with ‘standing crop’, we provided false clues for optimality. If this hypothesis is correct, offering a more natural foodstuff, such as grass sods, in a similar setup and thus providing ‘true’ clues should result in optimal foraging decisions by the animals, without the animals sampling more than once.

After the animals had foraged for 7 hours, a grazing gradient was formed that was skewed towards the burrow (prediction 4). This is a pattern seen in many species foraging from a refuge (European rabbit *Oryctolagus cuniculus*, Farrow 1917, Tansley & Adamson 1925; pika *Ochotona princeps*, Huntly 1987; rock hyrax *Procavia capensis*, Kotler, Brown & Knight 1999). In the present study, the skewness towards the refuge of foraging impact and thus of food density was weaker in the low quantity (prediction 5) and small quality (prediction 6) treatments.

Animals left patches at higher densities, when low quality pellets were offered. This indicates that GUDs are higher when foraging on low quality patches. The animals seemed to forage from different trays, moving in an order of riskier and riskier trays, until a certain ratio of remaining densities between trays was reached (Figure 5). From then on, trays were depleted in such a way that this ratio stayed roughly the same. When low quality or low quantity was offered, this ratio of trays was reached sooner. In the low quality, low quantity treatment, the nearest trays were depleted fully and the pattern of evenly increasing GUDs per tray broke up.

In this experiment, we showed that refuge-living herbivores foraging on a homogeneous resource initially follow a zero-one rule: a preference for the optimal patch, where intake is highest. Other patches were sampled. In the long term, depletion of the safest patch caused a foraging gradient, with most foraging happening close to the refuge and least foraging at distant patches. This resulted in the formation of spatial patterns in remaining food density in the long term. These patterns were affected by food quality and quantity: they were more skewed towards the refuge, as the initial food quantity and the quality of the forage were higher. This study stresses that there are different strategies and rules of thumb for optimal foraging that operate on different time scales. It is important to analyse foraging patterns using the hypotheses generated for the time scale of the data analysed.

Acknowledgements

The authors would like to thank Anne-Marie van den Driessche for her help with the chemical analysis of the vegetation samples. Unifarm in Wageningen provided the indoor facility in which the experiment was performed.

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Chapter 4

Effects of seasonal variation in resource growth on central place foraging herbivores

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Abstract

Herbivores forage on a resource that is constantly changing: growth rate varies through the year and vegetation deteriorates in quality as it matures. Because of this, herbivores must concentrate their foraging on smaller and smaller areas in spring. As growth rate declines, free ranging herbivores can shift to new foraging locations but central place foragers are bound to their burrow when the vegetation 'dries up'. We predict that because of this, a quality and quantity gradient is formed, that the area grazed increases as growth rate of the vegetation increases, and that foraging time increases through the season.

To test these predictions, we staged rabbits *Oryctolagus cuniculus* in sward strips for a growing season. Behaviour and location of the animals and abundance, structure and growth rate of the vegetation was measured.

After a full growing season, spatial variation in grazing pressure resulted in a gradient in vegetation quality and quantity. The area the animals used for grazing increased as growth rate of the vegetation decreased. As growth rate declined, growth did not replenish off-take any more and the animals needed to expand their foraging area. Foraging time increased as the season progressed. We attribute this to an increased requirement for food, as forage quality declined, and an increased search and handling time, due to a deterioration of plant structure on the more distant locations.

Central place foragers are essentially different from free ranging herbivores in interactions with their resource. Seasonal variation in depletion and renewal rates of the vegetation has a big impact on these animals: being tied to their burrows, they must deal with decreasing renewal of the vegetation close to their refuge at the end of the growing season. Natural fluctuations in population size or facilitative grazing by large herbivores may lessen these problems.

Introduction

For herbivores, the main variable used for explaining foraging behaviour and animal distribution is food density: in order to maximize its fitness, an animal tries to gather food as efficiently as possible (Stephens & Krebs 1986). As forage intake rate increases with the amount of available forage (Gross *et al.* 1993), distribution of individuals or of foraging effort over space is then directly related to the distribution of forage over space, following an ideal free or ideal despotic distribution (Fretwell 1972).

In a simple form of a herbivore-plant system, the animal forages until the required energy is gathered and plants regrow at a certain rate. For a hypothetical constant growth and consumption rate, there is an area where growth and depletion of the plants are similar and the area over which the animals distribute their foraging is a constant. However, growth rate is variable: for example, in the northern temperate zone, grass grows from April to October following a hyperbole, with a smaller second growth peak later in the year in harvested swards (see for example Spedding (1971) for grass cultures). So in spring, with an increasing plant growth rate, the size of this required area decreases, and animals can be and are even forced to aggregate, as was hypothesised by Fryxell (1991) and shown for geese (Bos, Van De Koppel & Weissing 2004).

Presumably, this focusing of grazing on smaller areas as productivity increases will be even more beneficial for small herbivores that forage from a central point, such as a burrow. These animals optimise their foraging behaviour, minimising predation risk and travel time (Brown 1999) or loss of foraging time due to vigilance (Chapter 2 of this thesis) by staying close to their refuges, depleting the closest patches first. As refuge-living animals defecate in the same areas as they forage, they increase nutrient turnover (Bakker *et al.* 2005). Also, in grasses repeated grazing can increase plant quality as forage by stimulating regrowth of nutrient-rich young leaves (Ydenberg & Prins 1981). Close to the refuge, these two effects should result in “self-facilitation” and the formation of a grazing lawn (McNaughton 1984): vegetation with an increased nutrient content and digestibility. This was shown to happen in swards grazed by rabbits (Bakker *et al.* 2005). Conversely, the more distant part of sward remains ungrazed and becomes more stemmy and less digestible as it matures (Van Soest 1982).

When the growth rate of the vegetation declines, or the density of the herbivores increases, the vegetation of the area grazed will not provide enough regrowth to counter the loss due to grazing. This is no problem for free ranging animals, which can deal with seasonal changes by migrating to other regions (for example wildebeest, Wilmshurst *et al.* 1999) or select other habitats within their immediate surroundings (for example bison: Larter & Gates 1991). However, animals that live in burrows are ‘stuck’: they need their refuge for shelter against predators or bad weather. These animals will need to increase the area grazed to obtain the required intake and ‘recapture’ the more distant, matured and less digestible part of the sward. They can do this by following an ideal free distribution or, when the animals compete for food, an ideal despotic distribution (Fretwell 1972). In the latter case, the higher ranking animals will force the lower ranking animals to forage at suboptimal locations, i.e. further from the refuge.

However, all animals will need to gather more food in autumn than in spring, as digestibility and nutrient contents of non-grazed vegetation has become much lower due to maturation. This will result in more foraging time needed to gather this larger amount and more time spent on vigilance: foraging further from the burrow requires more scanning for the presence of predators (Chapter 2 of this thesis).

In this paper, we describe the interactions between the vegetation and a central place foraging herbivore throughout the growing season and test the following predictions:

1. Decreasing grazing pressure with distance from the burrow results in a biomass, height and quality gradient, from a short, cropped, high quality grazing lawn to tall, low quality sward.
2. The area that is grazed decreases with increasing growth rate of the resource.
3. Time needed for foraging increases as the season progresses.

These predictions were tested in an experimental setup, using domesticated rabbits, typical refuge-living small herbivores in sward strips during a full growing season.

Methods

Three pairs of two year old female domesticated rabbits *Oryctolagus cuniculus* L. of two kg were staged on a fenced, 4 by 50 metres strip of *Lolium perenne* sward in Achterberg, the Netherlands (51°59´ N, 5 °38´ E). These strips were interspaced with similar sized unused strips, to prevent contact between the animals in different strips. The vegetation on these strips was homogeneous at the beginning of these experiments: we did not find significant correlation between vegetation height and distance or vegetation biomass and distance. Artificial refuges of 1.5 by 1.5 metres were provided at one end of each strip. Small stakes were placed at the sides of the strip every 2 metres.

The animals were allowed to forage *ad libitum* from 0730 until 1930 hours. During the night they were locked in the refuges to prevent escape or predation. Water was given *ad libitum*. A small cardboard box placed inside the artificial refuge was provided as cage enrichment. The animals were weighed every five weeks. They were observed for a full grazing day twice a week, the behaviour and location of each animal being logged for 2 minutes every half hour using a handheld computer and Observer software (Noldus BV, Wageningen, The Netherlands). The behavioural states we distinguished were eating, vigilance, resting/sitting, running and other (grooming, digging, drinking etc.). Behavioural states were considered as mutually exclusive. Location was determined to within two metres and expressed as distance to the refuge.

Grass height was measured every month using the drop disc method (Stewart, Bourn & Thomas 2001), taking 5 measurements per distance plot. Grass growth rate in each strip was estimated by placing two mesh exclosures of 25x25 cm on the plots of 0-2 meter, 10-12 meter, 20-22 meter, 30-32 meter, 40-42 meter and 48-50 meter from the refuge. When these exclosures were placed (t=0), a 20x20 cm sample of similar grass height was harvested by clipping vegetation 1 cm above the ground ("grazed vegetation samples"). After three to four weeks (t=1), the inner 20x20 cm in the exclosure was harvested by clipping all vegetation 1 cm above the ground ("ungrazed vegetation samples"). Samples were dried for 48 hours at 70°C. Growth rate was estimated per exclosure by taking the difference in biomass between the dry biomass weight of the plot exclosed at t=0 and harvested at t=1 and the dry biomass weight of plot harvested at t=0, divided by the number of days between t=0 and t=1. This procedure was repeated during the experiment, in weeks 1 (starting on 19 April 2004), 4 (17 May 2004), 7 (7 June 2004), 10 (28 June 2004), 13 (19 July 2004), 17 (16 August 2004), 21 (11 September 2004), 25 (11 October 2004) and 27 (25 October 2004).

We used two approaches to measure the differentiation of the sward at the end of the season: the ratio of leaf to stem and dead material and percentage Nutrient Detergent Fibre (% NDF). The weight ratio of leaves to stems and dead material (L: SD) is a good indication of quality for the herbivore. The larger this ratio, the more leaves there are. Rabbits usually select only leaves for foraging, as these are more palatable and contain more nutrients, so an animal will need less time to select these leaves when L:SD is large. Percentage NDF is a good predictor of the energy content of the rabbits' diet (Fernandez-Carmona *et al.* 1996). We determined these variables for 12 ungrazed vegetation samples taken at plots 10 and 50 metres from the refuges at the start of the experiment and for 12 samples from the plots 0 and 50 metres from the refuge, taken near the end of the experiment. Samples were dried for 48 hours at 70 °C and manually separated into dead material, leaves and stems, then weighed. The leaves were then ground and NDF per dry leaf was determined using the ANKOM filter bag procedure (ANKOM Technology, Macedon, NY, USA) with omission of the sodium sulphite and the heat resistant α-amylase, and with Neutral Detergent Solution prepared following Goering & Van Soest (1970). One sample was dropped from the analyses of percentage NDF as it was contaminated during grinding.

The experiment ran from 19 April until 29 October 2004. One animal fell ill during the experiment, and was substituted. The experiment was assessed and permitted by the Institutional Animal Care and Use Committee of Wageningen University (entry code 2004036.b).

Data analyses

To generate time-distance maps of foraging time and height and biomass of the vegetation, the data were averaged over the strips and interpolated using linear interpolation of neighbouring values (Matlab 7.1, The Mathworks Inc., Natick, USA). Testing for differences in distance to the refuge during foraging and differences in behaviour between the two rabbits in each enclosure was done by selecting only those behaviour scans where the animal was foraging. As these data were not normally distributed, and could not be transformed to normality, we used the median test to identify differences between animals in median distance during foraging. Because an animal in one of the enclosures had to be replaced during the experiment, we split the data for that pair into a set with data gathered before and a set with data gathered after replacement.

As we were interested in the spatial distribution of foraging of the 'population' to the vegetation, the time both animals spent on that plot was summed. We tested for temporal trends in behaviour or location with a simple linear regression when the data were normally distributed, and with a general linear model with Poisson error term and log link function when it was not.

Growth rate and daily grazing time were collected on different temporal scales: the former was collected every four to five weeks, the latter weekly. To determine their relationship, we selected the grazing area per strip of the week in the middle of the period over which the growth rate was determined. The daily grazed area is defined as the total area of the plots that were grazed by the two rabbits during the observations. The strength of relation between vegetation growth rate and area grazed by the animals was tested using Pearson's correlation coefficient.

Results

The weight of the animals dropped in the first weeks of the experiment, but stabilised at 2.2 (± 0.3 SE) kg for the remaining 5 months. The animals did not graze more on plots where vegetation was sampled than on unsampled plots (ANOVA of square-root transformed time spend grazing, $F_{1,148} = 0.21$, $P = 0.65$).

Vegetation

At the end of the strips, furthest from the refuge, the vegetation developed freely, following a normal pattern: quick growth, reaching a maximum height and biomass in week 10 of the experiment (the week of 30 June 2004), when it flowered and decreased in height and biomass. Close to the refuge however, increases in height and biomass were much smaller (Figure 1). The grasses in the nearest, heavily grazed plots, did not produce seeds. The ratio of leaf to stems and dead material (L:SD) was much larger at the beginning of the experiment than at the end (Table 1, $F_{1,20} = 178.18$, $P < 0.001$), and was larger in the plots close to the refuge than those far from the refuge at the end of the experiment (Table 1, week-distance interaction term, $F_{1,20} = 6.35$, $P = 0.02$). Percentage NDF of the leaves was not different in plots that were

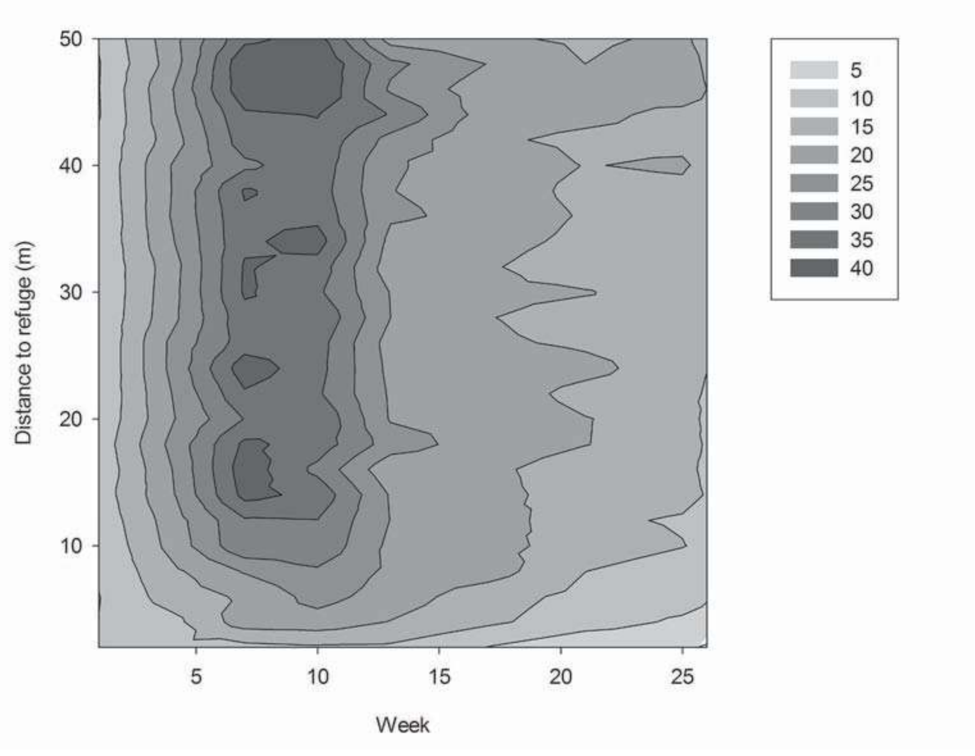

Figure 1a. Average height of grazed vegetation (cm) and median (thick line) and 90% percentile (thin line) foraging distance. Over the experiment, vegetation height was measured 5 times per distance, averaged per plot and then averaged over the three strips. The average standard deviation of the mean height was 5.3 cm (range 0.4 – 17.4) within the distance plots and 3.3 cm (range 0.2-15.0) over the strips. Week 1 is the first week of the experiment; measurements were done in weeks 1, 4, 7, 10, 13, 17, 21, 25 and 27.

Table 1. Weight ratio of leaves to stem and dead material and the percentage NDF calculated per dry weight of leaves (averages ± 1 SD) of 24 samples taken near to and far from the refuge, at the beginning and the end of the experiment. Ratio leaf: stem and dead material was larger at the beginning of the experiment than at the end ($F_{1,20}$= 178.18 , $P < 0.001$), and larger far from the refuge at the end of the experiment ($F_{1,20}$ = 6.35, $P = 0.02$). Percentage NDF was smaller at the beginning than at the end of the experiment ($F_{1,19}$ = 52.29, $P < 0.001$).

	Leaf : (Stem + Dead)		% NDF	
	near	far	near	far
beginning	3.1 ± 0.77	3.9 ± 0.73	46.6 ± 2.3	48.8 ± 1.8
end	0.7 ± 0.34	0.2 ± 0.03	80.0 ± 12.3	69.3 ± 13.1

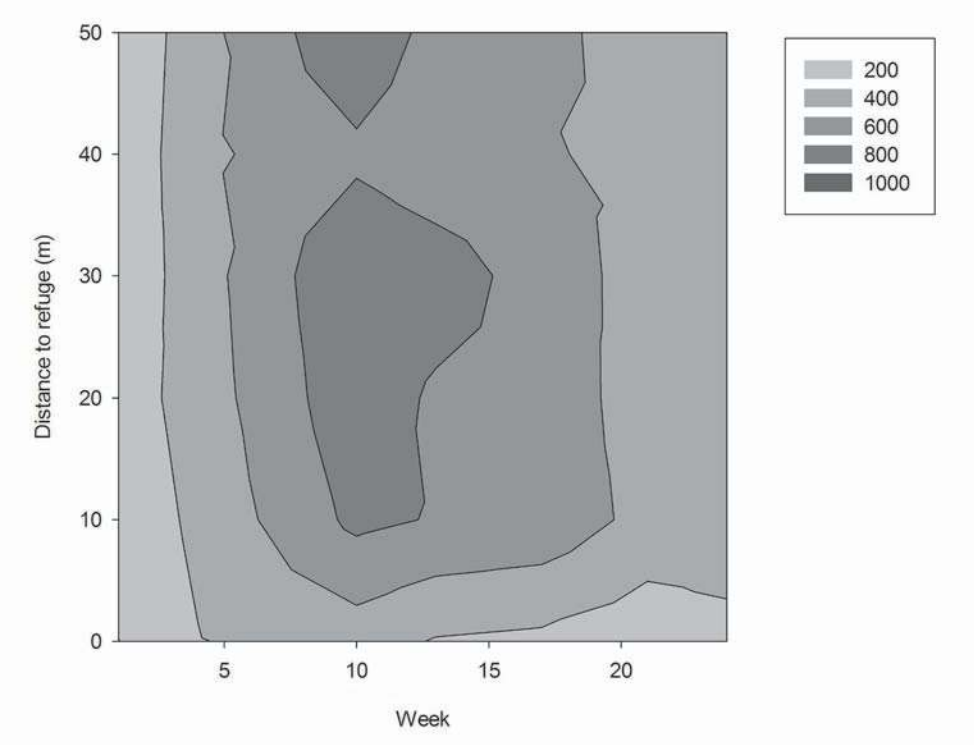

Figure 1b. Average dry biomass (in g m^{-2}) of grazed vegetation in the three sward strips and median (thick line) and 90% percentile (thin line) of the animals' foraging distance. Distance to the refuge is on the x-axis, week of measuring on the y-axis. The standard deviation of the biomass measurements between distances was 157.3 (range 63.4 – 256.6) g m^{-2}.

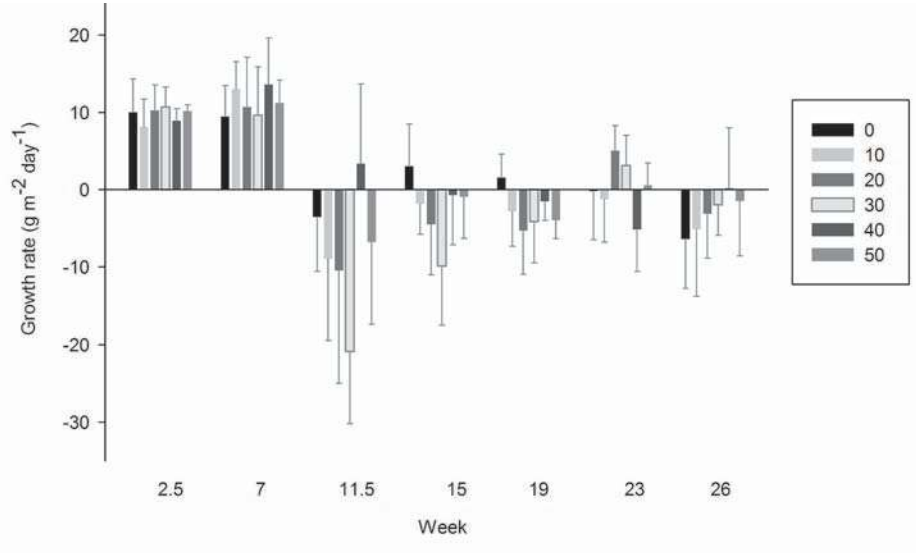

Figure 2. Average growth rate of biomass with 95% confidence intervals (g m^{-2} day^{-1}) on 6 different distances from the refuge over the course of the experiment. Growth rate was estimated by selecting similar plots, harvesting one, excluding the other from grazing for a number of weeks and harvesting it. The growth rate is then estimated by subtracting the dry weight of the latter from that of the former, divided by the number of days between the two harvests. Note that in week 23 onward, growth at distance 20 is different from 0.

close to or far from the burrow, but percentage NDF did increase over the season and was significantly higher at the end of the season ($F_{1,19} = 52.29$, $P < 0.001$).

The vegetation showed a large growth rate in the first 10 weeks of the experiment, and a decline in weeks 10-13, which is especially marked in the middle of the strips, at 30 metres from the refuge (Figure 2). After this period, the confidence limits include a growth rate of 0, and thus are not significantly different from zero growth, except for plot 20, which shows a second growth peak during week 23 of the experiment.

Animal behaviour

The animals stayed close to the refuge for the first part of the experiment, foraging on a mean of 4 metres from the refuge. They foraged further from the refuge from week 5 onward (Figure 3). The area the animals used for grazing follows the way the animals distributed their foraging time over the area (Figure 4): the area grazed is about 25 m^2 for the first weeks, then increases to about 80 m^2 for a number of weeks, and then increases again to 100 m^2, with a short decrease during weeks 20-21. The grazing area increased as growth rate decreased (Figure 4; $r_p(21) = -0.63$, P

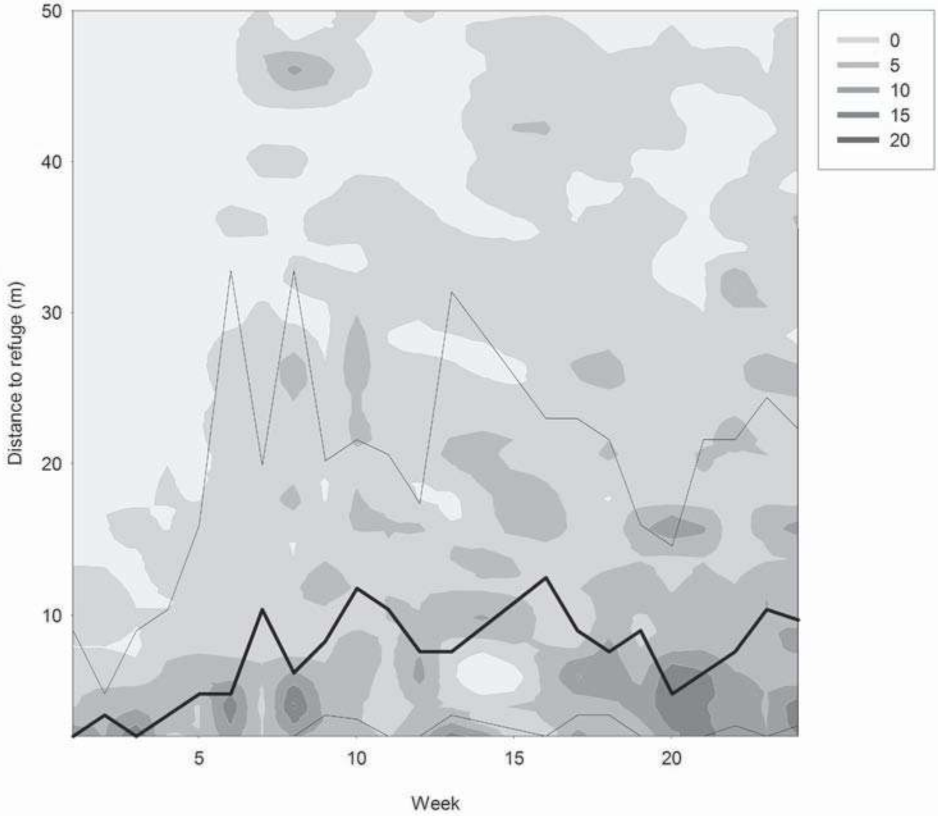

Figure 3. Foraging time in space and through time. Hue stands for average number of minutes the pair of rabbits foraged on that distance during observations. Thick black line: the median foraging distance of the animal in that week, thin black line: 90% percentile of the foraging distance of the animal in that week.

= 0.002). The time budget changed over the experiment: the percentage of the day that was used for foraging increased during the experiment (Figure 5, $R^2 = 0 .70$, $P < 0.01$), as did the percentage of the day that the animals attributed to vigilance (GLM, deviance/DF = 1.91, $P < 0.001$).

The individual rabbits in each pair differed in space use during foraging. Within one pair, median location during foraging was 6 metres from the refuge for one individual versus 12 metres for the other individual over the whole experiment ($\chi^2_{1,\ 1554} = 48.23$, $P < 0.001$); within the other pair the median location during foraging was 10 metres from the refuge for one individual versus 12 metres for the other individual over the whole experiment ($\chi^2_{1,1916} = 11.13$, $P = 0.001$). In the third pair, one rabbit was replaced due to illness. Here, the animals differed in distance

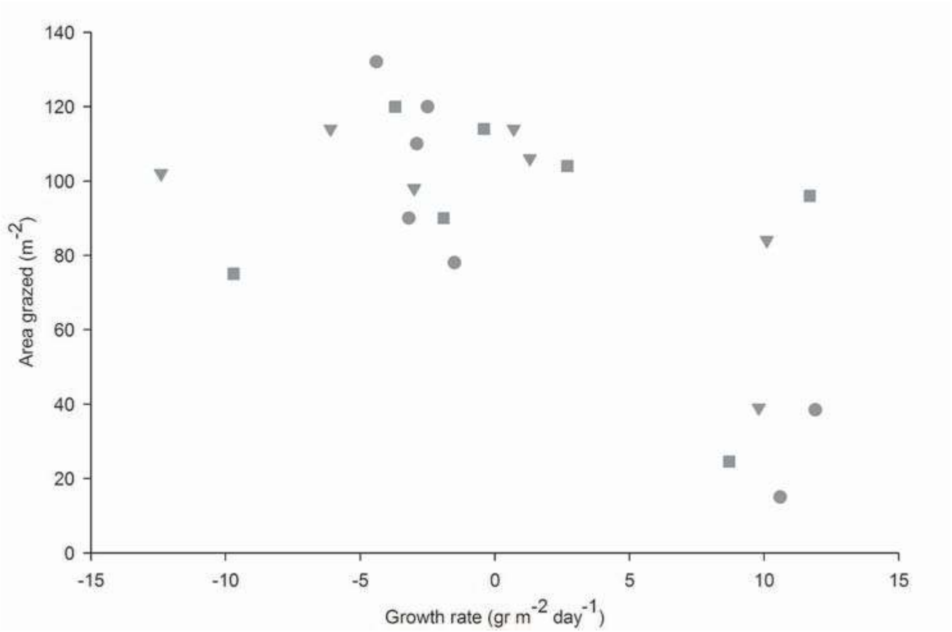

Figure 4. Growth rate of vegetation (g m^{-2} day^{-1}) and area used for grazing by both animals (m^{-2} day^{-1}). Area grazed is the area grazed by both animals. Different symbols stand for the three different sward strips. Area grazed decreases with increasing growth rate of the vegetation, $r_p(21) = -0.63$, $P = 0.002$).

to the refuge during foraging. However, before replacement, the median distance of the animal that was not replaced was the largest (12 metres versus 10 metres; $\chi^2_{1,1224} = 16.48$, $P<0.001$), while after one of the animals in the pair was replaced it was smaller (6 metres versus 14 metres; $\chi^2_{1,695} = 23.14$, $P< 0.001$). The animals of one pair did not differ in the amount of time they attributed to foraging, but in two pairs, the animals that foraged on larger distances spent more time on vigilance ($\chi^2_{1,33} = 3.88$, $P = 0.05$; pair before replacement: $\chi^2_{1,98} = 6.90$, $P = 0.01$). The total time the animals were active did not differ within the pairs.

Discussion

Over the course of the experiment, the animals attributed the majority of their grazing activity to plots close to their refuge (Figure 3). This resulted in a short lawn close to the refuge that stayed relatively short over the whole experiment (Figure 1). Farther from the refuge, the maximum standing crop was higher and the grasses developed into tall vegetation during summer. The ratio of leaves to stem and dead material, an indicator of forage quality, was higher close to the refuge than further away. So, as we expected (prediction 1), a gradient in biomass and quality had formed. However, the other quality indicator, percentage NDF of leaves, was the same for these plots. Hence repeated grazing and regrowth resulted in a grass

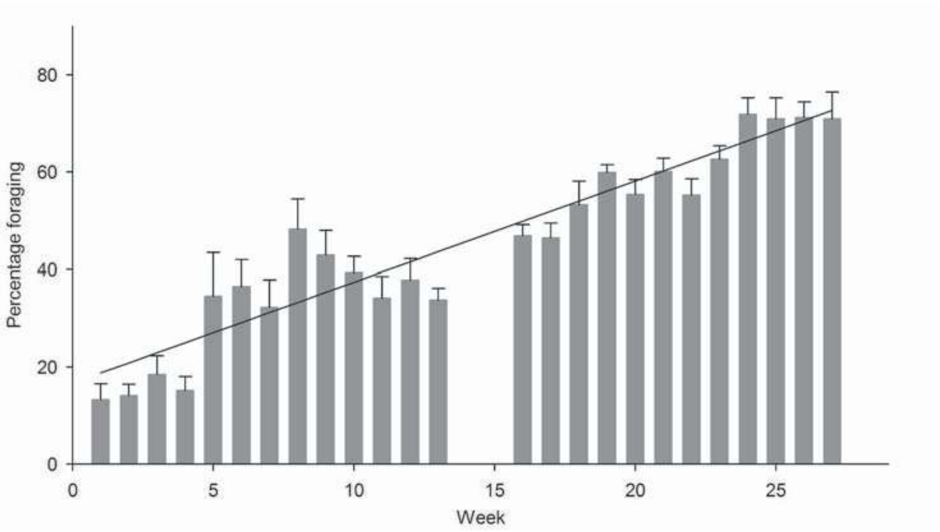

Figure 5. Average percentage of daily time budget spent on foraging. Error bars are standard errors. The average percentage of time the animals used for foraging increased through the experiment (linear regression, percentage foraging = 16.67 + 2.073·week, R^2=0 .70, P < 0.01). Note that the animals were in the sward for 12 hours a day.

sward that was higher in quality structure-wise, although grass leaves in all plots, regardless of locations showed the same estimation for digestibility.

The plots close and further from the refuge differed in growth: although the vegetation showed a growth peak at all distances from the refuge, only one of the closer and intermediately grazed plots showed a second growth peak, later in the season.

The area over which the animals foraged would increase as growth rate decreased. Although we started the experiment when the sward was already growing and so could not show the aggregative response in our experiment, we found that the growth rate of the vegetation and the area used for grazing were inversely related, partly confirming prediction 2. The animals foraged on a small area close to the refuge for the first five weeks: the vegetation near the plots, under rapid growth, seemed to be able to compensate for the grazing in this period. As the rate of growth declined the animals started foraging on larger distances from the refuge, and the area used for grazing increased about threefold (Figure 4). So, animals concentrated their foraging at a high growth rate and, as shown in the present study, must expand their foraging activity again as the growth rate decreases. When growth approaches zero, the area used for grazing keeps expanding, due to depletion of the sward by the animal.

As shown in Figure 5, this increase in area coincided with an increase in time used for foraging (prediction 3). This increase could be caused by three factors: increasing energy requirements, decreasing forage quality, or changes in forage structure. Increasing energy requirements could increase foraging times by increasing the required amount of food. The main factor affecting energy expenditure of an individual is the ambient temperature (Anderson & Jetz, 2005). If this factor would play a role, one would expect foraging times to inversely follow ambient temperatures, with a minimum during summer, in the middle of the experiment. Foraging time, however, increased throughout the whole experiment. Therefore, the factor of increasing energy requirements can be ruled out. The quality of the vegetation decreased over the season (Table 1), so the animals needed to eat more food to meet the same energy requirements. Additionally, the taller older vegetation contained more stems and dead material, which should result in an increase in the time needed to search and handle leaves during foraging and thus in an increase in the time needed for foraging. The increased foraging time in non-growth seasons also seems to occur in rabbits living in the wild. Gibb, Ward & Ward (1978) found that rabbits in a semi-natural setting used more time for foraging in autumn and winter than in spring and summer.

Within the three pairs of rabbits, there were significant differences in foraging location: one animal consistently foraged closer to the refuge than the other. In two of the pairs, this caused the animals foraging further from the refuge to spend more time on vigilance. We attribute this difference in foraging location and time budget to competition for the best foraging locations. As our animals avoided each other and hardly interacted, the degree of dominance ranking using conflict-flight methods could not be determined. We assume that the dominant animal is the one that stays closest to the refuge. Forage competition has to our knowledge not been described for rabbits, despite the many studies done on social behaviour of this species: the existence of a ranking in dominance in rabbits is attributed to competition for burrows for breeding between females and competition for females between males (Bell 1983; Cowan & Garson 1985). In our study, where only non-reproducing females were used, the dominant animals apparently used their rank to claim the best foraging locations. Although not described before, this is not surprising, as foraging at the best locations should lead to a better body condition, and a better body condition increases survival (Gibb, Ward & Ward 1978) and breeding success (Rödel *et al.* 2004).

Based on a field study on Eurasian rabbits, Bakker *et al.* (2005) hypothesised that in refuge-living herbivores, the concentration on foraging in an area close to the refuge is nutrient driven. They found that the vegetation close to the animals' refuge contained more nitrogen, so that the rabbits concentrated their foraging on these nearest locations and that adding nutrients to patches further from the refuge increased foraging on these patches, but adding predator cues did not decrease it. We show here that this preference for locations close to the refuge is also present when the vegetation is homogeneous. Spatially differentiated foraging transforms homogeneous distributed vegetation into a heterogeneous sward that increases in standing crop, but also in maturity with distance to the refuge.

Implications for population dynamics

As we illustrate with our experiment, refuge-living herbivores such as the rabbit live in two worlds: in spring they forage close to safety without depleting these patches and by doing so they even keep their forage in a more nutritious state (Bakker *et al.* 2005). However, as (re)growth of the vegetation decreases, these patches get depleted and the animals are forced to forage on the neglected, more distant plots. So, one would expect larger home ranges in winter than in spring and summer. The only two studies on rabbits to our knowledge that give home ranges per season indeed show that these were larger in winter than in summer (Moseby *et al.* 2005; Stott 2003), while the latter showed that for hares, a free ranging small herbivore, it stayed the same size. In our experiment, the animals could recolonise the rougher matured swards, but at a cost of more foraging and more vigilance. Our experiment ended in October, so there was still almost half a year of foraging on a non-renewing resource before the vegetation starts growing again

How do these animals tackle this problem? In extreme conditions, refuge-living herbivores such as pikas and marmots store forage and body fat in the spring and summer and hibernate in winter. Another strategy may be to not aggregate as closely to the refuge as depletion rates allow, but to keep the vegetation in check over a larger area than strictly needed, and to provisionally improve the sward needed for winter, i.e. to optimise for the long term instead of the short term. That this strategy is hardly possible may be illustrated by the following -crude- calculation. A rabbit eats around 70 g day^{-1} of *Lolium perenne* (unpublished data N Heuermann & JJA Dekker). Assuming that by grazing the animal keeps the sward in an optimal, high leaf, low dead material and stem situation of 385 g m^{-2}, roughly the height the animals kept the vegetation near the refuge in our study. Let's further assume that the animal can use the full standing crop of that grass. It can then be calculated that for 6 months of no growth of the vegetation, a rabbit would need an area of 180 days x (385 g m^{-2} / 70 g day^{-1}) = 990 m^2 of sward. However, at the height of the growing season, when growth rate is 10 g day^{-1}, one rabbit can only remove grown vegetation on 7 m^2 of the sward. So the rabbit inevitably loses control.

Still, it is possible that the effect of declining growth and associated increases in foraging area, foraging distance and foraging time are not as extreme as shown in this experiment with a stable population: natural populations of non-hibernating refuge-living animals such as rabbits show large fluctuations in size due to reproduction and increased mortality at the end of the reproduction period. These population fluctuations often coincide with the changing growth of the vegetation (for example in rabbits: Gilbert *et al.* 1987). The resulting increase in off-take by the herbivore population could equal the increasing growth rate. At the end of the season, populations decline, leaving the remaining animals with grass that is in good shape: short enough to forage on, but of good quality due to continued grazing. Lastly, if large herbivores are also present in the area, they can keep a large area in a non-matured, high quality state: the large herbivore would then act as a facilitator for smaller herbivores. Large herbivores such as cattle and bison can improve swards for small herbivores such as rabbits (Bakker *et al.* 2004) and prairie dogs (Knowles 1986, Krueger 1986), under a certain range of grazing pressures (Cheng & Ritchie 2006).

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Chapter 5

Plant productivity and free-ranging herbivores impact spatial foraging patterns and population dynamics of refuge-living herbivores

Jasja JA Dekker & Frank van Langevelde

Abstract

To study how plant productivity and grazing by free-ranging herbivores affect foraging patterns and population dynamics of refuge-living herbivores, we developed a mechanistic model. In this model, forage intake of the individual is a determined by plant biomass, but time is lost because time must be used for vigilance, which increases with distance to the refuge. Both a asymptotic functional response and a unimodal functional response were implemented in the model.

The model yielded circular patterns in grazing distribution and in the grazed vegetation around the refuge, resembling the patterns found in the field. An increase in productivity resulted in foraging on smaller.

Dynamic populations of small refuge-living herbivores showed an increase with plant density, but a decreased in the area used for grazing, as opposed to free-ranging herbivores: in those, area increased with population density. When foraging according to a unimodal functional response, grazing lawns emerged: due to vigilance, animals repeatedly grazed the closest locations, bringing it to a state in which intake was higher than at locations that were not grazed.

Adding large herbivores to the model showed that facilitation can only occur if the small herbivore forages according to a unimodal functional response. Small herbivores with such a functional response reached a lower population density with large herbivores than without them at low plant productivity: competition. At high plant productivity, cattle lowered vegetation density to a level at which the small herbivore reached higher intake rates, resulting in a larger refuge-living herbivore population: facilitation.

Introduction

When it comes to foraging, herbivores that use refuges (burrows, crevasses, etc.) are different than free-ranging herbivores. Free-ranging herbivores can select locations to forage where intake rates are maximal, while refuge-living herbivores forage under a spatial constraint: they must return to their refuge after feeding. For the refuge-living herbivores, the time needed to reach this refuge when they flee from predators increases with distance. This results in an increase in the time that is needed for scanning for predators with increasing distance between the animal and its refuge (Chapter 2 of this thesis). As vigilance often inhibits foraging (Underwood, 1982, Prins & Iason, 1988, Fortin *et al.* 2004), for refuge-living animals the intake rate at any location is not only a function of food density, but also of the distance from this location to the refuge (Chapter 4 of this thesis). This results in a reduced intake rate when foraging farther from the refuge (Chapter 4 of this thesis). Therefore, it is expected that the refuging herbivores should forage as closely to their refuge as possible. Here, the time needed for vigilance is minimal.

Indeed, herbivores that live in refuges often show less foraging activity as distance to their refuge decreases, for example in pika *Ochotona princeps* (Huntly 1987) and European rabbit *Oryctolagus cuniculus* (Bakker *et al.* 2006, Dekker, Groeneveld & Van Wieren 2006). Subsequently, vegetation around the refuge increases in density or height with increasing distance to the refuge, for example in rabbit (Farrow 1917; Tansley & Adamson 1925), pika (Huntly 1987) and prairie dogs Cynomys ludovicianus (Osborn & Allan 1949). In this paper, we model refuge-living herbivores to predict the consequences of this spatial constraint in their foraging on their foraging patterns and population dynamics.

Distance to the refuge and food availability determine the distribution of foraging, while the number of foragers and grazing time are influenced by the balance between local depletion and (re)growth of the vegetation. Depletion of the nearest locations forces the animals to forage at larger distances, whilst rapid regrowth of the vegetation can partly or wholly balance the consumption by the herbivore that allows the animals to forage closer to the refuge (Chapter 4 of this thesis). When the rate of regrowth is high (i.e., in areas with high productivity), small areas around the refuge are used for foraging, whereas a low growth rate (i.e., low productivity) results in larger areas used for foraging (Chapter 4 of this thesis). Plant productivity is thus expected to have a large influence on the pattern of foraging around the refuge.

Refuge-living mammalian herbivores typically have relatively low body mass compared to many free-ranging mammalian herbivores. Intake rates of these small herbivores are lower on tall and old grass than on short and young grass due to an increase in handling and search time, which results in a decrease in the intake rate at higher levels of grass biomass, a so-called unimodal ('type IV') functional response (Prins & Olff 1998, Durant et al 2003, Drescher *et al.* 2006, Heuermann *et al.* in prep.) instead of a type II asymptotic functional response (Holling 1959). Such a unimodal functional response is predicted to allow facilitation by other species of herbivores: the larger free-ranging herbivores graze the tall vegetation at which the smaller herbivores experience low intake rates to smaller vegetation height and better forage quality, where these smaller herbivores have higher intake rates (Vesey-Fitzgerald 1960, Prins & Olff 1998). This facilitative effect could also be brought about by humans: it has been suggested that mowing is the cause for the relatively high density of rabbits in city parks in the Netherlands (Akkermans 2006). We developed a simple model to study how plant productivity and grazing by free-ranging herbivores affect foraging patterns and population dynamics of refuge-living herbivores. This study will allow us to analyse whether plant productivity or the presence of free-ranging herbivores determine population size of refuge-living herbivores.

Model

First, we use the model to investigate how plant productivity affects spatial patterns in foraging in a static, non-reproducing population of refuge-living herbivores. Next, we allow this herbivore population to respond to available forage by increase or decrease in numbers, and study the effect of the unimodal functional response on the foraging patterns and population dynamics of the refuge-living herbivores. Finally, we include grazing by large free-ranging herbivores. We parameterise the model for rabbits, as this species is particularly well studied (Thompson & King 1994). The symbols used in the model, their interpretation, units and estimated values are given in Table 1.

Grass dynamics with constant herbivore population

We discern two mutually exclusive activities of refuge-living herbivores: foraging and vigilant behaviour, i.e., scanning their surroundings to detect predators. As the fraction of time that animals need to scan their surroundings increases with its distance from the refuge (Chapter 2 of this thesis), we can suffice with a 1-dimensional spatial model. We model the fraction of time needed for scanning, $v(x)$, as function of the distance from the refuge as:

$$\nu(x) = \nu_o + v_m x \qquad (1)$$

where v_o is the baseline vigilance, i.e. the vigilance close to the refuge, required to detect, recognize and respond to predator in time, and v_m is the rate of increase in vigilance with distance from the refuge: the time required to detect a predator in time to reach the refuge (Chapter 2 of this thesis). Maximally, $v(x) = 1$. It is assumed that scanning is vital for survival, and that the fraction of time the animal must be vigilant in order to detect predators early enough to escape at a certain location is fixed. The time that is not needed for vigilance can be used for foraging, the time needed for other foraging-associated activities such as travelling from the refuge to foraging locations surrounding the refuge and back is assumed to be negligible in relation to the time used for foraging (for example Chapter 2 of this thesis). In contrast to refuge-living herbivores, free-ranging herbivores are modelled by assuming vigilance as a constant which is independent of location, i.e., $v_m=0$.

The available grass biomass, $G(x)$, at a certain location x determines the intake rate animals can obtain at this location. Initially, we model the relation between vegetation biomass and instantaneous intake rate as an asymptotic functional response which is found in herbivores (Shipley 1994; Iason *et al.* 2002):

$$IR(x) = I_m \frac{G(x)}{G(x) + k_I} \qquad (2)$$

where I_m is the maximum specific intake rate and k_I is the half saturation constant: the grass biomass where the specific intake rate is half of its maximum.

We also analyse the effect of aging of the vegetation on intake by adding the following term (Owen-Smith 2002):

$$1 - q\,G(x) \qquad (3)$$

where q is a quality coefficient that determines the decrease of forage quality with increasing grass biomass. Combining equations (2) and (3) yields a hump-shaped relation between forage density and intake rate as:

$$IR(x) = I_m \frac{G(x)}{G(x) + k_I}\big(1 - q\,G(x)\big) \qquad (4)$$

The intake rate at a specific location x is also determined by the fraction of time that is left over for foraging from being vigilant at that location x (equation 1). Thus, we formulate the possible intake rate as a function of distance and forage density as:

$$PI(x) = \big(1 - \nu(x)\big) IR(x) \qquad (5)$$

The animals forage according to the following rule: each animal, one by one, forages at the location with the maximum value for *PI(x)*, and forages on that location for 1 minute. Then, the animals again select the location to forage with the next highest value for *PI(x)*. This procedure is repeated until all individuals have gathered their required intake for minimal basal metabolism and activities, *R*, or until there is no more time left in the day (maximum foraging time *T* is assumed to be 24 hrs x 60 minutes).

Having derived the spatially explicit consumption of vegetation by the foragers, we can now model the grass dynamics. These follow a simple discrete logistic equation minus the consumption by the herbivores:

$$G(x,t+1) = G(x,t) + \Delta G(x) \qquad (6)$$

$$\Delta G(x) = \frac{r(1-G(x,t))}{K} G(x,t) - \sum_{i=1}^{H} I(x,i) \qquad (7)$$

where *r* is the growth rate at low grass biomass, *K* the maximum grass biomass, *I(x,i)* the total amount vegetation over the day consumed at distance x by individual herbivore *i*, and *H* the number of refuge-living herbivores. The time steps of the model are minutes. The model simulates the changes in grass biomass due to growth and foraging around the refuge.

Dynamic herbivore population

To add population dynamics of the refuge-living herbivores to the model, we assume that the reproducing animals maximise their daily intake, as this improves body condition, and leads to large litter sizes and increased survival of the litter (for rabbits: Poole 1960; Rödel *et al.* 2005). In the dynamic herbivore model, the herbivores forage until their gut capacity is reached, or until there is no more time left in the day. When the daily food intake is equal to the required intake *R*, no litters are produced. When intake is larger than this requirement *R*, litters are produced and the population grows. When it is smaller than *R*, no litters are produced, animals die and the population decreases. Additionally, density dependent mortality as shown to act in rabbits (Gibb, Ward & Ward 1978; Rödel *et al.* 2004) is added:

$$H(x,t+1) = H(x,t) + \Delta H(x) \qquad (8)$$

$$\Delta H = H(t)c\left(\sum_{i=1}^{H(t)}\left(\int_{x=0}^{\infty} I(x,i)\,\mathrm{d}x\right) - R\right) - m\,H(t)^2 \qquad (9)$$

where c is the conversion factor from excess food intake to reproduction per herbivore, and m the density dependent mortality rate.

Grazing of large free-ranging herbivores

In order to study facilitative or competitive effects of large free-ranging herbivores on refuge-living herbivores, we add a second herbivore to the model. The foraging by large free-ranging herbivores is modelled in the same way as the foraging of the small refuge-living herbivore, but with constant level of vigilance. The additional large free-ranging herbivore population is not dynamic: they are assumed not to depend solely on the area covered by the model. The large herbivores are parameterized using data from free-ranging cattle (Table 1).

Simulations

We first analysed the model with a constant population of refuge-living herbivores with both the asymptotic and the unimodal functional response in a range from 1 to 100 animals living in the refuge, and for a maximum grass biomass in a range from 100 to 1400 grams dry matter m^{-2}. The low biomass corresponds to alpine or desert systems, the high densities to highly productive grasslands in the temperate zone. The model simulated 100 days of foraging, enough to reach a stable state. We also ran simulations with vigilance of the herbivores as a constant, i.e., the free-ranging herbivores.

Comparison of model predictions with field data

In order to test the model, we compare the predictions for foraging patterns to data from field studies. As the spatial distribution of grazing around refuges is rarely given, we use home range sizes of refuge-living herbivores to test the model. Although this measure of spatial behaviour is not only related to food abundance, but is also affected by intraspecific social interactions (e.g., Cowan 1987, Dekker, Groeneveld & Van Wieren 2006), it is reported in many studies performed in a wide range of biotopes and geographic regions. Where authors reported values for male and female animals or for summer or winter separately, these were used separately in the analysis. Annual net primary production (ANPP) or even the standing crop of the vegetation of the study site was given only given in 2 of the studies. We therefore estimated ANPP from the average yearly precipitation following Noy-Meir (1973):

$$ANPP = 0.6\,(p - 56) \qquad (10)$$

where is p is annual precipitation in mm. For yearly precipitation for the study sites, data from the Worldclim dataset (Hijmans *et al.* 2005) were used. As factors such as defence of mates or resources can also influence home range size, we analysed the relationship between the natural logarithm of home range size and productivity using quantile regression (Cade & Noon 2003). For testing the estimated quantile regression coefficient against the null hypothesis of being zero, we used a permutation test for the quantile rank score statistic (Koenker 1994). These analyses were performed using Blossom (Version W2005.11.23, Fort Collins Science Center, U.S. Geological Survey, Fort Collins, CO., USA).

Results

Plant productivity and foraging patterns

In general, herbivores in the model foraged within a certain distance from the refuge. When intake rate declined as the nearest locations were depleted, the animals foraged on locations further from the refuge, while vegetation (partially) grew back after being grazed. After a certain period of time, this depletion and regrowth became equal, resulting in a distribution of foraging that gradually declines with distance from the refuge (Figure 1). The distribution of consumption by the refuge-living herbivore was more skewered towards the refuge as maximum plant productivity increases and the area around the refuge that was used for grazing decreases with increasing

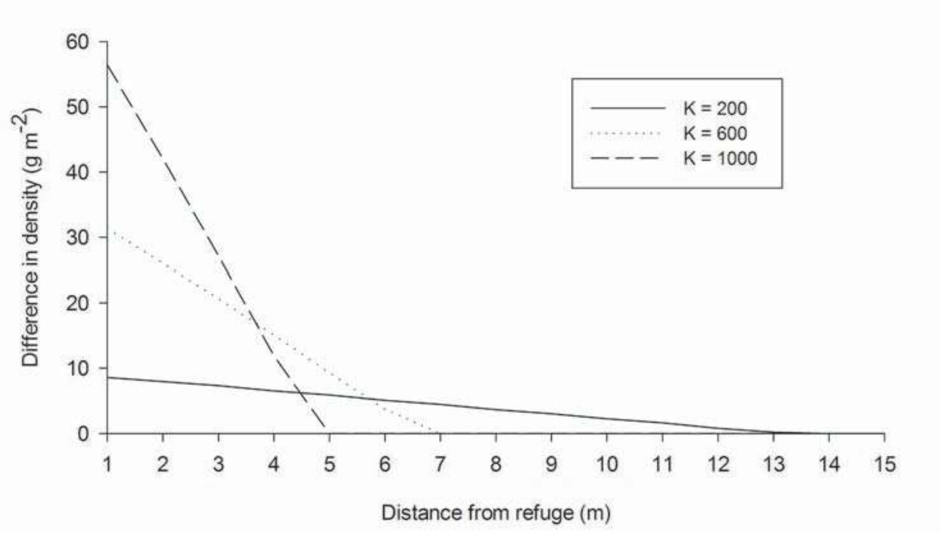

Figure 1. Density pattern in the vegetation caused by foraging of refuge-living herbivores for different values of the maximum plant density (K=200, 600 and 1000 g m^{-2}). Shown is the difference in density between the grazed vegetation at location x and ungrazed vegetation (at day 100 of the simulation. Refuging herbivore density H=25. Parameter values as in Table 1.

productivity (Figure 2a). At low plant productivity, locations close to the refuge were quickly depleted and intake rate declines. The highest intake rates were found at the locations further from the refuge, despite higher costs due to vigilance, resulting in a larger area used for grazing. At high plant productivity, the locations close by could be grazed longer before the density is so low that the corresponding intake rate is lower than intake rates minus loss to vigilance at more distant locations. With a larger population foraging from the refuge, the locations close to the refuge were depleted quicker, resulting in a larger foraging area. When the functional response was unimodal, the animals required a larger foraging area at low productivity (as our parameter values result in lower intake rate at low grass biomass), but this rapidly declined with higher plant productivity (i.e., higher than 500 g m^{-2}, Figure 2b). At locations with high productivity, the herbivores could not meet their requirements due to the decreasing intake rate at high grass biomass.

Free-ranging herbivores used a much larger area than refuge-living herbivores. For these animals, vigilance is equal everywhere, so to obtain the highest intake rate the animals forage at each location once, deplete it and so move to a untouched location to obtain the highest intake available, and so on. The area used for foraging was therefore much less influenced by productivity (Figure 2c), but does decline a little with maximum plant density. This is because, as intake rate is higher, the required intake is reached sooner and the herbivores stop foraging sooner.

Dynamic herbivore population

In the model with herbivore dynamics, the population size of refuge-living herbivores increased with plant productivity, but the area the population uses for foraging decreased (Figure 3a). When the refuge-living herbivores had a unimodal functional response, their resulting population density also had a unimodal relationship with productivity (Figure 3b). In the free-ranging herbivore model, both the population size as the area the population uses for foraging increased with productivity (Figure 3c).

We found that the area used for grazing declines with population size of the refuge-living herbivore model, whilst it increases with population size of the free-ranging herbivore model (Figure 4).When the functional response of the refuging herbivores has a unimodal relationship with grass biomass, the relationship between the area used and population size is less well-defined. The area used for foraging is large at low productivity, and small at high productivity. Initial population density did not affect the final population sizes and resulted in only slightly different outcomes.

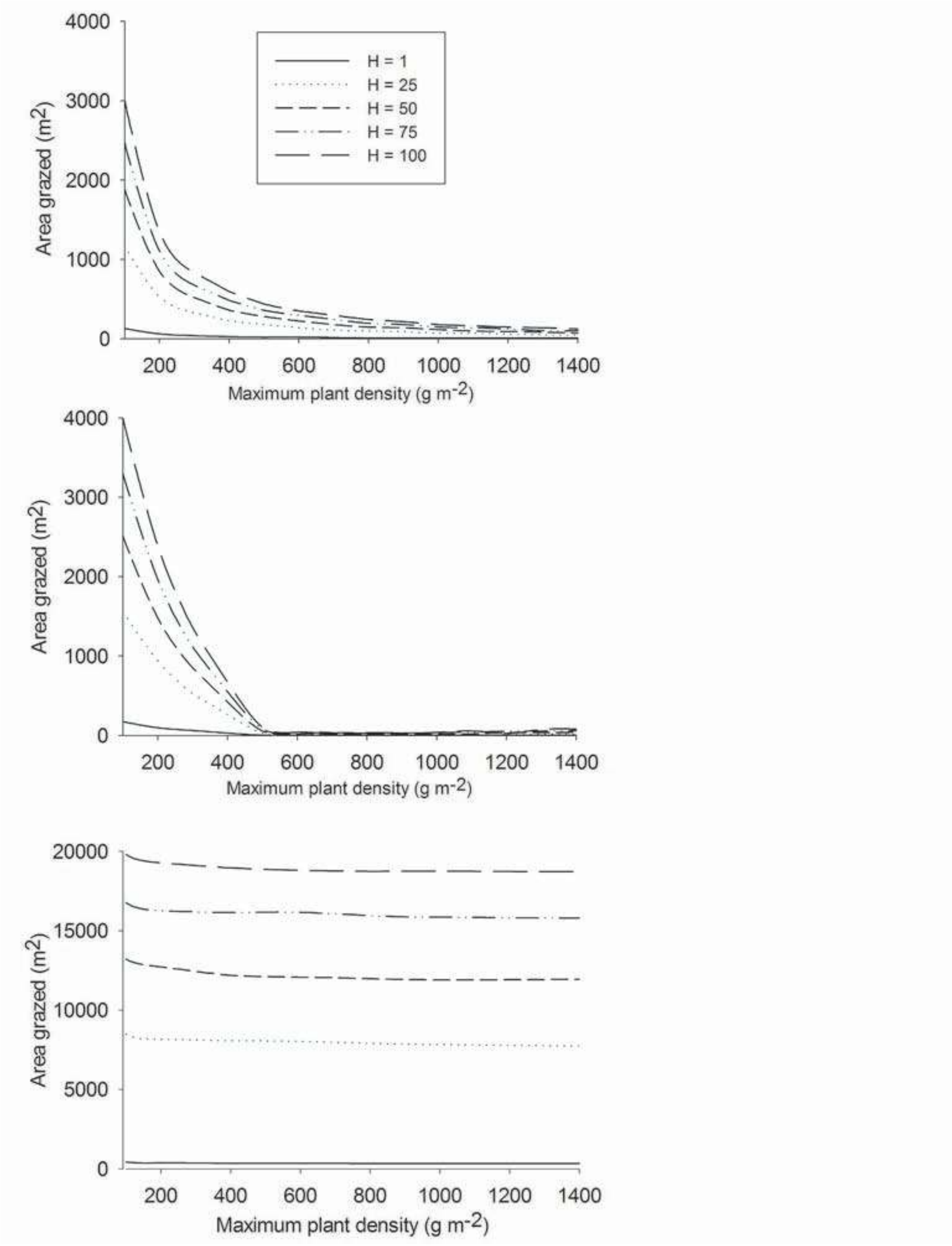

Figure 2. Area grazed by the refuge-living herbivores (upper graph), refuge-living herbivores with a unimodal function response middle graph), andfree-ranging herbivores (lower graph). Results of simulations for different values of a constant herbivore density (H = 1, 25, 50, 75 and 100 individuals). Parameter values as in Table 1.

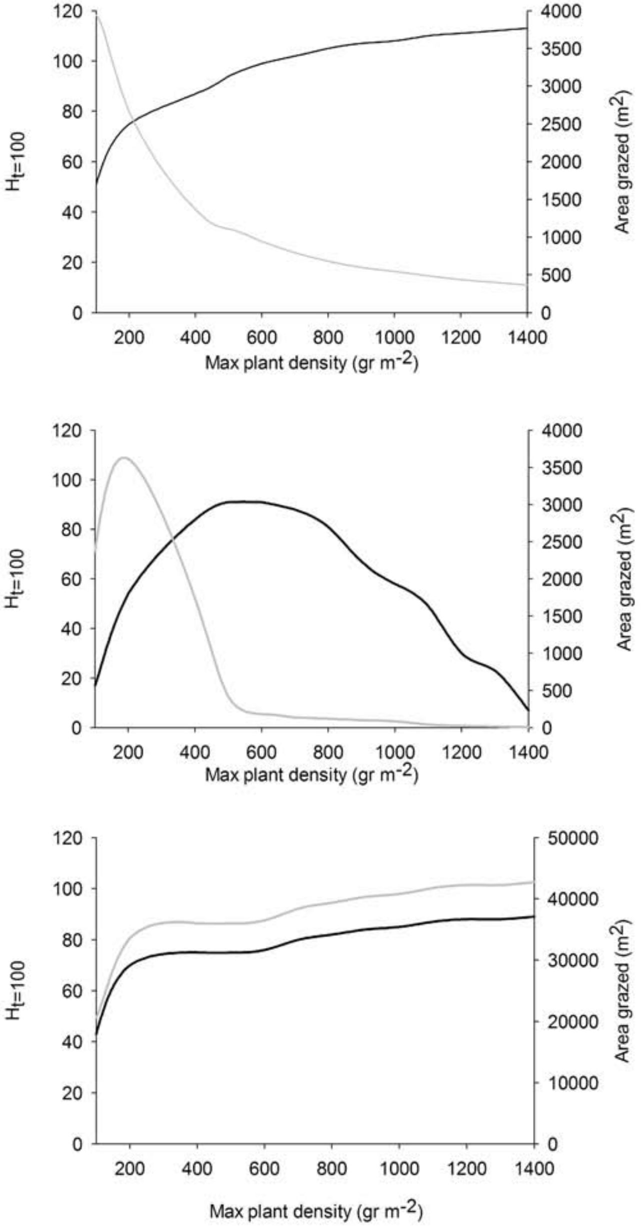

Figure 3. Population density of dynamic populations of small refuge-living herbivores (black line) and the area used for foraging (grey line) over a productivity gradient. For refuge-living herbivores (upper graph), refuge-living herbivores with a unimodal functional response (middle graph) and free-ranging herbivores (lower graph) and . Parameter values as in Table 1.

Refuge-living and free-ranging herbivores

Adding large free-ranging herbivores to the refuge-living herbivores had either a competitive or a facilitative effect on the refuge-living herbivores, depending on the shape of the functional response of the refuge-living herbivores. When the small refuge-living herbivore had an asymptotic functional response, large free-ranging herbivores did not affect their population dynamics at high plant productivity (Figure 5). The relatively small decline of plant density due to the consumption of the large herbivores did not translate to lower intake rate in the small refuge-living herbivores. However, at low plant productivity, the large herbivores largely depleted grass biomass, resulting in a low population size of refuge-living herbivores (Figure 5). This also occurred when the refuge-living herbivores had a unimodal functional response. At high productivity, the population size of refuge-living herbivores was higher when the free-ranging herbivores were present than when these were absent (Figure 5). Here, free-ranging herbivores depleted the vegetation to levels at which the intake rate of the refuge-living herbivore became higher.

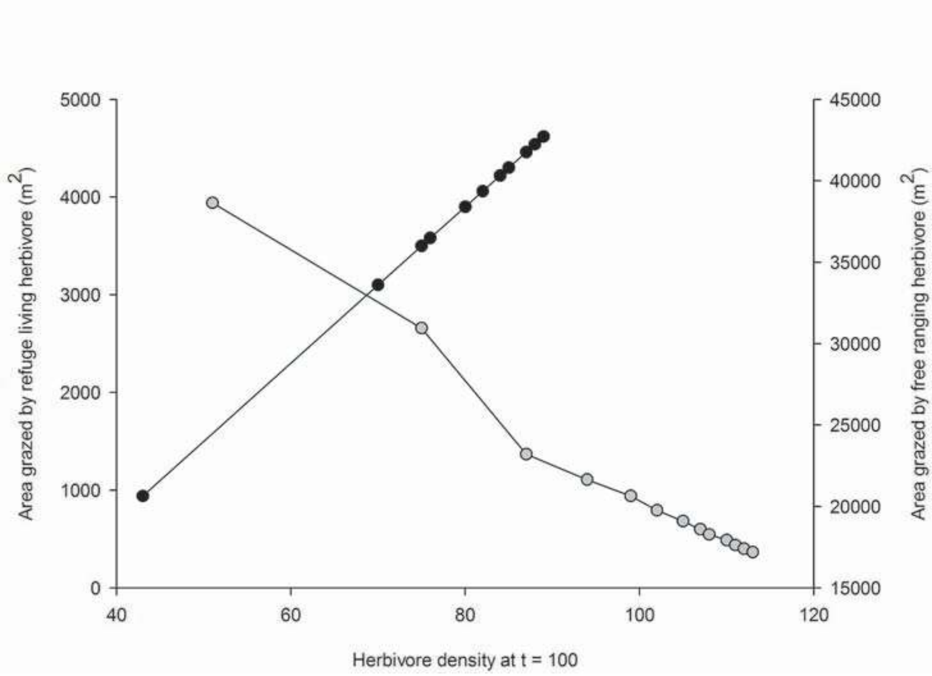

Figure 4. The area used for foraging as function of the population size of refuge-living herbivores (black circles) and free-ranging herbivores (grey circles) resulting from the simulations of dynamic herbivore populations. Left y-axis belongs to the central place foraging herbivore simulation results. Right y-axis belongs to the free-ranging herbivore simulation results. Area grazed increases in free-ranging herbivores, and decreases in central place foraging herbivores with population size. Parameter values as in Table 1.

Comparison of model predictions with field data

By combining home range data of rabbits from studies done at a range of sites in Europe and Australia, we could determine the relationship between home range of this refuge-living herbivore with productivity. The best fitting regression curve, a regression to the 80% quantile of the data curve shows a steady decrease of the home range with estimated annual plant productivity (Figure 6).

Discussion

In this paper, we show that adding one spatial constraint of foraging, i.e. the increase of time needed for vigilance with distance to the refuge, to a model of foraging herbivores results in foraging patterns concentrated around the refuge, which largely depend on plant productivity and the presence of free-ranging herbivores. These relationships are similar to those in refuging herbivores in the field and in experiments. Based on field data from a range of sites, we could predict the decrease the home range size of refuge-living herbivores decreases with productivity (Figure 2 and 3). This matches the pattern in the analysis from combined field studies (Figure 6).

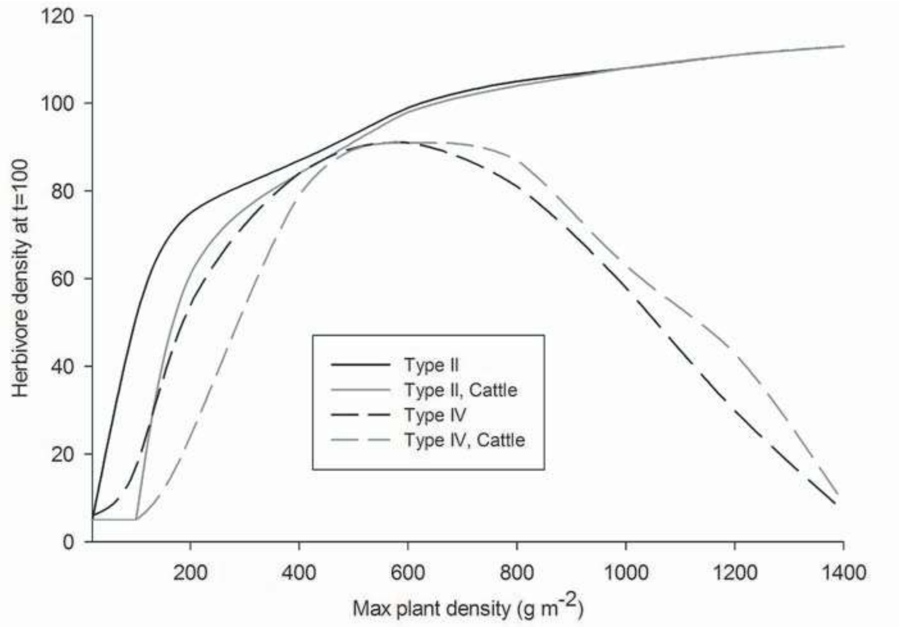

Figure 5. The effect grazing by large free-ranging herbivores has on population size of refuge-living herbivores. Black lines: large herbivores are not included in the model (see Fig 3a). Grey lines: large herbivore is included in the model. Solid lines: the refuge-living herbivores forage according to an asymptotic (type II) functional response. Dotted lines: the refuge-living herbivores forage according to a unimodal (type IV) functional response. Parameter values as in Table 1. Free-ranging herbivore (cattle) density is 20 animals ha^{-1}.

What determines refuge-living herbivore populations?
In populations of refuge-living herbivores with an asymptotic functional response, population size increases with plant productivity (as generally predicted for herbivores (Coe, Cumming & Phillipson 1976), whilst the area the population used for foraging decreases although there is much more vegetation available than is being grazed. Foraging without the spatial constraint of being not too far from the refuge would yield higher intake rates, but results in increased vigilance and thus decreases food intake. In refuge-living herbivores, vigilance costs limit further increase of herbivore numbers. Our finding that spatially increasing vigilance costs limit the population size of refuge-living herbivores is illustrated by the contrast between refuge-living and free-ranging herbivores: the area used for grazing increases with population size of the latter, whereas the first experiences a decrease in area used for grazing with population size (Figure 5).

The two different functional response types, the asymptotic and the unimodal, led to different relations between plant productivity and population size

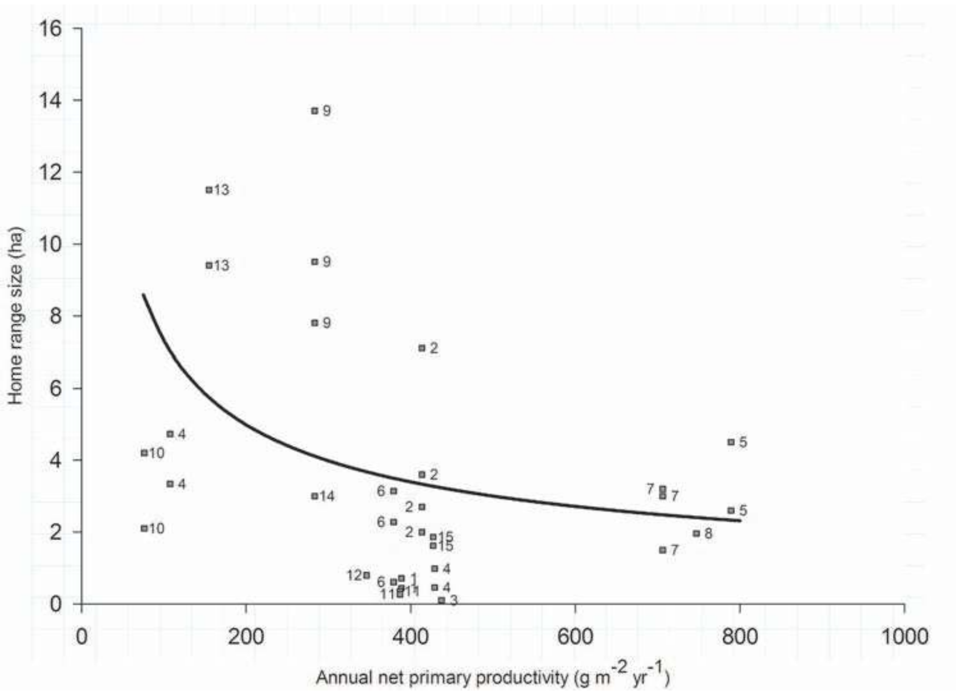

Figure 6. Effect of annual net primary productivity of the vegetation on home range size of rabbits. Line: 80% quantile regression (significantly different from a null-model, p = 0.04, n=34).
[1]Cowan 1987. [2]Daniels *et al.* 2003. [3]Dekker, Groeneveld &Van Wieren 2006. [4]Fullagar 1981. [5]Gibb 1993. [6]Henderson 1979. [7] Hulbert-Ian, Iason & Racey 1996. [8]Kolb 1991. [9]Lombardi *et al.* 2002. [10]Moseby *et al.* 2005. [11]Rödel, unpublished data. [12]Southern, 1940. [13]Stott 2003. [14]Villafuerte 1994 [15]White et al 2003.

of the refuge-living herbivores. In populations of refuge-living herbivores with a unimodal functional response, vigilance limits the population density at intermediate vegetation productivity: there is ample forage, but this is unreachable due to vigilance. In situations with high production (when plants are not accessible or digestible for small refuge-living herbivores) and low productivity, their numbers are limited by food availability. This decline in population size of refuge-living herbivores with productivity, however, does not follow the decrease in intake rate with productivity: the functional response starts declining at 400 g m^{-2}, but the population density does not decline until a maximum plant density of 750 g m^{-2}). Due to vigilance, the animals focus their foraging to a fixed area, closed to the refuge and remove between 100 to 200 g of vegetation daily. This way, they bring the vegetation surrounding the refuge to a density of 350-360 g m^{-2}, a density at which intake rate is optimal. This means that the realised individual intake is more than to be expected from the intake rate (Figure 7): grazing lawns (McNaughton 1976, McNaughton 1984) emerge when herbivores experience a spatial constraint in their foraging, i.e., refuge-living herbivores around their refuge, and forage according to a unimodal functional response. In our model, vegetation becomes impossible to control for the refuge-

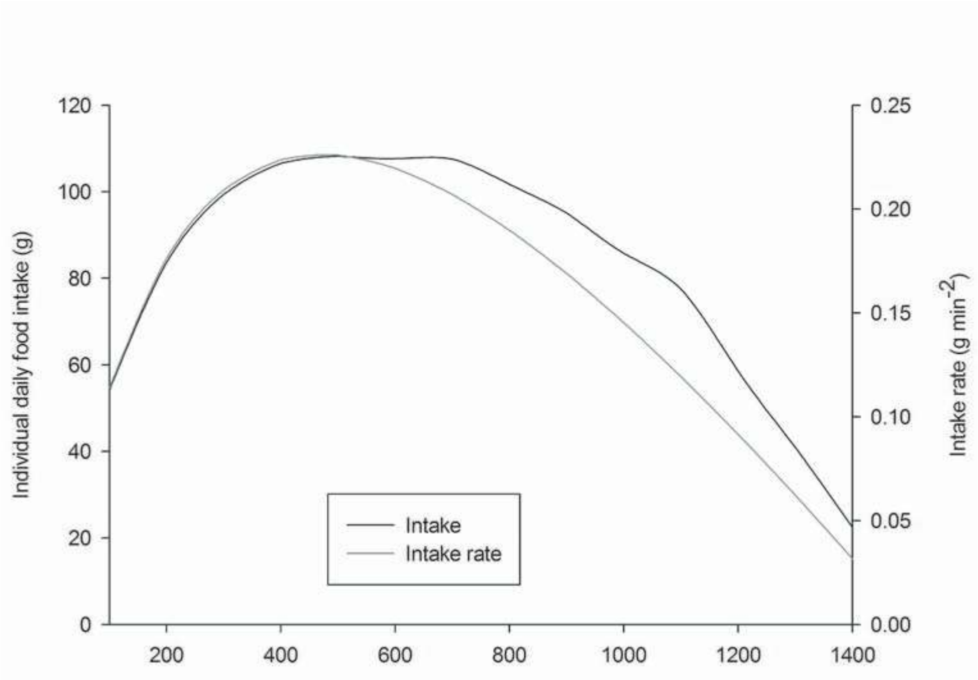

Figure 7. Realised individual daily intake (black line, left axis) and functional response (grey line, right axis) of refuge-living herbivore foraging according to a unimodal functional response.

living herbivores when maximum plant densities is higher than 800 g m^{-2}. At such densities, the facilitation by large herbivores is required to reach higher densities.

Facilitation

Ecological theory predicts facilitation when small and large herbivores co-occur (Prins & Olff 1988, Farnsworth, Focardi & Beecham 2002, Arsenault & Owen-Smith 2002). In the present paper, we show that this facilitation occurs at high levels of productivity, and only when the small herbivores have a unimodal functional response i.e. have problems ingesting or digesting high density forage. At low productivity, the large herbivores largely deplete the available vegetation, resulting in a low population size of refuge-living herbivores (Figure 7). This food competition also occurs when the refuge-living herbivores have a unimodal functional response. Facilitation increases both the population and area grazed of small refuge-living herbivores.

We can thus conclude that large free-ranging herbivores can have a facilitating effect at sites of high plant productivity when the refuge-living herbivores forage according to a unimodal functional response, but they have a neutral or even negative effect due to competition at sites with low plant productivity.

Implications for nature management

Due to the decrease of rabbits in the Netherlands resulting from diseases (Bijlsma 2004), grazing by large free-ranging herbivores is used as a substitute for this species to counter grass and bush encroachment and subsequent loss in species richness. Our results show that the re-occurrence such of small refuge-living herbivores can profit from the presence of these large free-ranging herbivores and can create spatial heterogeneity in the vegetation (Figure 1, Bakker, 2005, Adler *et al.* 2001, Chapter 4 of this thesis), which in turn can increase biodiversity (for example Sumption & Flowerdew 1985.).

Acknowledgements

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Table 1. The symbols used in the model, their interpretation, units and, for parameters, their estimated values. All plant values are dried plant matter weight. Parameters are for rabbit as small herbivore, and heifers with a weight of 500 kg Parameter sources: [1] Iason *et al.* 2002.[2] Dekker, unpublished results. [3] based on 5 surviving young animal^{-1} year^{-1}. [4] Wallis de Vries & Schippers 1994. [5] Wallis de Vries 1996.

Variable	Description	value	units
$G(x)$	resource density at location x		g m^{-2}
x	distance from the refuge (x = 0 at the refuge)		m
r	intrinsic growth rate of the resource	0.4	-
K	maximum resource size	20-1000	g m^{-2}
$\tau(x)$	fraction of the time the animal grazes at location x		-
$I(x)$	intake of forage at location x		g DM
H	herbivore population size		number of individuals
$IR(x)$	intake rate at location x		g min^{-1}
I_m	maximum specific intake rate of small herbivore	0.25[1]	g min-1
	maturation effect:	0.61	
k_I	half saturation constant of intake rate of small herbivore	44[1]	g
	maturation effect:	400	g
q	forage density - quality coefficient	1/1500	-
$PI(x)$	intake rate after loss to vigilance time at location x		g min^{-1}
v_m	maximum fraction of time that is spent on vigilance, at infinite distance from the refuge. Can not be larger than 1; all time spent on vigilance.	0.1[2]	
$I(x)$	total amount foraged at distance x		g
R	required minimal daily intake for energetic equilibrium	69[2]	g
gc	gut capacity of small herbivore	1202	g
c	conversion factor of food to reproduction/mortality	0.00133	
m	density dependent mortality rate	0.0005	
Im_{lh}	maximum specific intake rate of large herbivore	38[4]	g min^{-1}
K_{lh}	half saturation constant of intake rate of large herbivore	90[4]	g
gc_{lh}	gut capacity of large herbivore	107005	g

Chapter 6

No effects of dominance rank or sex on spatial behaviour of rabbits

Jasja JA Dekker, Monique Groeneveld & Sipke E van Wieren

Abstract

The home range is an important measure of the spatial behaviour of animals. In rabbits (*Oryctolagus cuniculus*), spatial behaviour may be affected by social rank and sex. Subdominant animals are expected to have a larger home range and to forage farther from the burrow than dominant animals. Females are expected to have a smaller home range than males.

To test these hypotheses, we determined home range size and distance to the burrow during foraging within a low density, semi-natural rabbit population in the Netherlands, using daytime observations of marked individuals.

Individual median distance to the nearest burrow during foraging ranged from 3 to 16 m. Home range varied between 0.01 and 0.43 ha, which is the smallest home range area reported for rabbits in Europe. We found no difference in home range or foraging distance between males or females, or between dominant and subdominant animals.

We postulate that this is caused by an interaction of two factors: low animal density and high availability of high quality food. This meant that there was no need to compete for best or safest foraging locations, and males did not need to protect females in their group against other males. This is also our explanation as to why the home ranges in our study are the smallest recorded.

Introduction

The home range, “that area traversed by the individual in its normal activities of food gathering, mating and caring for young” (Burt 1943: 351), has been called the fundamental measure of space use of animals (Hemson *et al.* 2005). Home range size is useful for a wide range of applications, such as habitat analyses and modeling of population dynamics. It reflects a range of ecological processes, such as the effects of body size (Jetz *et al.* 2004), habitat quality (Herfindal *et al.* 2005) and mating behaviour (Sandell 1989).

In rabbits (*Oryctolagus cuniculus*), home ranges are usually situated around the burrow of the animals, which they use as nests for their young and as shelter against predators. It is to be expected that two characteristics of an individual animal can affect its home range size: social rank and sex. Rabbits have a linear dominance hierarchy for males and females separately (Von Holst *et al.* 2002). This hierarchy is attributed to competition for females in males, and competition for the best breeding facilities (burrows) in females (Cowan & Bell 1986, Von Holst *et al.* 2002). As larger distances from the burrow result in more time spent looking for predators (Chapter 2 of this thesis), one would expect rabbits to compete for the safest foraging locations close to the burrow, with the dominant animals winning this competition. Sex also has an influence on home range size: males maximize survival by defending the females living in a burrow. This results in larger home ranges than those of females (Cowan 1987).

In this paper, we focus on the influence of dominance hierarchy and sex on spatial behaviour. We determine the home ranges of a low density, confined population of rabbits in winter and test the hypotheses that males have larger home ranges than females, and that dominant animals have smaller home ranges and forage closer to the burrow than subdominant animals.

Methods

Study site and population

A population of wild rabbits was established in a 2 ha enclosure in Wageningen, The Netherlands (51.99° N, 5.66° E). The enclosure was fenced off with dense mesh and an electric fence. Three artificial burrows, consisting of a large wooden 2 x 5 m box, with ten interconnected chambers and eight PVC entrance pipes were placed halfway into the earth. The burrows were located 90, 100 and 130 m from each other (Figure 1). Self dug burrows were also in use during the study, and some separate pipes were sporadically in use as short-stay refuges. A regular grid of colour-coded pickets interspaced at 20m was used to facilitate determination of the locations of the

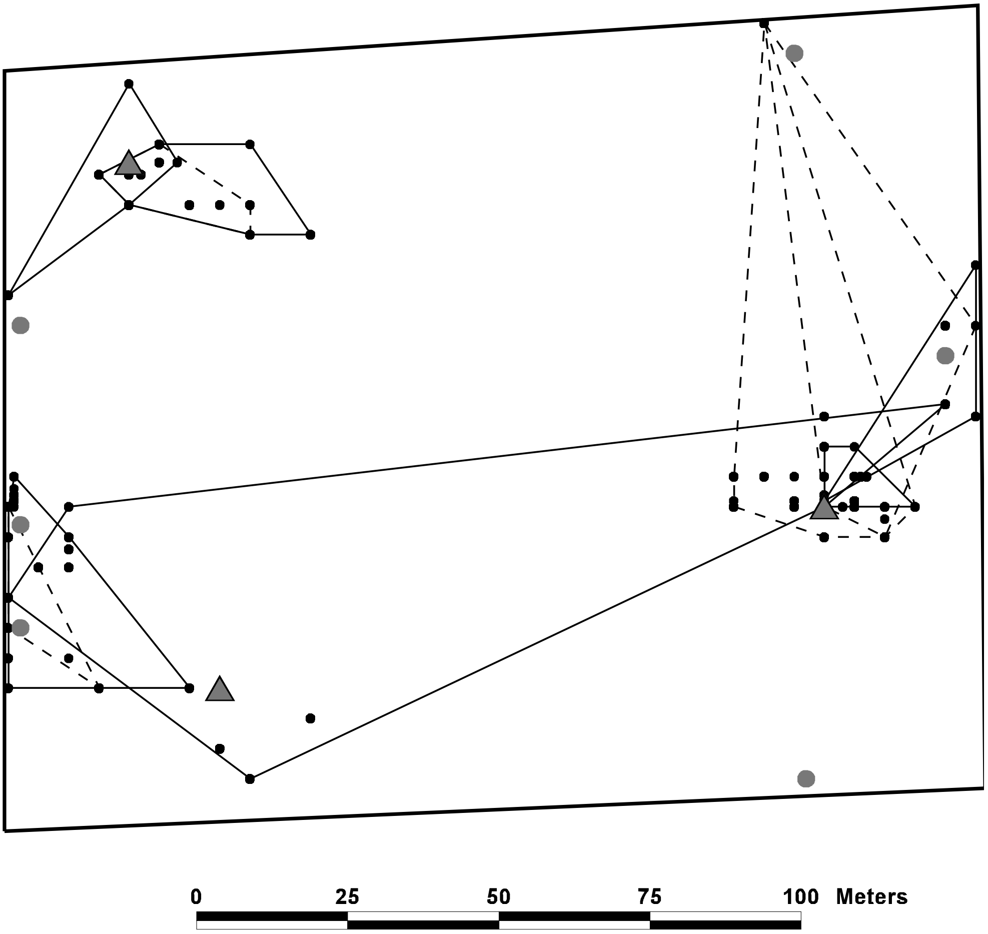

Figure 1. Burrows, rabbit locations and 100% MCP home ranges. The thick line represents the fence around the enclosure. Black circles stand for rabbit locations; grey houses for artificial burrows; grey circles for natural burrows. Male home ranges are solid lines; female home ranges dotted.

animals. At the time of the present study (January and February 2003), six male and four female adult wild rabbits (Table 1) were present in the enclosure, i.e. 5 animals ha^{-1}. The animals were marked using ear tags (Dalton Continental BV, Lichtenvoorde, The Netherlands) with an extra strip of aluminium with an individual colour coding and a number tattooed in the ear. Once a month, animals were trapped with live traps, and weighed. The animals were vaccinated against myxomatosis and Rabbit Hemorrhagic Disease.

The grassland in the enclosure consisted mainly of Yorkshire fog (*Holcus lanatus*), red fescue (*Festuca rubra*) and common bent (*Agrostis capillaris*). It was grazed by six heifers from April to December of 2002, which resulted in homogeneous, short vegetation. The grass height was mapped in January by 10 evenly distributed height measurements in 49 plots of 10 x 10 m across the enclosure. The actual height was measured by lowering a circular polystyrene disc with a central slot (a 'drop disc') down a vertical ruler until it rested on the grass (Stewart, Bourn & Thomas 2001). The distance to the ground was then read from the ruler. Vegetation heights within the plots were averaged, and then averaged over the plots. The average ± 1 SE over the plots was 4.9 ± 0.96 cm.

Dominance hierarchy

The dominance hierarchy was determined by observing which animal supplants which: it is assumed that the dominant animals initiate and win more aggressive interactions than subdominant animals (Martin & Bateson 1993). We observed the animals using a focal sampling method, observing each animal for 30 minutes during 10 days. During these scans we noted the initiator and winner of aggressive interactions. Based on these data, we separately ranked the males and females by the number of supplantments. We tested for difference in weight between dominant and subdominant animals using an ANOVA.

Spatial behaviour

The locations of the animals were estimated using an instantaneous scan sampling design: positions of all animals are determined ('scanned') at a regular time interval. We scanned every 30 seconds, between 15:00 to 17:00. We did this over 13 days, between the 17th of January and the 11th of February 2003. Locations were entered in a Geographic Information System (ArcView 3.2, Environmental Systems Research Institute Inc., Redlands, USA) for further analyses.

Home ranges were estimated using the minimum convex polygon (MCP) method (Mohr 1947): the home range is estimated by the minimum size polygon that encloses all the locations of an individual. This method is a robust non-parametric method that allows comparisons with most other studies. The MCPs were calculated using the software 'Home Range Extension' for ArcView (Rodgers & Carr 1998). We also calculated the distance from each location to the nearest artificial or self dug burrow.

As home range size and distance to the burrow were not normally distributed, we tested for differences in home range and distance to burrow between males and females and dominant and subdominant animals using a two-tailed Mann-Whitney U-test. Since we used each dataset for two tests, we applied a Bonferroni-correction to the critical values, rejecting null hypotheses only when P-values were below a critical value of $\alpha = 0.025$. We used Spearman's rank correlation coefficient to test for the relation between body weight and home range.

The study was assessed and approved by the Institutional Animal Care and Use Committee of Wageningen University (experiment code 1025).

Results

Dominance hierarchy

During this study, rabbits formed two groups of two males and one female, and one group with two males and two females. The males of each group showed a clear linear ranking (Table 1). In the group of four animals, the females also showed a dominance ranking. Dominant animals were not heavier than subdominant animals ($F_{1,7}$ =0.543, P=0.49). One male animal, Geen1, moved between several burrows, but was only interacting with animals from one group. There were no aggressive interactions between males or females of different groups.

Spatial behaviour

The animals stayed near the artificial or natural burrows (Figure 2): they were foraging within 5 m of a burrow in almost 50% of the observations. All home ranges contained at least one artificial burrow (Figure 1). The animal, Geen1, that moved between groups had a relatively large home range.

The individual median distance from the nearest burrow ranged from 3 to 16 m (Table 1). There was no difference in median foraging distance between male and female animals (U=7, Z=-1.14, n_{males} =6, $n_{females}$ =4, P=0.35) or between dominant and subdominant animals (U=3, Z=-2.08, n_{dom} =6, n_{subd} =4, P=0.07).

Table 1. Home range and median distance to the nearest burrow during foraging activity between January 17 and February 11, 2003. Home ranges were estimated using 100% MCP methods (see text). Dominant: 1 = dominant, 0 = subdominant animal. n = number of locations used for calculation of the 100% MCP home range. [a]: weight measured one month before the study.

Rabbit	Group	Sex	Dominant	Weight (g)	MCP (ha)	n	Median distance (m)
Oranje	1	M	1	1580	0.06	565	5
Geen1	1	M	0	-	0.43	151	16
BZZ	1	F	1	1875	0.02	218	3
WWB	2	M	1	1630	0.03	243	6
WRB	2	M	0	1710	0.03	94	5
RGG	2	F	1	2020	0.02	271	5
ZRZ	3	M	1	1710	0.01	231	5
GRW	3	M	0	1220	0.03	103	8
Geen3	3	F	1	1500	0.14	333	5
GBG	3	F	0	18	0.13	400	7

MCP home range size ranged from 0.01 to 0.43 ha (Table 1). Home ranges of males totally overlapped those of females in two groups (Figure 1). Two females from group 3 made excursions far from the burrow, which resulted in a larger home range (Table 1, Figure 1). The MCP home ranges did not differ between males and females (U=12, Z=0, n_{males} =6, $n_{females}$ =4, P=1.0), nor between dominant and subdominant rabbits (U=7, Z=-1.07, n_{dom} =6, n_{subd} =4, P=0.35). There was no relation between weight of an animal and its home range (Spearman's correlation coefficient, P=0.19).

Discussion

Although the population studied is not a natural population of rabbits, we feel that the results are comparable with natural free-living populations: the animals showed similar behaviour compared to wild rabbits in natural conditions in the way they reacted to each other and to predators.

As in other studies of rabbit home ranges, all the observations were done during day time when the animals were most active. We assume that space use is not fundamentally different at other times of the day. This assumption is supported by anecdotal observations and by pellet counts: at both night and in the day time

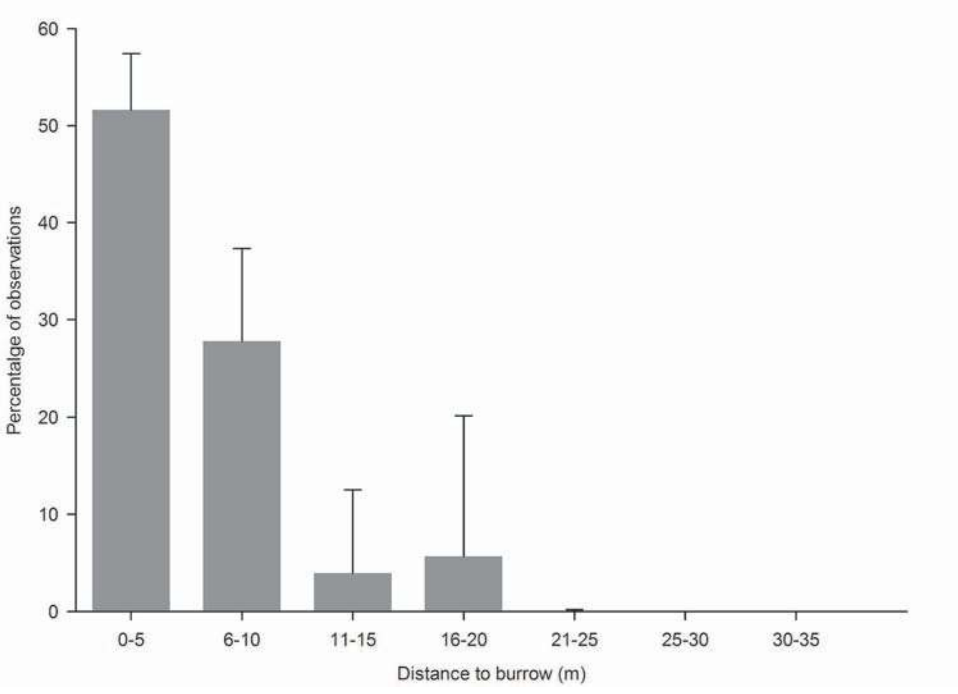

Figure 2. Frequencies (median and 3rd quartile) of observations per distance to the nearest burrow during foraging (n rabbits = 10). The observations were classified in 5-metre classes per individual animal and recalculated to percentages of total observations that fell in that class.

animals also stayed close to the burrow. Faecal pellet numbers roughly reflect spatial use of the population, and were highest close to the refuge, especially when corrected for latrines (Dekker, unpublished data).

Effects of rank and sex on spatial behaviour

Three other European studies compare the home range size of males and females separately. Cowan (1987) and Mcdonald (1989) found that home ranges of males were larger than those of females. Immink (1982) also found indications for this, but he could not test for differences due to a small sample size. In our population, there was no difference in home range size for the two sexes, although there were indications that males did defend the females against the other males living in the same burrow: home ranges of males entirely overlapped those of females in two of the three groups. In our study site, the animals formed pairs instead of breeding groups, often with an additional male, probably due to the low density. In such cases, there is no need to defend several females. Defending one female against other males will hence not lead to a difference in home range between the sexes.

We detected no difference in home range size or in distance to the burrow between dominant and subdominant animals. Again, we attribute this to the absence of competition due to the abundance of resources, in this case foraging space close to the burrow.

Sex and rank can interact however, especially during the breeding season, at high densities. Dominant male rabbits then have a larger home range than subdominant males, in the order of tenths to hundredths of hectares. This is probably caused by defending several females against mating attempts. Subdominant and dominant females have been found to have a much smaller home range (Myers & Poole 1961). The same dominance effect was probably a factor in a study of three rabbits in a dune area in the Netherlands. Animals with larger body weight, which may reflect dominance rank, had larger home ranges (Immink 1982). So, for dominant males the defence of females outweighs risk of being predated.

The subdominant male animal with the relatively large home range, Geen1 (Table 1), is probably a so-called floater: a low ranking, (often) young, male animal without a fixed territory. This animal moved between two artificial burrows, foraging farther from these burrows, and was often chased away by the males from the two groups. Its median distance to the nearest burrow is also larger than that of the other rabbits. Floaters occur in many species, from lizards (Stapley & Keogh 2005) to red foxes (Vulpes vulpes) (Dekker, Stein & Heitkönig 2001). Lockley (1961) describes this phenomenon amongst rabbits. In that study, the floaters were in bad condition, whilst in our study, the weight of the animal was well within the range of the other animals.

Comparison of spatial behaviour in European populations

The home range size we observed in our population is the smallest found in Europe. Macdonald (1989) found home ranges of 0.13 ha for males and 0.11 ha for females in Holy Island, UK, but used a 95% harmonic mean estimator, which makes it difficult to compare these results to our study. Rödel (unpublished data) found MPC home ranges of 0.35 ha for females just before the onset of breeding and of 0.27 ha for females during the breeding period, in a confined population of 38 animals ha^{-1} in Bayreuth, Germany. Immink (1982) reported home ranges of 0.53 ha for male rabbits and of 0.44 ha for female rabbits in a dune-area in the Netherlands. A comparison with this data is difficult since this author used a unconventional method to estimate home ranges. Cowan (1987) reported an average MCP home range of 0.71 ha for males, and 0.44 ha for females for rabbits on chalk grasslands in the south of the UK. Henderson (1979) found MCP home ranges of 0.3 ha to 0.8 ha for non-breeding females, using trapping locations. Other studies, performed in Scotland, found even larger home ranges (Hulbert *et al.* 1996, Kolb 1991a, Kolb 1991b).

In our study, the animals concentrated their foraging close to the burrow. The only other authors that report the distribution of activity as a function of distance to the burrow are Armstrong (1987, sightings of animals), Bakker *et al.* (2005, as number of pellets and counts of movement) and Monclús & De Miguel (2003, as number of pellets). Compared to these studies, our data seem most skewed towards the burrows.

We postulate that the small home range and skewness of foraging distance to the burrow found in our study are the result of an interaction between two factors: population density and food quality. The density in our population was 5 animals ha^{-1}, which was the lowest of all the above mentioned studies that report rabbit density: density was 15 animals ha^{-1} at Cowan's (1987) study site, 22 animals ha^{-1} at McDonald's (1989) study site, and 38 animals ha^{-1} in that of Rödel (H. Rödel, unpublished data). It is possible that with higher densities, lower ranking animals are forced to forage farther from the burrow, increasing the average home range. Another possible consequence of high density is an increasing number of floaters in the population, which results in a larger average home range. In a dense population rabbits do not form pairs but breeding groups of males and several females. In that case a male will have to increase its home range size because it has to defend more than one female.

In sub alpine areas of Australia, home ranges expand when growth rate of the vegetation declines (Myers & Bults 1977). It is therefore surprising that in our study winter home ranges were so small, when compared to the year-round ranges in other studies. This could be caused by the type of vegetation in our enclosure: the enclosure was grazed by cattle all summer. Grazing by larger herbivores can keep vegetation in a short state, with many tillers and nutrient-rich leaves (McNaughton 1984), a structure that rabbits prefer for foraging (Iason *et al*. 2002).

Conclusion

Although the rabbits in our study showed a dominance ranking, this did not result in differences in home range size or distances to the burrow between sexes or ranks, as reported in other papers. We attribute this to the low population density and good food quality, allowing animals to freely choose their feeding location. Our study was undertaken in a ‘boring’ time of the year for the researcher, but a calm time for the animals: there was no competition for space or females. This corroborates with Von Holst *et al.* (1999), who show that in winter months the number of aggressive interactions, offensive behaviour between individuals and stress hormone levels of rabbits are much lower than during mating and breeding in spring and summer.

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Chapter 7

Large herbivore grazing induces a shift in activity patterns of small herbivores

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Abstract

Studies of herbivore communities mostly are concerned with trophic interactions, such as large herbivores facilitating for or competing with small herbivores. However, by grazing, large herbivores modify vegetation structure, potentially changing the microhabitat for small herbivores, which could result in non-trophic interaction. In this paper, we test if this occurs in the European wild rabbit *Oryctolagus cuniculus*. The European rabbit prefers vegetation cover during the day and open spaces at night. This means that animals living in an area of ungrazed, dense, tall vegetation should become active earlier than animals living in a grazed, open area.

We tested this hypothesis by measuring the activity patterns of one population of rabbits living in a grazed enclosure and one population living in an ungrazed enclosure. Contrary to our prediction, the population of the field with short vegetation showed an earlier peak in activity than the population of the field with tall vegetation. We attribute this to an interaction of relatively low ambient temperatures and a lower number of predators.

We conclude that by grazing, large herbivores influence small herbivores not only through trophic interactions but also through physical ecosystem engineering: the alteration of the amount of cover.

Introduction

There is an ongoing debate about what shapes herbivore communities. This debate has primarily been concerned with indirect trophic interactions, such as facilitation and competition through food. When a limited resource must be shared, large and small herbivores will compete. Conversely, in more productive systems, grazing by large herbivores could alter vegetation from being old, woody and hard to digest to being more nutritious, easier to digest and palatable, facilitating small herbivores (Prins & Olff 1997, Arsenault & Owen-Smith 2002, Bakker *et al.* 2004).

Apart from such trophic interactions, animals can also affect each other through indirect non-trophic interaction. An example of such interaction is that of physical ecosystem engineering, the modification of the physical structure of the environment (Wilby, Shachak & Boeken 2001). There is potential for such interaction in large and small herbivores: grazing modifies vegetation structure, and for many small herbivores vegetation not only functions as food but also as physical cover against predators (Mitchell & Kirby 1990, Manson & Stiles 1998, Iason *et al.* 2002, Bakker *et al.* 2005).

The European rabbit is such a small herbivore. This species is reported to prefer vegetation cover in the day but open spaces at night (Moreno, Villafuerte & Delibes 1996, Gibb 1993, Martins *et al.* 2003). It was suggested that this shift in microhabitat preference is caused by a change in predation risk: this risk would be greatest in open areas during the day due to diurnal birds of prey, but would be greatest in dense vegetation during the night, due to nocturnal carnivorous mammals (Moreno, Villafuerte & Delibes 1996).

In this paper, we focus on how vegetation structure affects the activity patterns of European rabbits. European rabbits are mostly active around dusk: emergence from burrows occurs rapidly around sunset (Southern 1940, Kolb 1986, Wallage-Drees 1989) or the numbers of rabbits that are active show a rapid rise through the afternoon, peaking at sunset (Dunnet 1957, Mykytowycz & Rowley 1958, Fraser 1993). Predation risk strongly affects these patterns. For example, daytime hunting by man can result in later emergence times (Dunnet 1957).

If there is a preference for dense vegetation during the day and for open areas at night, it is to be expected that rabbits that cannot choose between open and closed vegetation structures and therefore cannot strive for a predator-free-space, will strive for predator-free-time. We predict that rabbits living in an area of short and open vegetation will show a relatively late activity peak, with more activity at night, and rabbits living in an area of tall vegetation will show a relatively early activity peak, ceteris paribus.

In order to test these predictions, we compared activity patterns of two rabbit populations in a temperate climate: a population living in an area with dense and tall ungrazed herbaceous vegetation and a population living in an area with vegetation kept short by large herbivores. As these two populations were separated, but were living within an area of 4 hectares, emergence times were similarly affected by sunset and sunrise times, human disturbance and predators present.

Methods

Study site and population

Two populations of wild European rabbits were established on two grasslands of 2 hectares in Wageningen, The Netherlands (51° 58´ N, 5° 40´ E). The grasslands were enclosed with dense mesh and an electric fence. Three artificial warrens were placed in each field. These warrens consisted of big wooden boxes, dug halfway into the ground, with separate chambers and PVC entrance pipes. The animals could dig additional burrows and breeding plugs. One of the fields was grazed by nine heifers from April until October, while one remained unmanaged. Temperature, measured at the Wageningen University Meteorology field station 2 km away, was never over 20°C during the study. Wild European rabbits were introduced in these fields, with respectively 12 and 9 adult animals living in the grazed and ungrazed enclosures at the time of the study.

The animals were cared for in accordance to the Guide to the Care and Use of Experimental Animals of the Canadian Council on Animal Care and the experiment was assessed and permitted by the Institutional Animal Care and Use Committee of Wageningen University, Wageningen, The Netherlands (entry code 2004036.b), as required by the Dutch Law on Animal Experiments

Vegetation

The dominant plant species in the two fields were the grasses Holcus lanatus and Agrostis capillaris. Vegetation height was mapped in October 2002 by measuring height in plots of 10 meters x 10 meters that were laid out uniformly every 20 meters across the two fields. Height was measured using the drop disc method (Stewart, Bourn & Thomas 2001): a circular polystyrene disc with a central slot, with a diameter of 9 cm and a weight of 6 grams, was lowered down a vertical ruler until it was resting on the grass. The distance to the ground was then read from the ruler. Height was measured 10 times per plot. To avoid pseudo replication, the average of the 10 measurements per plot was used for calculating mean vegetation height per field.

Rabbit activity

The animals' activity was measured from 25 September 2002 until 22 December

2002 using infrared trail monitors (Trailmaster 1500, Goodson & Associates, Inc., Lenexa, Kansas, USA). These monitors consist of a transmitter and a receiver of infrared light, with the receiver connected to a time logger. When the infrared beam between the transmitter and the receiver is broken, the time and date of that 'event' are logged. The infrared trail monitors were mounted on poles at two artificial burrows per field in such a way that animals had to pass a trail monitor to leave the burrow mound. As the animals were mostly active around the burrow (Dekker in press), we assume that the occurrence of events stands for activity of these rabbits and not only for emergence.

Data analysis

We compared the distribution of events over the day in the two populations using a Mardia-Watson-Wheeler test for differences between two samples of circular data (Batschelet 1981). Because this test does not indicate the difference between samples, we also analysed the distributions of activity over the day using two derived measures of the activity patterns: time of onset of daily activity and time of daily peak in activity. These measures were derived by classifying the data into 15 minute bins. The daily peak of activity was defined as the bin in which the maximum number of events of that day (0:00-23:59 hours) occurred. Onset of activity was defined as the first of a consecutive series of three bins in which the number of events is at least 20% of the peak number of events of that day. We tested for differences in mean vector of these two derived variables between the two populations using a Watson-Williams F-test (Batschelet, 1981). Due to the circular nature of the data, mean vectors instead of means were calculated for times of peak activity and onset of activity.

Results

Heifer grazing had a clear effect on the vegetation: in the grazed field, the vegetation was shorter than in the ungrazed field ($F_{1, 103} = 279.93$, $P < 0.001$). In October 2002, mean height ± SD was 6.4 ± 3.26 cm (n=49) in the grazed field and 23.8 ± 6.50 cm (n=58) in the ungrazed field.

The only predators seen in the fields were buzzard *Buteo buteo* and polecat *Mustela putorius*. Buzzards were usually seen perched on posts, and sometimes walking through the field.

In both fields, the distribution of events over the day showed that there was little activity in the morning, but a long period of activity in the evening (Figure 1). The distribution of activity over the day seemed to reach a maximum earlier in the grazed field. There is a significant difference in the distribution of activity over the day between the populations ($n_{ungr}=22164$, $n_{gr}=23011$, $W=462.23$, $P<0.001$).

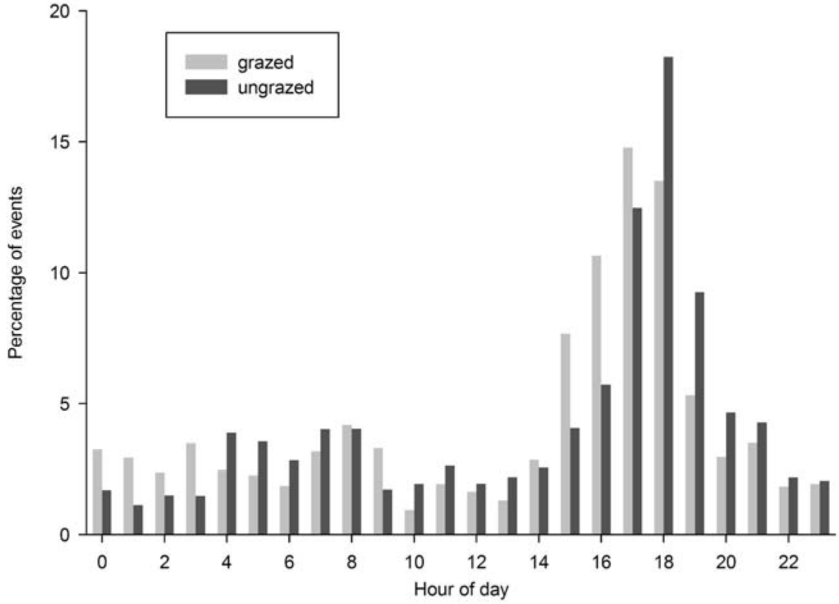

Figure 1. Distribution of all events over the day during the experiment per treatment.
▨ : activity of the rabbit population on the grazed field with short vegetation.
■ : activity of the rabbit population on the ungrazed field with tall and dense vegetation.

There was no difference in mean vector of the onset of activity between the rabbits of the two treatments, but the distribution of onset times was significantly different between the treatments ($n_{ungr}=68$, $n_{gr}=48$, W=28.22, P<0.001), with a mean vector (± 95% CI) of time of onsets of 17:27 ± 0:59 hour in the rabbit population of the ungrazed field and 16:10 ± 1:19 hour in the rabbit population in the grazed field.

Mean vector of time of peak activity significant differed between treatments ($n_{ungr}=78$, $n_{gr}=78$, W=5.00, p=0.03), with mean vectors ± 95% CI of peak activity of 19:07 ± 1:46 hour in the ungrazed field and 17:15 ± 1:07 hour in the grazed field.

Discussion

The rabbits in our study showed a pattern in activity that is common for the species: most activity in the afternoon, with a peak around sunset (Southern 1940, Dunnet 1957, Mykytowycz & Rowley 1958, Kolb 1986, Wallage-Drees 1989, Fraser 1993). There were, however, clear differences in both the distribution of activity over the day and the time of peak in activity between the two rabbit populations. The activity peak was earlier in the afternoon in the field with short vegetation than in the field with tall vegetation: timing of activity and microhabitat affect each other. But contrary to our prediction stemming from the shift in microhabitat preference over the day (Moreno, Villafuerte & Delibes 1996), emergence and the peak activity in the afternoon occurred earlier in the grazed fields with short, open vegetation than in the field with tall vegetation. This unexpected result may have been caused by a less diverse predator community than in the study area of Moreno, Villafuerte & Delibes (1996). In Chile, where rabbits occur but predators are much less numerous and diverse than in Spain, habitat use by rabbits in early spring was skewed towards sites with low shrub cover, while it was skewed more towards high shrub cover in Spain (Jaksic & Soriguer 1981, Jaksic personal communication). The only predators seen at our field site were buzzard and polecat, whereas 29 species of predator were identified in Spain (Jaksic & Soriguer 1981). Adding to this, buzzards are active in the daytime and catch prey from perches, on foot or from flight (Cramp & Simmons, 1980) and prey on rabbits of up to 60 days old (Bijlsma, 2004). The rabbits were all adult at the time of this study, so the only predator actually able to capture the studied animals is the polecat. Polecats chiefly use their sense of smell for finding and stalking their prey (Zielinksi 2000). If the rabbits allocate their activity to the time of least predation risk, they should shift their activity to daylight, when they can detect stalking polecats easily. This is corroborated by a study at a site in the Netherlands, where plots treated with faeces of mink, a species closely related to the polecat, caused a relative shift in the number of visits to these plots from night-time to daytime (Bakker *et al.* 2005). In another study, done in the UK, rabbits also preferred plots with short grass to those with tall grass during the daytime (Iason *et al.* 2002).

However, there is another potential factor in the temporal difference in daytime and night-time habitat preferences, namely heat. The preference for cover in the daytime may be caused not only by the need to avoid predators, but also to avoid the heat of the sun. That heat can cause a preference for shadow - i.e., vegetation cover - during foraging was elegantly shown for degus Octodon degus in Chile (Bacigalupe *et al.* 2003). Rabbit activity over the day is indeed negatively influenced by high temperatures (Villafuerte *et al.* 1993), and two of the three studies that detected preference for cover during the day and preference for open areas at night (Moreno, Villafuerte & Delibes 1996, Martins *et al.* 2003) were performed in warm climates. A third study was performed in a more temperate region. Here, the overall difference in microhabitat use between day and night were less pronounced than in the other two, and less so in winter (Gibb 1993). This hints that both predation and temperature are factors in the temporal patterns in microhabitat preference.

It seems that the temporal pattern of preference for cover versus open areas is different in temperate climates than in Spain. The observation that cover is safe during the day but dangerous at night in Spain is not a general pattern for the species. We postulate that this is because, apart from avoidance of predation, avoidance of heat also is a factor in microhabitat selection. The present study could be seen as the control treatment in a test of this hypothesis: temperatures were not high and there seemed to be little predation risk (Table 1).

The effects of predation risk on behaviour are complex and difficult to study (Lima & Dill 1992). To gain more insight in the causality in temporal shifts in microhabitat preference, an experiment is required in a region with low predation risk, in which perceived predation risk can be manipulated or at the least measured reliably, and which is repeated in a hot summer and a mild winter. Only then can the interacting effects of predation and temperature on microhabitat use be separated.

Large herbivore grazing and activity of small herbivores

From the present study, it is clear that altering vegetation structure in the environment of large herbivores not only results in trophic competitive or facilitative interactions with small herbivores (Arsenault & Owen-Smith, 2002), it can also affect the behaviour of small herbivores. By grazing, large herbivores induced a shift in timing of activity by small herbivores. We expect that this impact on activity patterns is more pronounced in the central place foraging rabbits than it is in free ranging small herbivores: the latter are more free to adapt to a habitat that becomes less suitable by moving to other habitat, as they have not invested energy in the construction of a burrow system.

Table 1. Effects of climate and predation risk (– : low, + : high) on timing of activity and on microhabitat preference of the European rabbit (Oryctolagus cuniculus). [a] Jaksic and Soriguer 1981, [b] the present study, [c] Moreno et al. 1996, collected in summer d Martins et al. 2003, X: no such study performed to our knowledge.

		Climate	
		Temperate or Mediterrenean (in winter)	Mediterranean (summer)
Predation	-	- higher abundance on low cover than high cover, over full day[a] - active earlier in day on short grassland than on tall grassland[b]	x
	+	x	- daytime: preference for cover night-time: preference for open areas [c, d]

Implications for management and monitoring
The fact that vegetation structure greatly influences the activity distribution of rabbits has several implications for the monitoring of these animals. Our results indicate that sight counting, a widely used and relatively quick and cheap monitoring technique (Poole, Cowan & Smith, 2003), is only suitable for within site comparisons. Even then, changes in vegetation could result in trends in counts that do not represent trends in the population. Also, counts are often done at the same time before sunset in order to standardize them, but our results indicate that onset of activity and peak of activity are independent of sunset. Cross-site comparisons should be done with caution, as our results indicate that counting at sites that differ in habitat, even when done at the same time, may result in counting different proportions of the various populations. In order to compare population density between habitats, standardized faecal pellet counts are a more robust, but more time consuming, method.

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Chapter 8
Synthesis

Vigilance and foraging patterns

This thesis started with a number of questions on patterns in foraging of refuge-living herbivores: can avoidance of predation explain the gradients in grazing around refuges? And how do characteristics of the forage, such as nutrient content, digestibility, density, productivity and growth rate influence grazing patterning? In my study, I used the European rabbit (*Oryctolagus cuniculus*) as a model species to investigate these questions.

Like all animals, herbivores must trade off the costs and benefits of foraging. For refuge-living herbivores (such as rabbits), these costs were expected to be spatially variable: perceived predation risk is higher as the animals are foraging farther from their central place. An experiment showed that vigilance did increase as the distance of the animal to its refuge increased (Chapter 2), which in turn resulted in a decrease in intake rate with distance to the refuge (Chapter 3). This means that for refuge-living herbivores, the intake rate is a not a function of plant density alone, but of both plant density on a location and its distance to the refuge. As a consequence, for refuge-living herbivores not all forage that is present is necessarily obtainable.

The costs of vigilance resulted in a preference for foraging closely to the refuge, when food was distributed homogeneously (Chapters 2 and 3). This causes refuge-living herbivores to make the spatial distribution of resources more heterogeneous by foraging (Chapter 3), in contrast to free ranging herbivores, which make it more homogeneous (Kotler, Gross & Mitchell 1994).

Depletion and forage quality

In an indoor experiment with controlled forage quality and quantity (Chapter 3), I showed that rabbits initially prefer the nearest patches to the refuge, where costs of vigilance and predation risk are lowest. However, depletion has a pronounced effect on the feeding preference on the longer term. Rabbits deplete patches until intake rate falls below the intake rate at the farther patch with higher vigilance costs. Then, they move to this more distant patch. After a day of foraging, a gradient in resource density is the result. Higher quality and quantity of food result in more skew of foraging towards the refuge. In field situations, refuge-living animals are thus predicted to forage farther from their refuge only if the quality of food there is higher, and to forage closer to their refuge at more productive sites.

Population density

To gain more insight in how population density of small refuge-living herbivores could be influenced by plant productivity and how they would be affected by different relations between forage intake rate and plant density, we constructed a simulation model based on the experiments described in this thesis. This model also allowed me to study how grazing by large herbivores would affect population densities of small refuge-living herbivores.

The model showed that adding vigilance-induced spatial variance in intake rate does result in the grazing patterns described in the literature and the experiments in previous chapters. These grazing patterns are strongly affected by plant productivity of a site: an increase in productivity resulted in foraging on smaller areas around their central place by the population. In dynamic populations of refuge-living herbivores, the area grazed by the population decreased as population density increased. In contrast, in free ranging herbivores the area grazed increased with population density (Chapter 5).

Variable plant growth

An important trait of plants is that they change: whilst (re)growing, they change in density, but also in quality as forage and by regrowing, they can “restore” parts removed by herbivores. With a constant growth rate and constant herbivore density, and thus a constant cropping rate and regrowth, a stable plant-consumer interaction would result. However, in plants, growth is seasonal, which will affect this interaction. To study how seasonality in growth rate affects refuge-living herbivores, we staged rabbits in a sward strip for one growing season (Chapter 4).

In this experiment, we found that in spring, when growth rate is high, the animal can keep foraging close to the burrow: a fixed area provides enough forage. When growth rate declined, however, the animals depleted the closest locations and had to move farther to forage. Therefore, the area that is used for grazing increased with decreasing growth rate.

So, during the peak of the growing season, the animals were able to create a grazing lawn of fixed size, whilst the more distant parts of the sward mature and deteriorated. As growth rate slowed down at the end of summer, the grazing lawn did not suffice, the animals had to move out and forage on the low quality parts of the sward, resulting in a drastic increase in the time animals used for foraging.

The experiment ended in October, at the end of the growing season. At this point, the sward had turned into a gradient of quality and quantity: from short, relatively high quality grass close to the refuge to tall, matured and low quality sward farther away. This maturation is not uncommon in the field, but free ranging

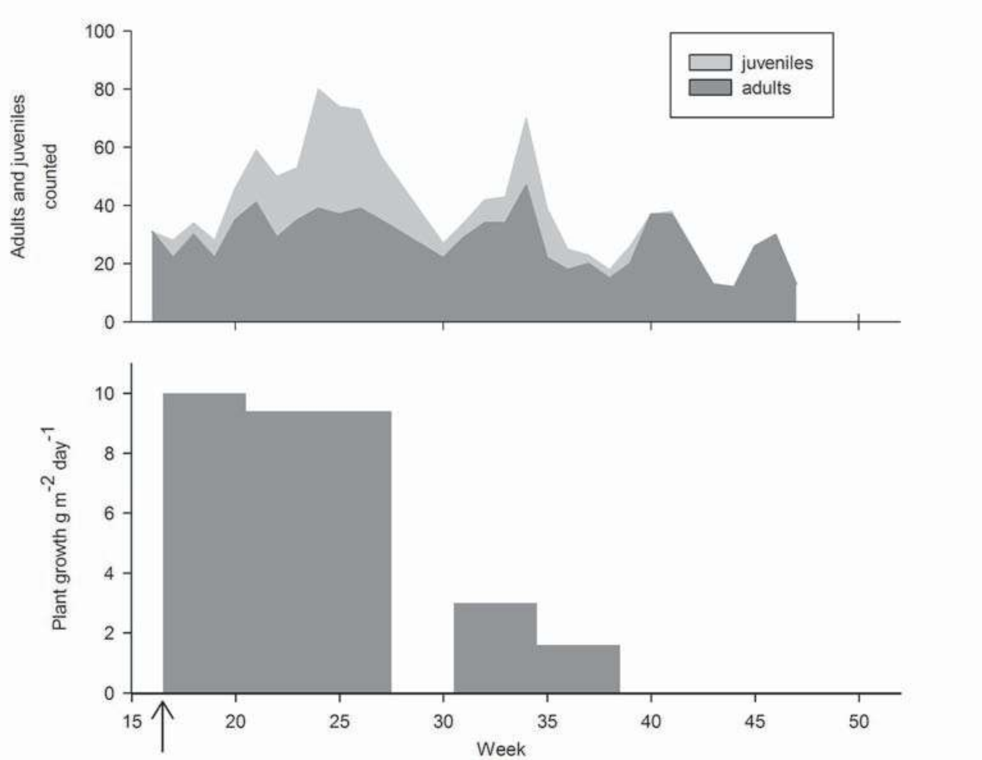

Figure 1. An example of the population dynamics of rabbits over the year and of a growth pulse of *Lolium perrene*. Weekly counts of the number of juvenile and adult rabbits were done on a fixed transect on ‘the Dreijen’, Wageningen in 2006 (Jasja Dekker, unpublished results). Sward growth rate was measured in rabbit-grazed plots at the Achterberg, Wageningen in 2004 (Chapter 4 of this thesis). Note that the data were gathered in different years, but in the same area. Both patterns are typical for respectively rabbit population growth patterns and grass growth patterns: a peak in spring and early summer, with a second small peak later in the year.

herbivores, such as large savanna grazers or geese, and also animals with a large home range, can move to other sites with higher quality forage or even migrate to areas where growth rates are high: ‘riding the green wave’, as Van Der Graaf (2006) described it. Rabbits or other refuge-living herbivores cannot move to greener pastures, as they are stuck to their burrow. Ideally, cattle or other large herbivores would graze the sward at the end of summer to ‘reset’ the area, but this is not always the case. How do refuge-living herbivores deal with this ‘drying up’ of their food source?

In fact, the outlook in autumn might not be as bleak for refuge-living herbivores in the field as one would extrapolate from our experiment. In the experiment, the population was stable: we stocked two non breeding females per sward strip, whilst in the wild, rabbits are proverbial reproducers and populations show strong peaks: births are in spring and summer, mortality acts mostly in autumn in winter (see for example Parer 1977, Gilbert *et al.* 1987). If these peaks coincide with the changes in growth rate, the dynamic population may be able to keep a fixed area short, and in that way keeping it in a palatable, nutrient rich condition: they create a grazing lawn.

Data on population dynamics, plant growth rates and areas used by the animals from a single area are disappointingly scarce. However, combining the best available data shows that this mechanism could function: peaks in rabbit offspring coincide with peaks in grass growth (Figure 1). If this were true, populations would be vulnerable to changes due to, for example, disease: a strong decline at the wrong time of the season would make the herbivores lose control after all.

Still, more solid data, not only of population dynamics and grass growth rates, but also of grazing distribution throughout the year, is required to really understand how continuous seasonality in resource quality and quantity affects the population dynamics of resident herbivores over multiple seasons, and whether a synchronisation of reproduction and plant growth pulses can avert the negative effects of sward maturation.

All in all, the question can be metaphorically worded as: are rabbits buoys instead of surfers, i.e., do they ride the green waves whilst staying at the same place?

Vigilance, social interactions and spatial patterns in grazing

The experiments discussed in this thesis were performed either with solitary rabbits (Chapters 2 and 3) or with two non-breeding animals of the same sex (Chapter 4) and focussed on effects of forage characteristics and space on the refuge-living herbivore, and so neglected a potentially important factor: intraspecific interactions. Intraspecific (social) interactions can also affect space use in foraging animals, for example by affecting vigilance. This is especially the case in animals that forage in groups. Foraging in groups can have costs, such as resource competition, and benefits, such as vigilance sharing (Krause & Ruxton 2002). Both are expected to affect spatial distribution of foraging. Again, this is illustrated by reviewing studies on rabbits.

When foraging in groups, animals can take turns in looking for predators. That way, groups of animals can reduce individual vigilance by sharing it (many eyes theory, Roberts 1996). Additionally, group formation can result in predator confusion, predator swamping or dilute encounter rates (Krause & Ruxton 2002). Consequently, grouping could reduce the effects of vigilance on the foraging behaviour of refuge-living herbivores: a group can therefore exploit locations farther from the refuge, which would not yield high enough intake rates due to high vigilance for a solitarily

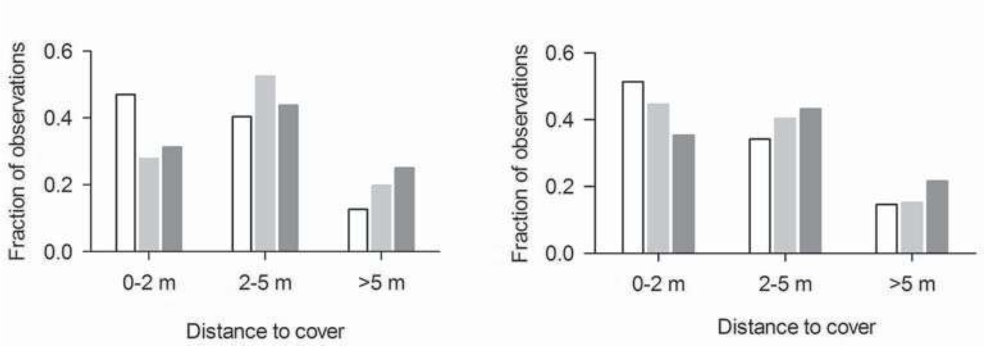

Figure 2. The effect of group size on its distance from cover at dusk in dense (left graph) and sparse (right graph) vegetation. □ : solitary animals, ▨ : pairs, ■ : groups of three or more animals. Data from Villafuerte & Moreno (1997).

foraging animal.

In rabbits, pairs indeed show lower vigilance per capita than solitary animals (Roberts 1988) and groups are observed farther from cover more often than solitary animals or pairs (Villafuerte & Moreno 1997; Figure 2). This pattern was clearest in sparse vegetation: here, using vigilance would be more prone to have results: advancing predators are spotted with more success, and members can spot each others reactions to predators more easily. However, the formation of groups during foraging will not necessarily result in a larger area grazed: when foraging in groups, animals are packed closer and graze a smaller area than when foraging solitarily.

Still, foraging in groups does not always lower vigilance, especially if members in a group compete for resources, such as food (Krause & Ruxton 2002) or mates. In rabbits in the breeding season, males decrease the rate of being vigilant when foraging with their mate compared to when foraging alone, but increased it when animals of the same sex were near (Roberts 1988). Roberts focussed on the vigilance of male animals, but as females compete for breeding burrows (Cowan & Bell 1986), it is likely that they will behave in a similar fashion. It is to be expected that this behaviour causes a population of animals foraging in pairs to distribute itself more evenly than would be predicted from vigilance-avoiding selection of foraging locations, and more than solitary animals. Interestingly, our enclosed population of rabbits showed no difference in vigilance between males and females or between dominant and subdominant animals outside the breeding season (Dekker, unpublished results).

Concluding, not only interspecific (Chapters 5 & 7), but also intraspecific interactions influence vigilance in foraging rabbits and in other species of herbivores (Krause & Ruxton, 2002). The effects of this interaction changes with breeding status of the population, with population density, with social rank of the individual animal and with food quantity and quality. The potential changes in vigilance level caused by these interactions are especially important for refuge-living herbivores: a change in vigilance can drastically alter the spatial layout of obtainable forage. That way, the optimal locations to forage can shift. How exactly the different factors interact requires additional research.

Facilitation

Small herbivores generally require short, high quality swards, whereas large herbivores need taller, low quality swards (Bell 1970, Jarman 1974, Prins & Olff 1998). Therefore, large herbivores can lower biomass density and increase sward quality by grazing, facilitating small (refuge-living) herbivores (Prins & Olff 1998, Farnsworth, Focardi & Beecham 2002).

In facilitation, one can distinguish between the short term process and the long term process: feeding facilitation and population facilitation (Arsenault & Owen-Smith 2002). The improving of vegetation for small herbivores by large herbivore grazing is feeding facilitation (Figure 2a), which can express itself as a preference for patches grazed by large herbivores, higher food intake rate, lower daily foraging times or intake of higher quality food of the small herbivore. Feeding facilitation by (simulated) large herbivores grazing has been shown to occur in a number of small mammalian and avian herbivores (Krueger 1986, Bakker *et al.* 2005, Van Der Graaf *et al.*, 2002), although different species respond differently to the changes in quality and quantity (Stahl *et al.* 2006). On the long term, facilitation, through higher intake, can lead to a better condition, higher reproduction and finally to a larger population: population facilitation (Figure 2b).

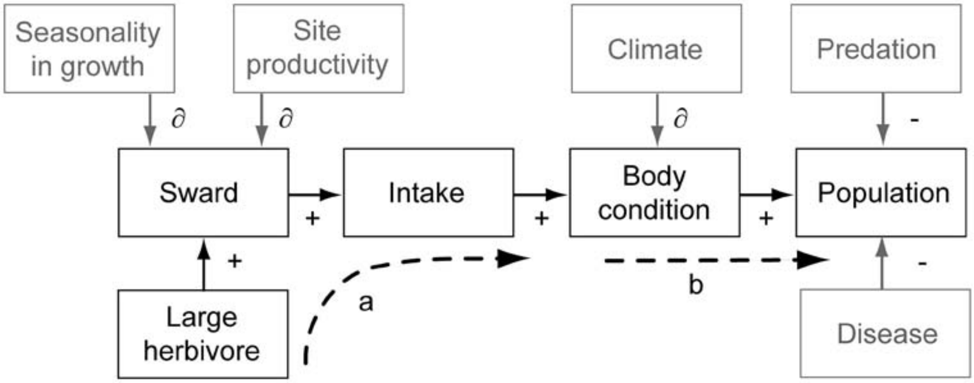

Figure 3. Conceptual model of the propagation of facilitation of small herbivores by large herbivores (black), and possible confounding factors (grey). The grey box represents the small herbivore. Arrow a represents feeding facilitation; arrow b stands for population facilitation.

Our simulation model showed that population facilitation of small refuge-living herbivores by large herbivores indeed can occur, but only when the functional response of the small herbivore had a unimodal shape (a type IV functional response; Drescher *et al.* 2006) and vegetation productivity was high (Chapter 5). When the productivity of the vegetation was low, densities of small refuge-living herbivores were lower when the non-dynamic large herbivores were included, than when they were not: competition. When the small herbivore foraged according to an asymptotic (type II) functional response, large herbivores hardly had an effect on population density at any plant productivity level.

Although population facilitation is predicted by theory and by our simulation model, it has not been detected in natural grazed assemblages (Arsenault & Owen-Smith 2005). This could have three causes.

Firstly, our model indicates that the role of vegetation productivity is an important factor in the occurrence of facilitation (Chapter 5), but it has not been included as an explanatory variable in analyses of assemblages with the potential for facilitation.

Secondly, maturation of plants, generating the unimodal functional response in small herbivores that is required for facilitation to occur (Prins & Olff 1998, Chapter 5 of this thesis), only happens at the end of the growing season (Chapter 3). Studies looking for facilitation should take this temporal aspect into account, but have so far focussed on the growing season itself (for example Arsenault & Owen-Smith 2002).

Thirdly, other factors such as disease, predators or non-trophic effects of the large herbivores (see Chapter 7) can have a confounding effect on the effects of feeding facilitation on small herbivores: the effects of feeding facilitation could become so diluted that they do not result in population facilitation.

All in all, population facilitation is a subtle process, and can be hard to detect. A well designed experiment or a thorough analysis of the within-year dynamics of populations of small herbivores and large herbivores, and the temporal dynamics of the productivity of the system in which they occur, is called for.

A good model system to perform such a study is that of rabbits and cattle. Rabbits occur almost in every nature conservation area in the Netherlands (Broekhuizen *et al.* 1992). In 68% of the cases that large herbivores are used as a management tool in nature areas in the Netherlands, it was to counter bush and grass encroachment (Kuiters, Hazebroek & Hennekens 2003), i.e. the maturation of the vegetation that grazing by large herbivores is to counter in facilitation. The other components for population facilitation also seem to be present in this system: we showed that the rabbit, a small herbivore, is negatively affected by maturation of the vegetation; foraging time increased as food quality decreased over the season

(Chapter 4), rabbits are attracted by grazed or mowed vegetation (Van Breukelen unpublished results, Bakker *et al.* 2005) and better body condition indeed results in larger litters and increased survival in the rabbit (Poole 1960; Rödel *et al.* 2005). It has been suggested that the high densities of rabbits found in urban and industrial areas can be attributed to facilitation by man: there, the vegetation is mowed and often even fertilized, keeping it in a good state for rabbits (Akkermans, 2006).

Refuge grazing and species diversity

Because refuge-living herbivores create a gradient in grazing pressure around the refuge, they should increase plant species diversity more than free ranging species do. The latter match their grazing impact to the potential intake i.e. the density of the vegetation and that way make an area more homogeneous (Kotler, Gross & Mitchell 1994), while the former distribute their grazing heterogeneously, according to location and achievable intake rate (this thesis).

As plant species differ in their tolerance to grazing, applying grazing will result in shifts of dominance by modifying competitive interactions of plant species (Crawley 1983, Crawley 1990). As grazing tolerance is different between plant species, this competitive release will have different outcomes depending on the amount of grazing taking place. In the case of refuge-living herbivores, this grazing pressure will not depend on the vegetation density alone, but also on the distance to the refuge. The decrease in grazing pressure with distance will result in a range of different niches, from intense grazed near the refuge, to no grazing on larger distances, potentially increasing plant species diversity in an area.

Do refuge-living herbivores indeed increase plant diversity? Few studies report species composition as a function of distance to the refuge. In a number of studies, plant diversity on plots with small herbivores included or excluded, or quadrates inside and outside herbivore borrows or colonies are compared.

The number of plant species in an area is higher where European rabbits can graze than where these are excluded (Bakker 2003, Sumption & Flowerdew 1985). Although the presence of some species is caused by creation of open places in the vegetation by digging (Bakker 2003), there is clearly a strong effect of rabbit grazing on species richness (Gillham 1955). The highest number of species is found at intermediate grazing pressure, the lowest at that part of a site that experiences is little or no rabbit grazing (Zeevalking & Fresco 1979). As these latter report the number of species per plot only, it remains unclear whether different species occur on different distances and if species diversity over the whole gradient is larger than on the ungrazed locations.

The relation between grazing by pikas (Ochotona sp.), another refuge-living small herbivore, and plant species richness is less clear cut. In one study area, species richness was higher in quadrates where American pikas *Ochotona princeps* were excluded than in quadrates where they grazed and species richness decreased with distance from the refuge (Huntly, Smith & Ivins 1986). In another study, excluding American pikas for three years resulted in increased plant richness close to the refuge, but had no effect on the number of plant species at larger distances (Huntly 1987). Both studies were performed over a distance of maximally 6 meters from the refuge, which are fully within the usual grazing distance of pika (Holmes 1991) and therefore do capture the potential additional effect of pika on species composition or species richness to the plant species occurring at ungrazed areas. In a second study area, it was found that species richness was highest close to the refuge of American pika (McIntire & Hik 2005). Daurian pika *Ochotona daurica* increases plant species richness in some studies (Dmitriev 1985, Smith *et al.* 1990), but in other studies it does not (Komonen, Komonen & Otgonsuren 2003). Daurian pikas can keep plant diversity relatively high by arresting succession through the eating of tree seedlings (Khlebnikov & Shtilmark 1965 in Smith *et al.* 1990). In plateau pikas *Ochotona curzoniae* plant richness within colonies is higher than outside them (Bagchi, Namgial, & Ritchie 2006).

Living in refuges versus ranging freely

So, refuge-living herbivores divide their grazing in a strongly skewed distribution within their home range and that way, in most cases, increase diversity, whereas free ranging herbivores distribute their grazing pressure over their home range according to attainable intake, which, in principle, should have less impact on diversity.

The comparison of the refuge-living rabbit to the free ranging European brown hare *Lepus europaeus* provides a nice illustration of this. Only double the weight of the wild rabbit, the closely related hare could be viewed as a free ranging rabbit. The hare has a much larger home range (Mann-Whitney U-test, $n1=34$, $n2=16$, $Z=-5.657$, $p<0.001$): an average of 3.4 ha for the rabbit (Cowan 1987; Daniels *et al.* 2003; Dekker, Groeneveld & Van Wieren 2006; Fullagar 1981; Gibb 1993; Henderson 1979; Hulbert-Ian, Iason & Racey 1996; Kolb 1991; Lombardi *et al.* 2002; Moseby *et al.* 2005; Rödel, unpublished data; Southern 1940; Stott 2003; Villafuerte 1994; White et al 2003) versus an average 77 ha for the hare (Broekhuizen & Maaskamp 1982; Hewson & Hinge 1990; Hulbert *et al.* 1996; Kovacs & Buza 1992; Kunst, Van Der Wal & Van Wieren 2001; Marboutin & Aebisher 1996; Parkes 1984; Reitz & Leonard 1994; Shaila *et al.* 2003; Stott 2003; Wolfe & Hayden 1996). The grazing of rabbits is focussed close to edges or refuge (this thesis) and (snowshoe) hare grazing pressure is distributed according to forage availability (Hodges & Sinclair, 2005), so one must assume that the hare divides its foraging impact over a much larger area. Adding to this, rabbits live and forage in groups, sharing a range (Chapter 6) while hare home ranges hardly overlap (Van Wieren, personal communication). So, the refuge-living rabbits create a gradient of grazing from their shelter outward, whilst free ranging hares distribute their grazing effort evenly. To my knowledge, effects of hare grazing on biodiversity have not been reported.

General conclusions

I argue that, as opposed to free ranging herbivores, it is inherent to refuge-living herbivores to divide their grazing pressure in a gradient. This spatial variation in grazing pressure applied by refuge-living herbivores, that is caused by spatial variation in vigilance, not only results in spatial patterns in vegetation density, but can also lead to spatial patterns in plant species composition, leading to increased biodiversity. In their role as an agent of increasing heterogeneity and biodiversity, refuge-living herbivores fulfil an important function in natural or semi natural ecosystems: nature conservators should strive to conserve species of refuge-living herbivores.

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Summary

Spatial patterns in vegetation biomass or plant species occur around refuges of small herbivores such as rabbits, pika and marmots. These patterns are caused by spatial variation in grazing pressure of these herbivores. In this thesis, I determine whether avoidance of predation explain gradients in grazing around refuges, and on how characteristics of the forage, such as nutrient content, digestibility, density, productivity and growth rate influence these grazing patterns.

In **Chapter 2**, I presented and tested a parsimonious mechanistic model that explains the patterns in grazing. Looking up and scanning for predators (vigilance) requires time that could have been attributed to foraging. If this vigilance increases, when an animal is more distant from its refuge, foraging intake is spatially variable and forage intake rate will decrease with distance. For a maximisation of forage intake, the animal should concentrate its foraging efforts close to its refuge.

I tested this model in two experiments: by staging domesticated rabbits on strips of fenced off grassland, with artificial refuges at one end, (**Chapter 2**) and in a similar setup, but with pelleted food (**Chapter 3**). Vigilance indeed decreased with distance (**Chapter 2**), and intake rate decreased with distance to the refuge (**Chapter 3**). The functional response of refuge-living herbivores is in fact a function of both plant density and distance to the refuge, which causes a preference for patches close to the refuge, when food is distributed homogeneously (**Chapter 2, 3**). This means that foraging of free ranging herbivores makes the spatial distribution of resources more homogeneous, whilst foraging of refuge-living herbivores makes it more heterogeneous.

By foraging, herbivores alter their food. In **Chapter 3**, I determined how the short term and long term foraging patterns of these herbivores are affected by the quantity and quality of their food, using predictions from optimal foraging theory.

Because the relation between quantity and quality in the vegetation are complex and their effect on behaviour hard to disentangle, I tested these predictions using artificial food: pellets of grass and different fractions of straw. I offered pellets at various distances to rabbits, in treatments ranging from low quality and small quantity to high quality and large quantity.

In the first hour of the trial, the rabbits foraged almost exclusively on the optimal tray, where intake rate was highest, with the other trays being sampled in a few trials. In the long term, depletion of the nearest patches and subsequent

foraging in farther patches resulted in a foraging gradient, which in turn resulted in the formation of spatial patterns in food density. These spatial patterns were affected by food quality and quantity: they were more skewed towards the refuge as the initial food quantity in the trays was larger and the quality of the forage was higher.

An important trait of plants is that they (re)grow and in that way can restore losses caused by herbivores. However, over the season, plant growth rate is not constant. In spring, growth rate is high, and the animal could stay close to the burrow. As growth rate declines, the animal depletes the closest locations, and must move to farther patches. I predicted that because of this, a quality and quantity gradient is formed, that the area grazed increases as growth rate of the vegetation increases, and that foraging time increases through the season. To test these predictions, I staged rabbits *Oryctolagus cuniculus* in sward strips for a growing season (**Chapter 4**).

At the end of the growing season, the spatial variation in grazing pressure resulted in a gradient in vegetation quality and quantity. As growth rate declined, the plant growth could not counter the foraging by the rabbits, and the animals needed to expand their foraging area: the area used for grazing increased with decreasing growth rate. The time animals used for foraging increased, which we attribute to a maturation and decrease in quality of ungrazed are, which likely caused increased searching and handling time.

The experiment showed that central place foragers will experience seasonal variation in the vegetation in a different way than free ranging herbivores. The latter can migrate, but being tied to their burrows, the refuge-living herbivore must deal with decreasing renewal of the vegetation close to their refuge at the end of the growing season. Natural fluctuations in population size or facilitative grazing by large herbivores may lessen these problems.

A mechanistic model, based on the first four chapters, was used to study how population dynamics of small refuge-living herbivores could be influenced by plant productivity, how they would be affected by different relations between intake rate and plant density, and how grazing by large herbivores would affect their population dynamics (**Chapter 5**).

The model showed that spatial variation in vigilance, that takes time away from foraging, will yield the patterns seen in the field. The spatial distribution of grazing is affected by plant productivity of a site: higher productivity resulted in foraging on smaller areas around their central place by the population.

In dynamic populations of refuge-living herbivores, the area grazed by the population decreased as population density increased. In contrast, in free ranging herbivores the area grazed increased with population density.

When the small herbivores foraged with a unimodal functional response instead of an asymptotic functional response, population density had a maximum at intermediate plant productivity, but at higher biomass density, the total intake was higher than would be expected from the intake rate: being forced to forage on the same locations around the refuge repeatedly, the vegetation was grazed to a density at which intake rate was higher: the population created grazing lawns.

Adding large herbivores to the model showed that positive interaction such as facilitation, can only occur if there is a unimodal functional response in the small herbivore, i.e., when vegetation matures. At high plant productivity, cattle lowered vegetation density to a level at which the small herbivore reached higher intake rates, resulting in a larger refuge-living herbivore population: facilitation, but at low plant productivity the refuge-living herbivores reached a lower population density with cattle than without cattle at low plant productivity: competition.

In rabbits, spatial behaviour may be affected by social rank and sex of the animal. Subdominant animals are expected to use more space and to forage farther from the burrow than dominant animals and females are expected to have a smaller home range than males. To test these hypotheses, home range size and distance to the burrow during foraging were determined within a low density, semi-natural rabbit population in the Netherlands (**Chapter 6**). I found no difference in home range or foraging distance between males or females, or between dominant and subdominant animals. I postulate that this is caused by an interaction of two factors: low animal density and high availability of high quality food. This meant that there was no need to compete for best or safest foraging locations, and males did not need to protect females in their group against other males. This is also the explanation as to why the home ranges in our study are the smallest recorded for wild rabbits: between 0.01 and 0.43 ha.

Studies of herbivore assemblages mostly are concerned with trophic interactions, such as large herbivores facilitating for or competing with small herbivores. However, by grazing, large herbivores modify vegetation structure, potentially changing the microhabitat for small herbivores, which could result in non-trophic interaction. In **Chapter 7**, we tested if this occurs in the wild rabbit.

The rabbit prefers vegetation cover during the day and open spaces at night. This means that animals living in an area of ungrazed, dense, tall vegetation should become active earlier than animals living in a grazed, open area. We tested this by determining the activity patterns of one population of rabbits living in a grazed enclosure and one population living in an ungrazed enclosure. Contrary to the prediction, the population of the field with short vegetation showed an earlier peak in activity than the population of the field with tall vegetation. I attribute this to an interaction of relatively low ambient temperatures and a lower number of predators, and conclude that by grazing, large herbivores influence small herbivores not only through trophic interactions but also through physical ecosystem engineering: the alteration of the amount of cover.

Because the intake rate at a location is a function of not only the biomass at a location, but also the distance to the refuge, refuge-living herbivores forage differently than free ranging herbivores. In **Chapter 8**, I discussed what this means for their interaction with the environment. Vigilance is not only affected by other species, but also by intraspecific interactions, such as mate competition. These interactions, and the way they could affect spatial distribution of grazing, are briefly discussed.

Refuge-living herbivores must deal with changes in growth rate and quality of the vegetation, whereas free ranging herbivores can move to other areas. One way to overcome this problem is by having a peak in reproduction that coincides with the peak in plant growth. That way, the intake of the population changes with the growth rate of the vegetation, and the population could graze a fixed area, keeping it from maturing and decreasing in quality.

Another way the negative effects of maturing of the vegetation could be deterred is by the foraging of large herbivores: facilitation. This has been shown to occur on the level of feeding facilitation: increased intake rates, or a preference for patches grazed by large herbivores. However, it has not been shown to result in an increase in the population density of small herbivores. This could be because the role of productivity is not incorporated in analyses properly, because only the period of high plant growth is studied, or because confounding factors such as disease or predation has a stronger effect on population size than the facilitative effect of large herbivores.

As opposed to free ranging herbivores, refuge-living herbivores show a heterogeneous distribution of grazing pressure over space. This spatial variation in grazing pressure results in spatial patterns in vegetation density, but can also lead to spatial patterns in plant species composition, leading to increased biodiversity. In their role as an agent of increasing heterogeneity and biodiversity, refuge-living herbivores fulfil an important function in natural or semi natural ecosystems. For this reason, nature conservators should strive to conserve or restore refuge-living herbivore species.

Samenvatting

Rond holen van kleine herbivoren zoals konijnen, pika's en marmotten zijn ruimtelijke patronen in de dichtheid of soortsamenstelling van de vegetatie te zien. Deze patronen worden veroorzaakt door ruimtelijke variatie in graasdruk van deze herbivoren. In dit proefschrift onderzoek ik of vermijding van predatie deze patronen kan verklaren en hoe karakteristieken van de vegetatie, zoals nutriëntengehaltes, verteerbaarheid, dichtheid, productiviteit en groei deze patronen beïnvloedt.

In Hoofdstuk 2 wordt een mechanistisch conceptueel model voorgesteld en getest, dat de patronen in begrazing kan verklaren. Dit model houdt in dat de tijd die wordt besteed aan waakzaamheid het opkijken en zoeken naar predatoren, toeneemt met afstand tot de burcht, en dat voor deze waakzaamheid tijd nodig is die niet meer besteed kan worden aan foeragen. De voedselinnamesnelheid van dieren die in holen leven neemt dan af met afstand tot dat hol, en de dieren zouden dus het beste dicht bij de burcht foerageren.

Dit conceptuele model werd getest door gedomesticeerde konijnen in stroken grasland, met aan een kant kunstmatige burchten (**Hoofdstuk 2**), en door een vergelijkbare proef, maar dan met korrels als voer (**Hoofdstuk3**). De tijd die aan waakzaamheid werd besteed nam inderdaad af met afstand tot de burcht (**Hoofdstuk 2**), en de opnamesnelheid van voedsel nam inderdaad ook af met afstand tot de burcht (**Hoofdstuk 3**). De opnamesnelheid is bij deze dieren dus niet alleen een functie van de dichtheid van voedsel, maar ook van de afstand van dat voedsel tot het hol. Dit veroorzaakt een voorkeur voor voedsel dicht bij het hol wanneer voedsel homogeen verdeeld is (**Hoofdstuk 2 & 3**). Dit betekent dat in tegenstelling tot free ranging dieren, die de verdeling van voedsel in principe homogener maken, holbewonende dieren als konijnen de verdeling heterogener maken.

Herbivoren veranderen hun voedsel door te eten. In **Hoofdstuk 3** bepaalde ik hoe de voedselkeuze op de korte en de langere termijn wordt bepaald door de kwaliteit en kwantiteit van het voedsel, waarbij voorspellingen uit de zogenaamde *optimal foraging theory* werden gebruikt.

Omdat kwaliteit en kwantiteit in plantaardig voedsel gecorreleerd is, en dus lastig te scheiden, gebruikte ik kunstmatig voedsel: korrels, gemaakt van verschillende verhoudingen gras en houtpulp. Deze korrels werden in bakjes op verschillende afstanden tot een kunstburcht aangeboden aan gedomesticeerde konijnen.

In het eerste uur van de proef aten de konijnen bijna alleen van de meest optimale dichtstbijzijnde bakjes korrels, waar de waakzaamheid het laagst was, en de opnamesnelheid van de korrels het hoogste. Op de lange termijn leidde het opraken van de meest optimale bakjes, en het daarop volgende foerageren in de minder optimale bakjes tot de vorming van ruimtelijke patronen in de dichtheden van achterblijvend voer. Deze patronen werden beïnvloed door de hoeveelheid en de kwaliteit van het aangeboden voedsel: de verdeling van ‘graasdruk was meer verschoven naar de burcht wanneer de voedselhoeveelheid groter was, en wanneer de kwaliteit hoger was.

Een van de karakteristieke eigenschappen van planten, en vooral van gras, is dat het blijft groeien, en op die manier verlies van biomassa door predatie door herbivoren kan herstellen. Gedurende een groeiseizoen verandert de groeisnelheid echter. In het voorjaar is de groeisnelheid hoog, waardoor de begrazing door holen bewonende herbivoren hersteld zou kunnen worden: de dieren kunnen dichtbij hun holen blijven. In de zomer en het najaar is de groeisnelheid lager, de dieren zullen daardoor de locaties dicht bij de holen uitputten, en zullen verder van hun hol moeten foerageren. We voorspelden dat dit groei- en graaspatroon een gradiënt in kwaliteit en kwantiteit in de grasmat zal veroorzaken, dat gedurende het seizoen het oppervlakte dat begraasd wordt toeneemt, en dat de tijd, die nodig is om te eten toeneemt. Om deze voorspellingen te testen, plaatsten we paren konijnen een groeiseizoen lang in langwerpige stroken gras (**Hoofdstuk 4**).

Aan het eind van het groeiseizoen was er inderdaad een gradiënt in kwaliteit en kwantiteit in de vegetatie gevormd. Toen de groeisnelheid afnam, werd de begrazing door de konijnen niet voldoende meer door de groei van de vegetatie gecompenseerd, en moesten de dieren het gebied waarover ze graasden vergroten: het begraasde oppervlakte nam toe met afnemende groeisnelheid.

De tijd die de dieren gebruikten om te eten nam over de maanden toe. We wijtten dit aan het ouder worden van de vegetatie, en het afnemen van kwaliteit van met name het vroeg in het seizoen nog niet begraasde deel, wat waarschijnlijk een toename van zoek-, bijt- en kauwtijd tot gevolg had.

Het experiment toonde aan dat dieren die in burchten leven op een andere manier te maken krijgen met seizoensvariatie in depletie en groei van de vegetatie, dan voor ‘vrije’ herbivoren zoals grote grazers. Aangezien de dieren aan hun holen gebonden zijn, moeten ze omgaan met afnemende groei van de vegetatie dicht bij hun hol, aan het eind van het groeiseizoen, en met de afname in kwaliteit van die vegetatie. In het veld zouden deze problemen echter minder kunnen zijn door natuurlijke seizoensfluctuaties in populatiegrootte of door faciliterende begrazing door grote grazers.

Om te bestuderen hoe de populatiedynamiek van kleine, holen bewonende herbivoren beïnvloed wordt door productiviteit van de vegetatie, hoe ze worden beïnvloed door verschillende typen functionele response, en hoe begrazing door grote herbivoren de populatiedynamiek kan beïnvloeden (**Hoofdstuk 5**), begruikte ik een mechanistisch mathematisch model, gebaseerd op bevindingen in de eerste 3 Hoofdstukken.

Dit model toonde dat ruimtelijke variatie in waakzaamheid inderdaad patronen in de vegetatie veroorzaakt, wanneer waakzaamheid foerageertijd kost. De ruimtelijke verdeling van de begrazing door de kleine herbivoren wordt beïnvloed door de productiviteit van de vegetatie: hoe hoger de productiviteit, hoe kleiner het begraasde oppervlak rond een hol.

In dynamische populaties nam het oppervlak dat rond de burcht begraasd werd af met productiviteit, terwijl de populatiegrootte wel degelijk toenam. Bij 'vrije' herbivoren was dit niet het geval: daarbij nam het begraasde oppervlak toe met de populatiegrootte.

Wanneer kleine herbivoren volgens een zogenaamde unimodale functionele response graasden, in plaats van met een asymptotisch verlopende functionele response, bereikte de populatie haar hoogste dichtheid bij een intermediare maximale vegetatiedichtheid, maar bij een hogere maximale vegetatiedichtheid was de inname hoger dan men zou verwachten op grond van de innamesnelheid bij die vegetatiedichtheid. Omdat de dieren aan hun burcht gebonden zijn, eten ze de vegetatie dichtbij de burcht tot een dichtheid waarbij de intake hoger was: de populatie maakte 'grazing lawns'.

Het toevoegen van grote herbivoren aan het model toonde dat er een positief effect op de populatiedichtheid van de kleine in holen wonende grazers kan zijn, maar alleen als die grazen volgens een unimodale functionele response, dus wanneer ze last hebben van bijvoorbeeld dichtere, verruigde vegetatie. In die situatie brachten de grote herbivoren in het model de vegetatie van een hoge dichtheid terug naar een dichtheid waarbij de klein herbivoren een hogere innamesnelheid haalden, wat weer resulteerde in een hogere populatiedichtheid: facilitatie. Bij een lage plantproductiviteit verlaagden de grote herbivoren de vegetatie naar een dichtheid waarbij de kleine herbivoren lagere dichtheden behaalden dan zonder grote herbivoren: competitie.

Het ruimtelijke gedrag van konijnen kan beïnvloed worden door de rang of door het geslacht. Ik voorspelde in **Hoofdstuk 6** dat subdominante dieren meer ruimte zullen gebruiken dan dominante, omdat ze op naar de verder van de burcht liggende, onveilige plekken worden gedrongen. Tevens verwachtte ik dat de mannelijke dieren, als in veel andere studies, meer ruimte zullen gebruiken dan de vrouwelijke:

zij moeten de vrouwen verdedigen tegen mannelijke concurrenten. Om deze hypotheses te testen bepaalde ik home range groottes en foerageerafstanden in een seminatuurlijke populatie konijnen van lage dichtheid (**Hoofdstuk 6**).

We vonden geen verschil in home range of foerageerafstand tussen mannelijke en vrouwelijke dieren, noch tussen dominanten en subdominante. Dit komt waarschijnlijk door een interactie van twee factoren: de lage dichtheid van de dieren, en het hoge aanbod van voedsel. Dit zorgde dat de mannelijke dieren de vrouwelijke dieren niet hoefden te verdedigen, en dat er geen noodzaak was voor competitie om veilige plekken, dicht bij de burcht: alle dieren bleven relatief dicht bij hun burcht. Dit verklaart waarom de door ons gevonden home ranges de kleinst bekende home ranges van konijnen zijn: tussen 0,01 en 0,43 hectare.

De meeste studies aan interacties tussen dieren richten zich op trofische interacties, zoals die van competitie of facilitatie tussen grote en kleine herbivoren. Door te grazen veranderen grote herbivoren echter niet alleen de vegetatie in haar functie als voedsel, maart ook in haar functie als structuur in het landschap. Hierdoor zouden grote herbivoren het microhabitat van kleine herbivoren kunnen veranderen. Of dit ook zo is, testte ik in **Hoofdstuk 7**, met behulp van koe en konijn.

Het konijn heeft een voorkeur voor dichte vegetatie overdag, en open ruimten in de nacht. Dit betekent dat dieren in een onbegraasde, dichte en hoge vegetatie vroeger actief zouden moeten worden dan dieren die een begraasd, open gebied bewonen. Deze hypothese testte ik door het activiteitspatroon van twee afgesloten populaties te vergelijken: een in een onbegraasd terrein, een in een begraasd terrein.

Tegen de hypothese in toonde de populatie in het veld met korte begraasde vegetatie en vroegere activiteitspiek dan de populatie die in hoge vegetatie leefde. Dit schrijf ik toe aan een interactie van relatief lage temperaturen en relatief lage dichtheden van predatoren, in vergelijking met de studies waarop de voorspellingen waren gebaseerd.

Begrazing door grote herbivoren beïnvloedt kleine herbivoren niet alleen trofisch, maar ook als physical ecosystem engineering: fysieke verandering van de leefomgeving.

Omdat de voedselinnamesnelheid op een locatie voor kleine, holbewonende herbivoren niet alleen een functie is van vegetatiedichtheid op een locatie, maar ook van de dichtheid tot hun hol, foerageren deze dieren anders dan grote, *free ranging* herbivoren. In **Hoofdstuk 8** bespreek ik wat dit voor effect heeft op de interactie met hun omgeving.

De mate van waakzaamheid wordt niet alleen benvloed door andere soorten, maar ook door intraspecifieke interacties, zoals competitie om partners. Deze interacties, en de wijze waarop ze ruimtelijke verdeling van graasdruk kunnen beïnvloeden, worden kort besproken.

In holen wonende herbivoren moeten omgaan met veranderingen in groeisnelheid en kwaliteit van hun voedsel, in tegenstelling tot *free ranging* herbivoren, die naar andere gebieden kunnen trekken. Een wijze waardoor deze problematiek voor kleine holenbewonende herbivoren veel minder zou zijn, is wanneer de piek in de populatie, veroorzaakt door reproductie samenvalt met de piek in plantengroei. Dan fluctueert de intake van de populatie met de verandering in groei, en zal de populatie een vast areaal begrazen, waardoor het niet verouderd, verruigt of in kwaliteit verminderd.

Een andere factor die de negatieve effecten van veroudering van de vegetatie op kleine herbivoren kan verkleinen is het foerageren door grote herbivoren: facilitatie. Facilitatie is aangetoond op kleine ruimtelijke en temporele schaal: dieren behaalde op door grote herbivoren begraasde patches hogere voedselinnamesnelheden, of een er was een voorkeur van kleine herbivoren voor zulke. Facilitatie op populatie-niveau, dus een verhoogde populatiegrootte van kleine herbivoren door begrazing van grote herbivoren is echter vooralsnog niet in het veld aangetoond. Dit kan komen doordat productiviteit van de vegetatie niet is opgenomen in de analyses, omdat slechts een bepaalde periode van het jaar is bestudeerd, of omdat andere factoren, zoals ziekten, sterker inwerken op de populatiedichtheid van de kleine herbivoren.

In tegenstelling tot *free ranging* herbivoren, verdelen kleine, holen bewonende herbivoren hun graasdruk heterogeen over de ruimte. Deze ruimtelijke variatie in graasdruk resulteert in ruimtelijke patronen in dichtheid van de vegetatie, maar kan ook leiden tot ruimtelijke patronen in samenstelling van plantensoorten, en zo tot hogere biodiversiteit leiden.

In hun rol als veroorzakers van vergrote ruimtelijke heterogeniteit en biodiversiteit, vervullen kleine, holen bewonende herbivoren een belangrijke rol in natuurlijke en halfnatuurlijke ecosystemen. Daarom zouden natuurbeheerder moeten streven naar behoud of herstel van holen bewonende kleine herbivoren.

Nawoord

Ik weet nog dat ik tijdens mijn sollicitatie-gesprek, een paar jaar geleden, een betoog hield voor meer onderzoek aan Nederlandse zoogdieren als het konijn: waarom zo'n zware focus leggen op de tropen, als er in Nederland nog zoveel te bestuderen viel? Na afloop van het gesprek bedacht ik me dat dat misschien niet heel handig was bij een sollicitatie bij de vakgroep Tropical Nature Conservation and Vertebrate Ecology. Toch werd ik aangenomen als promotie-kandidaat op het onderwerp 'Facilitative and competitive interactions between large and small herbivores: the role of density and effects of vegetation structure', dat uitgemondde in dit proefschrift. Op dat proefschrift staat weliswaar mijn naam, maar een flinke hoeveelheid mensen hebben bij de totstandkoming ervan bewust of onbewust, op directe of op indirecte wijze aan bijgedragen. Die wil ik hier graag bedanken.

Ten eerste mijn promotor Herbert Prins en co-promotor Sip van Wieren. Zij gaven me de kans dit onderzoek te doen en gaven me de ruimte en mogelijkheden een andere richting te zoeken toen het oorspronkelijke experiment anders liep dan we gepland hadden. Naast alle zaken over wetenschap en onderzoek bedrijven, leerden ze me dat het ook belangrijk is dat onderzoek doen leuk is.

Frank van Langevelde liet me vrij zelf te pielen en te schaven aan het model dat beschreven wordt in hoofdstuk 5, al zullen zijn handen af en toe hebben moeten jeuken om het over te nemen. Ik kijk uit naar onze verdere samenwerking! Hij en Fred de Boer hielpen ook mee met het ontwerp van, en bij de begeleiding in het MSc/PhD experiment dat beschreven wordt in hoofdstuk 2.

Een speciaal woord van dank aan Nicol Heuermann: het is apart samen een onderzoek uit te voeren als dat inhoud dat je elkaar daardoor net nooit ziet. Toch was het 24-uurs-observatie-experiment een enorm leuke samenwerking. Ook de gedachte dat ik niet de enige was die uren in Achterberg luierende, of erger, voor de regen schuilende dieren aan het observeren was betekende een hoop voor me.

In dat 24-uur observatie experiment en de experimenten van hoofdstukken 2 en 4 was de hulp van Teus Bleijenberg onmisbaar. Hij zette een groot deel van de dagen de konijnen-hokken open en sloot de dieren 's avonds weer op, maar ook voor duizenden konijnenkeutels rapen draaide hij zijn hand niet om.

Unifarm zorgde voor de velden, koeien en loodsen, zonder welke dit proefschrift niet gelukt was! Gerard Müskens (Alterra) leende me een aantal bunzing/konijnenvallen, waarvoor ik hem bijzonder dankbaar ben.

Another enormous help was the advice on large scale enclosures and practice in rabbit trapping and handling I got from Dr. Heiko Rödel of the University of Bayreuth, Germany. Heiko, you taught me the only true argument to study rabbits: because they are incredibly cute (and extremely fascinating)! Thank you en Raquel for your hospitality, and for making it possible to finally meet the Easter-rabbit in person.

Ik heb tijdens dit AIO-schap een fiks aantal MSc studenten mogen begeleiden. Soms vraag ik me af dat ik meer geleerd heb van jullie dan jullie van mij! Ard Zwijnenburg, Marjolein van Adrichem (zie Chapter 7!), Monique Groeneveld (zie Chapter 6!), Dominique de Koning, Marleen Broekhuijse (zie Chapter 2!) en Femke Schepers: dank!

In random order de collega's van TNV/REG en NCP: barakkers Barend, Michael, Juul, Jasper, Eelke, Euridice, Thomas, Geerten, Anna, Christiaan, Rampal, Jantineke, Nicol, Jort, Angela, Yolanda, Cornelius, Bjorn, Roy, Gabriela, Jinze, en staffers Ignas, Arend, Milena, Herman, Gerda, Willemien, Margeet, Jan, Frans en Annemarie. Een speciaal dank-je-wel daarbij voor Liesbeth Bakker. Haar onderzoek op het Junner Koeland was, getuige de vele citaties naar haar papers in de diverse hoofdstukken, een belangrijke inspiratie voor mijn werk.

Een mens kan maar een beperkt aantal uren per dag over konijnen nadenken zonder door te draaien. Gelukkig was er in weekenden en vrije avonden de nodige afleiding. Zo waren er de huisgenoten en buren van de rustieke Vrijstaat Droevendaal, met wie ik uitgebreide veganistische diners, kampvuurtjes en aziatische film-marathons deelde. Dus veel dank aan Jasper, Elise, Euridice, Tijl, Vena, Paulien, Gertjan, Agata, Linda, Tuur, Chris, Karin, Claire, beide Jeroenen, Menno, Eelke, Lidewij, Arnoud, Yoran & Mark.
Een andere manier van ontspannen was het plegen van sectie op 'vers' ontdooide bunzing- of steenmarterlijkjes met Maurice en Raymond: een bijna Zen-achtige bezigheid die ik iedereen kan aanraden.

Speciale vermelding verdient de Monday Boulder Crew, die vreemd genoeg vaker op woensdag dan op maandag bij elkaar kwam, maar welke dag ook, wat is er beter dan onder het mom van sporten wat bij te kletsen en een biertje te drinken? Roemer, Pim, Joost, Michiel, maar af en toe ook Sanne, Joris en David, ik beloof weer eens wat vaker te komen klimmen. Echt!

Naast klimmen was musiceren een goede uitlaatklep van opgebouwde spanning rondom konijnen-vretende, ongrijpbare bunzingen, onwillige manuscripten en weerbarstige data. Marchien en Alex, superveel dank voor de leuke tijd met de Pitts. Later was er ook de klimband de Seven Summits: Sanne, Mariska, Pim, Lotte, Wouter en Saakje! Weer eens jammen? In het staartje van deze promotie hielpen ook Chris Smit en Thomas Groen voor de eco-muzikale ontspanning tussen de soep en de patatten. Dank allemaal!

Maja was tijdens een groot deel van deze promotie mijn steun en toeverlaat. Dank je wel!

Dan mijn ouders Ton en Marianne wil ik danken voor alles wat jullie voor me betekenen. Ook dank aan Nynke & Henkjan plus Tijmen, Hidde en Renske , Sanne & David, ook voor de hulp bij de bovenbuurt-distels snoeien en de klim-uitjes, en Eelke, ook voor zijn hulp bij grafische zaken en het maken van het filmpje over het Bovenbuurt-onderzoek.

En natuurlijk Ans, niet alleen omdat je het belang van konijnen in de wereld altijd in perspectief wist te zetten, maar voor alles!

Curriculum vitae

Jasja Johannes Antonius Dekker was born in Alphen aan den Rijn on 28 October 1975. After graduating from the Coornhert Gymnasium in Gouda in 1994 and a gap year working as strawberry-picker, cheese-tumbler, assembly-line worker and busker in the UK and the Netherlands, he moved to Wageningen University in 1995 to study biology.

He obtained a Master Degree in 2000, after doing three MSc-theses: on the spatial behaviour of the red fox in Meijendel under the supervision of Jaap Mulder, Alfred Stein en Ignas Heitkönig (Dekker *et al.* 2001), on the relation between grasshopper diversity and intensity of landscape-use in North-Eastern Poland (through Alterra) and on the genetic variation of the extinct otter population of the Netherlands, under the supervision of Hugh Jansman (Dekker & Jansman 2000; Jansman *et al.* 2003). During the last years of his study, he became interested in mustelids, dissecting polecats and martens under guidance of Sim Broekhuizen en Gerard Müskens of Alterra. They also provided the opportunity to gain more experience in radio tracking geese and beech martens.

After receiving his degree, he worked for a producer of nature documentaries, collected habitat data of the Root Vole for the Society for the Study and Conservation of Mammals (Zoogdiervereniging VZZ) and worked as a managing editor for the popular scientific mammal magazine “Zoogdier”.

In January 2002, he started a PhD project at the Resource Ecology Group, on a project entitled ‘Facilitative and competitive interactions between large and small herbivores: the role of density and effects of vegetation structure’ which resulted in this thesis.

In 2002, he joined the editorial board of Lutra, a peer reviewed journal published by the Society for the Study and Conservation of Mammals.

Despite his vows never to work on a species as elusive, nervous and difficult as the rabbit or indeed on any animal larger than insects again, he now works for the Society for the Study and Conservation of Mammals, where he can combine applied ecological research with the conservation of, amongst other species, the wild rabbit….

List of publications

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PE&RC Ph.D. Education Statement

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 22 credits (= 32 ECTS = 22 weeks of activities)

Review of Literature (4 credits)

- Facilitation and vertebrate herbivores/facilitation and competition between large and small herbivores (2002).

Post-Graduate Courses (3 credits)

- Spatial modelling in ecology (PE&RC) (2002)
- Spatial ecology (PE&RC) (2003)
- Advances in wildlife health (Dutch Society for Wildlife Health) (2006)

Deficiency, Refresh, Brush-up and General Courses (2 credits)

- Basic & advanced statistics (PE&RC, SENSE) (2002, 2003)

PhD Discussion Groups (5 credits)

- Forest and conservation ecology (2002-2006)

PE&RC Annual Meetings, Seminars and Introduction Days (2 credit)

- Annual meeting (PE&RC) (2002)
- Current themes in ecology (2002, 2003, 2006)

International Symposia, Workshops and Conferences (4 credits)

- Verweij meeting (RUG, Texel, The Netherlands) (2002)
- Eureco (Univ. Lund, Sweden) (2002)
- Second World Lagomorph Conference CIBIO/UP (Univ. of Porto, Vairao, Portugal) (2004)
- Benelux Conference of Zoology (KNDV, Wageningen, The Netherlands) (2005)

Laboratory Training and Working Visits (2 credits)

- Rabbit handling, setup experiments (Univ. of Bayreuth) (2002)
- Visit to rabbit introduction scheme, discussing research (Univ. of Cordoba)