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The impact of sward height, forage quality and competitive conditions on foraging behaviour of free-ranging rabbits (*Oryctolagus cuniculus* L.)

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ABSTRACT. The habitat choice of the small hindgut fermenter, the European rabbit (*Oryctolagus cuniculus* L.), was studied in relation to sward height, forage quality, population size fluctuations and spatial distribution of burrows in a temperate grassland. In a multi-phase differential clipping experiment with alternating short and tall vegetation strips, rabbits tended to graze near the closest burrows in situations of equal vegetation heights, while a clear preference for short swards was found during summer (July). In this period, general crude protein content was significantly lower than in spring (April) and autumn (September), apparently leading to a potential forage quality deficit. The summer behavioural pattern with short sward preference coincided with the relatively higher crude protein content of short swards as compared to tall swards in this period, and with higher intraspecific competition, due to significantly larger numbers of animals present in summer. In autumn, rabbit densities decreased, while crude protein content of both short and tall vegetation increased to a higher, though not significantly different level, comparable with spring crude protein content. In those conditions, significant preference for low vegetation height could no longer be detected. Data suggest that selection for nutritive quality appears when intraspecific competition is high and nutritive quality remains under a certain threshold value. When, in autumn, competition decreases and nutritive quality increases again, short sward preference disappears. We conclude that short sward preference is primarily caused by the better forage quality of re-growth in periods of forage quality limitation, while this preference disappears when forage quality limitation no longer occurs.

KEY WORDS. rabbit, forage quality, vegetation height, crude protein.

INTRODUCTION

The optimal foraging theory states that herbivores maximize their net energy intake per unit time (MacArthur & Pianka, 1966; Stephens & Krebbs, 1986), which implies that foraging animals tend to select high quality forage as long as the energy gain exceeds feeding costs (e.g. searching and handling time and efforts, predation avoidance). While food intake rate by mammalian herbivores is predicted to increase asymptotically with food density (Lundberg, 1988; Lundberg & Astrom, 1990; Gross et al., 1993), food requirements can be expected to vary among mammal species with different body mass. Whereas larger herbivores may tolerate forage of low nutritional quality if available in sufficiently large quantities, the high metabolic rate and small digestive system of small grazers entails a need for higher-quality forage, albeit in smaller quantities (Demment & Vansoest, 1985; Olff et al., 2002).

Given the fact that fibre content of above-ground grassland vegetation increases - and nitrogen content decreases - during ageing (Pavlů et al., 2006), a grassland consisting of fully-grown, mature plant leaves is on average of lower nutritional quality than one consisting of re-growing shoots with short swards. Hence, food intake rates by small herbivores are expected to be lower under high availability of low-quality food, and higher under low to intermediate availability of high-quality food (Type IV functional response) (Dekker & van Langevelde, 2007), as reflected by unimodal, dome-shaped response curves (Durant et al., 2003; van Langevelde et al., 2008). Consequently, it is expected that when given the choice, small herbivores will prefer small to intermediate quantities of high-quality food instead of large quantities of low-quality food, although other factors, such as predation avoidance, interfere with feeding behaviour (Bakker et al., 2005; Lima & Dill, 1990).

The European rabbit (*Oryctolagus cuniculus*) is a medium-sized hindgut fermenter (Demment & Vansoest, 1985), which, due to its digestive system and medium-sized stature, relies on high quality, quickly digestible forage. While rabbits are expected to select foraging sites with short swards and high nutrient contents, other studies reveal contrasting patterns. For instance, strictly-controlled, experimental studies confirm a preference of rabbits for short swards (Iason et al., 2002; Bakker & Olff, 2003) while correlative field studies draw attention to the optimum grazing efficiency for swards of medium standing crop (van de Koppel et al., 1996) or temperature-dependent habitat selection (Villafuerte et al., 1993). Small refuge-living herbivores are also known to exhibit spatial foraging patterns determined by the location of their burrows (Dekker, 2007). As the proportion of time spent on vigilance increases with distance from the nearest burrow, rabbits tend to graze in proximity to refuges until the food source is depleted (Dekker et al., 2007).

To study if and to what extent, free-ranging small herbivores select for vegetation height or forage quality, we conducted a clipping experiment in a homogeneous grassland habitat in which the mammal herbivore community is dominated by European rabbits. To determine whether sward height preference could be attributed to structural or forage quality differences, we measured sward height in the field and analyzed standard forage-quality-determining variables (neutral detergent fibre, acid detergent fibre and acid detergent lignin, crude protein and mineral content (phosphorous and potassium)). The location of all rabbit holes near the study site was recorded in order to discriminate between habitat preference induced by habitat quality (sward height and nutritive content) and the proximity of burrows.

In this study we answer two main research questions:

1. Do free-ranging rabbits select for short or tall vegetation? If rabbits show a preference for a certain vegetation height, is this preference affected by seasonal changes in rabbit densities or forage quality or by the location of burrows?
2. What is the underlying mechanism for selecting short or tall vegetation? Do rabbits actively and in all circumstances select for high quality forage?

MATERIALS AND METHODS

Clipping experiments

We selected two flat, nearby, monotonous dry grasslands (500 m apart, separated from each other by two Poplar plantations. They are located in the Flemish Provincial Domain 'Puyenbroeck' (Wachtebeke, Belgium, 51°9'11"N, 3°52'43"E). Both were co-dominated by the grass species *Holcus lanatus* and *Agrostris capillaris* with *Cerastium fontanum, Ranunculus repens, Prunella vulgaris* and *Veronica chamaedrys* as constant dicotyledonous species. Both were bordered by plantations of *Populus* X *canadensis* under which rabbit burrows were concentrated. According to burrow distribution patterns, both Poplar stands were populated with different rabbit populations, ensuring foraging of both grassland stands by different rabbit populations. Within each grassland, a 72m x 30m study plot was delineated (Fig. 1a-c). Both plots were subsequently divided into eight strips of equal

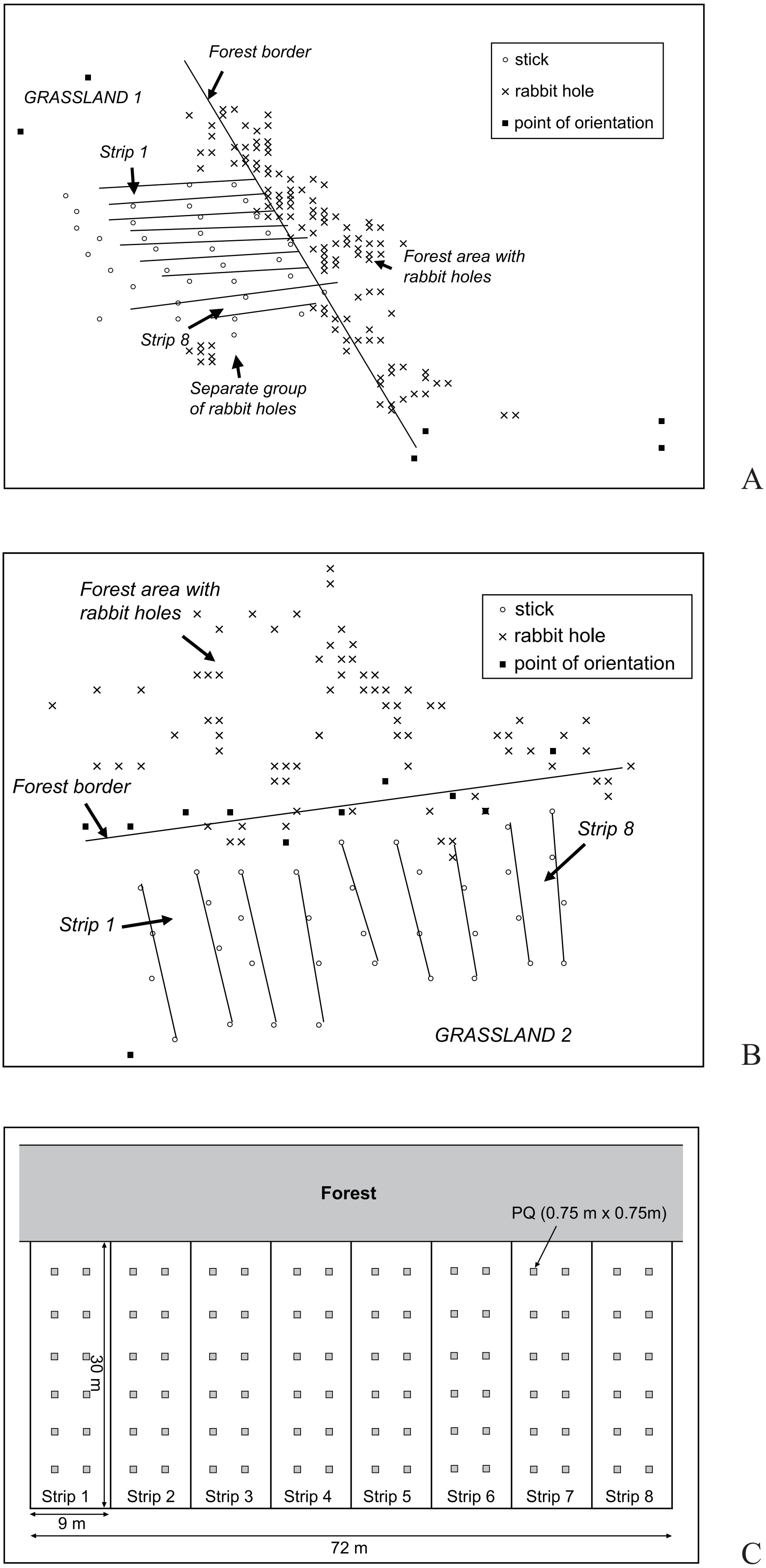

Fig. 1 – Schematic representation of experimental design. (A-B): both grassland sites with location of rabbit burrows (based on GPS coordinates), forest borders and grassland strips that were subjected to differential clipping treatments. (C): details of single grassland strip with indication of permanent quadrants for pellet counts. See text for details.

width and length (9x30m, numbered 1-8 in Fig. 1c), and twelve 75 x 75 cm permanent quadrates (PQs) were delineated in a systematic order within each strip (totalling 96 PQs per grassland). To structurally homogenize both plots all grassland strips were initially clipped at an equal height of 4.2 ± 2.61 cm (t_{-1}), which resulted in an average sward height of 6.6 ± 3.4 cm after 3 weeks of re-growth ('equal' (spring) treatment; t_0=25-26 April 2006). After 12 weeks, even numbered strips were clipped at equal height, while odd strips were left untouched (summer treatment; t_1=10-12 July 2006). After another 12 weeks, even strips were left untouched, and odd strips were clipped at equal height (autumn treatment; t_2=26-27 September 2006). Clipping can be considered as an extreme simulation of grazing, e.g. by other larger herbivores. Under the assumption that the latter have a general impact on sward height and consecutive re-growth of vegetation, conclusions drawn from this clipping experiment could give an estimate of possible facilitative or competitive interactions between both mammal herbivore types, although large herbivores give rise to structural diversity, which is absent in uniformly clipped fields.

Rabbit presence and burrow locations

Rabbit presence was estimated by the pellet counting method (WOOD, 1988; PALOMARES, 2001; BAKKER et al., 2005). Before the first general clipping event all rabbit pellets were removed from the PQs and immediately before both other clipping events, the total number of pellets per PQ was counted and then removed. Latitude-longitude coordinates of all rabbit burrows located in and within a range of 50 m around both grasslands were recorded using a Garmin GPS map76 (Fig. 1a and 1b) and distances between every PQ and the nearest rabbit burrow were calculated.

Vegetation parameters

At the start of the experiment (03/04/2006) and at the end of each experimental treatment (25/04/2006, 10/07/2006 and 26/09/2006 for respectively the equal spring, and the differential summer and autumn treatment), vegetation height was measured at the centre of each PQ as the height at which a disc (diameter 15 cm) with a central slot around a vertical ruler touched the vegetation first (combination of "drop disc method" and "sward stick method" described by STEWART et al., 2001). General vegetation composition of each site was measured in summer (July). Before each clipping event, vegetation samples were collected in the PQs in both grasslands and dried at 60°C to constant weight. Subsequently, the dried samples were milled through a 0.8 mm sieve and analysed using Near-Infrared Spectroscopy (NIRS) (GIVENS et al., 1997). The following measures of nutritive value were determined: concentrations of crude protein (%CP), neutral detergent fibre (%NDF), acid detergent fibre (%ADF), acid detergent lignin (%ADL), phosphorous (%P) and potassium (%K). A sub-sample of 10% of all vegetation samples was randomly selected for direct chemical analysis to fine-tune NIRS calibration lines; the latter are based on a wide range of grassland species of temperate grasslands. %N (needed to calculate %CP) of the samples was determined using the Kjeldahl technique (AOAC 1990), while cell wall components (%ADF) were determined using the method described by Van Soest *et al.* (1991). Cell wall components were analyzed using an ANKOM-220 fibre analyzer (ANKOM Technol. Corp., Fairport, NY) by sequentially adding neutral detergent (for %NDF), acid detergent (for %ADF) and 72% (wt/wt) sulphuric acid (for %ADL). Results of the chemical analysis were merely used for calibration purpose, while the results of the NIRS-analyses were used in the statistical analysis.

Statistical analysis

In the statistical analysis six treatments were distinguished: "short1" (t_{-1}, start of the experiment), "tall2" (t_0, equal spring treatment), "short3" and "tall3" (t_1, respectively the even and odd strips in the differential summer treatment),

TABLE 1

Average values and standard deviations for vegetation height, rabbit activity (number of pellets) and forage quality measures (CP, NDF, ADF, ADL, P and K). Different letters in the same column indicate significant differences between treatments.

Period	Treatment	Strip	Vegetation height (cm)	Pellet count (m^{-2})	%CP	%NDF	%ADF	%ADL	%P	%K
t_{-1}	Control	even = short1	4.3 ± 2.8 a	-	17.93 ± 4.49 c	37.12 ± 2.72 a	17.31 ± 1.04 a	2.53 ± 0.89 a	0.28 ± 0.05 c	2.01 ± 0.25 b
		odd = short1	4.1 ± 2.4 a	-	19.23 ± 2.95 c	35.02 ± 6.16 a	16.64 ± 1.98 a	3.11 ± 0.96 a	0.3 ± 0.04 c	2.14 ± 0.29 b
t_0	Equal spring treatment	even = tall2	6.5 ± 3.3 ab	2.5 ± 7.2 a	18.06 ± 3.16 c	35.93 ± 4.89 a	18.65 ± 1.52 a	2.66 ± 1.31 a	0.28 ± 0.03 c	2.14 ± 0.16 b
		odd = tall2	6.7 ± 3.6 ab	3.6 ± 8.5 a	17.43 ± 3.98 c	38.07 ± 5.17 a	19.71 ± 2.78 a	3.32 ± 0.28 a	0.28 ± 0.04 c	2.11 ± 0.24 b
t_1	Differential summer treatment	even = short3	8.8 ± 3.4 b	18.6 ± 49.6 b	12.73 ± 1.97 b	41.52 ± 3.65 a	22.83 ± 0.8 a	3.79 ± 0.41 a	0.22 ± 0.02 b	1.91 ± 0.16 b
		odd = tall3	31.6 ± 21.1 d	5.8 ± 12.9 a	10.14 ± 0.69 a	43.27 ± 13.77 a	24.46 ± 6.07 a	4.08 ± 0.87 a	0.18 ± 0.01 a	1.66 ± 0.1 a
t_2	Differential autumn treatment	even = tall4	15.2 ± 5.2 c	2.1 ± 6.1 a	17.59 ± 2.20 c	39.2 ± 3.57 a	22.37 ± 0.97 a	4.15 ± 0.41 a	0.25 ± 0.02 c	2.16 ± 0.06 b
		odd = short4	9.1 ± 2.3 b	0.8 ± 3.8 a	18.83 ± 2.09 c	44.11 ± 2.34 a	24.18 ± 1.85 a	4.09 ± 0.92 a	0.28 ± 0.03 c	2.28 ± 0.13 b

and “tall4” and “short4” (t_2, respectively the even and odd strips in the differential autumn treatment).

Treatment effects of clipping regime on vegetation height were determined using analysis of variance (ANOVA) and Tukey HSD tests. Effects of clipping regime on rabbit densities were tested with linear mixed models with factors vegetation height, month and distance to the nearest rabbit hole as response variables, and factors grassland and strip as random effects. Furthermore, to test for treatment effects irrespective of distance to burrows, ANOVA and Tukey HSD tests were performed with rabbit densities and treatment as fixed factors. Effects of different clipping regimes on forage quality measures and vegetation height were tested with Wilcoxon rank sum tests. All statistical analyses were performed with R 2.13.0 (R Development Core Team, 2011).

RESULTS

Vegetation height

Average clipped vegetation height did not differ significantly either between even and odd strips in the control treatment or between the re-growth in even and odd strips in the equal spring treatment, indicating unbiased clipping methods and similar regeneration potential in even and odd strips (Fig. 2). In both differential treatment periods (even summer and odd autumn treatments) similar vegetation height was measured in clipped strips, whereas vegetation was significantly taller in unclipped than clipped strips. Average vegetation height in unclipped strips was significantly higher in summer than in autumn (Fig. 2 and Table 1).

Rabbit presence

During the equal treatment, the number of faecal pellets was negatively correlated with the distance to the nearest burrow ($p<0.05$), while a similar, albeit not significant, relationship was found in the differential treatment periods,. Furthermore, negative correlations between pellet numbers and both season and vegetation height ($p<0.05$) were detected in the differential treatment periods (Table 2).

The number of faecal pellets did not differ significantly between even and odd strips in the control treatment, while subsequent differential clipping treatments resulted in significant differences in pellet numbers. Significantly more droppings were found in the short strips in the

TABLE 2

Results of the linear mixed effects models with pellet counts as dependent variable, distance to nearest burrow, vegetation height and season as response variables, and grassland and strip as random effects, for equal and differential treatments. Significant interactions are in bold.

Treatment	Factor	Value	Std.Error	DF	t-value	p-value
Equal treatment	(Intercept)	1.4998529	0.4735357	175	3.167349	**0.0018**
	Distance nearest burrow	-0.0406124	0.0195366	175	-2.078788	**0.0391**
Differential treatment	(Intercept)	14.346682	2.7271512	365	5.260684	**0.0000**
	Distance nearest burrow	-0.041426	0.045371	365	-0.913049	0.3618
	Season	-3.139754	0.689741	365	-4.552077	**0.0000**
	Vegetation height	-0.055591	0.0246432	365	-2.255843	**0.0247**

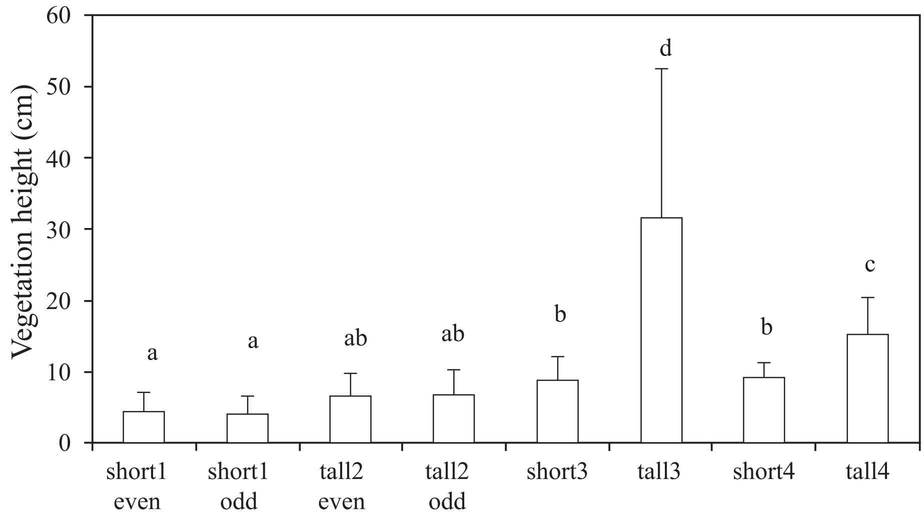

Fig. 2. – Comparison of vegetation height between treatments using ANOVA and Tukey's HSD tests. Different letters indicate significant differences between treatments (F= 104.84; p=0.0000).

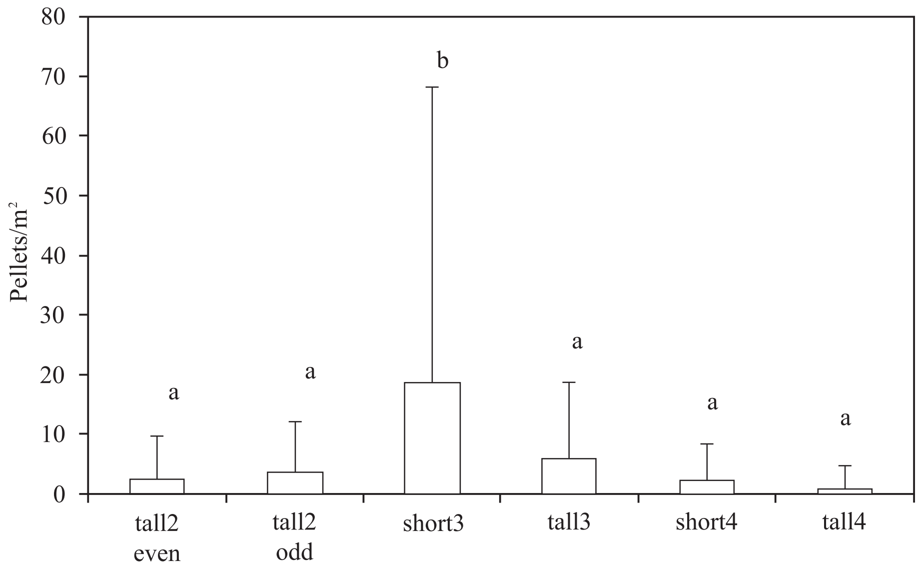

Fig. 3. – Comparison of pellet counts between treatments using ANOVA and Tukey's HSD tests. Different letters indicate significant differences between treatments (F= 8.9429; p=0.0000).

TABLE 3

Comparison of forage quality measures (CP, NDF, ADF, ADL, P and K) for different treatments and test periods (Wilcoxon rank sum test). Significance levels: NS: p>0.10, *: 0.10<p<0.05, **: 0.05<p<0.01, ***: p<0.01.

Period	Treatment	Strip	%CP	%NDF	%ADF	%ADL	%P	%K
t_{-1}	Original situation	short1: even - odd strips	NS	NS	NS	NS	NS	NS
t_0	Equal treatment	tall2: even - odd strips	NS	NS	NS	NS	NS	NS
t_1	Even treatment	short3 - tall3	**	NS	NS	NS	**	**
t_2	Odd treatment	short4 - tall4	NS	NS	NS	NS	NS	NS
t_1-t_2	Even vs. odd treatment	short3 - short4	**	NS	NS	NS	**	*
t_1-t_2	Even vs. odd treatment	tall3 - tall4	**	NS	NS	NS	**	**

differential summer treatment period, while a similar, though not significant trend was found in the differential autumn treatment period (Fig. 3 and Table 1). A peak in overall pellet numbers was found in summer (July) with in total 586 droppings, whereas a total of 146 droppings was counted in spring (April) and only 69 in autumn (September).

Forage quality

No significant differences were found between even and odd strips in both the control and autumn treatment in any of the forage quality variables, while significantly higher CP, P and K concentrations were found in the short sward strips during the summer treatment as compared with the long sward strips. As opposed to the

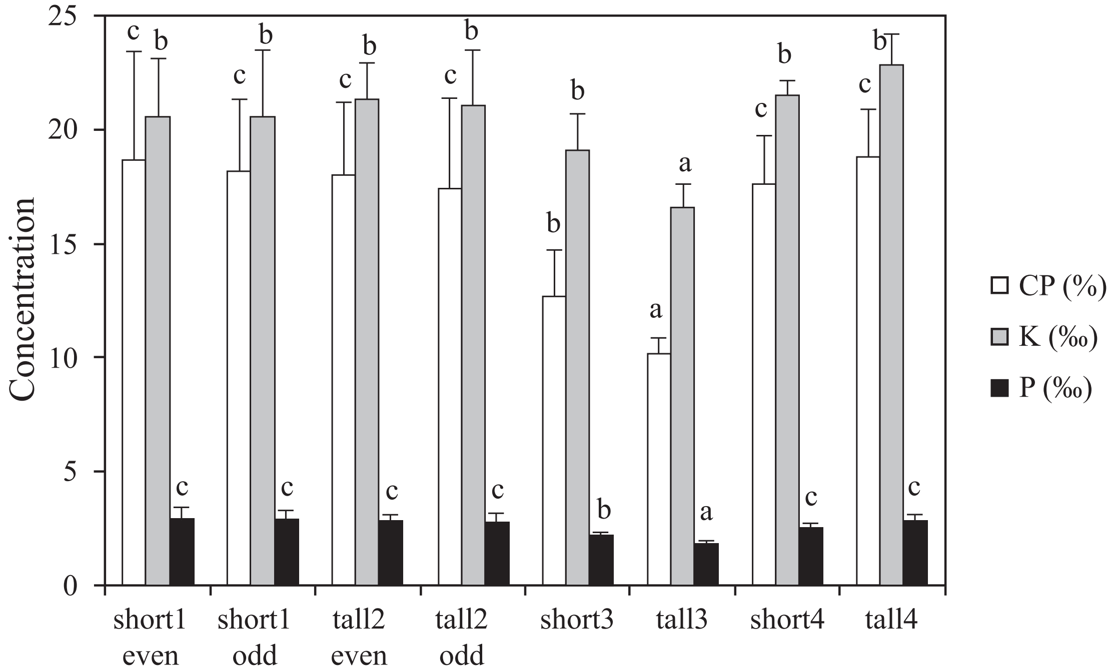

Fig. 4. – Comparison of forage quality concentration (crude protein, potassium and phosphorous) between treatments. Different letters indicate significant differences between treatments.

summer treatment, no significant differences in forage quality measures were found between tall and short vegetation after the autumn treatment. Additionally, when comparing both differential treatment periods, significantly higher concentrations for CP, P and K were found in general (short and tall combined) in autumn versus summer, indicating overall seasonal variations in these forage quality variables with a general forage quality dip in summer (Fig. 4 and Table 3).

DISCUSSION

Low versus tall sward preference

In line with preference patterns emerging from strictly-controlled laboratory and field experiments (Iason et al., 2002; Bakker & Olff, 2003), results from our field experiments support the hypothesis that free-ranging rabbits prefer low above taller vegetation when offered a direct choice. As control and treatment plots were reversed during consecutive experiments, preference for vegetation height was not confounded by possible site preference.

No overall correlations between forage quality traits and vegetation height were found. Although in the first differential summer clipping experiment forage quality measures for crude protein, potassium and phosphorous content were significantly higher in short swards, no significant forage quality differences between cutting treatments were found in the second differential autumn experiment. Nonetheless, a positive correlation between crude protein content and cutting frequency has been demonstrated by many authors. In temperate grasslands in France, Pontes et al. (2007) found a positive correlation between crude protein content and cutting frequency. A sequential clipping trial in an Icelandic hayfield, Fox et al. (1998) caused elevated protein content of *Phleum pratense* leaves from 7-13%. Other studies also demonstrated that grazing or clipping resulted in vegetation re-growth with higher crude protein content (Mayhew & Houston, 1999; Pavlů et al., 2006; Li et al., 2010 for *Poa pratensis*).

Forage quality threshold value as sward selection criterion

Apart from cutting or grazing effects (e.g. Pavlů et al., 2006), crude protein content in grasslands also tends to fluctuate with seasons. In a sown pasture vegetation (including both grasses and herbs) differences appeared but without a clear seasonal pattern (Pavlů et al., 2006), while a selection of grasses cultivated in monocultures, showed a significantly lower %CP in spring than in summer and autumn, the last two seasons not significantly different from one another (Pontes et al., 2007). Also in Puyenbroeck, seasonal fluctuations in crude protein concentration were measured, with the highest concentrations at the end of the growing season for both short and tall stands. Seasonal patterns were also found by Peitz et al. (1997) for cottontail rabbits in Oklahoma where summer forage quality was extremely low in all essential amino acids for all life processes whereas winter diets were probably adequate for maintenance and growth. In contrast with the findings of Pontes et al. (2007), in our experiment crude protein concentrations of the vegetation showed a significant dip in summer, when average values for %CP ranged between 12.73% for short swards and 10.14% for tall swards. Worth mentioning is that Pontes et al. (2007) only dealt with grass species, while in our experiment dicotyledonous plant species were an important vegetation component, among which *Veronica chamaedrys* and *Prunella vulgaris* were the most prominent. Both may have far slower re-growth response to clipping than the grass species involved (*Holcus lanatus* and *Agrostis capillaris*).

Taking into consideration that de Blas & Mateos (1998) recommend forage with a crude protein content of 15.3-18.4% for meat rabbits, we hypothesize that crude protein levels in summer are around or even below a certain forage quality threshold, forcing the wild rabbits to select for the best quality levels. Hence, we assume that rabbits are attracted to the nutritionally more attractive short grasslands. This could be true for %CP, but also for %K and/or %P, but we found no literature references to underpin this for the latter two variables. A laboratory experiment (SOMERS et al., 2008), has already shown that rabbits are able to differentiate between forage of different quality (expressed in protein content), which supports the hypothesis that also in the present study, rabbits actively selected sites with a higher forage quality when forage quality in general was low. It is interesting to mention that forage quality levels of the cultivated grasses used in the feeding trial of SOMERS et al. (2008) were similar to the summer %CP levels of vegetation at our study site (i.e. 10.18 ± 0.30 versus 13.46 ± 0.30 for both low and high quality food in the feeding trial while 10.14 versus 12.72 for both tall and short swards in summer in the present field experiment). Consequently, as the feeding experiment of SOMERS et al. (2008) revealed that domesticated rabbits actively choose for the more protein-rich option, we can assume that this is also the case for the wild rabbits in the presently discussed field experiment. As a response to seasonal and spatial variation in forage quality small herbivores tend to actively select plants or vegetation patches with a high nutritional content (HOLMES, 1991; DRENT & VAN DER WAL, 1999; MARTINS et al., 2002; BAKKER et al., 2005). MARTINS et al. (2002) illustrated the diversity of the diet of wild European rabbits with a seasonal shift in preferred foraging habitats according to forage availability. When combining both seasonal and spatial variation in our field experiment, crude protein levels in summer were significantly lower than in spring and autumn, but between short and tall strips it was still significantly higher in the first, which could drive rabbits to these short strips due to the slightly higher forage quality. This hypothesis is supported by the fact that in contrast with the equal treatment, during both differential clipping treatments no correlation was found between distance to burrows and defecation area, indicating that the availability of patches with a higher forage quality results in higher foraging efforts. In other studies rabbits also tended to forage further from their refuges once high quality food sources near the burrows became depleted (DEKKER, 2007).

Population dynamics

According to the pellet counts, rabbit numbers in summer were four times higher than in spring and even eight times higher than in autumn. This high summer level of rabbit population size can be explained by the breeding season rather than by migration from other territories, as the population was significantly reduced in autumn. This pattern corresponds with the high juvenile mortality found in other studies, e.g. VON HOLST et al. (2002) found a low survival of juveniles after weaning due to starvation, diseases and predation (11.4% for males vs. 15.6% for females). Also, at the start of the reproductive season, more does are reproducing and litter size tends to be higher than at the end of the breeding season (VON HOLST et al., 2002), which could explain the observed population size in summer. Nonetheless, the importance of other population regulating factors, such as migration, predation, diseases and seasonal variability in habitat preference, remains unknown. Irrespective of the cause of the fluctuation in population size, the combination of high population pressure and low nutritional quality in the summer period can at least partly explain the enhanced preference for short sward, having slightly higher nutritional value than the tall sward in this period. Also, due to the nutritionally unfavourable conditions in summer, intraspecific competition might lead to higher juvenile mortality and hence lower animal densities in autumn.

Sward height preferences caused by factors other than forage quality

However, rabbits may also prefer short vegetation for reasons other than forage quality, such as higher visibility of predators in more open vegetation (IASON et al., 2002; see also KOTLER & BLAUSTEIN, 1995). On the other hand, the location of burrows is more restrictive for rabbit movement patterns in short grasslands as short vegetation provides less protection against predators than tall swards (LOMBARDI et al., 2003). Earlier field experiments confirmed that rabbits are sensitive to perceived predation risk

(Bakker et al., 2005; Dekker, 2007), although such risk did not alter the spatial distribution of grazing individuals but rather resulted in shifts in foraging time versus vigilance. In other studies, sward height selection varied according to day/night activity patterns and temperature, with preference for dense vegetation during warm summer days (Villafuerte et al., 1993; Lombardi et al., 2003). Rueda et al. (2008) found season- and age-dependent habitat preferences in Central Spain, where adult rabbits preferred low volume swards in summer while juvenile distribution was dictated by the location of the warrens. Also, the selection for open vegetation may result from higher foraging efficiency, due to lower handling time, in low-open compared to tall-dense vegetation (van de Koppel et al., 1996), especially in summer when resource quality is low.

CONCLUSIONS

Although the selection for short sward cannot unambiguously be attributed to its better forage quality, our data nonetheless suggest that selection for nutritive quality appears when intraspecific competition is high and nutritive quality remains under a certain threshold value; in the experiment both factors coincide during summer (July). When, in autumn (September), competition decreases and nutritive quality increases again, short sward preference largely disappears. We conclude that short sward preference is primarily caused by the better forage quality of re-growth in periods of forage quality limitation, while this preference largely disappears when forage quality limitation no longer occurs.

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