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Food quality affects diet preference of rabbits: experimental evidence

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ABSTRACT. When foraging, small mammalian herbivores do not show a preference for the forage with the highest biomass, which can be explained by several hypotheses (e.g. antipredator considerations, more difficult handling of tall swards and/or the higher nutritional quality of shorter grasses). We tested the ability of rabbits to discriminate between plants of different nutritional value and whether they prefer the most nutritious. A feeding trial in which rabbits (*Oryctolagus cuniculus* (Linnaeus, 1758)) were offered two different types of grasses (fertilised and unfertilised) was executed under experimental conditions. The rabbits preferred the grasses with the highest protein percentage, when conditions were controlled for sward height/plant biomass. This observation is equivalent to results obtained in geese and provides experimental evidence about the capability of rabbits to select for plants with the highest nutritional quality.

KEY WORDS : diet selection, feeding trial, grazing, herbivore, rabbit

INTRODUCTION

Predicting the impact of herbivores on their environment requires insight into the criteria by which grazers select food patches. The mechanism of functional response (reviewed in CRAWLEY, 1983) predicts herbivores to prefer patches with the highest biomass and plant size (LUNDBERG, 1988; GROSS et al., 1993), in order to obtain as much forage as possible in a given time period. However, some studies evidenced that small herbivores, such as rabbits (*Oryctolagus cuniculus* (Linnaeus, 1758)) and geese, prefer rather swards of intermediate height (OLFF et al., 1997; WILMSHURST et al., 2000; HASSALL et al., 2001; IASON et al., 2002; BAKKER et al., 2005). Several explanations for this phenomenon have been mentioned. IASON et al. (2002) and VAN DE KOPPEL et al. (1996) suggested that rabbits and hares, *Lepus europaeus* (Pallas, 1778), prefer vegetation with medium standing crop swards because predators are most likely to occur in the cover offering higher vegetation. Moreover, a tall sward is more difficult to handle for small animals. A dislike for tall swards by brent geese, *Branta bernicla bernicla* (Linnaeus, 1758), and barnacle geese, *Branta leucopsis* (Bechstein, 1803), was explained by the larger costs of handling, more difficult locomotion, and decreased predator detection in the taller vegetation (VAN DER GRAAF et al., 2002).

However, preference for shorter swards may also be related to their higher food quality: grazing creates fast-growing and nutritionally-rich vegetation (so called 'grazing lawns', MCNAUGHTON, 1984), due to plant compensatory mechanisms operating after defoliation (MATTSON, 1980; MCNAUGHTON, 1983). Large herbivores need a larger plant biomass, but can tolerate low plant quality, while smaller herbivores can persist on small quantities of food on the condition that the plants are of high nutritional quality (OLFF et al., 2002). Small hindgut fermenters (e.g. the rabbit) depend on highly digestible forage because they have high metabolic requirements and their digestive system is very small (DEMMENT & VAN SOEST, 1985). The creation of grazing lawns by large herbivores may hence result in 'feeding facilitation' (ARSENAULT & OWEN-SMITH, 2002) benefiting smaller grazers. Hunger may strengthen this preference for nutritionally-rich forage (CRAWLEY, 1983).

The wild rabbit is considered to have a preference for shorter swards. For example, MORENO & VILLAFUERTE (1995) noticed that rabbit grazing pressure was higher in fresh, re-growing vegetation (after burning). Being a central-place forager (SCHOENER, 1979), this herbivore concentrates foraging in the neighbourhood of the burrow (DEKKER, 2007), less than 20m from cover (MORENO & VILLAFUERTE, 1995). With increasing distance from the burrow, grazing pressure of rabbits gradually decreases, causing a gradient pattern. Consequently, vegetation height increases and nitrogen content of forage decreases, due to repeated grazing of the rabbits, stimulating fresh regrowth (BAKKER et al., 2005). BAKKER et al. (2005) conclude that the grazing pattern has to be explained by food quality.

Univocal discrimination of factors determining feeding preferences is only possible in strictly controlled choice experiments (so-called 'cafeteria-trials'; CRAWLEY, 1983). Experimentally enhancing food quality in field experiments by fertilisation increases both biomass (BALL et al., 2000) and plant height. Moreover, feeding preferences are very difficult to measure in the field (CRAWLEY, 1983). For these reasons, we conducted a laboratory experiment to test the ability of rabbits to discriminate between grasses of low and high nutritional quality, while controlling for sward height or vegetation biomass. We predicted that rabbits would prefer grasses of the highest forage quality either when offered grass swards of comparable height or cut grasses of the same biomass.

MATERIALS AND METHODS

Study species

Twelve domestic rabbits (six males and six females, all between 1 and 3 years old) of the breed 'Steenkonijn' were used. The Steenkonijn is the oldest Belgian rabbit breed, and is most closely related to the wild rabbit (WERNER, 1980). Therefore, the behaviour of these animals is supposed to be comparable to the behaviour of their wild ancestor. The rabbits were housed in wire mesh pens (65cm x 110cm, height: 60cm) such that each individual could see a single other individual. This allowed social contact between the animals (DUNCAN et al., 2006). A vaccination against myxomatosis and viral haemorrhagic syndrome was administered. All the individuals received water *ad libitum*, and were fed with a mixture of commercial rabbit pellets and grains (Bonito 96, Aveve, Belgium). From the first day of the feeding trials, the pellet feeding was discontinued, so that the rabbits depended for their feeding on the experimental plants, supplemented with straw, which was provided in the pens.

We used *Festuca rubra* as forage in all trials. *Festuca rubra* plants were grown from seeds (Herbiseed, Twyford, England), sown on a mixture of 50% dune sand and 50% potting soil, in seed trays of 40cm by 45cm during July – October 2004. Immediately after sowing, half of the seed trays (selected at random) received 30g of organic fertiliser (8% nitrogen, 6% phosphorus, 7% potassium, 3% magnesium and 38% organic matter), further referred to as 'fertilised plants' (F^+). All trays received an inorganic fertiliser twice (once one month after sowing and once in March 2005). The 'fertilised plants' received 7.5g of inorganic fertiliser (20% nitrogen, 5% phosphorus and 8% potassium) at a time; the 'unfertilised plants' (F^-) received 2.5g at a time.

The trays were put inside the greenhouse immediately after sowing, and were watered every two days. From December 2004 until March 2005, the trays were put outside for better aeration. Fungicide (sulphur) was added twice to cope with a mildew infection, and an infection of aphids was treated by using a mix of piperonylbutoxide and pyrethrine.

Experimental design

The feeding trial took place in an experimental pen (Fig. 1) of 104cm depth, 91cm width and 73cm height, connected to a smaller pen (36cm by 26cm by 30cm) from which the rabbit was not able to see the surroundings. Two grass swards (trimmed just before the start of the trial to a height of 13cm (further called short swards ('S')) or of 33cm (tall swards ('T'))) or two dishes with clipped grass (100g per dish) were put in the larger pen, on the opposite side of the entrance from the small pen. A partition of 40cm high (in the middle between the two swards or dishes) divided the large pen into two halves.

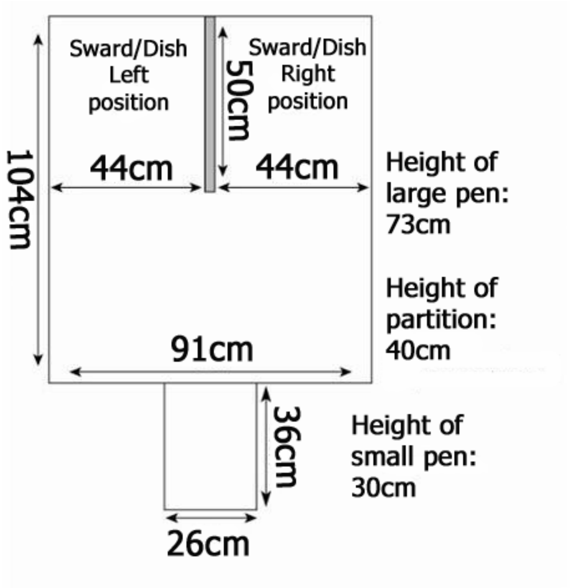

Fig. 1. – Design of the experimental pen.

In the sward trial (22-29 April 2005), there were four groups of three rabbits and two treatments (two combinations of swards): F^+T versus F^-T and F^+S versus F^-S. Each two groups of rabbits received the treatments in a different order. This total design was replicated once, but with a reverse of the left-hand and the right-hand sward. During the clipping trial (2-5 May 2005), the rabbits received dishes with clipped fertilised grass on one side of the pen, and unfertilised grass on the other side (F^+ versus F^-). In the replicate of the clipping trial, the position of F^+ and F^- was reversed. Since the design was randomized and fully balanced, possible effects of the order of treatments were minimized.

Before the start of the feeding trial, four learning days were organised: the rabbits were placed in the pen to habituate to the pen, the grass and the observer. Research carried out with ruminants shows that food preferences develop because of the experience of post-ingestive effects (satiety or malaise) and their interaction with the senses of mainly taste and smell (PROVENZA, 1995). Herbivores learn about grass quality through foraging consequences, which they link with pre-ingestive cues necessary to recognize the value of the forage (GINANE et al., 2005). Although this was only evidenced for ruminants, it is reasonable to assume that ruminants and non-ruminants do not differ in the non-cognitive aspects of how feedback is processed (PROVENZA, 1995). Non-ruminants have indeed been found to be able to discriminate between foods, even when the differences are relatively small (POST, 1993). This means that the rabbits would only be able to select the most nutritious food if they had the opportunity to experience the differences in post-ingestive effects between F^+ and F^-grasses. This condition was fulfilled through the learning days preceding the experiment.

At the start of each experimental session, the individual was weighed (to estimate its degree of hunger) and placed in the small pen. When the entrance to the experimental pen was opened and the rabbit approached the feeding trays, we started an observation session of 20 minutes, from a central point which did not interfere with the experiment. A detailed description of the foraging behaviour of the rabbit was noted.

Forage quality analysis

After each session, plant material that had not been consumed was removed from the pen and dried at 60°C (WTB Binder with controller RD 2 EED/FED (Binder, Tuttlingen, Germany)), until no more mass loss was detected, after which the dried plants were ground. The percentage of crude protein (CP) and of cell wall constituents (cellulose, hemicellulose and lignin, which were derived from NDF (neutral detergent fibre), ADF (acid detergent fibre) and ADL (acid detergent lignin)) were obtained by Near Infrared Spectroscopy (NIRS – for more information see GIVENS et al. (1997)). A FOSS Feed and Forage Analyzer was used, combined with Winisi software (FOSS, Brussels, Belgium). The calibration for the NIRS was carried out by performing wet analyses for approximately 10% of the samples, following the method of Kjeldahl for CP and following the protocols of GOERING & VAN SOEST (1970) and VAN SOEST et al. (1991) for cell wall constituents.

The amount of digestible protein (DP) was calculated by multiplying CP by the mean digestibility coefficient of CP in grasses (value of 0.70; MAFF, 1986). DE (Digestible Energy) was calculated based on ADF, by multiplying GE (Gross Energy, value based on MAFF M (1986)) by GE_D (coefficient of digestibility of Gross Energy, in which GE_D is defined as follows: GE_D=0.867–0.0012 ADF (g/kg DM) (DE BLAS et al., 1992)). The DP/DE ratio was also calculated since this ratio has been proven to be very valuable in evaluating forage quality for rabbits (FRAGA, 1998).

Statistical analysis

All statistical analyses were performed using SAS 9.1 (SAS Institute Inc., Cary, North Carolina).

The feeding preference of rabbits for different types of grasses was tested by Mixed Linear Models, with "individual" as random effect and "relative foraging time" as dependent variable. This last variable was calculated by timing individual feeding bouts per sward or dish, starting from the moment when the experimental individual had tasted from either both swards or both dishes until the end of the session, divided by the total time left until the end of the session. As vegetation height or biomasses were controlled for, differences in handling time were not expected, so that the relative foraging time can be considered a good measure for intake rate. Furthermore, the level of satiety after eating (PROVENZA, 1995; GINANE et al., 2005) will have been higher for the more nutritious grasses. Since mammals learn to link the taste of the forage to the satiety level, directed foraging behaviour can only start from the moment they have tasted both grasses. Therefore, the relative foraging time, as defined above, is the most appropriate measure describing their preference.

Four independent categorical variables were included in the model: fertilisation (0/1), position of the sward or dish (left or right), day and sex. We started with a full model including all two-factor and higher-order interactions and applied a backward stepwise selection procedure.

The effect of fertilisation on forage quality was analysed by a General Linear Model. We tested the effect of fertilisation as a categorical variable separately on the percentages of CP, cellulose, hemicellulose, lignin, DP, DE and DP/DE. Mixed regression analysis modelling repeated measurements at individual level was used to examine shifts in weight during the feeding trials.

RESULTS

Table 1 summarizes the effect of fertilisation, day, sex and the position of the sward or dish (and all possible interaction terms) on the relative foraging time. Fertilised swards and dishes were preferred over unfertilised ones, as can be seen in Fig. 2: the mean of the relative foraging time was lower for F^-plants (sward trial: mean=20.02%±3.31 SE, N=48; clipping trial: mean=18.25±4.74%, N=24) than for F^+plants (sward trial: mean=31.26±3.31%, N=48; clipping trial: mean=37.13±4.74%, N=24).

The effects of fertilisation on forage quality measures are shown in Table 2, which highlights some significant differences between fertilised and unfertilised plants. CP and cellulose percentages were significantly higher in the F^+plants, as well in the sward trial as in the clipping trial. In the clipping trial, also the hemicellulose percentage was higher in the F^+plants, while the lignin percentage was lower in these plants. The value of digestible protein percentage was significantly higher in the F^+plants, compared to the F^-plants. This applied to the sward trial as well as to the clipping trial. The same result was obtained for the DP/DE-ratio. Also, the DE percentage differed significantly between F^+ and F^-plants, with a higher DE percentage in F^-plants, in the sward trial, but not in the clipping trial.

The effect of day on the relative foraging time was not significant, although the rabbits lost weight during the trials. These losses were statistically significant in both trials (sward trial: $F_{1,11}$=519.51, estimate for time effect=-22.74, P<0.001; clipping trial: $F_{1,11.3}$=7.11, estimate for time effect=-18.50, P=0.02).

DISCUSSION

The results of the experiment showed that only fertilisation had a significant influence on the preference of the animals: the relative foraging time was longer for the fertilised forage, both in the sward and in the clipping trial. The forage quality analysis revealed a higher percentage of both crude and digestible protein in F^+plants, compared to F^-plants. This was to be expected, since nitrogen is a principal component of the used fertilisers and its content is strongly related to protein content. We also observed a higher percentage of cellulose and hemicellulose, although the latter only in the F^+plants from the clipping trial, in which lignin decreased. As forage quality is believed to be enhanced by the protein level (LANGVATN

TABLE 1

Results of the Mixed Linear Model testing for the effect of the four main factors (fertilisation, position, day and sex) and interactions, on the relative foraging time, during a backward stepwise selection. The relative foraging time was calculated by timing individual feeding bouts per sward or dish, starting from the moment when the experimental individual had tasted from either both swards or both dishes until the end of the session, divided by the total time left until the end of the session. The p-values are those from the last step before the respective variable was removed. Num d.f.=numerator degrees of freedom, den d.f.=denominator degrees of freedom.

	Fixed effects	num d.f.	den d.f.	F	P
Sward trial	Fertilisation (F)	1	94	5.74	0.02
	Day (D)	7	87	1.21	0.3
	Position grass (P)	1	86	0.84	0.36
	Sex (S)	1	85	0.35	0.56
	F*P	1	84	0.85	0.36
	P*D	7	77	1.05	0.4
	D*S	7	70	0.9	0.51
	F*S	1	69	0.3	0.59
	P*S	1	68	0.02	0.89
	F*D	3	65	0.19	0.9
	F*P*D	3	62	1.72	0.17
	F*D*S	7	55	1.08	0.39
	P*D*S	3	52	0.29	0.83
	F*P*S	1	51	0.03	0.87
	F*P*D*S	3	48	0.23	0.87
	Random effect	*estimate*	*residual*		
	Individual	0	525.03		
Clipping trial	Fertilisation (F)	1	46	7.86	0.01
	Sex (S)	1	45	3.45	0.07
	Day (D)	1	44	0.08	0.78
	Position grass (P)	1	43	0	0.97
	F*S	1	42	2.97	0.09
	D*S	1	41	0.3	0.59
	P*D	1	40	0.26	0.61
	P*S	1	39	0.22	0.64
	F*D	1	38	0.2	0.66
	F*P	1	37	0.04	0.85
	F*D*S	1	36	0.98	0.33
	F*P*D	1	35	0.21	0.65
	P*D*S	1	34	0.1	0.76
	F*P*S	1	33	0.04	0.85
	F*P*D*S	1	32	0.13	0.72
	Random effect	*estimate*	*residual*		
	Individual	0	633.67		

& HANLEY, 1993) and to be diminished by the fibre content (OLFF et al., 1997), the question arises whether fertilisation effectively resulted in a higher food quality. Moreover, in the sward trial, the F^{+}plants even had a lower digestible energy content. However, it is reasonable to assume that the increase of digestible protein is the most important factor determining forage quality. Since some amino acids cannot be synthesized by the animal's body itself, organisms need amino acids, immediately available from the forage to maintain body conditions constant (FRAGA, 1998). The close agreement between the sum of individual amino acids levels in the body of the rabbit and the CP content (FRAGA, 1998), indicates that CP content provides a good estimate of forage quality. The DP/DE-proportion is mentioned to be an even better predictor (FRAGA, 1998). This ratio also proved to be significantly higher in the F^{+}plants, in both trials. We can hence conclude that the rabbits selected the forage with the highest nutritional quality.

This preference for high quality forage has been suggested for rabbits (KUIJPER et al., 2004; RÖDEL, 2005) and also for other relatively small mammal herbivores, e.g. small ruminants (WILMSHURST et al., 2000) and mountain hares (*Lepus timidus* (Linnaeus, 1758)) (LINDLÖF et al., 1974). However, studies eliminating the correlation between forage quality and sward height/biomass are scarce. Therefore, it is difficult to know whether the animals are really able to select for the higher nitrogen content, or whether this selection is just coincidental related to the selection of swards with medium standing crop. Some studies concerning geese (HASSALL et al., 2001; BOS et al., 2002; HASSALL & LANE, 2005) showed the capability of these birds to discriminate between high and low quality forage, by eliminating the relationship between forage quality and sward height. BAKKER et al. (2005) executed a field experiment which eliminated the relationship between distance from the rabbit burrow and forage quality, and showed that forage of a higher quality

TABLE 2

Results of the General Linear Model testing for the effect of fertilisation on forage quality measures of standing crop (sward trial) and clipped grass material (clipping trial). F^-plants=unfertilised plants, F^+plants=fertilised plants. CP=% Crude Protein, DP=% Digestible Protein, DE=% Digestible Energy. Num d.f.=numerator degrees of freedom, den d.f.=denominator degrees of freedom.

	num d.f.	den d.f.	F	P	mean F^-plants ± SE	mean F^+plants± SE
Sward trial						
CP (%)	1	94	60.95	<0.001	10.77±0.28	13.91±0.28
Cellulose (%)	1	94	19.99	<0.001	21.86±0.25	23.43±0.25
Hemicellulose (%)	1	94	0.21	0.65	22.62±0.25	22.79±0.25
Lignin (%)	1	94	0.36	0.55	3.17±0.07	3.23±0.07
DP (%)	1	94	60.95	<0.001	7.54±0.20	9.73±0.20
DE (%)	1	94	24.46	<0.001	10.54±0.05	10.17±0.05
DP/DE	1	94	86.67	<0.001	0.71±0.02	0.96±0.02
Clipping trial						
CP (%)	1	46	57.65	<0.001	10.17±0.30	13.44±0.30
Cellulose (%)	1	46	10.32	<0.001	21.55±0.22	22.56±0.22
Hemicellulose (%)	1	46	17.22	<0.001	21.54±0.19	22.65±0.19
Lignin (%)	1	46	19.5	<0.001	2.77±0.07	2.32±0.07
DP (%)	1	46	57.65	<0.001	7.12±0.21	9.41±0.21
DE (%)	1	46	2.69	0.11	10.70±0.05	10.57±0.05
DP/DE	1	46	49.18	<0.001	0.67±0.02	0.89±0.02

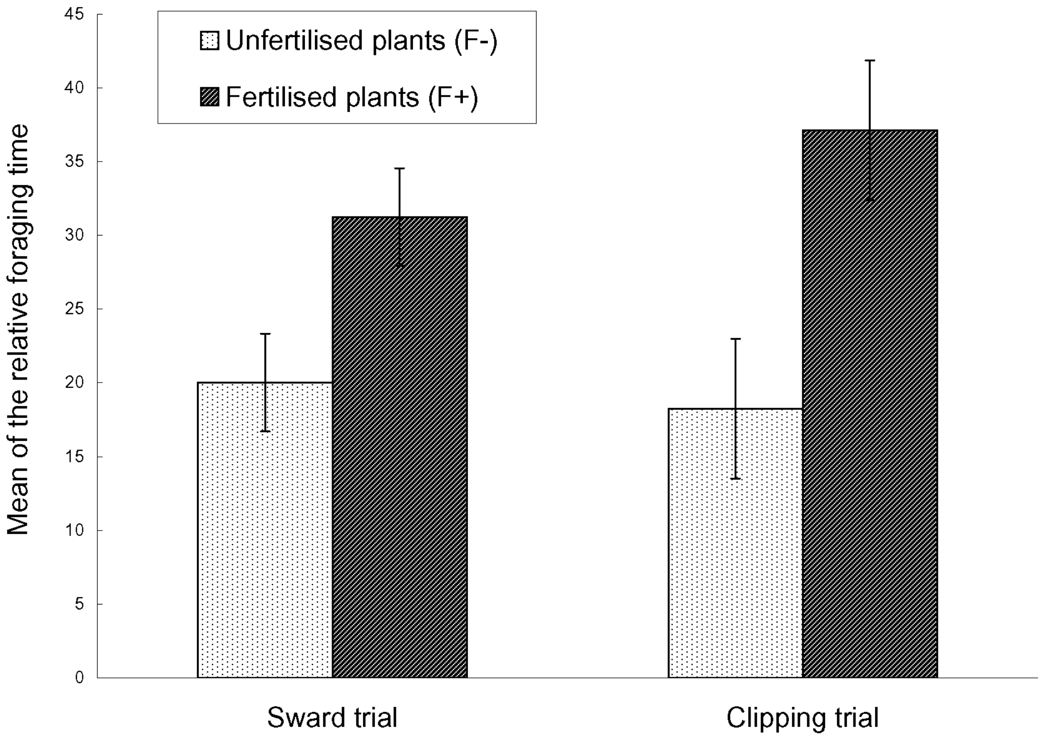

Fig. 2. – Mean and standard error of the relative foraging time of rabbits, when offered the choice between fertilised and unfertilised grasses, controlling for sward height (sward trial) or plant biomass (clipping trial). The relative foraging time was calculated by timing individual feeding bouts per sward or dish, starting from the moment when the experimental individual had tasted from either both swards or both dishes until the end of the session, divided by the total time left until the end of the session.

is preferred, even when farther from the burrow (and thus with a higher sward height). However, the highest (and farthest) swards in this trial were on average approximately as high as the short swards in our study. Therefore, it is possible that sward height in their trial did not show enough variation to really affect the rabbit behaviour. However, their results are confirmed by the results of the present study, controlling for plant height and biomass, which clearly indicate that plant quality, particularly nitrogen and related protein content, is a crucial factor for selecting foraging patches in rabbits.

The other factors included in the model (position of the sward or dish, experimental day and sex) did not significantly influence the food preference of the rabbits. The day of feeding was of no importance; although CRAWLEY (1983) mentions that a hungry animal will be more selective. Since the animals lost weight during the experiments, it could be expected that the animals would become more selective towards the end of the experiment, but this was not confirmed. Similar results were obtained by DUNCAN et al. (2006) who found no evidence that nutritional plane had an overall effect on the proportion of several plant species eaten during preference tests carried out with herbivores. The authors relate this to the more extreme forage deficits in the wild. Similarly, the scarcity of food during winter time in the temperate regions will cause stronger feelings of hunger than the rabbits in our experiment experienced.

Although we evidenced that food quality is important for determining preferences, we were not able to exclude the importance of anti-predation considerations and other sward height-related issues in diet selection: other factors, besides nutrient content, may also have played a role during the decision process of the rabbits. Other research indeed showed that rabbits also choose the swards with the lowest biomass, when there are no nutritional differences between the swards of different heights (IASON et al., 2002). However, the field experiment of BAKKER et al. (2005) demonstrates that the presence of predators causes a shift in the moment of feeding, but does not affect patch preferences. The presented results clearly showed that nutritional content plays an important role in the observed preference of small herbivores for swards of intermediate size, but further research is needed to unravel the relative importance of other potentially contributing factors.

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