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Digestive strategies in two sympatrically occurring lagomorphs

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Abstract

Separation of low digestible fibres and fermentation of the digestible part of the food in the caecum is an adaptation of some small herbivores to cope with low-quality forage. The caecum content is later re-ingested as soft faeces so that the herbivore can benefit from this protein-rich material. This is known as caecotrophy and is a common phenomenon in species of leporids, although differences exist between hares and rabbits. Hares have amorphous soft faeces and the amount of soft faeces produced is smaller compared to that of rabbits. Both factors suggest that hares have smaller benefits from re-ingestion of the caecal contents compared with rabbits and, as a consequence, have a less efficient digestion (mainly of nitrogen) compared to rabbits. The assertion was tested whether digestive efficiency is different between the two herbivores and how this affects the choice of food plants in a natural situation. A feeding trial was conducted using hares and rabbits fed with diets with a range of fibre contents. Dry matter digestibility was not different, but nitrogen digestibility was lower in hares than in rabbits, indicating a less efficient digestion of protein. Both taxa showed a different response to increased fibre content in the diet. Rabbits maximized digestibility by increasing retention time of the food, hares maximized digestion rate by increasing the passage rate of the food through the digestive tract. The daily digestible nitrogen intake was higher in hares *Lepus europaeus* than that in rabbits *Oryctolagus cuniculus*, indicating that hares compensated for their lower nitrogen digestibility. Hares were predicted to select for higher quality plant species in a natural situation, but they had, on average, a lower nitrogen and higher total fibre content in their diet compared to sympatrically occurring rabbits. This indicated that hares did not compensate for their lower digestive efficiency by selecting higher quality food plants. The present experiment shows that hares and rabbits have different digestive strategies to cope with low quality forage. Rabbits had a higher N-digestibility by increasing the retention time, whereas hares appeared to compensate for their lower N-digestibility by increasing the processing rate, when food quality deteriorated.

Key words: hare, *Lepus europaeus*, rabbit, *Oryctolagus cuniculus*, caecotrophy, fibre, nitrogen digestion

INTRODUCTION

Small herbivores have evolved several mechanisms that enable them to cope with forage containing a high fibre content (Foley & Cork, 1992; Justice & Smith, 1992). One mechanism is the selective separation of fibres from the digestible fraction of the food. Its basic function is to excrete quickly poorly digestible large particles but retain fine food particles in the caecum for fermentation (Björnhag, 1994). This results in the production of two types of faeces; hard faeces that mainly consist of poorly digestible food particles and soft faeces composed of the material retained and fermented in the caecum. These soft faeces are normally re-ingested after excretion (caecotrophy), to make use of the end products of fermentation and the microbial proteins present in the soft faeces (Hirakawa, 2001).

Although caecotrophy is a common phenomenon in leporids (Hirakawa, 2001), several studies suggest a difference in the digestive system between rabbits *Oryctolagus* spp. and hares *Lepus* spp. First, the type of soft faeces that is produced is different. Rabbits produce soft faeces with a tough surface membrane, whereas hares produce amorphous soft faeces without a membrane (Hirakawa, 2001). The faeces with a surface membrane remain intact in the stomach for several hours after re-ingestion. This allows microbial activity to continue inside the acid environment of the stomach (Griffiths & Davies, 1963). The amorphous type of faeces is mixed with other materials in the stomach from which it is hardly distinguishable (Hewson, 1963; Hirakawa, 1995). Second,

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the amount of soft faeces produced may be different. We are aware of only two published studies which report on the proportion of soft faeces that are produced by rabbits and hares. Jilge (1974) found that soft faeces made up to 40% of daily faeces production in laboratory rabbits, while Pehrson (1983) observed that only 24% of daily faeces production consisted of soft faeces in caged mountain hares *Lepus timidus*. Although this suggests a large difference between rabbits and hares, differences in diet need to be taken into account when comparing the results of both studies. However, another study in which brown hares *Lepus europaeus* and rabbits *Oryctolagus cuniculus* were fed the same diet, showed a similar pattern. On average five soft faeces in the digestive tract of hares were found compared to 99 in rabbits (Van Laar, pers. comm.). These two factors, the type and amount of soft faeces produced, suggest a difference in the digestive system based on caecotrophy between hares and rabbits. Hares seem less able to separate poorly digestible fibres from the digestible fraction of the food and hence produce smaller amounts of soft faeces. Combined with the amorphous type of soft faeces produced, we hypothesize that hares have smaller benefits from re-ingestion of the caecal contents compared with rabbits.

Based on these differences between hares and rabbits, we wanted to test whether the digestive strategies of these two herbivores are different and whether this affects their feeding strategy. As re-ingestion of the caecum contents is an important source of proteins for herbivores (Iason & Van Wieren, 1999; Hirakawa, 2001), we hypothesized that rabbits have a higher nitrogen digestibility, especially when diets contain high levels of fibres. We tested this by comparing the digestive efficiency of rabbits *O. cunniculus* and European brown hares *L. europaeus* in a feeding trial using diets with increasing fibre contents. Differences in the digestive system might have important consequences for the feeding strategy of both herbivores in a natural situation. A herbivore might compensate a low digestive efficiency by selecting high-quality food plants (Karasov, 1990). We hypothesized that in an area where both herbivores occur, hares select forage of higher protein content and lower fibre content. This was tested by comparing the selection of food plants in a high-salt marsh system where both hares and rabbits occurred sympatrically.

METHODS

Animals

Five European brown hares born in captivity were obtained from the breeding stock of the Research Institute of Wildlife Ecology of the University of Vienna. Five domesticated Hollander rabbits were purchased from registered breeders.

This is an ancient rabbit breed, with a body weight that is within the range reported for wild rabbits (1.2–2.5 kg; Lange *et al*., 1994). One male and 4 females, all fully grown adults (between 1 and 2 years) were selected to be used in the feeding trials. One rabbit (male) showed a sharp decrease in body weight during the experimental period. It turned out to have a deformation of the incisors and was excluded from all analyses. The 5 hares averaged 3.4 kg (range 2.8–3.7 kg) and the 4 female rabbits used averaged 2.4 kg (range 2.3–2.6 kg). The animals were housed in outdoor pens of 1.5 × 1 m with a wooden box for shelter of (40 × 40 × 50 cm). The outdoor pens were covered with a roof. The floor consisted of mesh wire (ø1 cm) where droppings could fall through. This did not prevent caecotrophy as soft faeces were directly taken from the anus for re-ingestion (pers. obs.). Animals were kept under natural daylight and temperature. The feeding trials were carried out in June–July with relatively constant weather conditions. The experiments were approved by the animal experiment commission (Dec nr. 2469).

Table 1. Ingredients and chemical composition of the experimental food pellets used in the feeding experiment. NDF, neutral detergent fibre; ADF, acid detergent fibre

% wheat straw	% *Lolium perenne*	% molasses	%NDF diet	%ADF	%N
0	95	5	42.3	27.1	2.6
10	85	5	45.6	28.5	2.4
20	75	5	48.9	32.0	2.4
30	65	5	52.2	34.4	2.1

Diets and experimental procedure

Four types of diet were provided in similar-sized, homogenous pellets to exclude any selection of food particles. The basis of the diets was high-quality dried ryegrass *Lolium perenne*. This was mixed with different amounts of wheat straw creating a range in fibre content (Table 1). Molasses (5% of pellet weight) was used to bind these ingredients in pellets. Outside the experimental periods the animals received *ad libitum* pellets of fresh dried grass and additional hay. In this way the animals were used to diets containing a high fibre content. Before the feeding trial of each diet, animals had a 7-day adaptation period in which they only received the experimental food. During the feeding trials, the animals did not have any food during daytime (09:00–18:00). In the evening (18:00) they received experimental food *ad libitum*. Next morning all remaining food and all droppings were collected, dried for 48 h at 70 °C, and weighed. The intake and amount of droppings were determined for 5 days for each diet. For each animal, the diet received was randomly selected, and thus the different diets were offered in a random order so that time effects were exclude. The experiments were carried out from May to July 2002.

Chemical analyses and calculations

Chemical analyses were performed on dried samples of food and droppings. Total nitrogen, as a measure of protein content (Van Soest, 1982), was determined by automated elemental analysis (Interscience EA 1110). Acid detergent fibre (ADF), a poorly degradable cell wall component of plants (Van Soest, 1982) was determined according to Goering & Van Soest (1970). Neutral detergent fibre (NDF) of the food was determined as a measure of total fibre content (Van Soest, 1982). A mixed sample of droppings per individual animal for each diet was created. On each day of each 5-day feeding trial, 10 random droppings were taken per individual animal. The resulting 50 droppings per animal were homogenized by grinding them to powder. Samples of each diet were taken by randomly selecting 10 pellets of food. Dry matter digestibility (DMD) was calculated according to Van Soest (1982):

$$\mathrm{DMD} = \frac{(Ii - Fi)}{Fi}$$

where Ii is the total intake of dry matter and Fi is the total dry weight of faeces per individual during each 5-day feeding trial.

Apparent nitrogen digestibility (AND) was calculated according to Van Soest (1982):

$$\mathrm{AND} = \frac{(Ni - Nf)}{Ni}$$

where Ni is the total intake of nitrogen (via food) and Nf is the total excreted nitrogen (via faeces). Again this was calculated for each individual during each 5-day feeding trial. The retention time of the food in the digestive tract can be calculated as the gut volume divided by the digesta flow rate (Owen, 1975; Sibly, 1981). The mean retention time was approximated (Prop & Vulink, 1992) as:

$$\mathrm{T} = \frac{\mathrm{LDT}}{(\mathrm{LD/I})}$$

where LDT = length of the digestive tract (cm), LD = length of dropping (cm), I = dropping interval (h). Length of the digestive tract (total length of intestines) was determined after dissection of 7 adult hares and 9 adult rabbits (of the Hollander breed) in another feeding experiment (Van Laar, pers. comm.). As no significant relation between body weight and intestine length was found (hares: $F_{1,7} < 0.061$, $P = 0.82$; rabbits: $F_{1,9} = 4.66$, $P = 0.068$) the average intestine lengths per species were taken (hare 278.1 cm SE = 29.3; rabbit 298.0 cm, SE = 10.7). Dropping length was determined by measuring 10 droppings to the nearest 1 mm per individual on the last day of each feeding trial. The dropping interval was calculated as the time divided by the total number of droppings produced per night per individual. This crude method of calculating mean retention time provided an average retention time of the food in the digestive tract. Real retention times of the different fractions of the food can only be determined by the use of internal markers (see e.g. Jilge, 1974; Fraga *et al.*, 1991). Therefore, this approximation of retention time was used to look only at qualitative differences in mean retention time of the food between species or between diets.

As metabolic requirements of mammals increase with body mass$^{0.75}$ (Nagy, 1987), the intake of dry matter was expressed in terms of the weight per animal$^{0.75}$ to compare both species. The daily intake of digestible nitrogen was calculated as the proportion of the nitrogen that was digested of the total ingested nitrogen of the food. To be able to compare hares and rabbits, this was also scaled per body mass$^{0.75}$.

Field data

To assess the selection of food plants by wild hares and rabbits in a natural setting, droppings of both species were collected in 1993 on the salt marsh of Schiermonnikoog, an island in the Dutch Wadden Sea (J. Snel, pers. comm.). The rabbits on this island, derived from domestic stock liberated in 1851 (Flux & Fullagar, 1992). Every week fresh droppings were collected on randomly spread fixed plots in an area (500 × 500 m) where both species occurred. As rabbit and hare droppings were found on all plots in this area, they experienced similar availabilities of food plants. Hare and rabbit droppings could be distinguished by the combination of the size, shape and contents of the droppings. Hare droppings were larger than rabbit droppings, were pointed instead of rounded and contained larger fragments than those in rabbit droppings. Dried samples were examined under the microscope and plant species were identified on the basis of epidermal fragments. Diet composition was determined using the line-intercept method described by Seber & Pemberton (1979). The period of collecting droppings (October–November) was subdivided in 4 equal periods of 12 days. A homogenized sample was analysed for each period.

In the same area, samples of plant species were picked by hand and dried for 48 h at 60 °C. Only leaf tips of plants were harvested as this most closely resembles the parts selected by hares and rabbits in the field (pers. obs.). The nitrogen content and the NDF content per species was analysed as described above. The average nitrogen and NDF contents of the diet of hares and rabbits was calculated by multiplying the N, NDF values of each plant species by the fraction in which the species occurred in the diet.

Statistical analyses

Univariate analyses of variance were used to test for the effect of diet and species (hare, rabbit) on the DMD, AND, dry matter intake and retention time of the food. Diet and species were entered as fixed factors (Zar, 1984). Differences between diets within each species were tested using Tukey's test for multiple comparison. Differences between species on each diet were tested using independent t-tests. Linear regression was used to test if any of these values showed a significant trend with increasing fibre content of the food. Whether the natural diet of hares and rabbits differed in the NDF and nitrogen content was tested with paired t-tests, matching the samples collected during 1 period.

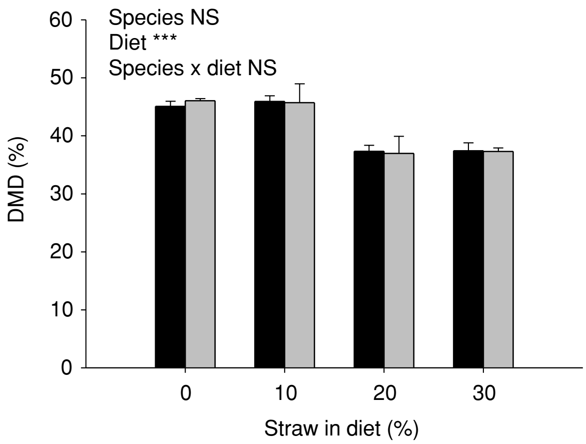

Fig. 1. Dry matter digestibility (DMD) of hares *Lepus europaeus* (■) and rabbits *Oryctolagus cuniculus* (■) that fed on the four experimental diets. Significance of the effect of species, diet and the interaction are indicated by asterisks: $^{***}P < 0.0001$.

Fig. 2. Apparent nitrogen digestibility (AND) of hares *Lepus europaeus* (■) and rabbits *Oryctolagus cuniculus* (■) that fed on the four experimental diets. Significant effects of species, diet and significant interactions: $^{*}P < 0.05$, $^{**}P < 0.001$, $^{***}P < 0.0001$. Asterisks in the graph indicate significant difference between hares and rabbits that fed on each diet.

RESULTS

Dry matter and nitrogen digestibility

Dry matter digestibility (DMD) did not differ between hares and rabbits ($F_{1,36} = 0.003$, $P = 0.958$; Fig. 1), but was significantly affected by the type of diet ($F_{3,36} = 18.05$, $P < 0.0001$). Animals fed with diets containing 20% and 30% of straw showed a lower DMD compared to the other two diets ($P < 0.05$). Both species had a similar decrease in DMD, indicated by the non-significant interaction between species and diet. In contrast, rabbits had a higher apparent nitrogen digestibility (AND) compared to hares on all diets ($F_{1,36} = 20.25$, $P < 0.0001$; Fig. 2). The AND did not change with increasing straw content of the diet ($F_{3,36} = 2.94$, $P = 0.06$).

Intake rate and mean retention time

As metabolic requirements of mammals increase with body mass$^{0.75}$ (Nagy, 1987), the intake of dry matter was expressed in terms of the weight per animal$^{0.75}$ in order to compare both species. Hares and rabbits showed a different reaction to increased straw content of the diet (Fig. 3). Hares tended to increase the dry matter intake per unit metabolic body weight ($r^2 = 0.17$, $F_{1,20} = 3.68$, $P = 0.07$) whereas rabbits decreased the intake with increasing straw content of the food ($r^2 = 0.31$, $F_{1,16} = 6.14$, $P = 0.027$). This resulted in a higher dry matter intake for hares compared to rabbits ($F_{1,3} = 63.48$, $P < 0.0001$). Only when fed with the diet containing no straw was intake per body mass similar in both species. Another difference between hares and rabbits was the higher mean retention time of the food in rabbits (Fig. 4; $F_{1,36} = 81.31$, $P < 0.0001$). Hares decreased the mean retention time when the fibre content of the food increased

Fig. 3. Dry matter intake (DMI) is expressed as a ratio of the body weight$^{0.75}$ of hares *Lepus europaeus* (■) and rabbits *Oryctolagus cuniculus* (■) that fed on the four experimental diets. Significant effects of species, diet and significant interactions: $^{*}P < 0.05$, $^{**}P < 0.001$, $^{***}P < 0.0001$. Asterisks in the graph indicate significant difference between hares and rabbits that fed on each diet.

($r^2 = 0.24$, $F_{1,20} = 5.59$, $P = 0.030$), whereas no trend could be observed in rabbits.

The digestible intake of nitrogen (DNI) is the result of intake rate (scaled per body mass) times the apparent nitrogen digestibility. The DNI is similar for hares and rabbits when fed with the diet containing 10% of straw (Fig. 5). When fed with diets with a higher percentage of straw, hares had a higher DNI ($F_{1,36} = 38.75$, $P < 0.0001$). DNI decreased in rabbits with increasing straw content of the food ($r^2 = 0.54$, $F_{1,16} = 16.16$, $P = 0.001$), whereas no trend could be observed in hares.

Fig. 4. Retention time of the food in the digestive tract of hares *Lepus europaeus* (■) and rabbits *Oryctolagus cuniculus* (■) that fed on the four experimental diets. Significant effects of species, diet and significant interactions: $^*P < 0.05$, $^{**}P < 0.001$, $^{***}P < 0.0001$. Asterisks in the graph indicate significant differences between hares and rabbits that fed on each diet.

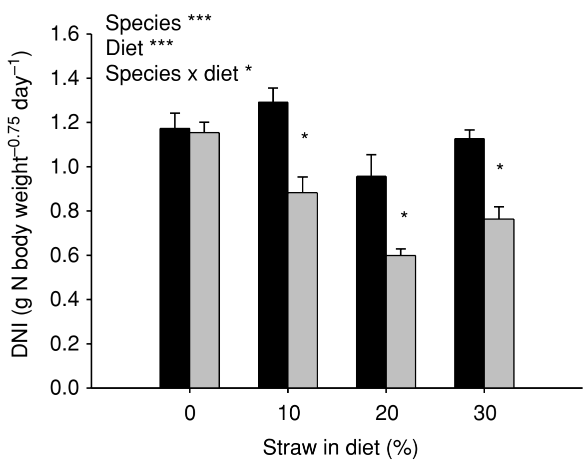

Fig. 5. Digestible nitrogen intake (DNI) per day of hares *Lepus europaeus* (■) and rabbits *Oryctolagus cuniculus* (■) scaled per body weight$^{0.75}$ that fed on the four experimental diets. Significance of the effect of species, diet and the interaction: $^*P < 0.05$, $^{**}P < 0.001$, $^{***}P < 0.0001$. Asterisks in the graph indicate significant difference between hares and rabbits that fed on each diet.

Selection of food plants by hares and rabbits

Hares and rabbits selected a wide range of plant species under free-ranging conditions on the high salt marsh. In total 15 species were found in the droppings of hares and rabbits. The plant species, which comprised the largest fraction of the diet in both animals, was the grass, *Festuca rubra* (68% in hares; 39% in rabbits). Although considerable overlap existed in the plant species selected, a higher proportion of dicotyledonous plants were found in the droppings of rabbits (36.5% in rabbits *vs* 12.5% in hares, $t_{3,8} = -6.72$, $P = 0.007$). As dicotyledonous plants generally have a higher protein content and lower fibre content, this resulted in a higher NDF content ($t_{3,8} = 5.78$, $P = 0.01$) and a lower nitrogen content ($t_{3,8} = -4.51$, $P = 0.020$) in the overall diet of hares compared to rabbits (Fig. 6). This selection of food plants is opposite to what was expected on the basis of the feeding trials.

DISCUSSION

Do hares and rabbits have a different digestive strategy?

Re-ingestion of the caecum contents is an important source of nitrogen for herbivores (Garcia, De Blas *et al.*, 1995; Takahashi & Sakaguchi, 1998; Iason & Van Wieren, 1999; Hirakawa, 2001). The importance of re-ingestion for the digestion of nitrogen was illustrated by a 10% reduction of the crude protein and nitrogen digestibility in rabbits that were deprived of caecotrophy (Grigorov, 1989). As hares produce amorphous soft faeces that directly disintegrate after re-ingestion (Hirakawa, 2001), and seem to produce a smaller amount of soft faeces (Pehrson, 1983; Van Laar, pers. obs.), the nitrogen digestion of this species was expected to be less efficient compared to rabbits. The results of the present study support this hypothesis. It was found that hares had a lower nitrogen digestibility for each diet that was tested. The difference in digestive strategy is further supported by the different reaction both species showed when the straw, and hence fibre, content of the diet was increased. The dry matter intake per unit metabolic body mass of hares tended to increase, whereas the intake rate of rabbits decreased. As a consequence, the mean retention time of the food decreased in hares and increased in rabbits when fibre content increased.

Caecotrophy elongates the retention time of the food in the digestive tract, as was illustrated for rabbits (Jilge, 1974; Fraga *et al.*, 1991; Sakaguchi, Kaizu & Nakamichi, 1992). The time period that food is retained in the caecum has been shown to account for > 60% of the total retention time of the food in rabbits and is responsible for the most variation in total retention time (Garcia, Carabano & De Blas, 1999). The increased mean retention time that was found in the present study suggests that rabbits relied more on fermentation in the caecum and re-ingestion via soft faeces when the fibre content of the food increased. The amount of nitrogen recycled from the caecum will be increased to compensate for the low digestibility of the food, as was also found by De Blas, Garcia & Carabano (1999).

Hares and rabbits thus follow different digestive strategies when food quality deteriorates. Rabbits maximize digestion of the food by increasing the mean retention time in the digestive tract and allowing longer microbial fermentation (Demment & Van Soest, 1985). Hares maximize the processing rate of the food by increasing intake rate and decreasing mean retention time at the cost of a lower efficiency for nitrogen digestion. This implies that hares rely less on caecotrophy and consequently show a less efficient digestion of nitrogen. The higher intake rate of food and the shorter retention

Fig. 6. The average percentage of neutral detergent fibre (NDF) and nitrogen (N) in the diet of hares *Lepus europaeus* and rabbits *Oryctolagus cuniculus* in a natural situation. Different letters indicate significant differences between species in NDF (small letters) and N (capital letters).

time in the digestive tract of hares did not result in a decreased dry matter digestibility. Earlier studies in small rodents showed than an increased gut capacity can partially offset the expected decrease in the digestibility of low-quality food (Hammond & Wunder, 1991; Loeb, Schwab & Demment, 1991; Toloza, Lam & Diamond, 1991). By increasing the processing rate of the food, hares were able to compensate for their lower nitrogen digestibility. The daily intake of digestible nitrogen per metabolic body weight was higher in hares when fed on diets with a high straw content.

Does digestive strategy affect feeding strategy?

In the present study, the digestive system of wild hares was compared with that of domesticated rabbits. One could argue that domestic rabbits have evolved special adaptations in their digestive system to cope with changed conditions in captivity. To what extent the digestive system of domesticated rabbits is different from that of wild rabbits remains to be studied. However, rabbits originating from domesticated stocks have been introduced in a number of places, such as on the island of Schiermonnikoog that was used in the present study (Flux & Fullagar, 1992). A difference in the efficiency of the digestive system is expected to affect the choice of food plants. In order to compensate for limited digestive capabilities, animals that retain food for a short period have to select high-quality food (Karasov, 1990). Therefore, hares with a lower nitrogen digestibility were expected to select plant species with a higher protein content. Most salt-marsh plants show a sharp decrease in their protein content during the growing season (Ydenberg & Prins, 1981; Prins & Ydenberg, 1985). A difference in the selection of food plants between the two herbivores should be most pronounced in autumn, when protein levels in plants are low. In contrast, it was found that the average diet of hares contained lower nitrogen and higher fibre contents compared to the amounts in the diet of sympatrically occurring rabbits. This suggests that the lower nitrogen digestibility in hares does not have profound effects on the selection of food plants. Direct competition between hares and rabbits for the same food plants (Homolka, 1987) could have caused a shift in the selection of food plants by hares. However, owing to the low density of both herbivores (1 hare/ha, 0.6 rabbit/ha; Snel, pers. comm.) in the present study area, competition intensity is expected to be low and does not seem a probable explanation for the observed selection of food plants. Hares and rabbits have been shown to occupy different ecological niches (Chapuis, 1989) and hence use different habitats, which is related to their feeding strategy (Hulbert, Iason, Elston *et al*., 1996; Hulbert, Iason & Racey, 1996). The grazing intensity of rabbits is closely related to the location of their burrows (Palomares & Delibes, 1997), whereas hares do not use burrows but sleep in forms, and range more widely. The average home range of hares is far larger than that of rabbits (Hulbert, Iason, Elston *et al*., 1996). Hares can search for high-quality food plants in a larger area; however, the intensive grazing by rabbits around their burrows will result in a young, protein-rich vegetation. By repeated grazing, rabbits can manipulate the quality and quantity of the food plant species they are eating (Ydenberg & Prins, 1981). This differential habitat use might largely explain the different selection of food plants and the different quality of overall diets observed between both types of herbivores.

Rabbits had a higher nitrogen digestibility compared to that of hares. They maximized digestion by increasing the mean retention time of food in their digestive tract when the fibre content of their diet increased. Hares are able to compensate for their lower digestive efficiency by increasing the intake and the passage rate of the food through the digestive tract. Hares and rabbits thus show different digestive strategies to cope with forage with a high fibre content. The strategy followed by hares seems a more successful way to cope with deteriorating food quality. As longs as the quantity of food is not limiting, they are able to reach a higher intake of digestible nitrogen. The lower digestive efficiency of hares, therefore, may not force them to select for higher quality food plant species. How these differences in digestive strategy affect the interaction between both species in a range of different landscapes, which differ in food plant quality and quantity, remains to be studied.

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