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Seasonal faecal excretion, gut fill, liquid and particle marker retention in mouflon *Ovis ammon musimon*, and a comparison with roe deer *Capreolus capreolus*

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Five mouflon [average body mass (BM) 33 kg] and two roe deer (average BM 20 kg) with rumen cannulas were kept in large enclosures under semi-natural conditions and were used for seasonal studies on gastrointestinal tract (GIT) indigestible fill and digesta passage kinetics. As the mouflon were not fully mature, both species had similar digesta volumes in the reticulorumen (RR; mouflon 5.5 ± 1.8% of BM; roe deer 5.4 ± 1.5% of BM); however, the mouflon had lower RR liquid flow rates (15.1 ± 4.3 ml h^{-1} $kg^{-0.75}$) than the roe deer (19.2 ± 0.2 ml h^{-1} $kg^{-0.75}$), and particle retention in the RR accounted for 68 ± 3% of total GIT retention in the mouflon versus 55 ± 6% in the roe deer. Annual average total GIT retention times for liquids and particles were longer in the mouflon (23.4 ± 0.9 h and 37.9 ± 4.0 h) than in the roe deer (18.4 ± 1.7 h and 22.4 ± 1.9 h). Similarly, annual average RR retention times for liquids and particles were longer in the mouflon (11.9 ± 0.9 h and 25.8 ± 3.3 h) than in the roe deer (8.1 ± 1.7 h and 12.5 ± 2.3 h). The factor of selective particle retention in the RR (retention of particles/retention of liquid) was 2.10 ± 0.09 in the mouflon versus 1.54 ± 0.01 in the roe deer. These observations are in accord with differences in digesta passage characteristics postulated between browsing and grazing ruminants. Total GIT indigestible fill was lower in the mouflon than in the roe deer (10.7 ± 2.1 g kg^{-1} and 13.3 ± 1.0 g kg^{-1}).

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Introduction

An anatomy-based classification of ruminants into three feeding types ("concentrate selectors"/browsers BR, intermediate feeders IM, grazers GR) was first

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developed using East African ruminants (Hofmann 1973) and later expanded to a wider range of ruminant species (Hofmann 1988). Within this system, mouflon *Ovis ammon musimon* Pallas 1811 have been classified as GR (Geiger *et al.* 1977) and roe deer *Capreolus capreolus* Linnaeus 1758 as BR (Hofmann *et al.* 1976), with roe deer having smaller rumens, weaker rumen pillars, lower reticular crests and smaller omasa, among other parameters. Drescher-Kaden (1976) demonstrated with a large sample that, in relation to body mass (BM), mouflon have more capacious reticulorumens (RR) than roe deer (RR ingesta mass 14.6 vs. 7.2% BM, respectively). Kamler (2001) demonstrated differences in forestomach papillation between these two species, with roe deer having larger papillae and a higher papillae density. Reports on the diet of free-ranging mouflon emphasize the importance of grass for this species (Mottl 1960, Tuercke and Schmincke 1965, Onderscheka and Jordan 1976, Hadjisterkotis 1996). In contrast, reports on the natural diet of roe deer confirm that this species consumes mainly browse and herbs, with grasses comprising only an annual average of about 5% of the diet (Cornelis *et al.* 1999).

One of the main postulated differences between GR and BR is that BR have faster ingesta passage rates (Kay 1987, Hofmann 1989), a claim that has been challenged statistically (Gordon and Illius 1994, Robbins *et al.* 1995). Several factors make a shorter ingesta retention time in browsers reasonable: the natural diet of BR has a higher proportion of indigestible lignin in the fibre fraction (Robbins 1993) which cannot be effectively exploited by longer fermentation. Browsers in general do not digest fibre as well as grazers do (Iason and Van Wieren 1999), which may be either an ultimate cause or an effect of faster passage rates. Finally, it has been shown that the cellulolytic activity in the RR of browsers is generally lower than in grazers (Prins *et al.* 1984) and that the cellulolytic activity in the RR of roe deer in particular is lower than that of sheep (Deutsch *et al.* 1998), which again would mean that long RR retention times would not be beneficial. A potential proximate cause for faster ingesta passage rates in BR could lie in an interplay of particular anatomical adaptations and characteristics of the natural forages (Clauss *et al.* 2003). In particular, it could be shown that, while the RR contents of sheep stratify (Sutherland 1988), RR contents of roe deer did not (Clauss *et al.* 2001). Based on these considerations, we predicted generally faster ingesta passage rates, and according higher food intakes (reflected in higher relative faecal production and gut fill), in roe deer than in mouflon.

In order to test these predictions, RR-cannulated animals under semi-free--ranging conditions were used with liquid and particle markers to determine patterns of faecal marker appearance, amount of indigestible residue in the gastrointestinal tract, and retention times.

Methods

Five mouflons and two roe deer were used between April 1997 and June 1998. All animals had been born between March and June 1996. The animals were fitted with rumen cannulas to enable a liquid and a particle marker to be given for the determination of passage rates and gut fill, and to sample rumen fluid for the determination of forestomach volume. Handling of these animals was ensured by hand-rearing them. However, of the six roe deer initially hand-reared, only two animals remained tolerant enough of an investigator's close contact as to be usable for this study. Even with the two remaining animals, the sound of gas escaping when the rumen cannula was opened often induced a flight reaction. The mouflon, on the other hand, were generally more tolerant of an investigator's presence, and tolerated short periods of manual restraint during marker dosing or sampling from the cannula. Manual restraint was not considered a viable option in the roe deer. The animals were weighed at the beginning and the end of the study, with the mouflon weighing between 27.5–35.5 and 29.5–37.0 kg, and the roe deer weighing 17.5 and 19.0 kg, and 22.5 and 25.0 kg. For comparisons with body mass, an average mass of 33 kg for the mouflon and 20 kg for the roe deer was used.

The mouflons were kept in a 1400 m^2 enclosure with a mixed lucerne and grass lawn (*Medicago sativa*, *Lolium perenne*). The roe deer were kept in a 4000 m^2 wild lawn enclosure with fruit trees (*Malus sylvestris*, *Prunus domestica*, *Pyrus domestica*, *Prunus avium*), conifers (*Pseudotsuga menziesii*, *Pinus silvestris*, *Picea abies*) and shrubs, and grasses. In addition to the natural vegetation, the roe deer were given fresh or dried browse (*Quercus robur*, *Betula pendula*, *Acer platanoides*, *Salix alba, Populus tremula, Populus nigra*) daily. Additionally, a pelleted cattle feed and oats (each 100 g per animal daily) were offered daily to both species. Carrots (1 kg per animal daily), apple pomace (0.5 kg per animal daily), and hay, pine browse (*Pinus sylvestris*) and beets were offered ad libitum during winter months. Assuming food intakes of 350 g DM in winter and 600 g DM in summer for an adult roe deer (Drożdż and Osiecki 1973), and given a DM content of 90% for the pellets and 88% for the oats, supplemental feeding should have, in theory, accounted for 51% of food intake in winter and 30% in summer. Water was available at all times.

The markers used, cobalt-EDTA (liquids) and chromium-mordanted fibre (< 2 mm) (particles) were prepared according to Udén *et al.* (1980), using hay particles that had been processed in a feed mill (Retsch Mühle SM1, Haan, Germany) with a pore size of 1.5 mm and subsequently been retained during wet sieving on a sieve with linear hole dimensions of 1 mm. Ten-20 ml Co-EDTA and 1–5 g Cr-hay (in frozen form) were dosed through the cannula into the RR. After marker dosing, RR fluids were sampled every 2 h for 24 h, and faeces were sampled every 2–4 h for 5 d (at night with the aid of floodlights). Animals defecated naturally and faeces were collected immediately after defecation. Constant observations of the animals during the collection periods guaranteed the identity of the faecal samples.

All samples were stored frozen until analysis. Faeces were dried at 80°C to constant weight for dry matter (DM) determination. Co and Cr were analyzed by atomic absortpion spectroscopy (Welz and Sperling 1997) after digestion in 72% sulfuric acid and filtration. Mean retention times (MRT) for Co and Cr were calculated according to Thielemans *et al.* (1978) as

$$MRT = \frac{\sum t_i C_i dt_i}{\sum C_i dt_i}$$

With C_i = marker concentration in the faecal sample at time t_i (hours after marker administration) and dt_i = the interval (hours) of the respective sample

$$dt_i = \frac{(t_{i+1} - t_i) + (t_i - t_{i-1})}{2}$$

Liquid MRTs for the RR were calculated as by Grovum and Williams (1973); this calculation is based on the decrease of the faecal liquid marker concentration C_i with time according to the equation

$$C_i = a\, e^{-kti} \quad \text{or} \quad \ln C_i = -k\, t_i + b$$

Liquid MRT in the RR then is k^{-1}. Liquid MRTs distal to the RR were calculated by difference; as liquids and particles move together distal to the RR (Lechner-Doll and von Engelhardt 1989), particle MRTs for the RR were calculated by subtraction of MRT distal to the RR from total GIT particle MRT. The selectivity factor was calculated by dividing RR and MRTs for particles and liquids. The amount of faecal DM excreted, and the amount of indigestible material in the GIT was calculated according to Holleman and White (1989) and Holand (1994), with the daily faceal dry matter excretion (Faecal DM_{24h}, in kg DM) resulting from the equation

$$\text{FaecalDM}_{24h} = \frac{\text{D } 24h}{\sum C_i dt_i}$$

where D is the marker dose given (in mg).

The amount of indigestible material (IM, in kg DM) in the total GIT (or the RR) is then calculated using particle MRT as

$$\text{IM}_{\text{GIT (RR)}} = \frac{\text{FaecalDM}_{24h}\,\text{MRT}_{\text{part GIT (RR)}}}{24h}$$

From the Co concentrations measured in RR fluid samples, RR liquid volume was calculated by dividing the Co dose by the extrapolated Co concentration at the time of dosing, and liquid flow rate from the RR was calculated by dividing the RR liquid volume by the RR liquid MRT.

Results are presented throughout as means ± standard deviation (SD); n is the number of individuals or measurements. Annual averages were calculated using data from July 1997 until June 1998. First, annual averages per indiviual were calculated, and individual averages were used to calculate species averages. For a seasonal comparison of mouflon data, four seasons were defined: summer (June–August 1997), autumn (September–November 1997), winter (December 1997–February 1998) and spring (March–May 1998), which were evaluated by repeated-measurement analysis of variance (RM-ANOVA) and subsequent post-hoc tests. In roe deer, such an evaluation was not possible due to the small sample size ($n = 2$). For the same reason, species comparisons were not evaluated statistically.

Results

Faecal production and gut fill

The daily amount of faeces produced was calculated using both the Co and Cr excretion patterns. The average relative deviation of the two results was 16.1 ± 15.2% ($n = 51$) in the mouflon and 16.4 ± 14.7% ($n = 16$) in the roe deer, and are probably due to a certain degree of absorption of the Co-EDTA marker (Udén *et al.* 1980). However, in order to facilitate a comparison with the highest number of measurements possible, values based on Co calculations are given here. The average annual faecal DM production was 273 ± 26 g d^{-1}or 8.3 g kg^{-1} d^{-1} in the mouflon and 255 ± 7 g d^{-1} or 12.8 g kg^{-1} d^{-1} in the roe deer.

The amount of indigestible material in the GIT ranged, in the mouflon, from 310 g DM in May to 505 g DM in August (Fig. 1), and in the roe deer, from 173 g DM in May to 365 g DM in October. The seasons differed significantly (RM-ANOVA, $p = 0.034$) in the mouflon; pair-wise differences could, however, not be confirmed in post hoc tests. Over the year, indigestible DM in the GIT was, on average, 10.7 ± 2.1 g kg^{-1} in the mouflon and 13.3 ± 1.0 g kg^{-1} in the roe deer.

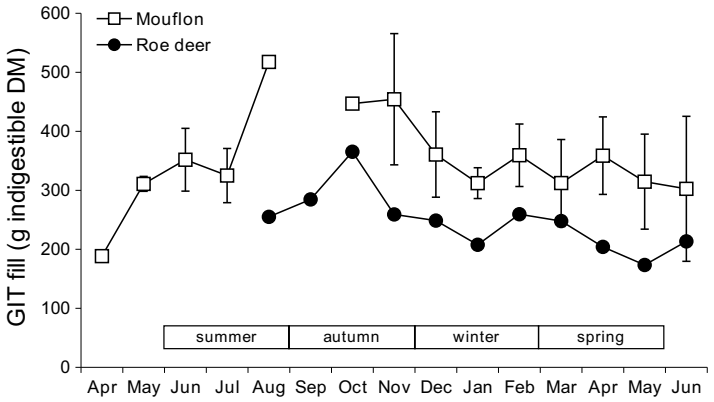

Fig. 1. Seasonal variation in indigestible dry matter content of the total gut (GIT) in mouflon and roe deer.

RR liquid volume was measured in summer only and was, in the mouflon, 1.82 ± 0.60 l or 5.53 ± 1.82% of BM. In the roe deer, the corresponding values were 1.09 ± 0.30 l or 5.43 ± 1.52% of BM.

Passage rates

Generally, kinetics of liquid and particle retention differed between the species (c.f. Fig. 2 and 3). Although the peak of liquid marker concentration in the faeces was reached, in both species, after about 12 h, the peak of particle marker concentration in the faeces occured later in mouflon (after 20–25 h) than in roe deer (17–19 h). In the mouflon, chromium concentrations decreased later than cobalt concentrations, whereas the decrease in faecal concentration was nearly simultaneous for both markers in the roe deer. Both markers were generally excreted completely within the 5 day collection period.

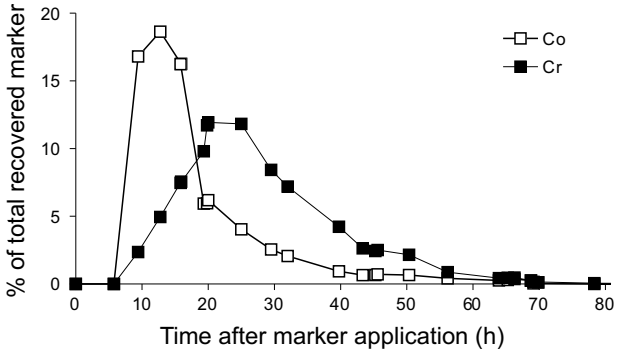

Fig. 2. Example of an excretion curve for liquid (Co) and particle (Cr) marker in a mouflon.

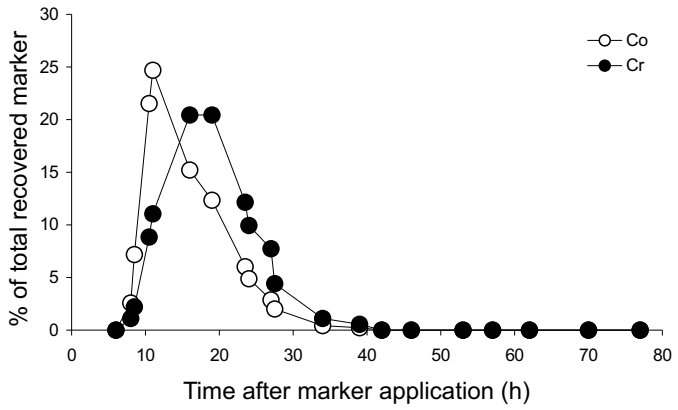

Fig. 3. Example of an excretion curve for liquid (Co) and particle (Cr) marker in a roe deer.

Annual average liquid and particle MRTs in the whole GIT in the mouflon were 23.4 ± 0.9 h and 37.9 ± 4.0 h, respectively, compared with 18.4 ± 1.7 h and 22.4 ± 1.9 h in the roe deer. The liquid and particle MRTs in the 15 months of measurement are displayed for both species in Fig. 4. In the mouflon, winter and spring liquid MRTs were longer than those measured in autumn (RM-ANOVA, $p = 0.015$, post hoc tests significant for autumn–spring and autumn–winter). For particles, this effect was not significant (RM-ANOVA, $p = 0.022$).

The annual average liquid and particle MRTs in the RR in the mouflon were 11.9 ± 0.9 h and 25.8 ± 3.3 h , respectively, compared with 8.1 ± 1.7 h and 12.5 ± 2.3 h in the roe deer. The seasonal RR liquid and particle MRTs are displayed for both species in Fig. 5. In the mouflon, there was a significantly shorter RR liquid MRT in

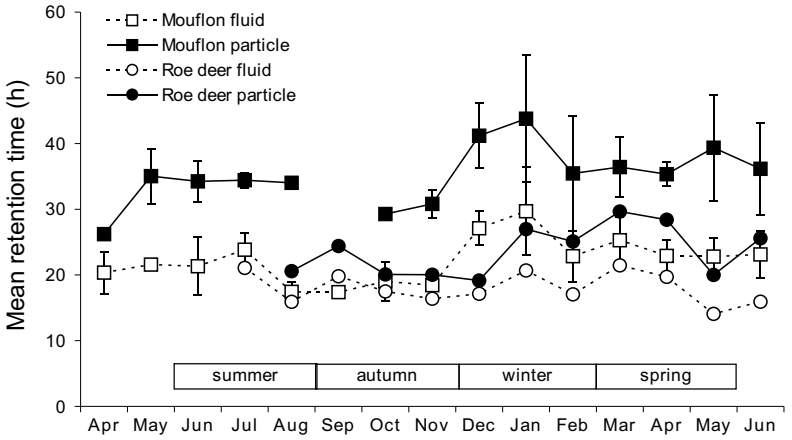

Fig. 4. Seasonal variation in total gut mean retention time for liquids and particles in mouflon and roe deer.

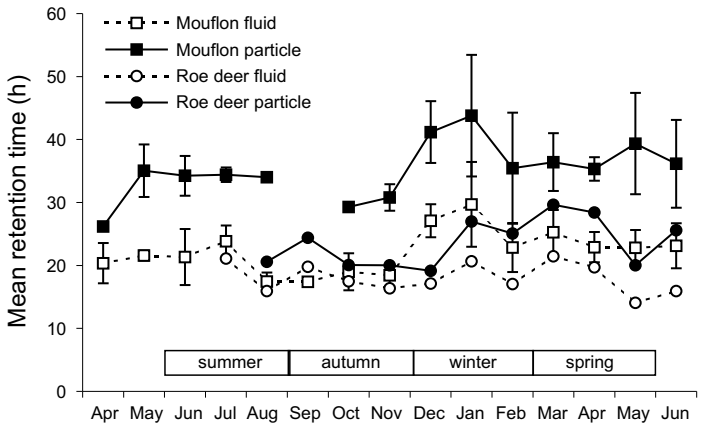

Fig. 5. Seasonal variation in forestomach mean retention time for liquids and particles in mouflon and roe deer.

summer compared to spring (RM-ANOVA, $p = 0.001$, post hoc tests significant for spring–summer). As for the whole GIT, this effect was not sig- nificant for RR particle MRT (RM-ANOVA, $p = 0.134$). In the mouflon, an increase of 15.9% in particle MRT in the RR could be observed between May/June 1997 and May/June 1998. In the mouflon, RR particle retention accounted for 68 ± 3% of total GIT particle retention; in the roe deer, this value was 55 ± 6%.

The selectivity factor (RR MRT particles/ RR MRT liquids) did not vary seasonally in the mouflon (RM-ANOVA, $p = 0.863$); the values averaged 2.10 ± 0.09 in the mouflon and 1.54 ± 0.01 in the roe deer. Liquid flow rates from the RR were 15.1 ± 4.3 ml $h^{-1}kg^{-0.75}$ in the mouflon and 19.2 ± 0.2 ml $h^{-1}kg^{-0.75}$ in roe deer. As an absorption of Co-EDTA from the RR cannot be excluded (Udén *et al.* 1980), these figures are probably slight overestimates. MRTs of both liquids and particles distal to the RR were, on annual average, 11.5 ± 0.7 h in the mouflon and 10.3 ± 0.0 h in the roe deer.

Discussion

The results for RR liquid volume of this work for the roe deer (1.1 l) are in good accord with data from the literature (1.5 l, Holand 1992). However, values measured in mouflon (1.8 l) are distinctly lower than literature data (4.1–7.2 l, Drescher-Kaden 1976). This discrepancy could be due to different growth rates of the two species; Whereas roe deer, in general, reach their maximum body weight within two years (Stubbe 1966), mouflon reach their maximum only after four years (Stubbe 1977). The apparent overall increase in RR particle MRT with time in the mouflon may reflect this continuous growth. If expressed as a function of BM, the mouflon and roe deer had similar RR liquid volumes, in contrast to comparisons

between fully mature specimens (Drescher-Kaden 1976; but note that Gill [1960] found total stomach contents of 5.5% of BM in a senile zoo mouflon). For the interpretation of the passage rate measurements, this implies that observed differences in MRT patterns for both liquids and particles cannot be explained by difference in RR volume alone but are likely to reflect a combination of different physiological processes in the RR and of different dietary choices between the two species. Even if this study cannot differentiate between intrinsic physiological animal factors and the influence of the diet selected by the animals, the results are an approximation of a diet-physiology interplay within the animal and therefore representative of actual differences in passage rates in free-ranging animals that select their forage according to their species' preferences.

The results of passage characteristics of this study are in accord with other observations. A comparison of the mouflon data with data from sheep (Lechner-Doll *et al.* 1990) demonstrates the importance of MRT distal to the RR in animals that operate under the necessity of water conservation. Whereas the mouflon and the African sheep displayed similar RR liquid MRTs and similar RR particle MRTs, the sheep in Africa had longer total GIT MRTs. Results for the roe deer of this study closely match those from Holand (1994) (Table 1). In general, the passage data of this study support the concept that free-ranging browsing ruminants have faster passage rates than grazing ruminants. Illius and Gordon (1992) postulated that total GIT particle passage in ruminants was independent of feeding type, and was: total GIT MRT particles (h) = $15.3\ BM^{0.251}$.

For a 20 kg roe deer and a 33 kg mouflon, this would mean particle MRTs of 32.5 and 36.8 h. The calculated value for the mouflon is in accord with the measured values (annual average: 37.9 h), but the calculated value for the roe deer is longer than the MRT measured in this study (annual average: 22.4 h). Robbins *et al.* (1995) postulated that RR liquid flow rate in ruminants was independent of feeding type, and was: RR liquid flow rate (ml h^{-1}) = $11.5\ BM^{0.98}$.

Table 1. Comparison of passage rates in the total gastrointestinal tract (GIT) and the reticulorumen (RR) determined in this study with literature data. MRT – mean retention time. All particle MRTs were determined using particles < 2 mm except data from Van Wieren (1996) who used stained feeds of varying particle size. [a] animals weighed between 19–55 kg, [b] animals had an average BM of 24.7 kg, [c] animals had an average BM of 17.2 kg.

	MRT liquids GIT (h)	MRT particles GIT (h)	MRT liquids RR (h)	MRT particles RR (h)
Mouflon, this study	17.4–29.7	29.3–43.8	9.1–15.3	20.1–29.4
Sheep (Lechner-Doll *et al*. 1990) [a]	31.5–37.7	37.6–49.3	9.1–16.1	19.7–28.8
Roe deer, this study	14.1–21.5	19.2–29.7	6.5–9.6	10.1–18.5
Roe deer (Holand 1994)[b]	17.9–26.7	19.6–31.1	9.6–14.1	8.7–19.1
Roe deer (Van Wieren 1996)[c]		15.7–21.0		

For a 20 kg roe deer and a 33 kg mouflon, this would mean flow rates of 216 and 354 ml h^{-1}, respectively. The calculated value for the roe deer is somewhat higher than the measured value (182 ml h^{-1}), and that calculated for the mouflon is substantially higher than the measured value (208 ml h^{-1}). Relative to metabolic BM, the roe deer had a higher RR liquid flow rate (19.2 ml h^{-1} $kg^{-0.75}$) than the mouflon (15.1 ml h^{-1} $kg^{-0.75}$). Particle retention in the RR accounted for 68% of total GIT MRT in the mouflon but only 55% in the roe deer; given the similar RR ingesta volumes of the species (5.4 and 5.5% of BM, respectively), this difference must be explained by different physiological processes in the RR. A potential explanation could be derived from the observations that in sheep, RR contents stratify into different layers (Sutherland 1988) but that, in roe deer, RR contents are unstratified and generally form a frothy, homogeneous mass (Clauss *et al.* 2001). The stratification of RR contents according to a functional density gradient is generally regarded as one of the main factors responsible for the selective retention of particles in the RR (Lechner-Doll *et al.* 1991). The selective retention of particles in the RR as compared to liquids was always higher in the mouflon (selectivity factor 2.10) than in the roe deer (1.54). The observation that there was no seasonal changes in the selectivity factor in mouflon is in accordance with a similar observation on sheep by Lechner-Doll *et al.* (1990).

The higher faecal output (12.8 g vs. 8.3 g DM d^{-1} kg^{-1}) and the higher relative gut content of indigestible material in the roe deer than in the mouflon measured in this study (13.3 and 10.7 g DM kg^{-1}) suggests either a higher fibre content in the roe deer's diet, or a lesser fibre digestibility in this species (Iason and Van Wieren 1999, Deutsch *et al.* 1998). On the other hand, the higher defecation rates could indicate a higher food intake by the roe deer. A shorter total GIT MRT and a lesser fibre digestibility must, by necessity, either be matched by generally lower metabolic demands or by higher food intakes. Higher food intakes in browsing ruminants have been suggested (Owen-Smith 1992, Prins and Kreulen 1991) but not been demonstrated to date.

The seasonal digestive physiology of temperate zone ruminants of any feeding type is characterised by a lower food digestibility, lower food intake, lower body weights, and lower maintenance requirements in winter as compared to summer (cf Hudson and White 1985). During summer, high food intakes – as indicated in this study by the increase in GIT fill and the faecal DM excretion in autumn – lead to faster passage rates. The correlation of faster ingesta passage and higher food intake has been repeatedly demonstrated in domestic ruminants (Offer and Dixon 2000). In the winter period, two opposing trends influence the ingesta volume in the RR: On the one hand, the lower digestibility of the food – expression of certain structural and chemical characteristics – results in a longer retention time in the RR with an associated increase in RR volume. Such an effect has been observed in African sheep and goats during the dry season (Lechner-Doll *et al.* 1990), and for moose (Gasaway and Coady 1974) and roe deer (Holand 1992) during the winter period. On the other hand, lower metabolism and lower food intake could lead to a

reduced RR fill. In the case of this study, the artificial food supplementation during the winter period is likely to have shifted this equilibrium towards reduced RR volumes. However, even for completely free-ranging roe deer, nadirs in ingesta volume have been described for the winter period (Hofmann *et al.* 1976).

Faster digesta passage rates in roe deer than in mouflon could explain several differences observed between these species. Drescher-Kaden and Seifelnasr (1977) compared the protozoal fauna of the two species. On the one hand, protozoa could not be found in the rumen of 19 out of 32 roe deer (59%) but were absent in only one out of 11 mouflons (9%). On the other hand, *Entodinium* spp. represented 100% of the total protozoa fauna in all roe deer with protozoa (a finding corroborated by reports of Buisson 1923, Brüggemann *et al.* 1967, Deutsch *et al.* 1998), but only 71–90% in mouflon. As *Entodinium spp*. are particularly fast-growing ciliates, it has been suggested that in browsing ruminants, other protozoa cannot establish viable populations due to the fast RR passage rates (Dehority 1986). Roe deer have a significantly higher content of polyunsaturated fatty acids in their body fat than mouflon (Meyer *et al.* 1998, Rowell-Schäfer *et al.* 2001), which can be explained by a faster escape of plant material from the RR and hence a less complete hydrogenation of double bonds by RR bacteria. In contrast to sheep, roe deer have a high abundance of sodium-dependent glucose-cotransporters in their duodenum (Rowell-Schäfer *et al.* 1999, 2001), indicating that in roe deer, some glucose must escape the RR unfermented. Amylase activities in pancreatic tissue of roe deer is higher than in that of sheep (Rowell-Schäfer *et al.* 2001), indicating that other soluble carbohydrates escape the RR in higher proportions. It has been suggested that in browsing ruminants, soluble nutrients could bypass the rumen – due to a reticular groove that maintains its viability even in adult animals (Hofmann 1989). However, the similarity of results achieved by Holand (1994), in which the water-soluble liquid marker was fed to the animals and therefore could have, according to the hypothesis, been dissolved in saliva and transported via the reticular groove directly into the lower GIT, and by this study, in which the marker was applied directly into the RR via a fistula, suggests that such a hypothesized ruminal bypass does not occur, at least not in significant proportions, and that in contrast the hypothesis of an increased ruminal escape due to faster passage rates (Rowell-Schäfer *et al.* 2001) should be further investigated.

That the differences in ingesta kinetics between mouflon and roe deer are representative of a general difference between browsing and grazing ruminants can be suspected, but should be corroborated in further studies.

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