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Comminution of roughages by red deer (*Cervus elaphus*) during the prehension of feed

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SUMMARY

The chewing behaviour of red deer (*Cervus elaphus*) during eating and the effectiveness of chewing on feed comminution was studied in two experiments. In Expt 1, deer were fed long or chopped lucerne (*Medicago sativa*) hay, and feed intake and chewing activity were recorded. In Expt 2, the rumen was emptied and test meals of fresh chicory (*Cichorium intybus* cv. Puna), lotus (*Lotus corniculatus* cv. Grasslands Goldie), ryegrass (*Lolium perenne* cv. Ruanui) forage and long lucerne hay were given, chewing activity recorded and the ingested forage quantitatively removed from the rumen. In Expt 1, the chopped hay was eaten more quickly than long hay (11·4 *v.* 8·3 g dry matter/min), and required fewer chewing bites per g dry matter eaten. In Expt 2, the four forages were consumed at similar rates (mean 4·3 g organic matter/min) and there was no significant difference in the chewing required to consume either total organic matter (OM) or cell wall OM. Deer chewed more quickly when eating lucerne hay than when eating lotus, and it was estimated that a greater number of chewing bites were required to form a bolus of lucerne hay than to form a lotus bolus. The proportion of ingested OM which was comminuted so as to pass a 1 mm sieve (efficiency of chewing) was greater for lotus (0·485) and lucerne hay (0·518) than for chicory (0·267). The efficiency of chewing ryegrass (0·366) was intermediate and not significantly different from any other forage. For all forages, the main effect of chewing during eating appeared to be the release of cell contents, rather than the comminution of cell wall. Physical breakdown to particles which passed a 1 mm screen but were retained on an 0·25 mm screen was low for fresh forages (0·074–0·086) but was slightly higher for lucerne hay (0·127). Deer reduced feed particle size during eating with a similar efficiency to sheep, but were less efficient than goats.

It is suggested that the chewing effort associated with forage consumption by red deer is related to the need to form a bolus. The amount of chewing may be as much influenced by the physical characteristics of the forage (e.g. leaf size and shape) as by its chemical composition, and the extent of comminution during eating may be determined by the processing needed to form a bolus and the resistance of the feed to bolus formation.

INTRODUCTION

Forages are a major component of the diets of farmed deer in New Zealand, so forage characteristics which influence feed consumption and the release of nutrients will have important effects on animal performance. Intake of forage dry matter (DM) by ruminants is affected to a large extent by the rate at which it is cleared from the reticulo-rumen by digestion and onward passage of undigested DM. In some circumstances the rate of passage of undigested feed may be more important than the rate of digestion (e.g. Mertens & Ely 1979; Poppi *et al.* 1981*a*). Spalinger (1986) has noted that the rate of small particle passage is an important determinant of intake in mule deer (*Odocoileus hemionus*) and the North American elk (*Cervus elaphus canadensis*). In the ruminant, there is substantial evidence that passage from the rumen of undigested feed depends on it being comminuted to a size which maximizes its probability of leaving the rumen. In many small ruminants, the critical particle size is *c.* 1 mm (e.g. Ulyatt *et al.* 1976; Poppi *et al.* 1981*b*) and it has been shown by Domingue *et al.* (1991*a*) that this critical

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Table 1. *Dry matter (DM), organic matter (OM), cell wall OM (CWOM) and total nitrogen (N) contents of the forages used in Expts 1 and 2*

Forage	DM (g/kg)	OM (g/kg DM)	CWOM (g/kg DM)	Total N g/kg DM)
Basal hay	869	881	485	34
Fresh chicory	142	770	132	31
Fresh lotus	163	881	208	48
Fresh ryegrass	164	863	369	47
Lucerne hay	814	906	414	31

particle size also applies in red deer. Particle comminution is achieved by chewing during eating and rumination (Ulyatt *et al.* 1986).

The work described in this paper was designed to investigate the degree to which commonly-used New Zealand forages are comminuted during eating by red deer.

METHODS

Animals, treatments and experimental design

The experiments were carried out in the (southern hemisphere) winter, at Palmerston North, New Zealand in 1991. Castrated male red deer, *c.* 3 years old, equipped with permanent rumen cannulae (rubber, 83 mm diameter) and accustomed to animal house conditions, were housed in metabolism cages (Milne *et al.* 1978) at ambient temperature and a regime of 9·75 h light, 14·25 h dark. They were maintained throughout the whole pre-experimental and experimental period on a medium quality lucerne/grass hay (the basal forage) given *ad libitum*, and with a multi-mineralized salt block (Dominion Salt Ltd.) and water *ad libitum*. At those times when chewing recordings were not being made, the basal forage was given at 08.30 h NZST and was available for 24 h.

There was a pre-experimental period of 21 days in which eight deer were introduced to the procedures (jaw movement recording and rumen emptying) and test feeds to be used in both experiments. Three animals did not tolerate these procedures and were not used. Each experiment involved four animals: three of the eight deer were used in both experiments, a fourth was used in Expt 1 and a fifth in Expt 2.

Expt 1 was an investigation of eating behaviour as influenced by the form of forage presentation, and Expt 2 an investigation of the degree to which a range of common forages were comminuted during eating. As there was no *a priori* reason for assuming carry-over effects of previous treatments (forages), each test forage was given to each animal in a randomized complete blocks design in which the animals constituted the blocks.

In the first experiment, the test feed was a mature lucerne (*Medicago sativa*) hay, offered either unchopped (stems up to 30 cm long with attached leaves) or chopped (pieces up to 4 cm long). Four forages were tested in the second experiment: lotus (*Lotus corniculatus* cv. Grasslands Goldie) leaves and stems, chicory (*Cichorium intybus* cv. Puna) leaves hand plucked from rosettes in a semi-dormant stage, ryegrass (*Lolium perenne* cv. Ruanui) cut near ground level from a sward *c.* 10–15 cm in height, and unchopped lucerne hay (similar to that used in Expt 1). The forages other than lucerne were offered fresh and in the form collected from the field. The chemical and particle size composition of the forages used in the two experiments are given in Tables 1 and 3.

Experimental protocols

In Expt 1, both forms of forage presentation were tested with each of the four animals on the same day. In Expt 2, one or two animal/forage combinations were examined on any one day, and at least 48 h elapsed between successive measurements with individual deer. The basal forage was withheld from 16.30 h (water and salt block remained available) on the day prior to a measurement period. Water and salt blocks were withdrawn during the measurement periods. In both experiments, each combination of animal and forage type was tested once.

Experiment 1

Deer were offered, separately, 200 g of each of the chopped and long lucerne hay for 20 min. Chewing was measured as described by Domingue *et al.* (1991*b*) in which a small compressible balloon is held by a harness under the animal's jaw and connected to a pressure transducer, with the signal output to a chart recorder set at a chart speed of 2·5 mm/sec. Uneaten feed was weighed and sampled at the end of each 20 min period and the harnesses were removed after each measurement.

Experiment 2

Immediately before test feeds were given, the rumen contents were removed by hand bailing and stored in a container immersed in water at 37 °C. Air was largely excluded by covering the rumen contents with a plastic bag also containing water at 37 °C. A test meal of 110 g long hay or 1000 g fresh forage was then offered, and jaw movements were recorded. Chewing measurements were recorded either until the test meal was consumed, or for 30 min. On completion of the feeding period, any uneaten feed was removed, weighed and sampled. The eaten material was recovered from the rumen, weighed and sampled, and the original rumen contents were replaced.

Chemical analyses and particle size determinations

The DM content of the feeds, refusals and ingesta recovered from the rumen were determined immediately after sample collection, in duplicate, by drying at 80 °C until constant weight.

Samples of lucerne feeds and refusals were stored prior to chemical analysis at ambient temperature in sealed plastic bags. Samples of ingesta and the fresh forages were stored frozen (−20 °C) and later prepared for chemical analysis by freeze-drying. All samples were ground (0·5 mm screen) before analysis for DM (100 °C for 16 h), organic matter (OM; 600 °C for 16 h), total N (by the Kjeldahl method) and cell wall organic matter (CWOM) by extraction with neutral detergent as described by Van Soest & Wine (1967) with correction for the ash content of the residue.

The particle size distributions in the forages and rumen ingesta from Expt 2 were determined in triplicate by wet sieving (Waghorn 1986), using sieves with apertures of 4, 2, 1, 0·5 and 0·25 mm. Most samples were sieved within 6 h of collection although some were stored at 5 °C before processing. The weights of material retained on each sieve were determined by drying (100 °C until constant weight), and then bulked within replicates for ashing (500 °C for 4 h). The weights of DM and OM which passed the final sieve (< 0·25 mm) were calculated by difference.

Mathematical and statistical analysis

'Prehension' and 'chewing' jaw movements during eating were identified; only chewing movements (called 'bites') were counted and used in the calculations described below.

The duration of eating was measured from the onset of the first prehension movements to the end of the final chewing movements, but excluding rest periods which occurred during the eating period. 'Consumption rate' (g feed constituent/min) and 'chewing rate' (number of chewing bites/min) calculations were based on this measurement. A 'chewing event' was defined as a period of chewing (of four or more bites) following a period of prehension. 'Chewing events' were considered to be similar to bolus formation, so that bolus size was estimated as (mass of feed constituent eaten)/(number of chewing events). Chewing activity was expressed in relation to feed consumed (bites/g feed constituent), and in relation to the number of bites in a chewing event (bites/bolus; i.e. excluding those bites which were not counted in 'events').

The effectiveness of chewing in reducing feed particle size was calculated by dividing the total number of bites by the amount of ingested OM which was comminuted to pass a 1 mm screen (Eqn (1)), and by calculating the proportion of food OM comminuted during chewing ((Eqn (2), this is similar to the ⟨C.EAT⟩ of Domingue *et al.* 1991*b*).

Two additional indexes were calculated (Eqns (3) and (4)), which corrected for the presence in the feed and the ingesta of very small particles and solubles (the fraction which passed the 0·25 mm screen).

The main effects (blocks and treatments) were compared by analysis of variance, using a procedure for balanced designs (Statistical Analysis Systems 1988).

Bites/g ingested OM comminuted

$$= \frac{\text{Total no. of chewing movements}}{(\text{Mass of ingesta OM}) * (\text{Proportion of ingesta OM} < 1{\cdot}0\text{ mm} - \text{Proportion of food OM} < 1{\cdot}0\text{ mm})} \quad (1)$$

Proportion of food OM comminuted

$$= \frac{(\text{Proportion of ingesta OM} < 1{\cdot}0\text{ mm} - \text{Proportion of food OM} < 1{\cdot}0\text{ mm})}{\text{Proportion of food OM} > 1{\cdot}0\text{ mm}} \quad (2)$$

Bites/g food OM comminuted to particles between 0·25 and 1 mm

$$= \frac{\text{No. of chewing movements}}{\left(\begin{matrix}\text{Mass of}\\ \text{ingesta OM}\end{matrix}\right) * \left(\begin{matrix}\text{Proportion of}\\ \text{ingesta OM}\end{matrix} < 1{\cdot}0 \text{ and } > 0{\cdot}25\text{ mm} - \begin{matrix}\text{Proportion of}\\ \text{food OM}\end{matrix} < 1{\cdot}0 \text{ and } > 0{\cdot}25\text{ mm}\right)} \quad (3)$$

Proportion of food OM comminuted to particles between 0·25 and 1 mm

$$= \frac{(\text{Proportion of ingesta OM} < 1{\cdot}0 \text{ and } > 0{\cdot}25\text{ mm} - \text{Proportion of food OM} < 1{\cdot}0 \text{ and } > 0{\cdot}25\text{ mm})}{(\text{Proportion of food OM} > 1{\cdot}0\text{ mm})} \quad (4)$$

RESULTS

The chewing records indicated two types of jaw movement during prehension and formation of the bolus (Fig. 1). Prehension movements were of high frequency and small amplitude, while chewing movements during bolus formation gave a lower frequency, large amplitude trace with a distinctive pause midway through each movement. Chewing movements (bites) were usually grouped in contiguous bursts of *c.* 10–30 movements (although sequences of > 50 bites were sometimes recorded) and were preceded by periods of prehension. This pattern was most obvious when lucerne hay was eaten. When fresh forages were consumed, chewing movements were often found interspersed with prehension movements.

Effects of long and chopped hay on eating behaviour

The chewing behaviour of deer eating chopped or long lucerne hay is reported in Table 2. In comparison to chopped hay, long hay required more chewing bites per g DM eaten ($P < 0.005$). The chewing rate (bites/min) of deer eating long hay was significantly ($P < 0.05$) faster. The estimated numbers of chewing bites required to form a bolus were 25·7 for long hay and 15·1 for chopped hay. The difference was not significant, although there were large variations between deer. There was no significant difference in estimated bolus size, or in the proportion of total chewing bites which were associated with chewing events (97 *v.* 93% of total chewing bites for long and chopped hays respectively).

Comminution of fresh and air-dried forages

The very large particle fraction of the ingesta (i.e. that OM which was retained on the 4 mm screen) contained easily identifiable, large pieces of stem and leaf. Some leaves (e.g. smaller chicory or ryegrass leaves) were largely intact and some (e.g. lotus and lucerne) were found still adhering to pieces of stem. Leaf and stem particles were also identifiable in the fractions retained on the 2 and 1 mm screens.

Table 2. *Consumption of dry matter (DM) and the characteristics of the chewing behaviour of deer eating long or chopped lucerne hay (Expt 1)*

	Feed type		S.E.
	Long	Chopped	(3 D.F.)
Consumption rate (g DM/min)	8·3	11·4	0·88
Chewing rate (bites/min)	73·3	42·9	5·50
Chewing activity			
Bites/g DM consumed	9·1	3·8	0·48
Estimated bites/bolus	25·7	15·1	4·29
Estimated bolus size (g DM)	3·2	4·4	0·69

Relative to the forages consumed, the principal effect of chewing was to reduce the proportion of very large particles (i.e. those retained on the 4 mm screen) and to increase that of material passing the 0·25 mm screen (Table 3). For all forages, > 30% of the ingested OM remained in the very large particle (> 4 mm) fraction, and between 48·1% (lucerne hay) and 65·2% (chicory) of the ingesta recovered from the rumen consisted of particles which were retained on screens with apertures of 1 mm or larger (Table 3). Significantly ($P < 0.05$) more chicory OM was retained by the 1 mm and larger screens than either lotus or lucerne hay.

Of the ingesta OM which passed the 1 mm screen, between 7·1 and 13% was in the 0·25–1 mm size fraction, and between 27·4 and 41·2% was in the very small particle (< 0·25 mm) pool. There was a significantly greater ($P < 0.005$) proportion of the lucerne hay OM than that of the other forages in the 0·25–1 mm pool.

Measurements of chewing, ingestion and ensalivation are given in Table 4. The four forages were consumed at similar rates (g OM/min) and there were no significant differences in the amounts of

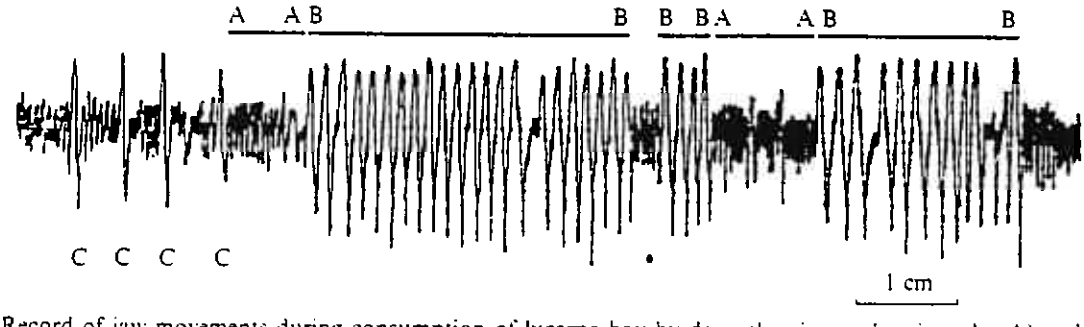

Fig. 1. Record of jaw movements during consumption of lucerne hay by deer, showing prehension (A—A) and chewing (B—B) sequences. Sequences of more than four contiguous chewing movements preceded by prehension movements are considered to represent the formation of a bolus. Four single chews (C) are also shown. (Chart speed: 1 cm corresponds to 4 seconds).

Table 3. *Distribution of particle sizes (g OM in given size range/g total OM) in forage and rumen ingesta S organic matter (OM) (Expt 2)*

Particle size (mm)*	Forage				
	Chicory*	Lotus	Ryegrass	Lucerne hay	S.E. (9 D.F.)
In forages					
> 4	0·881	0·949	0·869	0·993	
> 1	0·889	0·965	0·869	1·002	
< 0·25	0·103	0·028	0·128	0	
In rumen ingesta					
> 4	0·497	0·323	0·436	0·307	0·0349
2–4	0·062	0·076	0·042	0·068	0·0053
1–2	0·093	0·100	0·074	0·106	0·0107
0·5–1	0·043	0·055	0·040	0·067	0·0045
0·25–0·5	0·030	0·035	0·031	0·063	0·0032
< 0·25	0·274	0·412	0·378	0·390	0·0352
> 1	0·652	0·499	0·552	0·481	0·0357
< 1	0·348	0·502	0·448	0·519	0·0357

* Because some particles pass lengthwise through the sieve, the maximum size of particles in each fraction will be larger than the nominal sieve mesh size.

Table 4. *Consumption of organic matter (OM), and measures of the chewing and ingestive behaviour of deer while eating fresh or air-dry forage (Expt 2)*

	Forage				
	Chicory	Lotus	Ryegrass	Lucerne hay	S.E. (9 D.F.)
Consumption rates and chewing activity					
Consumption rate (g OM/min)	4·3	5·6	3·6	3·7	1·32
Chewing rate (bites/min)	43·4	37·9	48·1	49·6	3·12
Chewing activity					
Bites/g OM consumed	11·8	10·3	15·6	18·7	3·32
Bites/g CWOM consumed	59·7	37·7	40·9	43·2	10·14
Estimated bites/bolus	11·1	9·5	9·7	14·3	1·07
Bolus formation					
Estimated bolus size (g OM)	1·2	1·5	0·8	1·1	0·32
Bolus DM content (g/100 g)	7·1	8·6	9·5	10·9	0·47
Indexes of chewing efficiency					
Bites/g OM comminuted					
To < 1 mm	50·5	23·5	48·1	37·9	8·64
To < 1 and > 0·25 mm	174	121	246	143	42.7
Proportion of OM comminuted					
To < 1 mm	0·267	0·485	0·366	0·518	0·0381
To < 1 and > 0·25 mm	0·074	0·086	0·078	0·127	0·0078
Apparent salivary water secretion					
G/g OM	9·4	7·8	5·9	9·7	0·87
G/bite	0·94	1·03	0·42	0·67	0·166

chewing required to consume either the OM or the CWOM of the different forages. The test feeds appeared to be formed into boli of similar sizes but it was estimated that a greater number of chewing bites ($P < 0·05$) was required to form a bolus of lucerne hay than a bolus of either lotus or ryegrass.

The chicory boli had less ($P < 0.01$) water than those of lucerne hay, but similar amounts of salivary water appeared to have been added during the formation of both chicory and lucerne hay boli. Less water ($P < 0.05$) was added during the formation of lotus and ryegrass boli.

Similar numbers of bites were required to comminute the forages to particles < 1 mm in size, although the difference between lotus (23·5 bites/g OM) and chicory (50·5 bites/g OM) approached significance at the $P < 0.05$ level. There was no difference in the number of bites needed to comminute the forages to particles between 0·25 and 1 mm in size. More ($P < 0.005$) of the OM in lucerne hay and lotus, than in chicory, was comminuted to particles < 1 mm in size (Table 4), and more ($P < 0.005$) lucerne hay OM was comminuted to particles between 0·25 and 1 mm in size than for any other feed.

DISCUSSION

Effect of rumen emptying on ingestion behaviour

The method used to collect chewed and swallowed forage in Expt 2 has been used previously with sheep and cattle (e.g. Waghorn 1986; Waghorn *et al.* 1989; Domingue *et al.* 1991*b*). The data presented in this paper are thus comparable with previously published work. Nevertheless, the data from Expts 1 and 2, where the deer were given long lucerne hay suggests that deer with emptied rumens eat more slowly, make fewer chewing bites/min and more bites/g of ingested material, and have a smaller bolus size, relative to deer whose rumens have not been emptied. However, this does not invalidate comparisons between forages where the rumen emptying technique was used in all instances.

Effectiveness of chewing during eating on forage comminution

There appears to be only limited comminution of forages when they are eaten by red deer. Four lines of evidence support this view: first, between 48 and 65% of the ingesta OM examined in Expt 2 consisted of particles > 1 mm (Table 3), and much of this (between 31 and 50% of the total OM) consisted of very large particles, i.e. material which was retained on the 4 mm screen. Second, the chewing efficiency indexes (Table 4) show that only some 27% (chicory) to 52% (lucerne hay) of forage OM initially > 1 mm was comminuted to particles < 1 mm. Third, most of the ingesta OM in the < 1 mm pool consisted of very small particles and soluble OM which passed the 0·25 mm screen (the 'VSPS') and was probably largely cell contents released through the breakage of cell walls, as Ulyatt *et al.* (1986) and Waghorn *et al.*

Table 5. *Comparison of chewing efficiency (percentage of feed particles initially > 1 mm, comminuted to pass a 1 mm screen) and the particle size profile of chewed and swallowed feed, measured in ruminants eating fresh and dried lucerne and ryegrass*

Species	Forage*	Chewing efficiency	Ingesta particle size profile (%)		Reference
			< 1 mm	< 0·25 mm	
Deer	Long LH	51·8	51·9	39·0	This paper
	Fresh PR	36·6	44·8	37·8	This paper
Sheep	Chopped LH	53·6	—	—	Reid *et al.* (1979)
	Chopped LH	37·1	40·7	22·9	A. John & C. S. W. Reid (unpublished)†
	Chopped LH	48·0	60·6	30·8	Domingue *et al.* (1991*b*)
	Fresh L	45·4	45·4	31·9	A. John & C. S. W. Reid (unpublished)
	Fresh PR	48·6	48·6	36·8	A. John & C. S. W. Reid (unpublished)
Cattle	Fresh AR	25·9	25·9	10·7‡	Pond *et al.* (1984)
	Fresh PR	44·2	–	–	Waghorn *et al.* (1989)
	Fresh L	43·3	–	–	Waghorn (1986)
	Fresh L	45·3	–	–	Waghorn *et al.* (1989)
	Long LH	44·9	–	–	Waghorn (1986)
Goats	Chopped LH	85·0	78·6	38·0	Domingue *et al.* (1991*b*)

* LH, lucerne hay; L, lucerne; PR, perennial ryegrass; AR, annual ryegrass.
† cited by Ulyatt *et al.* (1986).
‡ < 0·3 mm.

(1986, 1989) have indicated that 40–80% of this fraction is 'solubles'. Fourth, for all four forages, much of the ingesta recovered from the rumen was still in a physical form similar to the original feed.

These results indicate that chewing by red deer during prehension and bolus processing expresses an amount of fine particulate and soluble material but is ineffective in reducing the particle size of the forage cell walls. Domingue *et al.* (1991*a*) have indicated that feed particles of > 1 mm have only a low probability of leaving the rumen of deer. This means that, for each of the forages fed in this experiment, approximately half of the OM recovered from the rumen would require considerable further comminution before it would be likely to pass out of the rumen.

The susceptibility of the different forages to comminution as they are eaten is best illustrated by the chewing efficiency index (proportion of forage OM > 1 mm which is comminuted to particles < 1 mm). Previous workers (e.g. those cited in Table 5) have used an 'uncorrected' index which includes the VSPS pool in the calculation. A second 'corrected' index (which excludes the VSPS pool) is also given in this paper to help to differentiate between chewing which comminutes cell walls and chewing which releases cell contents. The size of the VSPS pool reflects first the proportion of cell contents in the forage, and secondly the degree to which the cell contents have been released by chewing. It is suggested that an index which includes the VSPS may give a misleading impression of the degree to which the cell wall material has been comminuted. The uncorrected indexes suggest that lotus, ryegrass and lucerne hay are comminuted to a similar extent, but when the 'VSPS-corrected' indexes are compared it is clear that the lucerne hay cell wall mass was more broken by chewing than that of the other forages.

Chewing during feed prehension and bolus formation by red deer appears to have effects on forages which are similar to those produced by sheep and cattle. The particle-size profiles of ingesta swallowed by cattle and sheep eating fresh lucerne or ryegrass, or chaffed lucerne hay (references in Table 5) are similar to those reported in Table 3, i.e. where 30% or more of the chewed material consists of particles retained on a 1 mm screen, and there is a substantial pool (30–45%) of very small particles and soluble dry matter. Sheep, cattle and red deer appear to comminute forages with similar efficiencies, although less efficiently than goats (Table 5).

Influence of physical form and cell wall content on the ingestion of forage and chewing behaviour

The importance of physical form is indicated in Expt 1. When the deer were fed long pieces of lucerne hay they responded by increasing their chewing rate (bites/min and bites/g DM consumed) but this could not compensate for the effects of the more difficult physical form and the rate of feed consumption fell.

Forages with higher cell wall or cellulose contents are eaten more slowly and require more chewing (Dulphy & Michalet-Doreau 1983), and the consumption rates (g OM/min) and chewing activity (bites/g OM consumed) in Expt 2 (Table 4) are consistent with this. Comparison of lucerne hay and chicory (the forages with the greatest and least concentrations of CWOM) shows that lucerne hay was comminuted the most completely (Table 3) and was associated with high efficiency indexes (Table 4) while chicory was comminuted less than all the other forages and had low indexes of chewing efficiency. These results are consistent with those of Poppi *et al.* (1981*b*) and Ulyatt *et al.* (1982) who fed mature and immature fresh or dried grass to sheep and cattle. However, there is an inconsistent relationship between chewing efficiency and CWOM content within the three fresh forages.

The bolus sizes reported here are derived from the chewing records rather than direct observation because the deer often did not eat if they were watched. As particular bursts of chewing could not be related to the formation of particular boluses, all chewing events were given equal weighting in bolus formation. With the bolus data calculated on this basis, there was no evidence in Expt 2 that the size of the swallowed bolus changed when forages with different morphologies were eaten, and consequently more bites were needed to form a bolus of lucerne hay than of lotus or ryegrass. Bolus formation was accompanied by the addition of similar amounts of salivary water (g/g OM) to both chicory and lucerne hay. As the amount of water added per bite was similar, this also indicates that both these forages received similar amounts of chewing during bolus formation. These data suggest that the deer had more difficulty in prehending and processing into a bolus those forages which were presented in larger pieces.

Factors which may influence forage comminution during chewing

The chewing effort associated with forage consumption by red deer may be as much influenced by the physical characteristics of the forage as by its chemical composition. The inconsistent relationship between the CWOM content and chewing effort (bites/g CWOM consumed) and addition of salivary water (g/g OM) (especially the chicory/lotus comparisons in Table 4), and the significant differences between forages which have different physical forms (e.g. estimated bites/bolus for lotus *v.* lucerne hay, and bites/g DM consumed for chopped *v.* long lucerne hay) support the importance of physical form. It is suggested that the chewing effort is associated with

the need to form a bolus and that the forage is chewed only as much as is required to achieve this purpose. The extent of comminution during eating may simply reflect the processing needed to form a bolus and the resistance of the feed to this.

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