J Comp Physiol B (2006) 176: 117–124
DOI 10.1007/s00360-005-0027-x

ORIGINAL PAPER

W. von Engelhardt · P. Haarmeyer · M. Kaske
M. Lechner-Doll

Chewing activities and oesophageal motility during feed intake, rumination and eructation in camels

Received: 19 May 2005 / Revised: 22 July 2005 / Accepted: 10 August 2005 / Published online: 23 November 2005

Abstract It was the aim of this study to characterize rumination behaviour, eructation and oesophageal motility in camels to identify similarities and differences between camels and domestic ruminants. Recordings were carried out in five camels fed on a hay-based diet. On an average, the duration of rumination, feeding and resting was 8.3, 5.6 and 10.1 h per 24 h, respectively. Rumination activity peaked in the morning between 9:00 and 11:00 and in the night between 02:00 and 04:00 a.m. During rumination periods, on an average 67 boluses were regurgitated per hour. Each bolus was chewed for an average of 45 s with 68 chews per min. The pause between two rumination cycles lasted on an average 9 s. Hay intake took 61 min/kg dry matter (DM), rumination lasted 71 min/kg DM of hay consumed. The regurgitation of a bolus started with a contraction of cranial compartment 1 (C 1) during a B-sequence, followed by a deep inspiration with closed glottis. Digesta enters the oesophagus, and an antiperistaltic wave transported the bolus orally. Eructation starts with a contraction of the caudal C1 during a B-sequence when the cranial C1 is relaxed. After entering the oesophagus, a rapid antiperistaltic wave transports the gas orally. Results revealed that the parameter values obtained in the camels were remarkably similar to those in domestic ruminants despite profound morphological differences and different patterns of forestomach motility.

Communicated by G. Heldmaier

W. von Engelhardt (✉) · P. Haarmeyer · M. Lechner-Doll
Department of Physiology, School of Veterinary Medicine,
Bischofsholer Damm 15/102,
30173 Hannover, Germany
E-mail: wolfgang.von.engelhardt@tiho-hannover.de
Tel.: +49-511-8567272
Fax: +49-511-8567687

M. Kaske
Clinic for Cattle, School of Veterinary Medicine, Hannover, Germany

Keywords Camel · Rumination · Eructation · Oesophagus · Motility

Introduction

Tylopoda and Ruminantia independently developed forestomach fermentation during evolution. Species of both suborders of Artiodactyla ruminate and have in common large forestomachs with extensive microbial digestion to achieve a superior digestibility of diets rich in cell wall constituents. However, gross anatomy and the microscopic structure of the forestomach mucosa are very different in camelids compared to ruminants (Vallenas and Stevens 1971; Cummings et al. 1972; Heller et al. 1984; Osman and von Engelhardt 1998; von Engelhardt 1998; Osman et al. 1999). In camelids, the forestomach consists of a voluminous compartment 1 (C 1) which is subdivided by a strong muscular pillar into a cranial and a caudal part, a relatively small compartment 2 (C 2) and a tubiform compartment 3 (C 3). The motility of the forestomach system is characterized in camelids by A and B sequences. An A sequence starts with a relaxation of the canal between C 2 and C 3, followed by a contraction of C 2, and is finally completed by a contraction of the caudal C 1. Each B sequence starts with a contraction of the cranial C 1, followed by a contraction of the canal and C2, and finally a contraction of the caudal C 1 and a second contraction of the canal (Heller et al. 1986; Osman and von Engelhardt 1998; Osman et al. 1999). Regurgitation in camels occurs during the peak of the contraction of the cranial C 1. The eructation of gas from the forestomach takes place during the peak contraction of the caudal C1 when the cranial C 1 is relaxed (von Engelhardt et al. 1992; Osman and von Engelhardt 1998).

The objectives of this study were to characterize chewing behaviour, circadian activies and oesophageal motility in camelids as such information is not available so far. Thereby, similarities and differences between these two distinct suborders of Artiodactylae should be identified.

Material and methods

Experimental animals

A total of five camels were used (Table 1). Jaw movements, pressure in the oesophagus and forestomach motility mostly were measured in four of these camels. Tracheal pressure was measured in one camel (Er) only. At least 6 months prior to the studies, all animals were fitted with a fistula in the caudal C 1. Camels were fed, daily about 3 kg carrots, 2 kg dried beet pulp and medium-quality meadow hay ad libitum. If not particularily stated, the feed and the new batch of hay was offered at 8:00 hours. Water and mineralized salt licks were freely accessible.

Pressure measurements

Pressure events in the oesophagus, the trachea and in the forestomach were measured with open end catheters and pressure transducers (Statam P23XL) representing a modification of the method described by Arndorfer et al. (1977). Signals were recorded using a four channel recorder (Watanabe WTR 331) as well as a PC-based digital recorder (486, ASI). Digitalization was achieved using a 12 bit 16-channel AD converter with a D 2-programme.

For the measurements in the oesophagus, a device was devolped consisting of a 2.8 m long flexible polyvinylchloride (PVC) tube (external diameter 8 mm) with openings in distances of 30 cm shifted by 90° from one opening to the other. A bundle of six PE tubes (internal diameter 0.63 mm each) were introduced in the PVC tube, and each of the PE tubes was fixed in one of the prepared opening of the large-diameter tube with silicon. Thereby, the narrow tubes ended outside. For positioning in the oesophagus, a conventional nasogastric tube (external diameter 8 mm) was introduced through the nose into the C 1 and was pulled out through the forestomach fistula. After that, the prepared PVC tube, containing the six small PE tubes, was attached to the end of the oesophagus tube and was positioned in the oesophagus by pulling back the nasogastric tube. The PVC tube was fixed with a sponge ring at the entrance of the nose. Thereby six pressure changes in the oesophagus could be measured simultaneously between a position distal to the larynx down to the chest part of the oesophagus over a length of 180 cm every 30 cm.

In one camel (Er), pressure changes were also recorded in the trachea. Therefore, a PE tube (internal diameter 0.63 mm) was put into the lumen of the trachea in the middle of the neck through a sterile disposable cannula (1.2 mm × 40 mm, Teruma Europe, Leuven, Belgium).

For measurements of pressure changes in the forestomach, open polyethylene (PE) tubes (internal diameter 1.2 mm) were placed through the fistula in the cranial C 1, caudal C 1 and in the C 2; they were kept in position by a small piece of lead.

Jaw movements

Chews were either recorded (1) by measuring pressure changes (1) or (2) by using magnets (2).

1. A piece of bicycle rubber tube (15 cm long, diameter 3 cm) was filled with foam rubber. The bicycle tube was closed on one side, and in the other opening a PVC tube (internal diameter 2 mm) was glued with silicon. The bicycle tube was positioned below the lower jaw at the halter of the camel and the PVC tube was connected to the pressure transducer and the recording system.
2. Similar to the pressure measurements, a bicycle tube filled with rubber foam was fixed below the lower jaw and the halter at the head. In the middle of the foam a magnet (0.5 cm long, diameter 0.5 cm) was glued. A magnetoresistive sensor (MRS, type KMZ 10A, Siemens, Fuerth) was fixed laterally at the halter. Changes in the distance between magnet and sensor alter the magnetic field strengths which were recorded on average (Lechner-Doll 2005).

Rumination behaviour

Four camels were kept in their familiar barn. Jaw movements were recorded continuously for 4 days and nights (96 h). The lengths of chewing periods, rumination periods and pauses were assessed. The number of jaw movements per ruminated bolus was calculated. Due to characteristic differences in chew patterns, feeding and rumination periods could be differentiated easily.

Table 1 Experimental animals

Name	Breed	Gender	Age (years)	Mean body weight (kg)
Ro	Cross breed (tulu)	Female	5	510
Sei	Cross breed (tulu)	Female	12	770
Em	Camelus bactrianus	Male (castrated)	7	600
Su	Camelus bactrianus	Male (castrated)	18	740
Er	Camelus bactrianus	Male (castrated)	20	660

A tulu is a cross breed between *Camelus dromedarius* and *Camelus bactrianus*

Statistics

Results were expressed as means and standard deviations. Differences between means were checked by one factorial variance analysis for significance ($P < 0.05$). N represents the number of animals and n the number of measurements.

Results

Feeding, resting and rumination activities

The camels were eating 5.6 ± 2.5 h, ruminating 8.3 ± 2.7 h and resting 10.1 ± 1.7 h per 24 h. Data were calculated from four camels (Ro, Sei, Su, Em) for 4 days each. The resting periods were more or less uniformly distributed throughout day and night. However, feeding peaked clearly between 05:00 and 07:00 and between 12:00 and 17:00 hours and elsewhere (Fig. 1) while a maximal rumination activity was observed between 9:00 and 11:00 and between 2:00 and 04:00 hours. It took on an average 61.3 ± 10.8 min (Su 53 ± 10, Ro 70 ± 13, Em 61 ± 9 min) to consume 1 kg DM hay, and 71.0 ± 9.7 min (Su 64 ± 10, Ro 78 ± 8, Em 71 ± 11 min) were spent for rumination of each kilogram DM hay consumed (50 estimations in each camel; consumption of hay dry matter had been estimated reliably only in three of the camels).

Motility and pressure waves in the oesophagus during rumination

Regurgitation of the bolus

The regurgitation of a bolus started always at the peak of a contraction of the cranial C 1 during a B sequence. The regurgitation is accompanied by a deep inspiration with closed epiglottis. Thereby, the pressure in the

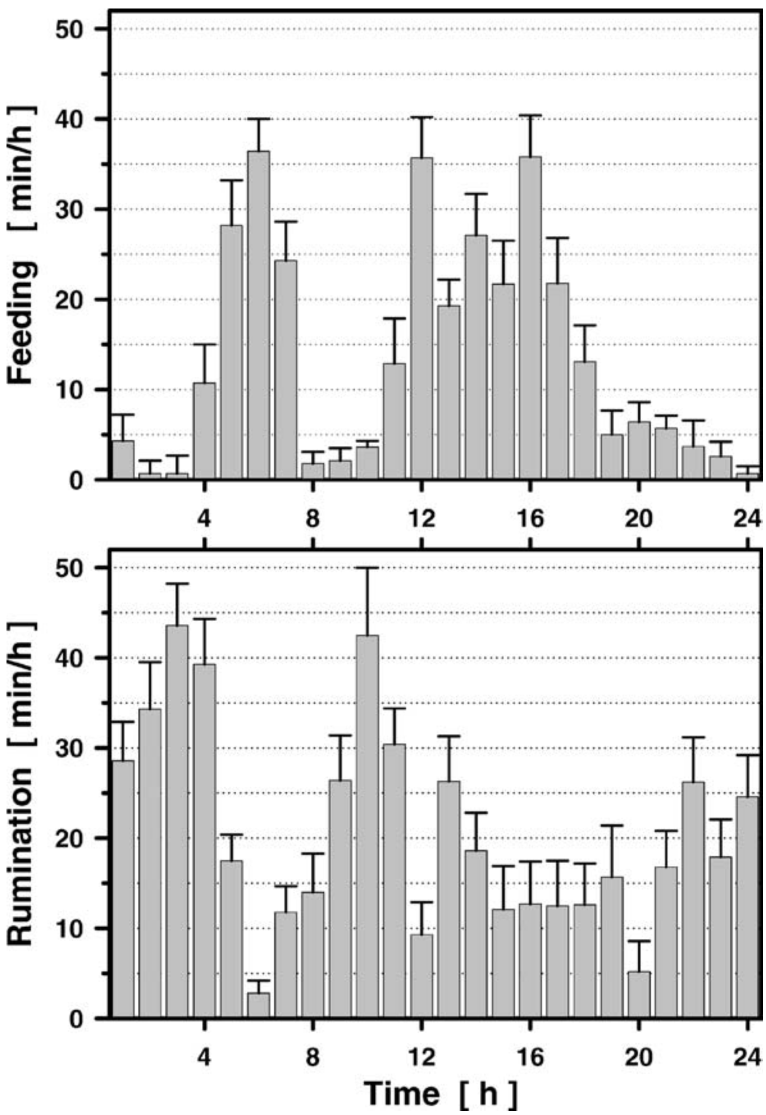

Fig. 1 Feeding and rumination activities expressed as chewing activities in minutes per 24 h (feeding upper drawing, rumination lower drawing). Hay was available ad libidum, a new batch of haw was added daily between 07:00–08:00 and 12:00–13:00. Means ± SD are given for four camels (Em, Ro, Sei, Su) recorded over a period of four days each

trachea decreased 1.0 ± 0.1 m H_2O (water column) below the baseline, and in the thoracic portion of the oesophagus the pressure decreased by 0.4 ± 0.1 m H_2O (Table 2). Due to the increased pressure in the cranial C 1 and the decrease of pressure in the oesophagus, digesta was aspirated into the oesophagus. Thereafter, an antiperistaltic wave starts in the most distal part of the oesophagus and transports the bolus into the mouth within 4.1 ± 0.2 s (Fig. 2). Thus, the mean speed of the antiperistaltic wave was 0.44 ± 0.15 m s^{-1} (30 estimations in each of the four camels Ro, Sei, Su, Em). The wave had a mean pressure peak of 1.5 ± 0.3 m H_2O.

The B sequence, in which the regurgitation of the bolus occurred, was followed in 62% by two sequences (B and A sequences), in 32% by three sequences (mostly B–A–B-sequences), and in 6% by only one B sequence. Swallowing of the chewed bolus was followed by a pause of 0.14 ± 0.03 min before the next regurgitation started.

Swallowing of the chewed bolus

Immediately after regurgitation some of the fluid that had entered the mouth with the bolus is swallowed (Fig. 2). Throughout the period of chewing, further fluid is swallowed one to three times. The final swallowing of the chewed bolus lasted 3.6 ± 0.2 s (similar to the swallowing of a bolus during feeding with 3.4 ± 0.2 s) and caused a pressure change in the oesophagus of 1.0 ± 0.07 m H_2O (bolus during feeding 1.10 ± 0.03 m H_2O). Swallowing of drinking water caused a significant lower pressure change (0.40 ± 0.07 m H_2O) in a shorter time (2.0 ± 0.2 s) (30 estimations in each of the four camels Em, Er, Ro, Su).

Jaw movements, frequency and duration of chewing and number of boluses during rumination

On an average, the camels chewed each bolus 61.5 times within 45.3 s which results in a chewing frequency of 68 chews min^{-1} (Table 3). The mean pause between two rumination cycles was 8.7 s. On average, 67 boluses were recorded per hour during the rumination periods. No differences existed between measurements with catheters and those carried out with magnets.

Eructation of gas

Eructation took place at the time of maximum contraction of the caudal C 1 during a B sequence. At that time, the cranial C 1 is relaxed. In contrast to the

Table 2 Magnitude and duration of pressure changes in oesophagus and trachea at the beginning and during regurgitation of a bolus and during eructation of gas. 30 estimations in oesophagus in each of four camels (Em, Ro, Sei, Su),and 50 estimations in trachea of camel Er. Values are means ± SD, different letters (a, b and A, B) indicate significant differences ($P < 0.05$)

	Regurgitation of bolus			Eructation
	During aspiration		During regurgitation	During eructation
	In trachea	In thoracic portion of oesophagus	In cervical and thoracical oesophagus	
Pressure [m H_2O]	−1.0 ± 0.1 a	−0.4 ± 0.1 b	1.5 ± 0.3 A	0.32 ± 0.2 B
Duration [s]	1.4 ± 0.2 a	1.5 ± 0.1 a	4.1 ± 0.2 A	1.8 ± 0.1 B

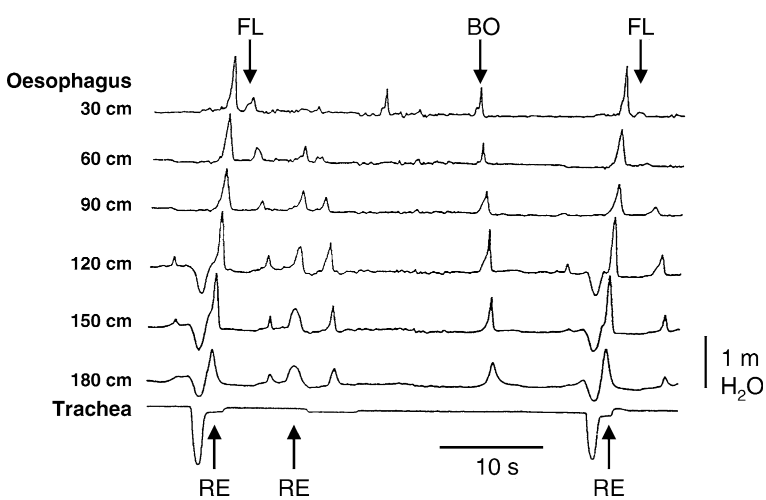

Fig. 2 Changes in pressure along the oesophagus 30, 60, 90, 150, and 180 cm from the nostril and in the cervical trachea (middle of the neck) during rumination (camel Er). Measurements with open catheters and pressure transducers. *RE* rejection of a bolus, *ER* eructation, *FL* swallowing of fluid, *BO* final swallowing of the chewed bolus

Table 3 Number, frequency and duration of jaw movements and number of boluses masticated during rumination. Measurements with open catheters or with magnets. 60 estimations in each of the four camels (Ro, Sei, Su, Em). Values are means ± SD

	Catheter	Magnet
Number of chews per bolus	59.2 ± 2.1	63.8 ± 3.0
Duration of chewing per bolus (min)	0.73 ± 0.2	0.78 ± 0.1
Frequency of chews (min^{-1})	67.4 ± 2.0	68.6 ± 1.5
Pause between two boluses (min)	0.14 ± 0.03	0.15 ± 0.02
Number of boluses (h^{-1})	68.9 ± 3.2	64.5 ± 4.5

regurgitation of a bolus, during eructation no decrease of pressure was observed in the trachea and in the chest part of the oesophagus. During the subsequent anti-peristaltic wave, pressure changes in the oesophagus (0.3 ± 0.2 m H_2O) are significantly smaller as compared to changes during bolus regurgitation (Table 2). The duration of the pressure wave in the oesophagus (1.8 ± 0.1 s) was found to be shorter, and the speed of the pressure wave (0.72 ± 0.10 m s^{-1}) was considerably faster than during bolus regurgitation.

Discussion

We wanted to determine the extent to which chewing activities, regurgitation, eructation and oesophagal motility might differ between the Tylopoda and Ruminantia representing two distinct suborders of Artiodactyla. Whereas numerous studies focusing on these issues in ruminants have been published, for camelids only little information is available.

Rumination, feeding and resting periods in camels and in cattle

Mean daily duration of rumination was similar in camels compared to cattle, sheep and goats (Table 4). Lechner-Doll (1986) and Kaske et al. (1989) reported longer periods for rumination in camels (on an average 11 h/day) from their studies in Sudan. However, both authors fed the animals with firm roughages with a high fibre content and low digestibility which were harvested in this semi-desert region. For breakdown of these roughages to small particles these camels needed obviously more time.

The time used for feed intake was roughly similar in camels, cattle, sheep and goats (Table 4). Also the resting time did not differ markedly among species. A markedly shorter resting time was observed only in those camels fed the low-quality Humaraya-hay (Lechner-Doll 1986). This may indicate that the well-known relation between cell wall contents of the diet and the length of the daily rumination activity in ruminants is also valid for camels (Welch and Smith 1969; Balch 1971; Van Soest 1982).

Frequency and duration of chewing during rumination in camels and cattle

The number of boluses ruminated per hour is similar in camels and in domestic ruminants (about 60 h^{-1} ; Van Soest 1994). Also the frequency of chews during rumination is in ruminants comparable to that in camels. A frequency of 62–75 chews per minute was recorded in hay-fed sheep (Kaske and Groth 1997; Kaske et al. 2002) and in cattle (Okine et al. 1994; Dado and Allen 1994, Hailu 2003). The rate of breakdown of feed particles into smaller particles is an important limiting factor for the passage rate of particles from the reticulum into the omasum (Poppi et al. 1980; Kaske and von Engelhardt 1990). The maximum size of particles in the intestine of ruminants (Smith et al. 1967; Reid et al. 1977; Poppi et al. 1980, Ulyatt 1982) as well as in that of camels (Lechner-Doll 1986) are less than 1–2 mm. Comminution of feed particles results mainly from chewing during rumination and only little to microbial activity (Pearce 1967; Troelsen and Campbell 1968;

Table 4 Comparison of rumination, feeding and resting periods (h/day) in camels, cattle, sheep and goats. Feed was mostly different in the various studies (silage, concentrates, grazing, hay of different quality)

Animals	Rumination (h/day)	Feeding (h/day)	Resting (h/day)	References
Camel	8.3	5.6	10.7	Present experiments
	10.9	7.9	5.2	Lechner-Doll (1986)
Cattle	6 – 10			Castle et al. (1950)
	7 – 8			Hardison et al. (1956)
	5.3–7.3			Welch et al. (1970)
	9.1	6.4	8.5	Deswysen et al. (1987)
	7.9	6.4	9.7	Luginbuhl et al. (1989)
	6.1 – 9.2	3.7 – 4.2		Grant et al. (1990)
	4.3 – 6.6	3.7 – 5.7	10.1 – 12.3	Okine et al. (1994)
Sheep	9.5	5.5	9.0	Deswysen and Ehrlein (1981)
	8.3	3.7	12.0	Domingue et al. (1991)
	9.1	7.7	7.2	Kaske and Midasch (1997)
	9.6	6.1	8.3	Kaske and Groth (1997)
	9.3	3.4	11.3	Kaske et al. (2002)
Goat	7.2	7.1	9.7	Lechner-Doll (1986)
	6.1	6.8	11.1	Domingue et al. (1991)

Welch 1982). In cattle rumination has been suggested to be responsible for 85% of comminution of feed particles (Kennedy 1985). Thereby and due to microbial activity, the density of feed particles increases which is a major precondition for the passage of particles out of the reticulorumen (Kaske and von Engelhardt 1990). Results indicate that important features of rumination activity are amazingly comparable in camels and in ruminants irrespective of their independent development during evolution.

Circadian rhythm in rumination and feeding activities in camels and ruminants

The main rumination activity of camels occurs in the late night and early morning rather independent of feeding time and feeding regime (Kaske et al. 1989). When goats and camels were fed the same hay ad libitum, the patterns of rumination activity did not differ significantly (Lechner-Doll 1986; Table 5). However, when goats and camels were fed in the morning exclusively, the second peak of rumination occurred about 7 h earlier in the goats than in camels. Also after feeding the animals exclusively in the early night hours, goats started to ruminate soon after feeding while in camels the rumination started with a delay of several hours. This more strictly circadian rhythm of rumination activity in camels compared to goats may be considered as a mechanism to achieve a prolonged retention time of particles in the forestomach system. Particles have to be reduced in size before they can pass into the C 3. If rumination occurs after a rather long lag period, particles remain for a longer time in the forestomach and cellulose digestibility may be improved.

In cattle and sheep fed ad libitum main rumination activities were also observed in the late night and early morning hours, with a maximum in the early morning (Welch and Smith 1968; Gordon and McAllister 1970). In other studies, rumination activity was more uniformly distributed over day and night (Deswysen et al. 1984; Hailu 2003).

Rumination and ructus in the relation to the pattern of forestomach motility in camels and in domestic ruminants

In agreement with observations by Heller et al. (1986), von Engelhardt et al. (1992) and Osman and von Engelhardt (1998), the regurgitation of a bolus for rumination started subsequent to a contraction of the cranial C 1 within a B-sequence. This contraction lifts up forestomach contents in front of the cardia. In domestic ruminants the regurgitation of a bolus starts with an additional contraction of the reticulum. In camelids a comparable extra contraction of the cranial C 1 has not been observed.

Similar to ruminants, the regurgitation of boluses by camels started with a deep inspiration and a closed epiglottis (von Engelhardt et al. 1992; Lechner-Doll and Hoffrogge 1994). Thereby, the pressure in the thoracic portion of the oesophagus is decreased, and forestomach contents are aspirated into the oesophagus. A rapid antiperistaltic wave transports the bolus up into the mouth. Also similar to ruminants, some fluid is swallowed by camels back into the forestomach immediately after the bolus had reached the mouth.

The courses of events during eructation are also comparable in camels and in ruminants. In camels due to the contraction of the caudal C 1 during a B sequence the gas layer is moved cranially in front of the cardia. In domestic ruminants, this movement of the gas is caused by a contraction of the dorsal rumen sac during the B cycle (only occasionally during an A cycle), and rumen contents in the rumen are held back by the cranial ruminal pillar. In camels as well as in ruminants, antiperistaltic waves transport the gas along the oesophagus cranially. In ruminants the soft palate elevates and closes the nasopharyngeal orifice when the gas reaches the cranial oesophageal sphincter, and all the gas enters from the pharynx into the trachea and the respiratory system. It is not known so far whether camels also inspirate the eructated gas into the lungs with the following inspiration, but observations suggest that this phenomenon occurs also in camels.

Table 5 Effects of feeding time on timing of the main feeding activity and on the main rumination activity in camels and goats fed medium or low quality roughage

Species	Feeding (time of day)	Main feeding activity (time of day)	Main rumination activity (time of day)		Reference
			First peak	Second peak	
Camels	Ad libitum	05–07 and 12–17	02–04	09–11	Present data
Camels	Ad libitum		02–06	11–12	Osman et al. (1999)
	20:00–02:00		00– 07	19–20	
Camels	Ad libitum	09–17	03–08	20–23	Lechner-Doll (1986)
	07:30–11:30	07:30–11:30	02–07	21–07	
	19:30–23:30	19:30–23:30	04–09	13–17	
Goats	Ad libitum	09–18	03–07	21–24	Lechner-Doll (1986)
	07:30–11:30	07:30–11:30	01–06	13–01	
	19:30–23:30	19:30–23:30	00–10		

Motility of the oesophagus during regurgitation and eructation

The calculated speed and pressure of the antiperistaltic waves in the oesophagus of camels and domestic ruminants (Sellers and Stevens 1966) were similar. During the eructation of gas the speed of the antiperistaltic waves in the oesophagus of camels (0.72 m s^{-1}) was twice that during regurgitation of a bolus (0.44 m s^{-1}). Amplitudes of the antiperistaltic waves were about twice as high during rejection of a bolus compared to the eructation of gas.

Conclusions

In camelids and domestic ruminants, the patterns of rumination were comparable in respect to daily duration and also in respect to the number of boli per hour, chews per min and pauses between consecutive rumination cycles. This may indicate that these patterns facilitate more or less an optimal utilization of diets with a high proportion of cell wall constituents, and this has developed accordingly in the distinct two suborders of Artiodactyla. The lag period between feeding and rumination in camels may promote even a superior utilization of low-quality roughage compared to ruminants.

References

Arndorfer RC, Steef JJ, Dodds WJ, Linehan JH, Hogan ME, Hogan W (1977) Improved infusion system for intraluminal esopgageal manometry. Gastroenterology 73:23–27

Balch CC (1971) Proposal to use time spent chewing as an index of the extent to which diets for ruminants possess the physical Property of fibrousness characteristic of roughages. Br J Nutr 26:383–391

Castle ME, Foot AS, Halley RJ (1950) Some observations on the behaviour of dairy cattle with particular references to grazing. J Dairy Res 17:215–229

Cummings JF, Munnel JF, Vallenas A (1972) The mucigenous glandular mucosa in the comlex stomach of two new-world camelids, the llama and guanaco. J Morphol 137:71–110

Dado RG, Allen MS (1994) Variation in and relationships among feeding, chewing, and drinking variables for lactating dairy cows. J Dairy Sci 77:132–144

Deswysen AG, Ehrlein HJ (1981) Silage intake, rumination and pseudorumination activity in sheep studied by radiography and jaw movement recordings. Br J Nutr 46:327–335

Deswysen AG, Bruyer DC, Vanbelle M (1984) Circadian rumination quality and voluntary silage intake in sheep and cattle. Can J Anim Sci 64(Suppl):341–342

Deswysen AG, Ellis WC, Pond KR, Jenkins WL, Conelly J (1987) Effects of monensin on voluntary intake, eating and ruminating behaviour and ruminal motility in heifers fed corn silage. J Anim Sci 64:827–834

Domingue BMF, Dellow DW, Barry TN (1991) The efficiency of chewing during eating and ruminating in goats and sheep. Br J Nutr 65:355–363

von Engelhardt W (1998) Forestomach motility in llamas and camels. Dtsch tierärztl Wochenschr 105:472–474

von Engelhardt W, Abbas AM, Mousa HM, Lechner-Doll M (1992) Comparative digestive physiology of the forestomach in camelids. In: Proceedings of the 1st international camel conference. R & F Publications, Newmarket, pp 263–270

Gordon JG, McAllister IK (1970) The circadian rhythm of rumination. J Agric Sci 74:291–297

Grant RJ, Colenbrander VF, Albright JL (1990) Effect of particle size of forage and rumen cannulation upon chewing activity and laterality in dairy cows. J Dairy Sci 73:3158–3164

Hailu Y (2003) Untersuchungen zur Bedeutung der Frequenz der Kieferschläge während des Wiederkauens für die Einschätzung der Wiederkauaktivität von Milchkühen. Vet Med Diss, Hannover

Hardison WA, Fisher HL, Graf GC, Thompson NR (1956) Some observations on the behaviour of grazing lactating cows. J Dairy Sci 39:1735–1741

Heller R, Gregory PC, von Engelhardt W (1984) Pattern of motility and flow of digesta in the forestomach of the llama (Lama guanacoe f. glama). J Comp Physiol B 154:524–533

Heller R, Lechner M, von Engelhardt W (1986) Forestomach motility in the camel (*Camelus dromedaries*). Comp Biochem Physiol A 84:285–288

Kaske M, von Engelhardt W (1990) The effect of size and density on mean retention time of particles in the gastrointestinal tract of sheep. Br J Nutr 63:457–467

Kaske M, Groth A (1997) Changes of factors affecting the rate of digesta passage during pregnancy and lactation in sheep fed hay. Repr Nutr Dev 37:573–588

Kaske M, Midasch A (1997) Effects of experimentally-impaired reticular contractions on digesta passage in sheep. Br J Nutr 78:97–110

Kaske M, Osman TEA, Lechner-Doll M, von Engelhardt W (1989) Circadian changes of forestomach motility and rumination in camels. Aust J Anim Sci 2:301–302

Kaske M, Beyerbach M, Hailu Y, Göbel W, Wagner S (2002) The assessment of the frequency of chews during rumination enables an estimation of rumination activity in hay-fed sheep. J Anim Physiol Anim Nutr 86:83–89

Kennedy PM (1985) Effects of rumination on reduction of particle size of rumen digesta in ruminants. Aust J Agric Res 36:819–828

Lechner-Doll M (1986) Selektive Retention von Futterpartikeln verschiedener Größe im Magen-Darmkanal von Kamelen im Vergleich mit Rindern und Schafen im Sudan. Vet Med Diss, Hannover

Lechner-Doll M (2005) The use of permanent magnetic fields in forestomach motility studies. In: F. Schober (ed) Proceedings of the 16th international symp biotechnology. Vienna, Austria 2001. Intern Soc Biotelemetry, Wageningen, Netherlands (in press)

Lechner-Doll M, Hoffrogge P (1994) Oesophagus manometry in camel. J Camel Pract Res 1:114–115

Luginbuhl JM, Pond KR, Burns JC, Russ JC (1989) Eating and ruminating behaviour of steers fed coastal bermudagrass hay at four levels. J Anim Sci 67:3410–3418

Okine EK, Khorasani GR, Kenelly JJ (1994) Effects of cereal grain silages versus alfalfa silage on chewing activity and reticular motility in early lactating cows. J Dairy Sci 77:1315–1325

Osman TEA, von Engelhardt W (1998) Motility pattern and flow of digesta in the forestomach of camel (*Camelus dromedarius*). J Camel Pract Res 5: 137–142

Osman TEA, Al-Busadah KA, von Engelhardt W, Lechner-Doll M (1999) Effects of ad libitum and restricted feeding on the circadian patterns of forestomach motility and rumination in camel (*Camelus dromedarius*). J Camel Pract Res 6:97–100

Pearce GR (1967) Changes in particle size in the reticulorumen of sheep. Aust J Agric Res 18:119–125

Poppi DP, Norton BW, Minson DJ, Henricksen RE (1980) The validity of the critical size theory for particle leaving the rumen. J Agric Sci 94:275–280

Reid CSW, Ulyatt MJ, Monro JA (1977) The physical breakdown of feed during digestion in the rumen. Proc N Z Soc Anim Prod 37:173–175

Sellers AF, Stevens CE (1966) Motor functions of the ruminant forestomach. Physiol Rev 46:634–659

Smith LW, Waldo DR, Moore LA, Leffel EC, Van Soest PJ (1967) Passage of plant cell wall constituents in sheep. J Dairy Sci 50:990–1002

Troelsen JE, Campbell JB (1968) Voluntary consumption of forage by sheep and it*prime*s relation to the size and shape of particles in the digestive tract. Anim Prod 10:289–296

Ulyatt MJ (1982) Plant fibre and regulation of digestion in the ruminant. In: Wallace G, Bell L (eds) Fibre in human and animal nutrition. Royal Soc NZ, Bulletin 20:103–107

Vallenas A, Stevens CE (1971) Motility of the llama and guanaco stomach. Am J Physiol 220:275–282

Van Soest PJ (1982) Nutritional ecology of the ruminants. O &B Books Inc, Corvallis

Van Soest PJ (1994) Nutritional ecology of the ruminants. Cornell University Press, Ithaca

Welch JG (1982) Rumination, particle size ans passage from the rumen. J Anim Sci 64(Suppl):324–325

Welch JG, Smith AM (1968) Influence of fasting on rumination activity in sheep. J Anim Sci 27:1734–1737

Welch JG, Smith AM (1969) Influence of forage quality on rumination time in sheep. J Anim Sci 28:813–819

Welch JG, Smith AM, Gibson KS (1970) Rumination time in four breeds of dairy cattle. J Dairy Sci 53:89–91