Effect of Level of Intake on Digestion, Rate of Passage and Chewing Dynamics in Hay-Fed Bactrian Camels *(Camelus bactrianus)*

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Four female Bactrian camels *(Camelus bactrianus)* were offered a diet of chopped mixed hay, composed predominantly of timothy, at three levels of intake. Digestibility of the hay was measured by total collection and rates of passage using cobalt (III) ethylene diamine tetra acetate and Chromium-mordanted hay. The time spent eating and ruminating per day was ascertained by continuous observation for 24 hours. Results from this experiment indicate that Bactrian camels appear to digest a predominantly grass hay to a similar extent seen with sheep and cattle, but at approximately 1 /4-1 /2 of the dry matter intakes (g/kg BW) observed with the latter species. Increases in daily metabolic faecal out-put and metabolic faecal N per kg DM intake compare favourably with ruminant data. Total mean retention (TMR) time of liquid and particulate markers was quite long but fall within a range exhibited by domestic ruminants fed restricted levels of roughages. The long TMR values were due to very long intestinal transit times. Fractional turn-over rates in the forestomachs and caecum-proximal colon were higher than would be expected for cattle at similar intakes. The observed relatively large changes in passage parameters but small depressions in digestibility with increasing intake are similar to that seen with sheep or cattle fed hay diets. This experiment also indicates that camels appear to spend an amount of time eating, ruminating or chewing per unit intake that is commensurate with that seen in adult cattle. However, at *ad libitum* (AL) intakes, the maximum amount of time spent ruminating was 5.39 h/d. Since camels possess an efficiency of rumination (min/g) similar to that of cattle but appear to be limited to 5-5.5 h of ruminating per d, the low AL intakes observed may be due to an inability to process highly fibrous forages as well as sheep or cattle.

Key words: Camels, Digestion, Digesta Kinetics, Chewing Dynamics

INTRODUCTION

Members of the family *Camelidae* are a source of food, fuel, fibre and traction in a number of countries world wide, yet little information is available on their digestive capacity. The present study examined the relationship of level of hay intake to digestion, rate of digesta passage and chewing parameters Bactrian camels *(Camelus bactrianus).*

MATERIALS AND METHODS

Four non-pregnant multiparous Bactrian camels (687 ± 55 kg) were used in an unbalanced latin square in which three levels (1 /3, 2/3, or 1/1 of *ad libitum)* of intake were imposed in a randomized sequential manner. A chopped (40-60 mm theoretical cut) mixed grass-legume hay, composed predominantly of timothy *(Phleumpratense),* was used in the study. Table 1 provides the chemical composition of the hay. Apart from mineral and vitamin supplementation, the diets were composed entirely of this chopped hay. Throughout the experiment camels received daily

supplements of 25 g of plain salt and 25 g of a mineral and vitamin supplement top-dressed on the chopped hay. The supplement composition was (as fed basis, g/kg) : Dry matter, 960; Ca, 140.0; P, 140.0; Mg, 40.0; NaCl, 160.0; Mn (mg/kg), 800; Cu (mg/kg), 200; Zn (mg/kg), 1000; Vitamin A (KIU), 88; Vitamin D (KIU), 30. Animals were fed twice daily at 09:00 and 16:00.

Each period lasted 21 days, with the first 7 days being used to establish AL intake, followed by 14 days on the assigned level of intake. Data collection for digestion (total collection) and rate of passage studies was accomplished during days 15 to 21, whereas chewing data was collected on days 20 to 21. Representative samples of faeces were collected daily and stored at -20 C prior to pooling (within period and animal), homogenizing, subsampling and sampling for dry matter (DM) determinations at the end of each period. Subsampled faeces were freeze dried prior to grinding (1 mm) and chemical analysis.

Dry matter determinations were conducted by drying material in a forced draft oven at 105 C for 24 h. Organic Matter (OM) was ascertained by dry-ashing at 550 C for 12 h. Neutral detergent fibre (NDF), acid detergent fibre (ADF), Lignin (72% H2SO4 or Klasson lignin), NDF bound N (NDFN) and ADF bound N (ADFN) were assayed as per Robertson and Van Soest (1980). Total nitrogen (N), and N in NDF and ADF was determined with a Kjelfoss Automatic 16210 Nitrogen Analyzer (Foss America Inc., Fish kill, NY) following procedures outlined by the AOAC (1984). Gross energy (GE) was measured using an adiabatic oxygen calorimeter (Parr Instrument Company, Moline, IL). Cell wall constituents were expressed as ash free NDF, ADF or Lignin. Neutral detergent solubles (NDS) were estimated by subtracting NDF values from 100%, hemicellulose (HCEL) by subtracting ADF from NDF, and cellulose (CEL) by subtracting Lignin from ADF. Under the assumption that all dietary neutral detergent soluble matter is fermented by foregut microbes and/or digested by the host animal, faecal output of NDS and NDSN were used as estimates of metabolic faecal output (MFO) and metabolic faecal N (MFN) production, respectively (Mason, 1969; Van Soest, 1982).

Chromium III mordanted cell wall (Cr-Hay, 52.9 g Cr/kg) and the Na salt of the monovalent cobalt ethylene diamine tetra acetic acid (Co-EDTA) anion (Uden et al., 1980) were used as particulate and liquid markers, respectively. One hundred grams of both Cr-Hay and Co-EDTA sprayed hay (Co-Hay g, 28, *Co/kg)* were mixed with 300 g of the a.m. meal and offered to the camels on day 15. Faecal samples were obtained from 10 to 170 hours post-dosing. Co and Cr concentrations in markers and oven-dried faeces were determined by the analysis of 51Cr and 60CO activities induced by neutron irradiation (Mineralogical Association of Canada, 1980). Faecal excretion curves of Cr and Co were analyzed by utilizing a model consisting of two exponential terms and a time delay (Grovum and Williams, 1977) of the form:

$$y = Ae^{-K1-(t-TT)} - Ae^{-K2(t-TT)}$$

for t > = TT and y = 0 for t < TT. Where y is Cr or Co concentration (mg/kg) in faeces, A is a scale parameter, t is sampling time (h post dosing marker) , TT is transit time or time of first marker appearance in the faeces (h), K^1 the fractional rate of turn-over of marker in the reticulorumen (C1/C2 in the camels) and K^2 is the fractional turn-over rate of marker in the caecum and proximal colon. The aforementioned parameters were estimated by fitting the model to marker excretion curves using a least squares, non-linear regression procedure (PROCNLIN,

iterative Marquardt method; SAS, 1982) described by Colucci (1984). Mean retention time in the different mixing pools was calculated to be 1/K. Total mean retention time of marker in the entire gastrointestinal tract was calculated as the sum of mean retention times of all gut segments (TMR = $1/K_1 + 1/K_2 + TT$) (Grovum and Phillips, 1973; Warner, 1981). It must be stressed that attributing K_1 to C1 /C2 and K_2 to the caecum and proximal colon of camels has not been conclusively justified from past research (Heller et al., 1986).

The time spent per day by each animal in eating (EATT, min/d) and ruminating (RUMT, min/d) was ascertained by 24 h continuous observation by two researchers working in shifts. Total amount of time spent chewing (CHEWT, min/d) was calculated as EATT + RUMT. A Tandy 102 portable microcomputer (Tandy Electronics Ltd., Barrie, Ontario, L4M 4W5), using software written in BASIC, was used to facilitate observational data acquisition. In addition to time spent eating and ruminating, the number of chews per ruminated bolus was ascertained on 30 different occasions, within a given period and animal, during the 24 h observation.

A multiple regression approach was adopted in the statistical analysis of the data. Animals and periods were class variables and animal intake, within period, be it DM or intake of a particular nutrient fraction, was a continuous variable. The GLM procedure of SAS (1982) was used to fit a model of the form:

$$Y_{ij}=\mu + PERIOD_i+ANIMAL_j +B_1\ INTAKE + E_{ij}$$

Where:

- Y_{ij} = the response variable value (observation in the ith period on the jth animal consuming a given amount of feed, Intake).
- μ = overall population mean.
- $PERIOD_i$ = overall period effect.
- $ANIMAL_j$ = overall animal effect.
- B_1 = the linear regression coefficient of intake on Y.
- INTAKE = intake of a particular nutrient fraction in kg/day, g/Kg BW/day, Mj GE/day or Kj GE/Kg BW/day.
- E_{ij} = random error associated with ijth observation.

Assumptions:

- 1) $E_{ij} = N\ (O,\sigma)$.
- 2) PERIOD, ANIMAL and INTAKE effects are additive.

A quadratic model which included the term B_2 INTAKE2 was also fitted to the data using the GLM procedure of the SAS (1982). Where B_2 is the quadratic regression coefficient of intake on Y and INTAKE is as previously defined.

A simplified version of the above models is presented in the text of the present paper and was arrived at as follows:

a = intercept (μ) + $1/3\sum$ Period; + $1/4\sum$ $Animal_j$ and
$y = a + B_1$ INTAKE ($+8_2$ $INTAKE_2$),

where:

Y, $PERIOD_j$ and $ANIMAL_j$ are as previously defined.
a = a combined intercept that includes the overall mean, or intercept, and the effects of PERIOD and ANIMAL.

In interpreting the equations presented in this paper the reader is reminded that r^2 values presented with the regressions pertain to the full model, that is to say animal and period variation have been taken into account. For this reason r^2 values may seem overly large. Also, when the influence of rate of passage parameters on digestibility was investigated, a similar approach to that discussed for the effect of intake was used except that the passage parameter was substituted for the intake term.

For the examination of AL intake data obtained within the first week of each period, a model of the form AL intake = U + $PERIOD_j$ + $ANIMAL_j$ + E_{ij} was fitted using PROC GLM of SAS (1982), with model parameters as previously defined. Variance analysis of the assigned DMINT was accomplished following similar procedures except that a treatment effect was included, where treatments were: 1/3, 2/3, or 1/1 of AL intake.

RESULTS

Dry Matter Intake.

Average ad libitum DM intake (ALDMINT) for the experiment was 4.10 (SE 0.247) kg/day or 5.85 (SE 0.377) g/kg BW/day and the average assigned DMINT for the trial was 2.60 (SE 0.228) kg/day or 3.72 (SE 0.293) g/kg BW /day. The effect of treatment was significant at $p < 0.10$, intake (kg/d) means being: 1/3 AL, 1.63; 2/3 AL, 2.65; 1/1 AL, 3.53; SE 0.455.

Digestibility Data

Table 2 provides the experimental means of the digestibility data. With the exception of HCEL, there was no significant ($P > 0.10$) effect of increasing intake on the digestion coefficient of a particular fraction. However, the linear regression coefficients for the effect of increasing intake on digestibility, while not significant, were negative for DM, OM, NDFN, NDF, ADF, CEL, and LIG. The coefficient of variation (CV) for DM digestibility in this trial was 1.63%, whereas that for LIGDIG was 43.83%. Lignin digestibility ranged from -0.11 to 0.20.

The significant ($P < 0.10$) linear effect of level of intake (kg HCEL/day) on hemicellulose digestibility (HCELDIG) was described by the equation HCELDIG = 0.685-0.066 (HCELINT); $r^2 = 0.738$. When HCELINT was expressed as g/kg BW /day (HCELINT1) there was also a significant ($P < 0.05$) linear effect on HCELDIG described by: HCELDIG = 0.690-.054 (HCELINT1); $r^2 = 0.791$. There were no significant ($P > 0.10$) quadratic effects of intake on digestibility.

Dry matter intake had a highly significant ($P < 0.001$) linear influence on daily MFN production. The relationship of MFN to DMINT (kg/d) was described by: MFN = 0.001 + 0.006 (DMINT); r^2

= 0.989. When MFN was regressed against DMINT expressed as g/kg BW /day (DMINT1), a similar significant ($P < 0.001$) relationship was described by MFN = 0.001 + 0.004(DMINT1); r^2 = 0.981. The quadratic term ($DMINT1^2$) resulted in a marginal reduction in the error mean square (data not shown). Dry matter intake (kg/d) also had a significant ($P < 0.001$) linear effect on MFO given by: MFO=0.0163+0.1465(DMINT); r^2=0.988. Again, when MFO was regressed against DMINT1 (g/kg BW) a significant ($P < 0.001$) linear relationship was observed: MFO = 0.0096 + 0.1 043 (DMINT1); r^2= 0.983.

Increasing DMINT (kg/day) had a significant ($P < 0.05$) linear effect on faecal DM concentration (FECDM; g/100g) described by the equation: FECDM=45.304-3.956(DMINT); r^2=0.790. An opposite effect ($P<0.10$) of intake was observed on faecal OM content (FECOM; g/100g DM): FECOM = 88.882 + 0.507(OMINT); r^2 = 0.763. Average faecal concentrations of DM and OM for the experiment were 35.01 (SE 1.116) g/100g and 90.12 (SE 0.167) g/100g DM, respectively.

Rate of Passage Data

The 2-compartment model of Grovum and Williams (1973) appeared to fit marker excretion data adequately (Co, average r^2 = 0.974; Cr, average r^2 = 0.954). Table 3 provides the experimental means of the rate of passage data using DMINT (kg/d) as the regressor variable. Average values of mean retention time (h) in C1/C2 ($1/K_1 = R_1$), caecum-proximal colon ($1 /k_2 = R_2$) and both mixing compartments ($R_1+R_2=R_{mix}$) were (SE): CoR_1 16.81 (0.504); CoR_2, 9.72 (0.737); COR_{mix}, 26.53 (0.857); CrR_1 27.97 (1.118); CrR_2, 22.83 (1.258); CrR_{mix}, 50.80 (1.906). Increasing DMINT significantly increased CoK_1 ($P < 0.05$) and CoK_2 ($P < 0.10$) and reduced CoTT ($P<0.01$), CoTMR ($P<0.01$) and CrTMR ($P<0.05$). Although not significant ($P > 0.10$) , the effect of intake on CrK_1 , CrK_2 and CrTT followed a similar trend to that of the corresponding Co parameters. CrTMR and CoTMR exhibited coefficients of variation of 8.25% and 7.96%, respectively, when DMINT (kg/d) was used as the regressor variable in the linear regression. Table 4 presents linear regression equations describing the effect of intake on the various passage parameters for liquid and particulate markers. Table 5 provides the corresponding significant ($P < 0.10$) quadratic equations. Linear regression equations were generally superior at describing intake effects on passage. Also, liquid passage parameters appeared to be more sensitive to changes in intake than their particulate counterparts. However, consistently significant ($P < 0.05$) linear declines for liquid and particulate TMR were observed when either DMINT (kg/d) or DMINT1 (g/kg BW) were used as regressor variables.

Chewing Behaviour

Experimental means for EATT , RUMT, CHEWT, RCHEW and parameters calculated from EATT , RUMT or CHEWT as they relate to intake are presented in table 6. Increasing DMINT (kg/d) significantly increased EATT ($P<0.01$), RUMT ($P<0.01$), CHEWT ($P<0.01$) and RCHEW ($P<0.05$) in a linear fashion. Table 7 presents linear regression equations describing the relationship between intake of DM or NDF and EATT, RUMT, CHEWT or RCHEW. Of the mastication behaviours examined in the present study, RUMT exhibited only marginally significant ($P < 0.10$) quadratic trends when regressed against DM and NDF intake (g/kg BW), however, CHEWT showed significant ($P < 0.05$) quadratic effects when regressed against any of the intake variables. Table 8 presents the significant ($P < 0.10$) quadratic regressions for RUMT

and CHEWT. The CV for EATT was 19.19%, for RUMT 20.69%, and for CHEWT 16.02% when DM intake (kg/d) was used as the regressor variable in the linear regression.

DISCUSSION

Intake

The average AL intake exhibited by camels in the present study is substantially lower than that generally reported in the literature. The closest literature value appears to be that provided by Foose (1982) who observed two Bactrian camels to consume a timothy hay at 8.6 g OM/kg BW. Values for Dromedaries on grass roughages include 8.8 g OM/kg BW provided by Foose (1982) and 9.8 g DM/kg BW obtained by Farid et al. (1980). Foose (1982) also observed mature sheep and cattle to consume a timothy hay at 9.8 and 10.1 g OM/kg BW respectively. Calculations based on data provided by the NRC (1975, 1984, 1987) for ruminants suggested that DM or DE intakes observed with the camels in the present study were 40 to 50% of those that would be expected with domestic sheep or cattle offered a similar hay. The findings of this trial appear to concur with the conclusion of Foose (1982) that camel ids exhibit lower AL DM intakes than true ruminants of similar body weights. A possible explanation for the low intakes observed in some studies with camels is the suggestion that camelids may possess slower fasting metabolic rates than predicted by the interspecies generalization 70BWo.75 (Engelhardt et al., 1975; Zine Filali and Guerouali, 1994).

Digestibility

Bactrian camels in Foose's (1982) study exhibited higher digestion coefficients than we observed while consuming a greater amount of a timothy hay similar in composition to the one used in present study. Based on information obtained over a variety of forages fed to domestic ruminants, the NDF, cellulose, and hemicellulose apparent digestibilities obtained in the present study are higher than average, but occur within observed ranges (Van Soest, 1982). The digestibility of cellulose in this trial compares favourably with results obtained by Thomas and Campling (1977) for sheep and cows consuming a rye grass at 6.35 and 7.62 g DM/kg BW. Cell wall digestibility in the present experiment was much higher than that reported by Uden and Van Soest (1982) for sheep, goats and heifers fed a timothy hay at maintenance levels of intake. However, these authors determined that digestive capacity increased with BW, and DM digestibility data for large heifers in their study were similar to those we obtained with the camels. Results from the present trial support the conclusions of Foose (1982) that digestive capability of camels may be higher than that observed in true ruminants but at the expense of lower intakes.

Increases in intake have been associated with digestibility depression in sheep (Blaxter et al., 1956; Leaver et al., 1969; Riewe and Lippke, 1970) and cattle (Makela, 1956; Leaver et al., 1969). However, with the exception of hemicellulose, level of intake did not significantly alter digestibility in the present trial. Other trials examining the relationship between intake and digestibility have also proved inconclusive or confusing owing to the small responses (often no larger than 2 to 4 percentage units) that are difficult to detect (Van Soest, 1982). Undoubtedly, the low AL intake levels we observed contributed to the nebulous response of digestibility to changes in intake. With forages, the majority of DM digestibility depression can be accounted for by the cell wall and the more potentially digestible the cell wall, the greater the potential for

digestibility depression (Riewe and Lippke, 1970; Van Soest, 1982; Mertens, 1986). It is, therefore, not surprising that hemicellulose exhibited a decline in digestibility with increasing intake as it represents part of the potentially digestible cell wall. That significant effects of intake on cellulose digestibility were not observed may be due to the observation that, in ruminants, most cellulose is digested in the rumen, but a substantial portion of hemicellulose escapes the rumen to be fermented in the lower tract (Waldo, 1969; Van Soest, 1982). Furthermore, in the present study, level of intake had a relatively greater effect on fractional turn-over of markers in the hindgut than in the forestomach; possibly explaining why hemicellulose digestibility, but not cellulose digestibility, was influenced by level of intake.

Excretion of Metabolic Faecal Matter

Van Soest (1982) suggested that over a variety of forages, the daily MFO (Kg) is given by 0.15 (DMINT; Kg) -0.3; $r = 0.95$, $p < 0.01$. The slope of this equation for domestic ruminants is identical to that obtained in the present study. In a trial utilizing a timothy hay similar to the one utilized in this experiment, Uden and Van Soest (1982a) determined that the MFO expressed as a proportion of DMINT (kg/d) gave similar values for cattle, sheep, goats, equines and rabbits (0.085 to 0.118). A value of 129.6 g MFO/kg DMINT was cited by Petit et al (1985) for Hereford steers consuming a variety of roughage diets. The MFO of Bactrian camels would appear to be quite similar to that of domestic ruminants.

Faecal excretion of N is typically the greatest source of N loss to a ruminant (NRC, 1985). From a summary of 75 different trials with both cattle and sheep fed dry roughages, the NRC (1985) suggests a MFN output of 4.8 g/kg DMINT. The value obtained in the present trial (6 g/kg DMINT) compares favourably with that cited by the previous authors; the 1.2 g/kg DMINT difference may be due to the observation that highly fibrous diets stimulate the faecal excretion of water soluble and endogenous N in both sheep and pigs (Mason, 1984). The study of Petit et al (1985) with cattle reported 5.74 g/kg DMINT while Foose (1982) obtained values of 3.52 g/kg DMINT for cows and 4.27 g/kg DMINT for sheep consuming a timothy hay at approximately 10 g DM/kg BW. Again, the conclusion reached is that camels appear to be similar to domestic ruminants in their excretion of MFN.

Faecal Concentrations of Dry Matter and Organic Matter

The significant decrease in DM content and increase in OM content with increasing DMINT (kg/d) in the camel faeces of this study have been observed to occur with sheep (Blaxter et al, 1956; Riewe and Lippke, 1970). However, the mean of 35% DM that we report is substantially lower than that cited by Vagil (1985) (48%) or Bhattacharya et al (1988) (49%) for Dromedary camels with ad libitum access to water.

Rate of Passage of Digesta;
Comparison with Other Studies Conducted on Camelids

Studies in which camelids have been fed fibrous grasses have reported a range of particulate TMRs similar to ours (70-99 h) (Foose, 1982; Heller at al. , 1986b). A noticeable exception is the work of Maloiy (1972) whose particulate TMR was about half of that observed in the present study.

The studies of Heller et al.(1986a) with Llamas and Heller et al (1986b) with Dromedary camels attempted to partition mean retention time of particulate matter to different sites within the gut. Mean retention time within C1/C2 of Bactrian camels in the present study (28 h) was half of that observed for the Dromedary research, being closer to that obtained by Heller et al. (1986a) for large hay particles in llamas fed a diet of 0.25 to 0.33 concentrate. Mean retention time in the intestines with the Dromedary study was calculated by subtracting C1/C2 MRT from the TMR and is presumably equivalent to the present $1/k_2$ + TT. However, these values for Dromedaries are more equivalent to the values of TT we observed (28-45 h). An average value for $1/k_2$ + TT for our Bactrian camels would be 22.8 + 34.3 = 57.1 h. Heller et at. (1986b) do not provide data on feed intake, making it difficult to identify factors responsible for providing a similar particulate TMR but different C1 /C2 and intestinal MRTs.

Mean retention time of a liquid marker in the gastrointestinal tract was similar in our Bactrian camels (50 h) to obtained with Dromedaries (52.9 h) by Heller et al. (1986b), fed a fibrous grass diet. Due to the great range in intakes of the present trial (1.55 to 5.88 g DM/kg BW) the range for CoTMR was 36-72 h; the lowest value of 36 h (corresponding to the highest intake) being the same as that obtained by Heller et al. (1986a) for llamas consuming a mixed diet at approximately 10-15 g DM/kg BW. In contrast to the shorter particulate R_1 obtained in our study relative to that obtained by Heller et al. (1986b), our average liquid R_1 was longer than their equivalent values. However, the range of our data (10-27 h) does include that reported by the previous authors (12-17 h). The value of 6.3 h obtained for a Dromedary by Maloiy (1972) is lower than presently observed, possibly due to a higher feed intake (g/kg BW). The intestinal MRT for a liquid marker reported by Heller et al. (1986b) is similar to our $1/CoK_2$ + CoTT = 33 h.

The comparison of the present data with that from other trials using camelids of lighter BW, higher feed consumption, different markers, sampling technique and mathematical analyses of marker excretion curves possesses its shortcomings. However, with the exception of the study by Maloiy (1972), it would appear that the Bactrian camels of the present study possess liquid and particulate TMRs which are similar to studies with other old world camelids fed dry grass roughages. In conclusion, retention times of liquid in any of the gut compartments of camels appears to be shorter than the corresponding particulate phase values. This observation concurs with marker kinetics in other foregut-fermenting herbivores (Warner,1981).

Comparison with Cattle and Sheep Data

In summarizing data from rate of passage trials, Warner (1981) provides average values for the total MRT of particulate matter in sheep (47.4 ± 26.5 h) and cattle (69 ± 28.2 h). These values are lower than that observed in the present experiment. However, in a summary of 5 studies using sheep fed all roughage diets at a fixed level to maintain BW, Warner (1981) reported the average TMR to be 85 (SE 16) h. Blaxter et al (1956) found the TMR of stained grass particles in sheep fed 600 g long grass hay/d to be 103 h. Also at low levels of grass hay intake (6.35 g/kg BW), Thomas and Campling (1977) observed sheep TMRs of 89 h. Although these studies represent extremes in low intake for sheep, they suggest that at the low intakes observed in our camels, TMRs between these two species might be similar. Recalculation of data presented by Makela (1956), using data from 9 cows with an average dry matter intake of 6.6 g/kg BW (2.40-4.14

kg/d) provided a lignin TMR of 103 h. Thomas and Campling (1977) also discovered long TMRs (79 and 89 h) with cows consuming 7.15 or 7.62 g DM/kg BW. These data also suggest that camels in our study exhibited TMR data similar to that of ruminants at low intake.

TMR data for liquid in sheep has been reported at 38 and 54.5 h (Grovum and Williams, 1977; Uden et al, 1982), for goats at 28 and 39 h (Uden et al, 1982; Quiroz et al, 1988) and for large (28 h) and small (30 h) heifers (Uden et al, 1982). The aforementioned values are substantially less than the 50 h obtained with Bactrian camels in the present study.

A review of cattle data by Owens and Goetsch (1986) indicates that, at intakes below 12.5 g/kg BW, roughage K, values average 0.018 h-' (29 observations). Values of K_1Cr for the present study are double that reported by the previous authors. Chromium K, values for the camels more closely approximated average roughage values of 0.039 h-' (26 observations) cited by these authors for cattle at intakes of 17.5-22.5 g/kg BW.

Narrowing the comparison to studies in which rations consisted predominantly of dry roughages fed at restricted levels to sheep, rumen particulate turnovers were 0.029 to 0.052 h^{-1} (Blaxter et al., 1956; Grovum and Williams, 1977; Varga and Prigge, 1982; Van Bruchem et al., 1984). At relatively high levels of intake, Uden et al (1982) observed rumen particulate turn-overs of 0.037 in sheep 0.038 h^{-1} in goats. From these observations it would appear that the average fractional turn-over of particulate marker in C1/C2 of our camels falls within the range of that for small ruminants at low intake, but that the K_1 values per unit intake might be higher. Recall that the camels exhibited an average CrK_1 of 0.037 h^{-1} at an average intake of only 3.72 g/kg BW.

A similar review of data for cattle offered unsupplemented grass hays obtained rumen particulate turn-overs of 0.014 to 0.041 h^{-1} (Poppi et al., 1981 b; Uden et al., 1982; Prigge et al., 1984; Miller and Muntifering, 1985; Fleck et al., 1988; Stokes et al., 1988). A recalculation of data from Makela (1956) with 9 cows at low intake provides a rumen lignin MRT of 73.4 h or a K_1 of 0.014 h^{-1}. It would appear that the particulate K_1 values for camels tend to be greater than those for cattle consuming dry roughages at low to moderate levels of intake. Similar to the conclusion made from data with sheep, the K_1 per unit intake for camels would appear to be much greater than that for cattle.

From a review of studies utilizing compartmental analysis, Warner (1981) determined an average ratio of rumen MRT to TMR to be 0.47 for sheep and 0.57 for cattle. Equivalent data for the camels would be 0.33, indicating that C1/C2 may not, quantitatively, play as important a role in digestion as the reticulo-rumen in true ruminants.

Van Soest (1982) suggests a range of liquid K_1 of 0.05 to 0.15 h^{-1}. Owens and Goetsch (1986) present an average value for cattle consuming less than 12.5 g/kg BW of 0.044 h^{-1}. Values for forage fed sheep and goats ranged from 0.038 to 0.073 h^{-1} (Grovum and Williams, 1977; Poppi and Minson, 1980; Uden et al., 1982; Varga and Prigge, 1982; Prigge et al., 1984; Van Bruchem et al., 1984). Equivalent values for cattle ranged from 0.056 to 0.075 h^{-1} (Poppi and Minson, 1980; Uden et al., 1982; Prigge et al., 1984; Stokes et al., 1988). Our values were greater than the average value for cattle at low intake reported by Goetsch and Owens (1986) , being closer to

their values (0.062 h^{-1}) for animals at intakes of 12.5 and 17.5 g/kg BW. However, the present values fell within the range of those reported in studies with both sheep and cattle fed roughages.

A review by Hoover (1978) suggests that mean retention of digesta in the hindgut of sheep may range from 29 h at an intake of 400 g/d to 10.5 h at intakes of 1200 g of forage/d. Values for liquid and particulate K_2 in sheep have been reported by Grovum and Williams (1977) to be 0.097 and 0.083 h^{-1} for sheep at low intake and by Van Bruchem et al. (1984) to be 0.103 and 0.041 h^{-1}. Additionally, Blaxter et al (1956) present values for particulate turnover in the hindgut of 0.031 to 0.038 h^{-1} for intakes ranging from 600-1500 g/d. Poppi and Minson (1980) also provide liquid K_2 values for sheep (0.303 h^{-1}) and cattle (0.181 h^{-1}). Again, the data for camelids appears to fall within the range of that for domestic ruminants.

The last passage parameter to be investigated was TT, or time for first marker appearance in the faeces. Published data for particulate TT indicates ranges of 11 to 36 h for sheep and goats (Blaxter et al., 1956; Grovum and Williams, 1977; Uden et al., 1982) and 13 to 28 h in cattle (Uden et al., 1982; Colucci, 1984). Equivalent data for liquid TT in sheep and goats was 10 to 17 h (Grovum and Williams, 1977; Pappi and Minson, 1980; Uden et al., 1982) and 10 to 12 h for cattle (Poppi and Minson, 1980; Uden et al., 1982). Apart from data for the stained hay of Blaxter et al (1956), the camel values of TT for both liquid and particulate markers are much longer than the equivalent ruminant data, suggesting the possibility of differences in the length and/or motility of the intestines. The long TT values are also probably a direct result of the very low intakes. There is also an indication that the relative differences in particulate TT and liquid TT are much larger in the camels. However, this again maybe due to the very low intakes; slight differences between particulate and liquid TT data at the relatively high intakes observed in sheep and cattle may be amplified at the low intakes seen in the camels.

Effect of Level of Intake on Passage Parameters

The reduction of CrTMR presently observed with the camels is in agreement with that observed for sheep and cattle fed all-forage diets (Blaxter et al, 1956; Makela, 1956; Grovum and Williams, 1977). Simple linear regressions of particulate TMR on intake of long hay derived from data presented by Blaxter et al (1956) yielded the following equation: TMR(h) = 121.7 - 38.52 (DMINT; kg), r =-0.96. A similar examination of treatment means presented by Grovum and Williams (1977) provided: TMR (h) = 67.60 -1. 54 (DMINT1 , g/kg BW), r = -0.98. Manipulation of raw TMR data from cows consuming 4.40-8.66 g/kg BW (Makela, 1956) yielded: TMR(h) = 188.16 -12.79 (DMINT1; g/kg BW), r=-0.862. The slope of the regression of TMR on intake (g/kg BW) in the camels (-6.38; $p < 0.05$) lies between the values presented by Grovum and Williams (1977) for sheep and Makela (1956) for cattle.

Few studies have examined the effect of intake of forage diets on TMR of liquid markers in the ruminant gut. However, calculations from the study of Grovum and Williams (1977) with sheep indicate that they observed a decline in liquid TMR with increasing intake (TMR(h) = 63.95-1.561 (DMINT1, g/kg BW), r=-0.985), but that their slope was substantially less than that observed for the present trial (-7.25; $P<0.001$). Although linear effects of intake on CrK_1 were not significant ($P>0.10$), there was a significant ($P < 0.05$) quadratic increase when DMINT (kg/d) was utilized as the independent variable (table 5). Increases in fractional turn-over of liquid and particulate markers in the rumen are generally observed in ruminants when intake is

elevated (Evans, 1981 a,b; Warner, 1981; Van Soest, 1982; Owens and Goetsch, 1986). Owens and Goetsch (1986), utilizing data of Makela (1956) and Paloheimo and Makela (1959), determined that as intake increased rumen volume of cattle increased but that this increase possessed a quadratic component; rumen volume and DM content of the digesta increased to a greater extent at higher intakes. These authors suggest that an increase in K_1 was responsible. A similar rational maybe responsible for the non significant linear but significant quadratic increase of CrK_1 with intake (kg/d) observed in the present trial.

Evans (1981 a) presents significant ($P < 0.05$) simple linear regressions describing the effect of dry matter intake on particulate K_1 for sheep ($K_1 = 0.0242 + 0.00119$ (DMINT1, g/kg BW), $r = 0.479$) and for cattle ($K_1 = 0.02960 + 0.00037$ (DMINT1, g/kg BW), $r = 0.281$). Although the effect of DMINT1 on CrK_1 was not significant, the regression coefficient in our experiment (0.0015) is similar to that described by the previous authors for sheep. Similar regressions for sheep have been calculated from data presented by Grovum and Williams (1977) ($K_1 = 0.0214 + 0.0018$ (DMINT1, g/kg BW), $r = 0.981$). A similar regression utilizing data from Makela (1956) with cows at low forage intake provided: $K_1 = 0.0018 + 0.0020$ (DMINT1, g/kg BW), $r = 0.790$. The two regressions possess similarities with those described for the camels in table 4. The quantitative significance of these similarities is difficult to assess, but there appears to be an indication that the fractional turn-over of particulate markers in C1/C2 of camelids responds to intake in a similar manner to that in domestic ruminants. It has already been mentioned that the effect of intake on fluid K_1 is similar to that for particulate K_1, indeed Evans (1981 b) and Goetsch and Owens (1986) indicate that this relationship is quantitatively more positive. Results from the present trial concur with the above given the significant linear (kg/d or g/kg BW) and quadratic (kg/d) effects of dry matter intake on CoK_1. Evans (1981 b) present regressions for sheep ($K_1 = 0.03734 + 0.00171$ (DMINT1, g/kg BW), $r = 0.610$) and cattle ($K_1 = 0.04413 + 0.00172$(DMINT1, g/kg BW), $r = 0.715$). A similar regression was calculated from data presented by Grovum and Williams (1977) for sheep ($K_1= 0.0185 + 0.0023$ (DMINT1, g/kg BW), $r=0.999$). Again, these regressions offer similarities with corresponding data obtained with the camels (table 4), most noticeably as concerns the intercept for cattle obtained by Evans (1981 b). However , the regression coefficient obtained with the camels was 2-3 times greater than that for the aforementioned studies, implying that fractional turn-over of liquid in the forestomach of camels maybe more sensitive to intake perturbations than that of domestic ruminants. Inclusion of a regression coefficient (positive relationship) for proportion of forage in the diet improved the prediction of fluid K_1 in the cattle equation of Evans (1981 b), suggesting that the regression coefficient for the effect of intake would probably be closer to that which we observed if only studies utilizing all forage diets had been considered by this author. Never-the-less, Evans (1981 b) concluded that feed intake was the major dietary factor that affects rumen liquid turn-over in both sheep and cattle. This author associated this phenomenon with the observation that water intakes generally parallel dry matter intakes. The positive relationship between intake and time spent chewing causing concomitant increases in saliva production has also been implicated in the changes seen in liquid K_1 values (Owens and Goetsch, 1986).

Passage rates within the post-ruminal gut are elevated with increasing intake (Hoover, 1978; Warner, 1981); these changes are proportionately greater in the hindgut (Warner, 1981). However, in the present study, CrK_2 values were not significantly ($P > 0.10$) influenced by intake, whereas CoK_2 values were linearly depressed when regressed upon DMINT (kg/d; $p < 0.10$)) or DMINT1 (g/kg BW; $P < 0.05$). A marginally significant quadratic component ($P < 0.10$) was also

evident when CoK_2 was regressed against DMINT (kg/d). Never-the-less, the linear regression coefficients for CrK_2 were 2.6 and 3.1 times greater than the corresponding CrK_1 coefficients when intake in the regressions was expressed as either kg/d or g/kg BW, respectively. Similar values for CoK_2 relative to CoK_1 were 3.7 and 3.8. These observations may indicate that, similar to ruminants (Warner, 1981), fractional turn-over rates within the caecum and proximal colon are quantitatively more sensitive to changes in intake than turn-over in the forestomach.

Influence of Passage Parameters on Digestibility

In order to quantify the effect of digesta passage on digestibility, the digestibility of different chemical fractions was regressed against the different passage parameters. Significant ($P < 0.10$) linear regressions are presented in table 9. The only quadratic regression to be significant involved the relationship between NDF digestibility and CoK_2: NDFDIG = 0.6548 -1.2485 (CoK_2) + 3.7254($CoK_2{}^2$), $r^2 = 0.997$. The linear ($P < 0.05$) and quadratic ($P < 0.10$) regression coefficients were significantly different from zero. Although the relationship between retention time and digestibility is well known, few studies have measured both parameters simultaneously and attempted to quantify the relationship (Goetsch and Owens, 1986). Although not significant ($P > 0.10$) , the linear regression coefficient of dry matter digestibility on CrTMR in the present study (0.00048, SE 0.000275) was similar to that described by Makela (1956), using lignin TMR, for hay fed cattle (0.00044). Utilizing data presented by Grovum and Williams (1977) with sheep fed lucerne chaff, regressions of OMDIG on liquid and particulate TMR were calculated: OMDIG = 0.6055 + 0.00093 (liquid TMR), r=0.964 and OMDIG = 0.6092 + 0.00093 (particulate TMR), r = 0.968. These regression coefficients were within the same order of magnitude that we observed and also indicate an identical effect of changing either liquid or particulate TMR on organic matter digestibility. Chromium TMR ranged from 70-99h and CoTMR from 36- 72 h, however, the range in organic matter digestibility in the camels was comparatively small (0.52-0.60). Grovum and Williams (1977) remarked on a similar phenomenon in their study, where retention times within the different sections of the gut were reduced by 50% as intake increased from 400 to 1300 g/d, but apparent organic matter digestibility only declined from 0.657 to 0.631. Makela (1956) reported a similar finding with cattle.

Given that, for forage diets, depressions in overall digestibility are due primarily to ruminal and hindgut escape of potentially digestible cell wall, the present observation that digestibility of the more available cell wall fractions (NDF and hemicellulose) was influenced by a greater number of passage parameters than the less available fractions (ADF and cellulose) may be justified. Without estimates of digestion rates within C1/C2 it is difficult to quantitatively partition the effects of intake on digestibility depression to different parts of the gut. However, CoK_1 appears to have had a significantly ($P < 0.10$) large negative relationship with digestibility of NDF and hemicellulose. A cursory examination of the regressions in table 9 appears to indicate a relationship between certain passage parameters and the digestibility of particular cell wall fractions. Cobalt K_2 was the only parameter to significantly affect both ADF and cellulose digestibility, whereas CrTMR, CrTT and CoK_1 were related to NDF and hemicellulose digestibility. These associations may be related to the relative importance of different sections of the gut to the digestibility of a particular cell wall fraction. For example, most cellulose is considered to be digested in the rumen, but a substantial proportion of hemicellulose escapes the rumen to be fermented in the lower tract (Waldo, 1969; Van Soest, 1982).

Chewing Behaviour

As previously mentioned, a major factor limiting the ALDMINT of ruminants on forage based diets is the accumulation of undigested feed within the reticulorumen. The production of small particles, which can move out of the reticulorumen, is accomplished by chewing during eating and ruminating and possibly cyclical motility or attrition within the foregut, but is also facilitated by microbial activity which weakens the structural cell wall during fermentation (Grovum, 1984). Chewing processes may therefore be important limiting factors in the determination of the rate of passage of digesta and in the control of voluntary intake in forage fed ruminants.

Eating

According to Dulphy et al (1980) the time spent eating is similar between ovines and low producing bovines, but shorter for adult wethers than for growing bulls and milking cows. These authors observed an average of 261 to 350 min/d spent in eating grass hay for wethers (18.6 g DM/BW) and lactating cows (23.1 g DM/BW). A value of 351 min/d was also obtained by Harb and Campling (1985) with non-lactating Friesian cows offered a mature rye-grass hay ad libitum. In a comparative study with cows and wethers consuming 15.5 and 11.2 g DM/BW respectively, eating times of 324 and 373 min/d were obtained by Thomas and Campling (1977). If the regression equation provided in table 7 is used to calculate time spent eating from an average ALDMINT of 4.1 kg/d observed in the present study, a value of 135 min/d is obtained. This is substantially lower than the aforementioned values for domestic ruminants consuming fibrous hay diets ad libitum. However, as previously mentioned, the ALDMINT, on a BW basis, was much lower for the camels than is traditionally observed with domestic ruminants. If corrected for intake, camels in this study ate for 33 min/kg DMINT, which is within the range of 20-40 min/kg DMINT suggested by Balch (1971) for cows consuming medium quality hay. Eating rate (g/min) is known to increase with BW (Thomas and Campling, 1977; Dulphy et al, 1980), and it would appear that Bactrian camels fit into this generalization, exhibiting values similar to those observed in cattle of comparable weight. It is interesting to note that Harb and Campling (1985) obtained a similar CV to the present study for the determination of min eating/d (21.4) when observing 14 cows at 2 min intervals.

Although level of intake did not significantly influence time spent eating per unit of feed (min/kg DMINT or min/kg NDFINT) with camels in the present study, it has been shown to influence eating rate in sheep (Dulphy et al, 1980; Thomas and Campling, 1977) and cattle (Thomas and Campling, 1977; Bae et al., 1981). A reduction in intake usually increases the rate of eating (reduction in min eating/g intake).

Ruminating

Van Soest (1982) postulates that the principal effect of rumination is to collapse and release intercellular spaces within the forage cell walls, thereby reducing the bulk density of ingested material and thus allowing the continued consumption of material. This author suggests that increasing amounts of rumination observed with greater intakes of cell wall may connect rumination to the limiting effects of cell wall upon intake.

As a general rule, sheep and cattle do not ruminate for more than 8 to 0 h/d (Van Soest, 1982; Welch, 1982; Bae et al, 1983), even when fed low quality, low intake potential forage. At an ad libitum DMINT of 4.1 kg/d the camels would be estimated to ruminate for only 5.35 h/d (table 7), even though they were on a fibrous diet. It might be that Bactrian camels possess a lower maximum for time spent ruminating per day, as compared to domestic ruminants. Alternatively, as previously mentioned, the camels may have consumed an ad libitum amount sufficient to meet their daily energy requirements. Given that the camels in this study fall within the range 0.11-0.15 min ruminating/g cell wall observed for cattle (Welch and Smith, 1970) over a variety of roughages, but they are perhaps limited to 5-5.5 h of ruminating/d, they might possibly be classed as restricted ruminators.

Camels are "brazers". A way to reduce the dietary load of unavailable lignified residue is to feed selectively (Van Soest, 1982; Van Soest et al, 1983). These authors suggest that selective feeding is probably the major adaptation of temperate browsers and tropical ruminants. Although the camels in this study were apparently able to digest cell wall fractions to a similar extent as domestic ruminants, their lower ALDMINTS might be due to an intolerance or inability to process (ruminate) highly fibrous forages as well as sheep or cattle. Alternatively, since rumination efficiencies of the camels were similar to those found in cattle of comparable weight, the lower ALDMINTS may be due to a smaller gut capacity in comparison to sheep or cattle. However, digesta contents (as a proportion of BW) in different parts of the camel gut appear to be similar to that found in cattle and sheep (Parra, 1978; Engelhardt and Rubsamen, 1980; Heller et al., 1986b). This observation suggests that camels should be limited due to gut fill, in the consumption of fibrous roughages, to a similar extent as cattle or sheep.

In a comprehensive summary of available data on lambs, goats, mature sheep, heifers of 3 different weight classes, and cows by Welch (1982), increasing efficiencies of rumination (ie. decreasing min/g cell wall) were again found with increasing BW. Body weights ranged from 39 kg for lambs to 561 kg for cows, with the corresponding rumination efficiencies ranging from 2.05 to 0.10 min/g cell wall respectively. The lack of animal numbers precludes any conclusive statements concerning the camels in this study, however, there was a non-significant trend for time spent ruminating/d to increase from the 2 heaviest camels to the lightest camels. A similar trend was also observed for min/kg DM or cell wall intake.

Although the total amount of time spent chewing may not necessarily be influenced by the cell wall content of forages, the efficiency of rumination is known to decrease, presumably because intake of the roughage declines (Dulphy et al, 1980; Balch, 1971). This relationship may possibly be due to a greater difficulty in particle size reduction of more fibrous feeds (Martz and Belyea, 1986). For 60 kg wethers consuming fresh forages, Dulphy et al (1980) report that each percentage increase in crude fibre content decreased voluntary intake by 38 g/d, decreased time spent eating by 4.1 min/d, and increased time spent ruminating by 6.6 min/d. Similarly, Balch (1971), citing results from a number of experiments with cows, reports that the min spent ruminating per kg of DMINT range from 94-133 for oat straw, 63-87 for medium quality hay, 55-74 for good quality hay, and 33-39 for dried grass. The corresponding value for camels in the present study consuming approximately 4.1 kg DM would be 78 min/kg DM. Given the relatively high content of cell wall constituents present in the hay utilized for the present study, it is, perhaps, not surprising that it falls within the range of minutes spent ruminating/Kg observed for medium quality hays.

Increasing levels of intake are generally known to augment the total amount of time that sheep and cattle spend ruminating per 24 h (Welch and Smith, 1969; Bae et al. , 1981). Camels in the present study seem to parallel domestic ruminants in this respect. Bae et al. (1981) observed an increase in min spent ruminating/24 h given by: 37.67 (DMINT, kg) + 105.10, r = 0.997. The slope of this equation is only 1/2 that observed for the camels, however, the intercept in the present study was lower (45.49). This would appear to indicate that Bactrian camels require a higher degree of triturition of feed residues than cattle, however, it must be noted that the cows in the study of Bae et al (1981) were consuming from 4.37 to 8.53 kg DM/d, whereas the DMINT of the camels ranged from 0.95 to 5.65 kg/d. Data for sheep indicate a curvilinear increase in time spent ruminating forages with increasing intake (Bae et al, 1979; Welch et al, 1969). Thomas and Campling (1977) suggest that, at low intakes, sheep ruminate more than cows, whereas at high intakes there is little difference between species (411 and 316 min/24 h for sheep and cows consuming 7.28 and 7.1 5 g DM/BW respectively and 540 and 542 min/24 h at 11. 2 and 1 5.5 g DM/BW). Using the regression equation provided in table 7, intakes of 7.28 and 7.15 g DM/BW in the camels would elicit rumination times of 396 and 389 minutes respectively. The coefficient of variation for the determination of min ruminating/d has been reported as being 9.7% (Dulphy et al, 1980) and 10.5% (Harb and Campling, 1985) for cows fed hay diets ad libitum. The value of 21% obtained in the present trial probably reflects the low number of animals utilized and possibly the presence of an important source of variation that was not taken into account.

Perhaps more important than the total amount of time spent ruminating is the effect of intake on min spent ruminating/kg DM or cell wall. Increasing levels of intake are generally accepted to cause reductions in the min spent ruminating per kg, or, conversely, increase the efficiency of rumination (g/min) , in both sheep and cattle (Welch and Smith, 1969; Bae et al, 1981; Harb and Campling, 1985). No significant change in ruminating efficiency was observed in the present study over a wide range of intakes. The nebulous response obtained in the present trial is probably due to a combination of the limited increase in ruminating efficiency traditionally observed with increasing intakes (Dulphy et al, 1980) and the small number of experimental animals utilized. As previously mentioned, the experimental mean for min ruminating per kg DMINT (92) is similar to that described by Balch (1971) for a medium quality hay. The average value of 0.011 g cell wall ruminated per min per kg BW is lower than the mean reported by Van Soest (1982) (0.02) across a number of large and small ruminants. Dulphy et al (1980) have suggested that reductions of voluntary intake in fibre-challenged animals are caused by a reduction in the time spent eating, but more importantly by decreases in both the eating rate and efficiency of rumination.

Number of Chews and Time Spent Chewing per Bolus

Bae et al (1979) have observed, with hay-fed rams, that as intake increases the number of boluses regurgitated per day and the number of chews/bolus increase. These authors concluded that since the number of boluses increased at a declining rate with intake, an increase in the size of the boli regurgitated is probably what augments the number of chews/bolus when intake increases. Similar results were obtained by Bae et al (1981) for cows fed hay based diets. Bae et al (1979) present a linear regression describing the effect of increasing intake in sheep on the number of chews/bolus: 32.79 + 16.4 (DMINT , kg). The equivalent regression for cows is described by 33.19 + 2.65(DMINT, kg) (Bae et al, 1981). The slope of the latter regression is very similar to

that observed for camels in the present trial (2.37) and may possibly be due to the similarity in BWs for the cows in the study of Bae et al (1980) (695-761 kg) and those for the camels (613-851 kg). The significant ($P < 0.05$) increase in chews/bolus observed in the present trial with increasing intake probably indicates a concomitant increase in bolus size. Although only examined in periods 2 and 3 in a cursory manner (10-20 observations per animal/24 h), the length of the rumination cycles exhibited by the camels also appeared to increase with intake (mean value of 51 sec/cycle). This value is within the range exhibited by wethers (45), ewes (65), and cattle (54), offered long hay diets ad libitum, as reported by Dulphy et al (1980).

Chewing

Several authors (Balch, 1971; Dulphy et al., 1980; Campling and Morgan, 1981) suggest that there is a complementary, reciprocal, relationship between time spent eating and ruminating, such that the total amount of time spent chewing/unit of feed intake is similar for anyone feedstuff. However, in their study with dairy cows, similar to results in the present study, Harb and Campling (1985) found a positive ($r = 0.64$) relationship between time spent eating and ruminating. Never the less, the variation in chewing time is smaller than that observed for time spent eating or ruminating (Balch, 1971 ; Dulphy et al, 1980). This has led to the proposal of a roughage index (total amount of time spent chewing [eating + ruminating]/kg DM) by which the physical property of ruminant diets can be quantitatively assessed (Balch, 1971). This index attempts to define a roughage with regard to its ability to promote optimum rumen function and the general metabolic well-being of the animal. This author suggests the following ranges in chewing (min)/kg DMINT: oat straw, 145-191; medium quality hay, 103-109; good quality hay, 87-105; dried grass, 44-53. Mertens (1986) provides values of 86-108 min/kg DMINT or 139-161 min/kg NDFINT for dried grass hays varying in NDF content from 65-72 g/100g and 153-170 min/kg DMINT or 194-218 min/kg NDFINT for oat straws containing 78-84 g/100g NDF. These observations suggest that chewing/kg NDF increases with increasing concentration of NDF in the forage. Although cattle tend to chew and ruminate a constant amount each day, even with increasing fibre content of the ration (Dulphy et al, 1980), Martz and Belyea (1986) explain the markedly lower ruminating and chewing efficiencies (ie. higher min/kg DMINT) for high fibre diets, to cattle eating less DM and spending less time eating high than low fibre diets. Martz and Belyea (1986) suggest that this relationship is due to a greater difficulty in particle size reduction in more fibrous rations.

In comparison with the observations of Balch (1971) and Mertens (1986) , the roughage index of the present trial (130 min/kg DMINT or 189 min/kg NDFINT) would appear to fall somewhere between that for a medium quality grass hay and straw. Mertens (1986) proposes a regression equation, for cattle consuming long hays, between NDF content (g/100g, X) and chewing activity (min/kg NDFINT, V): $V = 2.59 (X)-19.0$; R-Square = 0.73. The predicted chewing activity for the present hay would be 158 min/kg NDFINT compared to the observed value of 189 min/kg NDFINT. The higher values observed for the camels might be related to their lower intake capacity for forages relative to that of cattle of similar BWs. The experimental values are, however, substantially less than that observed for sheep and goats (545- 725 min/kg DMINT) by Dulphy et al (1980) and that reported by Aitchison et al (1986) (729 min/kg DMINT or 1118 min/kg NDFINT) for sheep (49-60 kg) consuming a coarsely chopped late-cut rye-grass hay at 18 g DM/BW.

Total amount of time spent chewing (min/d) has been shown to increase with increasing level of intake. Thomas and Campling (1977) observed sheep to chew for a total of 500 min/d when consuming hay at 7.28 g/BW and 913 min/d at 11.2 g/BW. The corresponding values for mature, non-pregnant, non-lactating dairy cows were 378 min/d at 7.15 g/BW and 866 min/d at 15.5 g/BW. Similarly, Bae et al (1981) observed an increase in total time spent chewing with increasing hay intake given by: 98.63(DMINT, kg)-57.58, correlation coefficient =0.997; or 152.01 (NDFINT, kg)-58.49, correlation coefficient = 0.996. The value of 93 min for each kg of DMINT observed with the camels is similar to that obtained by Bae et al (1981). However, the total time spent chewing reported by Thomas and Campling (1 977) for cows at a restricted level of intake (378 min/d) is an hour longer than the experimental mean observed for the camels (317 min/d) consuming only half as much DM. The increase in chewing time with increasing intake in the present trial appeared to respond in a significant ($P < 0.05$) quadratic manner, with the increase in CHEWT being less for each successive amount of food consumed. In the case of both time spent eating or ruminating/d no significant quadratic component was observed in their increase with greater intake. The quadratic effect exhibited by CHEWT with increasing intake may be due to the lower incremental increase in time spent eating/d in comparison to time spent ruminating/d.

The roughage index, expressed as min/kg intake, largely eliminates differences from variation in the amount of food consumed and differences from the time of access to food (Balch, 1971). In the present study there was no significant effect of intake on min chewing/kg DMINT or NDFINT. This was also observed by Bae et al (1981) and presumably by Thomas and Campling (1977) for cows. Bae et al (1981) suggest that the constant roughage index indicates that ingested roughages require a constant amount of triturition, either by eating or ruminating.

SUMMARY

Ad libitum DM intakes (g/kg BW) in the present study were much lower than would be expected for sheep or cattle consuming a similar diet. They were also lower than intakes generally observed with other camelid species. Possible reasons for these results have been discussed. One explanation was the possibility that the observed intakes fulfilled the energy requirements of the camels, based on limited data suggesting that camelids and other desert ruminants possess lower fasting metabolic rates than predicted from the interspecies equation of $70BW^{0.75}$. An apparent maximum of 5-5.5 h ruminating per d observed in this study may also indicate that camels are less capable of processing (comminuting) cell wall than ruminants, providing another possible explanation for the low intakes.

Although camels in this study digested feed fractions to an extent also expected with ruminants, they did so at much lower levels of intake than would be seen with the latter species. The relatively insignificant effect of intake on digestibility might be explained on the basis of the low intakes and on the high ADF and lignin content of the diet. Excretion of metabolic faecal matter and metabolic faecal N per unit intake was similar to that from ruminants consuming a high roughage diet.

Although TMR of the markers in the camel gut were similar to that expected of ruminants fed roughage diets at restricted intakes, the fractional turn-over of particulate marker in C1/C2 and the caecum -proximal colon was higher than expected. However, TT was relatively longer than

that generally seen in ruminants. The significant relationships observed between passage parameters and digestibilities were expected given that the effects of intake on digestibility are primarily mediated through rate of passage. However, reductions in digestibility were quite small relative to the effect of intake on rate of passage.

The examination of mastication parameters suggested that Bactrian camels spend a similar amount of time chewing per unit intake as cattle. However, the maximum total amount of time per day spent in ruminating maybe lower for camels than ruminants. The amount of time the camels spent ruminating per day may be related to the fact that they are predominantly a browsing animal. The number of chews per bolus and length of rumination cycles appears to fall within observed values for sheep and cattle.

Results obtained from the present study indicate that future research should be directed at defining the metabolic rate of camelids, the digestive capacity of camels fed browse plant species, the partitioning of digestion and digesta passage to different sections of the camel gut and conclusively ascertaining if camels do possess a maximum total amount of time available for ruminating per day that is lower than ruminants.

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TABLE 1. Chemical composition of experimental hay

Feed Fraction	Concentration (g/Kg)
Dry Matter	901.0
----------Dry Matter Basis--------	
Organic Matter	938.4
Total Nitrogen	22.0
Neutral Detergent Fibre Nitrogen	
Acid Detergent Fibre Nitrogen	2.9
Neutral Detergent Fibre	
Acid Detergent Fibre	472.3
Cellulose	386.3
Hemicellulose	212.0
Lignin	
In vitro rumen 48h digestibility	
Organic matter	0.630
Neutral Detergent Fibre	0.466

TABLE 2. Experimental means for the apparent digestibilty coefficients of different feed fractions in hay-fed Bactrian camels[+]

Feed Fraction	Digestion Coefficient	SEM
Dry Matter	0.543	0.0026
Organic Matter	0.563	0.0030
Energy	0.531	0.0030
Energy (MJ/kg DM)	10.077	0.0572
Nitrogen (N)	0.590	0.0072
Neutral Detergent Fibre-Bound N	0.696	0.0051
Neutral Detergent Fibre	0.571	0.0053
Acid Detergent Fibre	0.537	0.0085
Hemicellulose	0.647*	0.0062
Cellulose	0.633	0.0076

[+] Intake (Kg or MJ/day) of a particular fraction was used as the regressor variable in determining the influence of intake level on digestibility.

* Influence of intake on digestibility was significant at $P<0.10$.

TABLE 3. Mean fractional rates of passage (/h) in the forestomach (K_1) and caecum-proximal colon (K_2), transit time through the intestines (TT, h) and total mean retention time in the gastrointestinal tract (TMR, h) of liquid (Co) and particulate (Cr) markers in hay-fed Bactrian camels[+]

Parameter		Mean	
K_1	Co	0.063**	0.0020
	Cr	0.037	0.0016
K_2	Co	0.115*	0.0100
	Cr	0.046	0.0030
TT	Co	23.6***	
	Cr	34.3	
TMR	Co	50.1***	
	Cr	85.2**	

[+] Dry matter intake (kg/day) was used as the regressor variable in determining the influence of intake on passage parameters.

* $P<0.10$, ** $P<0.05$, *** $P<0.01$

TABLE 4. Linear regression equations describing the relationship between intake and fractional rates of passage (/h) in the forestomach (K_1) and caecum-proximal colon (K_2), transit time through the intestines (TT, h) and total mean retention time in the gastrointestinal tract (TMR, h) of liquid (Co) and particulate (Cr) markers in hay-fed Bactrian camels

Response Variable		Combined Intercept	Linear Regression Coefficient	Intake Parameter	r^2
Cr	K_1	0.0299	0.0024NS	DMINT	0.749
	K_2	0.0309	0.0062NS	DMINT	0.768
	TT	47.146	-4.954NS	DMINT	0.523
		108.058	-8.666**	DMINT	0.865
Co	K_1	0.0464	0.0067**	DMINT	0.939
	K_2	0.0455	0.0246*	DMINT	0.710
	TT	36.727	-5.438***	DMINT	0.940
		75.312	-9.985***	DMINT	0.955
Cr	K_1	0.0307	0.0015NS	DMINT1	0.716
	K_2	0.0299	0.0047NS	DMINT1	0.786
	TT	48.229	-3.798NS	DMINT1	0.577
		108.978	-6.378**	DMINT1	0.886
Co	K_1	0.0450	0.0051**	DMINT1	0.958
	K_2	0.0381	0.0194**	DMINT1	0.785
	TT	36.796	-3.863***	DMINT1	0.925
	TMR	76.030	-7.255****	DMINT1	0.967

DMINT, dry matter intake (kg/d); DMINT1, dry matter intake (g/kg BW).

NS, not significant. * $P<0.10$, ** $P<0.05$, *** $P<0.01$, **** $P<0.001$.

TABLE 5. Significant ($P<0.10$) quadratic regression equations describing the relationship between intake and fractional rates of passage (/h) in the forestomach (K_1) and caecum-proximal colon (K_2), transit time through the intestines (TT, h) and total mean retention time in the gastrointestinal tract (TMR, h) of liquid (Co) and particulate (Cr) markers in hay-fed Bactrian camels

Response Variable	Combined Intercept	Linear Regression Coefficient	Quadratic Regression Coefficient	Intake Parameter	r^2
CrK_1	0.0493	-0.0137**	0.0025**	DMINT	0.971
CoK_1	0.0208	0.0280***	-0.0033***	DMINT	0.997
CoK_2	-0.0678	0.1187**	-0.0148*	DMINT	0.927
CrTT	112.880	-42.493**	4.642**	DMINT1	0.928

DMINT, dry matter intake (kg/d); DMINT1, dry matter intake (g/kg BW/d).

* $P<0.10$, ** $P<0.05$, *** $P<0.01$).

TABLE 6. Mean time (min/d) spent eating (EATT), ruminating (RUMT) or chewing (CHEWT = EATT + RUMT) and number of chews per bolus when ruminating (RCHEW) in hay-fed Bactrian camels[+]

Parameter	Mean	SEM
EATT	96.2**	5.33
RUMT	220.4**	13.17
CHEWT	316.6**	14.64
EATT		
/g DMI	0.038NS	0.0016
/g NDFI	0.056NS	0.0023
RUMT		
/g DMI	0.092NS	0.0061
/g NDFI	0.133NS	0.0080
CHEWT		
/g DMI	0.130NS	0.0063
/g NDFI	0.189NS	0.0082
RCHEW	29.2*	0.80

DMI, dry matter intake; NDFI, neutral detergent fibre intake.

[+]Regressor variable was dry matter intake (kg/d), except for EATT/g NDFI, RUMT/g NDFI and CHEWT/g NDFI when NDFI (kg/d) was used, in determining the influence of intake on mastication parameters.

NS, not significant ($P>0.10$). * $P<0.05$, ** $P<0.01$.

TABLE 7. **Linear regression equations describing the relationship between intake and time (min/d) spent eating (EATT), ruminating (RUMT), chewing (CHEWT = EATT + RUMT) or number of chews per bolus when ruminating (RCHEW) in hay-fed Bactrian camels**

Response Variable	Combined Intercept	Linear Regression Coefficient	Intake Parameter	r^2
EATT	28.19	26.11***	DMINT	0.912
EATT	24.41	19.28***	DMINT1	0.933
EATT	30.47	36.43***	NDFINT	0.904
EATT	25.81	27.30***	NDFINT1	0.928
RUMT	45.49	67.22***	DMINT	0.879
RUMT	37.36	49.20***	DMINT1	0.902
RUMT	48.12	95.58***	NDFINT	0.885
RUMT	37.53	70.99***	NDFINT1	0.913
CHEWT	73.69	93.33***	DMINT	0.924
CHEWT	61.77	68.48****	DMINT1	0.948
CHEWT	78.59	132.01***	NDFINT	0.924
CHEWT	63.34	98.29****	NDFINT1	0.954
RCHEW	22.98	2.37**	DMINT	0.771
RCHEW	23.22	1.59*	DMINT1	0.736
RCHEW	22.95	3.44**	NDFINT	0.787
RCHEW	23.12	2.34*	NDFINT1	0.751

DMINT, dry matter intake (kg/d); DMINT1, dry matter intake (g/kg body weight); NDFINT, neutral detergent fibre intake (kg/d); NDFINT1, neutral detergent fibre intake (g/kg body weight).

* $P<0.10$, ** $P<0.05$, *** $P<0.01$, **** $P<0.001$.

TABLE 8. Significant (P<0.10) quadratic regression equations describing the relationship between intake and time (min/d) spent ruminating (RUMT) and chewing (CHEWT = eating + ruminating)

Response Variable	Combined Intercept	Linear Regression Coefficient	Quadratic Regression Coefficient	Intake Parameter	Statistical Significance of Intake Parameter		
					Linear	Quadratic	r^2
RUMT	-115.59	138.36	-10.91	DMINT1	**	*	0.964
RUMT	-94.84	182.62	-19.64	NDFINT1	**	*	0.969
CHEWT	-57.23	196.39	-16.29	DMINT	***	**	0.975
CHEWT	-98.88	162.13	-11.46	DMINT1	***	**	0.983
CHEWT	-50.93	277.01	-32.30	NDFINT	***	**	0.981
CHEWT	-76.94	216.59	-20.82	NDFINT1	***	**	0.986

DMINT1, dry matter intake (g/kg body weight); NDFINT1, neutral detergent fiber intake (g/kg body weight); DMINT, dry matter intake(kg/d); NDFINT, neutral detergent fiberintake (kg/d).
*P<0.10, **P,0.05, ***P<0.01.

TABLE 9: Significant ($P<0.10$) linear regression equations describing the relationship between liqiuid (Co) or particulate (Cr) fractional rates of passage (/h) in the forestomach (K_1) and caecum-proximal colon (K_2), transit time through the intestines (TT, h) or total mean retention time in the gastrointestinal tract (TMR, h) and digestibility of different fractions in hay-fed Bactrian camels

Response Variable	Combined Intercept	Linear Regression Coefficient	Passage Parameter	r^2
DM	0.5751	-0.6873**	CrK_2	0.987
OM	0.5068	0.0006*	CrTMR	0.972
OM	0.5313	0.0006*	CoTMR	0.973
OM	0.6124	-0.7938*	CoK_1	0.972
OM	0.5976	-0.7608**	CrK_2	0.979
OM	0.5835	-0.1980*	CoK_2	0.974
NDF	0.4931	0.0009**	CrTMR	0.980
NDF	0.5283	0.0008*	CoTMR	0.977
NDF	0.6407	-1.1492**	CoK_1	0.986
NDF	0.6118	-0.9412*	CrK_2	0.980
NDF	0.5989	-0.2869**	CoK_2	0.989
NDF	0.5313	0.0011*	CrTT	0.973
ADF	0.5581	-0.2539*	CoK_2	0.984
HCEL	0.4945	0.0018**	CrTMR	0.911
HCEL	0.7799	-2.0335*	CoK_1	0.848
HCEL	0.5719	0.0023**	CrTT	0.870
CEL	0.6600	-0.2986**	CoK_2	0.983
DE (Mj/kg DM)	9.3718	0.0141*	CoTMR	0.959
DE (Mj/kg DM)	9.4808	0.0260*	CoTT	0.962

DM, dry matter; OM, organic matter; NDF, neutral detergent fibre; ADF, acid detergent fibre; HCEL, hemicellulose; CEL, cellulose; DE, digestible energy (MJ/kg DM).
* $P<0.10$, ** $P<0.05$).