



Review article

Voluntary feed intake and digestibility of four domestic ruminant species as influenced by dietary constituents: A meta-analysis



M.Q. Riaz^a, K.-H. Südekum^{a,*}, M. Clauss^b, A. Jayanegara^c

^a Institute of Animal Science, University of Bonn, Endenicher Allee 15, 53115 Bonn, Germany

^b Clinic for Zoo Animals, Exotic Pets and Wildlife, University of Zurich, Winterthurerstrasse 260, 8057 Zurich, Switzerland

^c Department of Nutrition and Feed Technology, Faculty of Animal Science, Bogor Agricultural University, Jl. Agatis Kampus IPB Dramaga, Bogor 16680, Indonesia

ARTICLE INFO

Article history:

Received 18 May 2013

Received in revised form

11 January 2014

Accepted 13 January 2014

Keywords:

Crude Protein

Digestibility

Fibre

Intake

Meta-analysis

Ruminant

ABSTRACT

This meta-analysis was performed to evaluate whether voluntary feed intake and digestibility of forage-based diets differ between four domestic ruminant species, i.e. sheep, goats, cattle and buffaloes, and secondly, whether dietary constituents, i.e. protein and fibre influence the respective variables. A dataset on voluntary feed intake, digestibility and composition of basal diets and supplements of the respective domestic ruminant species was compiled by pooling data from previously published studies. A total of 45 studies were found to meet the required criteria. Data were analysed by mixed model regression methodology. Discrete (domestic ruminant species) and continuous predictor variables (chemical composition of diet) were treated as fixed effects, while different studies were considered as random effects. Significant linear relationships were observed between log-transformed body weight and log-transformed dry matter intake (DMI) for all ruminant species ($P < 0.05$). Within species, this scaling factor was lower for sheep and goats than for cattle and buffalo. Crude protein (CP) concentration affected DMI of ruminants positively with variations among the species; buffaloes were more responsive to CP, followed by sheep, goats and cattle. In contrast, acid detergent fibre (ADF) negatively influenced DMI across all species except buffaloes, and had a much stronger effect on DMI of sheep and cattle than on DMI of goats. The impact of CP on DM digestibility (DMD) was similar to its influence on DMI. The strongest effect was observed in cattle and was only significant in cattle and buffaloes ($P < 0.05$). Neutral detergent fibre reduced DMD only in cattle, while sheep were positively influenced and goats tended to be positively affected. The ADF lowered DMD in sheep, goats and cattle with significant effect for sheep and goats.

© 2014 Elsevier B.V. All rights reserved.

Contents

1. Introduction	77
2. Materials and methods	77

* Corresponding author. Tel.: +49 228 732287; fax: +49 228 732295.

E-mail address: ksue@itw.uni-bonn.de (K.-H. Südekum).

2.1. Description of database	77
2.2. Statistical analyses	78
3. Results	78
4. Discussion	80
4.1. Relationship between dry matter intake and body weight of animals	80
4.2. Dependency of voluntary dry matter intake of ruminants on dietary constituents	80
4.3. Dependency of digestibility on dietary constituents	81
5. Conclusions	82
Conflicts of interest statement	82
Acknowledgements	82
Appendix. List of references used to construct the data base	83
References	84

1. Introduction

Numerous studies have compared feed intake and digestibility of various nutrients between sheep and goats (e.g. [Abidi et al., 2009](#); [Molina Alcaide et al., 2000](#); [Yañez-Ruiz and Molina Alcaide, 2008](#)) and between sheep and cattle (e.g. [Kawashima et al., 2007](#); [Mulligan et al., 2001](#); [Südekum et al., 1995](#)). Fewer studies have made comparisons between cattle and buffaloes (e.g. [Ichinohe et al., 2004](#); [Lapitan et al., 2008](#); [Pearson and Archibald, 1990](#)). Also relatively few published studies are available for comparison of feed intake and digestibility among more than two ruminant species (e.g. [Burns et al., 2005](#); [Sharma and Murdia, 1974](#); [Sharma and Rajora, 1977](#)). Therefore, we assumed that it may be a useful and informative addition to the limited literature to investigate the influence of different dietary factors on voluntary intake and digestibility of more than two domestic ruminant species simultaneously.

For comparisons of voluntary feed intake across ruminant species of varying body weights (BW), a reference scaling unit is needed to achieve comparability, because large ruminants will usually eat less relative to BW than small ones. Thus, different scaling factors have been applied to compare feed intake among ruminants of various sizes. Traditionally, for sheep and cattle feed intake comparisons in Europe, metabolic body size (MBS, i.e. $BW^{0.75}$; [Kleiber, 1961](#)) is used as a scaling factor and researchers in North America usually express dry matter (DM) intake (DMI) related to $BW^{1.0}$ ([Mertens, 1994](#)). Researchers in Australia and New Zealand frequently use the reference unit of $BW^{0.90}$ based on the recommendations of [Graham \(1972\)](#) for feed intake comparisons. The scaling unit of $BW^{0.90}$ has been verified by several other researchers, supporting its use for feed intake comparisons among different livestock species ([Hackmann and Spain, 2010](#); [Minson and Whiteman, 1989](#); [Reid et al., 1990](#)). These different scaling factors have also been found in datasets comparing mammalian herbivores beyond ruminants. Across all available species ranging from small rodents to elephants, dry matter intake scales more or less to MBS (reviewed in [Clauss et al. \(2007\)](#) and [Meyer et al. \(2010\)](#)). If, in contrast, only large species with a BW above 10 kg are considered, the scaling exponent is higher at $BW^{0.84}$ ([Müller et al., 2013](#)). The relevance of these different scaling exponents lies in their use when comparing data on DMI between animals of different BW within and between

species. If for example a lower scaling exponent (e.g. $BW^{0.75}$) is used for comparisons than the actual one (e.g. $BW^{0.84}$), then the relative intake of the larger animals (expressed per unit $BW^{0.75}$ in this example) will be artificially increased compared to that of the smaller animals. For the same reason, it is important to know whether the same scaling exponents can be used in inter- and intraspecific comparisons.

Inconsistencies between the outcomes of individual studies may result from differences in the specific experimental conditions, the diets used and their chemical composition. Combining data from various reports into a meta-analysis can be a useful tool to deal with the inconsistencies exhibited across a variety of experimental conditions of different studies ([Charbonneau et al., 2006](#); [Sauvant et al., 2008](#)). Therefore, we performed a meta-analysis of various studies to determine whether there is a common scaling exponent for DMI among domestic ruminant species or if this exponent is species specific, and to investigate the influence of dietary nutrient composition on DMI and digestibility.

2. Materials and methods

2.1. Description of database

A dataset summarizing voluntary feed intake, digestibility, and composition of basal diets and supplements of forage-based diets fed to domestic sheep, cattle, goats and buffaloes was compiled by pooling data from scientific literature (references listed in [Appendix](#)). The total number of studies meeting the inclusion criteria was 45, which were divided into 3 main categories that comprised comparisons between sheep and cattle ($n=10$), sheep and goats ($n=25$), and cattle and buffaloes ($n=10$). The corresponding numbers of individual observations for sheep, goats, cattle and buffaloes were 139, 78, 91 and 30, respectively. Detailed composition of diets evaluated in the present study can be obtained from the corresponding author upon request. The prerequisites for a study to be included in the dataset was that DM digestibility (DMD, in g/kg), BW of animals (individual BW (kg)) of animals used in an experiment or mean value of a group of animals given for a certain trial, and feed intake (expressed as DMI, g/day) of any two or more of the above mentioned domestic ruminant species was reported for ad libitum feeding conditions. Chemical characteristics of the diets

(i.e. neutral detergent fibre (NDF), acid detergent fibre (ADF) and/or crude protein (CP)) were included as available. Feed intake data given as kg/day, % of BW or g/kg BW^{1.0}, g/kg BW^{0.90} or g/kg BW^{0.75} were converted to g/day.

An allometric relationship between DMI and BW was constructed according to the following model:

$$\text{DMI} = a\text{BW}^b,$$

where a is a constant and b is the scaling factor. The respective model was transformed into its logarithmic equation to obtain a linear relationship between DMI and BW, where the scaling factor is the slope of the equation:

$$\log \text{DMI} = \log a + b \log \text{BW}$$

In a first step, scaling factors were estimated for each ruminant species separately. The scaling factor was then used to obtain species-specific MBS, i.e. BW^{scaling factor} for each species. Feed intake was then expressed as g DMI per unit of species-specific MBS. To know whether there is a common scaling factor for all four ruminant species or not (i.e. each species has its specific scaling factor), interaction between species and log BW on log DMI was statistically tested.

2.2. Statistical analyses

Data were analysed using mixed model regression methodology (St-Pierre, 2001; Sauvant et al., 2008). Models with either discrete a predictor variable (domestic ruminant species) or continuous predictor variables (chemical composition of diets: CP, NDF or ADF) were assessed individually. The respective predictor variables were considered as fixed effects. Different studies were considered as random effects. The model statistics used for this study was Akaike's information criterion (AIC). The AIC was applied in model selection to measure the relative goodness of fit of a statistical model. In this study, AIC was used to select whether a model is quadratic or linear (lower AIC is better model), together with the P-value (explained below). Accordingly, for the continuous predictor variable (chemical composition of diet), the following model was used:

$$Y_{ij} = B_0 + B_1X_{ij} + B_2X_{ij}^2 + s_i + b_iX_{ij} + e_{ij},$$

where Y_{ij} =the dependent variable, B_0 =overall inter-study intercept (fixed effect), B_1 =the overall linear regression coefficient Y on X (fixed effect), B_2 =the overall quadratic regression coefficient Y on X (fixed effect), X_{ij} =the value of the continuous predictor variable, s_i =the random effect of the i th study, b_i =the random effect of study on the regression coefficient of Y on X , and e_{ij} =the residual error. When a quadratic model did not significantly explain the relationship between independent and dependent variables, the model was modified into a linear model by taking out the $B_2X_{ij}^2$ term. For the discrete predictor variable (domestic ruminant species), the following model was applied:

$$Y_{ijk} = \mu + s_i + \tau_j + s\tau_{ij} + e_{ijk},$$

where Y_{ijk} =the dependent variable, μ =overall mean, s_i =the random effect of the i th study, τ_j =the fixed effect of the j th

level of factor τ , $s\tau_{ij}$ =the random interaction between the i th study and the j th level of factor τ , e_{ijk} =the residual error.

Data were weighted by the number of animals in each study. Tukey's test was applied as a post hoc test to compare the differences among means in the case of discrete predictor variables.

3. Results

In some studies not all the variables of interest were reported, therefore, the number of observations across variables was not uniform (Table 1). There were large differences between minimum and maximum values in the database for dietary constituents (NDF, ADF and CP) between buffaloes and the other three species; for these three species, however, the nutrient ranges of the diets were relatively similar.

Table 1

Statistical description of the dietary and response variables in the database.

Species	Variables ^a	n^b	Mean	SD ^c	Minimum	Maximum
Sheep	Body weight, kg	139	41.6	17.3	10.2	82.6
	Feed nutrients, g/kg DM					
	NDF	69	520	168	134	768
	ADF	53	364	154	94	870
	CP	126	124	68	16	422
	DMI, g/kg MBS	139	898	435	139	2530
Goats	DMD, g/kg DM	92	580	95	243	815
	Body weight, kg	78	26.0	15.0	7.0	67.8
	Feed nutrients, g/kg DM					
	NDF	35	457	184	134	764
	ADF	25	347	164	94	870
	CP	78	121	75	25	422
Cattle	DMI, g/kg MBS	78	600	300	150	1520
	DMD, g/kg DM	45	611	102	312	869
	Body weight, kg	91	391.0	136.5	103.0	674.0
	Feed nutrients, g/kg DM					
	NDF	38	603	83	406	768
	ADF	43	403	128	221	661
Buffaloes	CP	68	114	66	16	313
	DMI, g/kg MBS	91	6857	3166	1680	19870
	DMD, g/kg DM	67	555	87	366	717
	Body weight, kg	30	329.0	137.8	150.0	722.0
	Feed nutrients, g/kg DM					
	NDF	5	606	54	510	632
Buffaloes	ADF	15	450	65	350	578
	CP	26	76	66	22	255
	DMI, g/kg MBS	30	5539	2055	2390	11200
	DMD, g/kg DM	15	478	79	366	610

References used to construct the data base are given as a separate list at the end of the article before the reference section.

^a NDF=neutral detergent fibre; ADF=acid detergent fibre; CP=crude protein; DM=dry matter, DMI=DM intake; DMD=DM digestibility; MBS=Metabolic body size.

^b n =Number of data used.

^c SD=Standard deviation.

Significant linear relationships were observed between log-transformed BW and log-transformed DMI of all domestic ruminant species in this study (Fig. 1). Individual regression equations for each ruminant species as shown in the footnote of Fig. 1 demonstrated that the scaling exponent for relative DMI (rDMI; intake expressed in relation to BW) is lower in small ruminants than in large ruminants. The differences for scaling factors among species were significant for each individual factor as

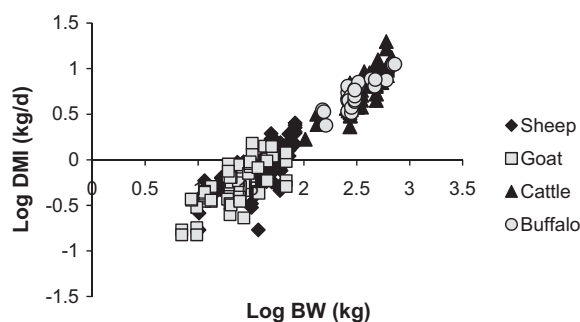


Fig. 1. Relationship between log body weight (BW) and log dry matter intake (DMI). The regression equation for each ruminant species is as follows (mean \pm 95% confidence interval): Sheep: $\log \text{ DMI} = -1.105 (\pm 0.290) + 0.639 (\pm 0.187) \log \text{ BW}$; $P < 0.001$; $r^2 = 0.49$. Goat: $\log \text{ DMI} = -1.231 (\pm 0.290) + 0.714 (\pm 0.212) \log \text{ BW}$; $P < 0.001$; $r^2 = 0.55$. Cattle: $\log \text{ DMI} = -1.461 (\pm 0.445) + 0.883 (\pm 0.175) \log \text{ BW}$; $P < 0.001$; $r^2 = 0.71$. Buffalo: $\log \text{ DMI} = -1.316 (\pm 0.602) + 0.818 (\pm 0.246) \log \text{ BW}$; $P < 0.001$; $r^2 = 0.75$. P -values: species, $P < 0.01$; log BW, $P < 0.001$; species \times log BW, $P < 0.01$.

Table 2

Equations for linear regression between chemical composition of feeds (independent variable; in g/kg dry matter) and dry matter intake (response variable); g/kg metabolic body size of sheep, goats, cattle and buffaloes.

Independent				Parameter estimates ^d						Model statistics ^e
Variables ^a	Species	Model ^b	n^c	Intercept	95% CI	$P_{\text{Intercept}}$	Slope	95% CI	P_{Slope}	AIC
CP	Sheep	Q	126	57.3	14.1	< 0.001	0.289	0.161	< 0.001	1157.1
	Goats	Q	78	43.9	12.3	< 0.001	-0.0005	0.0004	0.014	
	Cattle	Q	74	22.9	7.0	< 0.001	0.211	0.125	0.002	
	Buffaloes	Q	26	32.1	7.0	< 0.001	-0.0004	0.0003	0.013	
	All	Q	304	42.4	11.4	< 0.001	0.199	0.092	< 0.001	
NDF	Sheep	L	67	106.5	25.1	< 0.001	-0.0005	0.0003	< 0.001	531.3
	Goats	L	34	69.3	19.1	< 0.001	0.364	0.152	< 0.001	
	Cattle	L	38	75.1	21.3	< 0.001	-0.0012	0.0005	< 0.001	
	Buffaloes	n.d.	5	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	
	All	L	144	95.5	19.4	< 0.001	-0.0012	0.0005	< 0.001	
ADF	Sheep	L	53	99.4	23.3	< 0.001	0.266	0.139	< 0.001	2917.0
	Goats	L	25	59.6	16.0	< 0.001	-0.0005	0.0004	0.008	
	Cattle	L	43	46.8	17.7	0.002	-0.032	0.055	0.263	
	Buffaloes	L	15	42.3	22.4	0.034	0.004	0.049	0.868	
	All	L	136	75.8	20.3	< 0.001	-0.031	0.048	0.214	

^a CP=crude protein; NDF=neutral detergent fibre; ADF=acid detergent fibre.

^b Q=quadratic; L=linear; n.d.=not determined; number of data for buffaloes was < 10.

^c n =Number of data used.

^d CI=Confidence interval.

^e AIC=Akaike's information criterion.

shown by the significant interaction between species and log BW ($P < 0.01$).

The regression analysis showed that CP concentration impacted positively on DMI of ruminants with variations among the species (Table 2). Quite large differences were found for slope values of regression equations among all four ruminant species. The impact of feed constituents on DMI of these four ruminant species is also shown in Fig. 2. Overall buffaloes were found to be more responsive to CP with slope value of 0.364, followed by sheep, goats and cattle, and this response was significant for all species. In case of NDF, the number of observations for buffaloes was low; therefore, it was not possible to include this continuous predictor variable in the analysis. However, NDF negatively affected DMI of the other three species yet with a significant effect in cattle only. In contrast, ADF negatively influenced DMI of all species except buffaloes, showing the strongest effect on DMI of sheep and cattle with slope values of -0.032 and -0.023, respectively. The DMI of goats was less influenced by ADF with a slope value of -0.005 (Table 2).

The regression analysis for the effect of dietary factors on digestibility of animals showed that CP was positively correlated to DMD across species. The effect was much greater in cattle than the other three ruminant species, and it was significant only for cattle and buffaloes ($P < 0.05$; Table 3). The database of buffaloes for NDF and ADF was small. Therefore, only sheep, goat and cattle data could be analysed for these chemical entities. The NDF depressed DMD only in cattle, whereas it positively

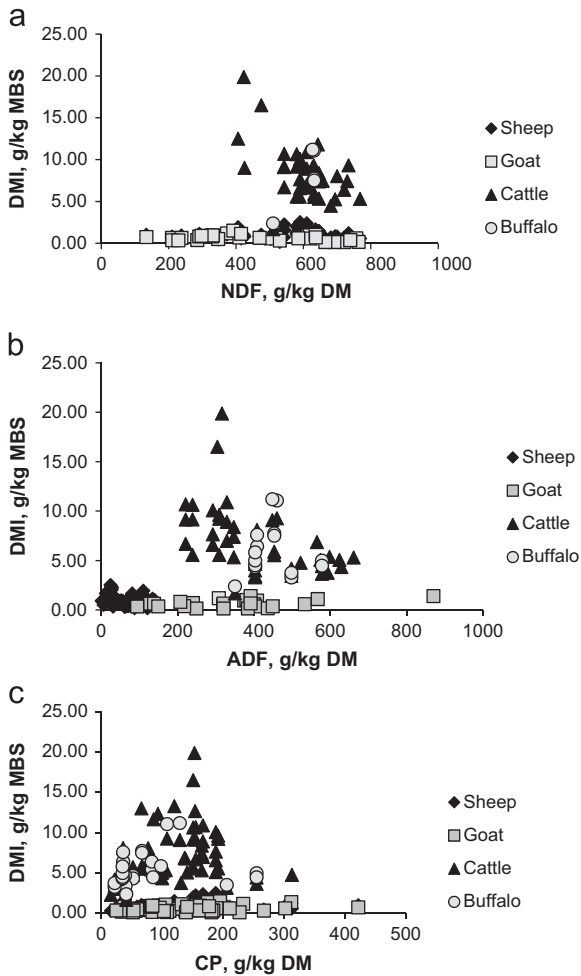


Fig. 2. The influence of various dietary constituents on dry matter intake (DMI) of sheep, goat, cattle and buffalo. MBS, metabolic body size.

influenced DMD in sheep and goats (Table 3; significant effect in sheep only). On the other hand, ADF lowered DMD in sheep, goats and cattle with a significant effect observed for sheep and goats. The species-specific response of DMD to dietary constituents is also highlighted in Fig. 3.

4. Discussion

4.1. Relationship between dry matter intake and body weight of animals

Voluntary feed intake is generally recognized as one of the most important factors influencing performance. Domestic ruminant species have substantially different BW, ranging from about 30–600 kg for matured dwarf female goat and cattle, respectively (Adejumo and Ademosun, 1991). Different opinions with regard to the effect of size on intake may be found in the literature. Kleiber (1961), for instance, stated that feed conversion in herbivores is dependent of body size because intake is directly proportional to maintenance requirement. As with

increasing size, maintenance requirements per unit of BW decrease, feed intake relative to BW will decrease to the same extent. On the other hand, Van Soest (1982) argued that gut size of animals acts as a limiting factor, and that, because gut capacity scales linearly with BW, intake of a given diet will be a constant fraction of BW irrespective of species size. In the present study, we obtained an allometric relationship between DMI and BW of animals confirming the findings of other researchers who also described the relationship between feed intake and BW (Peyraud et al., 1996; Favardin, 1999). The different scaling factors were found species-specific with lower values for small ruminants (sheep, goats) and higher values for large ruminants (cattle, buffalo), supporting previous studies on ruminant and non-ruminant herbivores (Clauss et al. 2007; Meyer et al., 2010).

More recently, Müller et al. (2013) suggested that the scaling of DMI is higher in larger as compared to smaller (< 10 kg BW) mammalian herbivores. Given the finding of the present study that the scaling factor was lower in goats and sheep than in cattle and buffaloes, it may be reasonable to suggest that potentially there even are differences in the intake scaling among the larger herbivores (> 10 kg BW) themselves.

When comparisons are intended to compare across different domestic ruminant species, various scaling factors are suggested by different researchers. For example, the use of 0.90 as scaling exponent for interspecies comparisons was suggested by Graham (1972), which has later been endorsed by other scientists (Minson and Whiteman, 1989; Reid et al., 1990; Hackmann and Spain, 2010). In contrast, if comparisons are to be made within species, other scaling factors may be more appropriate, which is supported by the results of the present study with lower scaling factors for small ruminants (sheep and goats) and greater exponents for large ruminants (cattle and buffalo).

The relevance of the magnitude of the scaling exponent was explained by Hackmann and Spain (2010) and Müller et al. (2013): The fact that rDMI scaling in large herbivores is higher than the scaling of energy requirements (which scale to about 0.75, e.g. Müller et al., 2012) suggests that larger herbivores cannot compensate for the poorer diet quality they have to accept in the wild by increasing digestive efficiency, but by increasing intake.

4.2. Dependency of voluntary dry matter intake of ruminants on dietary constituents

The CP concentration had a positive effect on DMI, whereas, fibre fractions of diets depressed DMI of the animals. This trend is consistent with previous studies (Molina Alcaide et al., 2000; Kawashima et al., 2007; Abidi et al., 2009). Overall, buffaloes appeared to be more responsive to CP content of diets at a given CP level than the other three ruminant species. The low quality diets with very low content of CP fed to the buffaloes used in the present study may be responsible, resulting in the positive response to increasing CP concentration. However, it is difficult to draw a concrete conclusion as the data size is small. The other three ruminant species responded similarly to an increase of CP concentration which has also

Table 3

Equations for linear regression between chemical composition of feeds (independent variable; g/kg dry matter) and dry matter digestibility (response variable; g/kg dry matter) of sheep, goats, cattle and buffaloes.

Independent				Parameter estimate ^d						Model statistics ^e
Variables ^a	Species	Model ^b	N ^c	Intercept	95% CI	P _{Intercept}	Slope	95% CI	P _{Slope}	AIC
CP	Sheep	L	82	545	47	< 0.001	0.21	0.21	0.059	943.6
	Goats	L	45	553	59	< 0.001	0.31	0.32	0.065	531.1
	Cattle	Q	53	374	66	< 0.001	2.34	0.87	< 0.001	
	Buffaloes	L	15	400	51	< 0.001	0.83	0.63	0.030	159.9
	All	Q	195	478	48	< 0.001	1.01	0.46	< 0.001	
							-0.0052	0.0026	< 0.001	615.2
							-0.0019	0.0011	0.001	2239.1
NDF	Sheep	Q	51	413	203	0.002	0.90	0.80	0.035	
	Goats	Q	23	437	236	0.007	0.94	1.02	0.094	587.2
	Cattle	L	32	590	321	0.037	-0.02	0.52	0.946	276.7
	Buffaloes	n.d.	4	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	363.5
	All	Q	110	414	155	< 0.001	0.92	0.60	0.004	n.d.
							-0.0011	0.0006	< 0.001	1257.9
ADF	Sheep	L	44	709	95	< 0.001	-0.36	0.21	0.002	484.3
	Goats	L	18	752	118	< 0.001	-0.49	0.31	0.012	199.9
	Cattle	L	34	656	225	0.011	-0.25	0.46	0.288	396.0
	Buffaloes	n.d.	8	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	All		104	726	82	< 0.001	-0.44	0.17	< 0.001	1173.4

^a CP=crude protein; NDF=neutral detergent fibre; ADF=acid detergent fibre.

^b Q=quadratic; L=linear; n.d.=not determined; number of data for buffaloes was < 10.

^c n=Number of data used.

^d CI=confidence interval.

^e AIC=Akaike's information criterion.

been reported previously. For example, [Quick and Dehority \(1986\)](#) observed only small differences between feed intake of sheep and goats. However, the authors also mentioned that there would probably be selectivity differences if the animals were kept under natural grazing conditions. Similarly, [Molina Alcaide et al. \(2000\)](#) found equal response of these species when fed medium to good quality diets in the absence of feed selection.

Goats appeared less responsive to increases in fibre fractions (NDF and ADF) than the other species such that these feed fractions had a less negative impact on their DMI. [Huston et al. \(1988\)](#) mentioned that sheep and goats were similar in terms of DMI when higher quality diets were fed; inconsistencies mostly occurred when low quality feeds were given with higher intake shown by goats and this observation is in agreement with the findings of the present study. In a review, [Brown and Johnson \(1984\)](#) indicated that intake was higher in sheep than in goats in most studies, with relatively greater intake by goats fed high fibre diets.

4.3. Dependency of digestibility on dietary constituents

Dietary CP had a positive influence on digestibility. The effect of CP on DMD in cattle was significant and higher than for the other species which may be partly be due to the structure of the data set which encompassed not only a range of diets but also different breeds within species which may also play vital role in feed selection of animals ([Huston, 1978](#)). Of the other three species, DMD of buffaloes responded stronger to an increase of CP,

however, this observation should be interpreted cautiously as the available dataset for buffaloes was small. The CP influenced DMD in sheep and goats almost in the same manner though non-significantly showing no large differences between the slope values of these species which is in contradiction to the generally accepted theory that goats are able to digest poor quality diets with high cell and low CP content better than other domestic ruminant species ([Adebowale, 1988](#); [Domingue et al., 1991](#); [Gihad, 1976](#)). [McCabe and Barry \(1988\)](#) suggested that goats are vastly superior to sheep in utilizing highly lignified diets. Similarly, [Al Jassim et al. \(1991\)](#) and [Domingue et al. \(1991\)](#) found that goats showed superiority over sheep when fed on low quality diets. The better utilization of fibrous diets by goats than other ruminant species may be due to higher fermentation rate ([El Hag, 1976](#)), higher rate of salivary excretion ([Seth et al., 1976](#)), or higher activity of cellulolytic bacteria ([Gihad et al., 1980](#)). Also [Doyle et al. \(1984\)](#) suggested that a greater ability of goats compared with sheep to digest low quality forages resulted from longer ruminal digesta retention times and possibly a higher capacity to recycle and conserve N within the body.

The content of NDF negatively influenced digestibility only in cattle, whereas sheep and goats responded positively with almost the same magnitude to this feed constituent. This finding is in contradiction to the generally accepted idea of reduced digestibility of high-fibre compared with low-fibre diets ([Poppi et al., 1980](#); [Woods et al., 1999](#)). Our observations on the effect of NDF on DMD should be interpreted carefully, since data selection can have an impact – data was collected across different

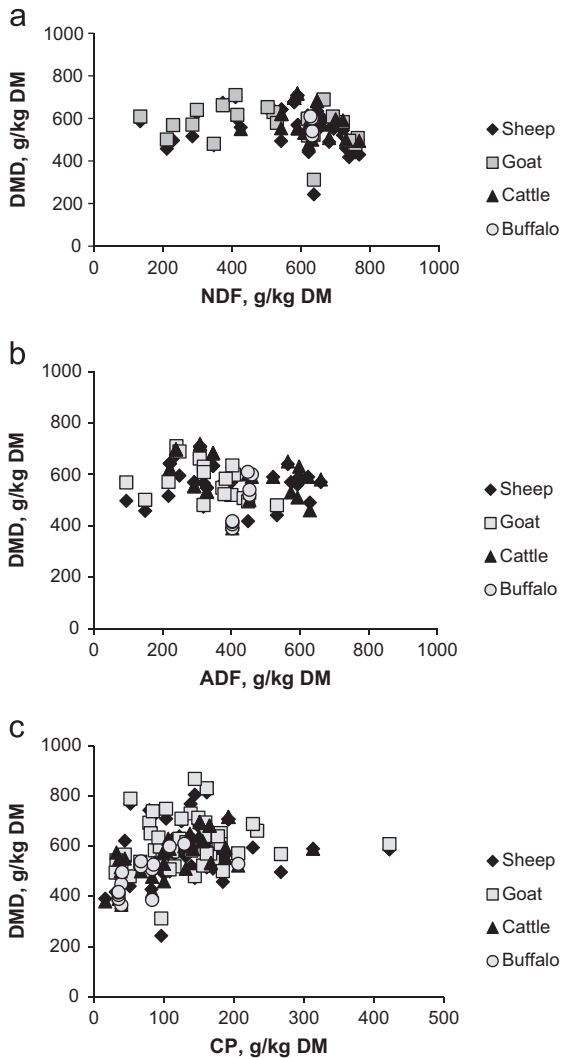


Fig. 3. The influence of various dietary constituents on dry matter digestibility (DMD) in sheep, goat, cattle and buffalo.

studies conducted in different parts of the world with large variations of environmental conditions, animal breeds and feeds.

The ADF negatively influenced DMD. This effect was most pronounced in goats followed by sheep and cattle. Usually goats are considered more robust to digest low quality diets with high fibre concentrations. Nonetheless, several authors have stated that digestibility of high quality diets is either similar among domestic ruminant species or goats are even superior to other domestic ruminant species. Jones et al. (1972) reported that goats digested CP better than dairy steers. Huston (1978) suggested that, in contrast to the general assumption of greater digestibility of low quality forages by goats, that goats would be less efficient in digesting low quality forages because of differences in the dynamics of the gastrointestinal systems between goats and sheep. This author proposed that this occurs because goats have a relatively smaller reticulo-rumen and shorter ruminal

retention times, and therefore, satisfy their nutrient requirements by higher daily forage DMI. Brown and Johnson (1985) found that digestibility of NDF and ADF was higher in sheep than in goats and suggested that goats can better exploit their potential on higher quality feeds. Again, the deviation of the outcome of the present data evaluation from the general trend – goats digesting fibrous diets better than other ruminants – may be due to data structure which encompassed different goat breeds; digestive efficiency of goats varies considerably with breed and strain (Huston, 1978).

For the other two species, cattle appeared to digest fibrous diets better than sheep. There are other studies which are in agreement with this finding. Prigge et al. (1984) reported that sheep showed a tendency to consume greater percentage of dietary CP which, vice versa, indicates that cattle do better on low quality diets which are typically low in CP. Similarly, Südekum et al. (1995) reported that cattle digested DM, NDF and ADF better than sheep. Also Woods et al. (1999) revealed that cattle digest fibre better than sheep. The ability of cattle to digest low quality rations better can be linked to the observation that they retain digesta longer in their rumen which may result in a greater digestive efficiency compared with sheep (Poppi et al., 1980).

5. Conclusions

Feed intake of ruminants is dependent upon their BW. Distinguishable, i.e. species-specific, scaling factors for the relationship between DMI and BW were estimated, and the difference was pronounced between small and large ruminants with lower exponents for sheep and goats and higher for cattle and buffaloes. Across all ruminant species, CP had a positive influence on intake and digestibility while fibre fractions influenced DMI negatively except for buffaloes who responded positively to ADF. Digestibility was also negatively influenced by ADF in all species, whereas NDF had a negative effect in cattle only. However, the magnitude of the response of feed intake and digestibility to varying concentrations of dietary constituents differed among the ruminant species.

Conflicts of interest statement

The authors declare that they have no conflict of interest.

Acknowledgements

The authors are grateful to the institute of Animal Science, University of Bonn, Germany for providing the financial support to conduct this study. Dr. Young Aniele is acknowledged for language editing of an earlier version of this manuscript.

Appendix. List of references used to construct the data base

- Abdullah, N., Nolan, J.V., Mahyuddin, M., Jalaludin, S., 1992. Digestion and nitrogen conservation in cattle and buffaloes given rice straw with or without molasses. *J. Agric. Sci.* 119, 255–263.
- Abidi, S., Ben Salem, H., Vasta, V., Priolo, A., 2009. Supplementation with barley or spineless cactus (*Opuntia ficus indica* f. *inermis*) cladodes on digestion, growth and intramuscular fatty acid composition in sheep and goats receiving oaten hay. *Small Rumin. Res.* 87, 9–16.
- Adebowale, E.A., 1988. Performance of young West African dwarf goats and sheep fed the aquatic macrophyte *Echinochloa stagnina*. *Small Rumin. Res.* 1988, 167–173.
- Adebowale, E.A., Ademosun, A.A., 1985. Studies on the utilization of brewers' dried grains by sheep and goats. II. Digestibility, metabolism and rumen studies. *Bull. Anim. Health Prod. Afr.* 33, 349–355.
- Adejumo, J.O., Ademosun, A.A., 1991. Utilization of leucaena as supplement for growing dwarf sheep and goats in the humid zone of West Africa. *Small Rumin. Res.* 5, 75–82.
- Alam, M.R., Poppi, D.P., Sykes, A.R., 1983. Intake, digestibility and retention time of 2 forages by kids and lambs. *Proc. N. Z. Soc. Anim. Prod.* 43, 119–121.
- Animut, G., Goetsch, A.L., Aiken, G.E., Puchala, R., Detweiler, G., Krehbiel, C.R., Merkel, R.C., Sahlu, T., Dawson, L.J., Johnson, Z.B., Kiesler, D.H., 2006. Performance by goats and sheep consuming a concentrate-based diet subsequent to grazing grass/forb pastures at three stocking rates. *Small Rumin. Res.* 66, 92–101.
- Antoniou, T., Hadjipanayiotou, M., 1985. The digestibility by sheep and goats of five roughages offered alone or with concentrates. *J. Agric. Sci.* 105, 663–671.
- Baiden, R.Y., Rhule, S.W.A., Otsyina, H.R., Sottie E.T., Ameleke, G., 2007. Performance of West African dwarf sheep and goats fed varying levels of cassava pulp as a replacement for cassava peels. *Livest. Res. Rural Dev.* 19 (article no. 35).
- Bird, P.R., 1974. Sulphur metabolism and excretion studies in ruminants. XIII. Intake and utilization of wheat straw by sheep and cattle. *Aust. J. Agric. Res.* 25, 631–642.
- Boer, M., Milton, J.T.B., Ternouth, J.H., 1982. The utilization of three roughage diets by sheep and angora goats. *Proc. Aust. Soc. Anim. Prod.* 14, 653.
- Bosma, R.H., Bicaba, M.Z., 1997. Effect of addition of leaves from *Combretum aculeatum* and *Leucaena leucocephala* on digestion of sorghum stover by sheep and goats. *Small Rumin. Res.* 24, 167–173.
- Brown, L.E., Johnson, W.L., 1985. Intake and digestibility of wheat straw diets by goats and sheep. *J. Anim. Sci.* 60, 1318–1323.
- Burns, J.C., Mayland, H.F., Fisher, D.S., 2005. Dry matter intake and digestion of alfalfa hay harvested at sunset and sunrise. *J. Anim. Sci.* 83, 262–270.
- Chandrasekharaiah, M., Reddy, M.R., Reddy, G.V.N., 1996. Effect of feeding urea treated maize stover on growth and nutrient utilization by sheep and goats. *Small Rumin. Res.* 22, 141–147.
- Colovos, N.F., Holter, J.B., Koes, R.M., Urban, Jr., W.E., Davis, H.A. 1970. Digestibility, Nutritive value and intake of ensiled corn plant (*Zea mays*) in cattle and sheep. *J. Anim. Sci.* 30, 819–824.
- Domingue, B.M.F., Dellow, D.W., Barry, T.N., 1991. Voluntary intake and rumen digestion of a low-quality roughage by goats and sheep. *J. Agric. Sci.* 117, 111–120.
- Domingue, B.M.F., Dellow, D.W., Barry, T.N., 1991a. The efficiency of chewing during eating and ruminating in goats and sheep. *Br. J. Nutr.* 65, 355–363.
- Gihad, E.A., 1976. Intake, digestibility and nitrogen utilization of tropical natural grass hay by goats and sheep. *J. Anim. Sci.* 43, 879–883.
- Greenhalgh, J.F.D., Reid, G.W., 1973. The effects of pelleting various diets on intake and digestibility in sheep and cattle. *Anim. Prod.* 16, 223–233.
- Hendricksen, R.E., Poppi, D.P., Minson, D.J., 1981. The voluntary intake, digestibility and retention time by cattle and sheep of stem and leaf fractions of a tropical legume (*Lablab purpureus*). *Aust. J. Agric. Res.* 32, 389–398.
- Howe, J.C., Barry, T.N., Popay, A.I., 1988. Voluntary intake and digestion of gorse (*Ulex europaeus*) by goats and sheep. *J. Agric. Sci.* 111, 107–114.
- Huston, J.E., Engdahl, B.S., Bales, K.W., 1988. Intake and digestibility in sheep and goats fed three forages with different levels of supplemental protein. *Small Rumin. Res.* 1, 81–92.
- Huston, J.E., Rector, B.S., Ellis, W.C., Allen, M.L., 1986. Dynamics of digestion in cattle, sheep, goats and deer. *J. Anim. Sci.* 62, 208–215.
- Jones, G.M., Larsen, R.E., Javed, A.H., Donefer, E., Gaudreau, J.-M., 1972. Voluntary intake and nutrient digestibility of forages by goats and sheep. *J. Anim. Sci.* 34, 830–838.
- Kennedy, P.M., Boniface, A.N., Liang, Z.J., Muller, D., Murray, R.M., 1992a. Intake and digestion in swamp buffaloes and cattle. 2. The comparative response to urea supplements in animals fed tropical grasses. *J. Agric. Sci.* 119, 243–254.
- Kennedy, P.M., McSweeney, C.S., Ffoulkes, D., John, A., Schlink, A.C., LeFeuvre, R.P., Kerr, J.D., 1992. Intake and digestion in swamp buffaloes and cattle. 1. The digestion of rice straw (*Oryza sativa*). *J. Agric. Sci.* 119, 227–242.
- Kilmer, L.H., Wangsness, P.J., Kesler, E.M., Muller, L.D., Griel, Jr., L.C., Krabill, L.F., 1979. Voluntary intake and digestibility of legume and grass diets fed to lactating cows and growing wethers. *J. Dairy Sci.* 62, 1272–1277.
- Larbi, A., Fianu, F.K., Akude, F.K., 1991. Voluntary intake and digestibility by sheep and goats of whole-plant, leaf and stem fractions of *Pennisetum purpureum* Schum. *Small Rumin. Res.* 6, 217–221.
- McCabe, S.M., Barry, T.N., 1988. Nutritive value of willow (*Salix* sp.) for sheep, goats and deer. *J. Agric. Sci.* 111, 1–9.
- McSweeney, C.S., Kennedy, P.M., John, A., 1989. Reticulo-ruminal motility in cattle (*Bos indicus*) and water buffaloes (*Bubalus bubalis*) fed a low quality roughage diet. *Comp. Biochem. Physiol.* 94 A, 635–638.
- Moran, J.B., 1983. Rice bran as a supplement to elephant grass for cattle and buffalo in Indonesia. 1. Feed intake, utilization and growth rates. *J. Agric. Sci.* 100, 709–716.
- Moran, J.B., Norton, B.W., Nolan, J.V., 1979. The intake, digestibility and utilization of a low-quality roughage by

Brahman cross, buffalo, Banteng and Shorthorn steers. *Aust. J. Agric. Res.* 30, 333–340.

Moran, J.B., Satoto, K.B., Dawson, J.E., 1983. The utilization of rice straw fed to zebu cattle and swamp buffalo as influenced by alkali treatment and *Leucaena* supplementation. *J. Agric. Res.* 34, 73–84.

Mousa, H.M., Ali, K.E., Hume, I.D., 1983. Effects of water deprivation on urea metabolism in camels, desert sheep and desert goats fed dry desert grass. *Comp. Biochem. Physiol.* 74 A (3), 715–720.

Pearson, R.A., Archibald, R.F., 1990. Effect of ambient temperature and urea supplementation on the intake and digestion of alkali-treated straw by Brahman cattle and swamp buffaloes. *J. Agric. Sci.* 114, 177–186.

Poppi, D.P., Minson, D.J., Ternouth, J.H., 1980. Studies of cattle and sheep eating leaf and stem fractions of grasses. 1. The voluntary intake, digestibility and retention time in the reticulo-rumen. *Aust. J. Agric. Res.* 32, 99–108.

Quick, T.C., Dehority, B.A., 1986. A comparative study of feeding behaviour and digestive function in dairy goats, wool sheep and hair sheep. *J. Anim. Sci.* 63, 1516–1526.

Rees, M.C., Little, D.A., 1980. Differences between sheep and cattle in digestibility, voluntary intake and retention time in the rumen of three tropical grasses. *J. Agric. Sci.*, 94, 483–485.

Reid, R.L., Jung, G.A., Cox-Ganser, J.M., Rybeck, B.F., Townsend, E.C., 1990. Comparative utilization of warm and cool-season forages by cattle, sheep and goats. *J. Anim. Sci.* 68, 2986–2994.

Sharma V.V., Murdia, P.C., 1974. Utilization of berseem hay by ruminant. *J. Agric. Sci.* 83, 289–293.

Sharma V.V., Rajora, N.K., 1977. Voluntary intake and nutrient digestibility of low-grade roughage by ruminants. *J. Agric. Sci.* 88, 75–78.

Silva, A.T., Greenhalgh, J.F.D., Ørskov, E.R., 1989. Influence of ammonia treatment and supplementation on the intake, digestibility and weight gain of sheep and cattle on barley straw diets. *Anim. Prod.* 48, 99–108.

Thomas, S., Campling, R.C., 1976. Relationship between digestibility and faecal nitrogen in sheep and cows offered herbage ad libitum. *J. Br. Grassl. Soc.* 31, 69–72

Wahed, R.A., Owen, E., 1986. Comparison of sheep and goats under stall-feeding conditions: roughage intake and selection. *Anim. Prod.* 42, 85–95.

References

Abidi, S., Ben Salem, H., Vasta, V., Priolo, A., 2009. Supplementation with barley or spineless cactus (*Opuntia ficus indica* f. *inermis*) cladodes on digestion, growth and intramuscular fatty acid composition in sheep and goats receiving oaten hay. *Small Rumin. Res.* 87, 9–16.

Adebowale, E.A., 1988. Performance of young West African dwarf goats and sheep fed the aquatic macrophyte *Echinochloa stagnina*. *Small Rumin. Res.* 1, 167–173.

Adejumo, J.O., Ademosun, A.A., 1991. Utilization of leucaena as supplement for growing dwarf sheep and goats in the humid zone of west Africa. *Small Rumin. Res.* 5, 75–82.

Al Jassim, R.A.M., Hassan, S.A., Al-Ani, A.N., Dana, T.K., 1991. Effects of undegradable protein supplementation and nitrogen balance in sheep and goats. *Small Rumin. Res.* 5, 57–63.

Brown, L.E., Johnson, W.L., 1984. Comparative intake and digestibility of forages and by-products by goats and sheep. A review. *Int. Goat Sheep Res.* 2, 212–226.

Brown, L.E., Johnson, W.L., 1985. Intake and digestibility of wheat straw diets by goats and sheep. *J. Anim. Sci.* 60, 1318–1323.

Burns, J.C., Mayland, H.F., Fisher, D.S., 2005. Dry matter intake and digestion of alfalfa hay harvested at sunset and sunrise. *J. Anim. Sci.* 83, 262–270.

Charbonneau, E., Pellerin, D., Oetzel, G.R., 2006. Impact of lowering dietary cation-anion differences in nonlactating dairy cows: a meta-analysis. *J. Dairy Sci.* 89, 537–548.

Clauss, M., Schwarm, A., Ortmann, S., Streich, W.J., Hummel, J., 2007. A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. *Comp. Biochem. Physiol.* A148, 249–265.

Domingue, B.M.F., Dellow, D.W., Barry, T.N., 1991. Voluntary intake and rumen digestion of a low-quality roughage by goats and sheep. *J. Agric. Sci.* 117, 111–120.

Doyle, P.T., Egan, J.K., Thalen, A.J., 1984. Intake, digestion and nitrogen and sulfur retention in Angora goats and Merino sheep fed herbage diets. *Aust. J. Exp. Agric. Anim. Husb.* 24, 165–169.

El Hag, G.A., 1976. A comparative study between desert goat and sheep efficiency of feed utilization. *World Rev. Anim. Prod.* 12, 43–48.

Faverdin, P., 1999. The effect of nutrients on feed intake in ruminants. *Proc. Nutr. Soc.* 58, 523–531.

Gihad, E.A., 1976. Intake, digestibility and nitrogen utilization of tropical natural grass hay by goats and sheep. *J. Anim. Sci.* 43, 879–883.

Gihad, E.A., El-Bedawy, T.M., Mehrez, A.Z., 1980. Fibre digestibility by goats and sheep. *J. Dairy Sci.* 63, 1701–1706.

Graham, N.McC., 1972. Units of metabolic body size for comparisons amongst adult sheep and cattle. *Proc. Aust. Soc. Anim. Prod.* 9, 352–355.

Hackmann, T.J., Spain, J.N., 2010. Ruminant ecology and evolution: perspectives useful to ruminant livestock research and production. *J. Dairy Sci.* 93, 1320–1334.

Huston, J.E., 1978. Forage utilization and nutrient requirements of the goat. *J. Dairy Sci.* 61, 988–993.

Huston, J.E., Engdahl, B.S., Bales, K.W., 1988. Intake and digestibility in sheep and goats fed three forages with different levels of supplemental protein. *Small Rumin. Res.* 1, 81–92.

Ichinohe, T., Orden, E.A., Del Barrio, A.N., Lapitan, R.M., Fujihara, T., Cruz, L. C., Kanai, Y., 2004. Comparison of voluntary feed intake, rumen passage and degradation kinetics between crossbred Brahman cattle (*Bos indicus*) and swamp buffaloes (*Bubalus bubalis*) fed a fattening diet based on corn silage. *Anim. Sci. J.* 75, 533–540.

Jones, G.M., Larsen, R.E., Javed, A.H., Donefer, E., Gaudreau, J.-M., 1972. Voluntary intake and nutrient digestibility of forages by goats and sheep. *J. Anim. Sci.* 34, 830–838.

Kawashima, T., Sumamal, W., Pholsen, P., Chaithiang, R., Terada, F., 2007. Comparative study on energy and nitrogen metabolism of Brahman cattle and sheep given ruzi grass hay with different levels of soybean meal. *Jpn. Agric. Res. Q.* 41, 253–260.

Kleiber, M., 1961. *The Fire of Life. An Introduction to Animal Energetics.* John Wiley and Sons, Inc., New York, NY, USA.

Lapitan, R.M., Del Barrio, A.N., Katsube, O., Ban-Tokuda, T., Orden, E.A., Robles, A.Y., Cruz, L.C., Kanai, Y., Fujihara, T., 2008. Comparison of fattening performance in Brahman grade cattle (*Bos indicus*) and crossbred water buffalo (*Bubalus bubalis*) fed on high roughage diet. *Anim. Sci. J.* 79, 76–82.

McCabe, S.M., Barry, T.N., 1988. Nutritive value of willow (*Salix* sp.) for sheep, goats and deer. *J. Agric. Sci.* 111, 1–9.

Mertens, D.R., 1994. Regulation of forage intake. In: Fahey Jr., G.C., Collins, M., Mertens, D.R., Moser, L.E. (Eds.), *Forage Quality, Evaluation, and Utilization*, ASA-CSSA-SSSA, Madison, pp. 450–493.

Meyer, K., Hummel, J., Clauss, M., 2010. The relationship between forage cell wall content and voluntary food intake in mammalian herbivores. *Mammal Rev.* 40, 221–245.

Minson, D.J., Whiteman, P.C., 1989. A standard livestock unit (SLU) for defining stick rate in grazing studies. *Int. Grassl. Cong. Proc.* XVI, Nice, France. pp. 1117–1118.

Molina Alcaide, E., Martin Garcia, A.I., Augilera, J.F., 2000. A comparative study of nutrient digestibility, kinetics of degradation and passage and rumen fermentation pattern in goats and sheep offered good quality diets. *Livest. Prod. Sci.* 64, 215–223.

Müller, D.W.H., Codron, D., Meloro, C., Munn, A., Schwarm, A., Hummel, J., Clauss, M., 2013. Assessing the Jarman-Bell Principle: scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. *Comp. Biochem. Physiol.* A 164, 129–140.

Müller, D.W.H., Codron, D., Werner, J., Fritz, J., Hummel, J., 2012. Dichotomy of eutherian reproduction and metabolism. *Oikos* 121, 102–115.

Mulligan, F.J., Caffrey, P.J., Rath, M., Callan, J.J., O'Mara, F.P., 2001. The relationship between feeding level, rumen particulate and fluid

- turnover rate and the digestibility of soya hulls in cattle and sheep (including a comparison of Cr-mordanted soya hulls and Cr₂O₃ as particulate markers in cattle). *Livest. Prod. Sci.* 70, 191–202.
- Pearson, R.A., Archibald, R.F., 1990. Effect of ambient temperature and urea supplementation on the intake and digestion of alkali-treated straw by Brahman cattle and swamp buffaloes. *J. Agric. Sci.* 114, 177–186.
- Peyraud, J.L., Cameron, E.A., Wade, M., Lemaire, G., 1996. The effect of daily herbage allowance, herbage mass and animal factors upon herbage intake by grazing dairy cows. *Ann. Zootech. (Paris)* 45, 201–217.
- Poppi, D.P., Minson, D.J., Ternouth, J.H., 1980. Studies of cattle and sheep eating leaf and stem fractions of grasses. 1. The voluntary intake, digestibility and retention time in the reticulo-rumen. *Aust. J. Agric. Res.* 32, 99–108.
- Prigge, E.C., Baker, M.J., Varga, G.A., 1984. Comparative digestion, rumen fermentation and kinetics of forage diets by steers and wethers. *J. Anim. Sci.* 59, 237–245.
- Quick, T.C., Dehority, B.A., 1986. A comparative study of feeding behaviour and digestive function in dairy goats, wool sheep and hair sheep. *J. Anim. Sci.* 63, 1516–1526.
- Reid, R.L., Jung, G.A., Cox-Ganser, J.M., Rybeck, B.F., Townsend, E.C., 1990. Comparative utilization of warm and cool-season forages by cattle, sheep and goats. *J. Anim. Sci.* 68, 2986–2994.
- Sauvant, D., Schmidely, P., Daudin, J.J., St-Pierre, N.R., 2008. Meta-analyses of experimental data in animal nutrition. *Animal* 2, 1203–1214.
- Seth, D.N., Rai, G.S., Yadav, P.C., Pandey, M.D., 1976. A note on the rate of secretion and chemical composition of parotid saliva in sheep and goat. *Ind. J. Anim. Sci.* 46, 660–663.
- Sharma, V.V., Murdia, P.C., 1974. Utilization of berseem hay by ruminant. *J. Agric. Sci.* 83, 289–293.
- Sharma, V.V., Rajora, N.K., 1977. Voluntary intake and nutrient digestibility of low-grade roughage by ruminants. *J. Agric. Sci.* 88, 75–78.
- St-Pierre, N.R., 2001. Integrating quantitative findings from multiple studies using mixed model methodology. *J. Dairy Sci.* 84, 741–755.
- Südekum, K.-H., Röh, H., Brandt, M., Rave, G., Stangassinger, M., 1995. Comparative digestion in cattle and sheep fed wheat silage diets at low and high intakes. *J. Dairy Sci.* 78, 1498–1511.
- Van Soest, P.J., 1982. *Nutritional Ecology of the Ruminant*. O and B Books, Inc., Corvallis, OR, USA.
- Woods, V.B., Moloney, A.P., Mulligan, F.J., Kenny, M.J., O'Mara, F.P., 1999. The effect of animal species (cattle or sheep) and level of intake by cattle on in vivo digestibility of concentrate ingredients. *Anim. Feed Sci. Technol.* 80, 135–150.
- Yañez-Ruiz, D.R., Molina Alcaide, E., 2008. A comparative study of nutrients utilization, alkaline phosphatase activity and creatinine concentration in the serum of sheep and goats fed diets based on olive leaves. *J. Anim. Physiol. Anim. Nutr.* 92, 141–148.