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Feed digestibility, digesta passage and faecal microbial biomass in desert-adapted goats exposed to mild water restriction

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Abstract

In arid and semi-arid environments, extensively managed ruminants regularly experience drinking water shortage, especially in the dry season. The present study therefore investigated the effects of mild drinking water restriction on feed intake, feed digestibility, solid digesta passage and composition of faeces including faecal microbial biomass. A feeding trial was conducted in Oman, during the dry summer months.

Nine adult male Batinah goats were subjected to three watering regimes in a 3 × 3 Latin Square design. Treatments were (1) water offered *ad libitum* (100%, W100); (2) water restricted to 85% *ad libitum* consumption (W85); and (3) water restricted to 70% *ad libitum* consumption (W70). Animals were offered Rhodes grass hay and whole barley grains (1:1 ratio) at 1.3 times maintenance energy requirements. Each of the three experimental periods comprised 16 days of adaptation and 8 days of measurements. During the latter, feed offered and refused as well as faeces were sampled and quantified. Gastrointestinal digesta passage was determined using ytterbium-labelled Rhodes grass hay. Ergosterol and amino sugars were used as markers for faecal microbial biomass, that is the sum of fungi and bacteria. Water restriction had no effect on feed intake and digesta passage. However, feed dry matter, organic matter and fibre digestibility increased ($p < 0.05$) in W70 compared with W85, and the excreted amount of faecal dry matter, organic matter, nitrogen and neutral detergent fibre decreased ($p < 0.05$) in W70 compared with W85. Even though water restriction did not affect total faecal microbial biomass carbon (C) concentration, that of fungal biomass C increased ($p < 0.05$) in W70 compared with W85. Therefore, mild water restriction seems unproblematic from a physiological and nutrient utilization perspective as it increases feed digestibility without compromising feed intake.

KEYWORDS
amino sugars, Batinah goats, ergosterol, faecal microbial composition, rumen retention, water consumption

1 | INTRODUCTION

Many areas of the world are currently affected by water shortage (Mancosu et al., 2015). This problem was first thematised in the 1800s, aggravated in the 1900s and increased drastically from 1960 onwards (Kummu et al., 2010). Water shortage is believed to worsen in the future due to population pressure (Kummu et al., 2010; UN, 2017), increasing production of water-intensive food and non-food crops (ActionAid, 2015; Varis, 2007) as well as climate change (Gosling & Arnell, 2016). This also affects the livestock sector, especially in regions such as the Arabian Peninsula, where water scarcity is a natural phenomenon (Procházka et al., 2018).

Across the world's arid and semi-arid environments, goats are the most numerous mammalian livestock species (Aboul-Naga et al., 2014), reflecting their adaptation to harsh dryland conditions (Silanikove, 2000; Silanikove & Koluman, 2015). Previous studies have shown that compared with the other ruminant livestock species, goats are least affected by successive drought events (Aboul-Naga et al., 2014) and can survive up to a week with little or no water intake (Igbokwe, 1997). Several studies investigated the physiological processes that enable goats—as well as sheep—to tolerate prolonged and severe restriction of access to drinking water (Hamadeh et al., 2006; Jaber et al., 2004,2013; Mengistu et al., 2007). Even though the water supply from feed and metabolic processes must not be ignored (Misra & Singh, 2002), the former is especially important when green feed is abundantly available, which is normally not the case under dry season grazing conditions. Compared with drinking water intake, the contribution of water freed in metabolic processes, namely carbohydrate, protein and fat oxidation, is rather modest (Misra & Singh, 2002). Drinking water restriction decreased voluntary feed intake (Abdelatif & Ahmed, 1994; Alamer, 2006), enhanced feed digestibility (Burgos et al., 2001) and increased mean retention time of feed in the digestive tract (Brosh et al., 1986; Hadjigeorgiou et al., 2000). Water restriction further improved nutrient utilization (Hadjigeorgiou et al., 2000) due to increased time available for rumen microbes to act on the feed (Ahmed & El Shafei, 2001).

Substantial research has investigated the impact of severe water restriction on ruminants (Bohra & Ghosh, 1977; Brosh et al., 1986; Jaber et al., 2013; Silanikove, 2000). However, in many extensive husbandry systems of dry tropical and subtropical areas, domestic animals are facing severe water shortage during a few weeks of the late dry season only, when they may remain without drinking water for several days. During most of the dry season, in contrast, they may be watered once a day or on alternate days (e.g. Feldt & Schlecht, 2016) and, thus, face only mild water restriction. Yet, the few studies determining the effects of mild drinking water restriction on small ruminants (Casamassima et al., 2008; Hadjigeorgiou et al., 2000) were focussing on feed intake and animal performance under quite low average daily ambient temperatures (6.08°C and 18–22°C, respectively), ignoring the much higher average daily temperature ranges of 25–35°C typical for dry tropical and subtropical regions.

Furthermore, while several of the above-mentioned studies paid great attention to rumen fermentation, hindgut fermentation was hardly considered, probably because its contribution to total-tract nutrient digestion is substantially less than that of rumen fermentation (Gressley et al., 2011). A long distal colon is reported for various desert-adapted African antelopes (Woodall & Skinner, 1993), which points to the importance of this organ in water-limited ruminants. Therefore, the microbial population of domestic small ruminants' hindgut might probably also contribute to an improved nutrient utilization in water-restricted animals. Hindgut fermentation has been deduced from microbial concentrations in faeces (Plaizier, Li, Tun & Khafipou, 2017), and faecal microbial biomass can be characterized via amino sugars (Al-Kindi et al., 2015; Jost et al., 2011,2013) and ergosterol (Jost et al., 2011; Meyer et al., 2019).

Against this background, the present study aimed at determining the effect of mild water restriction on the digestibility of feed and its proximate nutrient and fibre fractions, solid digesta passage rate and composition of faecal microbial biomass in a desert-adapted goat breed during the normal hot summer conditions of a dry subtropical region. We hypothesized that in analogy to water deprivation, mild water restriction will (1) increase feed digestibility due to prolonged digesta retention time in the gastrointestinal tract and (2) increase faecal microbial biomass due to intensified hindgut fermentation.

2 | MATERIALS AND METHODS

2.1 | Experimental design

A trial was conducted during the dry summer period (August–October 2014) at the Animal Experimental Station of the Department of Animal and Veterinary Sciences, Sultan Qaboos University, Oman. Nine adult male Batinah goats of similar age (13 months) and live weight (26 kg, SD 5.3) were used as experimental animals. The horned Batinah breed is of medium size with mature male weight reaching about 33 kg. The long coarse hair can be of dark brown, light brown or black colour; white spots in the face, belly and lower limbs are frequent. The goats are reared for meat production and are managed in grazing-based medium-input systems (FAO Domestic Animal Diversity Information System; http://www.fao.org/dad-is/browse-by-country-and-species/en/). During the three experimental periods, the average daily ambient temperature, relative air humidity and the temperature–humidity index (THI) were 31.3°C, 63.5% and 81.9, respectively, with no rainfall occurrence (Table 1). Animal care and use were in accordance with the country regulations; the experimental protocol and procedures employed were ethically reviewed and approved by the Animal Ethics Committee at Sultan Qaboos University (SQU/AEC/2017-18/5A).

A pre-trial was conducted one month before the commencement of the first measurement period to determine the *ad libitum* water consumption for each animal. Animals were fed at a ratio of 1:1 with Rhodes grass hay (*Chloris gayana* Kunth.) and whole barley grains (*Hordeum vulgare* L.). They were offered 4 l of drinking water in two

TABLE 1 Meteorological data (period averages) as measured at Sultan Qaboos University, Muscat, Oman, during the three experimental periods

Parameter	Experimental periods in 2014		
	1 (13th–20th August)	2 (6th–13th September)	3 (30thSeptember–7th October)
Maximum daily ambient air temperature (°C)	34.8	35.5	37.2
Minimum daily ambient air temperature (°C)	26.7	27.1	24.8
Mean daily ambient air temperature (°C)	30.9	31.0	31.3
Relative air humidity (%)	70.5	70.1	50.0
Temperature–humidity index[a]	82.9	82.8	80.0

[a]The temperature–humidity index was calculated using the equation of NRC (1971): THI = (1.8 *T°C + 32)–[(0.55–0.0055 *RH %) *(1.8 *T°C–26)]. where T°C is the average daily air temperature [°C] and RH is the relative humidity [%].

TABLE 2 Chemical composition [g kg^{-1} DM] of Rhodes grass hay and barley grains as the experimental diet[a] components offered to the goats during the feeding trial

Component	Rhodes grass hay ($n = 6$)	Barley grains ($n = 4$)
DM [g kg^{-1} FM]	841 ± 3.0	927 ± 5.8
OM	910 ± 1.3	970 ± 2.4
N	7.3 ± 0.38	15.9 ± 0.35
NDFom	631 ± 8.2	245 ± 79.7
ADFom	358 ± 5.7	491 ± 3.2

Note: Values are arithmetic means ± standard deviation of six and four samples, respectively, across the three experimental periods.

Abbreviations: ADFom, Ash-free acid detergent fibre; DM, Dry matter; FM, Fresh matter; N, Nitrogen; NDFom, Ash-free neutral detergent fibre; OM, Organic matter.

[a]The mineral blocks contained 380,000 mg kg^{-1} sodium, 5000 mg kg^{-1} magnesium, 1,500 mg kg^{-1} iron, 300 mg kg^{-1} copper, 300 mg kg^{-1} zinc, 200 mg kg^{-1} manganese, 150 mg kg^{-1} iodine, 50 mg kg^{-1} cobalt and 10 mg kg^{-1} selenium.

portions at 08:00 h and 16:00 h for one week. The amounts of water and feed refused per animal and day were measured and recorded. Thereafter, the average water intake per day (ml d^{-1}) and per unit of dry matter intake (DMI; ml g^{-1} DMI) were calculated for each animal. The *ad libitum* water consumption for each animal was then defined with respect to its individual DMI.

The main experiment was subsequently conducted as a complete Latin Square (3 × 3) with the following regimes for the provision of drinking water (treatments): 1) water offered *ad libitum* (100%; treatment W100); 2) water restricted to 85% of individual *ad libitum* consumption (W85); and 3) water restricted to 70% of individual *ad libitum* consumption (W70). Water was offered in two equal portions (at 8:30 h and 16:30 h; each time roughly 30 min after feeding). The experiment entailed three periods, each comprising 16 days of adaptation and 8 days of measurement. During adaptation, the animals were individually housed in paddocks of ca. 2.25 m^2 in a large roofed stable with open sides. During measurement periods, the goats were kept in individual metabolic crates designed to ease collection of urine (not reported here) and feed samples, while faecal bags were used to collect faeces. All animals were weighed before morning feeding on two consecutive days before and after each experimental period, using a mechanical scale. The mean live weight (LW) of the animals in the beginning of the first phase of the main experiment was 26.4 kg (SD 5.24).

2.2 | Feed and feeding

Animals were fed at 1.3 times individual maintenance energy requirement according to NRC feeding standards (NRC, 2007). Before commencing the experiment, all rations for every meal and animal were weighed and stored in paper bags until feeding. This was done to ensure that the diet's chemical composition (Table 2) between the experimental periods was similar. Feed was offered in two equal portions at 8:00 h and at 16:00 h, with barley grains offered first. After the barley grains were completely consumed (within 5–10 min), the Rhodes grass hay was offered. Protein-free mineral blocks were made available to each animal throughout the experiment.

2.3 | Determination of feed and water intake

During each measurement period, about 250 g fresh matter (FM) of each of the feeds offered were collected in duplicate and stored in paper bags at room temperature. There were no refusals of barley. Hay refusals were collected for each animal separately twice daily before every meal during the measurement period. At the end of a measurement period, hay refusals for each animal were pooled and thoroughly mixed. Two representative sub-samples of approximately 100 g DM each were then taken from the pooled samples and stored in paper bags at room temperature until analysis.

The volume of drinking water offered to each animal (with reference to the water treatment) was measured using a calibrated cylinder and supplied in buckets in two equal portions at 08:30 h and 16:30 h. One hour before morning as well as evening feeding, the buckets were removed from the metabolic cages and the water

refused was recorded for each animal. After washing the buckets, fresh water was offered according to the treatment for each animal. Drinking water intake (further on termed water intake) was determined as the difference between water offered and refused for each individual animal.

2.4 | Determination of particulate passage rate

Fibre particles marked with ytterbium (Yb) were used to determine the passage rate of solid digesta through the gastrointestinal tract. Rhodes grass hay was chopped to about 3 cm-long pieces, then sieved through a 2 mm mesh to remove small particles. Pieces remaining on the sieve were boiled in EDTA-free neutral detergent solution for one hour and then rinsed repeatedly with tap water until all detergent was removed. Washed hay particles were dried at 70°C and afterwards soaked for 24 h in 12.4 mmol l^{-1} aqueous solution of $Yb(CH_3COO)_3 . 4H_2O$ (Teeter et al., 1984). To ensure that all particles were marked, the soaked fibre was mixed twice within 24 h and subsequently thoroughly rinsed with tap water. Afterwards, the particles were soaked for 6 h in a solution of 100 mmol l^{-1} of acetic acid to discard unabsorbed Yb, and again thoroughly rinsed with tap water and dried at 70°C. About 25 g of the marked fibre was kept for determination of the Yb concentration.

On the first day of each measurement period, each animal was offered a small quantity of marked fibre particles corresponding to 5.6 mg Yb kg^{-1} LW. In instances where goats refused to consume the marked fibre immediately, 5–30 g hay was mixed with the marked fibre. Starting time (t_0) for determination of marker passage for each goat was defined as the time when the animal had completely eaten the marked fibre. In situations where the ingestion of marked fibre took longer than 30 min, t_0 was set at half time of marker consumption. Faecal bags were emptied at 0, 6, 12, 18, 24, 30, 36, 42, 50, 58, 66, 74, 86, 98, 110, 122, 134, 146 and 158 h after dosing the Yb-marked fibre. Samples were identified by animal, day and collection time. The total amount of faeces (on FM basis) was recorded at each time of collection. A thoroughly homogenized sub-sample of 50–60 g of faecal FM was kept each time the bag was emptied and was dried at 60°C for the determination of air-dry matter; afterwards, all samples were stored in sealed paper bags at room temperature until Yb analysis.

2.5 | Determination of total faecal output

After taking sub-samples for Yb and microbial biomass determination (see 2.4 and 2.8), all faeces remaining were stored at 4°C until the end of the measurement period. Pooled faeces were then thoroughly homogenized and two representative sub-samples of about 250 g FM each were stored at −20°C for proximate analysis. Total faecal output per animal and measurement period was calculated as the sum of the amount of bulked faeces plus sum of sample weights collected for Yb and microbial biomass determination.

2.6 | Proximate nutrient and fibre analyses of feed and faeces

Faecal samples were thawed before commencement of analysis. Rhodes grass hay offered and refused, offered barley grains and faeces were oven-dried at 60°C and ground to pass through a 1-mm screen (Retsch ZMI mill). Analyses were done according to the methods of VDLUFA (2012; method numbers given in parenthesis). The samples were analysed for their dry matter (DM) concentration by drying to constant weight for 24 h at 105°C (method 3.1). Crude ash (CA) concentration was determined in dried solids after DM analysis by incineration at 550°C in a muffle furnace for 7 h (method 8.1). Organic matter (OM) concentration was calculated as the difference between DM and CA. All analyses were conducted in duplicate.

Neutral detergent fibre (NDF) and acid detergent fibre (ADF) in feed and faecal samples were determined in duplicate using an Ankom^{220} Fibre Analyser (ANKOM Technology), thereby following the procedure of Van Soest et al. (1991). Alpha-amylase and sodium sulphite were used for NDF analysis. ADFom and NDFom concentrations were expressed without residual ash. Nitrogen (N) contents of oven-dried feed and faeces were determined in duplicate by means of a VarioMax CHN (Elementar Analysensysteme, Hanau, Germany). All analyses were repeated when the results for duplicate determinations deviated by more than 5%.

The quantitative intake of nutrients and fibre fractions and the quality of the ingested diet were calculated based on the respective differences between the offered feed and the feed refusals. The apparent total-tract feed digestibility (for simplicity termed 'digestibility' in the following text) of chemical constituents was calculated from the difference between the quantity of constituent ingested minus the quantity of constituent excreted in faeces divided by the quantity of constituent ingested. Digestibility was expressed in [g kg^{-1}] of the specific nutrient.

2.7 | Faecal ytterbium concentration

The concentration of Yb was determined following the method of Heinrichs et al. (1986) with some modifications. About 200 mg of the oven-dried (60°C) samples of marked fibre and faeces were treated with 0.5 ml double-distilled water and later mixed with 1 ml hydrogen peroxide and 3 ml of 65% (v/v) nitric acid. The sample was then digested at 198°C for 1 hour in Teflon® vessels. The residue was rinsed with double-distilled water into a 50-ml flask and filtered over ash-free Whatman 40 filter paper. Of the sample, 1 ml was further diluted to 10 ml before analysis. The Yb concentration of each sample was determined as the average of three independent readings using an inductively coupled plasma mass spectrometer (ICP-MS; Optimass 9500, GBC Scientific Equipment Australia) and was detected at a wavelength of 396.4 nm.

2.8 | Microbial biomass analysis

Microbial residues in faeces were identified on the basis of amino sugars occurring in the cell walls of bacteria and fungi (Al-Kindi et al., 2015; Jost et al., 2011,2013). To differentiate between the latter two groups, fungal biomass was determined based on ergosterol, an important constituent of fungal cell walls (Jost et al., 2011). Freshly excreted faecal samples were collected by emptying the faecal bags at one hour after morning feeding on days 2, 4 and 6 of each measurement period. About 30 g of fresh faeces were collected and immediately frozen at −20°C. Samples from the three days per measurement period were pooled, thoroughly homogenized, and a subsample of 50 g of the pooled material was freeze-dried, ball-milled and stored at room temperature until analysis.

Extraction of ergosterol was done following the method of Zelles et al. (1987), applying modifications as described by Wentzel and Joergensen (2015). Reversed-phase high-performance liquid chromatography was used to establish ergosterol concentrations, which were detected at a wavelength of 282 nm. The amino sugars muramic acid, mannosamine, glucosamine and galactosamine were determined by chromatographic separation using *ortho*-phthaldialdehyde reagent as described by Indorf et al. (2011). Analyses were repeated for both ergosterol and amino sugars if triplicate determinations for each pool sample deviated by more than 8%. Fungal C was calculated as follows:

mmol fungal C = (mmol glucosamine-2 × mmol muramic acid) × 9 (Engelking et al., 2007).

Bacterial C was calculated as an index for bacterial residues by multiplying the concentration of muramic acid by 45 (Appuhn & Joergensen, 2006). Microbial C was calculated as the sum of fungal C plus bacterial C.

2.9 | Statistical analyses

Quantitative outflow of Yb, that is its concentration in faeces DM multiplied by faecal DM excreted at the respective point in time, was used to calculate parameters of solid digesta passage through the gastrointestinal tract, applying the models of Richter and Schlecht (2006). Ytterbium leaching due to disassociation from fibre particles was observed in four cases, to which the disassociation model ('Type-D model') was applied. The normal model ('Type-N model') was used in all other cases (Richter & Schlecht, 2006).

Model computation (PROC NLIN method = dud) was used to determine time of first marker appearance in faeces (TT), passage rate of fibre-bound marker through the rumen (λ, Gamma-2 parameter), half time of marker in the rumen (T_{50}: $0.8392 \times 2\lambda^{-1}$), particle mean retention time in the rumen (CMRT: $2\lambda^{-1}$) and particle mean retention time in the total tract (TMRT: $TT + 2\lambda^{-1}$).

In total, 27 observations were obtained for data on water intake, feed intake, feed digestibility, parameters of digesta passage, faecal quantity and microbial biomass (3 periods × 9 animals). The data were tested for normal distribution using the Shapiro–Wilk test (UNIVARIATE procedure). All data sets were normally distributed. Analysis of variance was thereafter conducted by means of a mixed-model procedure with treatment and period as the fixed effects and animal as a random factor. The model used was:

$$y_{ijk} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + T_k + e_{ijkl}$$

where y_{ijk} is the value of the response variable for a particular ijk case, μ is the overall mean, α_j and β_k are the fixed effects of treatment and period, respectively, $\alpha\beta_{ij}$ is the interaction of treatment and period, T_k the random effect variable (animal), and e_{ijkl} is the residual error.

Interactions between period and treatment were derived from the model using type-3 tests of fixed effects. Means of treatments, periods and treatment x period interactions were compared using the Tukey post hoc test, and significance was declared at $p < 0.05$. To test the relationship between individual variables of diet quality, quantitative intake of feed and water and individual rate of passage parameters, linear correlation statistics and probabilities were computed using the REG procedure. All statistical analyses were performed using SAS 9.3 (SAS Institute).

3 | RESULTS

3.1 | Water intake, feed intake, faecal excretion and digestibility

Accounting for the animals' weight, water consumption [ml $kg^{-0.75}$ LW] was 1.12 times lower ($p > 0.05$) in goats subjected to W70 than that of goats at W85. Similarly, water intake per unit of ingested feed [ml g^{-1} DMI] was numerically lower in W70 than in W85 goats (Table 3). However, water intake of W85 goats was numerically higher ($p > 0.05$) than of W100 goats, and there were significant interactions between treatment and experimental period for the tested water intake variables (Table 3). This is due to the fact that in experimental periods 1 and 2, goats allocated to W85 were heavier than those of W100 (period 1: 26.4 vs. 23.9 kg LW; period 2: 24.5 vs. 23.8 kg LW; $p > 0.05$). Even though daily amount of water offered per animal was lower for W85 than for W100 (period 1: 1477 vs. 1783 ml; period 2: 1493 vs. 1603 ml), the daily water refusals per animal were higher in W100 than in W85 (period 1: 889 vs. 306 ml; period 2: 657 vs. 423 ml). This resulted in a lower drinking water intake of W100 as compared to W85 animals in two out of three experimental periods and a slightly higher overall water consumption of W85 as compared to W100 goats across the whole experiment. Therefore, in the following, the effects of mild water restriction are primarily examined by comparing W70 to W85. Since data provided by the meteorological station were averaged per measurement period, it was not possible to test whether period differences in ambient temperatures and air humidity, or THI, were causal for statistically significant effects of period or treatment x period interactions.

Daily intake [g $kg^{-0.75}$ LW] of DM, OM, N, NDFom and ADFom was not affected by treatment (Table 3), but intake of N and NDFom

TABLE 3 Live weight, intake of water and feed, faecal excretion and diet digestibility as measured in adult male Batinah goats exposed to treatments (Trt) of no (W100) or mild restriction to 85% (W85) and 70% (W70) of individual *ad libitum* water consumption. Values are arithmetic means of (n = 9) goats per Trt across three experimental periods (Per)

	Treatment				*p*-values		
Variable	W70	W85	W100	SEM	Trt	Per	Trt × Per
Live weight [kg]	26.1	26.5	26.3	0.97	0.99	0.72	0.06
Water intake per day [ml animal^{-1}]	965	1083	1033	35.6	0.30	0.54	0.03
-"- [ml g^{-1} DMI]	1.6	1.8	1.8	0.05	0.20	0.20	0.02
-"- [ml kg$^{-0.75}$ LW]	84	94	89	2.4	0.17	0.95	0.05
Feed intake per day [g kg$^{-0.75}$ LW]							
DM	52.2	52.2	51.2	0.85	0.46	0.44	0.30
OM	49.3	49.3	48.4	0.92	0.46	0.43	0.30
N	0.67	0.66	0.66	0.010	0.62	0.01	0.54
NDFom	22.2	22.5	21.8	0.54	0.57	0.01	0.27
ADFom	9.9	10.2	9.7	0.27	0.50	0.20	0.21
Faecal excretion per day [g kg$^{-0.75}$ LW]							
DM	14.5^{b}	16.5^{a}	14.3^{b}	0.44	0.04	0.58	0.26
OM	13.1^{b}	14.9^{a}	12.8^{b}	0.42	0.04	0.57	0.27
N	0.24^{b}	0.27^{a}	0.24^{b}	0.007	0.06	0.65	0.70
NDFom	7.3^{b}	8.3^{a}	7.2^{b}	0.24	0.03	0.48	0.24
ADFom	4.4	4.8	4.2	0.15	0.15	0.54	0.41
Apparent digestibility [g kg^{-1}]							
DM	722^{a}	683^{b}	723^{a}	7.5	0.04	0.21	0.21
OM	734^{a}	696^{b}	737^{a}	7.5	0.05	0.23	0.26
N	637^{a}	581^{b}	632^{a}	13.4	0.05	0.01	0.68
NDFom	668^{a}	630^{b}	667^{a}	8.3	0.08	0.03	0.49
ADFom	553	528	571	10.9	0.32	0.23	0.76

Note: Within rows, means with different superscripts differ at $p < 0.05$ (Tukey post hoc test).

Abbreviations: ADFom, Ash-free acid detergent fibre; DM, Dry matter; DMI, Dry matter intake; LW, Live weight; N, Nitrogen; NDFom, Ash-free neutral detergent fibre; OM, Organic matter; SEM, Standard error of the mean.

TABLE 4 Composition of ingested feed (ingesta) and faeces as measured in adult male Batinah goats exposed to treatments (Trt) of no (W100) or mild restriction to 85% (W85) and 70% (W70) of individual *ad libitum* water consumption

	Treatment				*p*-values		
Variable	W70	W85	W100	SEM	Trt	Per	Trt × Per
Ingesta composition [g kg^{-1} DM]							
OM	945	944	945	4.3	0.27	0.86	0.45
N	12.0	11.9	12.1	0.18	0.12	0.01	0.12
NDFom	424	432	425	9.1	0.32	0.01	0.38
ADFom	189	194	188	2.2	0.62	0.29	0.22
Faeces composition [g kg^{-1} DM]							
OM	902^{a}	905^{a}	894^{b}	1.8	0.02	0.38	0.88
N	16.6	16.6	17.2	0.34	0.13	0.52	0.03
NDFom	504	505	508	8.8	0.96	0.86	0.21
ADFom	305	291	289	4.8	0.25	0.88	0.33

Note: Values are arithmetic means of (n = 9) goats per Trt across three experimental periods (Per). Within rows, means with different superscripts differ at $p < 0.05$ (Tukey post hoc test).

Abbreviations: ADFom, Ash-free acid detergent fibre; DM, Dry matter; N, Nitrogen; NDFom, Ash-free neutral detergent fibre; OM, Organic matter; SEM, Standard error of the mean.

was affected by measurement period. Thereby, N intake was higher ($p < 0.001$) in period 3 (0.66 g N $kg^{-0.75}$ LW) than in periods 1 and 2 (0.58 and 0.61 g N $kg^{-0.75}$ LW), whereas intake of NDFom was higher ($p < 0.001$) in period 1 (23.7 g NDFom $kg^{-0.75}$ LW) than in periods 2 and 3 (18.0 and 18.9 g NDFom $kg^{-0.75}$ LW). None of the intake variables [DM, OM, N, NDFom, ADFom; g $kg^{-0.75}$ LW] was related to water consumption per kilogram of metabolic weight ($r^2 < 0.07$ in all cases).

The quantitative excretion [g $kg^{-0.75}$ LW] of faecal DM and OM was lower ($p < 0.05$) in W70 goats as compared with W85 goats. Also, faecal excretion of NDFom decreased by 14% with W70 as compared with W85 (Table 3), whereas no treatment differences were observed for the faecal excretion of ADFom. As a consequence, there were no treatment differences in the digestibility of ADFom. Compared with W85, the digestibility of DM and OM increased by 5% ($p = 0.03$) and the digestibility of NDFom by 6% ($p < 0.05$) with W70 (Table 3). N digestibility in period 3 was higher than in periods 1 and 2 (881 vs. 852 and 844 g kg^{-1}; $p < 0.01$), and digestibility of NDFom was higher in period 1 than in period 3 and period 2 (706 vs. 656 vs. 584 g kg^{-1}; $p < 0.05$).

3.2 | Diet composition, faecal quality and digesta passage

Water restriction to 85% and 70% of *ad libitum* intake had no effect on the quality of the actually consumed diet (Table 4), that is the concentration [g kg^{-1} DM] of OM, N, NDFom and ADFom. Ingesta concentrations of N as well as of NDFom were significantly different in each period (periods 1, 2 and 3: 11.7 vs. 12.5 vs. 13.7 g N kg^{-1} DM; $p < 0.05$; 475 vs. 370 vs. 393g NDFom kg^{-1} DM; $p < 0.05$). Faecal OM concentration [g kg^{-1} DM] increased with W85 and W70 as compared with W100 ($p < 0.05$). Faecal ADFom concentration only numerically increased when water was restricted at W70. There were no significant interactions between treatment and measurement period for ingesta and faeces quality parameters.

Across treatments, all parameters of solid digesta passage were similar (Table 5), even though transit time (TT) of fibre particles through the lower gastrointestinal tract and TMRT were numerically shortest ($p > 0.05$) with W70 as compared with the two other treatments. There were no interactions between treatment and period for all parameters of particle passage, but there was a significant effect of period on T50 and CMRT, with, in both cases, a higher ($p < 0.05$) value in period 3 (T_{50}: 37.1 h; CMRT: 44.3 h) as compared to periods 1 and 2 (T_{50}: 32.8 and 32.1 h; CMRT: 39.1 and 38.3 h). Simple linear regression analysis indicated that λ, T_{50}, CMRT and TMRT were significantly related to the animals' LW ($r = 0.65$; $p < 0.001$ for λ, T_{50} and CMRT; $r = 0.52$; $p < 0.01$ for TMRT). The daily amount of water drunk was significantly related to all passage rate parameters except TT (Table 6), but correlations disappeared when water intake was corrected for metabolic weight. Water drunk per kilogram of ingested feed DM only correlated with TMRT. TT, on the other hand, was positively related to the daily intake [g $kg^{-0.75}$ LW] of DM, OM and ADFom (Table 6), but was not affected by daily N intake ($r^2 < 0.075$ for TT and all other passage rate parameters). By contrast, TMRT was negatively correlated with daily intake of DM, OM, NDFom and ADFom. The digestibility of any of the proximate constituents (DM, OM, N, NDFom, ADFom) was at best weakly correlated to individual parameters of particulate passage, with the highest regression coefficient obtained for the (negative) correlation between OM digestibility and λ ($r^2 = 0.127$, $p > 0.05$).

3.3 | Faecal microbial composition

The faecal ergosterol concentration was numerically highest with W70 as opposed to the other two treatments (Table 7); however, ergosterol concentrations were also higher ($p < 0.05$) in period 1 (1.91 μg g^{-1} DM) than in periods 2 and 3 (both 1.60 μg g^{-1} DM). The faecal concentration of fungal glucosamine was higher ($p = 0.01$) with W70 compared with W85. On the other hand, there were no treatment differences for faecal concentrations of muramic acid, galactosamine and mannosamine. Significant period effects and treatment by period interactions manifested for fungal glucosamine, which decreased from 1.41 μg g^{-1} DM in period 1 to 1.32 and 1.12 μg g^{-1} DM in periods 2 and 3 ($p < 0.05$).

TABLE 5 Parameters of the gastrointestinal passage of feed particles in adult male Batinah goats exposed to treatments (Trt) of no (W100) or mild restriction to 85% (W85) and 70% (W70) of individual *ad libitum* water consumption

	Treatment				*p*-values		
Parameter	W70	W85	W100	SEM	Trt	Per	Trt × Per
TT [h]	16.7	17.1	17.3	0.63	0.94	0.68	0.25
λ [h^{-1}]	0.053	0.054	0.050	0.0023	0.49	0.14	0.67
T_{50} [h]	32.5	33.4	35.1	1.53	0.46	0.04	0.78
CMRT [h]	38.7	39.8	41.9	1.82	0.46	0.04	0.80
TMRT [h]	55.4	56.9	59.1	1.86	0.55	0.10	0.98

Note: Values are arithmetic means of ($n = 9$) goats per Trt across three experimental periods (Per).
Abbreviations: CMRT, Particle mean retention time in the rumen; SEM, Standard error of the mean; $T_{50,}$ Half time of marker in the rumen; TMRT, Particle mean retention time in the total tract; TT, Time of first marker appearance in faeces; λ, Passage rate of fibre-bound marker through the rumen.

TABLE 6 Correlation coefficients (r) and significance levels[a] of the individual linear relationships between drinking water intake, ingesta composition and quantitative intake with parameters of particulate passage in adult male Batinah goats exposed to treatments of no or mild restriction of drinking water consumption

	Passage rate parameter				
Variable	**TT [h]**	**λ [h^{-1}]**	**T_{50} [h]**	**CMRT [h]**	**TMRT [h]**
Water intake per day [ml $animal^{-1}$]	-0.02	−0.50**	0.51**	0.51**	0.49*
-"-[ml g^{-1} DMI]	0.20	−0.29	0.33	0.33	0.39*
-"- [ml $kg^{-0.75}$ LW]	0.34	0.05	−0.04	−0.04	0.08
Ingesta composition [g kg^{-1} DM]					
OM	-0.17	−0.55**	0.59**	0.59**	0.53**
ADFom	0.34	0.54**	−0.62**	−0.62**	−0.48*
Intake per day [g $kg^{-0.75}$ LW]					
DM	0.33	0.64***	−0.68***	−0.68***	−0.55**
OM	0.33	0.63***	−0.68***	−0.68***	−0.55**
NDFom	0.11	0.40*	−0.43*	−0.43*	−0.39*
ADFom	0.35	0.60**	−0.66***	−0.66***	−0.52**

Note: All coefficients are based on 27 observations per variable.

Abbreviations: ADFom, Ash-free acid detergent fibre; CMRT, Particle mean retention time in the rumen

DM, Dry matter; DMI, Dry matter intake; LW, Live weight; NDFom, Ash-free neutral detergent fibre; OM, Organic matter; $T_{50,}$ Half time of marker in the rumen; TMRT, Particle mean retention time in the total tract; TT, Time of first marker appearance in faeces;.λ, Passage rate of fibre-bound marker through the rumen.

[a]Significance levels: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; insignificant relationships between variables have no asterisk.

TABLE 7 Concentrations of ergosterol, amino sugars, microbial C, fungal and bacterial C in faeces excreted by adult male Batinah goats exposed to treatments (Trt) of no (W100) or mild restriction to 85% (W85) and 70% (W70) of individual *ad libitum* water consumption

	Treatment				*p*-values		
Variable	**W70**	**W85**	**W100**	**SEM**	**Trt**	**Per**	**Trt ×Per**
Ergosterol [μg g^{-1} DM]	1.8	1.7	1.7	0.11	0.64	0.025	0.54
Amino sugars [mg g^{-1} DM]							
Mannosamine	0.22	0.28	0.25	0.02	0.39	0.84	0.58
Muramic acid	0.62	0.65	0.61	0.04	0.89	0.58	0.16
Galactosamine	1.7	1.7	1.5	0.07	0.44	0.29	0.13
Glucosamine	2.3	2.1	2.1	0.10	0.51	0.22	0.29
Fungal glucosamine	1.4^{b}	1.2^{a}	1.3^{ab}	0.08	0.03	0.01	0.01
Microbial C [mg g^{-1} DM]							
Fungal C	12.2^{b}	10.4^{a}	11.7^{ab}	0.74	0.03	0.01	0.01
Bacterial C	28.0	29.1	27.7	1.64	0.93	0.52	0.20
Microbial C	41.0	40.1	38.9	1.72	0.87	0.58	0.40
Fungal to bacterial C ratio	0.51	0.38	0.46	0.038	0.22	0.09	0.23
Fungal to microbial C ratio	0.33	0.27	0.30	0.017	0.28	0.14	0.16

Note: Values are arithmetic means of ($n = 9$) goats per Trt across three experimental periods (Per). Within rows, means with different superscripts differ at $p < 0.05$ (Tukey post hoc test). Ergosterol = constituent of fungal cell walls. Mannosamine and galactosamine = found in both, fungal and bacterial cell walls. Muramic acid = found exclusively in bacterial cell walls. Glucosamine = found mostly in fungi, but also in some bacterial cell walls.

Abbreviation: C, Carbon; SEM, Standard error of the mean.

Faecal microbial C concentration tended to be higher ($p > 0.05$) with W70 as opposed to the other two treatments (Table 7). While bacterial C concentration of faeces was not affected by treatment, fungal C concentration in faeces increased by 1.79 mg g^{-1} DM with W70 compared with W85. In consequence, the fungal to bacterial C ratio was—numerically—higher with W70 than with the other two treatments. In parallel to fungal glucosamine, fungal C was significantly affected by period and treatment by period interactions and decreased from 12.5 mg g^{-1} DM in period 1 to 11.7 mg g^{-1} DM in period 2 and 10.0 mg g^{-1} DM in period 3 ($p < 0.05$).

4 | DISCUSSION

4.1 | Effects of mild water restriction on feed intake, digesta passage and feed digestibility

No changes in feed intake were observed when water intake was reduced in the present study. This contrasts the established view that drinking water restriction reduces voluntary feed intake due to changes in metabolic energy and water fluxes (Kaliber et al., 2015; Silanikove, 1989,1992). Brosh et al. (1986) reported a drop in feed intake by 40% when daily water intake in Bedouin goats fed alfalfa hay decreased by 109 ml $kg^{-0.75}$ LW. The current results are most likely due to the fact that daily drinking water intake at W70 was only 10 and 5 ml $kg^{-0.75}$ LW (11% and 6%) lower compared with W85 and W100, respectively, which may not have been so severe as to have a negative impact on feed intake. Our findings are in line with those obtained in Comisana sheep fed a diet of mixed field hay, alfalfa pellets and pelleted concentrate and being restrained to 60% of *ad libitum* water consumption (Casamassima et al., 2008). Feed intake was also not affected in Karagouniko sheep fed alfalfa hay when water intake was restricted to 65% of *ad libitum* consumption (Hadjigeorgiou et al., 2000). It therefore seems that a mild restriction of water consumption has no effect on feed intake regardless of the type of feed offered.

Level of water intake and, when accounting for the animals' metabolic weight, also the absolute reduction in drinking water intake, did not significantly affect mean gastrointestinal retention time of feed particles in the present study, probably due to the positive relationship between feed intake and reticulo-rumen fill (Clauss et al., 2016). Since feed intake was not affected by treatment, the gastrointestinal fill may have been similar across treatments, leading to a constant particle mean retention time even when water intake was restricted. This may also explain the observed positive correlation between intake of DM, OM, NDFom and ADFom, and the rate of particle passage through the rumen (λ), which is however a frequently observed phenomenon (Doreau et al., 2003). Contrary to our findings, mean particle retention time in the gastrointestinal tract has been shown to increase with decreasing water intake (Brosh et al., 1986; Hadjigeorgiou et al., 2000). The incongruity of our findings with Brosh et al. (1986) may be explained by the more severe water restriction to their Bedouin goats that were watered only once every 4 days and kept outdoors at ambient temperatures of up to 35°C. However, the average TMRT of 57 h recorded in the present study was very similar to the values reported for desert-adapted goats watered once daily and fed Rhodes grass hay (Silanikove et al., 1993), whereby these authors did not report drinking and total water intake.

The digestibility values of DM, OM and ADFom increased with decreasing water intake in the present study. This is consistent with results obtained for sheep by Nejad et al. (2014) and with those of Muna and Ammar (2001) who reported an increase in the digestibility of DM, OM and crude fibre in Sudanese desert goats. Yet, these authors fed high-quality alfalfa hay and reported a much lower water intake (570 ml per animal and day) compared with the present study. Enhanced digestibility following water restriction is believed to be associated with depressed feed intake and an associated increase in the mean digesta retention time (Ghassemi et al., 2014; Singh et al., 1976), but in the current study neither feed intake nor mean retention time of digesta were significantly affected by the level of water intake, although numerically digesta was retained for a shorter time when water intake decreased from W100 to W85 and W70. However, passage rate parameters did neither correlate with the amount of water drunk per kilogram of metabolic weight or kilogram of ingested feed DM, respectively, nor with the digestibility of proximate nutrient and fibre constituents. This disagrees with our first hypothesis that feed digestibility will increase due to longer mean retention time of digesta in the gastrointestinal tract if water restriction increases. Our results indicate that water restriction affected the digestibility of feed in other ways than through altered digesta kinetics at the investigated levels. Factors that may have been involved in the better feed digestibility for W70 as compared with W85 could be the relatively high proportion of grain in the animals' diet and hence increased rumen fermentation (Igbokwe, 1997) independent of the watering treatment.

4.2 | Effects of mild water restriction on quantitative faecal excretion

Total faecal DM, OM, N and NDFom excretion significantly decreased when water intake was reduced in the present study. This was expected considering the increased digestibility of the above-mentioned nutrients at reduced water intake. Similarly, quantitative faecal OM and N excretion decreased when South African Mutton Merino sheep fed a low-N diet were restricted to 50% of their *ad libitum* water intake (Van der Walt et al., 1999). The decrease in faecal DM excretion when water intake declines is thought to be a water conserving mechanism adopted by ruminants facing drinking water shortage (Adogla-Bessa & Aganga, 2000). During water restriction, the hindgut plays a regulatory role by re-absorbing moisture from boluses, thereby reducing the amount of faecal output (Bohra & Ghosh, 1977). However, water content of fresh faeces was similar for all current treatments; this is in line with Clauss et al. (2016) who reported that, in contrast to physiological changes in reticulo-rumen and small intestine, water reabsorption in the large intestine does not flexibly adapt to variations in feed intake or water restriction in sheep. A reduction in the total amount of faeces excreted therefore seems crucial for the maintenance of the water economy, especially when water intake is limited.

4.3 | Effects of mild water restriction on faecal microbial biomass

The present faecal concentrations of the different amino sugars as well as the calculated values of bacterial, fungal and total microbial C were similar to those reported for Boer goats fed temperate meadow

grass hay and a concentrate mix and having *ad libitum* access to drinking water (Al-Kindi et al., 2015). Furthermore, differences in total faecal microbial biomass between our watering treatments did not reach the significance level, which contradicts our second hypothesis that faecal microbial biomass will increase when water intake is restricted. This is most likely due to the relatively mild level of water restriction imposed on the animals in the present study.

Despite the unaltered total faecal microbial biomass concentration in water-restricted goats in the present study, the faecal microbial community structure shifted towards fungi when water intake was restricted. In the large intestine, digestion of the remaining diet components depends on the availability of unfermented and undigested carbohydrates (Van Vliet et al., 2007). Due to the high NDFom concentration in the diet offered to the goats in the present study, a certain share of this fraction may not have been fully fermented in the rumen, rendering it available to microbial fermentation in the hindgut. Yet, fibre entering the hindgut is much more difficult to degrade and the time available for degradation is shorter; this is due to the smaller volume of the hindgut as compared with the rumen (Gressley et al., 2011; Zeitz et al., 2016). Consequently, higher oxygen concentrations in the hindgut and the increased presence of undigested cell wall components promote saprotrophic fungi (Meyer et al., 2019), which are the dominant decomposers of lignified cellulose (Lynd et al., 2002). In contrast, the time for fibrolytic bacteria is too short to establish or proliferate in the hindgut (Zeitz et al., 2016). This was affirmed by De Oliveira et al. (2013) who reported an absence of *Fibrobacter* spp. in faeces of Brazilian Nellore steers. As water restriction is associated with an increased feed digestibility (Burgos et al., 2001), which was confirmed in the present study, the digestion of the remaining fibre fractions is associated with an increase in fungal biomass in the hindgut.

4.4 | Potential benefits of mild water restriction on nutrient cycling

Goat faeces are an important soil amendment in Oman (Siegfried et al., 2013) and other subtropical and tropical countries. Consequently, the fibre fractions present in the faeces are of importance as they will be slower decomposed by soil microorganisms, when used as fertilizer (Al-Asfoor et al., 2012). The faeces excreted by W70 goats were rich in ADFom, consisting essentially of lignified cellulose (Yan et al., 2018). For this reason, decomposition in the soil will be relatively slow and will lead to stronger N-immobilization (Jost et al., 2013) compared with faeces with a lower ADFom concentration excreted by goats watered *ad libitum*. However, studies have shown that ruminant faeces N is released by soil microbial decomposition in the long term and is eventually taken up by plants (Chadwick et al., 2000; Morvan & Nicolardot, 2009; Peters & Jensen, 2011). Thus, the decelerated decomposition of faecal N and C constituents may reduce methane as well as nitrous oxide emissions and nitrate leaching from faeces of water-restricted goats. This might be even true under the high temperatures and regular irrigation regimes that characterize crop farming in semi-arid and arid areas of the Near and Middle East and beyond (Siegfried et al., 2011,2013).

5 | CONCLUSIONS

A mild restriction of drinking water consumption in desert-adapted goats does not compromise their feed intake. Goats were able to improve feed utilization through increased digestibility when restricted to 70% of *ad libitum* water intake. A higher concentration of slowly decomposable carbohydrates in faeces of water-restricted animals may contribute to a stable soil organic carbon pool if such faeces are used as manure. Mild water restriction, as regularly encountered during the long dry season of arid and semi-arid regions, can therefore be considered harmless or even beneficial in terms of feed utilization and advantageous for nutrient recycling via manure at farm level.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest concerning the publication of this manuscript.

ANIMAL WELFARE STATEMENT

The authors confirm that the ethical policies of the journal have been adhered to and the appropriate ethical review committee approval has been received. The authors confirm that they have followed the host country's (Sultanate of Oman) standards for the protection of animals used for scientific purposes.

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