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Diurnal patterns of urination and drinking by grazing ruminants: a development in a mechanistic model of a grazing ruminant, MINDY

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Abstract

Measurement of water consumption and urinary nitrogen (UN) excretion of individual grazing ruminants is difficult, time-consuming and expensive. Therefore, prediction and modelling are critical for research to improve N and water use efficiency. The objective of the current work was to use a mechanistic model of a grazing ruminant, MINDY, to represent drinking and urination diurnal patterns, and the resulting pattern of UN excretion. This work is primarily an integration of existing knowledge of basic urination physiology and water dynamics in ruminants. MINDY reproduces observed patterns of urination achieving the correct temporal occurrence, relative volumes and nitrogen (N) concentration of individual urination events for a grazing dairy cow, comparable with those reported in the literature. The model simulates daily water imbibed and UN realistically, as well as ingestion rates for herbages with different protein content and contrasting grazing managements. Results of a cross-validation indicate that the root mean square prediction error and mean absolute error as % of the observed mean, respectively, were 26 and 23% for daily water imbibed, 26 and 27% for urination volume, and 25 and 19% for the frequency of urination. Although further parameterization and validation are needed, for a new development in an exploratory model like MINDY, these numbers are encouraging and reflect that the concepts encoded capture many of the underlying biological mechanisms that drive the diurnal pattern and daily UN excretion, as well as thirst, acceptable.

Introduction

Cattle grazing temperate swards do not use nitrogen (N) and water efficiently (Satter & Roffler 1975; Jarvis 1993; Van der Hoek 1998). At least 0·70 of the N they ingest is not stored or secreted in saleable products (e.g. milk, live weight gain) and >0·60 of that N is excreted with water as urinary nitrogen (UN) (Kebreab *et al.* 2001; Gregorini *et al.* 2010, 2016). Discharge of UN onto pasture is the greatest contributor to leached N in temperate grazing environments (Di & Cameron 2002; Selbie *et al.* 2015). Therefore, in association with intensive livestock production and increased demand for water and nutrients (Pimentel *et al.* 2004; Hoekstra & Chapagain 2007), these inefficiencies frequently deplete and/or contaminate water sources (Jongbloed & Lenis 1998; Ilea 2009). Individual measurements of UN excretion and water consumption by grazing ruminants are difficult, time-consuming and expensive; therefore, prediction and modelling are critical for research to improve N and water use efficiency.

The need to know about the diurnal pattern of urination relates to the great variability of N concentration, volume and diurnal frequency of individual urination events throughout the day (Betteridge *et al.* 2013). For beef cattle and non-lactating dairy cows grazing temperate swards, N concentration, volume and diurnal frequency of individual urination events vary considerably, 0·8–14·1 g/l, 0·3–10 litres and 13–73 times/d, respectively (Betteridge *et al.* 1986, 2013). Similar variations have been reported for lactating dairy cows in New Zealand (Shepherd *et al.* 2017). These variations have been related to animal N and water metabolism (Maltz & Silanikove 1996; Appuhamy *et al.* 2014), as well as grazing management (Clark *et al.* 2010*b*; Gregorini *et al.* 2017), and dietary and animal features (Betteridge *et al.* 1986). Collectively, they represent feeding and grazing management opportunities to modulate urination patterns and N excretion and discharges onto pastures (Gregorini *et al.* 2017).

Much empirical data and mathematical representations of water consumption and UN have been accumulated and summarized (Murphy 1992; Silanikove 1992; Castillo *et al.* 2001) and attempts to model them have been diverse (Winchester & Morris 1956; Holter & Urban Jr 1992; Bannink *et al.* 1999; Cardot *et al.* 2008; Khelil-Arfa *et al.* 2012; Appuhamy *et al.*

2014). However, many N cycles and farm models use UN as input data or only predict daily averages of UN, ignoring the known variability of N concentration, volume and diurnal frequency of daily individual urination events. The latter can create either under or overestimations of UN, scaling errors and thereby false perceptions (good or bad) of particular feeding and grazing managements. Mechanistic and dynamic approaches that simulate UN and water consumption are scarce, and to our knowledge, there are no current models on the diurnal patterns of urination and drinking by grazing ruminants.

MINDY is a deterministic, mechanistic and dynamic model of a dairy cow representing diurnal patterns of ingestion, digestion and metabolism, and production based on explicit relationships among direct (ingestion, digestion and metabolism) and indirect (feeding environment) controls of motivation to feed (Gregorini *et al.* 2013, 2015*b*). MINDY is a cluster of six models: (1) Molly models digestion, metabolism and production of a dairy cow (Baldwin 1995), as modified by Gregorini *et al.* (2015*a*); (2) diurnal fluctuations in feeding motivation; (3) sward canopy structure and herbage quality; (4) grazing behaviour; (5) dietary preference and forage selection; and (6) foraging bioenergetics. MINDY also integrates functional relationships between forage ingestion, oral physiology and swallowing, and rumen digestion responsible for variations in liquid outflows from the rumen (Gregorini *et al.* unpublished). The primary objective of the current work was to represent diurnal urination and drinking patterns, and the resulting pattern of UN in MINDY. The effort integrates existing knowledge of basic urination physiology (Andersson & Arner 2004) and water dynamics in ruminants (Silanikove 1994; Maltz & Silanikove 1996; Kadzere *et al.* 2002), which are responsible for frequency and variations in the volume and N concentration of urination events. The mathematical formulation, first principles, model parameters and function, as well as preliminary evaluation (cross-validation) of the new development in MINDY are described and presented, respectively, in the current paper. Also, and for illustrative and conceptual evaluation of the new model development, the hypothesis that herbage crude protein and specific grazing management strategies alters UN and drinking patterns were tested.

Rationale and Description of the Model Development

This development (Fig. 1) is a mechanistic and dynamic representation of water consumption (ingested with food and imbibed) and urination pattern by grazing ruminants within MINDY (Gregorini *et al.* 2013, 2015*b*). The code was developed and simulations were conducted using ACSLXtreme (Aegis Technologies Group, Austin, TX, USA). Numerical integration was conducted using a fourth-order, fixed-step, Runge–Kutta method. The maximum integration interval was set to 0·001 d. The results presented in the current paper were collected after 5 d of simulation to ensure the model had reached a steady state.

Water consumption

Amount of water imbibed

The rumen is the main water reservoir for ruminants (Church 1988). This water is used for metabolic, cooling and digestive processes (Van Soest 1994). Ruminants attempt to maintain an optimal rumen function (Yokoyama & Johnson 1988; Van Soest 1996), and a key requisite for that is stable microbial populations (Bergen 1977; Hobson & Stewart 1997). To thrive and survive, rumen microbial populations require water in a range between 0·80 and 0·85 of rumen contents (if water is accessible), independent of diet, season and type of ruminant (Van Vuuren 1993; Gregorini *et al.* 2007, 2009*b*; Seo *et al.* 2007). In addition, animals attempt to maintain blood volume, mobilizing water from various pools of the body if necessary but mainly from the rumen
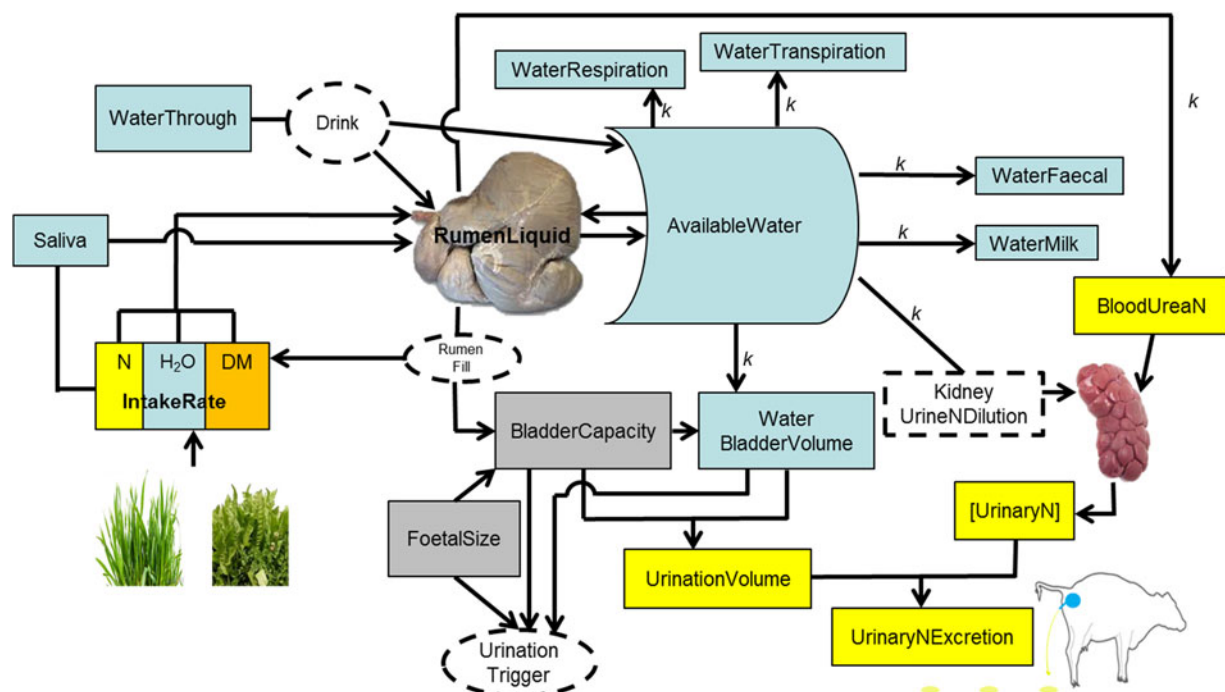

Fig. 1. Schematic representation of the processes of drinking and ingestion of water, urination and nitrogen (N) concentration in urine.

(Miaron & Christopherson 1992), to avoid haemo-concentration (Jain 1986). Therefore, it was assumed that the amount of water in the rumen is 'sensed' by the animal, and in conjunction with continuous 'sensing' of variations of water level in the body (*WaterBody*) stimulates the motivation to drink, i.e. thirst.

The amount of water imbibed is represented in MINDY as a function of rumen dry matter (DM) content (*RumDM*) and *WaterBody* as follows:

If water is available, and *RumDM* ⩾ *RumDMUpperLimit* or *WaterBody* ⩽ *WaterBodyTrigger*, then MINDY stops other activities (grazing, ruminating, idling) and drinks. MINDY drinks at a rate of 18 litres/min corrected for body size (*AnimalBodySize*, kg) (Pinheiro Machado Filho *et al.* 2004). MINDY stops drinking when *RumDM* ⩽18·4% or reaches a maximum volume of the rumen and *WaterBody* is ⩾*WaterBodyTrigger* (constant, 69·7%, water content of fat-free body (Springell 1968)).

Rumen liquid, and thereby *RumenDigesta*, are affected by the inflow and outflow of liquids to, from, and by-passing (water that goes directly to the abomasum, passing fleetingly through the top of the rumen and into the reticulum) the rumen. The model assumes 0·0115 of the water imbibed (*WaterImbibed*, litre/min) bypasses (*WaterBypass*, litre/min) the rumen (Woodford *et al.* 1984). For details on the mechanistic and dynamic representation of digesta outflow from the rumen (solid and liquid) in MINDY (Gregorini *et al.* 2015*a*; Gregorini *et al.* unpublished). The inflow of liquid to the rumen is calculated as follows:

$$WaterInflow = WaterImbibed + WaterIngestion + Saliva$$
$$+ WaterOsmolarity - Waterbypass \quad (1)$$

where *WaterIngestion* (litre/min) is the product of herbage (or any feed) intake rate and its moisture content. MINDY accounts for changes in herbage moisture content throughout sward canopy strata, during the day and throughout the year according to the season (Delagarde *et al.* 2000; Gregorini *et al.* 2008, 2009*c*; Gregorini 2012). *Saliva* is the inflow of saliva (litre/min) to the rumen and depends on the activity. Salivation rate is 2·4 litres/d while ruminating and 0·85 litre/d during idling (Maekawa *et al.* 2002); while eating, the rate of salivation (litre/min) depends on the characteristics of the ingestive bolus and number of jaw movements (severing and mastication) per bolus. MINDY simulates differential jaw movement rates according to behavioural actions (rumination, severing bites, oral processing, bolus formations) and internal state (hunger), which are influenced by fibre content of the forage (Gregorini *et al.* 2013; Gregorini *et al.* unpublished). *WaterOsmolarity* (litre/min) is water exchange across the rumen wall between rumen fluid and blood through osmolality as previously described (Gregorini *et al.* 2015*a*).

WaterBody is the continuous variable percentage of water in the body. It is the ratio between water pool in the body (*WaterPool*), excluding the rumen, and the body weight (BW) excluding the gravid uterus. *WaterInflowIntoWaterBody* is calculated as follows:

$$WaterInflowIntoWaterBody = WaterOutflowRumen$$
$$+ Waterbypass - Saliva$$
$$- WaterExcretion \quad (2)$$

WaterOutflowRumen is the momentary outflow of liquid from the rumen (See Gregorini *et al.* (2015*a*) for details of the

equations), and *WaterExcretion* is the water excreted as respiration (*kWaterRespired* = 0·033 litre/kg BW/d, assuming half the maximal respiratory rate, Murphy (1992)), transpiration (*kWaterTranspired*, 0·0185 litre/kg BW/d, assuming 0·25 of the maximal sweating rate), defecation (*kWaterDefecated*, 0·77, assuming 23% faecal DM Murphy (1992)), urination, and milk production (assuming 0·01 of ash in milk, while lactose, fat, protein and total milk are simulated mechanistically).

Water excretion as urine

Animal extra cellular water (*WaterPool* in MINDY) is the main source of water for urine production and dilution of N (Appuhamy *et al.* 2014). Cattle produce urine with a fixed ceiling for urine osmolality, ∼1000 mmol/kg BW (Maltz & Silanikove 1996). If urea concentration in the kidney is high, water is withdrawn from cellular water (*WaterPool*) because ruminants, as opposite to monogastrics, cannot concentrate urine above this ceiling (Silanikove 1994; Maltz & Silanikove 1996). Thus, increments in osmotic loads, e.g. by increases in N supply to the animal (i.e. intake and digestion) are associated with excessive urine production (Maltz & Silanikove 1996). Based on these concepts and data, plus basic urinary bladder physiology (Andersson & Arner 2004), urination behaviour in MINDY is represented as follows:

The bladder stores urine. Urine enters the bladder from the kidneys. The bladder of cattle can hold a variable volume (*BladderVolume*, litres) of urine. When the level of urine reaches about half this volume, the pressure of the accumulating fluid stimulates nervous impulses that relax the external sphincter and urination occurs. Subsequently, when MINDY's bladder is half full, 'she' urinates. Bladder capacity (*BladderCapacity*, litres) changes throughout pregnancy related to foetal size and within the day in relation to rumen fill. Both pregnancy and rumen fill reduce *BladderCapacity* and increase urination frequency, as well as reducing the volume of individual urination events. Then, if *BladderVolume* ⩾ *BladderCapacity*, MINDY empties the bladder, i.e. urinates.

MINDY's *BladderVolume* represents the current water content in the bladder. *BladderCapacity* is the current bladder capacity, which is calculated as the product of the maximum capacity of the bladder (*MaxBladderCapacity*, litres), pregnancy effect (*BladderPregnancyFactor*, proportion) and rumen volume effect (*BladderRumenVolumeFactor*, proportion). *MaxBladderCapacity* is a constant (8·0 litres) derived from model parameterization (see next section on model parameterization) modulated by body size. *BladderPregnancyFactor* is calculated as:

$$BladderPregnancyFactor = PregnancyFactor^{kPregMaxBladder} \quad (3)$$

$$PregnancyFactor = 1 - \frac{GravidUterus}{AnimalBodySize} \quad (4)$$

PregnancyFactor ranges between 1 (non-pregnant) and ∼0·85 before calving. *GravidUterus* is the fresh weight (kg) of the foetus plus the uterus, and *kPregMaxBladder* is a constant (1·2) that controls the reduction in urination trigger level as the foetus grows, due to the increased pressure on the bladder. *BladderRumenVolumeFactor* is

calculated as:

$$BladderRumenVolumeFactor$$
$$= 1 - 0.8 \times e^{-kRumVolMaxBladder \times RumenVolumefactor} \quad (5)$$

$$RumenVolumeFactor = Max\left(0, 1 - \frac{RumenDigesta}{MaximunRumenCapacity}\right) \quad (6)$$

kRumVolMaxBladder is a constant with a value of 3, which lowers the urination trigger level as the rumen fills up, due to increased pressure on the bladder. *MaximunRumenCapacity* (kg) is the capacity of the rumen to store fresh digesta. *RumenVolumeFactor* ranges between 0 (rumen full) to 1 (rumen empty).

The volume of each urination event equals the *BladderVolume* that triggers MINDY to empty the bladder. *BladderVolume* equals *WaterUrine* (litre/d), which drains any surplus water from *WaterBody* into the bladder. If this is not enough water to dilute UN as expected, it draws water from *WaterBody* even if there is no surplus; making MINDY thirsty, which stimulates 'her' to replenish *WaterBody* by drinking.

$$WaterUrine = MAX(MinimunWaterUrineDilution,$$
$$MinimunWaterSurplusResidence) \quad (7)$$

Urinary nitrogen concentration

The UN concentration (g/l) of each urination event at each urination time is calculated as follows:

$$UN = \frac{UNAccumulatedSinceLastUrination}{BladderVolume} \quad (8)$$

where *UNAccumulatedSinceLastUrination* (g) is accumulated urea in the blood since the last urination, and the *BladderVolume* is given by *WaterUrine* (Eqn (7)).

$$MinimumWaterUrineDilution = 1000 \times \frac{UN}{TargetConcentrationUN} \quad (9)$$

$$TargetConcentrationUN = MaximumConcentrationUN$$
$$\times \left(1 - e^{-(kConcentrationUN \times UN)/(AnimalBodySize)}\right) \quad (10)$$

$$MinimumWaterSurplusResidence$$
$$= \left(WaterPool - WaterPoolTaget\right) \times kWaterUrine$$
$$\times AnimalBodySize \quad (11)$$

where *MinimumWaterUrineDilution* (litre/d) is the minimum rate of water flowing to the bladder to achieve target dilution of the momentary N excretion rate. *MinimumWater SurplusResidence* (litre/d) is the minimal amount of water flowing to the bladder required to excrete water surplus. *TargetConcentrationUN* (g/l) is the maximal concentration of N for the current N excretion rate

as UN. *MaximumConcentration UN* (10·56 g/l) is a constant representing the maximum concertation of UN at each urination event. *MaximumConcentrationUN* value was fitted to the UN data (corrected by BW) reported by Nennich *et al.* (2006), Broderick (2003), Wattiaux & Karg (2004), Burgos *et al.* (2005), Woodward *et al.* (2013) and Betteridge *et al.* (1986). *kConcentrationUN* (unitless) is an exponential decay constant fitted as *MaximunConcentrationUN*. *kWaterUrine* is an exponential constant (0·18) determining the flow (litre/d) of water to the bladder.

Model Parameterization and Cross-validation

Ten data sets (Betteridge *et al.* 1986; Dado & Allen 1993, 1994; Aland *et al.* 2002; Jago *et al.* 2005; Cardot *et al.* 2008; Oudshoorn *et al.* 2008; Clark *et al.* 2010*a*, *b*) were used to (a) parameterize the model, using the 'Learn from All' methodology described by Witten *et al.* (2011); (b) calculate each parameter's standard error using the bootstrap method (Efron 1982, 1983); and (c) calculate the model's predictive error using the cross-validation method (Witten *et al.* 2011). These data sets included cows with different characteristics and diverse diets, reported pattern of water imbibed and urination and provided daily volumes of water in and urine excreted.

Model parameters standard errors were estimated using the bootstrap method (Efron 1982, 1983; Witten *et al.* 2011) as follows: (1) selecting items (treatments means) from the whole data set randomly, so some items appeared more than once in the selection; (2) for each parameter, fixing all parameters except one to the best values from the cross-validation phase; (3) finding the best value for this parameter (i.e. the one that was fixed); (4) repeating steps 2 and 3 for each parameter; (5) repeating steps 1–4 with 5 different random selections and (6) calculating each parameter's standard error, from the X values collected, to get the standard errors of the model parameters. The model parameter estimates and standard errors are presented in Table 1. In all cases, the model parameters were well defined by the data as evidenced by the low standard errors (<10% of the respective estimates) of the parameter estimates.

The Cross-Validation phase was performed using methodology described by Witten *et al.* (2011): First, allocating the data (treatments' means of data sets in this case) randomly into P groups, then excluding one group at a time – finding best parameters, collecting individual bias measurements for the excluded group, and repeating steps 1, 2 and 3 M times with different random allocation each time. Finally, averaging and reporting all the M × P deviance measurements from step 3 (i.e. all the excluded

Table 1. Model parameters estimates and standard errors (s.e.)

Parameter	Value	s.e.
RumDMLowerLimit	0.180	1
RumDMUpperLimit	0.184	0.0017
WaterBody	0.697	0.0050
kPregMaxBladder	0.59	0.044
kRumVolMaxBladder	3.00	0.055
kWatterUrine	0.180	0.0023
MaxBladderCapacity (litres)	8.0	0.21

groups). The assessment of the model's predictive error was conducted using the mean square prediction of error (MSPE), the square root of MSPE and MSPE decomposition in mean and systematic bias and random error, as well as the mean absolute error (MAE) (Bibby & Toutenburg 1977; Tedeschi 2006). MAE measures the average magnitude of the errors in a set of predictions, without considering their direction. It is the average over the test sample of the absolute differences between prediction and actual observation where all individual differences have equal weight. MSPE was calculated as follows:

$$\text{MSPE} = \frac{\sum_{i=1}^{n} [\text{Observed} - \text{Predicted}]^2}{n}$$

The MSPE measures the distance between observed and predicted values, and its square root, RMSPE, is used to obtain the same units as the observed and predicted values. The RMSPE gives an estimation of the mean error amplitude, a RMSPE <10% and between 10 and 25% of observed mean indicates, respectively, satisfactory and acceptable predictions (Fuentes-Pila *et al.* 1996).

Results of the cross-validation indicate that MINDY predicts daily water imbibed, urination volume and frequency of urination with a RMSPE and MAE as % of the observed mean of 26·33 and 23·30%; 25·80 and 27·14%; 25·10 and 18·76%, respectively. The model displayed the following mean bias, systematic bias, and random error (MSPE decomposition, Tedeschi (2006)) for daily water imbibed, urination volume and frequency of urination, respectively: 4·93, 33·75 and 61·31%; 90·19, 9·06 and 0·75%; and, 6·83, 8·42 and 84·74%. Decomposition of the MSPE, then, indicates that the structure of this new module in MINDY still needs improvement, especially in terms of daily water imbibed (model over-prediction) and daily urination volume (model over-prediction). This MSPE decomposition also indicates that considerable more, and more accurate (e.g. urination volumes and individual water imbibed under pastoral conditions) and specific data (e.g. bladder volume of dairy cows of various size and age) is needed to further parameterization and validation of MINDY's new module to ensure no lack-of-fit and account for non-random variation better. However, for a new development in an exploratory model like MINDY, these numbers (predictive errors) and the random errors, especially for urination frequency and water imbibed are encouraging, and reflect that the concepts encoded capture 'relatively acceptable' many of the underlying biological mechanisms that drive the diurnal pattern and daily UN excretion, as well as thirst.

MINDY's illustrative prediction of urination and UN patterns, as presented in the following section, suggests a realistic model response to herbage chemical composition and grazing managements. Model outputs are in close agreement with data reported by Shepherd *et al.* (2017), when evaluating urine excretion from dairy cows under different farm systems. This indicates the model predicts UN concentration at the level of urination event within one standard deviation (S.D.) of the observed means.

Illustrations and Discussion

The current work has formulated and described a new development in MINDY, with a preliminary conceptual validation conducted under a range of feeding scenarios. Validation means the model is acceptable for its intended purpose because it meets specified performance requirements (Rykiel 1996). The purpose of the present development was to integrate knowledge of urination physiology (Andersson & Arner 2004) and water dynamics (Silanikove 1994; Maltz & Silanikove 1996; Kadzere *et al.* 2002) responsible for frequency and variations in volume and UN into MINDY's framework. The context of the model is a 'foraging ruminant'. Model performance was also assessed by MINDY's ability to simulate sensible diurnal patterns of urination and drinking in response to various grazing scenarios, commonly used in intensive pastoral dairy farms.

To illustrate these simulations, MINDY was presented to: (1) herbage with contrasting contents of crude protein; (2) different timings of pasture allocation; and (3) a period of restriction in available grazing time to determine whether MINDY's diurnal urination and drinking patterns were sensitive to herbage crude protein content or intake and management of grazing patterns, and if so, whether that would change daily excretion of N and water imbibed. In all simulations, the outputs required from MINDY were: intake rates of water and herbage, N concentration, frequency, volume and diurnal distribution of urination events, as well as frequency, volume and diurnal distribution of drinking events.

The effect of crude protein content of herbage on urinary nitrogen excretion pattern and water consumption

Urinary N excretion is related directly to N intake (Castillo *et al.* 2001; Gregorini *et al.* 2016). As N intake increases, UN excretions increase exponentially (Kebreab *et al.* 2002). Although this phenomenon is well documented and several models simulate it, there is a lack of information on the effect of crude protein in herbage on diurnal patterns of UN excretion and water consumption. Then a scenario where MINDY (initialized as a pregnant Friesian dairy cow (500 kg liveweight) in mid-lactation (150 day in milk)) grazed a *Lolium perenne* L. sward (9 cm height and 3000 kg DM/ha) under set stock grazing management with herbage containing either 200 or 300 g crude protein (CP)/kg DM was simulated. These levels of CP reflect the effect of low *v.* high levels of N fertilization (0–50 *v.* 205–300 kg N/ha) on pastures (Goswami & Willcox 1969).

Figure 2 and Table 2 present MINDY's simulated diurnal patterns and daily values of UN excretion and water consumption, respectively, according to herbage crude protein content (g/kgDM). These results also account for different herbage intake patterns (meals' frequency, duration and intensity). It must be noted that, in MINDY chemical composition, and dry matter content of herbage fluctuates during the day and amongst sward canopy strata (See Gregorini *et al.* (2013) for details on equations)). Intake pattern, in conjunction with diurnal fluctuations in moisture content of the herbage (loss of moisture from dawn to dusk due to transpiration and evaporation and accumulation of dry matter (photosynthates)) determine water ingestion patterns throughout the day; which in turn determine daily water ingestion (64 *v.* 61 litres for 200 and 300 g CP/kg DM, respectively; Table 2).

Herbage with high crude protein led MINDY to excrete a considerably greater amount (72% more) of UN compared with that excreted when grazing swards with low levels of crude protein. Similar results (115 *v.* 348 g UN/d) have been reported by Delagarde *et al.* (1997) (cited by Castillo *et al.* 2000) for dairy cows grazing *Lolium perenne* L. swards fertilized with 0 and 250 kg N/ha, respectively. Patterns of urination also differed between treatments. Grazing swards with high crude protein led
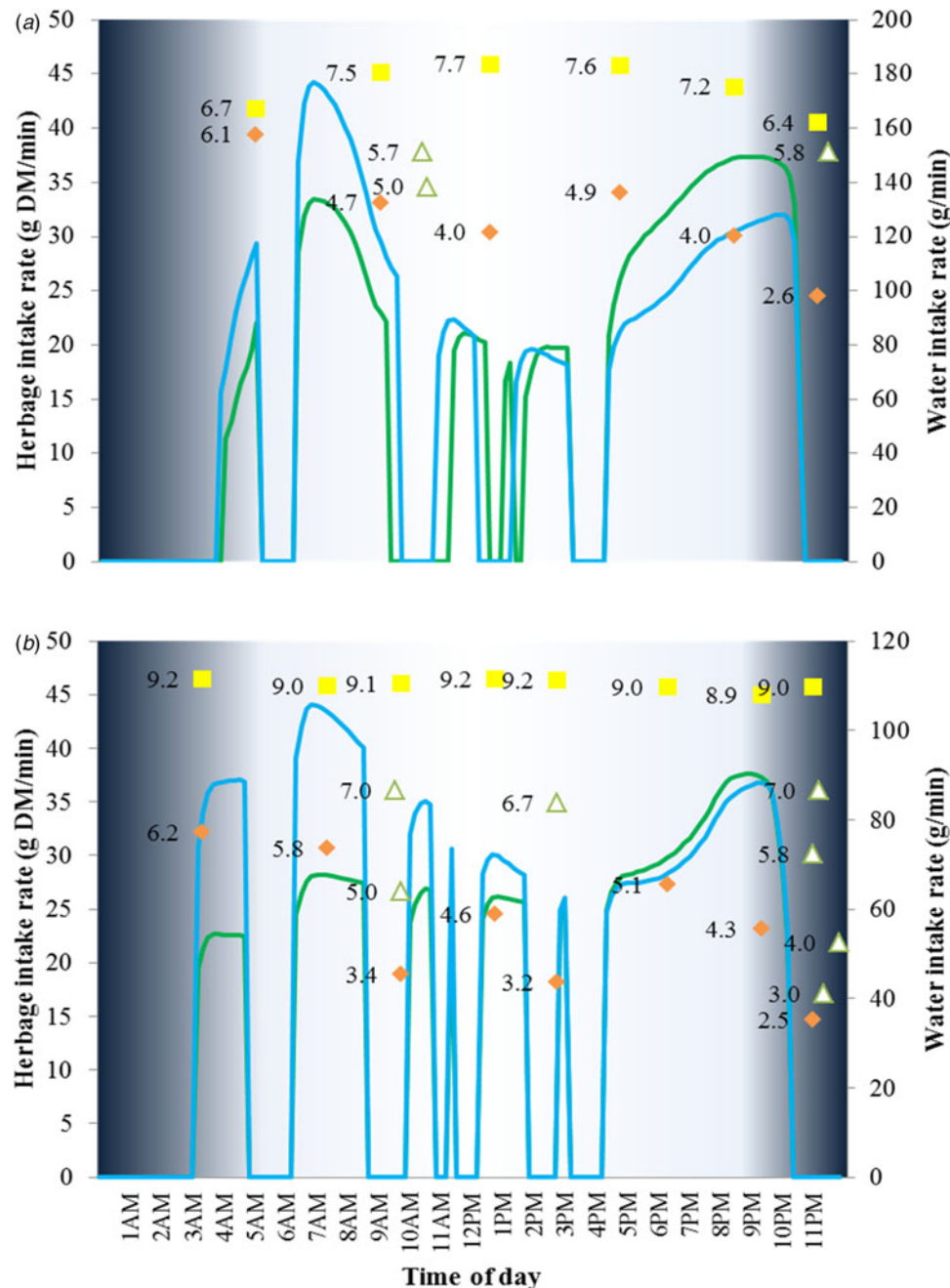
Fig. 2. Predicted values of the effect of herbage crude protein content ((a) 200 *v.* (b) 300 g/kg DM) on urinary nitrogen (N) excretion and water consumption patterns of a dairy cow (500 kg liveweight, ~150 days in milk) grazing a *Lolium perenne* L. sward under set stocking grazing management (9 cm height and 3000 kg DM/ha)*. **x*-axis is time of day, *y*-axis (green) is herbage intake rate, and *z*-axis (blue) water ingestion. Yellow squares are urinary N concentration for each urination event, Orange diamonds are individual volumes of urination events, and White triangles are drinking events with their respective volume of water imbided.

MINDY to have a greater urination frequency and a greater and steady concentration of N in each urination event (the difference between the highest and the lowest UN concentration were 0·3 *v.* 1·3 g/l for the low and high crude protein herbage, respectively).

Diurnal patterns of urination volumes were similar, with the greatest volumes overnight and early in the morning and the lowest after or within meals. This pattern reflects the eating pattern and the effect of rumen fill on bladder capacity. Such a pattern is supported by Betteridge *et al.* (2013) and Shepherd *et al.* (2017). When MINDY grazed herbage with a high level of crude protein, individual volumes of urination events were

greater. This difference and the greater urination frequency led MINDY to produce eight litres extra of urine per day on the high crude protein diet.

As discussed above, cattle produce urine with a fixed ceiling for urine osmolality, ~1000 mmol/kg live weight (Maltz & Silanikove 1996). If the urea concentration in the kidneys is high, more water is required to dilute the urine (Silanikove 1994; Maltz & Silanikove 1996), and water intake by drinking increases. Thus, 'toxic' increments in N supply to the animal, by ingestion and or digestion, lead to greater water excretion in urine and or excessive urine production; i.e. diuresis (Maltz & Silanikove 1996;

Table 2. Predicted values of the effect of herbage crude protein content and grazing managements on daily values of urination and drinking behaviour variables

Variable	Grazing methods[a]				
	SSLN	SSHN	AM	PM	PMSO
Herbage dry matter intake (kg/d)	15.6	15.1	16.2	16.5	13.2
Milk yield (kg/d)	19.2	22.3	14.2	14.5	13.7
Urinary nitrogen (kg/d)	0.188	0.324	0.293	0.278	0.259
Urinary volume (litre/d)	26.3	34.0	41.1	31.9	28.9
Urinations/day	6	8	17	11	9
Water ingested (litre/d)	64.5	61.4	81.2	77.2	57.7
Water imbibed (litre/d)	19.2	36.2	14.7	11.7	24.5
Drinks/day	3	7	3	2	5

[a]SSLN, set stocked grazing low N ryegrass herbage; SSHN, set stocked grazing high crude protein herbage; AM, strip-grazed with the daily pasture strip allocated in the morning, 8 a.m.; PM, strip-grazed with the daily pasture strip allocated in the afternoon, 4 p.m.; and PMSO, strip-grazed with the daily pasture strip allocated in the afternoon, 4 p.m. and stood-off from pasture between milking events (6.00 and 15.00 h).

Appuhamy *et al.* 2014). The upper volume of non-diuresis for dairy cows is around 15 litres/d (Maltz & Silanikove 1996). At relatively similar water ingestion, MINDY imbibed 17 litres more water when grazing high compared with low crude protein herbage, evidencing the greater need (also evidenced by the drinking frequency, seven *v.* three imbibing events) for water to dilute the increased surplus of N when consuming high compared with low crude protein herbage. These modelling results support the concept of diuresis and suggest feeding regimens with excess N cause diuresis. Associated phenomena, such as an excess of N intake and water consumption, are of particular interest from environmental, nutritional and animal welfare standpoints, as feed induced diuresis results in inefficiencies in water and N use by the animals.

The effect of grazing management on urinary nitrogen pattern and water consumption

Dietary management to dilute excess N in herbage from temperate swards, effectively reducing the N: fermentable carbohydrates ratio, reduces UN (Castillo *et al.* 2000; Gregorini *et al.* 2010, 2016). Thus grazing management that matches intake patterns with diurnal fluctuations in herbage chemical composition can reduce UN, as reported by Bryant *et al.* (2010) and Gregorini *et al.* (2010). However, most of the effort has focused on daily UN and production variables (Gregorini 2012). To reduce UN load onto pastures, more information is needed on the effect of grazing management on the temporal distribution of urination and related N excretion.

Reducing grazing time on pasture can alter intake patterns of dairy cows without significant losses in milk production, and reduces UN load onto pastures (Oudshoorn *et al.* 2008; Gregorini *et al.* 2009*a*; Clark *et al.* 2010*b*). Quantifying the effect of pasture restriction on diurnal patterns of UN and UN load (individual urination volume and N) onto pasture is not easy, and has not yet been investigated and reported thoroughly.

Three scenarios were simulated, where MINDY (initialized as a pregnant Friesian dairy cow (500 kg live weight) in late-lactation (200 day in milk)) strip-grazed a *Lolium perenne* L. sward (30 cm height (extended tiller length) and 3000 kg DM/ha), with strips (100 m^2/d) allocated either after morning (8 a.m.) or afternoon milking (4 p.m.), or stand-off (restricted) from pasture between milkings with the new pasture strip allocated at 4 p.m. The mean crude protein and fibre contents of herbage were 240 and 480 g/kg DM, respectively (Note: In MINDY, the chemical composition of herbage fluctuates during the day and amongst sward canopy strata (see Gregorini *et al.* 2013 for details on equations)).

Figure 3 and Table 2 present MINDY's diurnal patterns and daily values of UN and water consumption, respectively, according to the timing of pasture allocation and the effect of a stand-off period from pasture. As in Fig. 2, these results also describe different herbage intake patterns, which influence water ingestion patterns throughout the day, and in turn the daily total ingestion of water (81, 77 and 58 litres/d for 8 a.m. and 4 p.m. pasture allocations and 4 p.m. with a stand-off period between milkings, respectively; Table 2).

Allocating the pasture after the afternoon milking *v.* the common practice of allocating it after the morning milking (Chris Glassey pers. comm.) led MINDY to excrete 29% less urine volume and 6% less UN. These results are explained by water ingestion and amount imbibed (14 *v.* 11 litres/d), as well as a reduction (∼10%) in N intake. These results also indicate that opportunities exist to alter urination patterns through the timing of pasture allocation (Gregorini *et al.* 2017). As mentioned, daily and diurnal patterns of UN simulated by MINDY are in close agreement with empirical data reported by Shepherd *et al.* (2017), when evaluating the UN excretion pattern of strip-grazed dairy cows under similar New Zealand conditions.

Excess N intake, and consequent diuresis is also described in the simulations with MINDY. The results are most dramatic in model outputs when a new pasture strip was allocated in the morning when herbages present the highest N: readily fermentable carbohydrate ratio (Gregorini 2012). Other evidence of the need to dilute excess N by kidneys is that, even though MINDY ingested a considerable amount of water (herbage has the highest moisture content in the morning), 'she' drinks soon after such a big intake of water (Fig. 3). In conjunction with the high intake rate in the morning, such a water flow (ingested and imbibed) into and out of the rumen increases urination frequency and reduces the volume of individual urinations. Reductions in UN concentration per urination are seen even later in the day (∼4 h) as a product of this phenomenon and the reduction of N intake in the hours subsequent to the late-afternoon early-evening meal.

The number of urination events (11 *v.* 17), mean volume (2·9 *v.* 2·4 litres) and their diurnal distribution (Fig. 3) when MINDY is allocated a new pasture strip at 4 p.m. is also different from morning allocations. With the afternoon allocation, the volume and UN deposited onto non-pasture surfaces (milking shed and races) was 0·130 and 0·032 of the respective totals, compared with 0·097 and 0·037 for the morning allocation. Overall, these results are close to the 0·85 of daily urine volume deposited onto pastures reported by Clark *et al.* (2010*b*) for late-lactation dairy cows strip-grazing *Lolium perenne* L. in New Zealand. These values are also similar to that (24 g N/d) for UN deposited on the non-pasture surfaces (Shepherd *et al.* 2017).

Clark *et al.* (2010*b*) also reported that reducing pasture accessibility by 8 h reduced urine volume deposited onto pasture by
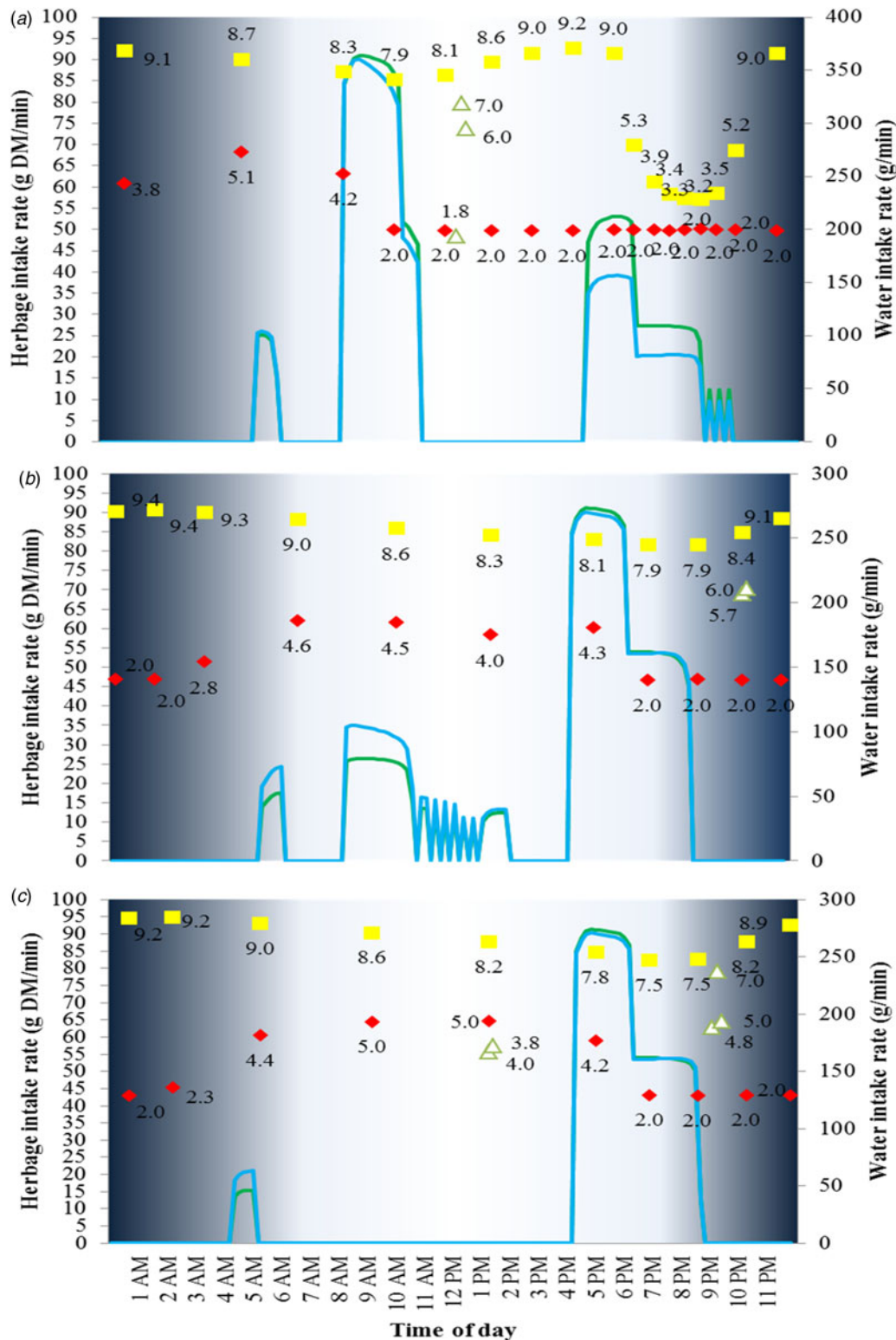
Fig. 3. Predicted values of the effect of timing of pasture strip allocation ((a), 8 a.m. *v.* (b), 4 p.m., after morning and afternoon milkings) and (c), a period of restriction of pasture (8 a.m. to 2 p.m.) between milking on urinary nitrogen (N) excretion and water consumption patterns of a dairy cow (500 kg liveweight, ~200 days in milk) strip-grazing a *Lolium perenne* L. sward. *x*-axis is time of day, *y*-axis (green) is herbage intake rate, and *z*-axis (blue) water ingestion. Yellow squares are Urinary N concentration for each urination event, Orange diamonds are individual volumes of urination events, and White triangles are drinking events with their respective volume of water imbibed.

50% when pasture was offered in two sets of 4 h after milking, and 56% when pasture was offered for eight continuous hours between milking events. Shepherd *et al.* (2017) reported that restricting pasture between milking events can reduce UN load by 36·5% (i.e. captures in the stand-off pad and races). The present simulation with MINDY indicates a 27% reduction. Thus,

MINDY's predictions of urination and UN patterns fall within expected ranges.

Summary and Concluding Remarks

The model development presented in the current paper makes explicit the functional relationships among direct and indirect controls of urination and UN, as well as the motivation of grazing ruminants to drink. Results of the evaluation indicate that the RMSPE and MAE, respectively, were 26 and 23% for daily water imbibed, 26 and 27% for urination volume, and 25 and 19% for the frequency of urination. Decomposition of the MSPE, i.e. mean biases and random errors, indicated that the structure of this new module in MINDY still needs some improvement and that more data is needed. Consequently, further parameterization and validation are needed. However, for a new development in an exploratory model like MINDY, these numbers are encouraging and reflect that the concepts encoded capture acceptably many of the underlying biological mechanisms that drive the diurnal pattern and daily UN excretion, as well as thirst.

MINDY reproduces patterns of urination acceptably, achieving the correct temporal occurrence and the relative volumes and N concentration of individual urination events of a grazing dairy cow as compared with the few reported in the literature. The model's response to those functional relationships also allows simulating daily UN and water ingestion in forage and imbibe for contrasting grazing managements and ingestion of herbages with different protein content. This is an advance in understanding and modelling of excretory and drinking behaviour patterns of free-range ruminants. Previous modelling efforts on N excretion or water intake have been either purely empirical or not comprehensive enough to include these more complex concepts. Therefore, MINDY represents a step forward.

REFERENCES

Aland A, Lidfors L and Ekesbo I (2002) Diurnal distribution of dairy cow defecation and urination. *Applied Animal Behaviour Science* **78**, 43–54.

Andersson K-E and Arner A (2004) Urinary bladder contraction and relaxation: physiology and pathophysiology. *Physiological Reviews* **84**, 935–986.

Appuhamy JA, Wagner-Riddle C, Casper DP, France J and Kebreab E (2014) Quantifying body water kinetics and fecal and urinary water output from lactating Holstein dairy cows. *Journal of Dairy Science* **97**, 6177–6195.

Baldwin RL (1995) *Modeling Ruminant Digestion and Metabolism.* London, UK: Chapman and Hall.

Bannink A, Valk H and Van Vuuren AM (1999) Intake and excretion of sodium, potassium, and nitrogen and the effects on urine production by lactating dairy cows. *Journal of Dairy Science* **82**, 1008–1018.

Bergen WG (1977) Factors affecting growth yields of micro-organisms in the rumen. *Tropical Animal Production* **4**, 13–20.

Betteridge K, Andrewes WGK and Sedcole JR (1986) Intake and excretion of nitrogen, potassium and phosporus by grazing steers. *The Journal of Agricultural Science, Cambridge* **106**, 393–404.

Betteridge K, Costall DA, Li FY, Luo D and Ganesh S (2013) Why we need to know what and where cows are urinating – a urine sensor to improve nitrogen models. *Proceedings of the New Zealand Grassland Association* **75**, 119–124.

Bibby J and Toutenburg H (1977) *Prediction and Improved Estimation in Linear Models.* New York, USA: Wiley.

Broderick GA (2003) Effects of varying dietary protein and energy levels on the production of lactating dairy cows. *Journal of Dairy Science* **86**, 1370–1381.

Bryant RH, Walpot V, Dalley DE, Gibbs SJ and Edwards GR (2010) Manipulating dietary N in perennial ryegrass pastures to reduce N losses in dairy cows in spring. In *Proceedings of the Australasian Dairy Science Symposium* (Eds G Edwards & R Bryant), pp. 97–101. Lincoln, New Zealand: Caxton Press.

Burgos SA, Robinson PH, Fadel JG and DePeters EJ (2005) Ammonia volatilization potential: prediction of urinary urea nitrogen output in lactating dairy cows. *Agriculture, Ecosystems and Environment* **111**, 261–269.

Cardot V, Le Roux Y and Jurjanz S (2008) Drinking behavior of lactating dairy cows and prediction of their water intake. *Journal of Dairy Science* **91**, 2257–2264.

Castillo AR, Kebreab E, Beever D and France J (2000) A review of efficiency of nitrogen utilisation in lactating dairy cows and its relationship with environmental pollution. *Journal of Animal and Feed Sciences* **9**, 1–32.

Castillo AR, Kebreab E, Beever DE, Barbi JH, Sutton JD, Kirby HC and France J (2001) The effect of protein supplementation on nitrogen utilization in lactating dairy cows fed grass silage diets. *Journal of Animal Science* **79**, 247–253.

Church DC (1988) *The Ruminant Animal. Digestive Physiology and Nutrition.* Englewood Cliffs, NJ, USA: Prentice Hall.

Clark C, Waghorn G, Gregorini P, Woodward S and Clark D (2010*a*). Diurnal pattern of urinary and faecal nitrogen excretion by dairy cows fed ryegrass pasture twice daily indoors. *Advances in Animal Biosciences* **2**, 269.

Clark CEF, Mcleod KLM, Glassey CB, Gregorini P, Costall DA, Betteridge K and Jago JG (2010*b*). Capturing urine while maintaining pasture intake, milk production, and animal welfare of dairy cows in early and late lactation. *Journal of Dairy Science* **93**, 2280–2286.

Dado RG and Allen MS (1993) Continuous computer acquisition of feed and water intakes, chewing, reticular motility, and ruminal pH of cattle. *Journal of Dairy Science* **76**, 1589–1600.

Dado RG and Allen MS (1994) Variation in and relationships among feeding, chewing, and drinking variables for lactating dairy cows. *Journal of Dairy Science* **77**, 132–144.

Delagarde R, Peyraud JL and Delaby L (1997) The effect of nitrogen fertilization level and protein supplementation on herbage intake, feeding behaviour and digestion in grazing dairy cows. *Animal Feed Science and Technology* **66**, 165–180.

Delagarde R, Peyraud JL, Delaby L and Faverdin P (2000) Vertical distribution of biomass, chemical composition and pepsin – cellulase digestibility in a perennial ryegrass sward: interaction with month of year, regrowth age and time of day. *Animal Feed Science and Technology* **84**, 49–68.

Di HJ and Cameron KC (2002) Nitrate leaching in temperate agroecosystems: sources, factors and mitigating strategies. *Nutrient Cycling in Agroecosystems* **64**, 237–256.

Efron B (1982) *The Jackknife, the Bootstrap and Other Resampling Plans.* Philadelphia, USA: SIAM.

Efron B (1983) Estimating the error rate of a prediction rule: improvement on cross-validation. *Journal of the American Statistical Association* **78**, 316–331.

Fuentes-Pila J, Delorenzo MA, Beede DK, Staples CR and Holter JB (1996) Evaluation of equations based on animal factors to predict intake of lactating Holstein cows. *Journal of Dairy Science* **79**, 1562–1571.

Goswami AK and Willcox JS (1969) Effect of applying increasing levels of nitrogen to ryegrass: I. Composition of various nitrogenous fractions and free amino acids. *Journal of the Science of Food and Agriculture* **20**, 592–595.

Gregorini P (2012) Diurnal grazing pattern: its physiological basis and strategic management. *Animal Production Science* **52**, 416–430.

Gregorini P, Gunter SA, Masino CA and Beck PA (2007) Effects of ruminal fill on short-term herbage intake rate and grazing dynamics of beef heifers. *Grass and Forage Science* 62, 346–354.

Gregorini P, Soder K and Sanderson M (2008) Case study: a snapshot in time of fatty acids composition of grass herbage as affected by time of day. *The Professional Animal Scientist* 24, 675–680.

Gregorini P, Clark CEF, Jago JG, Glassey CB, Mcleod KLM and Romera AJ (2009a). Restricting time at pasture: effects on dairy cow herbage intake, foraging behavior, hunger-related hormones, and metabolite concentration during the first grazing session. *Journal of Dairy Science* 92, 4572–4580.

Gregorini P, Soder KJ and Kensinger RS (2009b). Effects of rumen fill on short-term ingestive behavior and circulating concentrations of ghrelin, insulin, and glucose of dairy cows foraging vegetative micro-swards. *Journal of Dairy Science* 92, 2095–2105.

Gregorini P, Soder KJ, Sanderson MA and Ziegler GR (2009c). Toughness, particle size and chemical composition of meadow fescue (*Festuca pratensis* Hud.) herbage as affected by time of day. *Animal Feed Science and Technology* 151, 330–336.

Gregorini P, Beukes PC, Bryant RH and Romera AJ (2010) A brief overview and simulation of the effects of some feeding strategies on nitrogen excretion and enteric methane emission from grazing dairy cows. In *Proceedings of the 4th Australasian Dairy Science Symposium* (Eds GR Edwards & R Bryant), pp. 29–43. Lincoln, New Zealand: Caxton Press.

Gregorini P, Beukes PC, Romera AJ, Levy G and Hanigan MD (2013) A model of diurnal grazing patterns and herbage intake of a dairy cow, MINDY: model description. *Ecological Modelling* 270, 11–29.

Gregorini P, Beukes P, Waghorn G, Pacheco D and Hanigan M (2015a). Development of an improved representation of rumen digesta outflow in a mechanistic and dynamic model of a dairy cow, Molly. *Ecological Modelling* 313, 293–306.

Gregorini P, Villalba JJ, Provenza FD, Beukes PC and Forbes JM (2015b). Modelling preference and diet selection patterns by grazing ruminants: a development in a mechanistic model of a grazing dairy cow, MINDY. *Animal Production Science* 55, 360–375.

Gregorini P, Beukes PC, Dalley D and Romera AJ (2016) Screening for diets that reduce urinary nitrogen excretion and methane emissions while maintaining or increasing production by dairy cows. Science of the Total Environment 551–552, 32–41.

Gregorini P, Villalba JJ, Chilibroste P and Provenza FD (2017) Grazing management: setting the table, designing the menu and influencing the diner. *Animal Production Science* 57, 1248–1268.

Hobson PN and Stewart CS (1997) *The Rumen Microbial Ecosystem.* Dordrecht, the Netherlands: Springer.

Hoekstra AY and Chapagain AK (2007) Water footprints of nations: water use by people as a function of their consumption pattern. *Water Resources Management* 21, 35–48.

Holter JB and Urban WE Jr (1992) Water partitioning and intake prediction in dry and lactating Holstein cows. *Journal of Dairy Science* 75, 1472–1479.

Ilea RC (2009) Intensive livestock farming: global trends, increased environmental concerns, and ethical solutions. *Journal of Agricultural and Environmental Ethics* 22, 153–167.

Jago JG, Roche JR, Kolver ES and Woolford MW (2005) The drinking behaviour of dairy cows in late lactation. *Proceedings of the New Zealand Society of Animal Production* 65, 209–214.

Jain NC (1986) The dog: normal hematology with comments on response to disease. In *Schalm's Veterinary Hematology*, 4th edn (Eds OW Schalm & NC Jain), pp. 103–125. Philadelphia, USA: Lea and Febiger.

Jarvis SC (1993) Nitrogen cycling and losses from dairy farms. *Soil Use and Management* 9, 99–104.

Jongbloed AW and Lenis NP (1998) Environmental concerns about animal manure. *Journal of Animal Science* 76, 2641–2648.

Kadzere CT, Murphy MR, Silanikove N and Maltz E (2002) Heat stress in lactating dairy cows: a review. *Livestock Production Science* 77, 59–91.

Kebreab E, France J, Beever DE and Castillo AR (2001) Nitrogen pollution by dairy cows and its mitigation by dietary manipulation. *Nutrient Cycling in Agroecosystems* 60, 275–285.

Kebreab E, France J, Mills JA, Allison R and Dijkstra J (2002) A dynamic model of N metabolism in the lactating dairy cow and an assessment of impact of N excretion on the environment. *Journal of Animal Science* 80, 248–259.

Khelil-Arfa H, Boudon A, Maxin G and Faverdin P (2012) Prediction of water intake and excretion flows in Holstein dairy cows under thermoneutral conditions. *Animal* 6, 1662–1676.

Maekawa M, Beauchemin KA and Christensen DA (2002) Chewing activity, saliva production, and ruminal pH of primiparous and multiparous lactating dairy cows. *Journal of Dairy Science* 85, 1176–1182.

Maltz E and Silanikove N (1996) Kidney function and nitrogen balance of high yielding dairy cows at the onset of lactation. *Journal of Dairy Science* 79, 1621–1626.

Miaron JOO and Christopherson RJ (1992) Effect of prolonged thermal exposure on heat production, reticular motility, rumen-fluid and-particulate passage-rate constants, and apparent digestibility in steers. *Canadian Journal of Animal Science* 72, 809–819.

Murphy MR (1992) Water metabolism of dairy cattle. *Journal of Dairy Science* 75, 326–333.

Nennich TD, Harrison JH, Vanwieringen LM, St-Pierre NR, Kincaid RL, Wattiaux MA, Davidson DL and Block E (2006) Prediction and evaluation of urine and urinary nitrogen and mineral excretion from dairy cattle. *Journal of Dairy Science* 89, 353–364.

Oudshoorn FW, Kristensen T and Nadimi ES (2008) Dairy cow defecation and urination frequency and spatial distribution in relation to time-limited grazing. *Livestock Science* 113, 62–73.

Pimentel D, Berger B, Filiberto D, Newton M, Wolfe B, Karabinakis E, Clark S, Poon E, Abbett E and Nandagopal S (2004) Water resources: agricultural and environmental issues. *BioScience* 54, 909–918.

Pinheiro Machado Filho LC, Teixeira DL, Weary DM, von Keyserlingk MAG and Hötzel MJ (2004) Designing better water troughs: dairy cows prefer and drink more from larger troughs. *Applied Animal Behaviour Science* 89, 185–193.

Rykiel EJ (1996) Testing ecological models: the meaning of validation. *Ecological Modelling* 90, 229–244.

Satter LD and Roffler RE (1975) Nitrogen requirement and utilization in dairy cattle. *Journal of Dairy Science* 58, 1219–1237.

Selbie DR, Buckthought LE and Shepherd MA (2015) Chapter four-the challenge of the urine patch for managing nitrogen in grazed pasture systems. *Advances in Agronomy* 129, 229–292.

Seo S, Lanzas C, Tedeschi LO and Fox DG (2007) Development of a mechanistic model to represent the dynamics of liquid flow out of the rumen and to predict the rate of passage of liquid in dairy cattle. *Journal of Dairy Science* 90, 840–855.

Shepherd M, Shorten P, Costall D and MacDonald KA (2017) Evaluation of urine excretion from dairy cows under two farm systems using urine sensors. *Agriculture, Ecosystems and Environment* 236, 285–294.

Silanikove N (1992) Effects of water scarcity and hot environment on appetite and digestion in ruminants: a review. *Livestock Production Science* 30, 175–194.

Silanikove N (1994) The struggle to maintain hydration and osmoregulation in animals experiencing severe dehydration and rapid rehydration: the story of ruminants. *Experimental Physiology* 79, 281–300.

Springell PH (1968) Water content and water turnover in beef cattle. *Australian Journal of Agricultural Research* 19, 129–144.

Tedeschi LO (2006) Assessment of the adequacy of mathematical models. *Agricultural Systems* 89, 225–247.

Van Der Hoek KW (1998) Nitrogen efficiency in global animal production. *Environmental Pollution* 102(Suppl. 1), 127–132.

Van Soest PJ (1994) *Nutritional Ecology of the Ruminant.* Ithaca, NY, USA: Cornell University Press.

Van Soest PJ (1996) Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. *Zoo Biology* 15, 455–479.

Van Vuuren AM (1993) *Digestion And Nitrogen Metabolism of Grass Fed Dairy Cows.* Wageningen, the Netherlands: Wageningen Universisty.

Wattiaux MA and Karg KL (2004) Protein level for alfalfa and corn silage-based diets: II. Nitrogen balance and manure characteristics. *Journal of Dairy Science* 87, 3492–3502.

Winchester CF and Morris MJ (1956) Water intake rates of cattle. *Journal of Animal Science* 15, 722–740.

Witten IH, Frank E and Hall MA (2011) *Data Mining: Practical Machine Learning Tools and Techniques.* Amsterdam, the Netherlands: Elsevier.

Woodford ST, Murphy MR, Davis CL and Holmes KR (1984) Ruminal bypass of drinking water in lactating cows. *Journal of Dairy Science* **67**, 2471–2474.

Woodward SL, Waugh CD, Roach CG, Fynn D and Phillips J (2013) Are diverse species mixtures better pastures for dairy farming? *Proceedings of the New Zealand Grassland Association* **75**, 79–84.

Yokoyama MG and Johnson KA (1988) Microbiology of the rumen and intestine. In *The Ruminant Animal: Digestive Physiology and Nutrition* (Ed. DC Church), pp. 125–144. Englewood Cliffs, NJ, USA: Prentice-Hall.