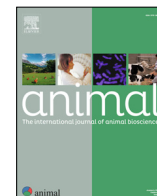




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On-farm evaluation of models to predict herbage intake of dairy cows grazing temperate semi-natural grasslands



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ABSTRACT

The objective of the present on-farm study was to evaluate the adequacy of existing models in predicting the pasture herbage DM intake (**PDMI**) of lactating dairy cows grazing semi-natural grasslands. The prediction adequacy of 13 empirical and semi-mechanistic models, which were predominantly developed to represent stall-fed cows or cows grazing high-quality pastures, were evaluated using the mean bias, relative prediction error (**RPE**), and partitioning of mean square error of prediction, where models with an $RPE \leq 20\%$ were considered adequate. The reference dataset comprised $n = 233$ individual animal observations from nine commercial farms in South Germany with a mean milk production, DM intake, and PDMI (arithmetic means \pm one SD) of 24 kg/d, (± 5.6), 21 kg/d (± 3.2), and 12 kg/d (± 5.1), respectively. Despite their adaptation to grazing conditions, the behaviour-based and semi-mechanistic grazing-based models had the lowest prediction adequacy among the evaluated models. Their underlying empirical equations likely did not fit the grazing and production conditions of low-input farms using semi-natural grasslands for grazing. The semi-mechanistic stall-based model Mertens II with slight modifications achieved the highest and a satisfactory modelling performance ($RPE = 13.4\%$) when evaluated based on the mean observed PDMI, i.e., averaged across animals per farm and period ($n = 28$). It also allowed for the adequate prediction of PDMI on individual cows ($RPE = 18.5\%$) that were fed < 4.8 kg DM of supplement feed per day. Nevertheless, when used to predict PDMI of individual animals receiving a high supplementation level, the model Mertens II also did not meet the threshold for an acceptable adequacy ($RPE = 24.7\%$). It was concluded that this lack of prediction adequacy for animals receiving greater levels of supplementation was due to a lack of modelling precision, which mainly could be related to inter-animal and methodological limitations such as the lack of individually measured supplement feed intake for some cows. The latter limitation is a trade-off of the on-farm research approach of the present study, which was chosen to represent the range in feed intake of dairy cows across the diverse low-input farming systems using semi-natural grasslands for grazing.

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Implications

Adequate estimates of the herbage intake of grazing dairy cows are essential to optimise grazing management. A semi-mechanistic model using animal-, milk-, and feed-related input parameters was identified which predicted the herbage intake of groups of dairy cows grazing semi-natural grasslands with satisfactory adequacy. The identified model can be applied for extension purposes and in decision-support tools to determine appropriate supplementation for dairy herds under low-input farming conditions. Inter-animal variation in feeding behaviour was not captured adequately by

the evaluated intake models. Hence, none of the evaluated models was applicable for predicting the herbage intake of individual cows.

Introduction

In contrast to improved or temporary grasslands, semi-natural grasslands can be defined as lower-yielding, multi-species permanent grasslands, with at least in part, lower nutritive value of herbage due to no or little treatment with fertilisers and pesticides, and reduced soil cultivation (Bruinenberg et al., 2003; Peeters et al., 2014). In regions with low mountain ranges, such as in great parts of Southern Germany, Austria, and Switzerland, semi-natural grasslands can constitute an import feed component for dairy cows (Akert et al., 2020). Accurate measurements of the pasture herbage DM intake (**PDMI**) of lactating dairy cows are essential to optimise

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grazing management and supplemental feeding (Tedeschi et al., 2019). For research purposes, a combination of external and internal markers to quantify the PDMI of cows is commonly used. This method, however, is labour- and cost-intensive, and invasive due to the need for daily faecal samples to quantify marker excretions (Hellwing et al., 2015). Alternatively, mathematical models have been developed to predict the feed intake of cows from animal, feed, and management characteristics. Such models can be applied for research but could also be integrated into decision-support tools for grazing and feeding management (Tedeschi et al., 2019).

Empirical models, based on regression equations using animal characteristics and productive parameters i.e., animal growth and milk yield, as input factors, are among the most widely applied intake models, but are criticised for being overfitted to the production conditions of the underlying empirical dataset (Tedeschi et al., 2019). Alternatively, mechanistic and semi-mechanistic models attempt to simulate the underlying processes regulating the voluntary feed intake of animals and are thus more applicable to a wider set of farming conditions (Pittroff and Kothmann, 2001). The majority of such mechanistic models rely on the principle that voluntary feed intake of cows is either determined by (1) the physical intake capacity governed by dietary fill-effect and rumen volume, or by (2) the physiological demand for feed intake, foremostly regulated by the animal's energy requirements (Pittroff and Kothmann, 2001). The underlying processes during grazing are, however, more complex than under stall-feeding conditions, because additional variation in feeding behaviour and energy expenditures need to be considered (Gregorini et al., 2015). Therefore, grazing-specific models with semi-mechanistic (e.g., e-cow; Baudracco et al., 2012) or empirical approaches using behavioural data to predict PDMI (e.g., Rombach et al., 2019) have been developed.

Most of these models were developed and their prediction adequacy was evaluated under high-input grazing conditions using improved, homogenous ryegrass-clover swards with high biomass yields for grazing (e.g., Baudracco et al., 2012; Roca-Fernández and González-Rodríguez, 2018). These conditions differ greatly from the production conditions on low-input farms using semi-natural grasslands for grazing, which, so far, have received less attention in research despite their common use for dairy production in grassland-dominated regions of Central Europe. It was hypothesised that existing models cannot adequately predict PDMI of dairy cows grazing semi-natural grasslands, due to the differences in yield, botanical composition, and nutritional value of the grassland vegetation, common animal breeds, and their milk yield and composition, as well as the herd, feeding, and grazing management factors between low-input and high-input dairy farming. The objective of the present study was, thus, to evaluate the adequacy (judged on the level of precision and accuracy; Tedeschi, 2006) of various existing models for estimating the PDMI of individual and groups of cows grazing semi-natural grasslands. For this, we chose an on-farm research approach to assure the transferability of our results to the wide variation in feed intake of grazing dairy cows across the diverse low-input farming systems using semi-natural grasslands for grazing. Preliminary results from the present study were previously published in abstract form (Perdana-Decker et al., 2021; Perdana-Decker et al., 2022).

Material and methods

Model selection

Literature research was conducted to identify existing models to predict daily feed intake of lactating cows on pasture. In total, 13 prediction models with four different approaches to estimate PDMI were selected (Supplementary Table S1). (1) Three

behaviour-based models using chewing behaviour, animal characteristics, and milk performance to predict PDMI (Rombach (Rombach et al., 2019: model GA7); Greenwood (Greenwood et al., 2017); Oudshoorn (Oudshoorn et al., 2013: model BT11T)), and (2) two semi-mechanistic models specifically developed to predict PDMI of grazing cows, called semi-mechanistic pasture-based models thereafter, using pasture characteristics, supplementation, and milk performance parameters (GrazeSim (Vazquez and Smith, 2001: modelPlsup); e-cow (Baudracco et al., 2012: Eq. (5) for a ryegrass-based pasture)). Additionally, models based on data from stall-fed animals were selected which predict total DM intake: (3) six empirical (AFRC (Vadiveloo and Holmes, 1979: model 1); Cornell (Fox et al., 2004); De Souza (de Souza et al., 2019); Gruber (Deutsche Landwirtschafts-Gesellschaft, 2006: Eq. (1); NRC (National Research Council (NRC), 2001); Sauvant (Sauvant et al., 2014)), and (4) two semi-mechanistic models (Conrad (Conrad et al., 1964; Kahn and Spedding, 1984); Mertens I (Mertens, 1987)). The latter eight empirical and semi-mechanistic stall-based models were used to predict PDMI indirectly by subtracting measured DM intake of supplemental feed (DMI_{supp}) from the models' predictions of total DM intake.

The Rombach model was slightly modified by using the DMI_{supp} as an input variable instead of corn silage intake and by using a constant value for postgrazing herbage mass i.e., the mean observed value of the model's development dataset (222 kg DM/ha), instead of a measured value. For the Cornell model, two different DM intake equations were applied (Fox et al., 2004): (1) one for lactating dual-purpose cows used for Simmental cows (Table 11: Eq. (9)) and (2) one for lactating dairy cows, which was applied for the remaining breeds (Table 11: Eq. (8)). The Mertens I model was modified assuming that grazing cows had a higher physical intake capacity, due to their high allowance to pasture herbage and forage supplements (Baudracco et al., 2012). Hence, a physical i.e., NDF, intake capacity of 1.65% of the animals' BW (Vazquez and Smith, 2001) was assumed for the model Mertens II, instead of the 1.30% of BW in the original Mertens I model. The model e-cow is a combination of models predicting milk yield, BW change, and PDMI. For the present study, instead of using e-cow's predictions of the animal's milk yield and BW change, the actual records of milk yield were used as an input factor to the PDMI module, and no changes in BW were assumed. For the calculation of metabolisable energy (ME) requirements and the model NRC, the energy-corrected and fat-corrected milk yields were calculated using Eqs. (1) and (2) (Gesellschaft für Ernährungsphysiologie (GfE), 2001; NRC, 2001):

$$\text{ECM} = (0.39 \times \text{fat} + 0.24 \times \text{protein} + 0.17 \times \text{lactose} + 0.1) \times \text{DMY} \div 3.28 \quad (1)$$

$$\text{FCM} = 0.4 \times \text{DMY} + 15 \times \text{fat} \times \text{DMY} \div 100 \quad (2)$$

where ECM is the energy-corrected milk yield (kg/d), fat the fat concentration in milk (g/100 g milk), protein the protein concentration in milk (g/100 g milk), lactose the lactose concentration in milk (g/100 g milk), DMY the milk yield (kg/d), and FCM the fat-corrected milk yield (kg/d). The models GrazeSim, e-cow, Mertens I, and Mertens II included the ME requirements for maintenance and milk production as input variable. For these models, an updated version of the German feeding recommendation system for dairy cows and heifers was applied to determine the daily ME requirements of cows, assuming that animals neither gained nor lost BW (Eq. (3)) (GfE, 2001; Gruber et al., 2021):

$$\text{ME}_{\text{req}} = 0.65 \times \text{BW}^{0.75} + 1.37 \times \text{ECM} \times 3.28 \quad (3)$$

where ME_{req} are the ME requirements for maintenance and milk production (MJ/d), $BW^{0.75}$ is the metabolic BW ($kg^{0.75}$), and ECM (kg/d) was calculated using Eq. (1). Furthermore, the energy expenditure of grazing animals for locomotion was considered. For this, additional daily ME requirements based on horizontal and vertical walking distance were added (2.6 J/kg BW and m horizontal walking distance and 28 J/kg BW and m vertical walking distance; Heard et al., 2004).

Reference data collection

Study farms and setup

The reference dataset for model evaluation was gathered on nine commercial organic dairy farms in South Germany in 2019 and 2020. Four farms were visited in both years, whereas five farms were only visited in 2020. Per year, every farm except one was visited for two examination periods to cover spring (May to July) and summer (August to October). Every examination period lasted for 11 d with an adaptation period from Days 1 to 5 and a sampling period for faeces, milk, pasture herbage, and supplement feeds from Days 6 to 11. Depending on herd size, 10–15 lactating dairy cows per farm and period were selected. Per farm, animals were chosen to obtain groups of cows with similar days in milk and number of parities across all periods. On two farms, two groups à 8–14 cows per period were used for testing supplementation treatments.

Animals grazed semi-natural grasslands with mean ME and CP concentrations of 9.3 MJ/kg DM and 16.1 g/100 g DM, respectively, across all sampling periods (Table 1). On five farms, the botanical composition of fresh aboveground herbage biomass of grazed paddocks was assessed visually once per examination period. For these paddocks, mean proportions of grasses, clover, and other forbs were 50.8, 20.4, and 28.8% of the entire aboveground herbage mass, respectively. Grazing took place for 4–20 h/d, during the day, at night, or full-time. The 1–8 paddocks per farm were either grazed continuously or rotated daily for the total herd of lactating dairy cows. Different combinations of concentrates, fresh forage of meadows or grass-clover leys, grass hay, grass silage, and maize silage were supplemented in the barn (Supplementary Table S2). Daily supplementation with concentrate feeds ranged from 0 to 5.6 kg DM and total supplementation (i.e., forage and concentrate feeds) between 0.5 and 18.2 kg DM/d.

The final evaluation dataset comprised 233 observations averaged per farm, period, and animal from a total of 176 animals (i.e., 44 animals were repeatedly sampled during 2–4 examination periods). The 233 observations were taken from 22 primiparous and 211 multiparous cows (Table 2) and different breeds (Simmental, $n = 156$; Brown Swiss, $n = 48$; Holstein-Friesian, $n = 70$; and cross-bred cows, $n = 7$). Mean (\pm one SD) milk production was 24 kg/d (± 5.6) and mean observed DM intake and PDMI were 21 kg/d (± 3.2) and 12 kg/d (± 5.1), respectively. On seven farms, animals were milked twice per day in the morning and afternoon, whereas automatic milking systems were used on two farms. All

animals had free access to water troughs, both, in the free-stall barns and on pasture.

Data and sample collection

Ambient air temperature and relative air humidity were recorded during the sampling period in a 1-h interval (HOBO® U23 Pro v2 External Temperature/Relative Humidity Data Logger, Onset Computer Corporation, Bourne, United States). Body weight of individual cows was estimated once per period by measuring the heart girth with a tape calibrated for common cattle breeds (Animeter, Albert Kerbl GmbH, Buchbach, Germany). Additionally, days in milk and parity of individual animals at the time of sampling were retrieved from milk reports by the Regional Association for Performance and Quality Inspection in Animal Breeding of Baden-Württemberg (LKV-Baden-Württemberg). Individual milk yield was measured, and individual milk samples were taken once daily from Days 6–11 alternating between morning and afternoon milking. For this, mobile milk meters provided by the LKV-Baden-Württemberg (HI, Tru-Test Datamars, Auckland, New Zealand) were used, or the farms' own in-parlour electronic milk meters or mobile milk meters (MK5, Waikato Milking Systems, New Zealand). Milk samples (40 ml) were conserved with 150 μ L Bronysolv (ANA.LI.TIK Austria, Vienna, Austria) and stored at 4 °C for later analysis.

A double-marker technique was used to determine daily DM intake of each cow, using faecal CP concentration as internal marker to estimate the apparent total tract digestibility of diet organic matter (OM) (Lukas et al., 2005), and titanium dioxide (TiO_2) as external marker to determine daily faecal output (Glindemann et al., 2009). For this, each cow orally received 24–28 g TiO_2 daily, depending on the expected DM intake and faeces excretion level, across the entire 11-d examination period. The marker was administered twice daily in two equal dosages after morning and evening milking. On one farm, animals received apples filled with the marker. The animals of five farms received the TiO_2 mixed into ~250 g fresh matter of concentrate feed per dosage. On the remaining three farms, the marker was fed via two daily doses à ~265 g fresh matter of pelleted concentrate mixed with TiO_2 (Ökokuh 164 Mais, Raiffeisen Kraftfutterwerk, Kehl, Germany). After morning and evening milking on Days 6–11, faecal grab samples (~300 g fresh matter) were taken from the animals' rectum, frozen immediately after collection, and stored at -20 °C. On farms with two supplementation groups per period, faecal samples of individual animals of each group were taken only once daily, alternating between morning and evening.

The amount of concentrate feed consumed by each cow at automatic feeding stations was automatically recorded. If cows were additionally supplemented with forages or partial mixed rations, the amount of each feed consumed by the entire herd or supplementation group of lactating cows was measured daily throughout the sampling period. For this, scales built into the forage wagons were used, whenever available, to determine the amount of feed offered to all dairy cows, or the offered feed mass on the feeding banks were weighed manually. To do so, feed mass in different seg-

Table 1

Chemical composition (g/100 g DM), organic matter (OM) digestibility, and metabolisable energy (ME) concentration of herbage on semi-natural grasslands grazed by lactating dairy cows on nine commercial organic farms in South Germany. Arithmetic means and one SD in parentheses.

| Year | Season ¹ | OM | CP | NDF | ADF | ME, MJ/kg DM | DOM _{in vitro} g/100 g OM |
|------|---------------------|-------------|-------------|-------------|-------------|--------------|------------------------------------|
| 2019 | Spring | 87.8 (2.74) | 15.7 (0.30) | 42.5 (2.63) | 24.3 (1.58) | 9.1 (0.46) | 67.7 (2.99) |
| 2019 | Summer | 88.5 (0.56) | 19.8 (2.14) | 43.0 (3.35) | 24.2 (1.52) | 9.1 (0.36) | 69.8 (1.49) |
| 2020 | Spring | 91.1 (0.57) | 14.8 (2.03) | 45.6 (2.81) | 22.1 (2.73) | 9.8 (0.51) | 71.4 (2.68) |
| 2020 | Summer | 89.7 (0.99) | 16.2 (2.50) | 46.0 (4.14) | 23.7 (2.65) | 8.9 (0.45) | 68.4 (3.99) |

Abbreviations: DOM_{in vitro} = apparent total tract digestibility of OM determined by *in vitro* incubation.

¹ Season: spring = May to July, summer = August to October.

Table 2

Arithmetic mean, one SD, minimum, and maximum of grazing conditions, and animal and feed intake variables of lactating dairy cows grazing semi-natural grasslands on nine commercial organic dairy farms in South Germany.

| Variables | n | Mean | SD | Minimum | Maximum |
|------------------------------------|-----|-------|--------|---------|---------|
| Grazing time, h/d | 28 | 11.5 | 5.27 | 3.5 | 20.0 |
| Herbage mass, kg DM/ha | 28 | 348.0 | 184.82 | 83.2 | 822.5 |
| Herbage allowance, kg DM/cow and d | 28 | 30.9 | 26.14 | 6.7 | 94.8 |
| Days in milk, n | 233 | 142.4 | 64.02 | 16.0 | 411.5 |
| Parity, n | 233 | 3.7 | 2.01 | 1.0 | 9.0 |
| BW, kg/cow | 233 | 700.0 | 82.77 | 408.0 | 1 000.0 |
| Milk yield, kg/d | 233 | 23.9 | 5.57 | 9.7 | 39.8 |
| Milk fat, g/kg milk | 233 | 39.2 | 5.52 | 23.7 | 60.4 |
| Milk protein, g/kg milk | 233 | 32.1 | 2.77 | 25.9 | 42.9 |
| PDMI, kg/d | 233 | 12.3 | 5.09 | 0.0 | 28.7 |
| DMLsupp, kg/d | 233 | 8.8 | 5.03 | 0.5 | 24.3 |

Abbreviations: DMLsupp = DM intake of supplemental feed; PDMI = pasture herbage DM intake.

ments (~3 m) of the feeding bank was weighed at each feeding, and the weight was extrapolated to the total length of the bank to estimate total offered feed mass. The total amount of daily feed refusals of the herd or treatment group was weighed. Samples of ~200 g fresh matter of offered and refused feeds were collected and weighed daily. Additionally, one sample of the pelleted concentrate mixture with TiO₂ was collected per farm and period. Samples of fresh forage and partial mixed rations were frozen immediately after collection (−20 °C), whereas samples of grass hay and concentrate feeds were stored at room temperature until analysis.

Grazing management decisions, such as timing, frequency, duration of daily pasture access, as well as stocking densities were recorded by the farm managers throughout the grazing period. Once per sampling period, the herbaceous vegetation on grazed paddocks was sampled in three or six representative points per paddock, depending on paddock size. Hence, 9 ± 5.7 pasture herbage samples were taken per farm and period. At each sampling point, herbage mass was manually harvested using electronic shears at an average cutting height of 3 cm above the ground surface to resemble grazing depth in a 1-m²-plot (0.5 m × 2.0 m) and weighed. The entire harvested herbage per sampling point was dried for 72 h at 45 °C, weighed, and its DM concentration determined. The pasture herbage available to each cow (i.e., herbage allowance, kg DM/cow and d) was estimated by dividing the mean aboveground herbage mass (kg DM/ha) by the stocking density on each paddock (n/ha). The mean herbage allowance across all grazed paddocks per farm and sampling period was used as model input.

Laboratory analysis

At the end of each period, all milk samples were analysed for fat, protein, and lactose by Milchprüfing Baden-Württemberg e.V. (Kirchheim/Teck, Germany) according to ASU L 01.00-78, 2018-06 (Milchprüfing Baden-Württemberg e.V., 2023). Results on milk yield and composition were averaged per cow and period. For this, records of milk yield and composition were only considered, if records of morning and evening samples of consecutive days were available. After thawing, faeces samples of each cow and period were homogenised, and aliquots of ~15 g fresh matter per sample were taken and pooled by cow and period. The pooled sample (~200 g fresh matter) was lyophilised for 72 h (LYO GT2 Basis, SRK Systemtechnik GmbH, Riedstadt, Germany). Samples of pasture herbage, offered feeds, and refused feeds were dried at 45 °C for 72 h, except of feed samples including silages that were lyophilised. Dried samples of faeces, pasture herbage, and offered and refused feeds were weighed, then ground to pass through a 1-mm-sieve (Retsch SM 100, Retsch GmbH, Haan, Germany). After

grinding, the whole samples of pasture herbage were pooled by paddock and period, and samples of offered and refused feed were each composited by farm and period. All faeces, pasture herbage, and feed samples were analysed in duplicate using the official analytical methods in Germany (Verband Deutscher Landwirtschaftlicher Untersuchungs- und Forschungsanstalten, 2007). All samples were analysed for DM and crude ash (methods 3.1 and 8.1, respectively). Concentrations of nitrogen in samples of pasture herbage, offered feed, and feed refusals were determined by Dumas combustion (method 4.1.2) using the Vario Max CN (Elementar Analysensysteme GmbH, Langensfeld, Germany). In faecal samples, nitrogen concentration was determined via Kjeldahl digestion (method 4.1.1; Vaportest 45 s, C. Gerhardt GmbH & Co. KG, Königswinter, Germany and behrotest K20L, Behr Labor-Technik GmbH, Düsseldorf, Germany). Subsequently, CP concentrations were calculated as nitrogen concentration × 6.25. The samples of herbage and offered feed were additionally analysed for NDF and ADF (methods 6.5.1 and 6.5.2, respectively) using an Ankom200 Fiber Analyzer (Ankom Technology, Fairport, US) and for crude lipid by ether extraction (method 5.1.1A) using a Soxtec System (HT 1043 Extraction Unit, Foss Tecator, Hillerød, Denmark). The Hohenheim Gas Test was applied to determine digestible OM (g/100 g OM) and ME concentrations of herbage and offered feed-stuffs in triplicate in two independent runs, according to the procedures and feedstuffs-specific equations described by Menke and Steingass (1988). Concentration of net energy for lactation in offered feed and pasture herbage was estimated from the ME concentration using an updated coefficient for lactation efficiency ($k = 0.73$; Gruber et al., 2021). Apparent total tract DM digestibility of herbage and offered feed was estimated from ADF and nitrogen concentrations in feed using Eq. (2) by Oddy et al. (1983). The TiO₂ concentration in faeces and pelleted concentrate mixtures with TiO₂ was determined in duplicate using the slightly modified method by Boguhn et al. (2009).

Chewing and locomotion behaviour

Ten of the experimental cows per period and farm were equipped with a sensor system to monitor their chewing behaviour, which combines a noseband-pressure sensor with a triaxial accelerometer (RumiWatch®, ITIN + HOCH, Liestal, Switzerland). On five farms, five of these animals were additionally equipped with Global Positioning System collars (VERTEX Lite Collars, Vectronics Aerospace, Berlin, Germany) to determine their walking distances during pasture access. The animals were equipped with the sensors 1.5 d prior to the 6-d-sampling period to allow for adaptation to the sensors. The chewing sensors recorded at a frequency of 10 Hz, whereas the Global Positioning System collars registered the Universal Transverse Mercator coordinates and the

altitude of the cows' location every 5 min. These registered Universal Transverse Mercator coordinates were then used to calculate the horizontal walking distance during pasture access using the Euclidean Distance with Eq. (4). The vertical walking distance was calculated from the recorded altitude (Eq. (5)):

$$\text{Horizontal walking distance} = \sum_{i=1}^n \sqrt{(Y_{i+1} - Y_i)^2 + (X_{i+1} - X_i)^2} \quad (4)$$

$$\text{Vertical walking distance} = \sum_{i=1}^n |A_{i+1} - A_i| \quad (5)$$

where horizontal walking distance was in m/d, Y_i is the y coordinate of the cow's location at time i , X_i is the x coordinate of the cow's location at time i , vertical walking distance was in m/d, and A_i is the altitude of the cow's location at time i in m. For calculating the ME requirements, the mean horizontal and vertical walking distances averaged per farm and period were used for each cow of the respective farm and period. For animals of farms where the Global Positioning System collars were not applied, the mean horizontal and vertical walking distances across all sampling periods and farms with Global Positioning System records were used. Using the RumiWatch Converter V0.7.3.36 (ITIN + HOCH, Liestal, Switzerland), jaw movement observations were converted to the total number of eat chews per day (i.e., mastication and prehension bites), bite rate (i.e., eat chews per minute of eating time), daily eating time on pasture, and daily number of prehension bites (i.e., only eat bites excluding mastication) in a 1-h resolution. Observations of these chewing variables were averaged for each animal per period and farm, but only mean values based on a minimum of four complete sampling days per animal were considered as model input.

Calculation of pasture herbage intake

Individual daily DM intake was calculated from the apparent total tract digestibility of ingested OM (**DOM_{CP}**, g/100 g OM) and daily faecal OM output. The **DOM_{CP}** was estimated using the CP concentration in faecal samples using the Gumpenstein/Hohenheim coefficient (Lukas et al., 2005). Faecal OM output (kg/d) was calculated by dividing the TiO_2 dosage (g/d) by the concentration of TiO_2 in faeces (g/kg OM). For the three farms on which TiO_2 was administered via pelleted concentrate mixtures, analysed TiO_2 concentration in concentrate pellets and daily pellet intake was used to calculate TiO_2 dosage. Total OM intake was determined by dividing faecal OM output by $[(1 - \text{DOM}_{\text{CP}})/100]$. Finally, DM intake was estimated by dividing OM intake by dietary OM concentration (kg/kg). The latter was estimated based on the ratio between PDMI and DMIsupp, forecasted using the ME requirements issued by the GfE (2001).

In case there were no records of individual DMIsupp from sole concentrate supplementation by feeding stations, it was determined proportionally to the animal's individual eating time in the barn using Eqs. (6) and (7):

$$\text{DMIsupp}_i = \frac{\text{eat}_i}{\text{eat}_{\text{sampled}}} \times \text{DMIsupp}_{\text{sampled}} \quad (6)$$

$$\text{DMIsupp}_{\text{sampled}} = \frac{\text{DMIsupp}_{\text{herd}}}{n_{\text{sampled}} \div n_{\text{herd}}} \quad (7)$$

where DMIsupp_i is the DM intake of supplemental feed of cow i (kg/d), eat_i the eating time in barn of cow i (min/d), $\text{eat}_{\text{sampled}}$ the sum of the time spent eating in barn across the cows with eat_i records per farm and period (min/d), $\text{DMIsupp}_{\text{sampled}}$ the sum of DMIsupp across the cows with eat_i records per farm and period (kg DM/d), $\text{DMIsupp}_{\text{herd}}$ the difference between the offered and

refused DM by the total herd (kg DM/d), n_{sampled} the number of cows with eat_i records per period and farm, and n_{herd} the total number of cows per herd, period, and farm. Finally, individual PDMI was calculated by subtracting the DMIsupp of each cow from its DM intake. Thus, individual PDMI could solely be calculated when complete behavioural records or measured individual DMIsupp values were available for the animal.

Statistical analysis

Evaluation of the models' prediction adequacy

Mean observations per farm and period of 296 animals were collected; however, only 233 were used for model evaluation. Sixty-three observations were excluded, because of missing records of chewing behaviour, due to technical issues with the sensors, or if animals refused to ingest daily TiO_2 dosages. Additionally, only 220 observations were used for evaluating the behaviour-based models Rombach and Greenwood, because these observations were missing the chewing behaviour data as input variables, whereas individual DMIsupp values were based on feed station measurements. For the evaluation of the model Oudshoorn, even less observations were considered ($n = 208$). In this case, the chewing behaviour sensors failed to record the prehension bites.

All following statistical analyses were conducted in R Version 4.2.0 (R Core Team, 2022). Mean bias (**MB**), mean square error of prediction (**MSEP**), and relative prediction error (**RPE**) were calculated to evaluate the models' prediction adequacy (i.e., accuracy and precision) (Tedeschi, 2006). The MB, MSEP, and RPE were calculated for both, the PDMI based on individual observations ($n = 233$, 220, or 208) and on mean basis, i.e., comparing the observed versus predicted PDMI averaged per farm, period, and supplementation group ($n = 28$). Equation (8) was used to calculate the MB (Tedeschi, 2006):

$$\text{MB} = \sum_i^n \frac{(\text{Obs}_i - \text{Pred}_i)}{n} \quad (8)$$

where MB is the mean bias per model, n the number of observations, Obs_i the observed PDMI of animal i (kg/d), and Pred_i the predicted PDMI of animal i (kg/d). A negative MB indicates an overprediction, a positive MB an underprediction of PDMI, and a $\text{MB} \leq 10\%$ acceptable modelling accuracy (Yungblut et al., 1981). The MSEP was used to decompose the source of prediction error and was therefore calculated as the sum of three error terms (Eq. (9)), representing the mean prediction bias, line bias, and random variation (Fuentes-Pila et al., 1996):

$$\text{MSEP} = (\overline{\text{obs}} - \overline{\text{pred}})^2 + s_{\text{obs}}^2(1 - b)^2 + s_{\text{pred}}^2(1 - R^2) \quad (9)$$

where MSEP is the mean square error of prediction per model, $\overline{\text{obs}}$ the mean observed PDMI (obs, kg/d), $\overline{\text{pred}}$ the mean predicted PDMI (pred, kg/d), s_{obs}^2 the variance of obs, s_{pred}^2 the variance of pred, b the slope of the regression between obs and pred, and R^2 the coefficient of determination of the regression between obs and pred. Whilst a large proportion of line bias (i.e., $s_{\text{obs}}^2(1 - b)^2$) is a sign for major systematic errors in the model structure and therefore not desired, a large proportion of random variation (i.e., $s_{\text{pred}}^2(1 - R^2)$) is an indicator for the model's high predictive adequacy where the greatest share of error is caused by variation in the observed data (Fuentes-Pila et al., 1996). The RPE (%) was calculated as the root of the MSEP divided by the mean observed PDMI. It was classified according to Fuentes-Pila et al. (1996), who assumed that the prediction adequacy is satisfactory with an $\text{RPE} < 10\%$, acceptable between 10% and 20%, and not acceptable with an $\text{RPE} > 20\%$.

Evaluation of the models' adequacy by animal subgroups

It was hypothesised that existing models were not suitable to predict PDMI of animals grazing on semi-natural grassland due to their inability to reflect the variable grazing and production factors under such conditions. Hence, the RPE was calculated separately for animal subsets differing in grazing or production levels. For this, the grazing factors daytime of pasture access, herbage allowance, stocking density, and DMIsupp, were considered and the production factors DM intake of concentrates, energy-corrected milk yield, feed use efficiency (kg energy-corrected milk/kg DM intake), and dietary ME and CP concentrations. For the quantitative factors, subgroups were formed by dividing animals into three groups of equal size per factor.

Analysis of residuals

To identify variables that explain the difference between observed and predicted values (i.e., the residuals), the most adequate models (i.e., with the lowest RPE) among the evaluated models were further examined using Bland-Altman plots, mixed-effects models, and stepwise regression. The Bland-Altman plots were used to visually assess the agreement between the observed and predicted PDMI and were created with the R package ggplot2 (Wickham, 2016). For this, the residuals were plotted against the means of the observed and predicted values. Additionally, the 95%-limits of agreement were calculated as $\pm 1.96 \times$ the SD of the residuals to quantify the residuals' spread (i.e., the models' precision; Bland and Altman, 1999).

Linear mixed-effects models were used to analyse the relation between the residuals of the most adequate prediction models and their respective input variables. The residuals were considered as the dependent variable, while the input variables of the respective prediction models were considered as independent variables. The animal was used as a random effect. Variables were considered significant at $P \leq 0.05$. For this analysis, the lme4 package was deployed (Bates et al., 2015). The marginal and conditional R^2 was calculated for each mixed model to determine the share of variation in residuals explained by the input variables (marginal R^2) and by the random effects (conditional R^2 minus marginal R^2). Mixed model and stepwise analyses were executed using three different variants of the residuals as dependent variable, with (1) absolute values (i.e., as difference between observed and predicted PDMI, kg DM/d), (2) relative values (i.e., the absolute value in percent of the respective observed PDMI (%)), or (3) relative values without negative signs (%).

Stepwise regression was used to analyse the relation between the residuals and potential independent predictors (i.e., the remaining variables excluding the model input factors). Forward, backward, and bi-directional elimination were applied to identify possible independent predictors of the residuals among the following candidate variables: grazing season (early or late), animal breed, parity, days in milk, milk yield, fat concentration and protein concentration prior to the examination period, feed use efficiency, DM intake of fresh forage, silage, hay, and concentrate, DOM_{CP}, grazing system (i.e., continuous, rotational, or short-grass grazing), length of daily pasture access, daytime of pasture access (i.e., night-time, daytime, full-time), herbage allowance, stocking density, stocking rate, herbage mass, ambient air temperature and relative air humidity, daily eating time, daily rumination time, daily eating time during grazing, daily rumination time during grazing, daily number of rumination chews, and daily number of rumination chews during grazing. Variables were entered and removed based on P -values, using the functions `ols_step_forward_p`, `ols_step_backward_p`, and `ols_step_both_p` by the R package `olsrr` (Hebbali, 2020). The resulting models after stepwise regression were checked for variable inflation factors (i.e., multicollinearity) using the VIF function of the R package `regclass` (Petrie, 2020).

Variables with a variable inflation factor ≥ 10 were removed successively from the statistical model until no variable with a variable inflation factor ≥ 10 remained. Finally, among the three resulting models from forward, backward, and bi-directional elimination, the model with the greatest R^2 and lowest Bayesian information criterion was reported in the present study. The relative importance of the predictor variables selected by stepwise regression (i.e., their individual contribution to the R^2 of the selected linear model) was quantified using the method by Lindeman et al. (1980) using the R function `lmg` by the package `relaimpo` (Grömping, 2006).

Results

Evaluation of the models' prediction adequacy

Based on the evaluation of individual animal observations, the MB was lowest for the stall-based models NRC, Mertens II, and De Souza with -0.1 , 0.3 , and -0.5 kg DM/d, respectively (Table 3). The behaviour-based models resulted in the greatest MB. The model Oudshoorn overestimated daily PDMI by 3.1 kg DM, whereas models Greenwood and Rombach underestimated daily PDMI by on average 2.6 and 3.3 kg DM, respectively. The models e-cow and GrazeSim overestimated PDMI by 3.2 and 1.0 kg DM/d, respectively. None of the fourteen evaluated models reached an RPE $< 20\%$, indicating that there was no model which predicted the PDMI with an acceptable adequacy when evaluated based on observed data from 208 to 233 individual animals (Table 3). The RPE for the behaviour-based as well as semi-mechanistic grazing-based models ranged from 41.9 to 52.0% , and the proportion of their MSEF attributable to the mean plus line bias ranged from 37.1 to 48.1% of total MSEF. The lowest RPE, and therefore the highest adequacy, was achieved by the semi-mechanistic stall-based model Mertens II (24.7%), closely followed by the empirical model NRC (25.3%) and the semi-mechanistic model Conrad (25.5%). For these three models, the greatest proportion of MSEF was the random error, ranging from 84.0 to 90.2% of total MSEF. When evaluated based on means per farm, period and supplementation group ($n = 28$), these three models and the original Mertens I model achieved an acceptable prediction adequacy (Table 4) with lowest RPE with 13.4% for Mertens II. The evaluation on mean basis did not substantially improve the prediction adequacy of the remaining models.

Evaluation for different animal subgroups

To evaluate the prediction adequacy of the models based on different levels of grazing (Table 5) and production factors (Table 6), the RPE was calculated separately for different subgroups of animals. Across all evaluated models, the RPE was lower in subgroups with full-time pasture access (i.e., 20 h/d) as compared to daytime (5 – 9 h/d) or night-time (9 – 12 h/d) access, and with DMIsupp < 4.8 kg/d as compared to the subgroups with medium and high DMIsupp, i.e., ≥ 4.8 kg/d. The RPE of the full-time access and low DMIsupp subgroups was below the threshold of 20% , for the models Cornell, NRC, Conrad, Mertens I, and Mertens II indicating an acceptable prediction accuracy for individual cow observations. Predictions by the models Conrad for animals with a feed use efficiency < 1.2 also had an RPE $< 20\%$. For the majority of models, the RPE was also lower for the subgroups on pastures with medium and high herbage allowance i.e., ≥ 14.3 as compared to a low herbage allowance < 14.3 kg DM/d, and for Brown Swiss and Holstein-Friesian cows as compared to Simmental cows. There was no substantial difference in the RPE between different levels of energy-corrected milk yield or dietary CP concentrations.

Table 3

Statistical evaluation of models to predict the individual pasture herbage DM intake (PDMI) of lactating dairy cows grazing semi-natural grasslands.

| Models | N | MB, kg DM/d | MB, % ¹ | MSEP, kg DM ² /d | Partitioning of MSEP, % | | | RPE, % |
|---|-----|-------------|--------------------|-----------------------------|-------------------------|-----------|--------------|--------|
| | | | | | MB | Line bias | Random error | |
| Behaviour-based ² | | | | | | | | |
| Rombach | 220 | 3.3 | 27.6 | 27.1 | 40.9 | 7.2 | 51.9 | 43.2 |
| Greenwood | 220 | 2.6 | 21.9 | 25.5 | 27.4 | 13.5 | 59.1 | 41.9 |
| Oudshoorn | 208 | −3.1 | −25.6 | 26.6 | 36.0 | 1.2 | 62.9 | 42.6 |
| Empirical stall-based ³ | | | | | | | | |
| AFRC | 233 | 5.2 | 42.6 | 35.6 | 77.5 | 0.7 | 21.8 | 48.5 |
| Cornell | 233 | 1.8 | 14.4 | 13.4 | 23.3 | 13.8 | 62.9 | 29.7 |
| De Souza | 233 | −0.5 | −4.4 | 16.6 | 1.8 | 32.1 | 66.1 | 33.1 |
| Gruber | 233 | 3.3 | 27.0 | 19.6 | 56.2 | 1.7 | 42.1 | 36.0 |
| NRC | 233 | −0.1 | −0.4 | 9.7 | 0.0 | 9.8 | 90.2 | 25.3 |
| Sauvant | 233 | 3.1 | 24.9 | 22.2 | 42.2 | 7.2 | 50.6 | 38.3 |
| Semi-mechanistic stall-based ⁴ | | | | | | | | |
| Conrad | 233 | −1.1 | −8.8 | 9.8 | 12.0 | 4.0 | 84.0 | 25.5 |
| Mertens I | 233 | 1.3 | 10.6 | 11.2 | 15.1 | 7.4 | 77.5 | 27.2 |
| Mertens II | 233 | 0.3 | 2.5 | 9.2 | 1.0 | 11.1 | 87.9 | 24.7 |
| Semi-mechanistic pasture-based ⁵ | | | | | | | | |
| e-cow | 233 | −3.2 | −25.6 | 31.0 | 32.0 | 8.5 | 59.5 | 45.3 |
| GrazeSim | 233 | −1.0 | −8.1 | 40.9 | 2.4 | 40.1 | 57.5 | 52.0 |

Abbreviations: MB = mean bias; MSEP = mean square error of prediction; RPE = relative prediction error, % of observed mean PDMI.

¹ MB, % of mean observed PDMI.² Rombach (Rombach et al., 2019), Greenwood (Greenwood et al., 2017), Oudshoorn (Oudshoorn et al., 2013).³ AFRC (Vadiveloo and Holmes, 1979), Cornell (Fox et al., 2004), De Souza (de Souza et al., 2019), Gruber (Deutsche Landwirtschafts-Gesellschaft, 2006), NRC (National Research Council, 2001), Sauvant (Sauvant et al., 2014).⁴ Conrad (Conrad et al., 1964; Kahn and Spedding, 1984), Mertens I (Mertens, 1987), Mertens II: modified Mertens I considering a higher intake capacity (Baudracco et al., 2012).⁵ e-cow (Baudracco et al., 2012), GrazeSim (Vazquez and Smith, 2001).**Table 4**

Statistical evaluation of models to predict the pasture herbage DM intake (PDMI) of lactating dairy cows grazing semi-natural grasslands based on the mean values per farm, period and supplementation group (n = 28). Only models with an RPE < 20% are reported.

| Models | MB, kg DM/d | MB, % ¹ | MSEP, kg DM ² /d | Partitioning of MSEP, % | | | RPE, % |
|-------------------------|-------------|--------------------|-----------------------------|-------------------------|-----------|--------------|--------|
| | | | | MB | Line bias | Random error | |
| NRC ² | −0.1 | −1.2 | 4.0 | 0.5 | 13.3 | 86.2 | 16.9 |
| Conrad ³ | −1.2 | −9.9 | 3.9 | 36.1 | 1.8 | 62.1 | 16.5 |
| Mertens I ⁴ | 1.3 | 10.5 | 5.4 | 29.4 | 9.2 | 61.3 | 19.4 |
| Mertens II ⁵ | 0.2 | 2.1 | 2.6 | 2.4 | 15.7 | 81.9 | 13.4 |

Abbreviations: MB = mean bias; MSEP = mean square error of prediction; RPE = relative prediction error, % of observed PDMI.

¹ MB, % of observed mean PDMI.² NRC (National Research Council, 2001).³ Conrad (Conrad et al., 1964; Kahn and Spedding, 1984).⁴ Mertens I (Mertens, 1987).⁵ Mertens II: modified Mertens I considering a higher intake capacity (Baudracco et al., 2012).

Analysis of residuals

The Bland-Altman graphs (Fig. 1) plot the residuals of the models NRC, Conrad, and Mertens II against the mean of the observed and predicted PDMI. The plots for the models NRC and Mertens II illustrate a uniform scatter of residuals around the zero-line, which resulted in a MB close to zero for these two models. The lower 95%-limits of agreement were located at −6.1, −6.9, and −5.6 and the upper 95%-limits at 6.1, 4.7, and 6.3 kg DM/d for the models NRC, Conrad, and Mertens II, respectively. This indicates a uniform, but wide distribution for 95% of the models' residuals.

The residuals for the models with the lowest RPE i.e., NRC, Conrad, and Mertens II, were analysed using mixed-effects models, and stepwise regression. The results of the mixed models using the input variables of the intake models as fixed effects and the relative residuals with positive and negative signs as dependent variable are summarised in Supplementary Table S3. The DMIsupp was the only significant input factor for the relative residuals of all three models. The marginal R^2 of the respective mixed models, however, indicated that the DMIsupp effect was negligible. For

the relative residuals, only 3–5% of the variation were explained by the fixed effects of the mixed models. In case of the absolute residuals, this share was greater (marginal R^2 between 14 and 23%).

Stepwise regression was used to identify potential predictors among a pool of independent grazing and production factors for explaining the relative residuals of the models NRC, Mertens II and Conrad (Supplementary Table S4). Backward selection rendered greater adjusted R^2 values and lower Bayesian information criterion values than forward or bi-directional selection for both analyses, based on relative residuals including or excluding negative signs. The adjusted R^2 values of the backward-selected models ranged between 0.03 and 0.05 (Table 7). When stepwise regression was performed for predicting the absolute residuals, the greatest adjusted R^2 and lowest Bayesian information criterion values were achieved by forward selection. For these forward-selected models, the adjusted R^2 ranged between 0.73 and 0.77. The predictor with the greatest relative importance (between 67.9 and 71.9 %) among the retained variables was feed use efficiency. It was related to absolute residuals of the models NRC, Conrad, and Mertens II by

Table 5

Relative prediction error (RPE, % of observed pasture herbage DM intake (PDMI)) of models to predict PDMI for different subgroups of lactating dairy cows grazing semi-natural grasslands, separated by different levels of grazing factors.

| Models | Daytime of pasture access ¹ | | | Herbage allowance ² | | | Stocking density ³ | | | DMIsupp ⁴ | | |
|--|--|-----------|------------|--------------------------------|--------|-------|-------------------------------|--------|------|----------------------|--------|------|
| | Daytime | Full-time | Night-time | Low | Medium | High | Low | Medium | High | Low | Medium | High |
| Behaviour-based⁵ | | | | | | | | | | | | |
| Rombach | 53.4 | 26.2 | 48.0 | 47.7 | 40.4 | 38.6 | 45.4 | 37.9 | 44.0 | 32.6 | 43.1 | 63.6 |
| Greenwood | 44.6 | 21.7 | 54.4 | 47.2 | 43.7 | 29.6 | 32.6 | 42.3 | 46.0 | 29.4 | 48.7 | 53.2 |
| Oudshoorn | 63.4 | 24.0 | 37.6 | 53.4 | 29.8 | 42.7 | 52.3 | 36.7 | 36.2 | 21.4 | 34.1 | 90.9 |
| Empirical stall-based⁶ | | | | | | | | | | | | |
| AFRC | 61.4 | 29.1 | 56.8 | 60.6 | 42.8 | 42.6 | 47.2 | 45.0 | 53.6 | 32.3 | 53.0 | 77.8 |
| Cornell | 42.4 | 16.7* | 31.2 | 33.5 | 25.3 | 30.2 | 36.1 | 26.7 | 26.0 | 17.5* | 30.7 | 54.9 |
| De Souza | 36.8 | 29.1 | 32.8 | 36.7 | 26.8 | 35.2 | 37.0 | 31.6 | 30.7 | 28.0 | 29.2 | 49.5 |
| Gruber | 42.5 | 19.1* | 46.6 | 44.5 | 33.0 | 30.9 | 34.7 | 33.4 | 40.2 | 22.7 | 40.8 | 58.1 |
| NRC | 32.9 | 17.0* | 27.1 | 30.7 | 23.7 | 21.7 | 25.2 | 26.4 | 23.8 | 18.3* | 25.8 | 40.4 |
| Sauvant | 52.4 | 23.0 | 41.2 | 42.0 | 33.8 | 38.8 | 45.5 | 30.8 | 39.0 | 24.1 | 38.7 | 69.4 |
| Semi-mechanistic stall-based⁷ | | | | | | | | | | | | |
| Conrad | 35.6 | 16.8* | 25.2 | 31.5 | 25.4 | 19.6* | 25.0 | 27.2 | 23.6 | 17.4* | 28.9 | 38.2 |
| Mertens I | 33.4 | 17.2* | 32.1 | 34.5 | 24.5 | 23.1 | 25.8 | 25.5 | 30.6 | 18.6* | 30.8 | 41.1 |
| Mertens II | 32.2 | 16.9* | 26.1 | 30.7 | 22.0 | 21.8 | 24.0 | 25.8 | 23.9 | 18.5* | 26.4 | 35.9 |
| Semi-mechanistic, pasture-based⁸ | | | | | | | | | | | | |
| GrazeSim | 71.8 | 31.1 | 55.3 | 54.2 | 45.6 | 54.8 | 60.1 | 50.6 | 44.1 | 33.6 | 50.9 | 94.5 |
| e-cow | 64.2 | 36.2 | 34.4 | 45.5 | 24.5 | 58.2 | 58.3 | 40.3 | 34.8 | 29.3 | 35.6 | 92.4 |

Abbreviations: DMIsupp = DM intake supplement feed.

¹ Daytime: pasture access during daytime for 5–9 h/d (daytime), during the night for 9–12 h/d (night-time), or for full day except for milking for 20 h/d (full-time).

² Herbage allowance: low (<14.3), medium (14.3 – 29.1), and high allowance (>29.1 kg DM/cow and d).

³ Stocking density: low (<10.9), medium (10.9 – 20.2), and high level (>20.2 cows/ha).

⁴ DMIsupp: low (<4.8), medium (4.8 – 11.1), and high level (>11.1 kg DM/d).

⁵ Rombach (Rombach et al., 2019), Greenwood (Greenwood et al., 2017), Oudshoorn (Oudshoorn et al., 2013).

⁶ AFRC (Vadiveloo and Holmes, 1979), Cornell (Fox et al., 2004), De Souza (de Souza et al., 2019), Gruber (Deutsche Landwirtschafts-Gesellschaft, 2006), NRC (National Research Council, 2001), Sauvant (Sauvant et al., 2014).

⁷ Conrad (Conrad et al., 1964; Kahn and Spedding, 1984), Mertens I (Mertens, 1987), Mertens II: modified Mertens I considering a higher intake capacity (Baudracco et al., 2012).

⁸ e-cow (Baudracco et al., 2012), GrazeSim (Vazquez and Smith, 2001).

* Groups with an RPE < 20%, i.e., acceptable prediction accuracy, are indicated by an asterisk.

Table 6

Relative prediction error (RPE, % of observed pasture herbage DM intake (PDMI)) of models to predict PDMI for different subgroups of lactating dairy cows grazing semi-natural grasslands, separated by different levels of production factors.

| Models | Concentrate DMI ¹ | | | ECM before trial ² | | | Feed use efficiency ³ | | | ME ⁴ | | | CP ⁵ | | | Breed ⁶ | | |
|---|------------------------------|--------|------|-------------------------------|--------|------|----------------------------------|--------|------|-----------------|--------|------|-----------------|--------|------|--------------------|------|------|
| | Low | Medium | High | Low | Medium | High | Low | Medium | High | Low | Medium | High | Low | Medium | High | Brown | Hf | Simm |
| Behaviour-based⁷ | | | | | | | | | | | | | | | | | | |
| Rombach | 39.2 | 37.5 | 52.2 | 41.4 | 41.5 | 43.5 | 49.8 | 39.6 | 31.4 | 43.0 | 39.7 | 42.8 | 38.2 | 46.6 | 39.7 | 28.0 | 40.2 | 48.7 |
| Greenwood | 50.8 | 33.6 | 38.7 | 43.2 | 41.5 | 35.2 | 50.3 | 33.9 | 32.2 | 44.1 | 43.5 | 32.9 | 41.8 | 42.6 | 37.1 | 34.5 | 28.8 | 51.0 |
| Oudshoorn | 36.5 | 30.9 | 61.1 | 40.7 | 41.4 | 39.6 | 31.5 | 42.2 | 53.1 | 30.8 | 45.6 | 50.3 | 41.2 | 40.1 | 44.6 | 41.1 | 34.9 | 48.1 |
| Empirical stall-based⁸ | | | | | | | | | | | | | | | | | | |
| AFRC | 56.9 | 40.2 | 50.2 | 51.8 | 51.7 | 41.3 | 58.6 | 45.0 | 33.7 | 44.8 | 59.7 | 41.2 | 52.7 | 43.8 | 49.1 | 48.1 | 37.9 | 56.4 |
| Cornell | 27.9 | 22.4 | 41.3 | 27.5 | 29.9 | 30.1 | 33.4 | 28.6 | 24.9 | 24.3 | 34.5 | 31.7 | 31.5 | 30.5 | 26.5 | 21.0 | 22.5 | 37.5 |
| De Souza | 26.5 | 31.7 | 40.6 | 30.3 | 37.0 | 29.5 | 26.7 | 32.2 | 41.3 | 32.9 | 33.7 | 32.3 | 34.5 | 33.1 | 31.5 | 32.9 | 33.8 | 32.6 |
| Gruber | 41.8 | 30.1 | 37.6 | 37.3 | 38.8 | 29.9 | 45.8 | 31.1 | 22.9 | 36.2 | 42.9 | 27.5 | 39.7 | 33.5 | 34.7 | 27.1 | 29.3 | 43.7 |
| NRC | 23.4 | 21.9 | 31.7 | 25.5 | 25.8 | 21.9 | 25.5 | 18.8* | 30.9 | 24.0 | 25.5 | 26.3 | 26.0 | 23.9 | 26.1 | 18.2* | 23.4 | 29.3 |
| Sauvant | 36.7 | 31.9 | 48.8 | 36.4 | 38.8 | 37.7 | 42.1 | 38.3 | 31.8 | 34.2 | 46.0 | 35.7 | 44.3 | 35.4 | 34.5 | 30.2 | 30.7 | 46.4 |
| Semi-mechanistic stall-based⁹ | | | | | | | | | | | | | | | | | | |
| Conrad | 23.9 | 21.0 | 33.2 | 24.6 | 26.7 | 23.2 | 19.6* | 17.8* | 37.7 | 22.2 | 26.0 | 28.8 | 26.6 | 24.9 | 24.9 | 18.5* | 23.1 | 29.9 |
| Mertens I | 29.1 | 24.0 | 29.5 | 30.7 | 28.0 | 22.5 | 32.4 | 22.4 | 24.0 | 27.2 | 30.1 | 24.0 | 29.7 | 22.9 | 29.4 | 23.5 | 24.8 | 30.9 |
| Mertens II | 25.2 | 21.4 | 28.7 | 26.3 | 24.7 | 21.8 | 26.8 | 18.8 | 27.5 | 23.9 | 26.4 | 23.8 | 24.8 | 23.1 | 26.4 | 21.3 | 21.6 | 28.4 |
| Semi-mechanistic, pasture-based¹⁰ | | | | | | | | | | | | | | | | | | |
| GrazeSim | 51.0 | 38.2 | 71.3 | 44.7 | 46.9 | 52.3 | 47.5 | 48.3 | 61.1 | 45.1 | 61.8 | 50.9 | 58.3 | 53.6 | 41.2 | 31.5 | 36.3 | 67.5 |
| e-cow | 34.1 | 36.2 | 66.5 | 35.7 | 48.5 | 43.8 | 28.8 | 50.0 | 56.7 | 34.1 | 56.4 | 47.6 | 51.5 | 40.4 | 43.7 | 46.1 | 33.3 | 52.6 |

Abbreviations: DMI = DM intake; ECM = energy-corrected milk yield; ME = metabolisable energy.

¹ Concentrate DMI: low (<0.5), medium (0.5 – 2.8), and high level (>2.8 kg DM/d).

² ECM before trial: low (<22.1), medium (22.1 – 27.1), and high level (>27.1 kg/d).

³ Feed use efficiency: low (<1.0), medium (1.0 – 1.2), and high level (>1.2 kg ECM/kg DMI).

⁴ ME: low (<9.2), medium (9.2 – 10.0), and high level (>10.0 MJ/kg DM).

⁵ CP: low (<14.3), medium (14.3 – 15.7), and high level (>15.7 MJ/kg DM).

⁶ Breed: Brown = Brown Swiss, Hf = Holstein-Friesian, Simm = Simmental.

⁷ Rombach (Rombach et al., 2019), Greenwood (Greenwood et al., 2017), Oudshoorn (Oudshoorn et al., 2013).

⁸ AFRC (Vadiveloo and Holmes, 1979), Cornell (Fox et al., 2004), De Souza (de Souza et al., 2019), Gruber (Deutsche Landwirtschafts-Gesellschaft, 2006), NRC (National Research Council, 2001), Sauvant (Sauvant et al., 2014).

⁹ Conrad (Conrad et al., 1964; Kahn and Spedding, 1984), Mertens I (Mertens, 1987), Mertens II: modified Mertens I considering a higher intake capacity (Baudracco et al., 2012).

¹⁰ e-cow (Baudracco et al., 2012), GrazeSim (Vazquez and Smith, 2001).

* Groups with an RPE < 20%, i.e., acceptable prediction accuracy, are indicated by an asterisk.

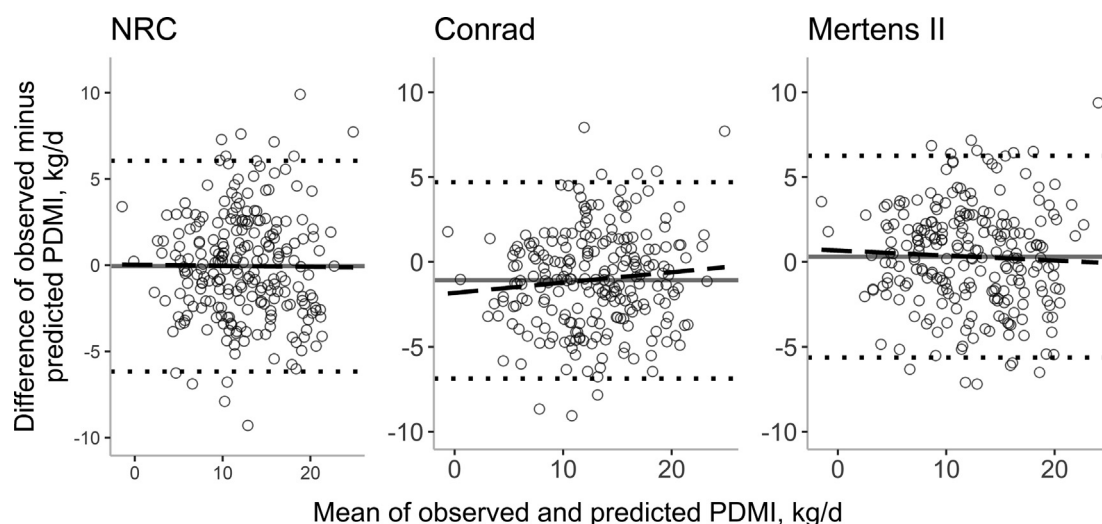


Fig. 1. Bland-Altman plots showing the relationship between the residuals and the mean of observed and predicted pasture herbage DM intake (PDMI) for the models NRC, Conrad, and Mertens II evaluated with a dataset with lactating dairy cows grazing semi-natural grasslands on organic dairy farms ($n = 233$). The dashed line corresponds to the simple linear regression line between residuals and mean of observed and predicted PDMI; the dotted lines indicate the lower and upper 95%-limits of agreement; the solid line indicates the mean bias between observed and predicted PDMI.

Table 7

Adjusted R^2 of linear regression models identified via stepwise regression to identify independent predictors for the residuals of pasture herbage DM intake (PDMI, i.e., observed – predicted PDMI) estimated by the models NRC,¹ Conrad,² and Mertens II³ for lactating dairy cows grazing semi-natural grasslands.

| Models | Absolute residuals | Relative residuals | Relative residuals without negative signs |
|------------|--------------------|--------------------|---|
| NRC | 0.77 | 0.05 | 0.04 |
| Conrad | 0.73 | 0.03 | 0.05 |
| Mertens II | 0.76 | 0.05 | 0.05 |

¹ NRC (National Research Council, 2001).

² Conrad (Conrad et al., 1964; Kahn and Spedding, 1984).

³ Mertens II: modified Mertens I considering a higher intake capacity (Mertens, 1987; Baudracco et al., 2012).

a decrease of 12.6, 12.7, and 12.5 kg PDMI/d per unit increase in feed use efficiency (kg energy-corrected milk yield/kg DM intake), respectively.

Discussion

The reference dataset represents the wide range of grazing and production factors found on commercial farms in South Germany using semi-natural grasslands for grazing, which differed substantially from the commonly studied temperate grazing systems with regard to their supplementation strategy and pasture conditions (Bargo et al., 2003; Pérez-Prieto and Delagarde, 2012). Cows in the present study were predominantly supplemented with forages (mean forage to concentrate ratio of DMIsupp: 71:29, on DM basis), such as grass hay, grass silage, or freshly cut forages. The type and combination of forage and concentrate supplements, however, differed greatly between farms, which is typical of the diversity of farm structures and management systems found in this region (Velasco et al., 2021). Further, a comparably low herbage mass (348 kg DM/ha) was measured on the grazed semi-natural grasslands of the observed farms. In contrast, herbage mass values between 1 800 and 3 700 kg DM/ha were identified in a meta-analysis characterising intensive strip-grazing systems with minimal supplementation (i.e., < 1 kg DM/d; Pérez-Prieto and Delagarde, 2012).

Limitations of reference dataset

The aim of the present study was to evaluate the adequacy of existing models to estimate the PDMI of individual and groups of

dairy cows grazing semi-natural grasslands, using the above-described on-farm reference dataset. As it is inherently challenging to measure the actual feed intake of individual grazing animals (Hellwing et al., 2015), a certain error in the reference PDMI values is expected due to (1) the chosen methodology to determine DM intake and (2) the method used to estimate individual DMIsupp.

The DM intake was determined by double-marker technique using TiO_2 as external and faecal CP as internal marker. There are limitations to the TiO_2 methodology related to total marker recovery and the use of faecal spot samples (de Souza et al., 2015; Guinguina et al., 2019). Yet, errors related to these limitations were minimised by several measures. Firstly, the TiO_2 was administered via concentrate mixtures and its complete ingestion was assured by feeding each animal an individual dosage, and by observing the animal until the total mixture was consumed. Thus, nine total cow observations were cleared from the dataset due to reluctance of animals to ingest the entire marker dosages. Secondly, faecal spot sampling started from Day 6 after five days of TiO_2 dosing to assure that the marker mixed homogeneously with digesta and thus a total faecal recovery of the TiO_2 marker. Moreover, to minimise diurnal variation in faecal TiO_2 excretion and to be able to collect representative samples, TiO_2 was administered and faecal samples taken twice daily (Glindemann et al., 2009). The DOM_{CP} of diets ingested by individual animals was estimated from faecal CP concentrations (Lukas et al., 2005) to account for selective foraging behaviour of cows on pasture and to capture possible interactive effects between different diet ingredients (Bruinenberg et al., 2003; Schneider et al., 2011). This equation was recently re-evaluated by Lukas et al. (2021), who confirmed its adequacy for determining the DOM_{CP} of diets ingested by lactating cows grazing intensive as well as extensive pastures and with a moder-

ate to high concentrate supplementation (3.2–7.7 kg DM/d). Overall, the chosen approach to determine the DM intake of individual cows resulted in realistic DM intake values, despite the mentioned limitations. The observed mean DM intake of 21.1 kg/d was comparable to values (20.7 kg/d) observed for lactating Simmental cows with a milk yield of 23.0 kg/d with a forage-dominant diet in a Swiss organic dairy farm (Leiber et al., 2015). Similarly, a mean DM intake of 21.6 kg/d was observed by Haselmann et al. (2020) in organic lactating Holstein-Friesian cows with an intake of 18.1 kg forage DM/d and 3.5 kg concentrate DM per day.

For 178 of 233 individual cow observations, individual DM_lsupp was not measured, but calculated using measured DM_lsupp on herd-level and the individual animal's eating time in barn. The mean time spent eating (560 ± 72.1 min/d) was comparable to values observed for grazing Holstein-Friesian cows with concentrate supplementation (527 min/d; Dohme-Meier et al., 2014) and for grazing Simmental cows receiving ryegrass or sainfoin pellets in barn (555 min/d; Kapp-Bitter et al., 2021). Eating time might not be the most adequate parameter for direct estimation of feed intake of dairy cows due to the substantial variation in eating rate between individual animals (Leiber et al., 2016). In view of the on-farm approach of the present study, this approach was the most sensitive alternative to capture the variation in individual DM_lsupp of the observed cows, although it does represent a limitation to the validity of the reference dataset. On-farm experiments may face methodological limitations but make use of the variation in target variables across farms which enables a greater transferability of the present findings to the diversity of practical grazing conditions.

Prediction adequacy across models

The models NRC, Conrad, and Mertens II resulted in the lowest RPE among the evaluated models. When evaluated based on the mean observed PDMI, their RPE values were comparable with the RPE of previous studies evaluating the adequacy of PDMI predictions by the model e-cow using weekly PDMI means for different Holstein-Friesian strains (9.1%; Baudracco et al., 2012) and the grazing-based model Grazeln using PDMI values on paddock level (10.0%; Roca-Fernández and González-Rodríguez, 2018). In case of the models Conrad and Mertens II, their acceptable prediction accuracy may be due to the semi-mechanistic nature of these models, which made them less prone to be overfitted to specific production conditions (Tedeschi et al., 2019). Among these two models, Mertens II was even more adequate with a lower MB and RPE than the Conrad model, both, when evaluated on individual cow basis or for animal groups. There were two options available to adapt Mertens II to the reference dataset: (1) by assuming a greater NDF intake capacity for animals used to forage-dominant diets and (2) by using an updated equation of the German recommendations for ME requirements of dairy cows. This adaptability and its semi-mechanistic nature made Mertens II the most promising model to predict the PDMI for cows grazing on semi-natural grasslands. The prediction adequacy of the model NRC for individual animals was comparable with the modelling performance of the Mertens II model, despite the empirical nature of the NRC model, which is likely related to the substantial size of its reference dataset ($n = 17\,087$ weekly cow observations), and the moderate performance level of cows in the NRC reference data (Rayburn and Fox, 1993: mean fat-corrected milk yield = 26.8 kg/d) that was similar to the mean milk yield in the present study.

None of the remaining models were nearly as adequate as the models NRC, Conrad, Mertens I or Mertens II, neither when evaluated based on individual cow observations nor when predicting the mean PDMI of different animal groups. A greater prediction adequacy was expected for the Gruber model, because it was developed from a wide dataset with cows from Germany, Switzerland,

and Austria and uses breed-specific coefficients for the same breeds as covered in the present study (i.e., for Holstein-Friesian, Simmental, and Brown Swiss). The Gruber model, however, relies on empirical equations, primarily based on the observed correlation between the DM intake and lactation stage of stall-based dairy cows, which likely overfitted the model for the stall-based diet and controlled production conditions of their dataset, while ignoring additional energy expenditures, for instance, due to stress or grazing activity (Dohme-Meier et al., 2014). Similarly, the De Souza model was developed using data of stall-fed Holstein-Friesian cows with a mean milk energy production of 29.8 Mcal/d, which substantially exceeded the mean milk energy yield in the present study (17.4 Mcal/d), implying considerable differences in the ME use efficiency between the cows of the De Souza reference dataset and the cows of the present study (Gruber et al., 2021). The empirical nature of the Gruber and De Souza models and the outlined fit of their equations to their underlying datasets are exemplary for explaining the poor modelling adequacy of empirical models for production conditions other than the conditions of the model development dataset.

Despite their adaptation to grazing conditions, the behaviour- and semi-mechanistic grazing-based models had the lowest prediction adequacy among the evaluated models. This was likely linked to (1) differences in sward characteristics and (2) herbage availability between the observed grazing conditions and those considered for model development. Firstly, Boval and Sauvant (2019, 2021) summarised that PDMI was determined by the interaction of sward characteristics, such as sward height and herbage mass, with the cows' ingestive behaviour during grazing. Their meta-analyses, for instance, revealed positive relations between sward height (cm) and intake rate (mg DM intake/kg BW and min) and sward height and bite mass (g/eat bite). Considering the lower herbage availability observed in the present study due to the low sward height (mean compressed sward height = 4.1 ± 1.44 cm), the predictive models likely overpredicted PDMI for cows grazing on low-yielding semi-natural grasslands, because they assumed a greater intake rate (e.g., Greenwood) or bite mass (e.g., Oudshoorn) than was attainable under the present grazing conditions. Further, the relationship between PDMI and herbage availability is considerably affected by the cutting height of the sampled herbage due to differences in pasture bulk density across the sward's strata (Pérez-Prieto and Delagarde, 2012). The e-cow model, for instance, uses an empirical relationship between PDMI and herbage biomass 4 cm aboveground. However, pasture herbage was harvested at 3 cm aboveground in the present study, which may have also contributed to the prediction bias. Another possible explanation for the low prediction adequacy of the behaviour-based models was related to the sensor-technology used. For the development of the two behaviour-based models, Oudshoorn and Greenwood, chewing behaviour of cows was measured by different sensors (accelerometer), for which different algorithms for the classifications of mastication, prehension, rumination, and eating chews or bites were used as compared to those used for determining the chewing behaviour in the present study (RumiWatch Converter V0.7.3.36). These sensor-related differences and the differences in the herbage characteristics between the observed grassland conditions and those considered for the models' development are potential reasons for the low prediction adequacy of the behaviour- and semi-mechanistic grazing-based models.

Prediction adequacy on individual animal basis

Prediction adequacy was lowest in Simmental cows

The RPE for different subgroups distinguished by grazing and production factors revealed substantial differences in the predic-

tion adequacy between different breeds, levels of DMIsupp, and animals with different timing and duration of pasture access. The PDMI predictions for Holstein-Friesian and Brown Swiss cows were more adequate than for Simmental cows across most models. The differences in prediction adequacy between breeds could, however, not be attributed to core systematic factors by the statistical analyses. According to the residual analysis, none of the considered production management and behaviour variables, which may differ between Simmental cows and other breeds, such as milk yield, BW, or chewing behaviour, were sources for systematic prediction biases. There was also no difference in the RPE of subgroups differentiated by feed use efficiency. [Prendiville et al. \(2010\)](#) and [Sæther et al. \(2006\)](#) reported differences in grazing behaviour and activity between different dairy breeds with potential influences on nutrient intake and intake rate on pasture. Such differences in grazing behaviour cannot be fully excluded, and might, at least partly, explain the differences in prediction adequacy between breeds. Moreover, lower prediction adequacy in Simmental cows can also be related to random variation in the predicted PDMI values. One source of random variation might be the measured BW. The BW is an input variable for estimating energy requirements for maintenance and locomotion, and, hence, for several PDMI prediction models ([Smith et al., 2021](#)). Variation in and mean of individual BW observations (710 ± 72.4 kg) are, however, comparable with values observed in Austrian Simmental dairy cows by [Köck et al. \(2018\)](#): 731 ± 85 kg) demonstrating that the BW of Simmental cows was adequately captured by the measuring tape. Thus, the lower prediction adequacy cannot be fully explained by systematic or random variation but should be kept in mind as this dual-purpose breed is common within organic and small-scale dairy farming, as seen in Germany, Austria, or Switzerland.

Prediction adequacy was greatest with low supplementation level and high daily pasture access

The RPE differed between animal subgroups with pasture access at different daytime or with different levels of DMIsupp. The models Cornell, Conrad, NRC, and Mertens I and II were able to predict the PDMI of individual cows with an acceptable adequacy, when animals had access to pasture at day and night (i.e., full-time), or when their DMIsupp was < 4.8 kg/d. Both factors were interrelated. Full-time grazing was only performed in periods when pasture herbage mass per paddock was high, which concurred with a low supplementation level. Possible reasons for differences in the adequacy of the estimation models depending on the DMIsupp level may have been (1) the methodological approach for calculating DMIsupp, or (2) differences in the grazing behaviour depending on the supplementation level or types of supplements. For 55 of the 233 observations, there was no need to estimate the individual DMIsupp via the individual eating time in barn, because measurements from feeding stations were available, or because no supplement feed was offered. All these observations belonged to the subgroup with a DMIsupp < 4.8 kg/d. Hence, the lower RPE for this subgroup may be, at least in part, associated to the lower error in DMIsupp values. Nevertheless, the greater RPE with high than with low DMIsupp may also be related to observations by [Wright et al. \(2016\)](#), who detected a greater between-cow variation in eating time on pasture and in barn with greater supplementation in barn. These inter-animal variations in eating behaviour potentially increased variation in individual PDMI, and thus RPE in the subgroups with a DMIsupp ≥ 4.8 kg/d.

Lack of precision affected prediction adequacy more than lacking accuracy

The models NRC, Conrad, and Mertens II achieved a satisfactory prediction accuracy for PDMI of individual cows with a MB $\leq 10\%$. However, the Bland-Altman plots showed a wide distribution of

the models' residuals around the MB i.e., a lack of precision ([Montenij et al., 2016](#)), indicating that the models' substantial MSEP i.e., prediction bias, was rather owing to a lack of precision than to low accuracy. The high share of random error in total MSEP, which constituted 84 to 90% of the MSEP of the models NRC, Conrad, and Mertens II, is another indication for the lack of precision. The random variation was likely related to inter-animal variation or methodological limitations. In this line, RPE of these three models greatly declined when they were evaluated using the mean PDMI per treatment group to 11.4, 16.5, and 16.9% for the models Mertens II, Conrad, and NRC, respectively, which removed the natural and measurement-related variance between individual animals. The remaining components of the MSEP showed that only 10–16% of the prediction bias was related to structural deficiencies in the models. Mixed model and stepwise analysis were used to identify variables that possibly explain this systematic bias. When the absolute residuals were used as outcome variable for these analyses, factors were selected, such as the daily milk yield or feed use efficiency, that were correlated to DM intake and PDMI. The latter variables, in turn, were related to the absolute residuals. The relative residuals, with and without negative signs, thus, represented a more sensitive basis for identifying potential bias factors independent of the level of the PDMI. The marginal R^2 of the mixed models (< 0.01) and the adjusted R^2 of the stepwise regression models (≤ 0.05) revealed that the selected significant fixed effects were of negligible importance for explaining the variation in the relative residuals of the models NRC, Conrad, and Mertens II. The remaining systematic bias of 10–16% could, thus, not be explained further by the methodology and considered predictor variables chosen for the analysis of the residuals.

Random error due to natural variation between individual cows

The relation between feed intake and productive performance i.e., feed use efficiency, is well known to greatly vary between individual animals despite similar diets, feed intake and performance levels, as well as husbandry and environmental conditions. This is not only attributable to differences in physical or physiological parameters but also to individual differences in energy losses and retention ([Guinguina et al., 2020](#); [Martin et al., 2021](#)), factors that may not be accounted for by mathematical intake models but add a source of natural variation that hampers the models' precision. For instance, [Gregorini et al. \(2015\)](#) and [Lahart et al. \(2020\)](#) found differences in the residual feed intake (as an indicator for feed use efficiency) between individual cows. The authors of both studies related this to between-cow differences in grazing behaviour. Hence, a negative correlation (Spearman's rank correlation: -0.24) between residual feed intake and grazing meal duration and a positive relation between number of grazing meals and residual feed intake (0.42) in the study of [Lahart et al. \(2020\)](#) indicated that more efficient beef cattle appear to have fewer, but longer grazing meals. Further, the ranking of animals according to their residual feed intake was not constant but varied depending on whether the cows received a stall-based or a grazing-based diet ([Lawrence et al., 2012](#); [Lahart et al., 2020](#)), implying diet-induced differences in the inter-animal variation in residual feed intake. Finally, selective grazing behaviour determines nutrient intake of grazing cows and could be another reason for between-cow variation in feed use efficiency. [Schneider et al. \(2011\)](#) compared the digestible OM of dairy cows receiving clipped herbage from grazed pastures to cows grazing on the same paddock. Although both groups were offered the same herbage, digestible OM values determined with the same methodology differed between cow groups, indicating differences in selective feeding behaviour between the grazing and stall-fed cows. Differences in residual feed intake, selective feeding behaviour, and thus in nutrient intake between and even within animals are sources of natural variation which

might at least partly explain the lack of precision in PDMI predictions observed in the present study.

Outlook to improve herbage intake models

The Mertens II model appeared to be the most promising amongst all tested models for predicting PDMI of lactating dairy cows grazing semi-natural grasslands. It achieved the highest modelling performance when evaluated based on the mean observed PDMI and allowed for adequate prediction of PDMI of individual cows with low DMIsupp level. Nevertheless, when used to predict PDMI of individual animals of other subgroups, this model also did not meet the threshold for an acceptable adequacy. It was concluded that the low prediction adequacy was predominantly related to a lack of precision, and hence, either to the model's inability to capture inter-animal variation in PDMI or to random variation pertaining to the present study's methodological limitations. Possible options for improving the precision and thus adequacy of the PDMI predictions by Mertens II, or possibly other PDMI models, could be the addition of further or alternative explanatory variables, the integration of sensor data, and/or the use of more sophisticated approaches in data analysis. Firstly, there might be merit in attempting to capture the influence of the amount of DMIsupp on PDMI by adding respective variables to the model. Secondly, the use of behavioural, sensor-based data allows for integration of measured, individualised data into prediction models in addition to, for instance, performance characteristics which are already part of the Mertens II model. This could help in accounting for inter-animal differences in feeding behaviour and thus PDMI. Nevertheless, the behaviour-based models evaluated in the present study could neither accurately nor precisely predict PDMI. This is likely since feeding behaviour and feed use efficiency vary between individual cows despite similar PDMI due to herd- and management-specific differences in the learned and socially driven behaviours of lactating dairy cows (Illius et al., 2004; Moreno García et al., 2020) and due to natural variation between cows (Guinguina et al., 2020). The consideration of behaviour-based data could be combined with new approaches in data analysis. For instance, the inclusion of non-linear components in existing PDMI models such as Mertens could account for the fact that the coefficients for the relationship between the number of bites and the PDMI are not constant but vary depending on animal traits, such as BW (Boval and Sauvant, 2019), or forage availability (Boval and Sauvant, 2021). However, the solution to increase the precision and accuracy of PDMI models should not be the development of even more complex mechanistic models (Tedeschi et al., 2019), but rather the adaptation of the existing models to better capture inter-animal variation in PDMI, e.g., using the individual or a combination of the aforementioned options. Alternatively or additionally, machine learning could be used to capture the inter-animal variation in feeding behaviour and efficiency by combining available data from sensor-based behavioural observations and milk performance records to adapt PDMI models for individual animals (Ellis et al., 2020).

Conclusions

Among the models evaluated in the present on-farm study, the slightly modified semi-mechanistic stall-based model by Mertens (1987) allowed for most adequate and acceptable prediction of the mean PDMI of groups and even of individual lactating dairy cows grazing temperate, semi-natural grasslands full-time and receiving limited amounts of supplemental feeds. Instead, existing empirical, behaviour-based, and semi-mechanistic grazing-based models cannot predict PDMI of lactating dairy cows with accept-

able accuracy and precision. The model Mertens II can be applied for groups of cows across a diverse range of practical farms using semi-natural grasslands for grazing, but lack of precision hampers the adequate prediction of PDMI of individual cows by the model Mertens II, likely owing to pronounced inter-animal variance in PDMI of individual animals as well as methodological challenges such as the determination of supplement feed intake of individual animals. Possible options to improve the precision of semi-mechanistic prediction models are the addition of further or alternative explanatory variables, the integration of sensor data, and/or the use of more sophisticated approaches in data analysis. Such improved models may allow for accurate and precise prediction of intake of individual dairy cows and thus for an optimised use of semi-natural grasslands in Central Europe for grazing-based milk production.

Supplementary material

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.animal.2023.100806>.

Ethics approval

The study was conducted according to the guidelines of the German animal welfare act and was approved by the Institutional Animal Care and Use Committee of the University of Hohenheim.

Data and model availability statement

The data/models were not deposited in an official repository. The data/models that support the study findings are available from the corresponding author upon request.

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Declaration of interest

None.

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