Wu, L., Harris, P., Misselbrook, T. H. and Lee, M. R. F. 2022. Simulating grazing beef and sheep systems. *Agricultural Systems.* 195, p. 103307. https://doi.org/10.1016/j.agsy.2021.103307

Simulating grazing beef and sheep systems

L. Wu[1*], P. Harris[1], T. H. Misselbrook[1], M. R. F. Lee[1, 2†]

[1]Sustainable Agriculture Sciences, Rothamsted Research, North Wyke, Devon, EX20 2SB, UK

[2]Bristol Veterinary School, University of Bristol, Langford, Somerset, BS40 5DU, UK

†Current address: Harper Adams University, Newport, Shropshire, TP10 8NB, UK

Correspondent author:

Lianhai Wu

Email: lianhai.wu@rothamsted.ac.uk

Abstract

Context

Ruminant livestock makes an important contribution to global food security by converting feed that is unsuitable for human consumption into high value food protein, demand for which is currently increasing at an unprecedented rate because of increasing global population and income levels. Globally, ruminant livestock will be important for the foreseeable future and demonstrating the sustainability of production will become increasingly important. Factors affecting production efficiency, product quality, and consumer acceptability, such as reduced animal fertility, health and welfare, will ultimately define the sustainability of ruminant production systems. These more complex systems can be developed and analysed by using models that can predict system responses to environment and management.

Objective

We present a framework that dynamically models, using a process-based and mechanistic approach, animal and grass growth, nutrient cycling and water redistribution in a soil profile taking into account the effects of genotype, climate, feed quality and quantity on livestock production, greenhouse gas emissions, water use and quality, and nutrient cycling in a grazing system.

Methods

A component to estimate ruminant animal growth was developed and integrated with the existing components of the SPACSYS model. Intake of herbage and/or concentrates and partitioning of the energy and protein contained in consumed herbage and/or concentrates were simulated in the component. Simulated animal growth was validated using liveweight data collected from over 200 finishing beef cattle and 900 lambs collected from the North Wyke Farm Platform (NWFP) in southwest England, UK, between 2011 and 2018. Simulated annual nitrous oxide (N_2O), ammonia, methane and carbon dioxide emissions from individual fields were examined.

Results and Conclusions

A series of statistical indicators demonstrated that the model could simulate liveweight gain of beef cattle and lamb. Simulated nitrogen cycling estimated N input of 190 to 260 kg ha^{-1}, of which 41 – 58% was removed from the fields either as silage or animal intake, 6 – 15% was lost through surface runoff or lateral drainage and 1.5% was emitted to the atmosphere as N_2O. About 12% of the manure applied to the NWFP and excreta nitrogen deposited at grazing was lost via ammonia volatilisation.

Significance

The extended model has the potential to investigate the responses of the system on and consequences of a range of agronomic management and grazing strategies. However, modelling of multi-species

swards needs to be validated including the dynamics of individual species in the swards and the impact on animal growth and nutrient flows.

Key words: SPACSYS; North Wyke Farm Platform; grazing; modelling; liveweight.

1 Introduction

We are at a critical juncture for global livestock production as competing requirements for maximal productivity and minimal pollution have driven the requirement for sustainable intensification (Springmann et al., 2018). Ruminants make an important contribution to global food security by converting feed that is unsuitable for human consumption into high value food protein, demand for which is currently increasing at an unprecedented rate because of increasing global population and income levels (Tilman and Clark, 2014). Reduction in red meat and dairy intake is increasingly seen as a pathway to improving human and environmental health (e.g. Westhoek et al., 2014), but globally, ruminant livestock will be important for the foreseeable future and demonstrating the sustainability of production will become increasingly important. Sustainable intensification of ruminant livestock may be applied to pastoral grazing, mixed-cropping, feedlot, and housed production systems. All these systems have associated environmental impacts such as water and air pollution where greenhouse gas (GHG) emissions, soil degradation and erosion are all of particular concern. In addition, factors affecting production efficiency, product quality, and consumer acceptability, such as reduced animal fertility, health and welfare, also impact on the sustainability of ruminant production systems. These challenges necessitate multidisciplinary solutions that can only be properly researched, implemented and tested in real-world production systems (Eisler et al., 2014). As a consequence, there is a call to ‘redesign’ livestock systems, including the integration of both crops and livestock (Dumont et al., 2014). These more complex systems can be developed and analysed by using models that can predict system responses to environment and management.

Several reviews of grassland-based ruminant production models have been published (Bateki et al., 2019; Bryant and Snow, 2008; Snow et al., 2014). In order to simulate ruminant livestock systems, the components of animal genetics (breed), nutrition (forage), management practices and their subsequent impact on the surrounding environment (emissions to air and water) must be considered as a whole in computational models. Several mechanistic process-based simulation models have attempted to simulate the whole system, e.g. the Hurley Pasture Model (Thornley, 1998) and its subsequent revisions - PaSim (Graux et al., 2011), WFM (Neil et al., 1999), GRAZPLAN (Donnelly et al., 2002), GrazeIn (Faverdin et al., 2011), SEDIVER (Martin et al., 2011), e-Dairy (Baudracco et al., 2013) and LiGAPS-Beef (van der Linden et al., 2019). Challenges remain in modelling ruminant systems, due to the symbiotic relationship between rumen microbial anaerobic fermentation and subsequent mammalian metabolism of a combination of derived rumen microbial biomass (microbial protein), fermentation by-products (volatile fatty acids and ammonia) and dietary components which by-pass rumen fermentation. As well as associated microbial activity which influences lipid profiles (biohydrogenation), atmospheric pollutants (methanogenesis) and which ultimately drives the partitioning and retention (milk, live weight, faeces, urine) of dietary nutrients. A systems approach to investigate ruminant production through modelling and simulation is therefore recommended (Dougherty et al., 2019; Hirooka, 2010).

The SPACSYS model (Wu et al., 2007) is a weather-driven dynamic simulation model at a field scale with up to a daily step. Since it was first published in 2007, it has been developed to provide added functionality, e.g. the impact of vernalisation on overwinter crops (Bingham and Wu, 2011), biological nitrogen (N) fixation by legumes (Liu et al., 2013), microbial-based N_2O emissions (Wu et al., 2015) and soil phosphorus (P) cycling (Wu et al., 2019). The model can simulate the interactions of soil carbon (C), N and P, plant growth and development, water re-distribution and heat transformation in agricultural fields. The model has been applied to grassland systems in the assessment of GHG emissions (Abalos et al., 2016), responses to environmental change (Ehrhardt et al., 2018; Wu et al., 2016) under various climatic and soil conditions, nutrient cycling (Carswell et al., 2019b) and C fluxes (Sándor et al., 2020). However, as there is no component to describe animal growth, simulations involving animals have required pre-processing and direct input of data on grass intake rate and nutrient returns in animals, rather than deriving directly from animal performance, constraining model application.

This study presents a framework that dynamically models animal and grass growth, nutrient cycling and water redistribution in a soil profile taking into account the effects of animal genotype, climate, feed quality and quantity on livestock production, GHG emissions, water use and quality, and nutrient cycling in a grazing system, using a process-based and mechanistic modelling approach. Simulated animal growth was validated using liveweight data collected from over 200 finishing beef cattle and 900 lambs collected from the North Wyke Farm Platform (NWFP) in southwest England, UK, between 2011 and 2018. The framework could potentially integrate economic, environmental and social factors to provide decision makers with the ability to forecast, interpret and respond to potential threats to UK livestock production systems.

2 Materials and Methods

2.1 SPACSYS model

In this study, a component to estimate ruminant animal growth, AnimalCom, was developed, implemented and integrated with the existing components of SPACSYS (Fig. Figure 1). Existing model components are published in detail elsewhere (Wu et al., 2019; Wu et al., 2007; Wu et al., 2015), while the new AnimalCom is described here.

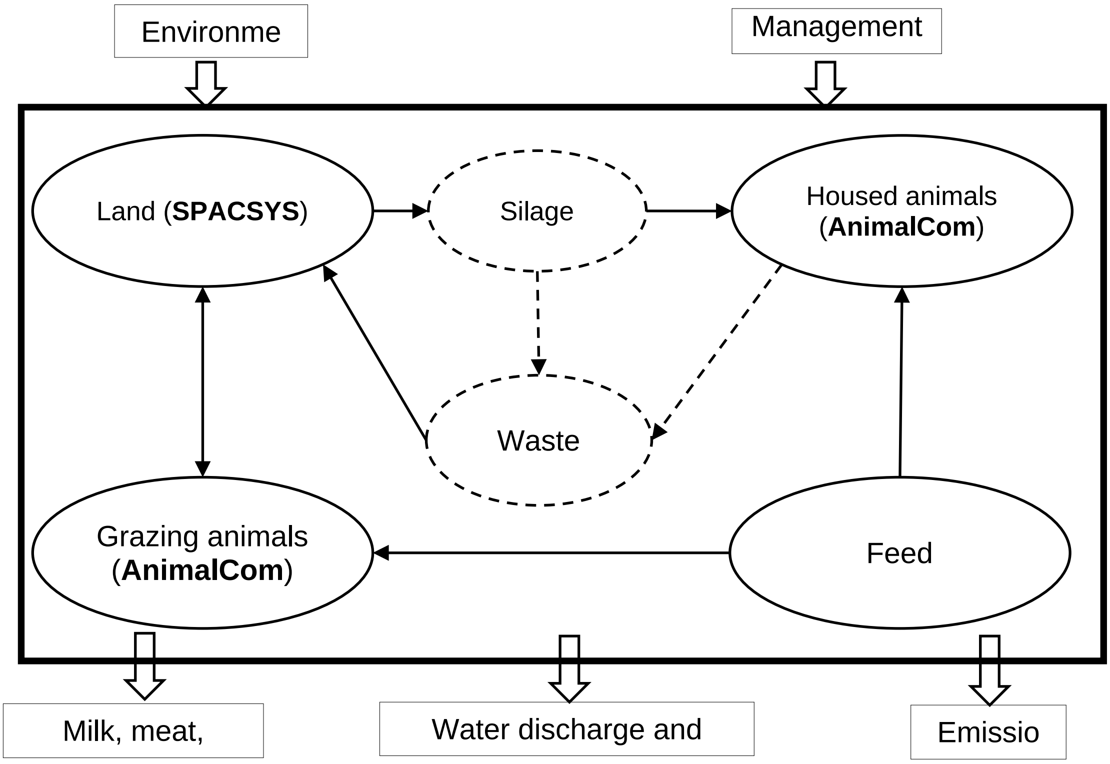


Figure 1. Extension of the SPACSYS model, component linkage and outputs. Solid lines show which processes are included in the latest version of the model.

2.2 AnimalCom

The AnimalCom component consists of two parts: intake of herbage and/or concentrates and partitioning of the energy and protein contained in consumed herbage and/or concentrates. Herbage intake by grazing ruminant livestock is assumed to be regulated by one of three factors (Loewer et al., 1983): a) the physiological limit on intake (or thermodynamic limit), b) the feed availability and c) the physical ability of the animal to consume feed (Fig.

Figure 2). The first factor is partially determined by the energy requirement of the animal. There are several systems developed for nutritional evaluation (Tedeschi et al., 2005), where the description below is mainly based on the UK Agricultural and Food Research Council metabolizable energy (ME) and protein (MP) system (Agricultural and Food Research Council, 1993) in which the dynamics of the rumen microbial population plays a vital role.

Metabolisable energy intake (MEI) through grazing and concentrate feeds is partitioned among that required for maintenance, pregnancy (for cow and dry ewe only), growth and fattening, and milk production (for cow and lactating ewe only). In general, the requirement for animal maintenance is given the highest priority, then pregnancy, and the lowest for milk production and liveweight gain.

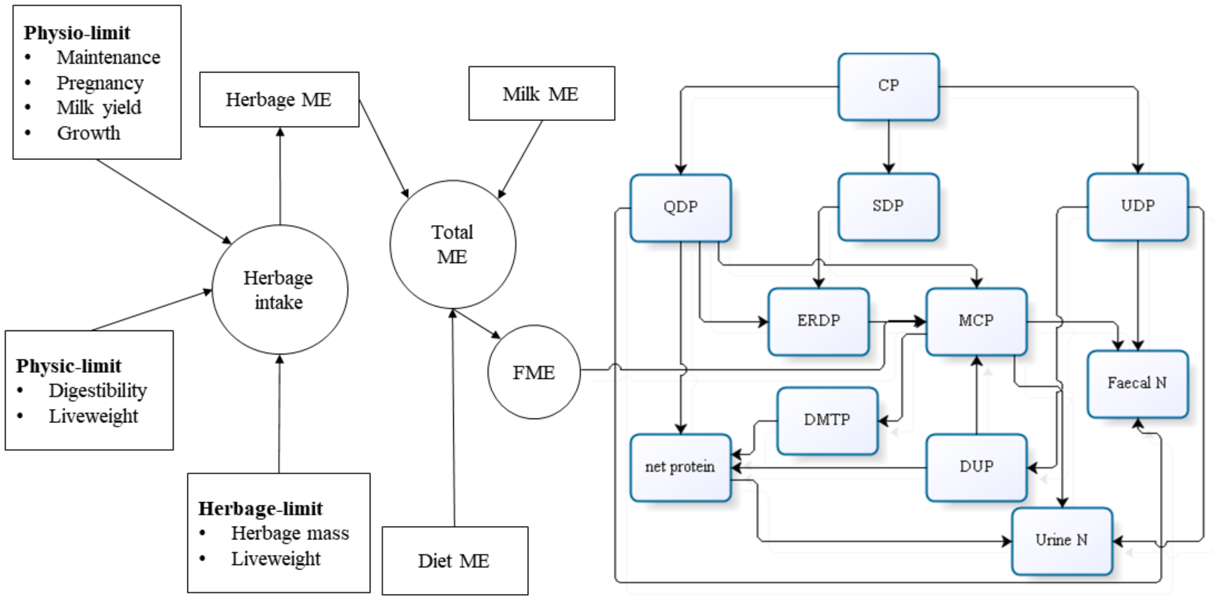


Figure 2. A schematic representation of the factors limiting intake and the metabolisable energy and protein system. ME: metabolisable energy; FME: fermentable metabolisable energy; CP: crude protein; QDP: quickly degradable protein; SDP: slowly degradable protein; UDP: undegradable dietary protein; ERDP: effective rumen degradable protein; MCP: microbial crude protein; DUP: digestible undegraded protein; and DMTP: digestible microbial true protein.

2.2.1 Energy requirements

Physiological ME requirement (E_{PH_C}, MJ head^{-1} day^{-1}) is defined by a generic term:

$$E_{PH\_C} = E_{req\ -\ growth} + E_{req\ -\ main} + E_{req\ -\ milk} + E_{req\ -\ preg} \tag{1}$$

where $E_{req\text{-}main}$ is the ME requirement for maintenance (MJ head^{-1} day^{-1}), $E_{req\text{-}growth}$ is the ME requirement for growth and fattening (MJ head^{-1} day^{-1}), $E_{reg\text{-}preg}$ is the ME requirement for pregnancy (MJ head^{-1} day^{-1}), and $E_{req\text{-}milk}$ is the ME requirement for milk production (MJ head^{-1} day^{-1}).

2.2.1.1 Energy requirement for maintenance

Following Agricultural and Food Research Council (1993), $E_{req\text{-}main}$ including fasting metabolism and activity allowance for the animal is estimated by:

$$E_{req\ -\ main} = \frac{\left[a\left(\frac{LWT}{1.08}\right)^{b}\right] + c \times LWT}{0.35q_m + 0.503} \tag{2}$$

where *LWT* is the live weight of the animal (kg), *a*, *b* and *c* are empirical parameters and q_m is the metabolisability of the gross energy of a diet at maintenance.

For sheep, it has been documented for some time that the AFRC (1993) model may underestimate maintenance energy requirement (e.g. Yang et al., 2019). The equation adopted here is therefore that used in the UK inventory model for agricultural GHG emissions, developed by Steven Anthony (pers comm. ADAS). Consequently, the requirement is estimated as:

$$E_{req\text{ - }main} = \frac{k_2 k_4 (LWT - 0.0097 \bullet LWT^{1.2735})^{0.75} \bullet e^{-k_3 \bullet Min\left(6, \frac{Age}{365}\right)} \bullet \left(1 + 0.26 \bullet \frac{Max(0, N - A)}{N}\right)}{0.35 q_m + 0.503} \quad (3)$$

where k_2, k_3 and k_4 are constants and setting 0.26, 0.03, and 1.0 (female and castrate male) or 1.15 (entire male), respectively; *N* is the weaning age of sheep; *Age* is the age of sheep and *A* is the age of the lamb (d); *Min* and *Max* are math functions for a minimum and maximum value of two values, respectively. This adaptation to AFRC (1993) added a further 9% of MEI to the requirement.

2.2.1.2 Energy requirement for liveweight change

$E_{req\text{-}growth}$ is based on the potential live weight growth rate that is expressed as the Gompertz function (Lewis et al., 2002; Taylor, 1968):

$$E_{req\text{ - }growth} = -\Delta W \cdot e_{req\text{ - }growth} \quad (4)$$

$$\Delta W = \frac{1}{g_f W_{mature}^{0.3}} \cdot LWT \cdot \ln\left(\frac{W_{mature}}{LWT}\right) \quad (5)$$

where g_f is a Gompertz constant that tends to be smaller as the mature size becomes larger (Emmans and Kyriazakis, 2000), W_{mature} is the average weight of the animal at maturity (kg), and $e_{req\text{-}growth}$ is the ME requirement per unit live weight increase of the animal (MJ kg^{-1}).

For finishing beef cattle, however, the potential energy requirement for growth and fattening is determined by the potential gain in protein (ΔP) and fat content (ΔF) of the empty body weight:

$$E_{req\text{ - }growth} = \frac{\Delta W}{e_{me\text{ - }eg}} \quad (6)$$

$$\Delta W = \Delta P \times P_e + \Delta F \times F_e \quad (7)$$

where P_e (MJ kg^{-1}) and F_e (MJ kg^{-1}) are the energy values of protein and fat, respectively, and $e_{me\text{-}eg}$ is the efficiency of the ME utilisation for growth and fattening, defined as (Agricultural and Food Research Council, 1993):

$$e_{me\text{ - }eg} = 0.78 M_e + 0.006 \quad (8)$$

where M_e is the metabolisability (MJ kg^{-1}DM) of fed dry matter (DM):

$$M_e = \frac{ME_{conc} + ME_{fod}}{(I_{conc} + I_{fod}) GE} \quad (9)$$

where ME_{conc} and ME_{fod} are the ME intakes of the concentrates and forage (MJ $head^{-1}$ d^{-1}), respectively, and I_{conc} and I_{fod} the concentrates and forage consumed (kg DM $head^{-1}$ d^{-1}), respectively. *GE* is the gross energy content of the feed (MJ kg^{-1}DM). Gross energy from concentrate can be obtained from the supplied product information and for grazed grasses (MJ kg^{-1}) was calculated as (Murray, 1991):

$$GE_{grass} = 0.0065CP + 17.7 \tag{10}$$

where *CP* is the crude protein content (g kg^{-1}DM) of the grass and estimated by the N content of the grass multiplied by 6.25.

2.2.1.3 Energy requirement for pregnancy

$E_{reg\text{-}preg}$ is estimated as (Agricultural and Food Research Council, 1993):

$$E_{req\text{ - }preg} = \frac{10^{\left(a_e - b_e \cdot e^{-c_e D_{preg}}\right)} \cdot d_e \cdot e^{c_e D_{preg}}}{e_{e\text{ - }preg}} \tag{11}$$

where a_e, b_e, c_e and d_e are parameters, D_{preg} is the pregnancy period (days) and $e_{e\text{-}preg}$ is the efficiency of utilisation of ME for the conceptus.

2.2.1.4 Energy requirement for milk production

Energy requirement for milk production from a lactating animal is estimated by:

$$E_{req\text{ - }milk} = \frac{Y_{milk} \times e_{req\text{ - }milk}}{e_{me\text{ - }m}} \tag{12}$$

where $e_{req\text{-}milk}$ is the energy requirement per unit milk produced, $e_{me\text{-}m}$ (= 0.35M_e + 0.503) is the use efficiency of ME for milk production and Y_{milk} is potential milk yield, that is controlled by a lactation curve described by Wood (1980) and then corrected by the period of milk production and the weeks of calving (and lambing) from the beginning of a year (Mainland, 1985).

$$Y_{milk} = Y_{init} T_w^{W_a} \cdot e^{-W_b \cdot T_w} \cdot (1 + f_w) \cdot (1 + f_c) \tag{13}$$

where f_w and f_c are parameters to reflect seasonal and calving (lambing) date effects on milk production, which are the tabulated functions of weeks from the beginning of a year.Y_{init} is the initial yield of milk and affected by lactation number; W_a, W_b and W_c are parameters and T_w is the lactation period in weeks.

2.2.2 Protein requirements

The protein requirement for milk production ($P_{reg\text{-}milk}$) is estimated by:

$$P_{req\text{ - }milk} = \frac{P_{per} \cdot M_{yield} \cdot f_{true}}{p_{e\text{ - }milk}} \tag{14}$$

where P_{per} is the protein percentage in milk, M_{yield} is actual milk yield, f_{true} is the fraction of true protein in milk and $p_{e\text{-}milk}$ is the efficiency of utilisation of protein for milk production.

The protein requirement for pregnancy ($P_{reg\text{-}preg}$) is estimated as (Agricultural and Food Research Council, 1993):

$$P_{req\text{ - }preg} = \frac{10^{\left(a_p - b_p \cdot e^{-c_p D_{preg}}\right)} \cdot d_p \cdot e^{c_p D_{preg}}}{p_{e\text{ - }preg}} \quad (15)$$

where a_p, b_p, c_p and d_p are parameters, D_{preg} is pregnancy period in days and $p_{e\text{-}preg}$ is the efficiency of utilisation of protein for the conceptus.

Following Hulme et al. (1986), the protein requirement for maintenance ($P_{reg\text{-}main}$) is estimated as:

$$P_{req\text{ - }main} = \frac{(0.35 + 0.018) \times 6.25W^{0.75}}{e_{p\text{ - }main}} \quad (16)$$

where $e_{p\text{-}main}$ is the conversion efficiency of metabolizable protein to net protein.

Protein requirement for growth is estimated as:

$$P_{req\text{ - }growth} = \frac{138.0 \times \Delta W}{f_{p\text{ - }growth}} \quad (17)$$

where $f_{p\text{-}growth}$ is the fraction of protein in faeces.

2.2.3 Herbage intake

Mechanisms for the long-term regulation on feed intake are still unclear and will differ between grazing and stall feeding. It was assumed that actual daily intake for the animal (*DMI*, kg DM head^{-1} d^{-1}) is determined by the most limiting factor among feed availability, and physical and physiological limits to intake:

$$DMI = \min\left(DMI_G, DMI_{PHYSICAL}, DMI_{PH}\right) \quad (18)$$

where $DMI_{PHYSICAL}$ is the physical limitation on the herbage intake rate (kg DM head^{-1} d^{-1}), DMI_{PH} is the physiological limitation on the herbage intake rate (kg DM head^{-1} d^{-1}) , and DMI_G is the intake rate (kg DM head^{-1} d^{-1}) based on herbage availability in the field.

2.2.3.1 Physical limit

Feed intake by the animal is controlled by the rate of passage through and the amount of undigested material in the digestive tract. For cattle, this is used (Kahn and Spedding, 1984):

$$DMI_{PHYSICAL} = \frac{F_a \times LWT}{1 - \frac{dg_{DM}}{1000}} \quad (19)$$

and for sheep (Blaxter et al., 1961):

$$DMI_{PHYSICAL} = \frac{F_a \times LWT^{0.734}}{1 - \frac{dg_{DM}}{1000}} \quad (20)$$

is used, where d_{max} and dg_{DM} are the average faecal DM output rate per unit liveweight (kg DM day^{-1}) and digestibility of feed, i.e. D-value (g kg^{-1} DM), respectively.

2.2.3.2 Physiological limits

DMI_{PH} is regulated by the daily ME requirement of the animal (Topp, 2001), and given by:

$$DMI_{PH} = \frac{E_{PH\_C} - M_{conc}}{M_{Fod}} \quad (21)$$

where M_{conc} is the daily ME intake rate of concentrates if supplied (MJ head^{-1} day^{-1}), and M_{Fod} is the ME (MJ kg^{-1}DM) of ingested herbage, defined by Pierret et al. (2005):

$$M_{Fod} = 0.017 \times dg_{DM} - 2.0 \quad (22)$$

However, the energy retention of ruminant livestock is not linearly related to intake; it is estimated to decline by between 0.3% and 1.4% per unit increase in feeding level. The ME intake (E_{PH_C}, MJ head^{-1} day^{-1}) required for the daily physiological production of milk and growth has consequently been corrected for feeding level (L_{Nut}), as recommended by the AFRC (1993), in the following manner:

$$E_{PH\_C} = E_{PH}\left[1 + 0.0018\left(\frac{E_{PH}}{E_{M}} - 1\right)\right] \quad (23)$$

2.2.3.3 Feed availability

When the quantity of herbage available for consumption is less than that required for 95% of maximum daily intake, the daily allowance of green herbage regulates intake. The green herbage allowance is taken to be the green herbage mass above the minimum herbage mass required for grazing. DMI_G was estimated as (Zemmelink, 1980):

$$DMI_G = I_{max}\left[1 - e^{-\left(\frac{H}{I_{max}}\right)^{p_{shape}}}\right]^{\frac{1}{p_{shape}}} \quad (24)$$

where p_{shape} is a constant, H is the daily allowance of green herbage for the animal (kg DM head^{-1} d^{-1}) and I_{max} is the maximum daily intake of herbage (kg DM head^{-1} d^{-1}) and is described by:

$$I_{max} = F_{max} \times LWT^{0.75} \quad (25)$$

where F_{max} is the maximum DM intake rate per kg of metabolic weight (kg DM (liveweight)$^{-0.75}$ head^{-1} d^{-1}).

2.2.4 ME intake partitioning

There are four possible scenarios to partition ME intake (Tess and Kolstad, 2000; Topp, 1999), meeting: 1) the physiological requirements of the animal (MEI $\geq E_{PH\_C}$); 2) the maintenance and pregnancy requirements but not the potential energy requirements for milk production and growth and fattening (E_{PH_C} > MEI $\geq E_{req\text{-}main} + E_{req\text{-}preg}$); 3) the maintenance requirements but not pregnancy and the potential energy requirements for milk production and growth and fattening are not fulfilled ($E_{req\text{-}main} + E_{req\text{-}preg}$ > MEI $\geq E_{req\text{-}main}$); and 4) no requirement (MEI < $E_{req\text{-}main}$).

2.2.4.1 Scenario 1

In this case, all the requirements can be met, and potential milk production (eq. 13) and growth (eq. 5 or 7) will be achieved.

2.2.4.2 Scenario 2

The energy requirements of the animal for maintenance and pregnancy (if possible) are met. The energy deficit (ME_d, MJ head^{-1} d^{-1}) for milk and liveweight change is:

$$ME_d = E_{PH\_C} - MI \quad (26)$$

It was assumed that the energy deficit is partitioned in equal amounts to reductions in potential energy requirements for milk and growth, i.e.

$$E_{a\_growth} = E_{req\text{ - }growth} - \frac{ME_d}{2} \text{ and } E_{a\_milk} = E_{req\text{ - }milk} - \frac{ME_d}{2} \quad (27)$$

If $E_{a\_growth} \geq 0$, milk production and growth are calculated based on E_{a_growth} and E_{a_milk}.

If $E_{a\_growth} < 0$, then maternal body tissue will be catabolised for milk production (ΔE_m) by:

$$\Delta E_m = \frac{\frac{ME_d}{2} - E_{req\text{ - }growth}}{2} \quad (28)$$

with the rate of change in body weight as:

$$\Delta W = -\frac{\Delta E_m}{N_l} \quad (29)$$

and milk production estimated as:

$$Y_{milk} = k_m \frac{ME_d}{2} + k_{bm} \Delta E_m \quad (30)$$

where N_l is the net energy produced per unit of catabolised liveweight (MJ kg^{-1}), k_{bm} is the efficiency of utilisation of maternal body tissue for milk production and k_m is the efficiency of ME utilisation for milk production.

2.2.4.3 Scenario 3

The ME requirement for pregnancy (ΔE_p) and milk production (ΔE_m) are met from maternal tissue catabolism:

$$\Delta E_p = (E_{req\text{ - }main} + E_{req\text{ - }preg} - MI)\frac{k_c}{k_{bc}} \quad (31)$$

and

$$\Delta E_m = \max(0, \frac{E_{req\text{ - }milk} - E_{req\text{ - }growth} - \Delta E_p}{2}) \quad (32)$$

where k_c and k_{bc} are utilisation efficiencies of ME for pregnancy and maternal body tissue for pregnancy, respectively.

Actual milk production and liveweight change rate are:

$$Y_{milk} = k_{bm}\Delta E_m \tag{33}$$

$$\Delta W = -\frac{\Delta E_m + \Delta E_p}{N_l} \tag{34}$$

2.2.4.4 Scenario 4

The ME required from maternal body tissue to meet the maintenance (ΔE_{ma}), pregnancy (if needed) and milk production that is estimated by eq. 33.

$$\Delta E_{ma} = (E_{req\ -\ main} - MI) \tag{35}$$

$$\Delta E_p = E_{req\ -\ preg}\frac{k_c}{k_{bc}} \tag{36}$$

$$\Delta E_m = \max(0, \frac{E_{req\ -\ milk} - E_{req\ -\ growth} - \Delta E_p - \Delta E_{ma}}{2}) \tag{37}$$

$$\Delta W = -\frac{\Delta E_{ma} + \Delta E_m + \Delta E_p}{N_l} \tag{38}$$

2.2.5 Nitrogen excretion from cattle

Excess dietary nitrogen intake, i.e. is neither in the form of DUP or incorporated into DMTP either directly or indirectly via salivary N re-circulation in the rumen, along with endogenous N will be deposited in housing or during grazing via faeces and urines (Fig.

Figure 2), which was estimated from mean nitrogen use efficiency values for cattle at pasture reported by the AFRC (1993).

2.2.6 GHG emissions

2.2.6.1 CO_2 emissions

Following Kirchgessner et al. (1991), CO_2 emission rate (g C head^{-1} d^{-1}) from a mature dairy or beef cow was estimated by:

$$E_{CO2} = (-1.4 + 0.43DMI - 0.045LW^{0.75}) \times 1000 \times \frac{12}{44} \tag{39}$$

However, for a lamb or ewe, the rate was estimated (CIGR, 2002; Haque et al., 2014) by:

$$E_{CO2} = \frac{HP \times 180 \times 24}{1000 + 4 \times (20 - T_a)} \times \frac{12 \times P_a}{8.31 \times (273.17 + T_a)} \times \frac{1}{1000} \tag{40}$$

where P_a is atmospheric pressure (Pa), T_a is air temperature and HP is heat production (Watt):

$$HP = \begin{cases} 6.4LW^{0.75} + 145 \times \Delta W \\ 6.4LW^{0.75} + 33 \times Y_{milk} \end{cases} \tag{41}$$

2.2.6.2 Methane (CH_4) emissions

For dairy and beef cattle, the regression equation from Yan et al. (2009) was used to estimate the enteric CH_4 emission rate (g CH_4 head^{-1}d^{-1}):

$$E_{CO2} = \left[\left(1.749 - 12.18\frac{ME}{GE} + 10.74\frac{DE}{GE}\right) \times GEI - 14.0\right] \times \frac{16 \times P_a}{8.31 \times (273.17 + T_a)} \tag{42}$$

where *GE, ME and DE* (MJ kg^{-1}DM)) are the gross energy, metabolisable energy and digestible energy in the dry matter intake, including forage and concentrate, respectively, and *GEI* is the gross energy intake (MJ d^{-1}). Values for *GE*, *ME* and *DE* were estimated as the weighted average across forage and concentrate.

Following Stergiadis et al. (2015), digestible energy from grass was estimated as:

$$DE_{grass} = -10.2 + \frac{45.1CP}{6.25 \times 1000} + 1.29GE_{grass} \tag{43}$$

Metabolisable energy from grass was calculated based on digestibility:

$$ME_{grass} = dg \times C_{d - M} \tag{44}$$

where $C_{d\text{-}M}$ is the conversion coefficient from digestible to metabolisable energy, with a default value of 16 MJ kg^{-1} (Agricultural and Food Research Council, 1993).

For sheep and lamb, the equation proposed by Blaxter and Clapperton (1965) was adopted:

$$E_{CH4} = \left[1.3 + \frac{11.2 \times DE}{GE} - L \times \left(2.37 - \frac{5 \times DE}{GE}\right)\right] \times \frac{1}{100} \times GE \times DMI \times \frac{1}{0.05565} \tag{45}$$

where 0.05565 (MJ g^{-1}) is the energy generated by CH_4 (de Haas et al., 2011), and *L* is the feed level:

$$LE_{PH\_C} = \frac{E_{PH\_C}}{E_{req - main}} \tag{46}$$

2.3 Case study grazing system

Simulated animal performance was validated with data collected from the NWFP from 2011 to 2018 (50°46’10’’N, 3°54’05’’W and 120-180 m a.s.l.). North Wyke has a temperate climate with average annual precipitation of 1030 mm and mean daily minimum and maximum temperatures of 7.0 and 13.6°C, respectively, from 1989 to 2018. The site overlays clay shales and the predominant soil type is a Stagni-vertic Cambisol under the FAO classification (Harrod and Hogan, 2008), which comprises a slightly stony clay-loam topsoil, overlying a mottled stony clay derived from the carboniferous culm measure. The platform is a 63 ha systems-based experimental facility divided into three 21 ha farmlets (small farms) with five hydrologically isolated sub-catchments in each. Over the simulation period, the farmlet treatments (pasture-type) were one of permanent pasture (PP) predominantly perennial ryegrass (*Lolium perenne* L.), monoculture reseed with high sugar perennial ryegrass (*Lolium perenne* cv Aber Magic) and a reseed mixture of high sugar perennial ryegrass and white clover (*Trifolium pratense* L.). From April 2011 to March 2013, the baseline period, all three farmlets were as one (PP) with no separate treatments in operation. From April 2013 to September 2015, the two reseed farmlets transitioned into a post-baseline phase with the third continuing as PP. Thus, some sub-catchments entered a post-baseline phase much earlier (say in 2013) than others (say in 2015). Given this and to furnish a long time series of consistent / coherent data for a robust calibration, validation and interpretation of the SPACSYS simulations, only outputs from the PP farmlet (Fig. Figure 3) were reported in this study. The size of each the five sub-catchments and the seven fields / paddocks for the PP farmlet together with management activities are shown in Table 1.

Table 1. Paddock size (ha) for various management activities on the permanent pasture (PP) farmlet

Field name	Hydrological area	Fenced area	Area for cutting	Area covered for chemical fertiliser	area covered for manure application
Bottom Burrows[†]	1.34 of 8.08	1.26	1.20	1.23	0.99
Burrows[†]	6.73 of 8.08	6.49	6.38	6.43	5.74
Golden Rove	3.95	3.86	3.77	3.78	3.28
Dairy North	1.87	1.78	1.73	1.74	1.39
Longlands South	1.81	1.75	1.69	1.69	1.42
Orchard Dean[††]	6.73	6.47	6.39	6.38	5.58
South	-	3.92		3.85	3.34
North	-	2.55		2.51	2.14

[†] together forms a single sub-catchment where a further field.

[††] sub-catchment split into two fields from mid-August 2015: Orchard Dean South and Orchard Dean North. We reported the results from these split fields as a single unit.

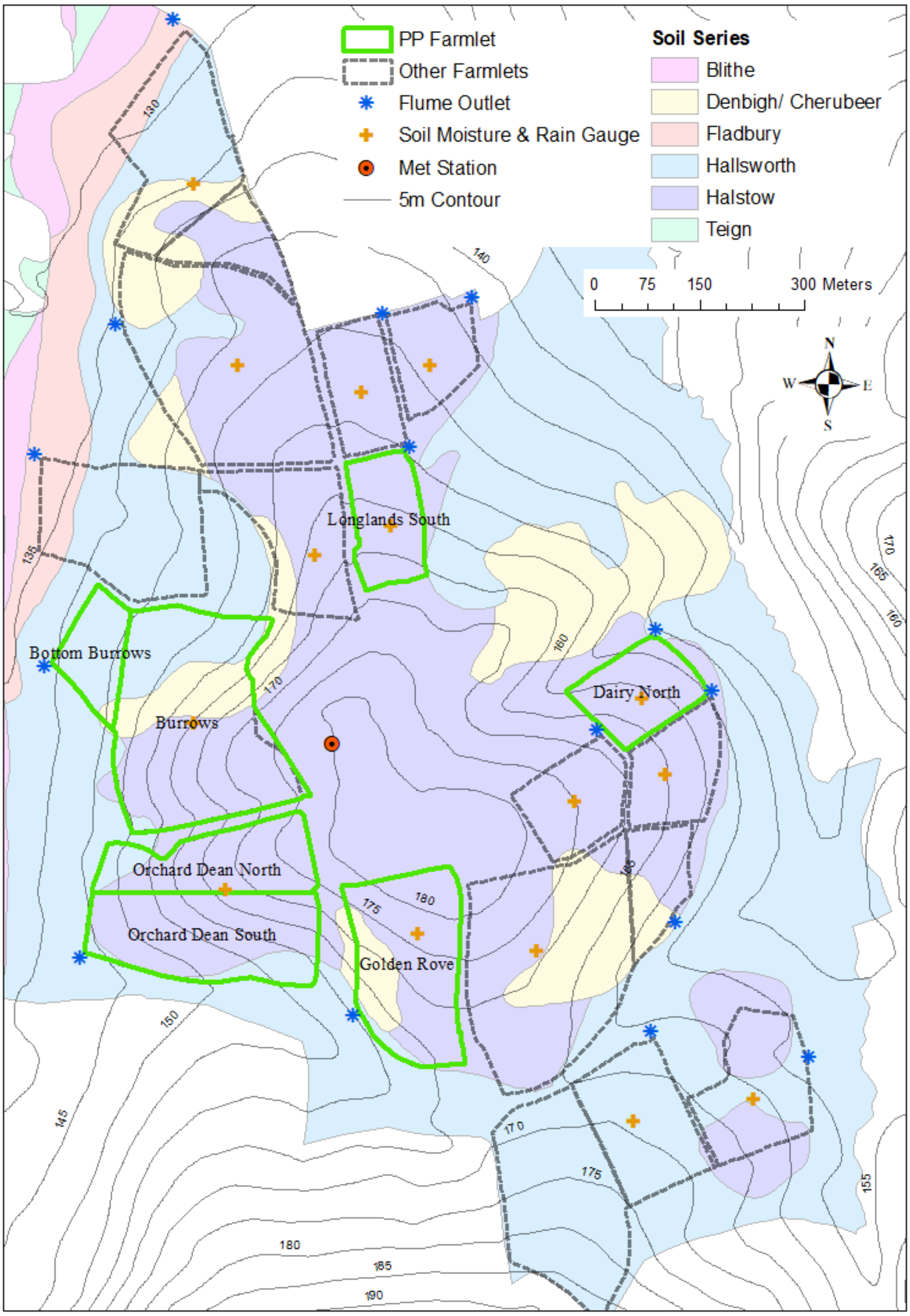


Figure 3. Map of the North Wyke Farm Platform (NWFP), showing the permanent pasture (PP) farmlet, sub-catchments, fields, soil class, topography and the locations of flume outlets where water and nutrient fluxes are measured. The soil moisture and rain gauge in Top Borrows is situated within the North Wyke Met station.

For the study period 2011 to 2018, each farmlet was grazed by 30 finishing beef cattle and typically 75 ewes with their lambs (typically 135 assuming a lambing rate of 1.8). Cattle were introduced to the farm platform after weaning, at 6 months of age, and were initially housed over the winter period (typically from October to March) and fed silage harvested from their respective farmlet, and then grazed on their respective farmlet at turnout until removed for slaughter on achieving a target weight of 555 kg (heifers) / 620 kg (steers) and fat class (4L). Ewes typically grazed into the winter season (late November to early January) and were then housed and fed off the platform prior to lambing; they were subsequently returned to the platform the following Spring (typically March) with their lambs, which were finished at a target weight of 43 kg and fat class (3L). All animal movements were recorded using unique identifier tags. Prior to 2017, a Hereford x Friesian herd provided predominantly Continental x calves, with heifers first calved to a Hereford bull. The breeding herd was subsequently transitioned to Stabilisers™. In total, seven breeds dominate: Charolais cross (CHX), Hereford (HEX), Limousin (LIMX), Stabiliser cross (STX), Stabilisers (ST), Simmental cross (SMX) and Belgian Blue cross (BRBX). Lamb were predominantly progeny of Suffolk x Mule (SUFMU) ewes crossed with Charolais (CHA) or Lleyn (LLE) rams.

In total, data for over 200 finishing beef cattle and 900 lambs were used in this study for the period 2011 to 2018. This resulted in n = 1383 periodic liveweight beef cattle measurements (across the above seven cattle breed combinations) and n = 3997 periodic liveweight lamb measurements (across the above two sheep breed combinations) for use in model performance assessment.

2.4 Simulation configurations

The SPACSYS model has previously been validated using the NWFP data in terms of water fluxes, N_2O emissions, grass biomass accumulation and soil C and N budgets (Carswell et al., 2019b; Li et al., 2017; Liu et al., 2018; Wu et al., 2016). Hence, all the initialised states and parameters for soil water redistribution, heat transformation, grass growth and soil C and N cycling were adopted from previous studies. Information on agronomic management, animal movement and liveweight was freely accessed and downloaded from the NWFP data portal (http://resources.rothamsted.ac.uk/farmplatform). In most study years, liveweight was measured once every two weeks, while in the latter years this was reduced to once every four weeks.

The growth rate of each animal was simulated from its first grazing day in a field of the PP farmlet to its last day in the PP farmlet. The record of the birth date and liveweight at the beginning of grazing for each animal was used as model input for the initial weight and age of the animal. For each animal, dates of movements between fields were used to determine the growing period within a given field. Weaning date for lambs each year is set at the end of June. For ewes, if there was no initial weight recorded, a default value of 70 kg was applied.

Simulated annual NH_3, CH_4 and CO_2 from both animals and soils and N_2O from soils were reported and N cycling in each field was analysed. A hydrological year from April to March was used to calculate annual values.

2.5 Statistical analysis

To assess the performance of the finishing beef cattle and lamb liveweight simulations, seven accuracy indices were found (the mean error (MErr), the mean absolute error (MAE), the normalized root mean square error (NRMSE), the percentage bias (PBIAS), the Nash-Sutcliffe efficiency (NSE), the index of agreement (*d*) and the Kling-Gupta efficiency (KGE)), which can be respectively defined as:

$$\mathrm{MErr} = \frac{1}{N}\sum_{i=1}^{N}\hat{z}_i - z_i \tag{47}$$

$$\mathrm{MAE} = \frac{1}{N}\sum_{i=1}^{N}|\hat{z}_i - z_i| \tag{48}$$

$$\mathrm{NRMSE} = 100\frac{\sqrt{\frac{1}{N}\sum_{i=1}^{N}(\hat{z}_i - z_i)^2}}{z_{max} - z_{min}} \tag{49}$$

$$\mathrm{PBIAS} = 100\frac{\sum_{i=1}^{N}(\hat{z}_i - z_i)}{\sum_{i=1}^{N}z_i} \tag{50}$$

$$\mathrm{NSE} = 1 - \frac{\sum_{i=1}^{N}(\hat{z}_i - z_i)^2}{\sum_{i=1}^{N}(z_i - \bar{z}_i)^2} \tag{51}$$

$$d = 1 - \frac{\sum_{i=1}^{N}(\hat{z}_i - z_i)^2}{\sum_{i=1}^{N}(|\hat{z}_i - \bar{z}_i| + |z_i - \bar{z}_i|)^2} \tag{52}$$

$$\mathrm{KGE} = 1 - \sqrt{(r - 1)^2 + \left(\frac{\sigma_{\hat{z}}}{\sigma_z} - 1\right)^2 + \left(\frac{\bar{\hat{z}}_i}{\bar{z}_i} - 1\right)^2} \tag{53}$$

Where N is the total paired number, $\hat{z}_i$ are simulated liveweight values, z_i are measured liveweight values, $\bar{\hat{z}}_i$ is the mean of the simulated values, $\bar{z}_i$ is the mean of the measured values, z_{max} and z_{min} are the maximum and minimum values among the measured data, respectively. Further, r is the Pearson product-moment correlation coefficient (between simulated and measured) and $\sigma_{\hat{z}}$ and σ_z are the standard deviations for the simulated and measured data, respectively.

The ideal value of the four error-based indices (MErr, MAE, NRMSE and PBIAS) is zero such that the closer to zero, the more accurate the model simulation. Negative MErr values indicate a tendency to under-prediction, while positive MErr values indicate a tendency to over-prediction of liveweight by the model. NSE takes values from $-\infty$ to 1, where unity corresponds to an exact match between simulated and measured data, zero indicates that the simulations are as accurate as the mean of the measured values and a negative value indicates that the simple arithmetic mean of the measured is a better predictor than the model. The index of agreement d is defined in the range 0 to 1, where unity shows perfect model performance and zero, no agreement at all. KGE incorporates the correlation coefficient r, the ratio between the means of the simulated and of the measured data and the variability ratio. As with NSE, KGE takes values from $-\infty$ to 1. Performances indices are calculated using the ‘hydroGOF' R package. An eighth model performance index is also reported with the usual R^2 value (the coefficient of determination) for a regression fit to the simulated and measured data. Performance indices are found across different animal ages, breeds and grazing years.

Using simulated outputs only, one-way ANOVAs were used to test differences in liveweight, growth rate, CH_4 and CO_2 emissions between cattle and sheep breeds. Note for CH_4 and CO_2 emissions, no model validation data exist.

3 Results

3.1 Model performance assessment with measured data

Model performance indices *per individual* liveweight measurement are presented in Table 2 and

Table 3. Performance indices (MErr, MAE, NRMSE, PBIAS, NSE, *d*, KGE and R^2) were found conditional to age, breed and grazing year. Graphical depictions of model performance according to breed are presented in Fig. Figure 4, where animal age was plotted against *average* liveweight for simulated and measured data. In each case, the plots for simulated and measured data were fitted with polynomial functions so that simulated (on average) growth curves could be visually assessed against measured (on average) growth curves. The first model assessment (Table 2 and

Table 3) is more detailed as it is conducted on each *individual* liveweight measurement, while the second assessment (Fig. Figure 4) is broader as it is conducted on *average* liveweights.

For beef cattle, all accuracy indices (Table 2) suggest model performance moves from a high to a low level of accuracy as animals age. There was no consistent over- or under-prediction given MErr and

PBIAS could be both positive and negative. Model accuracy was poor for animals that were aged around 600 days and over (e.g., with NSE dropping to 0.19 and R^2 dropping to 0.29 for the 600- to 660-day class). Although this threshold coincided with a sharp decrease in observations as animals reached their target weight ready for slaughter. For cattle breed, all accuracy indices suggest little difference in model performance, where prediction accuracy was commonly strong, and where under-prediction was more likely than over-prediction (as MErr and PBIAS tended to be negative). Strongest levels of model accuracy were found for the SMX breed (with NSE, *d*, KGE and R^2 values all close to unity), while weakest levels of accuracy were found for BRBX cattle. Both SMX and BRBX breeds were relatively small in number, where the predominant breeds (LIMX, HEX and CHX) were all predicted with strong levels of accuracy. For cattle by grazing year, all accuracy indices indicate strong levels of model performance with say, R^2 values > 0.80 and NSE values > 0.75, but with the notable exception of the 2013 grazing year where R^2 = 0.66 and NSE = 0.63. In summary, overall model accuracy for simulating cattle liveweight (regardless of age, breed or grazing year) was strong with NSE = 0.85, *d* = 0.96, KGE = 0.90 and R^2 = 0.85 (i.e. all four indices were close to unity).

Similar to cattle, all indices for lambs (Table 3) suggest model performance moves from high to low levels of accuracy as animals age. However, for lambs, prediction accuracy became weak at a relatively early age, with NSE dropping to 0.09 and R^2 dropping to 0.47 for animals in the 140- to 160-day class (and this performance became weaker still for all remaining ages). There was also a consistent over-prediction of liveweight for each age class given that MErr and PBIAS were always positive. For lamb breed, the accuracy indices were more diverse and harder to interpret, where moderate to strong levels of accuracy were found for the dominant SUFMU and CHA breeds (with R^2 and NSE values of 0.80 and 0.64, and 0.70 and 0.47, respectively), while moderate to weak levels of accuracy were found for the LLE breed (i.e. an R^2 = 0.67 coupled with a poor NSE = -1.45). Again, there was a consistent over-prediction of liveweight given that MErr and PBIAS were always positive. For lambs by grazing year, most accuracy indices suggest moderate to strong levels of model performance across all eight years with, R^2 values > 0.60, KGE values > 0.74 and *d* values > 0.83. However, the NSE index only suggested moderate to strong levels of model performance for some years (say 2011, 2012, 2014, 2017 with NSE > 0.51) and not others (say 2013, 2015, 2016, 2018 with NSE < 0.51). In summary, overall model accuracy for simulating a lambs liveweight (regardless of age, breed or grazing year) was moderate to strong with NSE = 0.50, *d* = 0.88, KGE = 0.83 and R^2 = 0.72 (i.e. two out of four indices were close to unity).

For the graphical descriptions of model performance, where *average* liveweights are assessed against age (Fig. Figure 4), liveweight for all seven cattle breeds was simulated with strong levels of accuracy (as the fitted polynomials were highly similar). However, such levels of accuracy could weaken as cattle get older, confirming that found above. For the BRBX breed, the study model tended to under-predict liveweight (as the fitted polynomial to the simulated data mostly lies below that for the fitted polynomial to the measured data), while conversely the model tended to over-predict liveweight for the LIMX breed. Such clear under- or over-prediction was not present for the remaining five breeds. Liveweights for the lambs tended to be over-predicted for all three breeds, where this over-prediction was stronger as the lambs aged for both CHA and LLE breeds. Overall, model simulation accuracy for a lamb's liveweight was weaker than that found for a cow's liveweight.

Table 2. Model performance on beef cattle by age (days), breed and grazing year

Age	All	<300	300-360	360-420	420-480	480-540	540-600	600-660	660-720	720-780	780+
Sample size	1383	18	55	236	360	398	206	34	43	22	11
MErr	-1.32	2.35	-2.54	0.23	-1.71	-4.20	-3.79	15.28	-4.33	22.30	41.67
MAE	21.63	2.37	10.41	11.65	18.41	22.34	29.42	42.15	42.68	56.12	42.70
NRMSE %	38.50	4.70	31.80	32.60	41.50	49.20	60.20	88.80	89.00	129.1	191.9
PBIAS %	-0.30	0.80	-0.70	0.10	-0.40	-0.80	-0.70	3.00	-0.80	4.10	8.30
NSE	0.85	1.00	0.90	0.89	0.83	0.76	0.64	0.19	0.19	-0.75	-3.05
d	0.96	1.00	0.97	0.97	0.95	0.93	0.87	0.71	0.68	0.32	0.56
KGE	0.90	0.99	0.92	0.92	0.90	0.81	0.69	0.46	0.39	-0.35	0.19
R^2	0.85	1.00	0.90	0.89	0.83	0.76	0.64	0.29	0.23	0.07	0.30

Breed	LIMX	HEX	ST	SMX	BRBX	CHX	STX
Sample size	199	168	64	40	57	771	84
Animal No.	27	32	10	7	8	130	14
MErr	13.23	-7.54	-4.53	-3.48	-3.56	-4.80	13.58
MAE	22.24	23.54	13.28	10.78	42.74	21.11	18.36
NRMSE %	37.20	45.60	29.50	18.60	52.00	38.80	40.30
PBIAS %	3.00	-1.60	-0.90	-0.70	-0.70	-1.00	2.60
NSE	0.86	0.79	0.91	0.96	0.72	0.85	0.84
d	0.96	0.94	0.97	0.99	0.90	0.96	0.96
KGE	0.93	0.86	0.87	0.95	0.69	0.91	0.91
R^2	0.89	0.80	0.92	0.97	0.75	0.85	0.89

Grazing year	2011	2012	2013	2014	2015	2016	2017	2018
Sample size	141	134	115	171	257	204	171	190
MErr	-4.16	14.35	5.52	-0.84	-20.77	5.23	0.87	2.47
MAE	11.94	25.79	30.43	20.74	34.47	16.24	13.02	17.54
NRMSE %	18.60	38.90	60.90	43.50	50.30	33.30	23.20	36.20
PBIAS %	-0.90	3.20	1.20	-0.20	-4.40	1.00	0.20	0.50
NSE	0.97	0.85	0.63	0.81	0.75	0.89	0.95	0.87
d	0.99	0.96	0.90	0.94	0.93	0.97	0.99	0.96

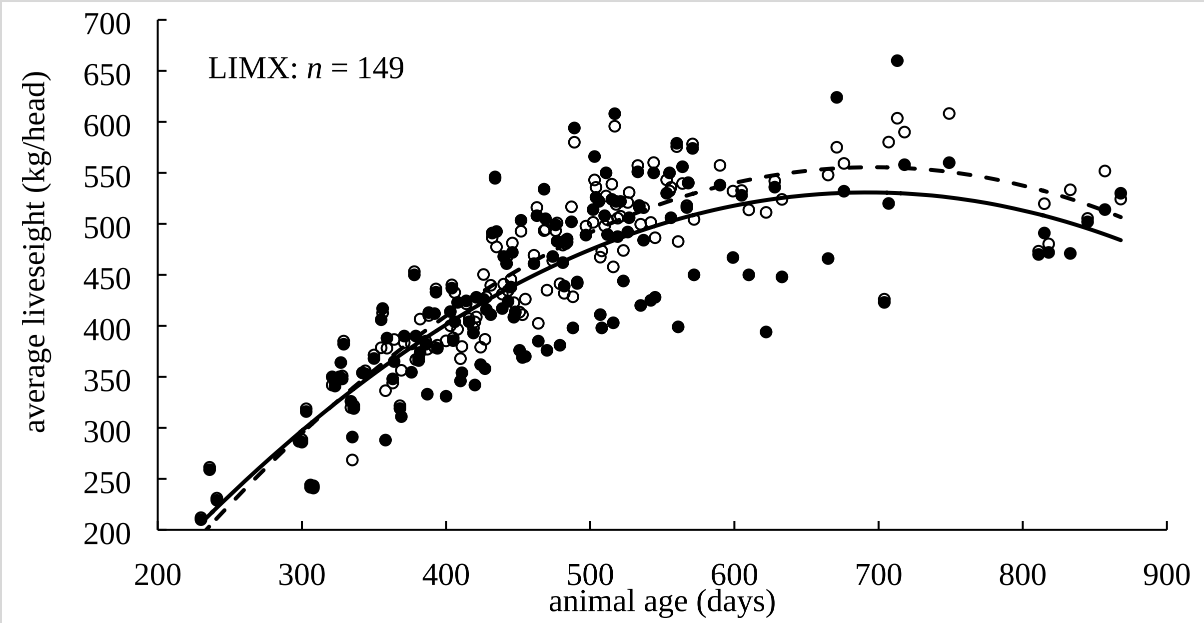
KGE	0.97	0.87	0.81	0.81	0.84	0.88	0.94	0.84
R^2	0.97	0.88	0.66	0.81	0.80	0.90	0.95	0.88

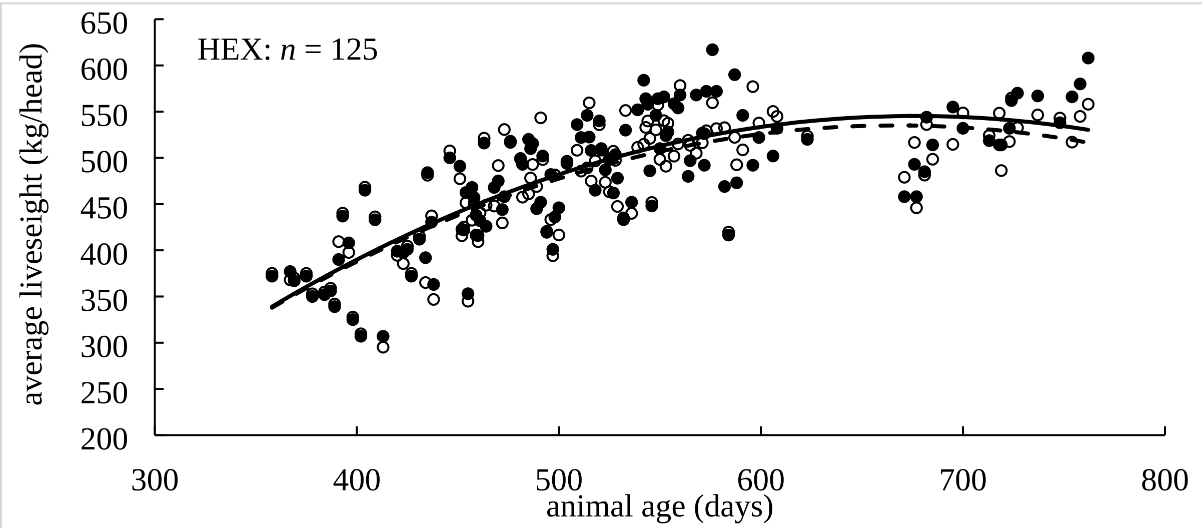
Table 3. Model performance on lamb by age (days), breed and grazing year

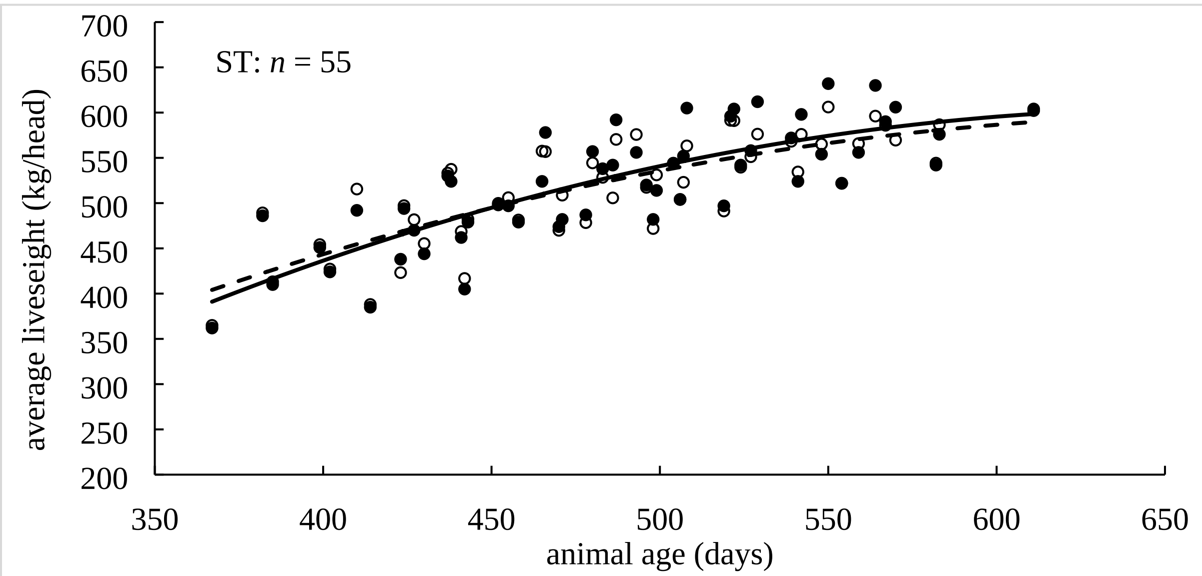
Age	All	<120	120-140	140-160	160-180	180-200	200-220	220-240	260+
Sample size	3674	1491	591	600	473	250	176	60	33
MErr	2.29	1.01	1.62	2.67	3.45	4.47	5.7	5.74	7.57
MAE	2.79	1.4	2.49	3.39	3.93	4.8	5.75	5.78	7.57
NRMSE %	70.4	34.3	64.6	95.3	110.3	150.3	151.4	149.6	198
PBIAS %	6.3	3.1	4.4	7	8.8	11.3	14.5	14.9	19.7
NSE	0.5	0.88	0.58	0.09	-0.22	-1.27	-1.3	-1.27	-3.04
d	0.88	0.97	0.87	0.74	0.66	0.51	0.5	0.6	0.41
KGE	0.83	0.91	0.74	0.61	0.52	0.32	0.22	0.57	0.13
R^2	0.72	0.92	0.7	0.47	0.41	0.16	0.16	0.36	0.08

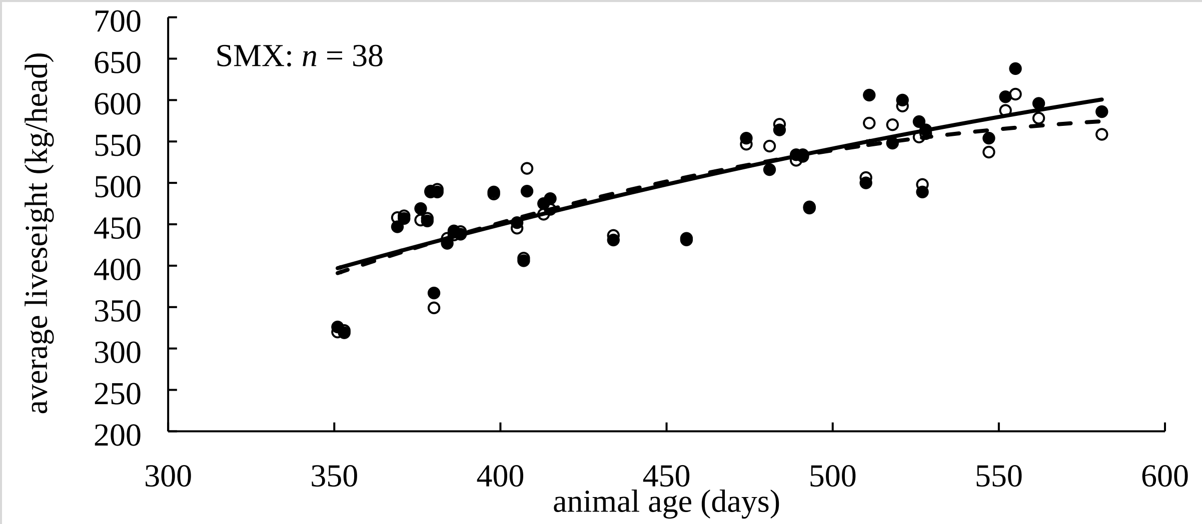
Breed	SUFMU	CHA	LLE
Sample size	671	2921	34
Animal No.	282	575	35
MErr	2.38	2.27	6.82
MAE	2.57	2.82	6.82
NRMSE %	59.6	72.8	154.2
PBIAS %	6.4	6.3	19.3
NSE	0.64	0.47	-1.45
d	0.91	0.87	0.68
KGE	0.88	0.82	0.43
R^2	0.8	0.7	0.67

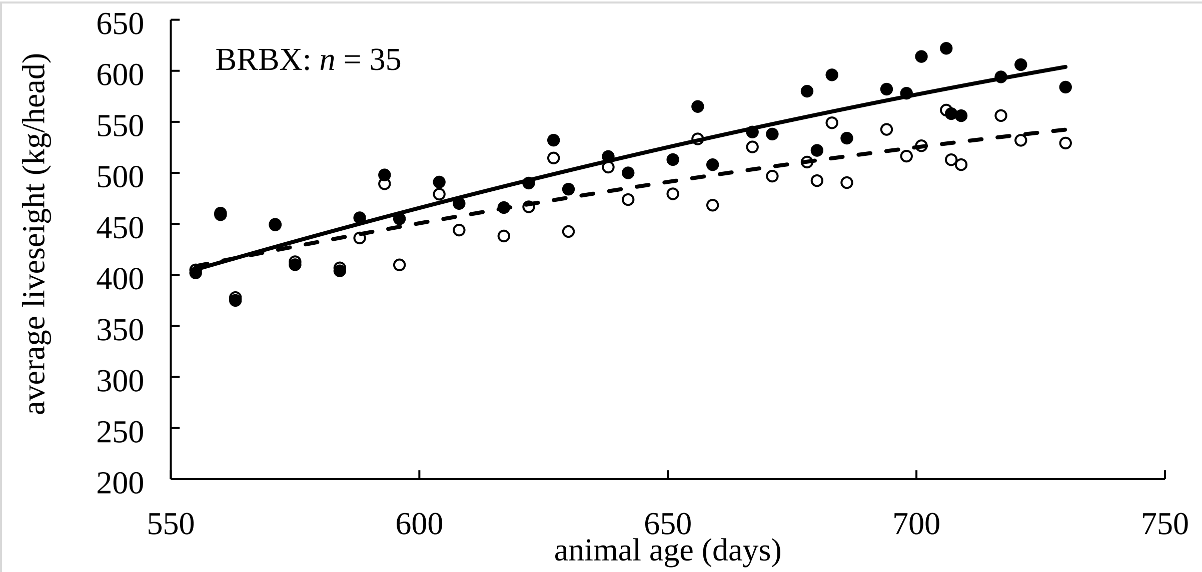
Grazing year	2011	2012	2013	2014	2015	2016	2017	2018
Sample size	341	356	203	286	317	730	731	710
MErr	1.04	2.1	2.73	0.45	0.81	3.42	1.54	3.86
MAE	1.96	2.6	3.45	1.7	2.12	3.5	2	3.93
NRMSE %	49.1	57.2	83	43.7	70.5	92.9	50.8	93.5
PBIAS %	2.7	5.8	7.3	1.2	2.1	9.7	4.3	11.2
NSE	0.76	0.67	0.31	0.81	0.5	0.14	0.74	0.12
d	0.93	0.92	0.85	0.95	0.87	0.83	0.94	0.83
KGE	0.87	0.86	0.74	0.87	0.77	0.79	0.9	0.75
R^2	0.8	0.78	0.64	0.82	0.6	0.73	0.83	0.73

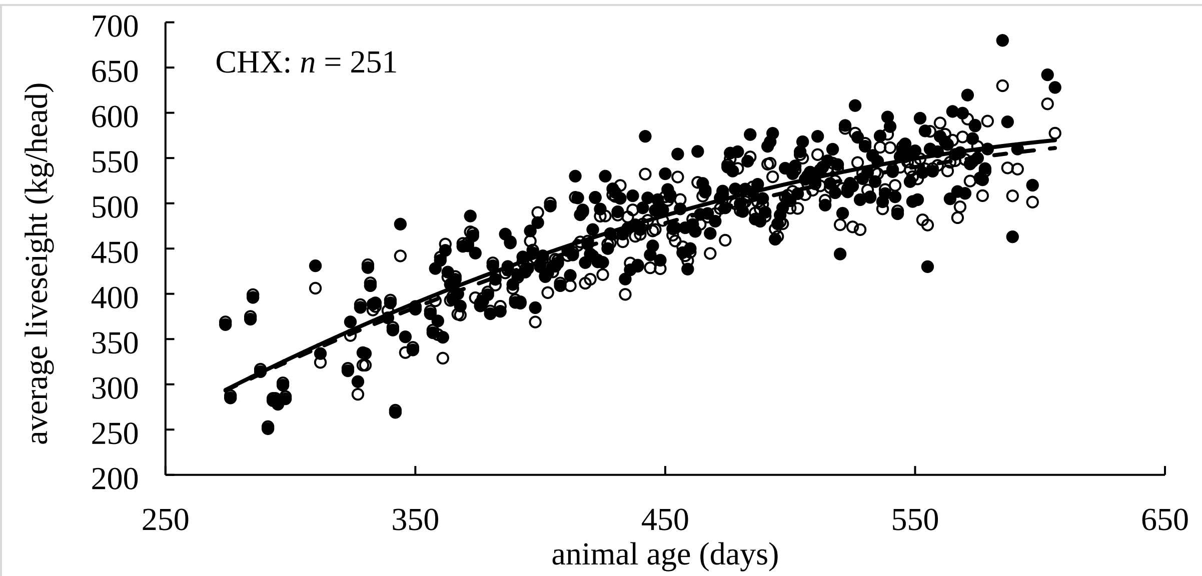

LIMX: n = 149
average liveseight (kg/head)
animal age (days)
700
650
600
550
500
450
400
350
300
250
200
200
300
400
500
600
700
800
900

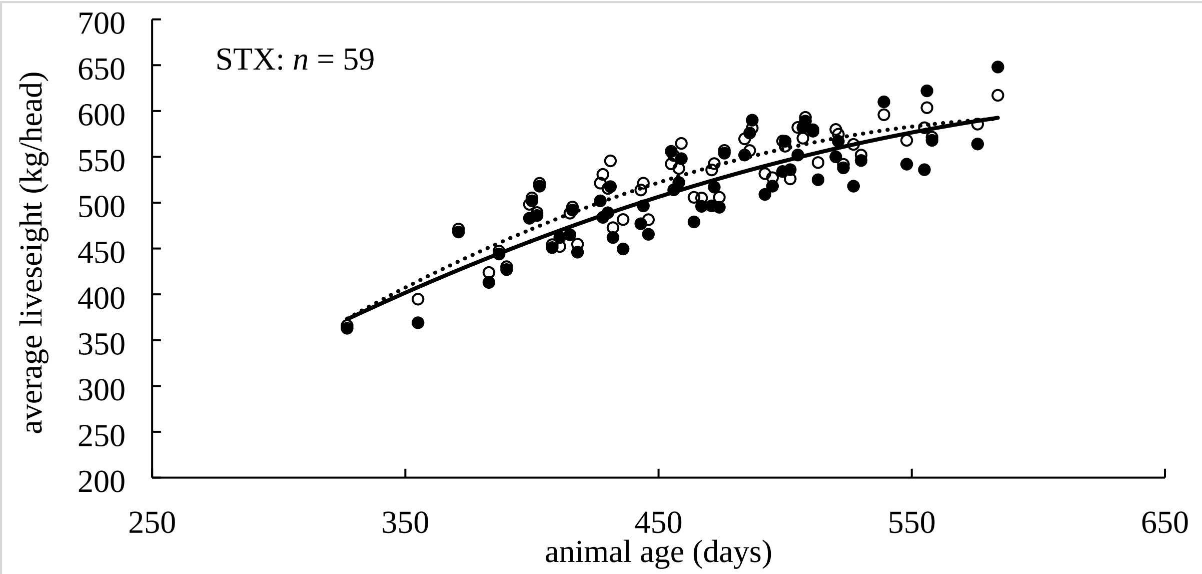

HEX: n = 125
average liveseight (kg/head)
animal age (days)
650
600
550
500
450
400
350
300
250
200
300
400
500
600
700
800

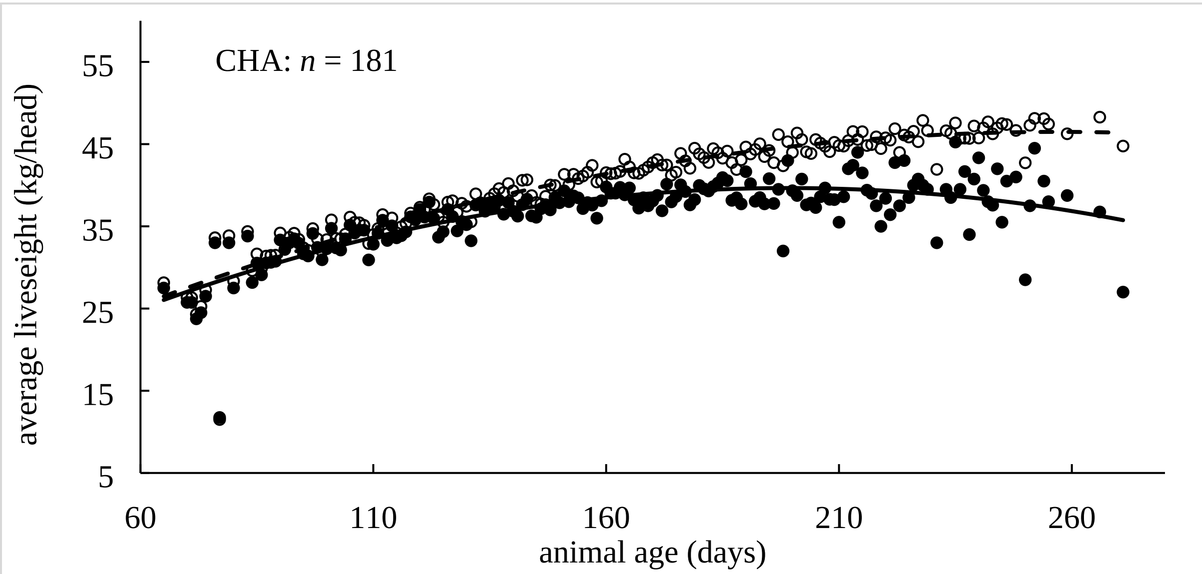

ST: n = 55
average liveseight (kg/head)
animal age (days)
700
650
600
550
500
450
400
350
300
250
200
350
400
450
500
550
600
650

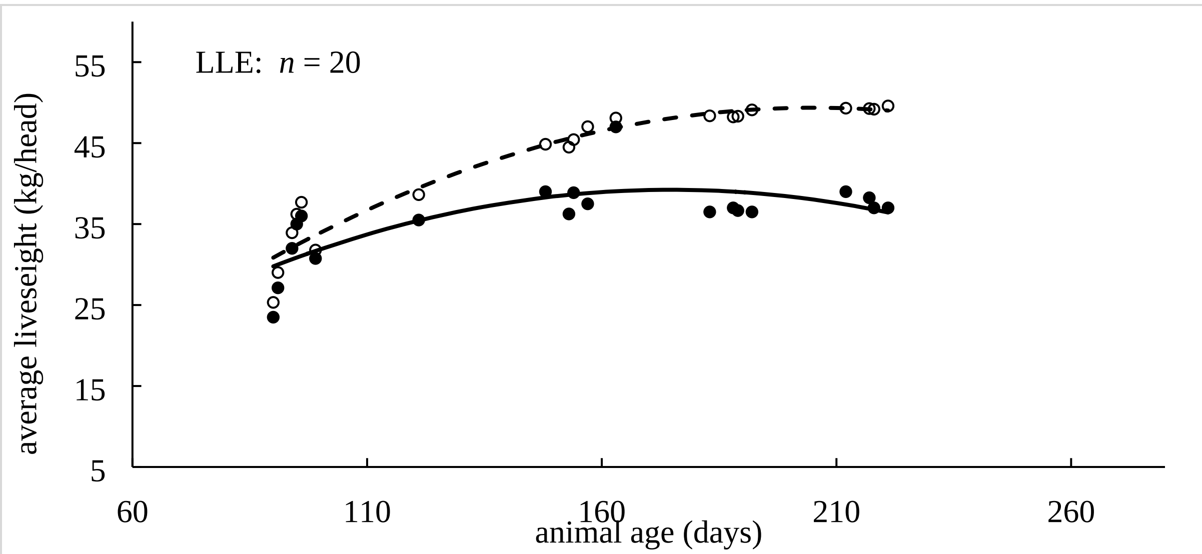

SMX: *n* = 38
average liveseight (kg/head)
animal age (days)
700
650
600
550
500
450
400
350
300
250
200
300
350
400
450
500
550
600


BRBX: *n* = 35
average liveseight (kg/head)
animal age (days)
650
600
550
500
450
400
350
300
250
200
550
600
650
700
750


CHX: *n* = 251
average liveseight (kg/head)
animal age (days)
700
650
600
550
500
450
400
350
300
250
200
250
350
450
550
650


STX: n = 59
average liveseight (kg/head)
700
650
600
550
500
450
400
350
300
250
200
250
350
450
550
650
animal age (days)


CHA: n = 181
average liveseight (kg/head)
55
45
35
25
15
5
60
110
160
210
260
animal age (days)


LLE: n = 20
average liveseight (kg/head)
55
45
35
25
15
5
60
110
160
210
260
animal age (days)

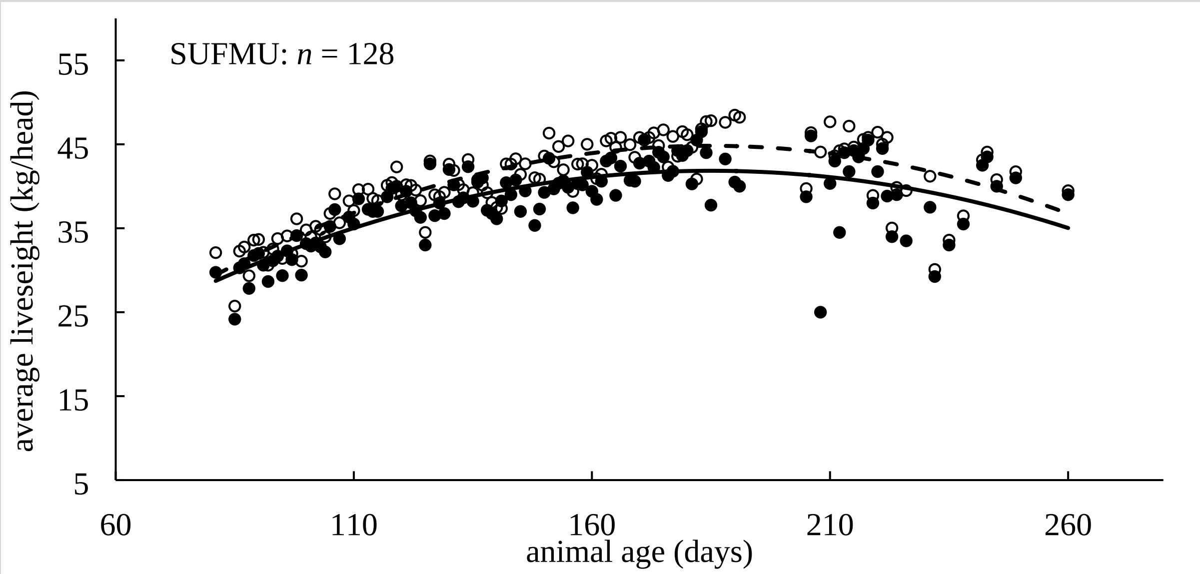


Figure 4. Comparison of measured and simulated animal liveweight by age for given breeds (BRBX, CHX, HEX, LIMX, SMX, ST and STX for cattle; CHA, LLE and SUFMU for lambs), where *n* is number of observations. Solid circles are measured average liveweight and open circles are simulated average liveweight. Solid and dotted lines are fitted polynomial functions for measured and simulated average liveweight against age, respectively.

3.2 Simulated performance for different breed combinations

Simulated liveweight gain and gaseous emissions rates during the grazing period from individual beef and sheep (lamb) breed combinations are shown in Table 4. For cattle, STX emitted the least CH_4 per head compared with other cattle breed combinations, while SMX had the highest emission. There was no significant difference in CO_2 respiration among the cattle breed combinations. There was a significant difference in the growth rate between sheep breed combinations, with LLE at the greatest rate and CHA at the least. Across the sheep breed combinations, CHA showed the lowest emissions of both CH_4 and CO_2.

Table 4. Simulated average daily liveweight gain (kg d^{-1}) and methane and carbon dioxide emissions (g $head^{-1}$ d^{-1}) during the grazing period for beef and sheep (lamb) breed combinations (different letters in a column either for cattle or sheep indicate a significant difference among breed combination, *p*<0.05)

Breed	Animal No.	Average liveweight (kg)	Growth rate (kg $head^{-1}$ d^{-1})	CH_4 (g $head^{-1}$ d^{-1})	CO_2 (g C $head^{-1}$ d^{-1})

Cattle					
CHX	130	475	0.80^{a}	265^{ab}	2045^{ab}
HEX	32	468	0.83^{a}	268^{ab}	2043^{ab}
LIMX	27	448	0.8^{a}	267^{ab}	1938^{a}
STX	14	533	0.72^{b}	242^{b}	2184^{b}
ST	10	525	0.70^{b}	245^{b}	2133^{ab}
BRBX	8	484	0.75^{ab}	259^{ab}	2028^{ab}
SMX	7	502	0.78^{ab}	289^{a}	2125^{ab}
Sheep					
SUFMU	282	41	0.23^{a}	26.9^{a}	294^{a}
CHA	575	40	0.17^{b}	22.3^{b}	273^{b}
LLE	35	41	0.29^{c}	30.7^{c}	313^{c}

3.3 Simulated gaseous emissions

Averaged annual emissions of GHGs and ammonia from different sources over the simulation period are shown in Table 5. There was less variation in N_2O and CO_2 emissions from plants and soils between fields than for NH_3, CH_4 and animal-derived CO_2 emissions, which relate to animal type (cattle or sheep), grazing density and duration in each field. For example, annual grazing density is 340 head·d ha^{-1} for cattle and 412 head·d ha^{-1} for sheep in Burrows but in Golden Rove annual grazing density is 224 head·d ha^{-1} for cattle and 1500 head·d ha^{-1} for sheep.

Table 5. Average annual (April – March) gaseous emissions (kg ha^{-1}) from soils, plants and animals when they grazed from 2011 to 2018 for each field of the PP farmlet

Field	N_2O - N	NH_3 - N	CH_4	CO_2		
				plant	soil	animal
Bottom Burrows	3.32	3.78	98	7520	5691	979
Burrows	3.64	7.82	105	6914	6277	854
Dairy North	2.55	5.04	171	6657	4963	1808

Golden Rove	3.17	4.38	101	6233	5289	892
Longlands South	2.71	4.16	189	6709	5302	1716
Orchard Dean†	3.76	6.92	91	6344	5522	790
Orchard Dean North‡	3.93	4.71	103	5112	5755	958
Orchard Dean South‡	4.09	5.96	124	6955	6099	941

† before the field was split; ‡ after the Orchard Dean field was split.

3.4 Nitrogen cycling

Averaged annual N inputs to and outputs from the individual fields over the simulation period are shown in Table 6. Total N input ranged from 190 to 260 kg ha^{-1}. Between 41 - 58% of the N added to the fields was removed through harvested biomass (silage) or animal intake, and 6 – 15% of N was lost through surface runoff or lateral drainage. Annual averaged gaseous losses of N_2O and NH_3 over the simulated period were 3.40±0.56 and 5.35±1.43 kg N ha^{-1}, respectively.

Table 6. Average annual (April – March) N inputs and outputs (kg N ha^{-1}) from each field of the PP farmlet from 2011 to 2018

Field	Input				Output				
	Deposition	Fertiliser	Manure	Excreta	Cut	Grazed	Volatilisation	Leach & runoff	Denitrification
Bottom Burrows	20.2	144.6	34.2	13.4	60.4	39.8	3.8	31.7	5.2
Burrows	20.0	164.3	63.8	15.4	58.4	49.6	7.8	24.6	6.4
Dairy North	20.0	142.3	0.0	25.1	13.5	68.2	5.0	21.1	4.1
Golden Rove	20.0	171.6	12.8	15.2	63.4	43.1	4.4	20.8	5.5
Longlands South	20.0	155.5	0.0	24.8	30.4	70.5	4.2	22.3	4.3
Orchard Dean[†]	20.5	158.8	60.1	14.6	62.7	46.4	6.9	27.6	6.8
Orchard Dean North[‡]	19.4	155.8	50.4	23.3	88.3	56.9	4.7	14.6	6.7
Orchard Dean South[‡]	19.3	146.6	48.5	15.7	42.9	57.7	6.0	16.8	6.8

[†] before the field was split; [‡] after the Orchard Dean field was split.

4 Discussion

4.1 Model performance of beef finishing cattle and sheep growth

For both beef cattle and sheep, individual animals will differ in their growth rate and their health status naturally within any livestock enterprise. Growth rates will similarly vary between breeds and the change in meteorological conditions for and during each grazing season. Given this, when objectively assessing model performance for simulating liveweight for cattle and sheep, for different age ranges, breed combinations and grazing seasons (Tables 2 and 3 and Fig. 4), the extended SPACSYS model could accurately simulate the dynamics of animal liveweight within the natural variations expected. Relatively, liveweight simulations for cattle were shown to be more accurate than those for sheep, where in both instances, simulation accuracy weakened as animals aged. Further, levels of accuracy differed more across sheep breeds than it did across cattle breeds. Grazing year could also influence simulation accuracy, although reasons for this are not entirely clear.

The extended SPACSYS model is capable of simulating not only animal growth but also other elements of livestock (either beef finishing cattle or sheep) production at a systems level. Therefore, the model has the potential to investigate the responses of the system on and consequences of a range of agronomic management and grazing strategies – i.e., not only those as analysed across the farmlet (small farm) of this research with its specific (single) management and (single) grazing approach.

4.2 Gaseous emissions from cattle and sheep

The simulated averaged CH_4 emission rate was between 242 and 289 g head^{-1} d^{-1} for beef cattle and between 22 and 31 g head^{-1} d^{-1} from sheep aged between three and seven months (Table 4). There are few measurement datasets available for UK grazing systems, but the simulated data are within the expected range according to those datasets that have been published and, more broadly, with the default values provided by the IPCC Guidelines for national GHG inventories (IPCC, 2019). Meo-Filho et al. (2021) reported average emission rates of 183 – 213 g head^{-1} d^{-1} for growing beef cattle grazing the same PP farmlet of the NWFP during late summer of 2019, measured using the SF_6 tracer gas technique (Berndt et al., 2014). Fraser et al. (2014), also using the SF_6 tracer gas technique, measured emissions from upland and lowland grazing beef cattle and reported emissions in the range 173 – 217 g head^{-1} d^{-1}. For sheep, using an emission chamber methodology and a cut and carry system for feeding fresh herbage, Moorby et al. (2015) measured emissions from mature ewes fed permanent pasture of 11 – 15 g head^{-1} d^{-1}, and Fraser et al. (2015) reported emission rates in the range 12 – 17 g head^{-1} d^{-1} for growing lambs. More generally, default emission rates provided by the IPCC (2019) equate to 142 and 25 g head^{-1} d^{-1} for finishing beef cattle and productive sheep in Western Europe, respectively. While there were significant differences between breed combinations in the simulated emissions per head for both beef cattle and sheep (Table 4), the literature evidence is that breed is a far less important variable (generally non-significant) influencing CH_4 emission than other factors such as diet characteristics and feed DMI (Duthie et al., 2017; Fraser et al., 2014; Fraser et al., 2015; Moorby et al., 2015). Any differences in emissions per head between breeds are generally accounted for through differences in body size, productivity or feed intake and, therefore, on an emission intensity basis (CH_4 kg^{-1} LWG) breed is considered relatively unimportant.

There was less variation in respiration rate between different beef and sheep breed combinations (Table 4) suggesting that breed plays only a minor role and that body size is the major determinant of respiration rate (data not shown). Although a direct comparison with measurement data is lacking, relative errors of less than 10% between the simulated and reported values for animals of the same size (Chaves et al., 2006; Gunter and Beck, 2018) support the model output. There have been few measurements, reported to date on CO_2 emissions from sheep. In an early study, Whitelaw et al. (1972) reported that an average of 232 g CO_2-C $head^{-1}$ d^{-1} was produced by sheep weighing 56 – 78 kg at 12 °C ambient temperature, which is slightly lower than we estimated.

4.3 Nitrogen cycling

Averaged annual N input to the individual farmlet fields ranged from 190 to 260 kg ha^{-1}, which mainly reflected variations in stocking density and duration across fields (Table 6). The estimated output components in N balance are within the range of the reported values. For example, an annual average loss rate through surface runoff or lateral drainage of 22.44 (±5.54) kg N ha^{-1} over the farmlet, which was close to the data-based estimate from the NWFP in a previous study (Carswell et al., 2019b).

An annual average of 3.40 kg N ha^{-1} N_2O over the simulated period was emitted to the atmosphere. Although as a proportion of the total input this is small and agronomically of little consequence, it is of environmental significance because of the high global warming potential of N_2O. Sources for this emission include the atmospheric N deposition, the applied fertiliser N and farm-yard manure (FYM) N as well as the in-field recycled N being deposited as dung and urine by the animals (making the N content of the grazed herbage available to the soil microbial processes of nitrification and denitrification) and N from senescent above- and below-ground plant material. The simulated N_2O emission was equivalent to 1.49±0.14% of the N input for these sources. This estimate is a composite of the various N_2O sources and therefore difficult to compare with emission factors reported elsewhere for individual N sources. It is in the range of 0.1 – 1.8 % given as the default emission factor (EF_1) by IPCC (2019) for fertiliser and FYM N additions to the soil, but above the range for the default IPCC emission factor (EF_3) of 0 – 1.4 % for cattle excreta returns during grazing (IPCC, 2019). It is also of a similar order of magnitude to empirical data from recent UK studies. Cowan et al. (2020) reported an average value of 1.33 % for synthetic N fertiliser (ammonium nitrate) based on 202 observations for grassland soils in the UK and Ireland. Thorman et al. (2020) reported an average emission for FYM applied to grassland of 0.37%, based on three experimental sites, with a value of

0.13% specific to the North Wyke site. Chadwick et al. (2018) analysed available UK data for N_2O emissions from cattle dung and urine returns to soil, developing average emission factors of 0.69 and 0.19% for urine and dung, respectively, based on five sites and applications at three times of the year across the grazing season. There are large uncertainties in these estimated emission factors for agricultural soils because of the many influencing environmental and management factors (Cowan et al., 2020).

Agriculture is the major source of NH_3 emissions to the atmosphere, primarily deriving from livestock excreta, including manure management, and urea / NH_3-based fertiliser applications (Behera et al., 2013). In SPACSYS, NH_3 volatilisation from chemical fertilisers is not yet considered. Ammonium nitrate was applied in this study, which is associated with much lower NH_3 emissions than other fertiliser types, e.g. urea (Forrestal et al., 2015), typically of less than 5% of the applied fertiliser N (e.g. Misselbrook et al., 2004). We simulated the NH_3 volatilisation from applied FYM and excretal grazing returns at an average annual value of 5.35±1.41 kg N ha^{-1} , equivalent to 11.9% of the FYM and excreta N. Ammonia emissions from applied FYM can be low, as the ammonium-N content of the FYM is typically low (Chambers, 2003), particularly for FYM that has previously been stored for some months, because of volatilisation losses and immobilisation processes during storage. Nicholson et al. (2017) quoted a mean emission for livestock FYM based on UK experiments of 4.5 % of the total N applied while Misselbrook et al. (2005) reported a loss of 69% of the available N at spreading, which equated to approximately 8% of the total N applied. Emissions from excretal returns at grazing derive primarily from the urine (Laubach et al., 2013) and previous experiments in the UK and Netherlands give emissions typically in the range 5 – 10% of urine N deposited (Bussink, 1994; Jarvis et al., 1991; Jarvis et al., 1989; Lockyer, 1984), although Laubach et al. (2013) reported somewhat higher values (c. 25%) from trials in New Zealand. As with N_2O emissions, NH_3 emissions can vary considerably according to application techniques, N forms, soil texture, soil wetness and weather conditions at the times of application to the field. However, the rate might be underestimated in the model and should be further investigated, including an implementation of the NH_3 volatilisation process from chemical fertilisers.

On average, the study farmlet annually received 208kg N ha^{-1} and took 122 kg N ha^{-1} from the system (Table 6), which resulted in a surplus of 86 kg N ha^{-1}. The imbalanced N budget suggested that the N application rate could be reduced to a certain extent or the livestock density might be increased to graze more forage during the grazing season. However, average simulated annual N uptake is 264 kg N ha^{-1} (data not shown). Considering the contribution from soil N mineralisation, the N budget could be balanced. Although volatilisation from FYM application or animal excreta has been considered, the loss from chemical N fertiliser through the process has not been included. It was reported that NH_3 emissions represented 7 - 21% of the total applied N for ammonium-nitrate and urea, respectively, on grassland in the UK (Carswell et al., 2019a). Not including this loss in the model adds uncertainty to the N cycle. We noted that the N_2O emissions accounts for half of total denitrification, with the ratio of $N_2O/(N_2O+N_2)$ being controlled by soil moisture. In an aerobic environment, the ratio is kept at a relative low level (Ciarlo et al., 2008). In addition, substrate concentrations will also control the ratio (Senbayram et al., 2012). Given the weather conditions when chemical fertiliser and FYM were applied in this study, the ratio of 50% might be slightly higher, and requires further investigation.

4.4 Future development

As shown in this study, the extended SPACSYS model can dynamically simulate animal and grass growth, nutrient cycling and water redistribution in a soil profile considering the effects of animal genotype, climate, feed quality and quantity on livestock production, GHG emissions, water use and quality, and nutrient budgets at a field scale. It is novel to link animal, plant, soil and atmosphere together into a whole system model to quantitatively investigate the dynamics of animal and grass production and nutrient fate, and their interactions under varied environmental conditions. Through this study, the configuration for a permanent pasture grazing system has been validated. All PP farmlet fields were reasonably homogenous and dominated (>60%) by perennial ryegrass, with a smaller biomass of creeping bent (*Agrostis stolonifera*), Yorkshire fog (*Holcus lanatus*) and marsh foxtail (*Alopecurus geniculatus*) also contributing to the sward; legumes, on the other hand, comprised <1% of the overall composition (Takahashi et al., 2018). As more diverse, multi-species swards with higher proportions of legumes and forbs in intensive grasslands are becoming more common in practice, the modelling of these more diverse botanical composition swards needs to be validated as a subject of future work. Such modelling could also include the dynamics of individual species in the swards and their impact on animal growth and nutrient flows. Furthermore, no components have been implemented to simulate the impacts of extreme events such as those for temperature, rainfall, systematic animal-mediated nutrient transfers, pests, weeds and plant and animal genetic characteristics - environment interactions (GxE) on an agricultural ecosystem, which is highly desirable (Bryant et al., 2011). Evidence suggests that current guidance (Agricultural and Food Research Council, 1993) on nutritional requirements needs to be updated, where the ongoing research project (https://www.cielivestock.co.uk/improve-beef-feed-guidelines/) may lead to revisions to the energy requirements of beef cattle.

5 Conclusions

In this study, the extended SPACSYS model was shown to accurately and dynamically model finishing beef cattle, lamb and grass growth, nutrient cycling and water redistribution in a soil profile considering the effects of genotype, climate, feed quality and quantity on livestock production, GHG emissions, water use and quality, and nutrient cycling in a permanent pasture grazing system consisting of seven fields. Averaged annual N input to the individual fields ranged from 190 to 260 kg ha^{-1}, of which 41 – 58% removed from the fields in terms of biomass cut or animal intake, and 6 –

15% through surface runoff or lateral drainage and 1.5% emitted to the atmosphere as N_2O. About 12% of the FYM and excreta N in the farmlet volatilised from the soil. There are significant differences in animal growth rate, CO_2 and CH_4 emissions between different sheep breeds. However, there are less differences between the cattle breeds. Although the extended model was validated with data specific to Southwest England and for a permanent pasture grazing system, the model has clear potential to explore more innovative practices to maintain / increase livestock production whilst reducing adverse environment impacts across different livestock breeds, climates and soil types.

Acknowledgement

This work was supported by the Biotechnology and Biological Sciences Research Council through the Soil to Nutrition Institute Strategic Programme grant (BBS/E/C/000I0320). The North Wyke Farm Platform is a UK National Capability supported by the Biotechnology and Biological Sciences Research Council (BBS/E/C/000J0100).

References

Abalos, D., Cardenas, L.M., Wu, L., 2016. Climate change and N_2O emissions from South West England grasslands: a modelling approach. Atmos. Environ. 132, 249-257.

Agricultural and Food Research Council, 1993. Energy and Protein Requirement of Ruminants. An Advisory Manual Prepared by the AFRC Technical Committee on Responses to Nutrients. CAB International, Wallingford, UK.

Bateki, C.A., Cadisch, G., Dickhoefer, U., 2019. Modelling sustainable intensification of grassland-based ruminant production systems: A review. Global Food Security 23, 85-92.

Baudracco, J., Lopez-Villalobos, N., Holmes, C.W., Comeron, E.A., Macdonald, K.A., Barry, T.N., 2013. e-Dairy: a dynamic and stochastic whole-farm model that predicts biophysical and economic performance of grazing dairy systems. Animal 7, 870-878.

Behera, S.N., Sharma, M., Aneja, V.P., Balasubramanian, R., 2013. Ammonia in the atmosphere: a review on emission sources, atmospheric chemistry and deposition on terrestrial bodies. Environ. Sci. Pollut. R. 20, 8092-8131.

Berndt, A., Boland, T.M., Deighton, M.H., Gere, J.I., Grainger, C., Hegarty, R.S., Iwaasa, A.D., Koolaard, J.P., Lassey, K.R., Luo, D., Martin, R.J., Martin, C., Moate, P.J., Molano, G., Pinares-Patiño, C., Ribaux, B.E., Swainson, N.M., Waghorn, G.C., Williams, S.R.O., 2014. Guidelines for use of sulphur hexafluoride (SF_6) tracer technique to measure enteric methane emissions from ruminants, in: Lambert, M.G. (Ed.), New Zealand, p. 166.

Bingham, I.J., Wu, L., 2011. Simulation of wheat growth using the 3D root architecture model SPACSYS: validation and sensitivity analysis. Eur. J. Agron. 34, 181-189.

Blaxter, K.L., Clapperton, J.L., 1965. Prediction of the amount of methane produced by ruminants. British Journal of Nutrition 19, 511-522.

Blaxter, K.L., Wainman, F.W., Wilson, R.S., 1961. The regulation of food intake by sheep. Animal Science 3, 51-61.

Bryant, J.R., Snow, V.O., 2008. Modelling pastoral farm agro-ecosystems: A review. New Zealand Journal of Agricultural Research 51, 349-363.

Bryant, J.R., Snow, V.O., Cichota, R., Jolly, B.H., 2011. The effect of situational variability in climate and soil, choice of animal type and N fertilisation level on nitrogen leaching from pastoral farming systems around Lake Taupo, New Zealand. Agric. Syst. 104, 271-280.

Bussink, D.W., 1994. Relationships between ammonia volatilization and nitrogen fertilizer application rate, intake and excretion of herbage nitrogen by cattle on grazed swards. Fert. Res. 38, 111-121.

Carswell, A., Shaw, R., Hunt, J., Sánchez-Rodríguez, A.R., Saunders, K., Cotton, J., Hill, P.W., Chadwick, D.R., Jones, D.L., Misselbrook, T.H., 2019a. Assessing the benefits and wider costs of different N fertilisers for grassland agriculture. Archives of Agronomy and Soil Science 65, 625-639.

Carswell, A.M., Gongadze, K., Misselbrook, T.H., Wu, L., 2019b. Impact of transition from permanent pasture to new swards on the nitrogen use efficiency, nitrogen and carbon budgets of beef and sheep production. Agric. Ecosyst. Environ. 283, 106572.

Chadwick, D.R., Cardenas, L.M., Dhanoa, M.S., Donovan, N., Misselbrook, T., Williams, J.R., Thorman, R.E., McGeough, K.L., Watson, C.J., Bell, M., Anthony, S.G., Rees, R.M., 2018. The contribution of cattle urine and dung to nitrous oxide emissions: Quantification of country specific emission factors and implications for national inventories. Sci. Total Environ. 635, 607-617.

Chambers, B.J., 2003. Manure ANalysis DatabasE (MANDE), Final Project Report to Defra, Project NT2006, UK.

Chaves, A.V., Thompson, L.C., Iwaasa, A.D., Scott, S.L., Olson, M.E., Benchaar, C., Veira, D.M., McAllister, T.A., 2006. Effect of pasture type (alfalfa vs. grass) on methane and carbon dioxide production by yearling beef heifers. Can. J. Anim. Sci. 86, 409-418.

Ciarlo, E., Conti, M., Bartoloni, N., Rubio, G., 2008. Soil N_2O emissions and $N_2O/(N_2O+N_2)$ ratio as affected by different fertilization practices and soil moisture. Biology and Fertility of Soils 44, 991-995.

CIGR, 2002. Climatization of Animal Houses: Heat and Moisture Production at Animal and House Levels, in: Pedersen, S., Sällvik, K. (Eds.). Research Centre Bygholm, Danish Institute of Agricultural Sciences, Horsens, Denmark.

Cowan, N., Carnell, E., Skiba, U., Dragosits, U., Drewer, J., Levy, P., 2020. Nitrous oxide emission factors of mineral fertilisers in the UK and Ireland: A Bayesian analysis of 20 years of experimental data. Environ. Int. 135, 105366.

de Haas, Y., Windig, J.J., Calus, M.P.L., Dijkstra, J., de Haan, M., Bannink, A., Veerkamp, R.F., 2011. Genetic parameters for predicted methane production and potential for reducing enteric emissions through genomic selection. J. Dairy Sci. 94, 6122-6134.

Donnelly, J.R., Freer, M., Salmon, L., Moore, A.D., Simpson, R.J., Dove, H., Bolger, T.P., 2002. Evolution of the GRAZPLAN decision support tools and adoption by the grazing industry in temperate Australia. Agric. Syst. 74, 115-139.

Dougherty, H.C., Ahmadi, A., Oltjen, J.W., Mitloehner, F.M., Kebreab, E., 2019. Review: Modeling production and environmental impacts of small ruminants—Incorporation of existing ruminant modeling techniques, and future directions for research and extension. Applied Animal Science 35, 114-129.

Dumont, B., González-García, E., Thomas, M., Fortun-Lamothe, L., Ducrot, C., Dourmad, J.Y., Tichit, M., 2014. Forty research issues for the redesign of animal production systems in the 21st century. Animal 8, 1382-1393.

Duthie, C.A., Haskell, M., Hyslop, J.J., Waterhouse, A., Wallace, R.J., Roehe, R., Rooke, J.A., 2017. The impact of divergent breed types and diets on methane emissions, rumen characteristics and performance of finishing beef cattle. animal 11, 1762-1771.

Ehrhardt, F., Soussana, J.-F., Bellocchi, G., Grace, P., McAuliffe, R., Recous, S., Sándor, R., Smith, P., Snow, V., De Antoni Migliorati, M., Basso, B., Bhatia, A., Brilli, L., Doltra, J., Dorich, C.D., Sciences, N., Doro, L., Fitton, N., Giacomini, S., Grant, B., Harrison, M., Jones, S., Kirschbaum, M., Klumpp, K., Laville, P., Leonard, J., Liebig, M., Lieffering, M., Martin, R., Massad, R.S., Meier, E., Merbold, L., Moore, A., Myrgiotis, V., Newton, P., Pattey, E., Rolinski, S., Sharp, J., Smith, W., Wu, L., Zhang, Q., 2018. Assessing uncertainties in crop and pasture ensemble model simulations of productivity and N_2O emissions. Global Change Biol. 24, e603-e616.

Eisler, M.C., Lee, M.R.F., Tarlton, J.F., Martin, G.B., Beddington, J., Dungait, J.A.J., Greathead, H., Liu, J., Mathew, S., Miller, H., Misselbrook, T., Murray, P., Vinod, V.K., Saun, R.V., Winter, M., 2014. Steps to sustainable livestock. Nature 507, 32-34.

Emmans, G.C., Kyriazakis, I., 2000. Issues arising from genetic selection for growth and body composition characteristics in poultry and pigs. BSAP Occasional Publication 27, 39-53.

Faverdin, P., Baratte, C., Delagarde, R., Peyraud, J.L., 2011. GrazeIn: a model of herbage intake and milk production for grazing dairy cows. 1. Prediction of intake capacity, voluntary intake and milk production during lactation. Grass and Forage Science 66, 29-44.

Forrestal, P.J., Harty, M., Carolan, R., Lanigan, G.J., Watson, C.J., Laughlin, R.J., McNeill, G., Chambers, B.J., Richards, K.G., 2015. Ammonia emissions from urea, stabilized urea and calcium ammonium nitrate: insights into loss abatement in temperate grassland. Soil Use Manage., n/a-n/a.

Fraser, M.D., Fleming, H.R., Moorby, J.M., 2014. Traditional vs modern: Role of breed type in determining enteric methane emissions from cattle grazing as part of contrasting grassland-based systems. PLOS ONE 9, e107861.

Fraser, M.D., Fleming, H.R., Theobald, V.J., Moorby, J.M., 2015. Effect of breed and pasture type on methane emissions from weaned lambs offered fresh forage. The Journal of Agricultural Science 153, 1128-1134.

Graux, A.-I., Gaurut, M., Agabriel, J., Baumont, R., Delagarde, R., Delaby, L., Sousssana, J.-F., 2011. Development of the pasture simulation model for assessing livestock production under climate change. Agric. Ecosyst. Environ. 144, 69-91.

Gunter, S.A., Beck, M.R., 2018. Measuring the respiratory gas exchange by grazing cattle using an automated, open-circuit gas quantification system. Translational Animal Science 2, 11-18.

Haque, M.N., Roggenbuck, M., Khanal, P., Nielsen, M.O., Madsen, J., 2014. Development of methane emission from lambs fed milk replacer and cream for a prolonged period. Animal Feed Science and Technology 198, 38-48.

Harrod, T.R., Hogan, D.V., 2008. The soils of North Wyke and Rowden. North Wyke Research, North Wyke, Devon.

Hirooka, H., 2010. Systems approaches to beef cattle production systems using modeling and simulation. Animal Science Journal 81, 411-424.

Hulme, D.J., Kellaway, R.C., Booth, P.J., Bennett, L., 1986. The CAMDAIRY model for formulating and analysing dairy cow rations. Agric. Syst. 22, 81-108.

IPCC, 2019. 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories, in: Calvo Buendia, E., Tanabe, K., Kranjc, A., Baasansuren, J., Fukuda, M., S., N., Osako, A., Pyrozhenko, Y., Shermanau, P., Federici, S. (Eds.). IPCC, Switzerland.

Jarvis, S.C., Hatch, D.J., Orr, R.J., Reynolds, S.E., 1991. Micrometeorological studies of ammonia emission from sheep grazed swards. The Journal of Agricultural Science 117, 101-109.

Jarvis, S.C., Hatch, D.J., Roberts, D.H., 1989. The effects of grassland management on nitrogen losses from grazed swards through ammonia volatilization; the relationship to excretal N returns from cattle. J. Agr. Sci. 112, 205-216.

Kahn, H.E., Spedding, C.R.W., 1984. A dynamic model for the simulation of cattle herd production systems: 2-An investigation of various factors influencing the voluntary intake of dry matter and the use of the model in their validation. Agric. Syst. 13, 63-82.

Kirchgessner, M., Windisch, W., Müller, H.L., Kreuzer, M., 1991. Release of methane and of carbon dioxide by dairy cattle. Agribiol. Res. 44, 91-102.

Laubach, J., Taghizadeh-Toosi, A., Gibbs, S.J., Sherlock, R.R., Kelliher, F.M., Grover, S.P.P., 2013. Ammonia emissions from cattle urine and dung excreted on pasture. Biogeosciences 10, 327-338.

Lewis, R.M., Emmans, G.C., Dingwall, W.S., Simm, G., 2002. A description of the growth of sheep and its genetic analysis. Anim. Sci. 74, 51-62.

Li, Y., Liu, Y., Harris, P., Sint, H., Murray, P.J., Lee, M., Wu, L., 2017. Assessment of soil water, carbon and nitrogen cycling in reseeded grassland on the North Wyke Farm Platform using a process-based model. Sci. Total Environ. 603-604, 27-37.

Liu, Y., Li, Y., Harris, P., Cardenas, L., Dunn, R.M., Sint, H., Murray, P., Lee, M., Wu, L., 2018. Modelling field scale spatial variation in water run-off, soil moisture, N_2O emissions and herbage biomass of a grazed pasture using the SPACSYS model. Geoderma 315, 49-58.

Liu, Y., Wu, L., Watson, C.A., Baddeley, J.A., Pan, X., Zhang, L., 2013. Modeling biological dinitrogen fixation of field pea with a process-based simulation model. Agron. J. 105, 670-678.

Lockyer, D.R., 1984. A system for the measurement in the field of losses of ammonia through volatilisation. Journal of the Science of Food and Agriculture 35, 837-848.

Loewer, O.J., Smith, E.M., Gay, N., Fehr, R., 1983. Incorporation of environment and feed quality into a net energy model for beef cattle. Agric. Syst. 11, 67-94.

Mainland, D.D., 1985. A note of lactation curves of dairy cows in Scotland. Anim. Prod. 41, 413-416.

Martin, G., Martin-Clouaire, R., Rellier, J.P., Duru, M., 2011. A simulation framework for the design of grassland-based beef-cattle farms. Environmental Modelling & Software 26, 371-385.

Meo-Filho, P., Rivero, M.J., Nightingale, P., Cooke, A., Berndt, A., Lee, M., Cardenas, L., 2021. Methane emission of beef cattle raised in different types of pastures in southwest of England, in: Ball, E.E., Bon, M.L., Brameld, J.M., Carter, A., Flood, D.J., Garnsworthy, P.C., Kelly, A.K., Kenny, D.A., Lively, F., Magowan, E., Mansbridge, S.C., Margerison, J.K., Marley, C.V., Mather, L., Morrison, S., Murphy, B.A., Murray, J., O'Shea, C.J., Pyatt, A.Z., Sinclair, K.D., Tennant, L., Warren, H.E., Waters, S.M., White, G.A., Wilde, D., Williams, J. (Eds.), Proceedings of the British Society of Animal Science Annual conference 2021, On-line Virtual Conference.

Misselbrook, T.H., Nicholson, F.A., Chambers, B.J., Johnson, R.A., 2005. Measuring ammonia emissions from land applied manure: an intercomparison of commonly used samplers and techniques. Environmental Pollution 135, 389-397.

Misselbrook, T.H., Sutton, M.A., Scholefield, D., 2004. A simple process-based model for estimating ammonia emissions from agricultural land after fertilizer applications. Soil Use Manage. 20, 365-372.

Moorby, J.M., Fleming, H.R., Theobald, V.J., Fraser, M.D., 2015. Can live weight be used as a proxy for enteric methane emissions from pasture-fed sheep? Scientific Reports 5, 17915.

Murray, M.G., 1991. Maximizing energy retention in grazing ruminants. J. Anim. Ecol. 60, 1029-1045.

Neil, P.G., Sherlock, R.A., Bright, K.P., 1999. Integration of legacy sub-system components into an object-oriented simulation model of a complete pastoral dairy farm. Environmental Modelling & Software 14, 495-502.

Nicholson, F., Bhogal, A., Cardenas, L., Chadwick, D., Misselbrook, T., Rollett, A., Taylor, M., Thorman, R., Williams, J., 2017. Nitrogen losses to the environment following food-based digestate and compost applications to agricultural land. Environmental Pollution 228, 504-516.

Pierret, A., Moran, C.J., Doussan, C., 2005. Conventional detection methodology is limiting our ability to understand the roles and functions of fine roots. New Phytol. 166, 967-980.

Sándor, R., Ehrhardt, F., Grace, P., Recous, S., Smith, P., Snow, V., Soussana, J.-F., Basso, B., Bhatia, A., Brilli, L., Doltra, J., Dorich, C.D., Doro, L., Fitton, N., Grant, B., Harrison, M.T., Kirschbaum, M.U.F., Klumpp, K., Laville, P., Léonard, J., Martin, R., Massad, R.-S., Moore, A., Myrgiotis, V., Pattey, E., Rolinski, S., Sharp, J., Skiba, U., Smith, W., Wu, L., Zhang, Q., Bellocchi, G., 2020. Ensemble modelling of carbon fluxes in grasslands and croplands. Field Crops Research 252, 107791.

Senbayram, M., Chen, R., Budai, A., Bakken, L., Dittert, K., 2012. N2O emission and the N2O/(N2O+N2) product ratio of denitrification as controlled by available carbon substrates and nitrate concentrations. Agriculture, Ecosystems & Environment 147, 4-12.

Snow, V.O., Rotz, C.A., Moore, A.D., Martin-Clouaire, R., Johnson, I.R., Hutchings, N.J., Eckard, R.J., 2014. The challenges – and some solutions – to process-based modelling of grazed agricultural systems. Environmental Modelling & Software 62, 420-436.

Springmann, M., Clark, M., Mason-D'Croz, D., Wiebe, K., Bodirsky, B.L., Lassaletta, L., de Vries, W., Vermeulen, S.J., Herrero, M., Carlson, K.M., Jonell, M., Troell, M., DeClerck, F., Gordon, L.J., Zurayk, R., Scarborough, P., Rayner, M., Loken, B., Fanzo, J., Godfray, H.C.J., Tilman, D., Rockström, J., Willett, W., 2018. Options for keeping the food system within environmental limits. Nature 562, 519-525.

Stergiadis, S., Allen, M., Chen, X.J., Wills, D., Yan, T., 2015. Prediction of nutrient digestibility and energy concentrations in fresh grass using nutrient composition. J. Dairy Sci. 98, 3257-3273.

Takahashi, T., Harris, P., Blackwell, M.S.A., Cardenas, L.M., Collins, A.L., Dungait, J.A.J., Hawkins, J.M.B., Misselbrook, T., McAuliffe, G.A., McFadzean, J.N., Murray, P.J., Orr, R.J., Rivero-Viera, J., Wu, L., Lee, M.R.F., 2018. Roles of instrumented farm-scale trials in trade-off assessments of pasture-based ruminant production systems. Animal 12, 1766-1776.

Taylor, S.C.S., 1968. Time taken to mature in relation to mature weight for sexes, strains and species of domesticated mammals and birds. Animal Production 10, 157-169.

Tedeschi, L.O., Fox, D.G., Sainz, R.D., Barioni, L.G., Medeiros, S.R., Boin, C., 2005. Mathematical models in ruminant nutrition. Scientia Agricola 62, 76–91.

Tess, M.W., Kolstad, B.W., 2000. Simulation of cow-calf production systems in a range environment: I. Model development, , Volume 78, Issue 5, May 2000, Pages , https://doi.org/10.2527/2000.7851159x. J. Anim. Sci. 78, 1159–1169.

Thorman, R.E., Nicholson, F.A., Topp, C.F.E., Bell, M.J., Cardenas, L.M., Chadwick, D.R., Cloy, J.M., Misselbrook, T.H., Rees, R.M., Watson, C.J., Williams, J.R., 2020. Towards country-specific nitrous oxide emission factors for manures applied to arable and grassland soils in the UK. Front. Sustain. Food Syst. 4.

Thornley, J.H.M., 1998. Grassland Dynamics - An Ecosystem Simulation Model. CAB International, Cambridge.

Tilman, D., Clark, M., 2014. Global diets link environmental sustainability and human health. Nature 515, 518-522.

Topp, C.F.E., 1999. The implications of climate change on forage - based livestock systems in Scotland. University of Glasgow, Glasgow.

Topp, C.F.E., 2001. Dairy production, in: Tijskens, L.M.M., Hertog, M.L.A.T.M., Nicolai, B.M. (Eds.), Food Process Modelling. Woodhead Publishing Limited, Cambridge, England, pp. 230-252.

van der Linden, A., van de Ven, G.W.J., Oosting, S.J., van Ittersum, M.K., de Boer, I.J.M., 2019. LiGAPS-Beef, a mechanistic model to explore potential and feed-limited beef production 1: model description and illustration. animal 13, 845-855.

Westhoek, H., Lesschen, J.P., Rood, T., Wagner, S., De Marco, A., Murphy-Bokern, D., Leip, A., van Grinsven, H., Sutton, M.A., Oenema, O., 2014. Food choices, health and environment: Effects of cutting Europe's meat and dairy intake. Global Environ. Change 26, 196-205.

Whitelaw, F.G., Brockway, J.M., Reid, R.S., 1972. Measurement of carbon dioxide production in sheep by isotope dilution. Quarterly Journal of Experimental Physiology and Cognate Medical Sciences 57, 37-55.

Wood, P.D.P., 1980. Breed variations in the shape of the lactation curve of cattle and their implications for efficiency. Animal Production 31, 133-141.

Wu, L., Blackwell, M., Dunham, S., Hernández-Allica, J., McGrath, S.P., 2019. Simulation of phosphorus chemistry, uptake and utilisation by winter wheat. Plants 8, 404.

Wu, L., McGechan, M.B., McRoberts, N., Baddeley, J.A., Watson, C.A., 2007. SPACSYS: integration of a 3D root architecture component to carbon, nitrogen and water cycling - model description. Ecol. Model. 200, 343-359.

Wu, L., Rees, R.M., Tarsitano, D., Zhang, X., Jones, S.K., Whitmore, A.P., 2015. Simulation of nitrous oxide emissions at field scale using the SPACSYS model. Sci. Total Environ. 530–531, 76-86.

Wu, L., Zhang, X., Griffith, B.A., Misselbrook, T., 2016. Sustainable grassland systems: A modelling perspective based on the North Wyke Farm Platform. Eur. J. Soil Sci. 67, 397-408.

Yan, T., Porter, M.G., Mayne, C.S., 2009. Prediction of methane emission from beef cattle using data measured in indirect open-circuit respiration calorimeters. animal 3, 1455-1462.

Yang, C.T., Wang, C.M., Zhao, Y.G., Aubry, A., Yan, T., 2019. Is the maintenance energy requirement for current sheep flocks higher than recommended?, Proceedings of the British Society of Animal Science, 9–11 April 2019, Edinburgh, p. 15.

Zemmelink, G., 1980. Effect of selective consumption on voluntary intake and digestibility of tropical forages, Agriculture Research Report 896, Wageningen, p. 100.