Adaptation of herd simulation models to predict the efficiency of the use of resources in tropical ruminant productions systems

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Christian Bateki Adjogo

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Examination committee

Supervisor and reviewer	Prof. Dr. Uta Dickhöfer
Co-reviewer and examiner	Prof. Dr. Eva Schlecht
Additional examiner	Prof. Dr. Georg Cadisch
Faculty representative	Prof. Dr. Martin Hasselmann

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Summary

Adaptation of herd simulation models to predict the efficiency of the use of resources in tropical ruminant production systems.

Agricultural systems in the (Sub-)Tropics are under increasing pressure to produce more food and satisfy the growing demand of a rapidly growing and more affluent human population for agricultural products. With growing rates of urbanization in these regions and the associated dietary changes, the demand for calories from animal-based foods like milk, meat, and eggs could increase by 74 to 114 % between 2010 and 2050. Ruminant livestock have the potential to contribute to satisfying the demand for animal-based foods in the (Sub-)Tropics, but also raise considerable environmental concerns, amongst others due to their emissions. The use of simulation models is a holistic approach to identify how to sustainably harness the potential of ruminants for animal-based food production in the (Sub-)Tropics. Although several ruminant herd models are relevant for studying tropical ruminant production systems, most of them were developed using data that quantify and characterize biological processes of ruminants in temperate regions. Therefore, the present thesis identified and adapted an existing ruminant livestock herd model to adequately predict resource use and the potential outputs from production systems in the (Sub-)Tropics.

A comprehensive literature review was conducted to identify future modelling needs and the suitability of five state-of-the-art ruminant herd models was assessed relative to these modelling needs. Key modelling needs that ruminant herd models should address include inter- and intra-species competition for resources, feeding behaviors of ruminant livestock, and their adaptive behavior to changing environmental conditions. These models also need to be able to predict emissions from tropical ruminant livestock systems, as well as be able to capture the role of policy on farmers' decision-making. Current state-of-the-art models are only partly suitable to address the proposed modelling needs due to, for instance, their inability to capture the environmental impacts associated with tropical ruminant livestock production systems. Thus, to adequately simulate the interactions between ruminant livestock and other components in tropical agricultural systems, the integration of ruminant herd models into other biophysical and socio-economics tools was suggested.

Next, a meta-analysis was used to adopt and adapt a semi-mechanistic conceptual mathematical model (**CMM**) to accurately predict voluntary dry matter intake (**DMI**) of different types and sizes of cattle fed a wide range of feed types in the (Sub-)Tropics. We focused on voluntary DMI, because it is the main driver of resource use and performance in ruminant product systems. Also, the magnitude of parameters that determine the physical and physiological regulation of voluntary DMI of cattle in temperate regions differ from those of cattle kept under tropical feeding and husbandry conditions. For example, cattle in tropical ruminant production systems have a higher daily average fecal dry matter and neutral detergent fibre intake capacity (both in kg/kg body-weight) than those in temperate production systems. Therefore, the CMM of Conrad et al. (1964) (**C1**) and Mertens (1987) (**M1**) were identified and modified to yield six (**C2** – **C4** and **M2** – **M4**) CMM. Of the eight CMM evaluated in our meta-analysis, four CMM could predict voluntary DMI of stall-fed cattle in the (Sub-)Tropics with acceptable accuracy (i.e., prediction bias < 10 % of the observed DMI). Adapting the relevant parameters in the CMM and also retaining the mean of the physically and physiologically regulated voluntary DMI rather than the lower of both estimates yielded the most adequate voluntary DMI model (i.e., M4).

Building on adequate DMI prediction models, simulation models are needed to capture resource use, as well as the outputs and environmental impacts associated with ruminant herds in the (Sub-)Tropics. Thus, we leveraged the increasing availability of data that quantify and characterize biological processes in ruminants in the (Sub-)Tropics, and modified the LIVestock SIMulator (**LIVSIM**) to accurately predict resource use and productive performance. These modifications included the adoption of M4 for voluntary DMI prediction, increased maintenance metabolizable energy (**ME**) requirements from 0.488 to 0.631 MJ ME/kg metabolic body-weight, and age-sex specific ME requirements for gain (MJ ME/kg body-weight). The resulting model (modified LIVSIM) predicted voluntary DMI, final body-weights, and daily milk yields more accurately (i.e., relative prediction error < 10 % mean observed value) than the original LIVSIM. Consequently, the modified LIVSIM is more adequate than the original LIVSIM in simulating tropical stall-fed dairy cattle production systems.

The present thesis showed that state-of-the-art ruminant livestock herd models used to simulate tropical production systems need further development to enable them to address the modelling needs identified. Instead of developing new models to address these modelling needs, existing simulation models could be adapted using the increasingly available data that quantify and characterize biological processes in ruminants in these regions. This approach will ensure that not only the direction of change for different management strategies will be identified for tropical ruminant production systems, but also the correct magnitude of resources use and productive and reproductive performance.

Zusammenfassung

Anpassung von Simulationsmodellen auf Herdenebene zur Vorhersage der Effizienz der Ressourcennutzung von tropischen Wiederkäuer-basierten Produktionssystemen

Agrarsysteme in den (Sub-)Tropen stehen unter dem Druck, den steigenden Bedarf nach landwirtschaftlichen Produkten zu decken, der aus der zunehmenden Bevölkerung und dem wachsenden Wohlhaben resultiert. Zusätzlich wird für die Nachfrage nach tierbasierten Lebensmitteln wie beispielsweise Milch, Fleisch und Eier aufgrund der fortschreitenden Urbanisierung dieser Region und des damit verbundenen Wandels der Nahrungsgewohnheiten ein Anstieg von 74 bis 114% zwischen 2010 und 2050 erwartet. Wiederkäuer-basierte Systeme zur Bereitstellung dieser Lebensmittel besitzen das Potential, zur Deckung dieses steigenden Bedarfs beizutragen, was jedoch auch mit berechtigten Bedenken wegen der damit verbundenen umweltbelastenden Emissionen einhergeht. Die Nutzung von Simulationsmodellen berücksichtigt einen ganzheitlichen Ansatz, um eine nachhaltige Einbindung von Wiederkäuern in die Lebensmittelproduktion in den (Sub-)Tropen zu unterstützen. Es existieren mehrere Modelle, die für die Untersuchung tropischer Wiederkäuerproduktionssysteme in Frage kommen, jedoch basieren diese hauptsächlich auf Daten, welche die biologischen Prozesse von Wiederkäuern aus gemäßigten Regionen quantifizieren und charakterisieren. Diese Doktorarbeit thematisiert daher die Ermittlung und Anpassung eines existierenden Modells zur Simulation der Produktivität und Ressourcennutzung von Wiederkäuerherden in den (Sub-)Tropen.

Eine umfassende Literaturrecherche wurde durchgeführt, um die sich veränderten Ansprüche an Herdenmodelle aufgrund der sich in Zukunft wandelnden Rahmenbedingungen zu identifizieren, und fünf existierende Herdenmodelle hinsichtlich ihres Potentials bewertet. Wesentliche Ansprüche an zukünftige Herdenmodelle sind, dass diese in der Lage sein sollten, den Wettbewerb um Ressourcen innerhalb einer und zwischen verschiedenen Tierspezies, das Fressverhalten von Wiederkäuern und ihre Anpassungsmechanismen an sich ändernde Umwelteinflüsse erfassen zu können. Zudem müssen diese Modelle imstande sein, Emissionen tropischer Wiederkäuersystemen und den Einfluss politischer Ereignisse auf die Entscheidungsfindung der Landwirte berücksichtigen können. Die aktuellsten Modelle erfüllen nur zum Teil diese Voraussetzungen, insbesondere da sie Umwelteinflüsse z.B. durch Emissionen der tropischen Wiederkäuerhaltung nicht oder nur teilweise vorhersagen können. Um die Interaktion zwischen den Nutztieren und anderen Komponenten tropischer Agrarsysteme verlässlich darstellen zu können, wurde die Integration der herdenbasierten

Wiederkäuermodelle in andere biophysische und sozioökonomische Instrumente vorgeschlagen.

Als nächstes wurde, basierend auf einer Metaanalyse, ein semi-mechanistisches, konzeptionelles mathematisches Modell (**CMM**) ausgewählt und angepasst, mit dem Ziel, die freiwillige Futteraufnahme von Rindern unterschiedlichen Alters und verschiedener Klassen und über ein breites Spektrum der Fütterung in den Sub-(Tropen) hinweg verlässlich vorhersagen zu können. Wir fokussierten uns hierbei auf die freiwillige Futteraufnahme, da sie den Haupteinflussfaktor unter anderem für die Ressourcennutzung und Leistung der Nutztiere darstellt. Dafür wurden die CMM von Conrad et al. (1964) (**C1**) und Mertens (1987) (**M1**) ausgewählt und so modifiziert, dass daraus sechs (**C2 – C4** und **M2 – M4**) verschiedene CMM entstanden. Nur eines (C1) der ursprünglichen Modelle, die unter gemäßigten Bedingungen entwickelt wurden, kann die freiwillige Futteraufnahme von tropischen Rindern unter Stallbedingungen mit annehmbarer Genauigkeit vorhersagen (d.h. mit einer Verzerrung < 10% der beobachteten Futteraufnahme). Die physischen und physiologischen Regulatoren der freiwilligen Futteraufnahme von Rindern unter gemäßigten Bedingungen unterscheiden sich jedoch von denen, die unter tropischen Haltungsbedingungen gelten. Rinder in tropischen Produktionssystemen weisen beispielsweise im Vergleich zu solchen in gemäßigten Regionen eine höhere tägliche Kotausscheidung auf und besitzen eine höhere Kapazität zur Aufnahme von neutraler Detergenzienfaser (beides in kg/kg Körpergewicht). Das zuverlässlichste Modell für die Vorhersage der freiwilligen Futteraufnahme (d.h. M4) wird durch die Anpassung dieser relevanten Parameter erreicht und unter Beibehaltung der mittleren physisch und physiologisch regulierten freiwilligen Futteraufnahme, anstatt der niedrigeren Schätzwerte.

Aufbauend auf adäquaten Modellen zur Vorhersage der Futteraufnahme, wurde sich im nächsten Schritt mit Simulationsmodellen zur Erfassung der Leistung, der Ressourcennutzung und der möglichen Umwelteinflüsse (sub-)tropischer Wiederkäuerherden befasst. Dafür nutzten wir die zunehmende Verfügbarkeit von Daten über die biologischen Prozesse (sub-)tropischer Wiederkäuer aus und modifizierten das dynamische Herdenmodell LIVestock SIMulator (**LIVSIM**). Zu den Modifizierungen gehörten die Einbindung von M4 für die Vorhersage der freiwilligen Futteraufnahme, eine Erhöhung des Erhaltungsbedarfs an metabolisierbarer Energie (**ME**) von 0,488 auf 0,631 MJ ME/kg metabolischen Körpergewicht und die Nutzung geschlechtsspezifischer ME-Bedarfswerte für die Zunahme an Körpergewicht (MJ ME/kg Körpergewicht). Das daraus resultierende Modell ergab im Vergleich zu LIVSIM genauere Vorhersagewerte für die freiwillige Futteraufnahme, für das finale Körpergewicht und für die Milchleistung (d.h. relativer Schätzfehler <10 % des beobachteten Mittelwerts). Das

modifizierte LIVSIM ermöglicht eine bessere Vorhersage der Futteraufnahme und Leistung und somit der Ressourcennutzung und der Produktivität in der tropischen stallgebundenen Rinderhaltung.

Die hier vorliegende Arbeit zeigte, dass es notwendig ist, die aktuellen Herdenmodelle für Wiederkäuersysteme weiterzuentwickeln, um den identifizierten Anforderungen für zukünftige Simulationen gerecht zu werden. Anstatt der Entwicklung neuer Modelle kann hierbei auf die Anpassung existierender Modelle zurückgegriffen werden und dies unter Einbeziehen der Verfügbarkeit von quantitativen Daten auch für tropische Tierhaltungssysteme hinsichtlich relevanter biologischer Prozesse. Dieser Ansatz ist zukunftsweisend für die Bewertung der Produktivität und Ressourcennutzung sowie möglicher Managementstrategien für Wiederkäuersysteme in den (Sub-)Tropen.

CHAPTER I

I General introduction

I.1 Global agricultural systems and future food supply

An agricultural system is a set of interacting components (e.g., people, soils, plants, and animals) whose overall purpose is to produce crops and raise livestock for food, fibre, fuel, and related products using the earth's natural resources (Jones et al., 2016). Worldwide, agricultural systems are increasingly under pressure to satisfy the growing demand for agricultural and food products (Gouel and Guimbard, 2019; Jones et al., 2016; Santeramo et al., 2018). For example, the conjoint effect of population growth and rising incomes could increase global food demand by 47 % between the year 2010 and 2050 (Gouel and Guimbard, 2019). As such, agricultural systems in the (Sub-)Tropics will particularly come under pressure to produce more food since over 89 % of the 2.1 billion human population increase expected by 2050, will occur in these regions (UNDESA, 2019). These regions are also home to most lower-middle and low-income countries, where significant changes in food consumption patterns will occur due to urbanization (Warr, 2018). One such important change in food consumption patterns will be the increased human consumption of animal-based foods in the (Sub-)Tropics. For instance, the human intake of calories from animal food products like milk, meat and eggs could increase between 74 – 114 % by 2050 in the (Sub-)Tropics (Gouel and Guimbard, 2019).

Livestock production is already the largest land use sector on the earth (Herrero and Thornton, 2013), either directly via grazing pastures worldwide (~ 34.8 Mi. km^2) or indirectly via consumption of feed grains and fodder crops (Bruinsma, 2003). So, the need to increase supply of animal-based foods could pose further pressure on tropical agricultural systems. The supply of animal-based foods in the (Sub-)Tropics could be increased by improving animal productivity (i.e., increased outputs per unit input) and/or increasing the total herd sizes (Bruinsma, 2003). Livestock productivity in many developing regions (e.g., Sub-Saharan Africa and parts of Asia) remains low, so that current and projected production until 2050 will not satisfy the local demand (Herrero and Thornton, 2013). As such, an increase in number of different livestock species is envisaged across the (Sub-)Tropics (Turk, 2016). Ruminant livestock occupy the largest area of land globally compared to other livestock species (Pulina et al., 2017) and their population size could more than double by 2050 in the (Sub-)Tropics (Turk, 2016). Ruminant livestock also produce the highest quantity of animal-based protein (i.e., meat and milk) in human diets in this region (Pulina et al., 2017), and could thus play an important role in sustainably satisfying the high demand for animal-based products that will ensue in the (Sub-)Tropics (Tedeschi et al., 2015).

I.2 The role of ruminant livestock in sustainable supply of animal source foods in the (Sub-)Tropics

Existing scientific literature abounds with various definitions of sustainability, so that providing a comprehensive overview of what this term means is beyond the scope of the present thesis. For the present thesis, sustainable ruminant production systems are those that exist in the overlap of what present generations want for themselves and future generations, and what is biologically and physiologically feasible in the future (Vavra, 1996). Present and future trends suggest that humans in the (Sub-)Tropics want (as shown by consumption patterns) more animal-based protein in their diets (Turk, 2016). Accordingly, ruminant livestock produce milk, meat, and associated products that contribute to the food and income security of millions of people in rural and peri-urban areas of the (Sub-)Tropics (Gill, 2013). Regarding what is biologically and physiologically feasible, there is much these animals already offer and could further offer in the (Sub-)Tropics. Integrating ruminants in cropping systems (e.g., feeding crop residues while using manure to cycle nutrients) improves the efficiency of limited resource use and the fertility of cultivated soils (Lemaire et al., 2014; Russelle et al., 2007), and reduces the vulnerability of farmers to climatic and environmental risks (Thornton and Herrero, 2010). Also, ruminant livestock can reduce the pressure on human-edible foods in the (Sub-)Tropics by utilizing fibre-rich feed resources from non-arable areas better than monogastrics, to produce high quality foods for humans (Gill, 2013). As such, they could reduce the pressure for converting arable land to permanent crop or pasture land.

Ruminant livestock also produce significant amounts of green-house-gas emissions, which are important drivers of climate change (Gerber et al., 2013). They contribute to nutrient (e.g., nitrogen and phosphorus) leaching to aquifers and surface water (Janzen, 2011). Ruminant livestock could also affect food security negatively when they are fed rations containing products that are human-edible, and when arable land is converted to agricultural land for producing animal feed (Mottet et al., 2017). More so, they have a relatively low efficiency to convert feed into food compared to other species like poultry and pigs. Therefore, although ruminant livestock hold legit promises for feeding the expected human population by 2050 across the (Sub-)Tropics, ruminant livestock also pose justifiable worries on how to sustainably harness their potential.

The questions that begs to be answered is which and how ruminant livestock production systems in the (Sub-)Tropics can secure a net increase in productivity and concomitantly reduce its negative impact on the environment. Using conventional experimentation (i.e., animal feeding or management trials), several strategies have been identified for improving productivity of tropical ruminant production systems (Enahor et al., 2019). For example, the use of urea treatment to improve the nutritional quality of roughage feeds, and supplementation using hays, silages, leguminous shrubs, and agro-industrial by-products during dry seasons (Enahor et al., 2019) would positively impact ruminant production in the (Sub-)Tropics. In addition, such strategies will not only benefit ruminant performance, but could also contribute to reducing some environmental impacts associated with ruminant livestock (Table I.1). For example, improving the quality of diets by improving the digestibility of stovers reduces the methane output per ton of milk or meat produced (Table I.1). As such, fewer animals are needed to reach the same level of performance in the improved feeding scenarios than the baseline (i.e., normal feeding) scenario considered in Thornton and Herrero (2010).

However, evaluating strategies to improve the productivity of ruminant livestock in the (Sub-)Tropics as stand-alone solutions as reported above could misinform researchers that the net effect at system level is positive. For instance, crop residues like stovers make up about 20 % of the biomass produced globally (FAO, 2011). Thus, feeding crop residues ruminants could over time result in soil carbon depletion at plot scale if organic matter (e.g., manure) is not returned to the plots from which these residues are collected (Pulina et al., 2017). As such, the available strategies should not be explored in isolation to other components of the system as is often the case when using conventional field experiments (Hirooka, 2010). Furthermore, the interactions between the different components of tropical ruminant production systems do not always behave linearly as is often assumed by conventional experiments (Hirooka, 2010). Therefore, a systems approach is needed to incorporate the understanding from individual components of tropical ruminant livestock production systems to understand the behavior and responses from the overall system.

Systems science is a scientific framework that studies complex real world “systems” by simplifying reality into models (Jones et al., 2016; Turner et al., 2016). Here, interacting system components (e.g., those in livestock production systems) are defined by various disciplines in a virtual laboratory containing different models. Using simulation models, system components are allowed to interact with each other and their environments to replicate the overall behaviour of the system under study, to identify desired and undesired effects of components’ interactions. Simulation models have proven to be useful tools for capturing interactions between different components of agricultural systems and providing plausible outcomes for any intervention simulated (Jones et al., 2016). Thus, such modelling tools could be used to support decision-making for going forward with ruminant livestock production in the tropics.

Table I.1. Mitigation potential of different strategies on methane (CH_4) emissions for different ruminant livestock production systems in Central and South America (CSA) and Sub-Saharan Africa (SSA). (Adapted from Thornton and Herrero, 2010)

Mitigation strategy evaluated	CH_4 produced (kg) per t of		Number of bovines ($x10^6$) needed to satisfy demand in 2030 for		Mitigation of CH_4 via reduced bovine heads (Mt CO_2-eq)	Total mitigation potential (Mt CO_2-eq)
	Milk	Meat	Milk	Meat		
Diet intensification; stover digestibility improvement in SSA:						
Production systems[¶]: MR and MI.						
Baseline diet	58	1,958	490.1	490.1	-	-
100% adoption[†] of stover with 50% digestibility (from 40%)	25	548	177.0	114.3	-	61.6
23% adoption[†] of stover with 50% digestibility (from 40%)	50	1,634	418.1	403.6	-	14.2
Diet intensification; grain supplementation in SSA:						
Production systems[¶]: MRH, MRT, MIH, and MIT.						
Baseline diet	58	1,958	148.0	148	-	
100% adoption[†] - increased grain supplementation from 0.5 to 2 kg/head/d	18	395	39.3	22.5	22.1	22.1
23% adoption[†] - increased grain supplementation from 0.5 to 2 kg/head/d	49	1,598	123.0	119.1	5.1	5.1
Changing large ruminant breeds; in CSA and SSA:						
Production systems[¶]: LG (meat) and MRH, MRT, MIH, MIT (milk).						
Local breeds	31	713	363.3	172.8	-	-
100% adoption[†] of crossbreds	26	568	171.6	77.8	19.5	19.5
29% adoption[†] of crossbreds	30	671	307.7	145.2	5.6	5.6

[¶] MR: mixed crop-livestock rain-fed systems, MI: mixed crop-livestock irrigated systems, MRH: mixed crop-livestock rain-fed systems in humid and sub-humid systems, MRT: mixed crop-livestock rain-fed systems in tropical highland systems, MIH: mixed crop-livestock irrigated systems in humid and sub-humid systems, MIH: mixed crop-livestock irrigated systems in tropical highland systems and, LG: rangeland-based systems; [†] adoption refers to the proportion of total milk and meat production in 2030 that results from the option implemented.

I.3 Modelling ruminant livestock systems in the (Sub-)Tropics

A model is a simplified mathematical representation of a system used for understanding, explaining, and/or improving the overall system represented (Murthy, 2003; Sayama, 2015). The use of models for projection and exploratory studies is well established in the literature (Antle et al., 2017; Reilly and Willenbockel, 2010; Schmitz et al., 2014; Stromberg et al., 2007). On the one hand, properly developed and validated models can be cost-efficient and rapid tools to test hypotheses and establish the effect of various management strategies on the behavior of parts or the entire livestock system being simulated (Herrero, 1997). Due to the wide scope of management strategies that models can explore, they can complement conventional experimentation where the costs and time required make it impossible to study the various strategies available (Herrero, 1997). Also, compared to conventional experimentation, creating models encourages researchers to explore across disciplines beyond their specific expertise at different spatial and temporal scales (Janzen, 2011). For example, an animal nutritionist may have to interact with an agronomist to understand how various crop management strategies will influence the quality of the residues obtained. In addition, constructing models plays an important role in exposing knowledge gaps, and highlighting aspects of a system that researchers understand the least (Janzen, 2011; Tedeschi et al., 2015).

On the other hand, the use of models is also associated with certain drawbacks. Simplifying a complex system in a model can be very time consuming and expensive due to the computational and staff infrastructure required (Krishnan et al., 2017). Also, developing models often requires considerable skills in statistics and programming which many livestock scientists may not possess. Another issue associated with developing models is the validation process required. Model validation is an important requirement for acceptance of any model but this process is quite challenging for agricultural systems in the (Sub-)Tropics due to the lack of required (i.e., quantity and quality) data. Ergo, the above challenges must be carefully addressed before embarking into model development and improvement for a specific system.

Several types of model structures exist and the choice of each depends on the purpose for which it will be used.

I.3.1 Types of model structures

Models can assume different structures as per the behaviour of the parameters considered for the system being simulated (Sayama, 2015). Three models structure groups exist including deterministic or stochastic, dynamic or static, and empirical or mechanistic in nature (France and Thornley, 1984; Murthy, 2003). A model can assume only one type within each model structure group mentioned above, as well as combine types from the different model structure groups. While researchers can choose from the above model structures, the choice is often based on the simulation objectives and characteristics of the specific system under study (Haddon, 2011; Sayama, 2015).

I.3.1.1 Deterministic versus stochastic models

Deterministic models give specific predictions based on established relationships amongst states and events without any element of randomness e.g., the energy and protein requirements of animals (i.e., the same results will always be obtained from the same initial conditions) (Haddon, 2001). Contrarily, stochastic (also called probabilistic) models possess at least one parameter which varies in a random way over time e.g., simulating conception in livestock (i.e., the same set of parameters and conditions may lead to different outputs).

I.3.1.2 Dynamic versus static models

Dynamic (also called continuous) models simulate how the behaviour of a system changes with time (i.e., time-dependent changes in the state of the system) (Thornley and France, 2007). For example, to dynamically simulate the change in live-weight of cattle over a year, the present change in live-weight depends on the change that occurred in the previous time step (e.g., day or month) to determine the next change. In contrast, static (also called discrete) models make time independent predictions of the state a system (i.e., steady state). An example will be a steady-state herd model, where herd growth is assumed to be zero.

I.3.1.3 Empirical versus mechanistic models

Empirical (also called descriptive) models aim to describe the responses of a system, using statistical or mathematical equations ignoring the biological principles governing the system (Thornley and France, 2007). Empirical models are similar to deterministic models but the main difference is that the former could also accommodate parameters that are probabilistic in nature while the latter. An example of an empirical model is a regression model for predicting voluntary dry matter intake of animals. Mechanistic (also called explanatory) models simulate the processes regulating the system using mathematically equations that try to account for the biological principles governing how the system components function (Haddon, 2001). Such models when complete, can capture some of the causal relationships within the system. Voluntary dry matter intake of animals can also be predicted mechanistically.

It is important to note that a simulation model can assume different structures for different components of the system being modelled.

I.3.2 Tropical ruminant livestock systems and the state of available modelling tools

Ruminant livestock production systems in (Sub-)Tropics are complex and dynamic systems, made up of components which do not always interact linearly. These systems are very diverse, occurring in solely livestock production systems, landless livestock production systems, grassland-based livestock production systems, and mixed crop-livestock production systems (Steinfeld and Mäki-Hokkonen, 1995). Other factors like the prevailing climatic conditions, the natural resources available, and the socio-cultural contexts also distinguish tropical ruminant production systems from each other, but also from those in temperate regions (Oosting et al., 2014).

Several livestock models have been developed and published around the world that are relevant for tropical ruminant livestock production systems. Some simulate biological processes at a microscopic scale like protozoa dynamics in the rumen (Dijkstra, 1994), nutrient digestion and partitioning, and methane production in the animal (Kebreab et al., 2004) or more tangible processes like feed dry matter intake (Baumont et al., 2004). Other models can simulate only single species livestock production systems (Bourdon and Brinks, 1987), mixed crop-livestock systems (Bell and Moore, 2012; Rufino et al., 2009), and pastoral systems (Baumont et al., 2004; Hahn et al., 2005). The different models also operate within a wide range of temporal scales including 0.01 day (Dijkstra, 1994) to a monthly (Rufino et al., 2009) time step. As such, there is a wide array of ruminant livestock models developed at disparate levels (i.e., rumen, animal, herd, and farm) that can be employed for studying ruminant livestock production systems in the (Sub-)Tropics.

To adequately assess productivity and the associated impacts of different ruminant management strategies in the (Sub-)Tropics using models, the herd level of farm organisation should be the focus of simulation. First, herd productivity is not equal to the sum of the productivity of individual animals in a herd (Pittroff et al., 1992). Certain performance traits like animal body-weight and product quality traits (e.g., fat content of milk) can be easily observed on individual animal level whereas others like fitness traits (i.e., survival and reproductive performance) are best measured at herd level (Pittroff et al., 1992). Second, the herd level of production systems’ organisation can permit modellers to capture the adaptive capacity of ruminant production systems in the face of changing climatic conditions and societal demands (Nozières et al., 2011). For example, combining different ruminant species (e.g., goats and cattle) in a herd can allow for better use of various feed resources owing to differences in feeding behaviours of the animals. This would then result in a higher productivity for the multispecies herd than a single-species herd. Therefore, simulating the herd level will permit modellers to identify the joint and interactive effects of ruminants in tropical production systems.

While several models are relevant for studying tropical ruminant production systems, most of them were developed either using ruminant feeding recommendations for animals in temperate regions or for feeding and husbandry conditions in temperate regions. The feeding recommendations most commonly used for ruminants in the (Sub-)Tropics include those developed for the British (AFRC, 1993), American (NRC, 2001), and French (INRA, 2018) production systems. However, ruminant livestock production systems in the (Sub-)Tropics differ from those in temperate regions, as to the types of animals kept, their nutritional requirements, and the environmental conditions that prevail (Chizzotti et al., 2007; Oliveira, 2015). These differences imply that, the feeding recommendation systems employed in ruminant herd models used in the (Sub-)Tropics may differ from the reality and thus lead to poor model predictions. In addition, using ruminant models (e.g., Baumont et al. (2004)) developed for production systems in temperate regions to simulate tropical systems often requires the use very detailed input data (e.g., protein fractions of different feeds). Yet, such detailed data is often lacking for tropical ruminant livestock systems (Otte and Chilonda, 2002). Therefore, existing ruminant herd models need to be adapted to feeding and husbandry conditions in tropical regions and the input data requirements simplified to facilitate the use of such models in the (Sub-)Tropics.

I.4 Objectives and research hypotheses

The fact that ruminant models developed using ruminant feeding recommendations for animals in temperate regions are used in tropical systems shows that the fundamental biological processes simulated are similar. Building new models specific for tropical ruminant livestock systems will be cost- and time-expensive efforts that simply duplicates efforts (Herrero, 1997). As such, to avoid duplicating efforts and maximise the resources available to researchers, existing ruminant herd models should be screened and the most suitable ones adapted to simulate ruminant systems in the (Sub-)Tropics.

Consequently, the main research objectives of the present thesis were to:

1. assess the suitability of existing ruminant livestock herd models to predict feed resource use, potential outputs (e.g., milk and manure) and associated environmental impacts of ruminants in the (Sub-)Tropics (Chapter II); and
2. improve the adequacy (i.e., accuracy and precision) of a selected ruminant herd model to simulate the use of resources and the potential outputs from different ruminant production systems in the (Sub-)Tropics (Chapters III and IV).

Accordingly, it was hypothesized that:

1. existing ruminant livestock herd models used in the (Sub-)Tropics are still inadequate to holistically assess feed resource use, potential outputs, and associated environmental impacts for different ruminant production systems; and
2. the adequacy of herd models to predict feed resource use and the potential outputs from different ruminant production systems in the (Sub-)Tropics can be improved by adapting the models to feeding and husbandry conditions in these regions.

I.5 Thesis outline

Chapter II focuses on Sub-Saharan Africa as a hot spot for population growth and vulnerability to climate change, as well as being home to the largest ruminant livestock herds world-wide. As such, the literature was reviewed to elucidate future modelling needs for evaluating the consequences of intensifying the predominantly grassland-based ruminant livestock systems in the region. In addition, five state-of-the-art ruminant livestock herd models were critically appraised based on the modelling needs identified. Then, suggestions were made on how to improve the next generation of models for holistically evaluating intensification options for grassland-based ruminant livestock systems in Sub-Saharan Africa.

In Chapter III, different semi-mechanistic models for predicting voluntary dry matter intake of stall-fed cattle were modified and evaluated. Voluntary dry matter intake was the focus, because it is the main determinant of animal productivity, and thus adequately simulating it across diverse tropical ruminant production systems is a requirement for estimating herds' feed resource use and productivity. These models were modified and evaluated using results published in studies performed under typical feeding and husbandry conditions in the (Sub-)Tropics.

In Chapter IV, a selected ruminant livestock herd model (i.e., the LIVestock SIMulator (**LIVSIM**)) was adapted and modified to: (i) improve the accuracy of feed resource use and performance (i.e., milk and body-weight changes) predictions for feeding and husbandry conditions in the (Sub-)Tropics; and (ii) reduce input data requirements for using the LIVSIM to simulate ruminant production systems in the (Sub-)Tropics. Moreover, the modified LIVSIM was evaluated using meta-data from a stall-fed feeding trial with dairy cattle in Ethiopia.

Then, in Chapter V, the general relevance of the findings made within the present thesis with respect to modelling tools used for studying sustainable intensification and expansion of ruminant livestock systems in the (Sub-)Tropics was assess. More so, the limitations of the present thesis are highlighted in the latter chapter and conclusions are drawn based on findings from the preceding chapters (i.e., II – IV).

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CHAPTER II

II Modelling sustainable intensification of grassland-based ruminant production systems: a review[Ŧ]

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Abstract

Intensifying grassland-based ruminant livestock systems (**GRLS**) in the African Guinea Savanna could contribute to food and income security of the increasing African population. Grassland-based ruminant livestock models (**GRLM**) may be useful to holistically assess the efficacy and sustainability of different intensification options. Therefore, we evaluated how adequately existing GRLM address future modelling needs required for assessing how sustainable and resilient different GRLS intensification options are relative to dynamic socio-economic, political, cultural, and environmental conditions.

Key aspects future GRLM should thus address include, inter- and intra-species competition for resources, feeding behaviour of ruminant livestock and their adaptive capacity to changing environmental conditions, emissions from GRLS, and the role of policy on farmers' decision-making. Current GRLM adequately simulate GRLS productivity, but only partly address proposed modelling needs. To improve these GRLM, coupling to or integration in modelling tools focusing on neglected issues and research on interrelationships between diverse GRLS components are suggested.

Keywords

African Guinea Savanna; Grassland; Livestock intensification; Modelling; Ruminants

II.1 Introduction

Global human population is expected to increase from 7.6 billion people currently to about 9.7 billion people by 2050 (UNDESA, 2017), with about half the increase to occur in developing countries (Thornton et al., 2009). Correspondingly, global demand for food and especially animal-derived food products (e.g., meat and milk) will sharply increase due to a simultaneous rise in per-capita income in these countries (Delgado, 1999). This increase in food demand will be particularly high in Sub-Saharan Africa. Here, the sub-tropical and tropical African Guinea Savanna (**AGS**), which covers about 600 million hectares, is considered a key resource for intensifying food production in the region (Morris et al., 2009). Within this context, grassland-based ruminant livestock systems (**GRLS**) could play an increasing role in enhancing food security by converting inedible, fibre-rich feed resources (in particular from underutilized and non-arable areas) to high-quality food products (Gill, 2013). This would therefore further contribute to food security of millions of rural and peri-urban smallholders, significantly increase their income earnings, and reduce the competition in natural resource use for food, feed, or fuel production. Yet, GRLS in the AGS are challenged by ongoing climate change, overgrazing, and progressive conversion of grassland to cropland, urban settlements, and industrial areas in recent years (Foley et al., 2011). Such conversions are commonly associated with widespread loss of available grazing areas and thus of grassland ecosystem productivity and functioning (e.g., biodiversity conservation, carbon sequestration, water storage, and filtration). Moreover, efficiency of resource use (e.g., in kg meat or milk per unit of feed, land, or water) by livestock in GRLS is low (Herrero et al., 2013), emphasizing the great scope as well as urgent need for their sustainable intensification (i.e., increasing productivity of crop and livestock farming while minimizing possible negative socio-economic, political, cultural, and environmental impacts which might be associated with these intensification processes). While several intensification options such as the use of more adapted livestock breeds (Thornton et al., 2011) or shifts in type of production systems (Thornton et al., 2011) including a closer integration of crop and livestock farming (Udo et al., 2011) have been suggested, their sustainability is yet to be evaluated.

Modelling tools enable researchers to simulate the non-linear interrelationships between multiple (agro-) ecosystem components at large temporal and spatial scales (Dixon, 2011; Reips, 2000). Therefore, these tools could allow for comprehensive evaluation of the effectiveness and sustainability of intensification options for GRLS under changing socio-economic, political, cultural, and environmental conditions. Many widely accepted models in use today were developed between the late 1980s and early 2000s (Jones et al., 2016; Snow et al., 2014) to address research foci that arose at that time. Although these models have been refined and amended to increase their modelling capacity, current research needs associated to new socio-economic, political, and cultural trends and environmental challenges may not yet be adequately captured in the models' simulations. Moreover, their simulation potential was limited by the data management and information technology tools available then (Antle et al., 2017). Data processing and modelling capacities have greatly advanced over the last decade, allowing for higher computational efficiency and speed, improved data storage capacity, and enhanced ability to model adaptive behaviour of systems (Nussinov, 2015).

Hence, the aim of this review was to assess the suitability of existing grassland-based ruminant livestock production models (**GRLM**) to holistically evaluate the sustainability of different GRLS intensification options. More specifically, the objectives were: (1) to identify future modelling needs for evaluating the consequences of intensified resource use in GRLS in the AGS under changing socio-economic, political, cultural, and environmental conditions; (2) to critically appraise whether existing GRLM can adequately address these modelling needs; and (3) based on the models' limitations, suggest needs and options for future models' improvement to allow for holistic evaluation of possible implications of the intensification of GRLS and of their contribution to food and income security of people in the AGS.

II.2 Methodological approach

To identify future modelling needs, we adopted the fundamental dimensions of sustainability (i.e., economic, social, cultural, and environmental dimensions) according to Hansmann et al. (2012) and Soini and Birkeland (2014) as the guiding framework for assessing whether or not existing GRLM can holistically assess the sustainability of intensification options for GRLS in AGS. Using this guiding framework, a comprehensive literature search was conducted using the Scopus, Google Scholar, and google search engines to identify the appropriate literature highlighting questions to be answered as per intensification of GRLS and also which modelling tools have been used so far within the literature. The search key words and phrases used in gathering literature included combinations of the following: grasslands, ruminants, intensification, livestock, models, modelling simulations, pastoral, bio-physical, socio-economic, policy, and environmental impacts. After the search, other relevant literature were identified by following up on related papers suggested in Science direct (http://www.sciencedirect.com/) and reference sections of the literature reviewed. The search resulted in 150 articles, books, book sections, and reports downloaded based on their titles and abstracts. These literature sources were then screened to identify future modelling needs with respect to sustainable intensification of

GRLS. Also, within the literature downloaded, a total of 33 models were identified for further evaluation.

Due to the large number of biophysical and agricultural models already published, some exclusion criteria were set to identify models to be evaluated for this review. A model was excluded if: (1) it was not a ruminant model (i.e., it focused only on simulating plant, soil and/or climate processes, or socio-economics); (2) it was not a grassland model or GRLM (i.e., to ensure that only models that fit the grassland context were evaluated); (3) the identified model had no citation in Scopus or Google Scholar (i.e., to ensure that all models reviewed had some minimum level of acceptance by the scientific community); and (4) the documentation of the model was completely inaccessible (i.e., to avoid a wrong or biased review of such models). After application of the exclusion criteria, six models were retained of which five were selected for appraisal in light of the future modelling needs identified in this review.

II.3 Modelling needs for assessing sustainable intensification options in grassland-based ruminant livestock systems

The GRLS are complex systems that comprise several components, which are self-organized in a hierarchy, interact non-linearly, and are influenced by the dynamic socio-economic, political, cultural, and environmental conditions of the AGS (Figure II.1). As such complexity can be expected to further increase in the future due to continuing GRLS diversification and greater spatiotemporal variation in their environmental conditions and thus the availability of natural resources (e.g., land, feed, and water) (Hoffman and Vogel, 2008). Hence, at GRLS level, if future GRLM should holistically assess and predict the manifold consequences of suggested intensification options, they need to be able to account for the increasing complexity and diversity of GRLS. For instance, supplementing grazing livestock with crop by-products could improve animal performance and thus enhance food and income security of farm households (Ben Salem and Smith, 2008; Ngongoni et al., 2007). However, the efficacy of this management strategy is determined by, amongst other factors, the animals’ nutrient requirements as well as the availability and nutritional quality of both, the pasture herbage and supplement feeds, which are in turn affected by various factors such as changing climatic conditions (Hoffman and Vogel, 2008; Thornton et al., 2009). Moreover, such a feeding strategy will modify manure amount and composition and therefore nutrient return to the grassland as well as quantity and quality of dung available for crop fertilization (Rufino et al., 2011; Saha et al., 2008), which would again influence soil fertility and thus yield and nutrient concentrations of food crops and their by-products (Delve et al., 2001).

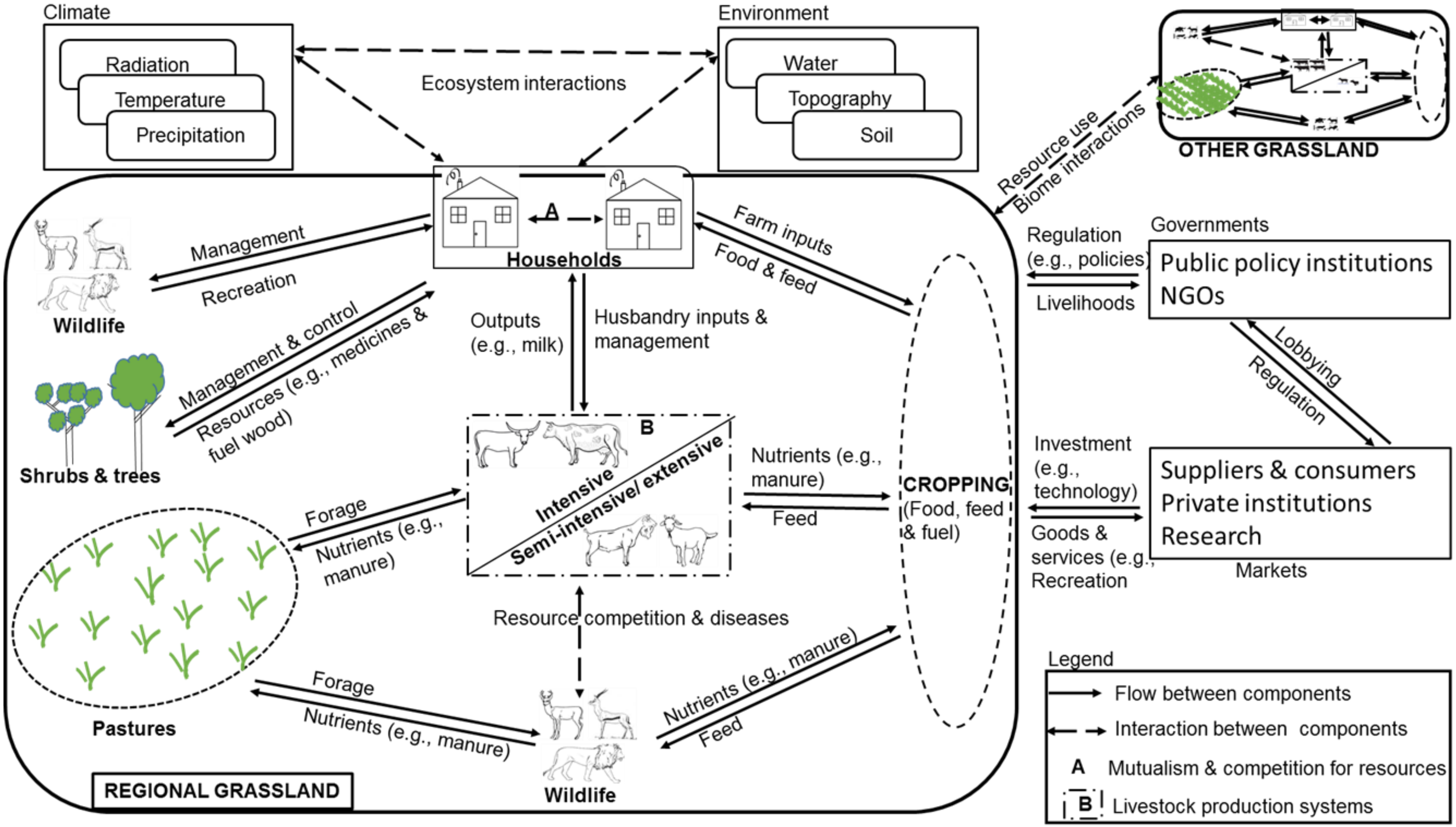

Figure II.1 Typical interactions between different components in the African Guinea Savanna grassland system.

Finally, farmers' management decisions depend on the required inputs and potential multiple outputs, and are embedded in the context of globalizing markets and government policies (Hobbs et al., 2008; Jayne et al., 2002), which for instance, determine market access and prices of animal products. Therefore, there is an urgent need to understand and consider the complex interactions between various components of GRLS when developing and assessing the sustainability of different intensification options (Sayama, 2015).

Furthermore, if future GRLM should adequately simulate the impacts of intensified resource use under changing socio-economic, political, cultural, and environmental conditions in the AGS, they need to capture the increasing diversity of GRLS. For instance, expanding cropland compounded with climate change will reduce available grazing areas, yet increase the quantity and variety of supplement feed resources such as crop residues or agro-industrial by-products available for livestock feeding (Thornton et al., 2011). As a result, GRLS may shift from nomadic to more sedentary systems with graded intensities in animal and grassland management and varying levels of integration of livestock with other GRLS components. Hence, if sustainable intensification options amongst those suggested for different GRLS under the dynamic conditions in the AGS should be identified, future GRLM should be able to simulate diverse GRLS along gradients of production intensity and crop-livestock integration so that appropriate comparisons can be made.

Similarly, future GRLM need to go beyond simulating single livestock species only (i.e., cattle in most cases), but also account for differences in intra- and interspecies resource use and competition at the livestock herd level (Ben Salem and Smith, 2008), as well as interactions between livestock and wildlife in the AGS. For instance, intensified grassland use and climate change may shift botanical composition of the grassland vegetation and favour proliferation of ligneous plants. These are more readily consumed by goats than by cattle, so that the implementation of mixed-species grazing could contribute to enhanced efficiency of available feed resources use, while preventing negative shifts in botanical composition of the grassland vegetation (Liu et al., 2015). Additionally, mixed-species grazing diversifies agricultural products, thereby improving food and income security and resilience of farm households (Udo et al., 2011). Moreover, future GRLM should be able to simulate the effects of multiple complementary livestock management strategies (e.g., feeding, grazing, health care, breeding) in order to identify which strategies are most sustainable for livestock in GRLS of the AGS, because a portfolio of effective options to improve animal nutrition, health, and performance in GRLS is available nowadays (Adjogo et al., 2018). As the effectiveness of these measures will differ for different animal species and categories (e.g., lactating, growing, non-producing animals), the GRLM should predict the effects of such management options separately for different animal sub-groups and thus provide an understanding how far these options can be sustainably employed for intensifying GRLS in the AGS.

Finally, if the multi-functionality of livestock and GRLS and the diverse socio-economic, cultural, and environmental implications of intensification strategies should be captured, future GRLM should simulate a wider variety of animal-related processes beyond those involved in conversion of feed or forage to animal products. For instance, there is increasing public concern about the emission of greenhouse gases from livestock and the contribution of grasslands to carbon sequestration and storage. Use of high-quality concentrate supplements to intensify GRLS may lower enteric CH_4 emissions per unit of product produced, but could increase total nitrogen release to the environment and modify partitioning in nitrogen excretion via urine or feces (Thornton et al., 2014). Therefore, it is paramount that future GRLM predict quantity and form of nutrient emissions in ruminant livestock in order to assess the consequences of intensification strategies on environmental emissions from GRLS. Additionally, there is an increasing public interest in improving animal health and welfare as well as quality and safety of food products (e.g., zoonotic diseases) from livestock farming (Clark et al., 2017), which should therefore also be reflected in GRLM. In this context, animal pests and diseases greatly impair productivity of GRLS and impose considerable risks for human health. Predicted changes in climatic conditions are expected to aggravate the occurrence and spread of animal diseases in the AGS (Jones et al., 2017). Thus, in order to capture these changes in the AGS, future GRLM should account for their effect on overall GRLS productivity and safety of animal-derived food products. More so, the socio-economic, political, and cultural aspects of GRLS intensification via the role of humans at market and policy levels could be further represented in future GRLM (Antle et al., 2017). For example, key services provided by the AGS could be evaluated (e.g., attaching a price tag) and linked to human decisions and policy tools using data management and information technology advances, so that GRLM can evaluate the socio-economic and cultural implications of GRLS intensification options (Lambin et al., 2000).

II.4 Existing grassland-based ruminant livestock models

II.4.1 LIVSIM model

The Livestock Simulator (**LIVSIM**) is a dynamic model, that simulates animal performance based on the animal's genetic potential and the availability and nutritional quality of feed using a 30-days time-step (Rufino et al., 2009). Different production units can be simulated, such as confined (e.g., dairy cows) and free-ranging (e.g., cows and small ruminants) ruminant systems. LIVSIM simulates maintenance requirements, animal growth, milk yield, amount of manure produced, greenhouse gases emissions, reproductive rates, and mortality in livestock systems. Furthermore, LIVSIM was coupled with a grazing routine based on functional relationships between animal behaviour and size, and intake and herbage mass (Rufino et al., 2011). Thus, LIVSIM simulated diet selection and feed intake restrictions during grazing (Rufino et al., 2011). It has also been used to evaluate the impact of feed management on life-time productivity of dairy cattle in the central highlands of Kenya (Rufino et al., 2009).

LIVSIM is also a part of the Farm-scale Resource Management Simulator (**FARMSIM**) model suite of the Department of Plant Sciences, Wageningen University (Tittonell et al., 2005). In addition to the LIVSIM, the FARMSIM model suite integrates a manure handling and storage module (**HEAPSIM**), a labour availability module (**LABOURSIM**), and a grass growth model (**GRASSSIM**) (Rufino et al., 2011).

II.4.2 SAVANNA ecosystem model

The SAVANNA model is a process-oriented model initiated in 1985 by Michael Coughenour in the context of the South Turkana Ecosystem Project in Kenya, but was further developed to simulate temperate grasslands (Coughenour, 1993). Detailed information on the model and its sub-models is provided in Coughenour (1993) and Coughenour et al. (2013). In brief, the model is spatially explicit and simulates the interactions between vegetation and herbivores in grasslands, shrublands, and forest ecosystems using a weekly time step (Boone et al., 2011; Coughenour, 1993). The SAVANNA model simulates carbon flows at four trophic levels (i.e., vegetation, herbivores, predators, and soil microbiota as decomposers). The above-ground vegetation and soil sub-models simulate plant biomass production and population dynamics, and soil organic matter dynamics, respectively. The ungulate sub-model simulates population dynamics, spatial distribution, herbivory, and energy balance of herbivorous wildlife and domestic ruminants (Coughenour, 1993). The wolf sub-model simulates the predation of wolves on wildlife and could be modified to serve as the basis for simulating predation on livestock.

The ungulate sub-model specifically simulates the following: (1) forage intake (i.e., intake rate depending on botanical composition (using preference weightings) and nutrient digestibility); (2) ungulate liveweight dynamics from the animals' energy balances estimated from forage intake and digestibility; (3) birth and death rates for different age and sex ungulate classes in response to the animals' body condition and different climate and weather scenarios; (4) spatial distribution of ungulate population in the study area depending on habitat suitability; and (5) effects of livestock herbivory on forage availability for herbivorous wildlife.

Further development of the SAVANNA model included the incorporation of the CENTURY's soil organic matter decomposition routine into its code and its coupling to the Pastoral Household Economics and Welfare Simulator (i.e., **PHEWS**) (Thornton et al., 2003) and the Spatially Integrated Disease Risk Assessment Model (i.e., **SIDRAM**) which simulates the spread and occurrence of animal diseases (Howe et al., 1999). In addition, it has also been coupled to the DECUMA model (Lesorogol and Boone, 2016), which predicts decision making and behaviour of pastoral household heads with respect to ecosystem services (Boone et al., 2011). These additions have tremendously extended the ability of the SAVANNA model, making it especially relevant for holistically assessing which intensification strategies are most sustainable for GRLS in the AGS.

II.4.3 PRY model

PRY is a steady-state livestock species independent model developed by Richard Baptist in 1988 (Pry, 2016; Baptist, 1987; Riedel et al., 2014). It combines deterministic and probabilistic modelling procedures to simulate livestock herds' population dynamics and productivity (PRY, 2016; Riedel et al., 2014). Using sex and age-specific rates for parturition, culling, and mortality, PRY estimates the size of the livestock population (Baptist, 1987). Total productivity is assessed using various parameters (Figure II.2) classified into two categories, including fitness traits and produce-related traits (Baptist, 1991). Then, based on these categories, PRY calculates annual animal productivity and gives outputs such as milk yields (Dickhoefer et al., 2012; Riedel et al., 2014).

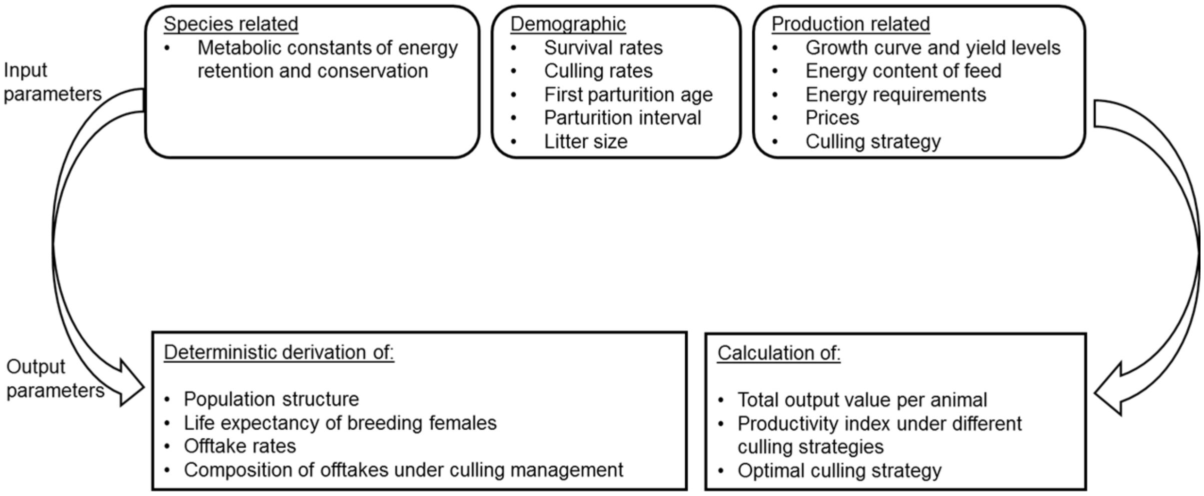

Figure II.2 Simplified structure of the PRY Herd Model, showing input and output parameters as well as data-processing steps (Riedel et al., 2014).

II.4.4 SPUR model

The **SPUR** (Simulation of Production and Utilization of Rangelands) model is a physically-based model developed in 1987 (Baker et al., 1993; Wight, 1983). It is dynamic, operates either at pasture or basin scales, and simulates the functioning of rangeland ecosystems and their responses to changing determinants and management practices (Foy et al., 1999). SPUR 2.4 is the latest version and comprises six sub-models, including a climate, hydrology, soil, plant, animal, and economic sub-model (Foy et al., 1999).

The climate sub-model stochastically generates climatic variables based on multiple, pre-entered weather parameters (e.g., daily precipitation and temperature) to drive the model. This component is closely related to the hydrology sub-model that simulates daily water balances and also includes a snowmelt routine. The plant sub-model, which covers both, crops and grassland vegetation, predicts forage availability for herbivorous livestock and wildlife, while also simulating the response of grassland vegetation to grazing (Wight, 1983). The economic sub-model of SPUR 2.4 focuses primarily on livestock outputs. It simulates the economic benefits from growing herd sizes or animal liveweight gains due to improved animal management and rangeland use on a monthly basis.

The animal sub-model covers herbivorous livestock and wildlife for which it simulates herbage selection and consumption based on changes in sward characteristics and animal preferences, as well as liveweight changes and reproductive rates (in livestock only) (Foy et al., 1999). Although the modelling objectives were not different from those of earlier versions of SPUR, SPUR 2.4 is more adequate than the previous versions for assessing different intensification strategies suggested for GRLS (Hanson et al., 1999). For example, linking it to the FORAGE model of Baker et al. (1992) simulating the animal-plant interface, and to the Colorado Beef Cattle Production Model (Bourdon and Brinks, 1987), that deterministically predicts changes in herd structure, intake, growth, lactation, and losses due to death, allows SPUR 2.4 to simulate different herd management and grazing strategies under different grassland conditions (Hanson et al., 1999).

II.4.5 Frame-based model

This model follows the “frames” modelling paradigm and combines several independent models into different frames (i.e., one model per frame) to represent distinct states of complex systems dynamically rather than spatially (Hahn et al., 1999; Starfield et al., 1993). This frame-based model was constructed for typical semi-arid savannah ecosystems to simulate vegetation (i.e., grasses and bushes) and livestock (i.e., cattle and goats) dynamics and was first tested in Southern Africa. Detailed information on the model is presented in Hahn et al. (1999).

In brief, the model is composed of six frames representing six specific vegetation states (Figure II.3), within which livestock are produced. Though the frames employ different time steps in simulating different processes, the outputs are given on a yearly basis divided between the rainy and the dry seasons.

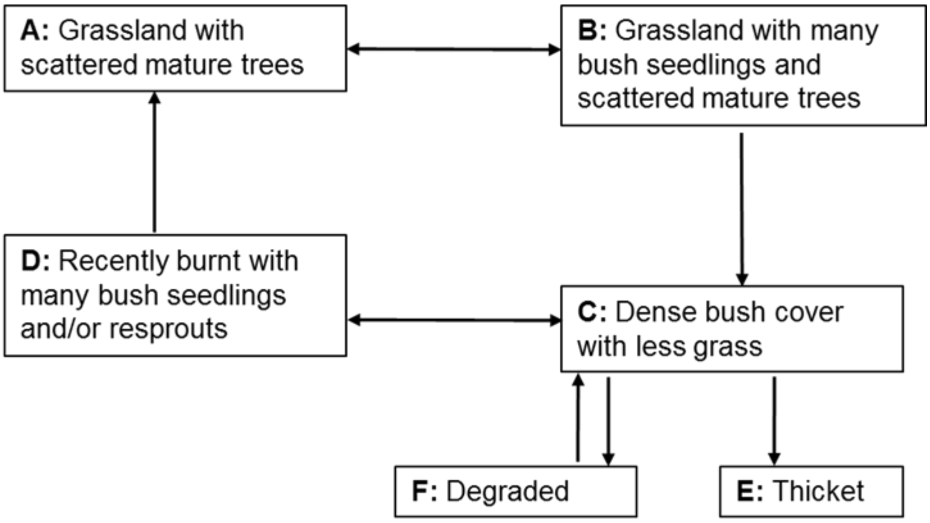

Figure II.3 Frames representing different grassland vegetation states and switches in the model of Hahn et al. (1999).

The model's frames are driven by a set of external (i.e., rainfall, frost, and bush fires) variables that are defined at the start of the simulation. The model also has internal variables (i.e., grass cover, bush seedlings, bush cover, and livestock populations), which are used to simulate key processes within each frame (Hahn et al., 1999). The total dry matter intake of each animal and total milk yield (for cattle) are estimated in a separate model called the "Production system model" (Richardson et al., 1998), based on the liveweight, physiological and nutritional status of the animal, and the quantity and nutritional value of forage available. These parameters are then inputted into the frame-based model and the performance of animals is predicted depending on their feeding strategy (i.e., grazing or browsing).

II.5 Comparative evaluation of reviewed livestock models

II.5.1 At grassland-based ruminant livestock system level

All GRLM reviewed focus predominantly on grassland and animal production dynamics within the GRLS, and have weaknesses regarding more holistically assessing GRLS and possible options for their intensification. In view of a holistic assessment of intensification options suggested at GRLS level, the GRLM are here evaluated based on (see section 3) their ability (i) to simulate a large diversity of GRLS; (ii) to capture the linkages and interactions between different GRLS components; and (iii) to reflect the multi-functionality of GRLS for sustainably intensifying agriculture in the AGS.

The most suitable of the five models reviewed for addressing the aforementioned modelling needs identified (see section 3) at GRLS level are the SAVANNA and SPUR models. Both models simulate livestock and wildlife within extensive GRLS and capture the linkages to the household, climate-driven changes in the quantity and nutritional value of the grassland vegetation and other feed resources over time, and can reflect the multi-functionality of livestock and GRLS beyond food and economic returns (Table II.1). However, both models are not applicable to a diversity of GRLS and in particular not to mixed crop-livestock systems, because they rather focus on extensive, purely grazing-based livestock systems. Nevertheless, the SAVANNA model is better suited to holistically simulate intensification of GRLS than the SPUR model, because it allows for simulation of multiple livestock species, grazing management based on a set of animal behavioural choices, implicit human herd management decisions (i.e., based on scenarios defined and not decisions from the model), and the contribution of GRLS to crop production through the supply of animal manure and use of crop residues as animal feed.

In terms of the diversity of GRLS, only LIVSIM and PRY can simulate a broad range of GRLS across a gradient of intensification (i.e., from extensive or pure grazing to intensive or zero-grazing systems). However, as PRY cannot simulate changes in GRLS over time due to its steady-state nature, it is less suitable for modelling consequences of an agricultural intensification at system level under increasingly variable socio-economic, political, cultural, and environmental conditions.

At GRLS level, none of the reviewed models can account for the role of either the policies driven by various stakeholders, who are a key component of GRLS (Figure II.1), nor of changing market situations. Yet, land tenure regulations, provision of social amenities, or the privatization of rangelands in the AGS by multinationals are, for instance, known to restrict pastoral land use systems and to favour their conversion to sedentary GRLS (Degen, 2011; Kamara et al., 2004; Korf et al., 2014), which in turn will alter natural resource use and GRLS productivity. Hence, if the socio-economic, political, and cultural consequences of suggested options for intensifying GRLS in the AGS should be adequately investigated, aspects relating to policies and markets need to be included in future GRLM.

Table II.1 Synopsis of model properties and simulation foci of reviewed grassland-based ruminant livestock production models

Model properties	**Grassland-based ruminant livestock models**[a]				
	LIVSIM[b]	**SAVANNA**	**PRY**	**SPUR**[c]	**Frame-based**
Type	Dynamic & mechanistic	Dynamic process -oriented	Static & deterministic	Dynamic	Dynamic
Time step	Monthly	Weekly	None	Monthly	Yearly[d]
Scale	Herd	Herd	Herd	Herd	Herd
Spatially explicit	Yes	Yes	No	Yes	Yes
Program language	Matlab 7.0.4	FORTRAN modules	R-program[e]	FORTRAN modules	Pascal program
Species simulated	Dairy cows & SR	Wild-life, cattle & SR	Cattle, SR, etc[f].	Cattle & Wild-life	Cattle & goats
Production system	Intensive & extensive	Extensive	Intensive & extensive	Extensive	Extensive
Coupled to other models	Yes	Yes	No	Yes	Yes
Simulation capacity					
Greenhouse gases	(Yes)	No	No	No	No
Manure production	Yes	(Yes)	Yes	No	No
Parasites & diseases	No	(Yes)	No	No	No
Forage-animal interface[g]	Yes	Yes	No	Yes	Yes
Predation	No	Yes	No	No	No
Inter-livestock competition	(Yes)	Yes	No	(Yes)	(Yes)
Impact of human decisions	(Yes)	Yes	Yes	Yes	Yes
Feed quality over time	No	Yes	No	No	No
Performance	Yes	Yes	Yes	Yes	Yes
Wild-life-livestock interactions	No	(Yes)	No	(Yes)	No
Economic returns	No	Yes	Yes	Yes	Yes
Policy regulations	No	No	No	No	No

[a] The synopsis given above applies primarily to the animal/livestock (i.e., Cattle, SR (i.e., goats and sheep) and wild-life) module of each model.

[b] LIVSIM (i.e., Livestock Simulator) is the livestock module within the FARMSIM model.

[c] SPUR (i.e., Simulation of Production and Utilization of Rangelands).

[d] Yearly for the Frame-based model is the time step for the overall outputs since the frames use different time steps.

[e] PRY uses R-programming for its latest version as earlier versions were Excel-based; (Yes) means the process is not simulated directly but inferred using data generated by the model.

[f] etc. refers to other animal species such as pigs, cattle, camels, guinea pigs, and many others.

[g] this interface basically refers to grazing (i.e., how the animal takes in food)

II.5.2 At livestock herd level

To holistically assess intensification options at herd level, the GRLM are here evaluated based on (see section 3) their ability (i) to model the reproductive and productive performance of livestock herds; (ii) to predict inter- and intra-species competition in and efficiency of natural, human, and financial resource use by livestock and wildlife; and (iii) to simulate animal health status and environmental impacts in GRLS as affected by environmental conditions and livestock management strategies.

All reviewed GRLM can predict reproductive and productive performance of livestock herds and therefore their potential contribution to the food and income security of farm households, which was expected, because they were primarily developed to simulate herd performances for specific livestock production systems. However, although the livestock herd level is already well represented in the reviewed GRLM, there is need to validate and refine the prediction approaches for some of the underlying processes, so that they can adequately simulate potential options for GRLS intensification. For example, the expected shifts in abundances of browse trees or shrubs, forage grasses, and forage legumes in (semi-natural grasslands due to rising atmospheric carbon dioxide levels (Thornton et al., 2014) will greatly affect plant-animal interactions and the ability of different livestock species to utilize available feed resources. In this line, further research is needed to understand diet selection of animals under grazing conditions in the AGS and to implement respective prediction approaches in GRLM. Such research is essential to reveal the true carrying capacity of the AGS, to assess the efficacy of grazing and livestock management options to sustainably intensify GRLS and increase their resilience to variable socio-economic, political, and environmental conditions, as well as to evaluate their implications for other grassland ecosystem functions such as being a habitat for local wildlife populations. In this line, all the GRLM reviewed can simulate resource use by different livestock species, breeds, and age or physiological state groups, but only the SPUR and SAVANNA can simulate the competition between livestock and herbivorous wildlife.

Furthermore, only SAVANNA simulates pests and diseases associated with livestock (Table II.1). In view of climate change and particularly the rising ambient air temperatures, pests and diseases will increasingly hamper productivity of GRLS (Jones et al., 2017) and represent an even greater risk for human health in the future (Naicker, 2011). Consequently, future GRLM should consider the spread and implications of important livestock pests and diseases. Moreover, except LIVSIM, none of the other four models simulate greenhouse gases and nutrient emissions associated with GRLS (Table II.1), although such environmental impacts should be quantified, if sustainability of intensification options for GRLS in the AGS shall be adequately and comprehensively assessed.

Hence, overall, LIVSIM appears to be the most suitable GRLM at herd level amongst those reviewed for assessing intensification options. It not only already simulates intra- and inter-species resource use and competition (except wildlife), feed intake of domestic ruminant species depending on the quantity and nutritional value of available feed resources, and the associated herd productivity, but also greenhouse gas and nutrient emissions from GRLS, which was a main limitation for all other models evaluated.

II.6 Outlook

Future GRLM could serve as very important tools for scientists from different disciplines to assess options for intensifying GRLS in the AGS and provide informed inputs to different stakeholders for decision-making at different levels. For holistic evaluation of possible implications of GRLS intensification and their contribution to food and income security of people in the AGS, coupling or integration of current GRLM to other models or model elements focusing on complementary GRLS components and processes (e.g., environmental impacts) is suggested to enhance their overall simulation capacity (Table II.1). In this line, SAVANNA (e.g., Thornton et al. (2003) for socio-economic aspects of pastoral livestock systems) or LIVSIM (e.g., Tittonell et al. (2005) for mixed crop-livestock systems) are already components of larger model interfaces. Such coupling efforts would encourage cooperation between modellers, reduce duplication of effort within GRLS research (Ahuja et al., 2002), and facilitate the creation of more comprehensive and accessible datasets which are currently unavailable due to the data being non-existent or scattered amongst different research institutions. For instance, socio-economic, political, and cultural concerns could be addressed in GRLM via coupling with agent-based models, which can simulate the economic behaviour of producers in relation to environmental processes and government policies, such as MPMAS (Berger, 2001) or DECUMAS, which has previously been used accordingly in pastoral systems (Boone et al., 2011). Similarly, for environmental impacts, coupling GRLM with an existing model that accurately predicts rumen fermentation and nutrient partitioning in ruminant livestock may allow more adequate simulation of greenhouse gases emissions from GRLS. Hence, the integrated mathematical dairy cow nutrient partitioning model was developed to evaluate the environmental impacts of dairy farming (Kebreab et al., 2004). This model combines four dynamic sub-models: a rumen model (Dijkstra, 1994), a CH_4 production model (Mills et al., 2001), and each a phosphorus and a nitrogen partitioning model (Kebreab and Vitti, 2005) and could thus be coupled to LIVSIM, SPUR, or SAVANNA to better account for such environmental impacts of GRLS in the AGS. However, improved understanding of underlying biophysical and socio-politico-cultural processes, and in particular of the interrelationships between various GRLS components, is essential for future conceptual and technical development of such coupled or integrated model suites and thus for holistic evaluation of the sustainability of different intensification options for GRLS in the AGS.

Finally, modellers need to choose between soft-coupling (which allows independent development of individual models and thus flexibility) and hard coupling (which slows the development and testing of individual model components) (Marohn et al., 2013). Yet, the over-arching challenge that must be over-come to successfully couple GRLM to other models is that of interoperability (i.e., how and in what format data exchanges between models happen) (Riley et al., 2004). Over-coming interoperability involves logical and correct data exchange, which requires technical computational skills that may often be lacking with agricultural and natural scientists. Also, communication and cooperation across scientific disciplines can be severely impeded simply by semantics and this problem should not be over-looked in the context of coupling models. Addressing these issues could facilitate model coupling or integration between different experts and thus contribute to improving future GRLM for holistic assessment of intensification options for GRLS in the AGS. However, model coupling should be done in such a way that the models stay in touch with reality rather than becoming too complex and thus exclusive for experts' use only.

II.7 Conclusions

Future GRLM should capture the increasing diversity, complexity, and multi-functionality of livestock and GRLS in order to reflect their sustainability, resilience, and possible contribution to food and income security of livestock-keeping households in the AGS. Consequently, the potential impact of different intensification strategies would be more quantifiable using the improved GRLM and thereby provide a more informed basis for decision-making at different farm management to policy levels on how to sustainably intensify GRLS in the AGS.

If future GRLM should adequately simulate the impacts of intensified resource use under changing socio-economic, political, cultural, and environmental conditions in the AGS, several important processes should be considered in GRLM such as the inter-and intra-species competition for resources (including wildlife), the (selective) feeding behaviour of ruminant livestock and their adaptive capacity to changing environmental conditions, the environmental emissions from GRLS, as well as the role of policy and global markets in farmers' decision-making. Current GRLM focus more on simulating GRLS productivity and only partly address these modelling needs. Amongst the five reviewed GRLM, SAVANNA and LIVSIM appear most promising at farm system and livestock herd level, respectively, for assessing available options for intensifying GRLS. Their coupling or integration with complementary modelling tools could facilitate simulation of complex interrelationships between diverse components of GRLS and thus the assessment of options for their sustainable intensification under increasingly variable socio-economic, political, cultural, and environmental conditions in the AGS.

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CHAPTER III

III Predicting dry matter intake using conceptual models for cattle kept under tropical and subtropical conditions[1]

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Abstract

Using empirical models to predict voluntary dry matter intake (**VDMI**) of cattle across production systems in the (Sub-)Tropics often yields VDMI estimates with low adequacy (i.e., accuracy and precision). Thus, we investigated whether semi-mechanistic conceptual mathematical models (**CMM**) developed for cattle in temperate areas could be adopted and adjusted to adequately predict VDMI of stall-fed cattle in the (Sub-)Tropics. The CMM of Conrad et al. (1964) (**C1**) and Mertens (1987) (**M1**) were identified and adopted for their simplicity in reflecting physico-physiological VDMI regulation. Both CMM use two equations that estimate the physiologically and physically regulated VDMI and retain the lower VDMI prediction as actual VDMI. Furthermore, C1 was modified by increasing the daily average faecal dry matter output from 0.0107 to 0.0116 kg/kg body-weight, yielding the modified model C2. For M1, the daily neutral detergent fibre intake capacity was increased from 0.012 to 0.0135 kg/kg body-weight and the daily metabolizable energy requirements for maintenance from 0.419 to 0.631 MJ/kg$^{0.75}$ body-weight, whereas the metabolizable energy requirements for gain was reduced from 32.5 to 24.3 MJ/kg body-weight gain, yielding the modified model M2. Lastly, also the mean of the physically and physiologically regulated VDMI rather than the lower of both estimates was retained as actual VDMI to generate the models C3 (from C1), C4 (from C2), M3 (from M1), and M4 (from M2). The eight CMM were then evaluated using a dataset summarizing results from 52 studies conducted under (sub-)tropical conditions. The mean bias, root mean square error of prediction (**RMSEP**), relative prediction error (**RPE**), and concordance correlation coefficient (**CCC**) were used to evaluate adequacy and robustness of all CMM. The M4, C2, and C1 were the most adequate CMM (i.e., lowest mean biases [0.07, -0.22, and 0.14 kg/animal and day, respectively], RMSEP [1.62, 1.93, and 2.0 kg/animal and day, respectively], and CCC [0.91, 0.86, and 0.85, respectively]) and robust of the eight CMM. Hence, CMM can adequately predict VDMI across diverse stall-fed cattle systems in the (Sub-)Tropics. Adjusting CMM to reflect the differences in feed quality and animal physiology under typical husbandry conditions in the (Sub-)Tropics and those in temperate areas improves adequacy of their VDMI predictions.

Keywords

Conceptual mathematical models; Dry matter intake; Model comparison; (Sub-)Tropics; Cattle

III.1 Introduction

Dry matter (**DM**) intake prediction in beef and dairy cattle production systems in temperate countries has received much attention and resulted in the development of several DM intake prediction models (Conrad, 1966; Forbes, 1983; Kahn and Spedding, 1984; Mertens, 1987; Allen, 2000; Forbes, 2007a,b). These DM intake prediction models differ in complexity, ranging from simple empirical to complex mechanistic models that account for different factors affecting DM intake regulation in ruminants.

Empirical DM intake models use statistical concepts to identify relationships that best describe the sampled population, at the expense of the underlying mechanisms that regulate DM intake (Amerdal, 2005; Oliveira and Ferreira, 2016). Consequently, changing the sampled population for which the model was fitted reduces the robustness and adequacy (i.e., accuracy and precision) of the model's prediction. Conversely, mechanistic prediction models are more population-independent, because they predict DM intake by describing the processes that regulate DM intake in ruminants. Therefore, mechanistic DM intake models are usually more robust than empirical models, while also providing more adequate predictions across different cattle populations (Haddon, 2001). An alternative to both, empirical and mechanistic models for predicting DM intake in cattle, are conceptual mathematical models (**CMM**). The CMM like the mechanistic dry matter intake prediction models are more population-independent than empirical models. However, CMM use simpler mathematical equations (i.e., semi-mechanistic) and fewer parameters (mainly parameters that have a biological definition) than mechanistic models (which often attempt to simulate all processes) to describe DM intake regulation in cattle (Mertens, 1987).

Although such a wide array of options exists, the empirical models are those mainly used to predict voluntary dry matter intake (**VDMI**) of cattle in farming systems in the (Sub-)Tropics (Souza et al., 2014; Oliveira and Ferreira, 2016). Yet, there is an increasing need to be able to predict VDMI across the diverse cattle production systems in the (Sub-)Tropics. Applying the empirical models across the diverse geographical contexts and cattle production systems in the (Sub-)Tropics significantly reduces the adequacy of VDMI predictions (Souza et al., 2014). While mechanistic VDMI models can be applied across different cattle production systems in the (Sub-)Tropics, they remain impractical due to the considerable data details required as model inputs (e.g., passages rates of feeds) (Amerdal, 2005; Ingvartsen, 1994). Consequently, using the population-independent CMM may be a promising option for predicting VDMI across the very diverse cattle production systems in the (Sub-)Tropics. Nevertheless, the adequacy of predictions from CMM and their robustness to predict VDMI across different cattle production systems in the (Sub-)Tropics has not yet been determined.

Accordingly, the present study aimed at evaluating whether CMM can adequately predict VDMI of stall-fed cattle kept under typical (sub-)tropical husbandry conditions and how robust the CMM are under these conditions. This was achieved by: (1) identifying different CMM used for stall-fed cattle in temperate countries and adjusting them for differences in feed quality and animal physiology parameters related to VDMI of stall-fed cattle in the (Sub-)Tropics; and (2) evaluating and comparing the adequacy of predictions and robustness of the identified and adjusted CMM in predicting VDMI of stall-fed cattle in the (Sub-)Tropics using data obtained from published feeding trials. It was hypothesized that (i) CMM can adequately predict VDMI of stall-fed cattle across different cattle production systems in the (Sub-)Tropics; and (ii) adjusting CMM to reflect the differences in feed quality and animal physiology between stall-fed cattle kept under typical husbandry conditions in the (Sub-)Tropics and those in temperate regions yet improves the adequacy of VDMI predictions and the robustness of the CMM.

III.2 Materials and methods

III.2.1 Identification and selection of conceptual mathematical models

The CMM were identified through a systematic online search (i.e., using Scopus, Google search, and Google Scholar search engines) and by examining bibliographies of journal articles, conference proceedings, and textbook sections. The searches were performed in English using the key phrases including: CMM for DM intake prediction in cattle; mathematical models for VDMI prediction in cattle; semi-mechanistic models for DM intake prediction in cattle; and VDMI prediction in cattle. Thirteen models were identified from the search and a CMM was selected for further evaluation, if (i) it considered animal and feed parameters (e.g., animal performance and feed chemical composition) to predict VDMI. This criterion arose because several authors (Faverdin et al., 1995; Allen, 2000; Forbes, 2007a) have suggested the use of both, animal and feed parameters for predicting VDMI rather than just either of them to obtain more robust VDMI models; and (ii) model parameters required were easily available (e.g., fibre fraction rather than fill units (Hyppola and Hasunen, 1970) and body-weight (**BW**) rather than animal frame size) on farms or reported for cattle experiments in the (Sub-)Tropics.

Two models including the CMM of Conrad et al. (1964) (**C1**) and Mertens (1987) (**M1**) were then retained to evaluate the adequacy of VDMI estimates for stall-fed cattle in the (Sub-)Tropics and the CMM robustness.

III.2.1.1 Conrad conceptual mathematical model

The C1 was developed in the United States and used data from 114 trials with stall-fed lactating cows to estimate the model's equation parameters that play a role in physical and physiological regulation of VDMI (Conrad et al., 1964). Conrad et al. (1964) employed the "first limiting factor" theory (Forbes, 2007a) and proposed that for feeds with an apparent total tract dry matter digestibility (**DMD**) ≥ 667 g/kg DM, VDMI is driven by the animal's energy requirements (i.e., physiologically regulated VDMI), whereas for feeds with a DMD < 667 g/kg DM, VDMI is controlled by the rate of passage from and the quantity of undigested material in the digestive tract (i.e., physically regulated VDMI). Therefore, according to Kahn and Spedding (1984), the predicted voluntary dry matter intake (**pVDMI**) retained for C1 equals the lower of the two VDMI estimates of either the physiologically or physically regulated VDMI.

Physiologically regulated VDMI (kg/animal and day) was estimated as follows (Kahn and Spedding, 1984):

$$VDMI = \frac{Digestible\ DM}{DMD} \qquad (1)$$

where digestible DM is the digestible dry matter intake requirement of the animal (kg/animal and day), and DMD the apparent total tract digestibility of dry matter expressed as a fraction per unit of diet dry matter intake.

Accordingly, the digestible DM intake requirements (kg/animal and day) were calculated (Kahn and Spedding, 1984) as:

$$Digestible\ DM = 0.526 + 0.333 * FCM + 0.056 * metabolic\ BW + 3.08 * BW\ change \qquad (2)$$

where FCM is the 4%-fat-corrected milk yield (kg/animal and day), metabolic BW the animal's metabolic body-weight (kg$^{0.73}$), and BW change the daily change in body-weight (kg/animal and day). The FCM yield (kg/animal and day) was calculated using the equation from Gaines (1928):

$$FCM = (0.4 * Milk\ yield) + (15 * Fat) \qquad (3)$$

where FCM is the 4%-fat-corrected milk (kg/animal and day), Milk yield the milk yield (kg/animal and day), and Fat the total fat yield in milk (kg/animal and day).

Physically regulated VDMI (kg/animal and day) was estimated using the following equation (Kahn and Spedding, 1984):

$$VDMI = \frac{0.0107 * BW}{1\text{-}DMD} \tag{4}$$

where 0.0107 is the average faecal dry matter output (kg/kg body-weight) as determined in lactating dairy cattle by Conrad et al. (1964), BW the animal's body-weight, and DMD the apparent total tract digestibility of dry matter expressed as a fraction per unit of ingested dry matter.

III.2.1.2 Mertens conceptual mathematical model

The M1 was also developed in the United States and used data from several studies with dairy cows to estimate the model's equation parameters that contribute to regulating physically and physiologically driven VDMI. Additionally, similar to C1, M1 equally considers the lower of either the physiologically or physically regulated VDMI estimates as the pVDMI. Yet, in contrast to C1, M1 uses neutral detergent fibre (**NDF**) (i.e., as an indicator for rumen fill) rather than DMD of the feeds to derive physically regulated VDMI (Mertens, 1987). Moreover, M1 used the net energy rather than the digestible DM intake requirements to estimate the daily energy and nutrient requirements of each animal and from this to derive its physiologically regulated VDMI. The metabolizable energy (**ME**) requirement system from the Gesellschaft für Ernährungsphysiologie (GfE, 2001) rather than that of the National Research Council (NRC, 2001) was used in the present study, because it requires basic animal parameters that are readily available when working with cattle in the (Sub-)Tropics, thus reducing the need to make assumptions for unavailable parameters (e.g., empty BW of animals).

Therefore, physiologically regulated VDMI (kg/animal and day) was estimated as:

$$VDMI = \frac{ME_{req}}{ME_{diet}} \tag{5}$$

where ME_{req} is the total daily metabolizable energy requirements (MJ/animal and day) estimated according to the GfE (2001), and ME_{diet} the dietary metabolizable energy content (MJ/kg DM).

The ME requirements (ME_{req}; MJ/animal and day) for lactation, maintenance, activity, and BW gain were estimated according to the GfE (2001), as shown in Eq. 6:

$$ME_{req} = ((0.95 + 0.38 * Fat + 0.21 * Protein) * \frac{Milk\ yield}{k_l})$$

$$+ (0.420 * metabolic\ BW) + (\frac{13}{k_g} * BW\ gain) + 1 \tag{6}$$

where Fat is the milk fat content (g/100 g milk), Protein the milk protein content (g/100 g milk), Milk yield the milk yield (kg/animal and day), and k_l the efficiency of ME use for lactation (0.6). For daily ME requirements for maintenance 0.420 MJ per kilogram of metabolic BW ($kg^{0.75}$) were considered. The ME requirements for BW gain (kg/animal and day) were estimated using an energy content of 13 MJ/kg gain and an efficiency of ME use for gain (k_g) of 0.4. Lastly, ME requirement for daily activities (e.g., walking) were accounted for by adding 1 MJ/animal and day (i.e., the equivalent of 0.5 - 1 km horizontal displacement [Jenet et al., 2004] and 300 kg BW with the approximate mean being 1 MJ/animal and day; Eq. 6).

Physically regulated VDMI (kg/animal and day) was estimated according to Mertens (1987) as shown Eq. 7:

$$VDMI = \frac{NDF\ intake\ capacity}{NDF} \tag{7}$$

where NDF is the neutral detergent fibre concentration in the diet (kg/kg dry matter) and NDF intake capacity the neutral detergent fibre intake capacity (kg/animal and day), which was calculated as:

$$NDF\ intake\ capacity = 0.012 * BW \tag{8}$$

where BW is the animal’s body-weight (kg), 0.012 the maximum daily amount of neutral detergent fibre (kg/kg BW) that can be consumed by high-yielding lactating cattle fed high-quality diets (Mertens, 1985a).

III.2.2 Adjustment of conceptual mathematical models

To test whether adjusting CMM to reflect the physical (e.g., rumen fill capacity) and physiological differences between stall-fed cattle kept under typical (sub-)tropical husbandry conditions and those in temperate regions improves the adequacy of VDMI predictions and robustness of CMM, the C1 and M1 were modified to reflect (i) the effect of poorer quality diets offered to cattle in the (Sub-)Tropics than in temperate countries; (ii) the differences in ME requirements between cattle kept in temperate countries and the (Sub-)Tropics (Salah et al., 2014); and (iii) the “blended” rather than mutually exclusive effect of the physiological and physical mechanisms regulating VDMI under typical husbandry conditions in the (Sub-)Tropics (Forbes, 2007a).

III.2.2.1 Increased daily faecal output rate in the Conrad conceptual model

Genotype x environment interactions associated with diet quality play a major role in determining the physical and physiological differences observed between stall-fed cattle kept under typical husbandry conditions in the (Sub-)Tropics and those in temperate regions (Vercoe and Frisch, 1992). Forages offered to cattle kept under typical husbandry conditions in the (Sub-)Tropics often have a lower digestibility than those used under temperate conditions due to high concentrations of total fibre and lignin (Ibrahim et al., 1995). Several studies (Frisch and Vercoe, 1977, 1984; Detmann et al., 2014) have shown that when cattle kept under typical husbandry conditions in (Sub-)Tropics are offered low-quality feed *ad libitum,* their VDMI is higher than for similar cattle in temperate systems offered the same feed. Consequently, cattle kept under typical husbandry conditions in (Sub-)Tropics have to ingest more feed per kg BW and with this more indigestible feed material than those in temperate regions.

Thus, we increased the daily faecal DM output (C2) from 0.0107 to 0.0116 kg/kg BW to predict physically regulated VDMI as per the findings of Elliot and Fokkema (1961) who observed a faecal DM output rate in lactating cows on natural pastures Southern Africa of 0.0116 kg/kg BW and day).

III.2.2.2 Increased physical and physiological voluntary dry matter intake capacity in the Mertens conceptual model

The NDF intake capacity of cattle varies based on how much NDF is included in the diets they receive during the growth and development stages of their lives (Mertens, 1985a; 1987). As cattle in the (Sub-)Tropics are accustomed to consume fibre-rich diets, their daily NDF intake capacity could be as high as 0.0135 kg/kg BW (Mertens, 1987, 2009). Therefore, we increased the daily NDF intake capacity from 0.012 to 0.0135 kg/kg BW to create M2. Furthermore, Salah et al. (2014) suggested a higher daily ME requirement for maintenance (0.631 MJ/kg$^{0.75}$ BW) and a lower ME requirement for BW gain (24.3 MJ/kg BW gain) in cattle in the (Sub-)Tropics than for cattle kept in temperate regions. Consequently, we also increased the daily ME requirement for maintenance from 0.419 to 0.631 MJ/kg$^{0.75}$ BW and reduced the ME requirements for BW gain from 32.5 to 24.3 MJ/kg BW gain in M2.

III.2.2.3 Blending physiological and physical regulation of feed intake to predict dry matter intake

The C1 and M1 both assume that VDMI is either physiologically or physically regulated, and the regulatory mechanism that is first constrained determines the daily VDMI of the animal (Forbes, 2007a). Although this theory has been extensively used to predict VDMI, its assumption of mutually exclusive regulatory mechanisms of VDMI has already been challenged (Poppi, 1996; Forbes, 2007a). Therefore, a blending of the physiological and physical VDMI regulatory mechanisms was suggested as a more realistic approach

(Forbes, 2007a). Thus, we decided to take the mean of the physiologically and physically regulated VDMI as the pVDMI to create C3 (from C1), C4 (from C2), M3 (from M1), and M4 (from M2). As such, rather than just being determined by one VDMI regulatory mechanism, each regulatory mechanism contributes to the pVDMI proportionally to its importance for the conditions being simulated.

III.2.3 Evaluation of conceptual mathematical models

III.2.3.1 Meta-analysis

An extensive online literature search was conducted using the Google, Google Scholar, and Scopus search engines. The search phrases to start the literature search included: DMI of cattle in the (Sub-)Tropics, dairy cattle performance in the (Sub-)Tropics, smallholder dairy cattle farming, Napier grass, Calliandra supplementation, Leucaena supplementation, milk yield in smallholder cattle systems, improved feeding in cut-and-carry cattle systems, effects of supplementation on *Bos indicus*, concentrate supplementation in smallholder cattle systems, and digestibility of tropical feedstuffs. In addition, the bibliographies of identified journal articles, conference proceedings, and master and doctoral dissertations were examined to find further studies with relevant data.

Data from a study was included into the meta-data set, if the study: (1) had been conducted under stall-fed conditions in the (Sub-)Tropics; (2) was conducted with cattle *ad libitum*; (3) recorded at minimum the following required by the CMM: measured VDMI (kg/animal and day), corresponding milk yield (kg/animal and day) and its fat and protein contents (g/100 g milk), BW (kg), and BW changes (kg/animal and day), as well as the ME (MJ/kg DM), crude protein, and NDF concentrations (g/kg DM), and the DMD (g/kg DM) of each diet or constituents of the diets. In studies that lacked one or two parameters, we equally attempted to complete the missing information from similar studies in the same area whenever possible or else the study was not included into the meta-dataset.

III.2.3.2 *Meta-data set description*

Out of 114 studies identified in the present study, 52 studies were retained (i.e., based on the inclusion criteria given above) containing 231 dietary treatments and 1,679 animal observations. These studies were conducted in 17 countries of South and Central America, Africa, South East Asia, and Australia during the last 34 years. The animal categories within the meta-data set (i.e., bulls, calves, dry or lactating cows, heifers, and steers) belonged to 37 local and exotic cattle breeds, and their cross-breds. Moreover, the feedstuffs offered in the studies covered those commonly offered to stall-fed cattle in the (Sub-)Tropics such as tropical forage grasses, browses and legumes (fed fresh, as hays, or as silages), crop residues (e.g., stovers), different cereal grains, and agro-industrial food by-products.

Only 58 dietary treatments (i.e., out of the 231 dietary treatments used in this study) completely met the inclusion criteria; meanwhile, for the remaining 173 dietary treatments, at least one of the dietary or milk composition parameters were not reported. To complete the missing parameters, we searched online feed databases (e.g., Feedipedia (https://www.feedipedia.org) and studies done in the same geographical area that reported the missing value). In case milk fat and/or protein contents were not reported for the lactating cows, the information was obtained from online literature or cattle breeding society websites in the (Sub-)Tropics. A descriptive summary of the meta-data set is shown in Table III.1.

III.2.3.3 *Meta-data subsets*

To evaluate how robust (i.e., model accuracy for various datasets with different characteristics) the CMM are, we divided our meta-data set into 11 meta-data subsets with the following characteristics. Firstly, we separated the 231 dietary treatments from the meta-data set into five subsets for the different animal categories (n=dietary treatments) observed in the data (i.e., bulls [n=48], calves [n=16], cows [n=97], heifers [n=23], and steers [n=47]). Secondly, since the data was not normally distributed, the median values from the descriptive statistics (Table III.1) were used as thresholds for creating six other subsets from the 231 dietary treatments. The additional six meta-data subsets included high (n=115) and low (n=116) NDF concentrations (i.e., > 580 or ≤ 580 g/kg DM), high (n=116) and low (n=115) DMD (i.e., > 610 or ≤ 610 g/kg DM), and high (n=119) and low (n=112) VDMI levels (i.e., > 7.1 or ≤ 7.1 kg/animal and day).

Table III.1 Descriptive statistics for animal and diet parameters in the meta-data used in evaluating the eight conceptual mathematical models[1]

Parameter	n	Mean	SD	Maximum	Minimum	Median
Animal						
Body-weight, kg	231	289	119	591	32.5	285
Voluntary dry matter intake, kg/day	231	7.7	3.8	21	1.3	7.1
Body-weight change, kg/day	122	0.5	0.4	1.4	-0.9	0.5
Milk yield, kg/day	88	7.9	6.4	29.6	0.4	6.6
Milk fat, g/100 g milk	88	4.0	0.6	4.9	2.7	4
Milk protein, g/100 g milk	88	3.4	0.8	6.1	2	3.2
Days in milk (n)	88	78.6	64	261	1	61
Diet						
DM, g/kg as-fed	231	560	289	956	76.4	538
Crude protein, g/kg DM	231	111	36.9	241	36	108
Neutral detergent fibre, g/kg DM	231	556	129	786	180	580
Metabolizable energy, MJ/kg DM	231	8.8	1.5	13.4	4.2	8.7
Dry matter digestibility, g/kg DM	231	610	93.3	855	318	610

[1] n = number of observations considered for summarizing the specific parameter; DM = dry matter; SD =standard deviation.

III.2.3.4 Statistical evaluation of conceptual mathematical models

The eight CMM were all evaluated for their accuracy, precision, and robustness. The mean bias (kg/animal and day) was estimated as the first measure of model accuracy as follows (Cochran and Cox, 1992):

$$Mean\ bias = \sum_{i}^{n} \frac{(oVDMI_i - pVDMI_i)}{n} \qquad (9)$$

where $oVDMI_i$ is the observed voluntary dry matter intake (kg/animal and day) for animal group i, $pVDMI_i$ the predicted voluntary dry matter intake (kg/animal and day) for animal group i, and n is the number of pairs of the oVDMI and pVDMI being compared.

Also, the mean bias was expressed as a proportion of the observed voluntary dry matter intake (**oVDMI**; i.e., prediction bias) to ascertain whether the pVDMI was within the acceptable range of 10 % of the oVDMI according to Yungblut et al. (1981). Additionally, to identify the contribution of different sources of errors in the pVDMI, the mean square error of prediction (**MSEP**) can be considered the sum of the error due to central tendency, error due to regression, and error due to disturbance (Bibby and Toutenburg, 1977). The error due to central tendency is the error due to the difference between the oVDMI and pVDMI (i.e., overall bias) (Jensen et al., 2015). The error due to regression accounts for the error of unequal variation in pVDMI and oVDMI estimates, and measures the deviation of the least square regression coefficient from 1 (Jensen et al., 2015). Thus, if the variance in pVDMI is equal to that in oVDMI, the error due to regression is 0. Then, the error due to disturbance explains the variance in oVDMI that is not taken into account by a least square regression of the oVDMI on pVDMI (Jensen et al., 2015). To estimate the MSEP and its components described above, we fitted a mixed model (Eq. 10) according Jensen et al. (2015), which also considers a random effect due to study and thereby captures the error between treatments within a study.

$$oVDMI_i - pVDMI_i = \alpha + E(study_i) + \beta * \left(pVDMI_i - mean(pVDMI)\right) + \varepsilon_i \qquad (10)$$

where $oVDMI_i$ is the observed voluntary DM intake for diet i, $pVDMI_i$ the predicted voluntary DM intake for diet i, α the regression intercept, $E(study_i)$ the random intercept due to study i, β the regression slope, and ε_i the error term.

As such, the MSEP can be decomposed to its individual components using Eq. 11:

$$MSEP = EPB + EPB(study) + ED + ER \qquad (11)$$

where EPB is the error due to overall bias of prediction, EPB (study) the error due to the overall bias of prediction as a result of differences amongst studies included in the meta-data, ED the error due to deviation of the regression slope from unity, and ER the error due random variation.

The error due to overall bias of prediction and error due to deviation of the regression slope from unity quantify the systematic error. Meanwhile, the error due to the overall bias of prediction as a result of differences amongst studies included in the meta-data and error due random variation quantify the random error in the model (Bibby and Toutenburg, 1977), the former being unwanted and should account for a smaller proportion of the MSEP than the latter.

Furthermore, to quantify the error within each model's prediction, the root mean square error of prediction (**RMSEP**) and the relative prediction error (**RPE**) were estimated as described by Tedeschi (2006). Additionally, a weighted RPE was calculated (using the number of dietary treatments aforementioned for each meta-data subset) and used to evaluate the robustness of the CMM across different subsets of the meta-data. Also, the concordance correlation coefficient (**CCC**) as a combined measure of accuracy and precision was estimated and partitioned into a correlation coefficient (**ρ**) (i.e., precision) and a bias correction factor (C_b) (i.e., accuracy) (Lin, 1989). Lastly, the CMM were ranked from best to worst based on which CMM had the lowest RPE. All statistical analyses were performed using the software R (version 3.4.0, the R foundation for Statistical Computing, Vienna, Austria). The lme4 (Bates et al., 2015) and ggplot2 packages (Wickham, 2009) were employed for fitting the mixed models and plotting the box and residual plots in the models' evaluation.

III.3 Results

III.3.1 Observed versus predicted voluntary dry matter intake

The median pVDMI (kg/animal and day) from the C1 (7.5), C2 (7.9), and M4 (7.6) were not different ($p > 0.05$) from the median oVDMI (7.1 kg/animal and day) as shown by the over-lapping notches in Figure III.1. Meanwhile, median pVDMI from all other CMM (i.e., C3, C4, M1, M2, and M3) differed ($p < 0.05$) from the median oVDMI.

Also, pVDMI estimates from C1 – C4 were numerically greater than the oVDMI and pVDMI from M1 – M4. Lastly, the residual plots derived from applying all eight CMM on the meta-data showed no clear patterns and revealed a similar distribution of plotted points around the line at 0 for all the CMM (Figure III.2).

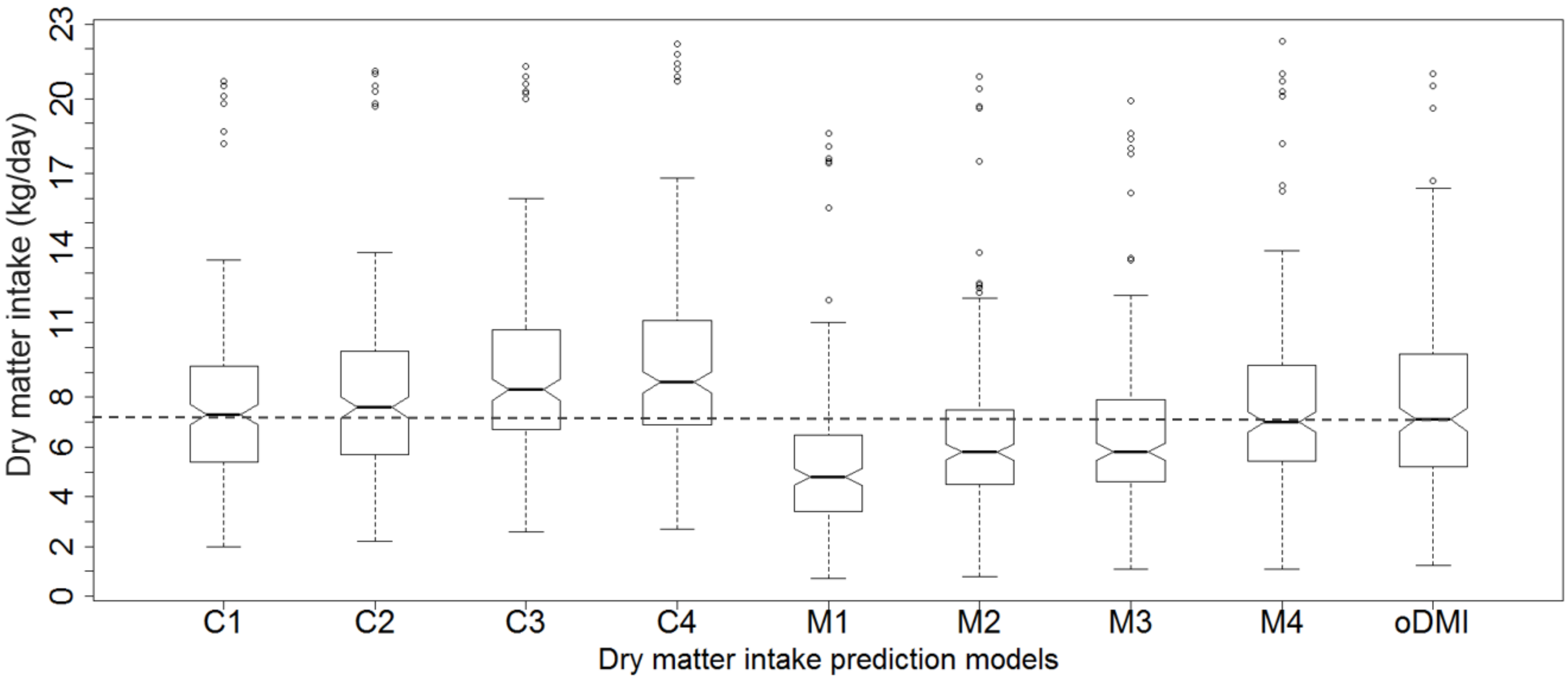

Figure III.1 Predicted relative to observed voluntary dry matter intake for eight models evaluated using meta-data from stall-fed cattle in the (sub-)tropics[1]

[1]C1= Conrad et al. (1964); C2 = Conrad et al. (1964) modified (modifications included an increase in the daily faecal dry matter output from 0.0107 to 0.0116 kg/kg body-weight); C3= C1 with average voluntary dry matter intake; C4 = C2 with average voluntary dry matter intake; M1 = Mertens (1987); M2 = Mertens (1987) modified (modifications included an increase in the daily neutral detergent fibre intake capacity from 0.012 to 0.0135 kg/kg body-weight and the metabolizable energy requirements for maintenance from 0.419 to 0.631 MJ/kg0.75 body-weight, and a decrease in metabolizable energy requirements for body-weight gain from 32.5 to 24.3 MJ/kg body-weight gain); M3 = M1 with average

voluntary dry matter intake; and M4 = M3 with average voluntary dry matter intake. Average voluntary dry matter intake describes a conceptual mathematical model where the mean of the physiologically and physically regulated voluntary dry matter intake is retained as the predicted voluntary dry matter intake rather than the lower voluntary dry matter intake estimates obtained from either of the two regulatory mechanisms. oVDMI = observed voluntary dry matter intake.

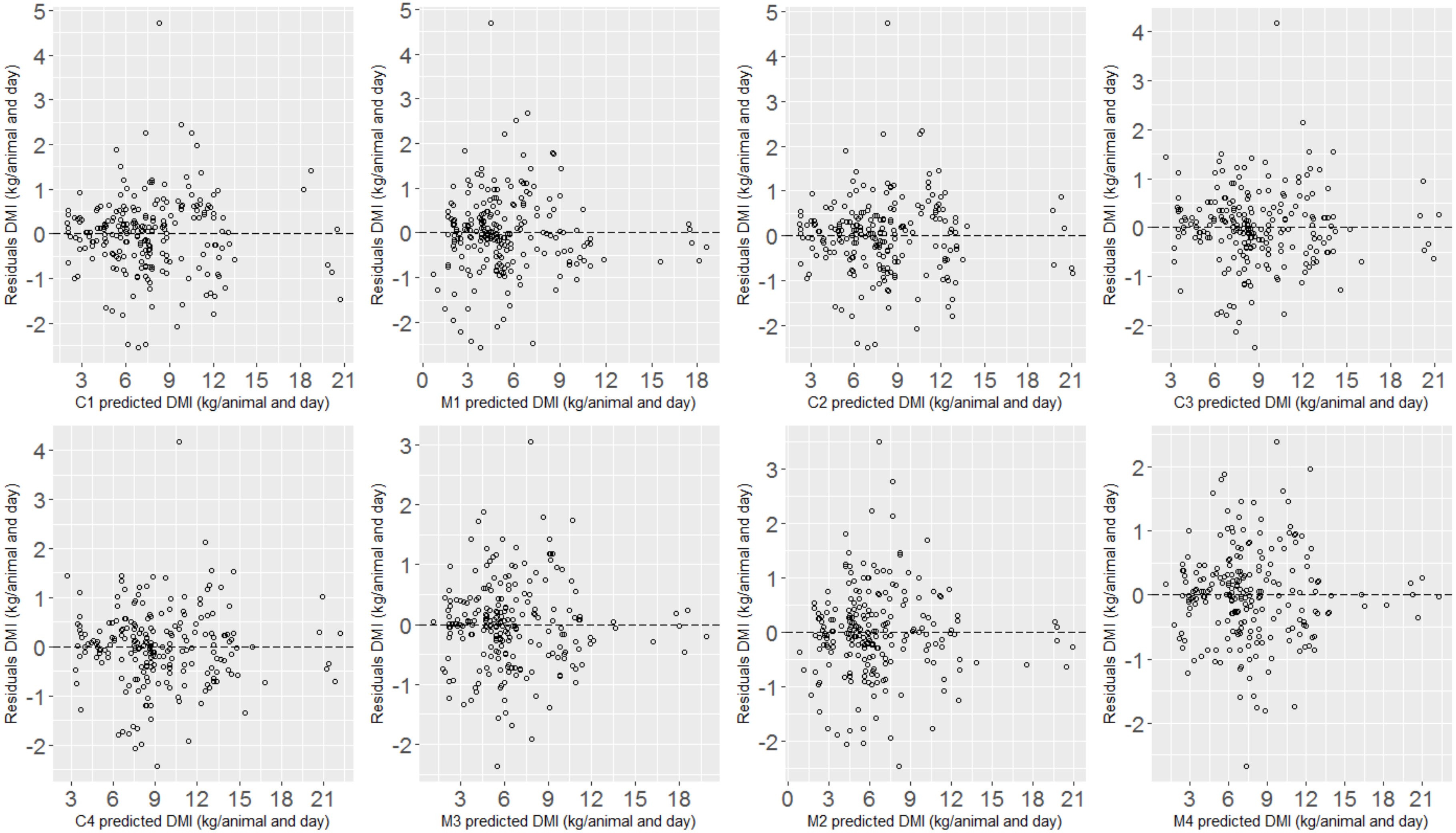

Figure III.2 Residuals versus predicted voluntary dry matter intake (VDMI) from eight conceptual mathematical models using meta-data from stall-fed cattle in the (sub-)tropics[1]

[1] C1= Conrad et al. (1964); C2 = Conrad et al. (1964) modified (modifications included an increase in the daily faecal dry matter output from 0.0107 to 0.0116 kg/kg body-weight); C3= C1 with average voluntary dry matter intake; C4 = C2 with average voluntary dry matter intake; M1 = Mertens (1987); M2 = Mertens (1987) modified (modifications included an increase in the daily neutral detergent fibre intake capacity from 0.012 to 0.0135 kg/kg body-weight and the metabolizable energy requirements for maintenance from 0.419 to 0.631 MJ/kg0.75 body-weight, and a decrease in metabolizable energy requirements for body-weight gain from 32.5 to 24.3 MJ/kg body-weight gain); M3 = M1 with average voluntary dry matter intake; and M4 = M3 with average voluntary dry matter intake. Average voluntary dry matter intake describes a conceptual mathematical model where the mean of the physiologically and physically regulated voluntary dry matter intake is retained as the predicted voluntary dry matter intake rather than the lower voluntary dry matter intake estimates obtained from either of the two regulatory mechanisms. oVDMI = observed voluntary dry matter intake.

III.3.2 Evaluation of the conceptual mathematical models

III.3.2.1 Accuracy and precision

The mean bias in pVDMI was smaller for C1 (0.14 kg/animal and day) than M1 (2.3 kg/animal and day), with MSEP for M1 (9.03) being more than twice as high than C1 (4.01) (Table III.2). The prediction bias was lowest for M4, C1, and C2 and greatest for C4 and M1. Over 60 % of the MSEP in pVDMI from M1 was inherent to the model performance, compared to 2 % for C1. Furthermore, partitioning the MSEP in pVDMI from C1 and M1 showed that 70 % and 26 % of MSEP, respectively resulted from bias in the oVDMI reported in the meta-data set. The RMSEP (3 kg/animal and day) in pVDMI from C1 was lower than M1. Consequently, RPE of pVDMI were ≤ 39 % and ≤ 26 % of oVDMI for M1 and C1, respectively. As such, CCC was greater for C1 (0.85) than M1 (0.69).

Increasing daily faecal DM output rate (g/kg BW) in C2 resulted in a higher mean bias, but in lower MSEP, RMSEP, and RPE and a higher CCC than in C1 (Table III.2). However, taking the mean of the physiologically and physically regulated VDMI as in C3 and C4 increased mean bias, MSEP, RMSEP, and RPE but lowered CCC. Similarly, all adjustments made for M2, M3, and M4 reduced mean bias, MSEP, RMSEP, and RPE, and increased CCC. While pVDMI from M4 had lowest mean bias, MSEP, RMSEP, and RPE and highest CCC of all eight CMM when applied to the whole meta-data set, pVDMI from M1 had highest mean bias, MSEP, RMSEP, and RPE and lowest CCC. In addition, partitioning of MSEP indicated that, except for M1, the largest proportion of MSEP of pVDMI from all other CMM was due to the bias in the studies included into the meta-data set.

III.3.2.2 Robustness of evaluated models

Although C1 and M1 had high RPE for several meta-data subsets, C1 had a lower weighted RPE than M1 across all the 11 meta-data subsets (Table III.3). C1 had the lowest RPE (< 23 %) for steers, cows, high VDMI, and high DMD subsets accordingly. Meanwhile, RPE were very high (≥ 35 %) for M1 pVDMI across all meta-data subsets.

Of the eight CMM evaluated, M4 had the lowest (22 %) and M1 the highest (39 %) weighted RPE (Table IV.3). The lowest weighted RPE were obtained in pVDMI from M4 for cows, high-VDMI, and low-NDF meta-data subsets by M4. Highest weighted RPE (82 %) was observed in pVDMI from C4 for the calves’ subset.

Table III.2 Statistical evaluation of eight conceptual models to predict voluntary dry matter intake using meta-data from stall-fed cattle in the (Sub-)Tropics[1]

Statistical measure	**Conceptual mathematical models**							
	C1	**C2**	**C3**	**C4**	**M1**	**M2**	**M3**	**M4**
Mean bias, kg/animal and day	0.14	-0.22	-1.19	-1.54	2.3	1.28	1.25	0.07
Prediction bias, % oVDMI	1.82	2.86	15.45	20.00	29.87	6.62	16.23	0.91
MSEP	4.01	3.74	4.66	5.74	9.03	4.82	4.42	2.64
Partitioning of MSEP, %								
error due to prediction bias	2.13	0.26	22.82	33.08	60.61	38.51	37.60	0.68
error due to prediction bias$_{studies}$	70.58	71.89	58.39	50.69	26.64	42.36	44.15	71.15
error due to regression slope ≠ 1	0.45	0.41	0.04	0.89	0.13	-0.79	1.22	0.10
error due to random variation	26.84	27.44	18.75	15.35	12.62	19.91	17.02	28.07
RMSEP, kg/animal and day	2.00	1.93	2.16	2.40	3.00	2.19	2.10	1.62
RPE, % oVDMI	26.08	25.19	28.09	31.19	39.12	28.57	27.37	21.13
CCC (0 to 1)	0.85	0.86	0.83	0.81	0.69	0.83	0.83	0.91
ρ	0.85	0.87	0.88	0.88	0.87	0.89	0.9	0.91
C_b (0 to 1)	0.99	1.00	0.94	0.92	0.80	0.94	0.93	1.00
Ranking	3	2	5	7	8	6	4	1

[1] C1 = Conrad et al. (1964); C2 = Conrad et al. (1964) modified (modifications included an increase in the daily faecal dry matter output from 0.0107 to 0.0116 kg/kg body-weight); C3 = C1 with average VDMI; C4 = C2 with average VDMI; M1 = Mertens (1987); M2 = Mertens (1987) modified (‡modifications included an increase in the daily neutral detergent fibre intake capacity from 0.012 to 0.0135 kg/kg body-weight and the metabolizable energy requirements for maintenance from 0.419 to 0.631 MJ/kg$^{0.75}$ body-weight, and a decrease in metabolizable energy requirements for body-weight gain from 32.5 to 24.3 MJ/kg body-weight gain); M3 = M1 with average VDMI; and M4 = M3 with average VDMI. Average VDMI describes a conceptual mathematical model where the mean of the physiologically and physically regulated VDMI is retained as the predicted VDMI rather than the lower VDMI estimates obtained from either of the two regulatory mechanisms. MSEP = mean squared error of prediction; RMSEP = root mean squared error of prediction; RPE = relative prediction error; CCC = concordance correlation coefficient; ρ = correlation coefficient estimate; and C_b = bias correction factor.

Table III.3 Evaluation of the robustness of eight conceptual models to predict voluntary dry matter intake (VDMI) using the relative prediction error (RPE; % of the mean square error of prediction) for different meta-data subsets from stall-fed cattle in the (Sub-)Tropics[1]

Data subsets (n)	**Conceptual mathematical models**							
	C1	**C2**	**C3**	**C4**	**M1**	**M2**	**M3**	**M4**
Bulls (48)	30	32	38	43	40	29	29	32
Calves (16)	65	63	77	82	36	33	32	31
Cows (97)	22	20	20	23	34	25	24	16
Heifers (23)	34	37	44	47	40	29	32	28
Steers (47)	17	17	21	26	47	30	29	18
Low DMD (115)	30	28	28	30	43	32	30	22
High DMD (116)	22	22	28	32	35	25	25	20
Low VDMI (112)	39	41	51	55	36	29	27	31
High VDMI (119)	21	18	18	21	37	26	25	17
Low NDF (116)	24	23	27	30	35	23	23	19
High NDF (115)	29	29	29	32	45	36	33	24
Weighted RPE	27	27	30	33	39	28	27	22
Ranking[2]	2	2	4	5	6	3	2	1

[1] number of dietary treatments considered for meta-data subset; C1 = Conrad et al. (1964); C2 = Conrad et al. (1964) modified (modifications included an increase in the daily faecal dry matter output from 0.0107 to 0.0116 kg/kg body-weight); C3 = C1 with average VDMI; C4 = C2 with average VDMI; M1 = Mertens (1987); M2 = Mertens (1987) modified (modifications included an increase in the daily NDF intake capacity from 0.012 to 0.0135 kg/kg body-weight and the metabolizable energy requirements for maintenance from 0.419 to 0.631 MJ/kg$^{0.75}$ body-weight, and a decrease in metabolizable energy requirements for body-weight gain from 32.5 to 24.3 MJ/kg body-weight gain); M3 = M1 with average VDMI; and M4 = M3 with average VDMI. Average VDMI describes a conceptual mathematical model where the mean of the physiologically and physically regulated VDMI is retained as the predicted VDMI rather than the lower VDMI estimates obtained from either of the two regulatory mechanisms. Low and high DMD = low and high DMD (≤ 610 and > 610 g/kg dry matter); low and high VDMI = low and high VDMI (i.e., ≤ 7.1 and > 7.1 kg/animal and day); Low and high NDF = low and high NDF (i.e., ≤ 580 and > 580 g/kg dry matter). All thresholds were determined based on the median values in the descriptive statistics. DMD = apparent total tract dry matter digestibility; NDF = neutral detergent fibre.

[2] The ranking is based on the weighted relative prediction errors shown in the table.

III.4 Discussion

III.4.1 Adequacy of the conceptual mathematical models

The most adequate and robust of the eight CMM (i.e., lowest MSEP, RPE, and highest CCC) were M4, C2, and C1 (in descending order as shown in Table III.2). While no consensus exists in the literature on the minimum level of adequacy required for satisfactory pVDMI estimates, Yungblut et al. (1981) in a study that tested the reliability of different VDMI prediction equations using data collected from 19 dairy herds, defined a satisfactory (i.e., accurate) pVDMI as one with a prediction bias ≤ 10 % of the oVDMI. Since Yungblut et al. (1981) used cattle herds with similar feeding and management regimes across herds, we suggest that achieving a prediction bias that is ≤ 10 % of the oVDMI will also be acceptable for the present study. The prediction bias in the pVDMI estimates from M4, C2, C1, and M2 were all < 7 % of the mean oVDMI compared to > 15 % prediction bias in pVDMI estimates from the other CMM (Table III.2). The low prediction bias observed in M4, C2, C1, and M2 pVDMI estimates corresponds with the low (all < 3 % of the MSEP) systematic error proportion observed in the MSEP in all but the M2 (< 37 % of the MSEP). Systematic errors are “one-sided” deviations from the observed value, that occur in a model due to inherent bias of the estimator parameters used, or poor simulation of the main processes regulating the variable being predicted (Meyer et al., 1989; Taylor, 1997). The small systematic error in the M4, C2, and C1, suggests that the physiological and physical regulation of VDMI were adequately simulated within the meta-data set. As such, the prediction bias observed in pVDMI from the latter three CMM resulted from random variation in oVDMI that cannot be accounted for by the CMM. It is however, unclear from our analysis why the low prediction bias in pVDMI estimates from M2 did not result into a corresponding small proportion for the systematic error. Nevertheless, the low prediction bias in pVDMI estimates and the small proportion of the MSEP due to systematic error from these three CMM shows that both, identified (C1) and adapted (C2 and M4) CMM can be used to predict VDMI satisfactorily across different stall-fed cattle production systems in the (Sub-)Tropics.

Yet, C3, C4, M1, and M3 did not meet the accuracy threshold suggested by Yungblut et al. (1981). The M1 had the highest MSEP of all models identified and evaluated, with > 60 % of its MSEP due systematic error compared to 22 % (C3), 34 % (C4), and 38 % (M3). The under-estimation (i.e., positive mean bias) of the VDMI by M1 could either be due to a poor estimation of the physiologically or physically regulated VDMI mechanisms when CMM developed in temperate countries are used without any adaptation for stall-fed cattle kept in the (Sub-)Tropics. Although, the modified CMM (C3, C4, and M3) had much lower systematic errors than the M1, about 20 % of the error in the pVDMI estimates from these three CMM resulted from weaknesses in the CMM. For C3 and C4, the increases in systematic error from C1 (2.5 % of MSEP) to 22 % and 33 % of MSEP suggest that the loss in adequacy lies in the changes made to C1, whereas the decreases from 60 % of MSEP (M1) to 38 % (M3) suggest that the changes made were not responsible for the poor adequacy of pVDMI estimates.

III.4.2 Robustness of the conceptual mathematical models

The robustness of the CMM was evaluated in the present study by how accurately (i.e., lowest RPE) they performed for the different meta-data subsets categories. Although the RPE was presented for the CMM over the entire meta-data set, it is a meaningful measure of model accuracy mainly in cases where the range of the observed and predicted values are small (Park and Stefanski, 1998) as in the case of the meta-data subset categories. As such, a CMM was considered robust for a meta-data subset category, if RPE was ≤ 20 % as recommended by Fuentes-Pila et al. (1996) who evaluated different equations for predicting VDMI of lactating Holstein cows fed total mixed rations.

The M4 resulted in satisfactory pVDMI estimates with RPE ≤ 20 % for five out of the 11 categories (i.e., cows, steers, high DMD, high VDMI, and low NDF). Instead, RPE of pVDMI were ≤ 20 % for only three categories (i.e., cows, steers, and high VDMI) for C2, two categories (i.e., cows and high VDMI) categories for C3, and one category (i.e., steers) for C1 (Table IV.3). Hence, M4 appears to be the most robust CMM, because it satisfactorily (RPE ≤ 20 %) predicted VDMI for more categories of the meta-data subsets than any other CMM. Additionally, the modified CMM (i.e., M4, C2, and C3) were most robust, suggesting that adjusting CMM to reflect the differences in feed quality and animal physiology between stall-fed cattle kept in the (Sub-)Tropics and those in temperate regions can improve their robustness. The highest RPE were observed for the calves (i.e., 82 % RPE for C4), heifers (i.e., 47 % RPE for C4), and bulls (i.e., 40 % RPE for M1), probably due to poor estimates of the physiologically regulated VDMI. In the present study, the ME requirements for BW gain and maintenance in cows (i.e., GfE, 2001; Salah et al., 2014) were applied to all animal categories; however in reality, the ME requirements per unit of BW gain and maintenance (i.e., per kg metabolic BW) vary for different animal categories within a herd (NRC, 1987; Flachowsky and Kirchgessner, 1998). Therefore, there is a need to determine and use more accurate values for ME requirements of different cattle categories in the (Sub-)Tropics and evaluate to which extent this can improve overall accuracy of pVDMI.

Furthermore, except for the M1, the CMM performed best for the high DMD (i.e., > 610 g/kg DM), high VDMI (i.e., > 7.1 kg/animal and day), and low NDF concentrations (i.e., ≤ 580 g/kg DM) categories. Thus, RPE was lowest for meta-data subsets whose feed and animal intake characteristics were similar to those of the datasets used by Conrad et al. (1964) and Mertens (1987) to develop their CMM. Hence, our results suggest that the CMM may not be completely population-independent, especially as some variable constants used in the CMM have been derived empirically (e.g., digestible DM and ME requirement estimates, faecal excretion rates, and NDF intake capacity). The lower RPE observed when using adjusted (i.e., M2 to M4, C2 to C4) as compared to adopted (i.e., M1 and C1) CMM shows that adjusting variable constants in CMM may make them more robust for predicting VDMI in cattle kept in the (Sub-)Tropics.

III.4.3 Adjustments made to the conceptual mathematical models

Based on the prediction bias (≤ 10 % of the oVDMI) and partitioning of the MSEP from the eight CMM evaluated in the present study, only M4, C2, and C1 (in descending order as shown in Table III.2) were adequate for predicting VDMI of stall-fed cattle in the (Sub-)Tropics. The adjustments in M4 included an increase in the daily NDF intake capacity and ME requirements for maintenance, a decrease in ME requirements per unit of BW gain, and retaining the mean of the physiologically and physically regulated VDMI as pVDMI. In C2, only the daily faecal DM output per kg BW was increased compared to the original CMM C1 from Conrad et al. (1964). It is important to note that the adjustments made to the CMM did not result in large changes or differences between oVDMI and pVDMI estimates and/or physically and physiologically regulated VDMI estimates, but rather small changes that affected the precision and accuracy of the pVDMI estimates.

III.4.3.1 Adjustments made to the Mertens conceptual mathematical model

Adjusting M1 resulted in more adequate (i.e., accurate and precise) VDMI predictions shown by the reduced mean bias, prediction bias, MSEP, and the increased CCC in pVDMI estimates from M2, M3, and M4 than in M1 as compared to those from M1. The prediction bias in pVDMI from M1 was > 29 % of the oVDMI, due to a considerable under-estimation of oVDMI and thus a large positive mean bias. In the (Sub-)Tropics, VDMI of stall-fed cattle is often limited by feeding high levels of fibre-rich roughages, with low rumen and apparent total tract digestibility (Allen, 1996; Souza et al., 2010). In the present study, physically regulated VDMI in M1 was more often (in 55 % of all cases) lower than the physiologically regulated VDMI, so that the former was more commonly retained as pVDMI. As such, one reason for the under-estimated oVDMI could be the low daily NDF intake capacity (i.e., 0.012 kg/kg BW) employed in M1. Also, in our meta-data, the average deviation from the oVDMI was greater for the physically regulated (26 % of the oVDMI) than the physiologically regulated (22 % of the oVDMI). Therefore, increasing the daily NDF intake capacity to 0.0135 kg/kg BW in M2 concomitantly with the adjusted ME requirements decreased mean bias in pVDMI (i.e., from 2.3 kg to 1.3 kg/animal and day) and prediction bias from 29 % to 6 % of the oVDMI.

The physiological and physical differences between cattle kept in the (Sub-)Tropics that have to cope with fibre-rich, slowly degradable diets and those raised in temperate regions are yet to be fully understood (Fisher, 2002; Forbes, 2007b). Such differences may include a larger gastrointestinal tract volume, greater ability to recycle endogenous nitrogen in the rumen (Hunter and Siebert, 1985; Souza et al., 2010), and a higher abundance of fibrolytic bacteria in the rumen (Nouala et al., 2009), and thus a greater extent and/or rate of fibre fermentation in the rumen of cattle in the (Sub-)Tropics than those in temperate regions. Taken together, the above differences increase VDMI, so that NDF intake capacity estimates derived from animals fed high-quality diets in temperate countries most likely under-estimate VDMI in cattle kept in the (Sub-)Tropics, which is confirmed by results of the present study. Although increasing NDF intake capacity in M2 as compared to M1 reduced mean bias, M2 still under-estimated VDMI of some cattle (e.g., cows) in the meta-data set, which could be because the daily NDF intake capacity from Mertens (2009) (0.0135 kg/kg BW) was measured in cattle fed poor-quality diets in temperate countries and may still be low for conditions in the (Sub-)Tropics. Additionally, NDF concentration is a good indicator of the total fibre concentration in a diet. However, it may not be the best parameter for simulating physical regulation of VDMI, because it does not account for differences in composition or degradability of the fibre fractions of ruminant feeds (Oba and Allen, 1999). Thus, including additional, readily available parameters in CMM (such as the acid detergent fibre to NDF ratio or the lignin proportion as well as the indigestible NDF) should be explored and evaluated to better capture physical regulation of VDMI of cattle in the (Sub-)Tropics.

The effects of the adjustments made in M1 to simulate physiologically regulated VDMI were explored by considering the cases where the latter was retained as pVDMI of cattle in out meta-data set (45 % of all cases). The pVDMI from the physiologically regulated VDMI were in > 80 % of cases lower than oVDMI, which suggested that ME requirements were under-estimated for cattle in our meta-data set. Increasing the daily ME requirements for maintenance (0.420 MJ to 0.631 MJ/kg$^{0.75}$ BW) and decreasing the ME requirements for BW gain (32.5 MJ - 24.3 MJ/kg BW gain), increased the total daily ME requirements for cattle in the meta-data set and thereby improved the adequacy of pVDMI estimates from M2 in the present study. The superior adequacy of pVDMI from M2 thus concurs with the findings from Salah et al. (2014) that at similar performance, cattle kept in the (Sub-)Tropics have higher ME requirements than those kept in temperate countries.

Furthermore, retaining the mean of the physiologically and physically regulated VDMI in M3 and M4 as pVDMI rather than the lower of the two estimates reduced mean bias when compared to those in M1 and M2. Depending on animals' physiological statuses, they often attempt to balance nutrient requirements and nutrient intake, and could eat more of the fibre-rich diets than the low-fibre diets to compensate for insufficient nutrient supply (Illius and Jessop, 1996), implying that the different mechanisms regulating VDMI blend. Such blending of physiological and physical mechanisms regulating VDMI are seen in empirical models predicting VDMI, where the individual effects of dietary and animal parameters are added up to determine VDMI (Amerdal, 2005). As such, the resulting regression models often achieve high accuracy and precision for the specific conditions under which they are developed. The superior adequacy of pVDMI estimates from M3 and M4 seems to support a blending of the VDMI regulatory mechanism rather than considering them as mutually exclusive.

III.4.3.2 Modifications in the Conrad conceptual mathematical model

Increasing the daily faecal DM output from 0.0107 kg (C1) to 0.0116 kg/kg BW in C2 decreased mean bias and improved the adequacy of pVDMI estimates, but did not alter the robustness (i.e., weighted RPE in Table III.3) of C1. Cattle kept in the (Sub-)Tropics and offered high levels of poorly digestible feed will normally excrete more faeces per kg BW (Allen, 1996; Souza et al., 2010) than animals at similar feeding levels on more digestible feed in temperate regions. As such, increasing the daily faecal output per kg BW in C1 reduced its systematic error from 2.6 % to 0.8 % of the MSEP in C2, suggesting that increasing daily faecal DM output rate was appropriate for predicting VDMI of the cattle in our meta-data set. However, pVDMI estimates from C2 over-estimated the oVDMI in the present study. The physically regulated VDMI estimates from C1 were often (in 67 % of cases) lower than the physiologically regulated pVDMI estimates, meaning the latter was more often retained as pVDMI rather than the former. Yet, the physically regulated VDMI estimates from C1 were also often (53 % of cases) higher than the oVDMI, thus, increasing the daily faecal output per kg BW in C2 further increased the pVDMI. The over-estimation of the oVDMI in C2 thus suggests that actual daily faecal output of the cattle in our meta-data set was lower than the assumed 0.0116 kg/kg BW and was most likely between 0.0107 kg to 0.0116 kg/kg BW. The physiologically regulated pVDMI estimates were mostly (80 % of cases) higher than the oVDMI, suggesting an over-estimation of the digestible DM intake requirements of the animals. The equation used in C1 and C2 to estimate the digestible DM intake requirements (Eq. 1) was fitted for dairy cattle in temperate regions and thus may explain the lack of adequacy when applied to a different cattle population. Also, rather than increase the physiologically regulated VDMI in C2 (i.e., as in the case of M2), there is a need to decrease the digestible DM intake requirements of the animals. Empirical models cannot be easily adapted for other conditions (Amerdal, 2005) than those for which they were fitted and thus we did not attempt to lower the digestible DM intake requirements for the animals in the present study. Also, substituting the digestible DM intake requirements with the ME requirement system from GfE (2001) within our meta-analyses did not yield more adequate results than those from C1 and C2 and thus, we did not investigate this option further.

Furthermore, in contrast to the M3 and M4, taking the mean of the physiologically and physically regulated VDMI rather than the lower of the two estimates in C1 and C2, did not reduce the mean bias of pVDMI estimates from C3 and C4 respectively. The mean of high physiologically and physically (i.e., in 53 % of cases higher than the oVDMI) estimated VDMI in C1 resulted in a greater mean bias in C3 and therefore an even greater mean bias in C4 than C2 due to over-estimated VDMI. Thus, to improve the adequacy of the pVDMI from C1 to C4, correct estimates for the physiologically and physically regulated VDMI should be made and tested to identify which values are most adequate and robust for cattle in the (Sub-)Tropics.

III.5 Conclusions

The CMM can provide adequate VDMI predictions for stall-fed cattle kept in the (Sub-)Tropics. Additionally, adjusting specific CMM parameters that regulate VDMI of cattle in the (Sub-)Tropics also increased the adequacy of predictions and robustness of CMM. These findings are important, because CMM could replace the empirical VDMI used in animal and herd simulation models, thus allowing for the use of the same model across different cattle production systems in the (Sub-)Tropics with no need to fit a new model equation for each cattle production systems. In addition, our findings suggest that M4 could be used to adequately estimate VDMI of cows and steers across different production systems in the (Sub-)Tropics. Lastly, the CMM made it possible to explore how different variables influenced physically and/or physiologically regulated VDMI of the animals in our meta-data set. Thus, CMM could allow researchers to further investigate and understand how VDMI is regulated using own or meta- data, to identify which parameters are most appropriate for simulating VDMI regulation in cattle kept in the (Sub-)Tropics.

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CHAPTER IV

IV Evaluation of the modified LIVestock SIMulator for stall-fed dairy cattle in the Tropics[2]

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Simple Summary

Models can play an important role in identifying and filling knowledge gaps related to sustainable resource use in (sub-)tropical livestock production systems. Yet, most simulation models used to study cattle production systems in the (Sub-)Tropics were developed using data that quantify and characterize biological processes of cattle kept in temperate regions, which may reduce the accuracy of predictions. Therefore, we adopted some published data that quantify and characterize biological processes of cattle kept in (sub-)tropical production systems to modify an existing ruminant livestock herd model. Then, the accuracy of predictions of feed intake and productive performance from the original and modified models were evaluated using meta-data from (sub-)tropical stall-fed cattle. The modified model predicted voluntary dry matter intake and productive performance more accurately than the original model. Consequently, adopting relevant data that correctly describe the biological processes in (sub-)tropical cattle production systems is the way forward for improving simulation models for these systems.

Abstract

Ruminant livestock systems in the (Sub-)Tropics differ from those in temperate areas. Yet, simulation models used to study resource use and productive performance in (sub-)tropical cattle production systems were mostly developed using data that quantify and characterize biological processes and their outcomes in cattle kept in temperate regions. Ergo, we selected the LIVestock SIMulator (LIVSIM) model, modified its cattle growth and lactation modules, adjusted the estimation of the animals’ metabolizable energy and protein requirements, and adopted a semi-mechanistic feed intake prediction model developed for (sub-)tropical stall-fed cattle. The original and modified LIVSIM were evaluated using a meta-dataset from stall-fed dairy cattle in Ethiopia, and the mean bias error (MBE), the root mean squared error of prediction (RMSEP), and the relative prediction error (RPE) were used to assess their accuracy. The modified LIVSIM provided more accurate predictions of voluntary dry matter intake, final body-weights 140 days postpartum, and daily milk yields than the original LIVSIM, as shown by a lower MBE, RMSEP, and RPE. Therefore, using data that quantify and characterize biological processes from (sub-)tropical cattle production systems in simulation models used in the (Sub-)Tropics can considerably improve their accuracy.

Keywords

Cattle; (Sub-)Tropics; Dry matter intake; Model accuracy; Ruminants; Fiber

IV.1 Introduction

Tropical livestock production systems are changing quickly in response to drivers, such as growing human population and increasing urbanization, that cause a rise in the demand for food, especially of animal origin [1]. Hence, livestock farmers in these regions could enjoy access to new markets, diversify production, and thus improve their income security, if they take advantage of the demand-driven markets. Many (sub-)tropical livestock production systems are considered as inefficient due to the limited use of inputs and low product yields [2,3]. However, available resources (e.g., feed, land, and water) are limited, so that livestock farmers in these regions need to shift towards more efficient resource use and sustainable production to ensure future income and food security. Therefore, researchers need to holistically re-assess livestock systems in order to identify the best interventions for improving productivity and sustainability of livestock systems in the (Sub-)Tropics under the rapidly changing environmental and socio-economic conditions.

Simulation models have often been used [2,4] to enhance researchers' knowledge on the feedforward and feedback interactions between different components (e.g., feed production, different animal herds, grazing land, and climate) of (sub-)tropical ruminant production systems. Such interactions are governed by biologically regulated processes (e.g., energy partitioning and use, feed intake regulation), which define the responses of ruminants to abiotic and biotic factors within a production system [5]. Ruminant production systems in the (Sub-)Tropics differ from those in temperate areas, for instance, in terms of the species or breeds of animals and their nutritional requirements [6,7], the availability and nutritional quality of feeds [8], and the prevalent environmental conditions. These differences should thus be correctly represented in simulation models to accurately evaluate resource use and productivity in ruminant production systems in the (Sub-)Tropics. However, most existing models (e.g., the LIVestock SIMulator (**LIVSIM**) and SAVANNA ecosystem models) used to simulate domestic ruminant herds in the (Sub-)Tropics and especially Sub-Saharan Africa reproduce biological processes based on data generated for ruminant production systems in temperate areas [9,10]. The present paper focuses on cattle, because they produce most of the meat and milk among all domestic ruminant species in the (Sub-)Tropics [11] and have thus been widely studied using simulation models.

Data to quantitatively characterize biological processes in (sub-)tropical cattle production systems are becoming increasingly available. Such data include estimates of the energy and protein requirements of cattle in the (Sub-)Tropics [6,7,12], their dry matter intake (**DMI**) capacity [13], and the nutritional composition of (sub-)tropical feedstuffs. We suggest that using such data in cattle simulation models for the (Sub-)Tropics could improve the accuracy with which feed resource use and productivity are simulated. Thus, the adjusted simulation models could serve as suitable tools to identify alternative feeding and management strategies for sustainable cattle production systems in the (Sub-)Tropics.

Building new simulation models is a more expensive and time-intensive process than adapting models already being used for (sub-)tropical cattle production systems [14]. As such, based on the review of five state-of-the-art models relevant for (sub-)tropical ruminant production systems [4], we selected the LIVSIM model for further modifications. The LIVSIM model was selected because it can predict feed resource use and performance of cattle and, unlike other models, also the associated environmental impacts of different feeding strategies [4]. The LIVSIM model is a dynamic model developed to assess the impacts of the allocation of feed resources on animal performance (i.e., productive and reproductive) in smallholder farming systems in Sub-Saharan Africa [15]. Using a monthly time step (i.e., 30.4 days), LIVSIM simulates cattle performance based on their genetic potential (i.e., breed-specific parameters) and the availability and nutritional quality of various feed resources. The energy and protein requirements of cattle in LIVSIM are estimated according to the recommendations of the Agricultural and Food Research Council (**AFRC**) [16] for dairy cattle. Lastly, LIVSIM can also simulate manure production and greenhouse gas emissions for different cattle production systems (e.g., confined dairy cows and/or free-ranging cattle).

Therefore, the present study aimed at modifying the predictions of some of the biological processes that govern cattle responses to feeding in LIVSIM and evaluating whether the modified model (hereafter called LIVSIM-mod) is more accurate in predicting voluntary DMI, final body weight (**BW**), and daily milk yields than the original LIVSIM. As such, we propose that modifying the simulation of biological processes in LIVSIM-mod based on data generated for (sub-)tropical cattle production systems will result in more accurate predictions of resource use and productive performance than from the original LIVSIM.

IV.2 Materials and methods

IV.2.1 Overview of the LIVSIM

The LIVSIM consists of three main components (Figure IV.1) including (i) a user-defined input component where details on the size and structure of the herd and related management decisions can be defined; (ii) various modules containing mathematical equations that describe different biological processes occurring in the animal; and (iii) an output component that summarizes the results from each simulation [10].

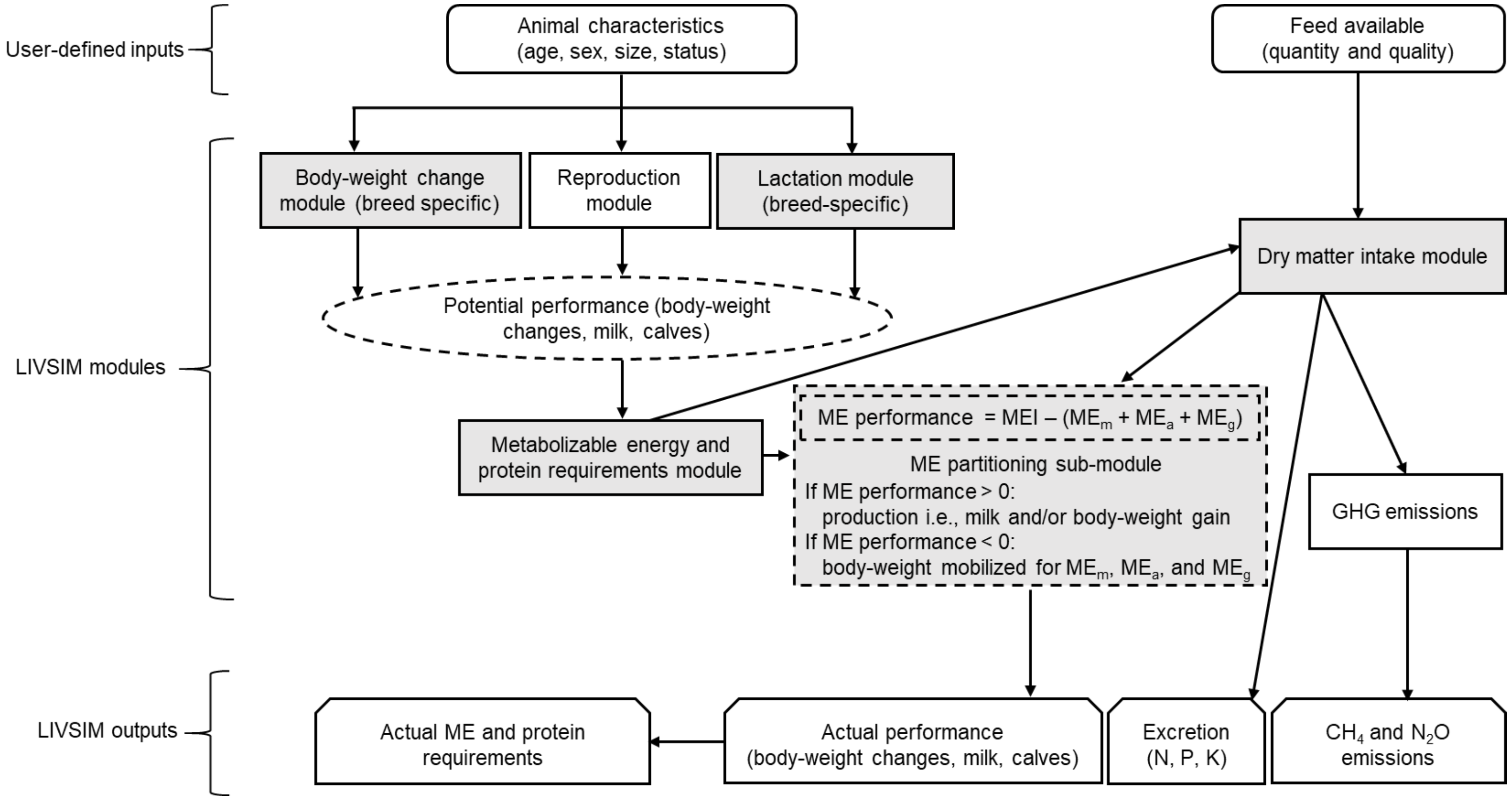

Figure IV.1 Schematic representation of the different components of the LIVestock SIMulator (LIVSIM) model. Grey boxes represent the modules in LIVSIM that were modified in the present study. Rectangular boxes with continuous lines represent LIVSIM modules and rectangular boxes with broken lines represent LIVSIM sub-modules. Rectangular boxes with smooth edges and trapezium-shaped boxes represent input and output components of the LIVSIM model, whereas the oval shape with broken lines contains the information being passed to the metabolizable energy and protein requirements module

ME performance: metabolizable energy available for productive performance, MEI: metabolizable energy intake, and ME$_m$, ME$_a$, and ME$_g$: the metabolizable energy requirements for maintenance, activity, and gestation, respectively, when applicable (all in MJ/animal and day); GHG: greenhouse gases, N: nitrogen, P: phosphorus, K: potassium, CH_4: methane, and N_2O: nitrous oxide.

IV.2.1.1 LIVSIM input component

The user-defined input component includes data on herd and herd-related management options such as (i) breed- and sex-specific parameters such as life-time BW developments, pregnancy and lactation lengths, and milk fat and protein concentrations (g/kg milk) of the animal; (ii) herd size and structure characteristics—i.e., each animal in the herd is described by its breed, sex, age (years), BW (kg), and reproductive status (comprising of the stage of pregnancy (months) and calving interval (years) [10]; (iii) herd management rubrique, where users can define the target herd sizes and structure, culling ages for male and female animals, and maximum number of lactations per animal; (iv) available feed quantity (kg/animal and day) and nutritional quality; and (v) feeding strategies (i.e., daily quantity of different feeds allocated to animals in different herd classes).

IV.2.1.2 LIVSIM modules

The LIVSIM model contains five modules (i.e., square boxes with continuous lines, Figure 1), each describing a biological process. Detailed information on the equations used for each module is provided in [10,15]. In brief, the BW change module uses a simplified Brody model [17] to describe the potential BW gain of animals of different breeds and sexes [10,15]. The reproduction module controls conception in mature non-lactating and non-gestating females. Conception can be triggered either deterministically or stochastically based on the preference of the modeler. Deterministically, it is based on age and BW combinations [15], whereas, stochastically, it uses probabilities associated with the calving rate, postpartum length, presence or absence of a bull, and body condition [10]. Further, the lactation module describes the average daily milk yield throughout lactation for each breed based on the animal’s age and body condition [10]. The outputs from the BW change, reproduction, and lactation modules are then used to estimate the potential performance of animals in the herd.

Total metabolizable energy (**ME**) and metabolizable protein requirements of the animals are estimated from their potential performance according to [16] in the ME and protein requirements module and used to determine the required feed in the DMI module. This module uses the conceptual voluntary DMI model of [18], which was originally developed for high-performing dairy cows in temperate regions. The voluntary DMI (kg/animal and day) determines the total intakes of nitrogen, phosphorus, and potassium as well as of ME intake (**MEI**), which are then used to predict the actual performance (e.g., BW gain or loss and milk yield), greenhouse gas emissions, and nutrient excretion via urine and feces from the animal.

IV.2.1.3 LIVSIM output component

The output component of LIVSIM is a spreadsheet that summarizes the changes in BW, reproductive status, and the actual productive and reproductive performance of each animal in the herd for each time-step (i.e., monthly) of a simulation. In addition, the nitrogen, phosphorus and potassium intakes, their excretion via urine and feces, their ME and metabolizable protein intakes, and the greenhouse gas emissions are reported on a monthly basis.

IV.2.2 Modification of LIVSIM

Modifying the underlying data that characterize the biological processes governing cattle responses in LIVSIM could enable the model to better simulate dairy cattle production systems in the (Sub-)Tropics. Thus, a ME partitioning sub-module (i.e., grey square with broken lines in Figure 1) was created and integrated into LIVSIM-mod to determine the actual productive performance of the animals based on their actual DMI. In addition, four modules (i.e., grey squares with continuous lines in Figure IV.1) of the LIVSIM model were modified to simulate the biological processes they represent under (sub-)tropical husbandry conditions.

IV.2.2.1 Metabolizable energy partitioning sub-module

The ME partitioning sub-module (i.e., grey box with broken lines in Figure IV.1) represents a set of equations interacting with the DMI, BW change, and lactation modules to estimate the actual productive performance of the animals. The DMI module estimates the actual voluntary DMI (kg/animal and day), which is then used to derive the daily MEI as follows (Equation 1):

$$\text{MEI} = \text{voluntary DMI x diet ME} \tag{1}$$

where MEI is the metabolizable energy intake (MJ/animal and day), voluntary DMI the voluntary dry matter intake (kg/animal and day), and diet ME the dietary metabolizable energy concentration (MJ/kg dry matter).

To empirically establish the fraction of MEI available for milk production during lactation, average estimates were obtained from [19], who described MEI utilization in several dairy cattle breeds fed different diets. Accordingly, for diets containing concentrates, 100%, 88%, and 80% of the MEI available for performance (i.e., after accounting for the ME requirements for maintenance as well as activity and gestation requirements, if applicable) were used for milk production during early, mid, and late lactation, respectively. For diets without concentrates, 100%, 85%, and 74% of the MEI available for performance were used for milk production during early, mid, and late lactation, respectively. Furthermore, dairy cattle mainly mobilize BW for milk production during early lactation (i.e., first three months of lactation) [19]. Ergo, unlike in the original LIVSIM where BW mobilization could occur throughout lactation to maintain milk production, we limited BW mobilization for milk production to the first three months of lactation in LIVSIM-mod. If MEI is below the ME requirements for maintenance during early lactation, a maximum of 0.23% of the animal's BW can be mobilized daily for either survival and/or milk production [20]. Beyond the first three months of lactation, milk production will cease, if MEI remains below the ME requirements for maintenance. In addition, if MEI is greater than the ME requirements for maintenance during early lactation, cows in LIVSIM-mod can mobilize BW for producing up to 60% of their potential milk yield predicted by the lactation module. Allowing for BW mobilization in LIVSIM-mod ensures that sufficient quantities of milk are available for calves when cows have a good body condition but their MEI is temporarily insufficient.

For the remaining phases of lactation, milk production is simply dependent on MEI available for performance as described for different diets above.

IV.2.2.2 Body-weight change module

Growth curves provide a mathematical description of the changes in BW of an animal from birth to when it attains its mature BW given adequate nutrition. In animal simulation models, growth curves are used to estimate the potential daily growth rate from which the nutritional requirements are estimated [21]. Several growth models are available [22,23] to describe growth patterns in cattle including the Brody model [17], the Gompertz model [24], and the von Bertalanffy model [25]. The original LIVSIM uses a simplified version of the Brody growth model [10] that assumes a constant potential exponential daily growth rate, which is independent of the animal's BW until the age of puberty [26]. However, the Brody growth curve tends to over-estimate BW changes [10,27]. Thus, in an attempt to better mimic the potential daily growth rate for cattle in the (Sub-)Tropics, a parameterized Gompertz model [28] was implemented in LIVSIM-mod (Equation 2). A potential advantage of the Gompertz curve is that it does not assume a constant potential growth for early phases of the animal's growth as in the case of the Brody model, but assumes a growth proportional to the animal's BW [26].

$$\frac{dBW}{dt} = \mu_0 \times BW \times \left(\frac{\ln(BW_f/BW)}{\ln(BW_f/BW_0)}\right) \tag{2}$$

where the first derivative of body weight with respect to time dBW/dt is the potential daily body weight growth rate (kg/day) [28], μ_0 the Gompertz coefficient specifying the initial body weight growth rate (0.015 per day for cattle) [28], BW the body weight of the animal (kg), BW_f the body weight (kg) at maturity (we assumed 90% of the maximum body weight attainable, because under (sub-)tropical feeding conditions cattle rarely attain the genetic final body weight [29]), and BW_0 the body weight (kg) of the animal at birth.

More so, to avoid unrealistic potential daily growth rates, the maximum daily growth was limited to 1.2 kg/animal as observed in an own (sub-)tropical meta-dataset [13]. The actual daily BW changes in LIVSIM-mod were then estimated (section IV.2.2.5) based on the MEI (MJ/animal and day) available for BW gain or ME mobilized from body reserves when MEI was insufficient to sustain the ME requirements for maintenance and early lactation.

IV.2.2.3 Lactation module

The lactation module in LIVSIM simulates the potential milk yield using lactation curves fitted from the literature data of the different breeds contained in the model. Lactation curves are used in animal simulation models to depict changes in daily milk yield from the time of parturition to the end of lactation [30], and thus to determine the potential milk yield. The predicted potential milk yield (kg/animal and day) is then modified by the age and body condition of the cow, as shown in [10]. The challenge with using this lactation module is that data must be obtained from the literature to fit the lactation curve for each new breed. In order to make the lactation module more generic and, at the same time, easy to parameterize, the lactation curve (Equation 3) used in [9] was implemented in LIVSIM-mod, which requires mainly the peak milk yield (kg/animal and day) achieved during lactation and the month (n) in which the peak occurs.

$$\text{potential milk yield} = \frac{n}{(a \times \exp^{(k \times n)})} \tag{3}$$

where potential milk yield is the potential milk yield during month n of the lactation cycle (kg/animal and day), n the time from calving (months), a the curve parameter, and k the shape parameter. The curve parameter (a) was calculated as [9]:

$$a = \frac{1}{(\text{peak milk yield} \times (1/T) \times \exp(1))} \tag{4}$$

where peak milk yield is the peak milk yield during lactation (kg/animal and day) and T the month in which the peak milk yield is obtained. The shape parameter (k) was calculated as [9]:

$$k = \frac{1}{T} \tag{5}$$

where T is the month in which the peak milk yield is obtained.

In the original LIVSIM, the final predicted potential daily milk yield was modified by the age and body condition factor of the cow [10]. This approach was therefore maintained when predicting the potential daily milk yield in LIVSIM-mod. The actual predicted milk yield (kg/animal and day) was, however, estimated based on the amount of the MEI available for lactation after ME partitioning.

IV.2.2.4 Metabolizable energy and protein requirement module

The recommendations for the ME and protein requirements used in the original LIVSIM were those according to the AFRC [16], estimated for dairy cattle in temperate production systems. To minimize potential errors in predicted cattle performance in (sub-)tropical systems, a modified factorial approach was used. This modified factorial approach builds on the German ME and protein requirement system (Gesellschaft für Ernährungsphysiologie (**GfE**) [31]) and the ME for growth requirement for cattle in warm areas of the French Institut National de la Recherche Agronomique (**INRA**) [32]. The GfE [31], the AFRC [16], and the INRA [32] ME recommendations all use a factorial approach to estimate the ME and protein requirements of cattle. However, the AFRC [16] and the INRA [32] systems require more dietary parameters (e.g., fermentable ME and metabolizability of the gross energy of the diet) than the GfE [31] system to match intakes and requirements of ME and protein in cattle. The fewer data requirements of the GfE [31] than the AFRC [16] and the INRA [31] system make it attractive for the (Sub-)Tropics, where detailed data on nutritional composition of diets are often lacking.

The ME requirements for each relevant metabolic function were calculated separately and then summed-up to yield the total ME requirements (MJ/animal and day), as shown in Equation 6:

$$\text{total ME requirement} = ME_m + ME_l + ME_a + ME_g + ME_{pf} \quad (6)$$

where total ME requirement is the total metabolizable energy requirements for all metabolic functions (MJ/animal and day), and ME_m, ME_l, ME_a, ME_g, and ME_{pf} the metabolizable energy requirements for maintenance, lactation, activity, gestation, and protein and fat deposition (i.e., growth), respectively (all in MJ/animal and day).

The ME requirements (MJ/animal and day) for maintenance in cattle in temperate production systems differ from those of cattle in the (Sub-)Tropics [12]. As such, we estimated the ME requirements for maintenance (ME_m) as (Equation 7):

$$ME_m = \text{metabolic body-weight} \times b \quad (7)$$

where metabolic BW is the animal's metabolic body-weight ($kg^{0.75}$ BW) and b the daily metabolizable energy requirements for maintenance per kg of metabolic body-weight ($MJ/kg^{0.75}$ BW) and. For calves, b was 0.53 $MJ/kg^{0.75}$ BW [33] and for all other animals 0.631 $MJ/kg^{0.75}$ BW [12].

The potential ME requirements (MJ/animal and day) for lactation were estimated according to [31] as (Equation 8):

$$ME_l = \text{ME for milk} \times \text{potential milk yield} \tag{8}$$

where ME for milk is the metabolizable energy requirement per kg of milk (MJ/kg milk) and the potential milk yield during month n of the lactation cycle in kg/animal and day (see Equation 3). The ME requirements per kg of milk (ME for milk) were estimated as (Equation 9):

$$\text{ME for milk} = \frac{(0.041 \text{ x milk fat}) + 1.51}{k_l} \tag{9}$$

where milk fat is in g/kg milk and k_l the efficiency of ME use for lactation (i.e., 0.6 for *Bos taurus* × *Bos indicus* crossbreds and 0.53 for *Bos indicus* breeds [6]).

The ME requirements (MJ/animal and day) for activity (ME_a) were estimated according to [16] (Equation 10), because the GfE [31] provides no recommendations for estimating those requirements for cattle:

$$ME_a = \frac{((2.6 \text{ x BW x horizontal distance})/10^6) + ((28 \text{ x BW x vertical distance})/10^6)}{k_a} \tag{10}$$

where 2.6 is the net energy (J) required to move 1 kg body-weight by 1 m horizontally (J/kg body weight and m), BW the body-weight (kg), horizontal distance is the horizontal distance (m) covered daily by the animal, 10^6 a factor to convert the net energy required from J to MJ, 28 the net energy required to move 1 kg body-weight by 1 m vertically (J/kg body weight and m), vertical distance is the vertical distance covered daily by the animal (m), and k_a the efficiency of ME use for activity (0.7).

The ME requirements (MJ/animal and day) for gestation (ME_g) were considered only for the last eight weeks of gestation and estimated as:

$$ME_p = \frac{0.044 \times \exp(0.0165 \times \text{gestation})}{k_g} \tag{11}$$

where gestation is the duration of gestation (days) and k_g is the efficiency of ME use for gestation (i.e., 0.2).

We adopted the ME requirements for growth recommended for cattle in warm areas by the INRA [32]. These energy and protein recommendations were not entirely adopted in LIVSIM-mod, because they require so many animal and feed parameters, making it quite impractical under typical (sub-)tropical husbandry conditions. Furthermore, the ME requirements per kg BW gain according to the AFRC [16], the GfE [31], and the INRA [32] are based on the animal’s current BW. Thus, these requirements assume that cattle are adequately fed and that their BW develops normally over time, as in most temperate systems. Yet, on-farm, animals in the (Sub-)Tropics often display retarded BW development relative to age, mainly due to poor breeding and undernutrition [34]. Thus, age-dependent ME requirements per kg BW gain were used in LIVSIM-mod to correctly simulate BW changes of cattle in the (Sub-)Tropics. First, the ME requirements according to the INRA [32] were regressed against the animals' corresponding BW reported in the recommendations. Then, selected BW were replaced with cattle ages reported for *B. taurus* × *B. indicus* crossbreds and *B. indicus* breeds in different studies to obtain age-dependent ME requirements per kg BW gain (Table IV.1). Ergo, the resulting ME requirements per kg BW gain for animals older than two years in LIVSIM-mod were 27% higher than for those recommended by the INRA [31] to account for retarded or slower BW development observed under (sub-)tropical husbandry conditions.

Table IV.1 Net energy requirements per kg of body-weight gain (MJ/kg body-weight; k_{pf} = 0.4) for female and male zebu cattle and crossbred cattle of different ages in the (Sub-)Tropics.

		Age (years)						
Sex	**Breed**	**0.0**	**0.1**	**1.5**	**3.0**	**4.5**	**5.5**	**20.0**
		Net energy requirements (MJ/kg body-weight)						
Female	*Bos indicus x Bos taurus*	3.4	4.0	9.6	16.5	23.4	23.4	23.4
	Bos indicus	3.4	3.9	8.6	12.9	16.2	17.0	17.0
Male	*Bos indicus x Bos taurus*	3.4	4.0	9.1	15.5	21.8	25.1	25.1
	Bos indicus	3.4	3.9	7.9	11.9	14.8	18.8	18.8

[1] k_{pf} is the efficiency of utilization of metabolizable energy for protein and fat deposition [31].

The ME requirements (MJ/animal and day) for potential protein and fat deposition (ME_{pf}; i.e., growth) were then estimated as (Equation 12):

$$ME_{pf} = \text{ME for gain} * \frac{dBW}{dt} \qquad (12)$$

where ME for gain is the metabolizable energy requirement per kg of body-weight gain at a given age (MJ/kg BW) and dBW/dt is the first derivative of body-weight with respect to time, which represents the potential daily body-weight growth rate (kg/animal and day).

The actual ME available for growth in LIVSIM-mod was determined by the MEI available for growth after ME partitioning. If MEI was less than ME requirements for maintenance, activity, and/or milk production in early lactation, net energy was mobilized from body reserves. The net energy was then used for different purposes (e.g., lactation) with an efficiency of 0.84 [31].

Similar to the ME requirements, metabolizable protein requirements (g/animal and day) of the AFRC [16] in the original LIVSIM were replaced by the utilizable crude protein (**uCP**) requirements (g/animal and day) according to the GfE [31] for each relevant metabolic function in LIVSIM-mod. The uCP is the sum of undegraded feed crude protein plus the microbial crude protein available in the duodenum of the cattle [35]. The metabolizable protein requirements differ from the uCP requirements in that the former is corrected for the proportion of true protein and its intestinal digestibility (i.e., truly digestible protein) while the latter is not (i.e., sum of the undegraded feed and microbial crude protein leaving the rumen). Thus, it is easier to estimate an animal's protein requirements on a uCP basis using feed data commonly available in the (Sub-)Tropics than on a metabolizable protein basis.

The uCP requirements for each animal were calculated factorially as shown in Equation 13.

$$\text{Total uCP requirement} = uCP_m + uCP_l + uCP_g + uCP_{pf} \tag{13}$$

where total uCP requirement is the total utilizable crude protein requirement (g/animal and day), and uCP_m, uCP_l, uCP_g, and uCP_{pf} the utilizable crude protein required daily for maintenance, lactation, gestation, and protein and fat deposition (i.e., growth), respectively (g/animal and day).

The uCP requirements for each metabolic function considered in Equation 13 were estimated as reported in the GfE [31]. The net requirements of protein per kg BW in (sub-)tropical cattle reported by Valente et al. [36] rather than those suggested by the GfE [31] were used to estimate the uCP requirements for daily growth. Then, similar to the age-dependent ME recommendations for BW gain presented above, we developed an age-dependent net protein content per kg BW, as shown in Table IV.2.

Table IV.2 Net requirement of protein per kg of body-weight gain for female and male zebu and crossbred cattle of different ages in the (Sub-)Tropics.

		Age (years)						
Sex	**Breed**	**0.0**	**0.1**	**1.5**	**3.0**	**4.5**	**5.5**	**20.0**
Female	*Bos indicus x Bos taurus*	236	182	174	171	170	170	170
	Bos indicus	236	182	173	170	168	168	168
Male	*Bos indicus x Bos taurus*	236	182	175	172	170	169	169
	Bos indicus	236	182	174	168	167	167	167

Therefore, the uCP requirements (g/animal and day) for BW gain (uCP_g) were estimated as:

$$uCP_g = \text{protein content in gain} * \frac{dBW}{dt} * 2.1 \tag{14}$$

where protein content in gain is the protein content per kg body-weight gain at a particular age (Table 2), dBW/dt the first derivative of body-weight with respect to time which represents the potential daily body-weight growth rate (kg/animal and day), and 2.1 the efficiency of utilizing the utilizable crude protein for body protein accretion.

The actual uCP requirements for gain were then determined based on the actual daily BW changes as predicted from the MEI available for growth from the energy partitioning sub-module.

IV.2.2.5 Dry matter intake module

Prediction of voluntary DMI in the original LIVSIM is based on the conceptual model of [18], developed for high-producing dairy cows in temperate regions. However, identifying a model that more accurately predicts voluntary DMI under (sub-)tropical feeding conditions has previously been recommended [10].

Bateki and Dickhoefer [13] identified and adjusted different conceptual models to adequately (i.e., accurately and precisely) predict voluntary DMI of stall-fed cattle in the (Sub-)Tropics. Consequently, the most adequate voluntary DMI prediction model identified by [13] for cattle under (sub-)tropical feeding conditions was adopted in LIVSIM-mod (Equation 15):

$$\text{voluntary DMI} = \left(\frac{\text{NDF intake capacity}}{\text{diet NDF}} + \frac{\text{total ME requirement}}{\text{diet ME}}\right) / 2 \tag{15}$$

where voluntary DMI is the voluntary dry matter intake (kg/animal and day), NDF intake capacity the neutral detergent fiber intake capacity (kg/animal and day), diet NDF the neutral detergent fiber concentration in the diet (kg/kg dry matter), total ME requirement the total potential metabolizable energy requirements (MJ/animal and day) estimated according to Equation 6, diet ME the dietary metabolizable energy concentration (MJ/kg dry matter), and 2 to account for the blending of physiologically and physically regulated voluntary dry matter intake [13].

The NDF intake capacity (kg/animal and day) was calculated as:

$$\text{NDF intake capacity} = 0.0135 * BW \tag{16}$$

where BW is the animal’s body-weight (kg) and 0.0135 is the maximum daily amount of neutral detergent fibre (kg/kg BW) that can be consumed by lactating cattle in the (Sub-)Tropics.

The fact that voluntary DMI is estimated using the potential total ME requirements implies that the above intake model (Equation 15) may over-estimate DMI. Potential productive performance of livestock is primarily driven by their genetic potential under optimum feeding conditions [37]. However, cattle in the (Sub-)Tropics are scarcely fed at optimum to fulfil their full productive genetic potential. Thus, to prevent over-estimation of the voluntary DMI in LIVSIM-mod, the predicted voluntary DMI estimate was multiplied by the BW condition index (Equation 17):

$$\text{BW condition index}_t = \frac{(\text{BW}_t - \text{BW}_{\text{min},t})}{(\text{BW}_{\text{max},t} - \text{BW}_{\text{min},t})} \tag{17}$$

where BW condition index$_t$ is the body-weight condition index at time t (kg/kg), BW$_t$ the current body-weight of the animal of a given age at time t (kg), BW$_{\text{min},t}$ the minimum possible body-weight of an animal of a particular age at time t (kg), and BW$_{\text{max},t}$ the maximum body-weight attainable by an animal of a particular age at time t (kg).

Similar to Equation 2, it was assumed that 90% of the maximum BW was attainable in LIVSIM-mod. The minimum and the maximum attainable BW were defined based on the literature data for each breed in the original LIVSIM [10].

IV.2.3 Evaluation of LIVSIM mod

IV.2.3.1 Dataset used for model evaluation

LIVSIM-mod was evaluated and compared to LIVSIM using data extracted from a study with stall-fed dairy cattle in Ethiopia [38], which evaluated the effect of lablab hay supplementation to 48 multiparous *B. indicus* × *B. taurus* cows fed forages from cereal–legume intercropping on feed voluntary DMI, apparent total tract digestibility, as well as on milk yield and milk composition. This study was selected because it lasted for 200 days (i.e., 60 days prepartum and 140 days postpartum), allowing for simulations over multiple time steps. For the present study, only data for the 140 days postpartum were used, because the average BW of the animals were not reported prepartum. Data (Table 3) for two dietary treatments (i.e., maize–lablab stover only and oats–vetch hay only fed ad libitum) out of the eight evaluated in [38] were chosen because of a lack of data on some dietary nutrient parameters (e.g., undegradable crude protein and fermentable ME of the diet) for the other six diets.

Table IV.3 Animal and dietary parameters from stall-fed dairy cattle in Ethiopia used for parameterizing and evaluating LIVSIM mod.

Parameter	**Treatments**	
	Maize-lablab	Oats-vetch
Animal		
Number of cows	6	6
Age[1], years	5.2	5.2
Body-weight at calving, kg	415	432
Body-weight at 140 days postpartum, kg	386	399
Voluntary dry matter intake, kg/animal and day	9.8	9.7
Lactation length, months	10	10
Peak milk yield[2], kg/animal and day	20	20
Month of peak milk yield[2]	2	2
Milk yield, kg/animal and day	8.25	6.82
Milk fat, g/kg milk	46.3	46.6
Milk protein, g/kg milk	29.0	31.2
Diet		
DM, g/kg as fed	890	888
CP, g/kg DM	93.1	87.5
Undegradable CP[3], g/kg CP	250	220
Acid detergent insoluble nitrogen[3], g/kg DM	0.9	1.1
CP fraction a [4]	0.24	0.18
CP fraction b [5]	0.57	0.57
CP fraction c [6]	0.04	0.05
Neutral detergent fibre, g/kg DM	550	610
Gross energy[3], MJ/kg DM	17.2	17.6
Metabolizable energy, MJ/kg DM	9.4	9.6
Fermentable metabolizable energy of diet[3], MJ/kg DM	7.2	7.4
DM digestibility, g/kg DM	659	683
Phosphorus, g/kg DM	4.5	3.6
Potassium, g/kg DM	25.0	29.8

CP, crude protein; DM, dry matter. [1] Not reported but estimated based on the average (i.e., 2–4) number of parity reported in the study; [2] adopted from [9] to parameterize the lactation curve; [3] obtained from own data and [16]; [4] the proportion of water-soluble nitrogen in total nitrogen of the diet, [5] the proportion of potentially degradable nitrogen other than water-soluble nitrogen of the diet, and [6] fractional rumen degradation rate per hour of the b fraction of feed nitrogen.

The original LIVSIM and LIVSIM-mod were parameterized using the animal and dietary parameters shown in Table 3 and run for five time steps (i.e., five months). The predicted final BW (kg/animal), voluntary DMI (kg/animal and day), and milk yield (kg/animal and day) from both LIVSIM versions were then compared with the corresponding data reported in [38].

IV.2.3.2 Statistical evaluation

The original LIVSIM and LIVSIM-mod were evaluated for their accuracy in predicting the final BW, voluntary DMI, and daily milk yields. As first measure of accuracy, the mean bias error (MBE) in predicted final BW (kg/animal), voluntary DMI (kg/animal and day), and milk yields (kg/animal and day) was estimated as follows [39]:

$$\text{MBE} = \sum_{i}^{n} \frac{(\text{observed}_i - \text{predicted}_i)}{q} \qquad (18)$$

where MBE is the mean bias error, observed_i the observed value for either final body weight (kg), voluntary dry matter intake (kg/animal and day), or daily milk yield (kg/animal and day) for animal group i, predicted_i the predicted value for each of the parameters obtained from the both the original LIVSIM and LIVSIM-mod, respectively, for animal group i, and q is the number of pairs of the observed and predicted values for parameters being compared.

Further, to quantify the prediction error (i.e., measure of accuracy) associated with the final BW, voluntary DMI, and milk yield predictions obtained from both LIVSIM versions, the root mean squared error of prediction (**RMSEP**) was estimated as presented in [40]. Lastly, the RMSEP was expressed as a percentage of the observed mean value to obtain the relative prediction error (**RPE**) [40]. All statistical analyses were performed using the R software (version 3.4.0, the R foundation for Statistical Computing, Vienna, Austria).

IV.3 Results

IV.3.1 Voluntary dry matter intake predictions

The voluntary DMI predictions from the original LIVSIM for the maize–lablab and oats–vetch dietary treatments were greater than those from LIVSIM-mod and the measured values reported in the meta-data (Table IV.4).

Table IV.4 Observed and LIVSIM predicted values for voluntary dry matter intake and productive performance of stall-fed dairy cows in Ethiopia.

Experimental diets	**Parameters**								
	Voluntary DMI (kg/animal and day)			Final body-weight (kg)			Milk yield (kg/animal and day)		
	observed	*LIVSIM*	*LIVSIM mod*	*observed*	*LIVSIM*	*LIVSIM mod*	*observed*	*LIVSIM*	*LIVSIM mod*
Maize-lablab	9.8	14.4	10.2	386	454	385	8.3	13.1	8.1
Oats-vetch	9.7	14.2	9.6	399	430	383	6.8	12.6	7.8

The MBE (Table IV.5) in the voluntary DMI predictions from LIVSIM (−4.6 kg/animal and day) was greater than that in predictions from LIVSIM-mod (−0.2 kg/animal and day). The RMSEP and the RPE were also greater in the predictions from the original LIVSIM than those from LIVSIM-mod (Table IV.5).

Table IV.5 Statistical evaluation of the different LIVSIM versions for predicting voluntary dry matter intake in stall-fed dairy cattle in Ethiopia.

Statistical Measure	**LIVSIM**	**LIVSIM-Mod**
MBE [†], kg/animal and day	−4.6	−0.2
RMSEP [††], kg/animal and day	4.6	0.3
RPE [†††], % mean observed value	47.0	3.0

[†] MBE = mean bias error; [††] RMSEP = root mean squared error of prediction; [†††] RPE = relative prediction error.

IV.3.2 Animal productive performance: final body-weight and milk yield predictions

The final BW (kg/animal) predictions after 140 days postpartum by the original LIVSIM were greater than those by LIVSIM-mod (Table IV.4). The MBE in the predicted final BW was greater for LIVSIM (−49.5 kg/animal) than LIVSIM-mod (8.5 kg/animal) in the present study. Accordingly, the RMSEP and the RPE in predictions from the latter were lower than from the former. The milk yields (kg/animal and day) predicted by the original LIVSIM were also greater than the observed values in the meta-data. As in the case of the voluntary DMI and final BW, the MBE, the RMSEP, and the RPE were all lower for predictions from LIVSIM-mod than for those from the original LIVSIM (Table IV.6).

Table IV.6 Statistical evaluation of different LIVSIM versions for predicting final body weight (kg/animal) after 140 days postpartum and milk yield (kg/animal and day) in stall-fed dairy cattle in Ethiopia

Statistical measure	**Predicted parameters**			
	Final body-weight		Daily milk yield	
	LIVSIM	LIVSIM-mod	LIVSIM	LIVSIM-mod
MBE [†]	-49.5	8.5	-5.3	-0.4
RMSEP [††]	52.8	11.3	5.3	0.7
RPE [†††], % mean observed value	13.5	2.9	70.5	10.0

[†] MBE = mean bias error; [††] RMSEP = root mean squared error of prediction; [†††] RPE = relative prediction error.

IV.4 Discussion

LIVSIM-mod was obtained by modifying the cattle growth and lactation modules of LIVSIM, adjusting the estimation of the animals' ME and protein requirements, and by adopting a feed intake prediction model developed for stall-fed cattle in the (Sub-)Tropics. LIVSIM-mod provided more accurate predictions of voluntary DMI of the animals, their final

BW 140 days postpartum, and their daily milk yields than the original LIVSIM, as shown by the MBE, the RMSEP, and the RPE.

IV.4.1 Accuracy of models' prediction

The accuracy of a model's predictions can be classified as excellent, good, fair, and poor, if the RPE is <10%, 10–20%, 21–30%, and >30%, respectively [41]. In the present study, the original LIVSIM predicted voluntary DMI and daily milk yield poorly, whereas the final BW predictions were good (Table IV.5 and IV.6). Meanwhile, the predicted voluntary DMI and final BW from LIVSIM-mod were excellent, and its predictions of daily milk yield were also good (Table IV.5 and IV.6). The accuracy of predicted animal performances from both LIVSIM versions resulted from the complex interactions between several processes including those needed to predict daily ME requirements, voluntary DMI, and ME partitioning [16,32,42]. Voluntary DMI is the most important determinant of productive and reproductive performance predictions in cattle simulation models [43]. The greater accuracy of LIVSIM-mod compared to the original LIVSIM in predicting voluntary DMI could be explained by two points. First, LIVSIM-mod employed the modified Mertens conceptual intake model [44], which was specifically adapted for stall-fed dairy cattle systems in the (Sub-)Tropics [13]. As such, the latter DMI model is more suitable for (sub-)tropical cattle production systems than the intake model of [18] used in the original LIVSIM, which was developed for high-producing dairy cows in temperate regions. Second, a BW condition index (i.e., Equation 17) was used in LIVSIM-mod to down-scale the predicted DMI based on the body condition of the animal at each time step during simulations. The two conceptual models used in the present study predict DMI based on the theoretic potential (i.e., as defined by genetic potential) rather than actual (i.e., as defined by the animal's status) productive performance of the animal. However, the potential productive performance of cattle kept in the (Sub-)Tropics is rarely achieved [37]. As such, using the estimated ME requirements for potential productive performance will lead to an over-estimation of DMI by any model.

Both the original LIVSIM and LIVSIM-mod over-estimated voluntary DMI (as shown by the negative MBE in Table IV.5). As such, in the original LIVSIM, both the final BW after 140 days postpartum and the daily milk yields were also over-estimated (−49.5 kg/animal and day and −5.3 kg/animal and day, respectively). In the case of LIVSIM-mod, only the daily milk yield was over-estimated (−0.4 kg/animal and day), whereas final BW after 140 days postpartum was under-estimated (8.5 kg/animal and day). The reason for the latter under-estimation is not clear but could probably be due to the ME partitioning during early lactation or the changes in ME requirements in LIVSIM-mod. In the present study, 100% of the MEI available for performance, and ME from mobilized body fat and protein (i.e., BW losses) was used to sustain up to 60% of the potential daily milk yield during early lactation

[19]. In mid lactation (i.e., last 50 days of present simulation), 85% of the MEI available for performance were used for milk production and the remaining 15% MEI used for BW gain [19]. As such, all the animals lost BW in early lactation and regained some in mid lactation, although the BW gain predicted by LIVSIM-mod was lower than the observed gain during this phase. Since LIVSIM-mod at the same time over-estimated daily milk yields, the proportion of MEI used for milk production should be lower than the assumed 85%, increasing the proportion of MEI available for BW gain. Furthermore, the ME requirements per kg BW gain were greater by 27.5% in LIVSIM-mod than in the original LIVSIM. The greater ME requirements per kg BW gain additionally resulted in lower final BW predictions in LIVSIM-mod than in the original LIVSIM. Yet, overall, the changes made in LIVSIM-mod allowed for more accurate predictions of voluntary DMI and performance of cattle compared to the original LIVSIM.

IV.4.2 Relevance of the modifications made in LIVSIM-Mod

Several livestock models exist that can be used to simulate cattle production systems in the (Sub-)Tropics, as shown by various reviews [4,45]. These livestock models differ in their assumptions and approach (e.g., steady state and dynamic) to simulate cattle production systems [45]. However, one of the challenges inherent to most livestock simulation models used in the (Sub-)Tropics is still the errors associated with predictions of resource use (i.e., feed intake) and productive performance (e.g., BW gain) [5,9]. Hence, improving the adequacy (i.e., accuracy and precision) of predictions should continue to receive attention to ensure that the basis on which conclusions will be drawn from simulation outcomes is reliable. Benchaar et al. [46] suggested that more accurate predictions from process-based models can be achieved by adjusting factors that regulate different biological processes. Thus, the present study leveraged existing data to characterize biological processes and modify how different processes are simulated for (sub-)tropical cattle production systems in order to enable LIVSIM-mod to better quantify the expected resource use and productive performance than the original LIVSIM. Moreover, fewer input data for dietary (e.g., acid-detergent insoluble nitrogen and fermentable ME) and animal (e.g., planes of nutrition to calculate ME requirement) parameters are required for LIVSIM-mod than for the original LIVSIM. Such lower input data requirements of LIVSIM-mod than of the original LIVSIM could enable users to easily parameterize and run it for (sub-)tropical cattle production systems.

IV.4.3 Limitations of the present study

First, LIVSIM-mod should be applicable to a wide variety of ruminant production systems including small ruminants and crop–livestock cattle production systems. However, the present study used only data from stall-fed dairy cattle systems, implying that further evaluation is needed to ascertain how well LIVSIM-mod simulates other husbandry systems such as those mentioned above. Second, the present study could not validate LIVSIM-mod due to a lack of access to suitable data. For instance, the number of mean observations of the meta-dataset used in the study were not enough to distinguish systematic errors from random errors associated with model predictions [47]. Further, the dataset used for the present evaluation is small and focuses only on a short time period. As such, it was not possible to assess how the modifications in LIVSIM-mod may affect the adequacy of predictions for different groups of animals (e.g., heifers and calves), the reproductive performance, or the overall development in the size and structure of cattle herds over time. Therefore, there is still a need for validating LIVSIM-mod using a more comprehensive dataset from the (Sub-)Tropics.

IV.5 Conclusions

LIVSIM-mod predicts feed resource use and productive performance of stall-fed dairy cattle in the (Sub-)Tropics more accurately than the original LIVSIM, as it accounts for differences in voluntary feed intake capacity, growth and lactation curves, and ME requirements for maintenance and BW gain of cattle between temperate and (sub-)tropical husbandry systems. It may thus be a useful tool to assess strategies for improving productivity and sustainability of stall-fed dairy cattle systems in the (Sub-)Tropics. Further research should assess how well LIVSIM-mod can simulate resource use and productive and reproductive performance of other cattle groups (e.g., calves and heifers) in diverse production systems in the (Sub-)Tropics.

Author Contributions:

Conceptualization: C.A. Bateki and U. Dickhoefer; data analyses: C.A. Bateki; writing-review and editing: C.A. Bateki and U. Dickhoefer; project administration and funding acquisition: U. Dickhoefer. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest:

The authors declare no conflict of interest.

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CHAPTER V

V General discussion

V.1 Tropical ruminant production systems and simulation models

Ruminant livestock production systems in the (Sub-)Tropics are under increasing pressure to satisfy the demand for animal-based foods of a population with rising incomes and increasing urbanization (Gouel and Guimbard, 2019; Popkin et al., 2012). These ruminant production systems however continue to be characterized by low animal productivity (Oosting et al., 2014). Consequently, an intensification of resources (e.g., land, feed, and water) currently used can be expected, as well as an increased demand for the limited natural resources still available to satisfy the growing demand for animal-based foods (Morris et al., 2009). Nevertheless, natural resources available for expanding ruminant production in the (Sub-)Tropics are limited, and ruminant production systems can also impact the environment negatively (Gerber et al., 2013; Janzen, 2011). Thus, there is a need to study ruminant production systems in the (Sub-)Tropics to improve the efficiency of resource use and identify sustainable options for intensifying them and increasing herd productivity (Tedeschi et al., 2015).

Within this context, simulation models (Chapter I) like the LIVstock SIMulator (**LIVSIM**) could be useful tools for studying tropical ruminant production systems from a systems approach. A systems approach is needed because several interacting constraints to increased productivity exist, including limited access to feed, low-quality feeds, high prevalence of diseases, and lack of market infrastructure. These interacting constraints need to considered when assessing the suitability of strategies for increasing productivity of tropical ruminant production systems. As such, simulation models can be used to capture these interactions, and assess alternative management strategies for greater spatiotemporal frameworks than what conventional experimentation can allow (Derner et al., 2012). Yet, the results from such models need to be reliable to identify optimum strategies under varying ruminant livestock production conditions (Hanigan and Daley, 2019).

The reliability of predictions from simulation models is mainly determined by the data underlying the equations used to mimic biological processes in the models (Derner et al., 2012). This was also observed in Chapters III and IV of the present thesis, where using data generated from ruminant production systems in the (Sub-)Tropics yielded more adequate (i.e., accurate and precise) predictions than when using data from temperate regions. Unlike in temperate systems, there is a severe lack of data characterizing the role and magnitude of different parameters in regulating biological processes in ruminants in tropical production systems, as well as data on the nutritional composition of the diets offered (FAO, 2014; Mottet et al., 2017). Consequently, the development and improvement of ruminant livestock models for the (Sub-)Tropics has lagged behind when compared to those used in temperate regions. However, the increasingly available sensor technologies (e.g., pedometers and accelerometers) and digital tools like mobile applications could enable researchers or farmers to continuously monitor and collect data at animal and herd level under tropical conditions (Morota et al., 2018). For examples, pedometers could be used to estimate the level of physical activities on of animals and the data used together with data on feed intake and body-weight changes to estimates energy requirements under tropical conditions (Løvendahl and Chagunda, 2010). Such data will help alleviate the huge data deficit in the (Sub-)Tropics, as well as provide a good database for developing robust decision support tools for ruminant livestock producers.

Furthermore, researchers in many regions of the (Sub-)Tropics have not picked up on modelling (Whitbread et al., 2010). This may be due to the high levels of frustration associated with first time exposure to most models which are quite complicated and with not very friendly user interfaces. Other reasons for the low interest in modelling may include lack of funding for modelling-based research, limited access to the required data, and low perceptions of the relevance or usefulness of modelling for addressing the constraints livestock producers face. As such, there is a need for developing the capacity of researchers in the (Sub-)Tropics, so that the link between field experiments and the data requirements for modelling can be reconciled.

V.2 Suitability of existing ruminant herd models to predict the use of feed resources, potential outputs, and associated environmental impacts in (Sub-)Tropics

The issue of how suitable ruminant herd models are for use in the (Sub-)Tropics arises from the economic, environmental, and socio-cultural context within which production is occurring. An assessment of grassland-based ruminant systems in the African Guinea Savanna (Chapter II) revealed that future suitable ruminant herd model should be able to capture the multi-functionality of ruminants and the increasing complexity and diversity of production systems that will ensue in the (Sub-)Tropics. The findings from the present thesis suggest that existing ruminant herd models are only partly suitable to predict the use of feed resources, potential outputs, and the associated environmental impacts from ruminants in the (Sub-)Tropics. This suggestion is hereafter evaluated at two levels including: (i) the herd level (i.e., how well is the ruminant herd simulated) and (ii) the system level (i.e., how are the interactions between the herd and other components of agricultural systems are captured).

At ruminant herd level, the majority of relevant models for production systems in the (Sub-)Tropics simulate the animals' potential outputs based on feed resources available

(Chapter II). But, only a few of these models can account for the environmental impacts associated with production. This is because many models relevant for these systems were developed between the late 1980s and early 2000s (Jones et al., 2016; Snow et al., 2014). As such, the goal was to increase production during this period, with little focus on environmental impacts. However, since the mid-2000s, livestock keepers and researchers have come under increasing pressure to account for the environmental impacts associated with production (Steinfeld, 2006).

Of the five state-of-the art models evaluated in the present thesis (Chapter II), only LIVSIM can account for some environmental impacts (i.e., green-house gases emissions) associated with ruminant production systems. This may have been included in the model because LIVSIM was developed after 2006, when environmental impacts associated ruminant livestock was the focus of many scientific discussions. As such, to properly inform decisions of different stakeholders on appropriate management strategies for intensifying or expanding ruminant production systems in the (Sub-)Tropics, simulation models should be able to capture environmental impacts associated therewith.

Evidence from Chapters three (i.e., intake prediction) and four (i.e., feed resources and potential outputs prediction) suggests that, even if a model can simulate an event or a production system in the (Sub-)Tropics, it may not be suitable to adequately predict resource use and the potential outputs. The suitability of a ruminant herd model also depends on how well it simulates such events (e.g., feed intake) or production systems (e.g., grazing or zero-grazing) for tropical husbandry feeding and management conditions. Much evidence exists in the literature which points to bio-physical differences (e.g., climate, animal metabolism) that exist between ruminant production systems in temperate and tropical regions (Chizzotti et al., 2007; Burrow, 2012; Salah et al., 2014). As such, using feeding recommendations developed for ruminants in temperate regions when simulating ruminant in the (Sub-)Tropics will yield inadequate predictions.

Researchers have continued to use feeding recommendation for animal in temperate regions in the (Sub-)Tropics due to the huge lack of data in terms of nutrient composition of diets offered and the associated metabolic processes during digestion. However, such data is increasing becoming available in the literature. Thus, in 2018, the French Institut National de la Recherche Agronomique (INRA) even published one of the first feeding recommendations for ruminants in the (Sub-)Tropics (INRA, 2018). Their recommendations support the findings of the present thesis that the data used to quantify and characterize biological processes in models used for tropical ruminant systems should differ from those used in ruminants in temperate regions. To our knowledge, most state-of-the-art models currently being used for ruminant herd simulation mainly use data generated from temperate regions to simulate the outcomes of nutrient digestion and utilization in tropical production systems. Therefore, the ruminant models used at herd level in the (Sub-)Tropics are still not adequate to predict resources use and potential outcomes for different production systems as hypothesized in Chapter I.

At ruminant production system level, the herd interacts across space and time with different components of the agricultural system (e.g., soil, vegetation, and climate) (Jones et al., 2016; Masikati et al., 2017). For instance, in mixed-crop livestock system, the quality and quantity of the feed used will influence the ruminants' performance, as well as the quality and quantity of the manure produced. When returned to the fields, the manure could then improve soil structure via addition of organic matter and increase nutrient availability to plants. Thus, there are several non-linear interactions which should be captured to correctly inform what the overall impact of a management strategy is at system level (Janzen, 2011).

No one stand-alone ruminant herd model can capture all these interactions, because they simply go beyond the scope of what individual models are often designed for. Also, the scientific community is increasingly interested in the whole picture of agricultural systems including greenhouse gas emissions, climate change mitigation and adaptation, and food security for example rather than just focusing on one component like livestock production (Holzworth et al., 2015). As such, some authors (Liu et al., 2015; Mottet et al., 2017) have suggested that integrating stand-alone models that adequately simulate individual components of agricultural systems will offer the most promising option at system level. Models' integration also has the advantage that researchers from different disciplines will collaborate to identify and develop models, as well as make recommendations at agricultural systems' level in the (Sub-)Tropics. Therefore, several modelling frameworks are needed that define how different models simulating separate components of the agricultural system could be integrated to one another to adequately simulate the entire system.

V.3 Relevance of adapting existing ruminant herd models for tropical systems

There is a dire need to improve the adequacy (i.e., accurate and precise) of existing ruminant herd models for tropical systems in order to correctly assess the use of resources, potential productivity, and any associated impacts (Jones et al., 2016). Concurrently, data describing biological processes in tropical ruminant systems are increasingly becoming available, and could be used to validate and improve simulation models used for these systems (INRA, 2018; Masikati et al., 2017). In Chapter III of the present thesis, we identified and improved the adequacy of a voluntary dry matter intake prediction model for cattle kept under tropical feeding and husbandry conditions. Dry matter intake is the main nutritive factor that determines the productive and reproductive performance of ruminants (Huhtanen et al., 2011; Krizsan et al., 2014). Feed intake is also an important indicator of feed resources use and can thus significantly influence production economics of farmers, as well as drive land use change, since the type of feed needed determine cropping patterns (Mottet et al., 2017). As such, ruminant intake prediction models determine the amount of nutrients and energy the animals ingest and have available for predicting production of milk yield, bodyweight changes, and nutrient use efficiency (Zom et al., 2012). Ergo, without a good feed intake prediction model, no simulation model can adequately predict feed resources use, the potential outputs and associated environmental impacts of ruminant systems in the (Sub-)Tropics. The large variation in chemical composition and nutritive values of feeds, together with the diversity of breeds found in the (Sub-)Tropics present a challenge for accurate predictions but increases the need for precise intake prediction models (Krizsan et al., 2014). In the present thesis, we adapted and modified different conceptual mathematical intake model, and that of Mertens (1987) was adopted, because it can be used to adequately predict intake of different tropical feed types and ruminant animals.

In Chapter IV, literature data that quantify and characterize biological processes in tropical ruminant production systems were used to modify LIVSIM. This resulted in more accurate predictions of resources use and productive performance from the modified than from the original LIVSIM. It is a misconception to think that a ruminant herd model is satisfactory for decision support or impact assessment, as long as it can correctly predict the direction of change for different management strategies being assessed (Thornton and Herrero, 2001). The magnitude of the errors when simulating different components of the production system can significantly change the outcome of a management strategy at herd level. This is because livestock production activities in the (Sub-)Tropics often involve a range of on-farm and off-farm activities competing for limited available resources (McDonald et al., 2019). Considering a hypothetical example with a herd of 10 cows, each eating 9 kg dry matter of Napier grass and producing 4 kg of milk daily. If the simulation model overpredicts voluntary dry matter intake by 1 kg daily for each cow, this represents an additional feed requirement of 300 kg dry matter of Napier grass per month or 3.6 tons of dry matter per year. Considering the high seasonality and associated prevalence of feed scarcity experienced in many ruminant livestock production systems in the (Sub-)Tropics, such overestimation of feed needs could mislead decision making of researchers. More so, such an overestimation will also carry important consequences on land use patterns (e.g., more land needed for feed production), labor allocation, and even nutrient fluxes at herd level (Thornton and Herrero, 2001). Thus, to avoid drawing wrong conclusions, it is important that ruminant herd models go beyond predicting the direction of change, but also adequately predicting the changes expected. The modifications made to LIVSIM did not only aim at improving the accuracy with which tropical ruminant herds are simulated, but also aimed at improving the flexibility and applicability with which the herd model can be applied (Chapter III and IV). Flexibility refers to the diversity of production systems to which the model can be applied, whereas the applicability refers to how easy it is to apply the model (Thornton and Herrero, 2001). Ruminant production systems in the (Sub-)Tropics are very diverse and often limited in the quantity of data available to characterize the production systems (Mottet et al., 2017). This means any model improvements should optimally increase its applicability and render it easier to parameterize using the data available under tropical conditions (Hirooka and Yamada, 1990; Zom et al., 2012). Our modifications included the use of an adequate semi-mechanistic feed intake model (Chapter II) that ensures robustness and eliminates the need for a new intake model or re-parameterization when simulating different tropical production systems. In addition, applicability was improved by using fewer dietary parameters in modified than in the original LIVSIM when simulating the amount energy and nutrients available to the animals from their diets. For instance, we used metabolizable energy (already used parameter in the model) rather than fermentable metabolizable energy for estimating microbial protein synthesis. Along with other parameters (e.g., acid detergent insoluble nitrogen and feeding levels), the latter parameters were dropped in favor of more easily available parameters in tropical ruminant production systems (Chapter IV).

Therefore, the present thesis provides a ruminant herd model (i.e., modified LIVSIM) that can be employed stand-alone to adequately predict resources use and potential outputs of alternative management strategies for diverse ruminant production systems in the (Sub-)Tropics. More so, its modular nature (i.e., sub-modules are separated from one another) makes the modified LIVSIM an attractive candidate for integration into more comprehensive modelling frameworks with other biophysical and economic models. Such modelling frameworks will be suitable tools for investigating sustainable options and strategies for feeding a growing human population.

V.4 Challenges and limitations of the present thesis

One challenged faced within the present thesis was the issue of poor documentation of the software code of LIVSIM. This occurs amongst scientists involved in modelling, because the code is often not the priority but rather delivering research outputs for the topic under investigation (Holzworth et al., 2015). We depended mainly on comments within the code lines of LIVSIM and exchanges with developers from Wageningen University to understand and re-use the code. Consequently, adequate documentation of the model software is needed to facilitate the use of the LIVSIM by other researchers in the future.

There are two potential limitations to the findings of the present thesis. First, relates to the use of constants (e.g., metabolizable energy requirements for activity and conception) obtained from recommendations for ruminants in temperate regions in the modified LIVSIM. This was inevitable, because these data are lacking for tropical ruminant production systems, but further research is needed to generate these data. Second, the modified LIVSIM does not yet account for the effects of the environment (e.g., weather conditions) on the performance of the animals. However, environmental stress can have negative effects on productive and reproductive performance of ruminant livestock (Baudracco et al., 2012). Future development of the modified LIVSIM could leverage existing experimental data from tropical ruminant production systems that quantify the effect of environment (e.g., heat stress) on the animals.

V.5 Outlook and recommendations

The validation of simulation models is an important step for establishing any model (Bellocchi et al., 2010). Model validation is needed to establish how well a model's predictions agree with observations made in the real system being simulated. However, access to suitable data sets for validating models developed for tropical livestock production systems remains a significant challenge (Holzworth et al., 2015; Mottet et al., 2017). In Chapter four, the modified LIVSIM was evaluated using data from two (i.e., maize-lablab and oats-vetch) diets and 12 dairy cattle observations presented in (Mpairwe et al., 2003). The latter dataset does not represent the diversity diets or animal types or even production systems found in ruminant systems in the (Sub-)Tropics. Ergo, a larger and more diverse dataset than the one used in the present thesis is needed to validate the modified LIVSIM for ruminant production systems in the (Sub-)Tropics. Meta-datasets are very useful for evaluating simulation models like. Yet, many meta-datasets often fail to provide sufficient details to allow for data re-use, because details (e.g., ages or body weights of animals or some dietary parameters) are missing. In cases, when the data are available with sufficient details, the time scale may be too short, making them inadequate for ex-post validation of developed or improved models (Thornton and Herrero, 2001). Therefore, it will be very beneficial to the scientific community of livestock researchers if scientific journals increasingly scrutinize submissions under review for completeness of the data presented to foster the re-use of published data.

Furthermore, a proper documentation of the python-based software is needed to facilitate the re-use of the modified LIVSIM. Many models developed by researchers in agricultural sciences are often not re-used due to a lack of sufficient documentation of the model's software (Holzworth et al., 2015). As such, appropriate guidelines for documenting software code would be identified and implemented for the modified LIVSIM to facilitate its adoption amongst researchers in the (Sub-)Tropics. In addition, there is a need to compile experimental data from tropical ruminant production systems to develop robust and harmonized datasets for validating models' improvement in these regions (Jones et al., 2016). Open data policies could also be enforced by funding agencies to facilitate the development of and access to such databases for researchers working in tropical ruminant production systems.

Ruminant production systems in the (Sub-)Tropics are not limited to stall-fed systems, but also include grazing animals (Chapter II), which were not considered in the LIVSIM's adaption within the present thesis. Although LIVSIM contains a grazing routine (Rufino, 2008), it cannot be used when running the model stand-alone, since the model is not spatially explicit, creating the need for future work on the model to implement grazing animal in a spatially explicit manner. Nevertheless, in its present state, the modified LIVSIM needs to be integrated into a spatially explicit model to simulate grazing ruminants (Holzworth et al., 2015). The present thesis is part of a model integration project entitled "Underutilized or unprotected? New methods for analyzing diverging perspectives on the large-scale conversion of tropical grassland eco-systems" (SAVANNA[3]). On the one hand, economic research has suggested that the African Guinea Savanna zone is underutilized due to its large potential to increase global supply of agricultural products (Morris et al., 2009). On the other hand, environmental research has indicated that such a large-scale land use change could have many negative environmental consequences with regard to soil fertility, plant and animal biodiversity, and carbon sequestration (Ceballos et al., 2010; Foley et al., 2011; Johnson et al., 2014). In addition, there are major knowledge gaps regarding the governance of land use in this region, so that expanding smallholder crop farming has resulted in crop-livestock conflicts and outbursts of violence (Deininger and Byerlee, 2011).

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[3] https://www.uni-hohenheim.de/en/organization/project/underutilized-or-unprotected-new-methods-for-analyzing-diverging-perspectives-on-the-large-scale-conversion-of-tropical-grassland-eco-systems

Integrated biophysical and socio-economic modelling has been suggested as a suitable approach for evaluating future land use changes in the African Savanna regions (Lambin and Meyfroidt, 2011; Verburg et al., 2004). However, ruminant livestock models are often not included in such integrated modelling frameworks (Agarwal et al., 2002; Eitelberg et al., 2015; Schmitz et al., 2014). Consequently, the present thesis contributes to the SAVANNA project by providing a suitable model for integration (Figure V.1) to the already coupled land use change impact assessment model (**LUCIA**) and mathematical programming-based multi-agent systems (**MPMAS**) (Marohn et al., 2013). Basically, the MPMAS simulates a farmer and defines the initial herd size and structure as well as animal management strategies, and this information is then transferred via the LUCIA to the LIVSIM. Concurrently, data on pasture quantity and quality are generated from LUCIA and converted in an interface model between LUCIA and LIVSIM (i.e., trapezium shaped box in Figure V.1). Using this information, the LIVSIM then simulates the animal related processes and provides feedback data on feed intake, productive and reproductive performance, and manure quantity and quality. The models' coupling has been pre-tested (Marohn et al., 2018) and is currently in the final stage of implementation. For our future research agenda, the grazing routine of the original LIVSIM will be implemented to enable the livestock to graze and evaluated within the integrated models' framework and improved to adequately capture the complex aspects of ruminant foraging behavior on tropical pastures.

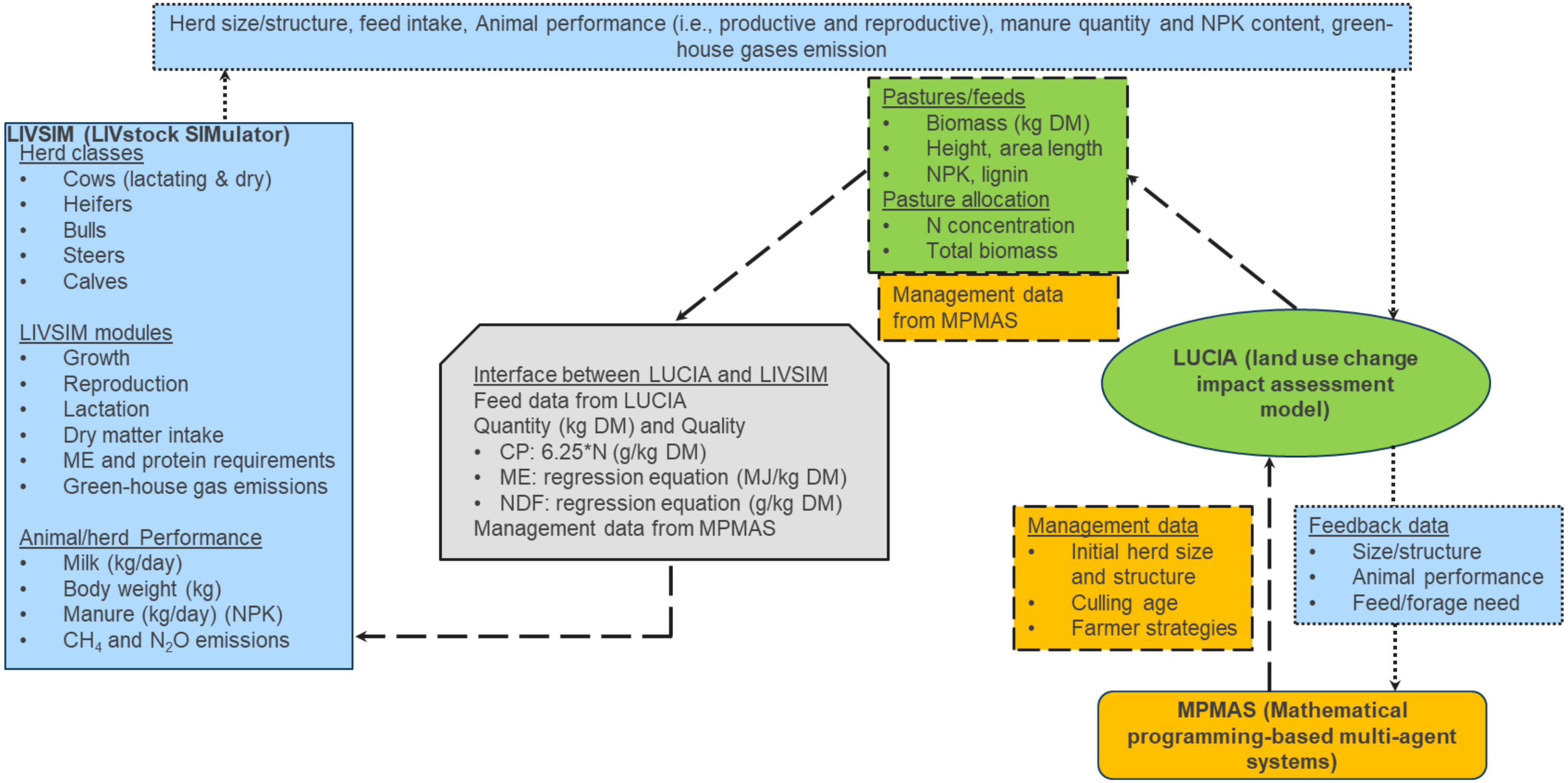

Figure V.1 Schematic representation of the data flow between the soft coupled LIVSIM to the already coupled LUCIA-MPMAS models. Rectangular boxes with broken lines represent data being exchanged between the models where each the colour of each box correspond to that of the model from which it originates. Arrows with broken lines show feedforward movement of data while those with dotted lines show feedback data reaching a particular model.
DM: dry matter, N: nitrogen, P: phosphorus, K: potassium, ME: metabolizable energy, NDF: neutral detergent fibre.

V.6 Conclusions

Ruminant livestock herd simulation models could play an important role in understanding and evaluating different management strategies for increasing resources use efficiency and productivity in the (Sub-)Tropics. The present thesis showed that existing state-of-the-art ruminant livestock herd models can assess resources use and potential outputs from different production systems in the (Sub-)Tropics. However, these models are still inadequate to holistically assess the environmental impacts associated with these production systems. This implies that further development of ruminant livestock herd models for tropical production systems needs to focus on improving the capacity of models to assess the different environmental impacts associated with production. Furthermore, results from the present thesis suggest that using data that quantify and characterize biological processes in tropical ruminant production systems rather than data from production systems in temperate regions can improve the prediction accuracy of existing ruminant herd models used in the (Sub-)Tropics. The latter finding confirms the fact that ruminant production systems in the (Sub-)Tropics differ from those in temperate regions and thus, models used in the former production systems need to be adapted using region specific data. Also, adapting existing state-of-the-art models as afore-suggested provided a more cost- and time-effective options than developing new models that can adequately to predict resources use and potential outputs of tropical ruminant systems.

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