

# Evaluation of LiGAPS-Beef to assess extensive pasture-based beef production in three agro-ecological regions in South Africa

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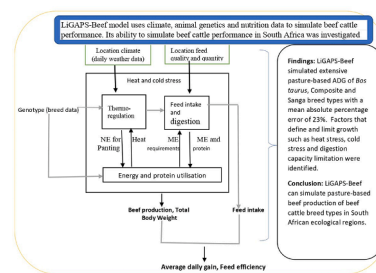
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## HIGHLIGHTS

- LiGAPS-Beef model was used to simulate growth of pasture-based beef cattle in South Africa.
- Simulated growth deviated 23%, or 0.078 kg per day from measured growth.
- The model identified factors that define and limit growth of beef cattle over time.
- Accurate estimates of metabolizable energy in feed are key when using LiGaps-Beef.
- The model can be used to develop resilience strategies for South African beef farms.

## GRAPHICAL ABSTRACT



## ARTICLE INFO

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## ABSTRACT

Quantifying the performance of beef cattle in diverse agro-ecological regions with different climatic conditions could be used by stakeholders to develop region-specific resilience strategies and optimize livestock production systems. This study evaluated the ability of the mechanistic LiGAPS-Beef model as a tool to quantify beef production of selected cattle breed types in diverse agro-ecological regions in South Africa. The average daily gain (ADG) was simulated for *Bos taurus*, composite and Sanga breed types in three different agro-ecological regions i.e. Bloemfontein (semi-arid), Phalaborwa (semi-desert) and Buffalo Berlin (temperate oceanic). Simulated ADGs were compared to measured ADGs from eight experiments for calibration and validation. After calibration, the model simulated ADG of breed types with a mean absolute percentage error (MAPE) of 23%. Simulated and measured values were positively correlated ( $r = 0.88$ ) and largely in agreement (index of agreement=0.92). Factors that define and limit growth, such as the genotype, heat stress, cold stress, and digestion capacity limitation, were identified. Consistent with literature, the model showed more heat stress on *Bos taurus* breed types than on composite and Sanga breed types in Phalaborwa, which was the warmest region included in the study. Sensitivity analysis by changing input parameters by  $\pm 10\%$  showed that the model was more sensitive to changes in metabolizable energy (ME) than crude protein (CP) implying that the accuracy of ME must be

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prioritised. Overall, the results showed that model performance was adequate and thus the LiGAPS-Beef model can be used to explore the effects of climate change and adaptive breeding strategies in future studies in South Africa.

## 1. Introduction

The negative impacts of climate change on agriculture in most African countries emanate mainly from an increase in ambient temperature, a decrease in precipitation and extreme weather events such as droughts and floods (Thornton et al., 2018). Over the past decades, the frequency of extreme weather events in South Africa has increased and average annual temperatures have risen by at least 1.5 times the global mean of 0.65 °C (Ziervogel et al., 2014). South African cattle production systems will need to adapt to hotter and drier conditions in particular, and to extreme weather events (Maluleke et al., 2020).

Livestock production is the largest sector of agriculture in South Africa, with a national cattle herd of 12.5 million beef and 1.6 million dairy cattle (Visser et al., 2020). Beef cattle production systems are dominated by extensive farming, with the most popular beef breeds being the locally developed Bonsmara and the indigenous Sanga (Nguni, Drakensberger, Tuli and Afrikaner) and some European (Hereford, Angus, Limousine, Simmentaler, Charolais and Dexter) breeds. Cattle production occurs in various agro-ecological regions e.g., semi-arid and temperate oceanic regions. The impact of climate change is likely to differ between cattle breeds and agro-ecological regions (Burrow, 2012; Traore et al., 2016; Descheemaeker et al., 2018). This must be addressed to improve and enhance resilience in cattle farming systems across regions (Lipper et al., 2014; Gil et al., 2017; Descheemaeker et al., 2018).

A comprehensive understanding of cattle performance and adaptation in their production environment under climate change is important for farmers and agricultural decision makers in developing strategies that result in resilient beef production systems (Descheemaeker et al., 2018). Simulation models are useful tools in evaluating and predicting the effects of climate change and the impacts of climate change adaptation on beef cattle production systems (Descheemaeker et al., 2018). However, simulation studies of livestock production are limited, especially of the possible effects of climate change on cattle production in various agro-ecological regions (Ramirez-Villegas et al., 2012; Descheemaeker et al., 2018; Rodriguez et al., 2017), because of a scarcity of appropriate simulation models.

Quantifying beef cattle production across heterogeneous production systems by simulation requires mechanistic models that integrate animals' genetics, climate, nutrition and herd management. This integration requires a hierarchy in growth factors. A framework that presents such a hierarchy in biophysical factors is referred to as the concepts of production ecology (Van de Ven et al., 2003; Van der Linden et al., 2015). This framework distinguishes potential, limited and actual production of livestock. Potential production is defined by the animals' genotype (i.e. breed) and the ambient climate. Limited production occurs when the defining factors such as genotype and climate as well as the limiting factors which include feed quality, available feed quantity and drinking water affect livestock production. The difference between limited production and actual production is caused by the reducing factors i.e. diseases, and stress (Van de Ven et al., 2003; Van der Linden et al., 2015).

The concepts of production ecology are the basis of the mechanistic model Livestock Simulator (LIVSIM) (Rufino et al., 2009), and the model family Livestock simulator for Generic Analysis of Animal Production Systems (LiGAPS). This model family consists of two mechanistic models, one for beef and one for dairy cattle (van der Linden et al., 2019a, 2021). LIVSIM has been applied to simulate smallholder dairy farms in the Kenyan highlands (Rufino et al., 2009), whereas LiGAPS-Dairy has been applied to simulate dairy cows in the Netherlands (van der Linden et al., 2021). LiGAPS-Beef has been used in

case studies in France, Australia, Uruguay and The Netherlands at animal and herd level (Linden et al., 2019a). LiGAPS-Beef and LiGAPS-Dairy are the only models based on production ecology that include the effect of climate on cattle growth and production mechanistically (Van der Linden et al., 2019a).

The LiGAPS-Beef model integrates three sub-models that jointly simulate production and growth of beef cattle. In its entirety, the model simulates the interactions between cattle genotype, climate, feed quality, and available feed quantity. Although this model has been evaluated for beef production systems in Europe, Australia and Uruguay (Van der Linden et al. 2019c), the extent to which it can be used to simulate cattle productivity in a South African context has not yet been investigated. This study aims to evaluate (through calibration and validation using experimental data) the LiGAPS-Beef model as a tool to assess pasture-based beef production as represented by the average daily gain (ADG) of selected cattle breed types under South African conditions.

## 2. Materials and methods

### 2.1. Study areas

The predictive capability of the LiGAPS-Beef model for ADG and the biophysical factors that influence growth was assessed in three agro-ecological regions (semi-desert, semi-arid, and temperate oceanic) located in three South African provinces (Free State, Limpopo, Eastern Cape). Since agro-ecological conditions differ in South African provinces, the locations Bloemfontein, Phalaborwa, and Buffalo Berlin were selected within Free State, Limpopo and Eastern Cape, respectively to represent semi-arid, arid/semi-desert and temperate oceanic agro-ecological regions. Beef cattle farming is dominant in these regions. Climate information of the study areas is shown in Table 1.

### 2.2. Description of Ligaps-Beef model

LiGAPS-Beef is an R-based model (R version 2.15.3; RCore Team, 2013) with a daily time step. The model is deterministic and integrates three sub-models, namely thermoregulation, feed intake and digestion, and energy and protein utilization, which jointly simulate production and growth of bovine animals. The thermoregulation sub-model specifically simulates heat release from the animal to the ambient environment, and its equations are based on McGovern and Bruce (2000) and Turnpenny et al. (2000a and 2000b). The feed intake and digestion

**Table 1**

Climatic characteristics of three locations included in the study.

Location	Climatic characteristics
Bloemfontein:	Altitude: 1227 m; Tropical and subtropical steppe (semi-arid) climate; Hot summers and cold, dry winters. Average summer temperature = 23 °C; average winter temperature = 8 °C Average annual rainfall: 300–600 mm
Buffalo Berlin	Altitude: 391 m; Temperate oceanic climate; Mild, generally warm and temperate climate Annual average temperature = 18 °C; average annual highest temperature = 30.6 °C; average annual lowest temperature = 7.9 °C Average annual rainfall = 850 mm
Phalaborwa	Altitude: 410 m; Hot semi-arid subtropical (hot semi-desert) climate; Hottest summers in South Africa, up to 45 °C, Average summer temperature = 30 °C; average winter temperature = 17 °C Average annual rainfall = 353 mm

Source: Climate data for cities worldwide (<https://en.climate-data.org/>).

sub-model simulates feed digestion based on the rumen model of [Chilibroste et al. \(1997\)](#). The outputs of this sub-model are ME and digested proteins which are inputs to the energy and protein utilisation sub-model. The energy and protein utilisation sub-model distributes the energy and protein to the various metabolic processes which include maintenance, physical activity, growth, gestation, and lactation ([Van der Linden et al., 2018a](#)).

Overall, the inputs to the LiGAPS-Beef model are 89 generic parameters for cattle, 27 breed-specific parameters (Table S1), 24 diet or feed composition parameters, and daily weather data ([Van der Linden et al., 2019a](#)). The minimum diet or feed composition input parameters required to simulate beef production are digestibility, metabolizable energy (ME) and crude protein (CP) (Table S2), while empirical equations were used to calculate some essential feed parameters (i.e. heat increment of feeding (HIF), fill units (FU), soluble non-structural carbohydrates (NSC)) from digestibility and CP. The main outputs of the model are ADG, beef production (boneless meat), feed efficiency (FE) (beef per kg dry matter consumed), feed intake, total body weight (TBW) (Table S3), and the biophysical factors that define and limit growth over time. Defining factors in the model are genotype and climate (heat and cold stress) and the limiting factors are feed quality and available feed quantity. Limitation related to feed quality occurs when the maximum capacity for feed digestion in the animal's gastro-intestinal tract is fully utilized and nutrient supply is insufficient to support potential growth. Limitation related to feed quantity occurs when the availability of feed limits intake and consequently nutrient requirements of the animals are not met ([Van Der Linden et al., 2019a](#)). This therefore results in protein or energy deficiency. [Van der Linden et al. \(2018a\)](#) and Supplementary Information of [Van der Linden et al. \(2019\)](#) provide a detailed description of the input and output parameters for LiGAPS-Beef.

### 2.3. Data collection

This study classified breeds in three breed types, namely exotic (*Bos taurus*), indigenous/Sanga (a cross between African taurine and *Bos indicus*) and composite, as was done by [Makina et al. \(2016\)](#). A composite is defined as a breed made up of at least two component breeds

(such as *Bos taurus* × Sanga), designed to retain heterosis in future generations. Genetic parameters for individual breeds were obtained as secondary data from literature and the SA Stud Book, which grouped the data as breed types. The genetic parameters used as input for the model included Gompertz curve parameters to describe growth such as, maximum bodyweight, birth weight, and carcass percentage as well as coat characteristics such as hair length (Table S1). Daily climate input data (temperature, rainfall, wind speed, vapour pressure, and solar radiation) from 2008 to 2020 were obtained from the South African Weather Service for the three agro-ecological regions. Climate data before the year 2008 were incomplete and were, therefore, not used as input for LiGAPS-Beef.

The pasture-based diets of beef cattle largely consisted of *Digitaria eriantha*, *Themeda triandra*, *Cymbopogon citratus* and *Eragrostis curvula* in Bloemfontein; *Panicum maximum*, *Digitaria eriantha*, *Themeda triandra*, *Eragrostis curvula*, *Penisetum clandestinum* and *Cynodon dactylon* in Buffalo Berlin; and *Eragrostis rigidior*, *Digitaria eriantha*, *Panicum maximum* and *Urochloa mozambicensis* in Phalaborwa ([Du Plessis et al., 2004, 2007; Esterhuizen et al., 2008; Muchenje et al., 2008; Mapiye et al., 2010; Mashiloane et al., 2012](#)). The average metabolisable energy (ME) content and crude protein (CP) content of these plant species for the specific experimental periods were collected through a review of published academic literature ([Feedipedia 2021; Engelbrecht, 2002; Gulwa et al., 2017; Ravhuhali et al., 2019](#)). The ME and CP content of the total cattle diet was calculated as the weighted average (DM basis) of the ME and CP contents of the individual plant species during the specific experimental period. Since there was a lack of data (in terms of longitudinal studies on pasture quality in South Africa), fixed averages were used (Table S2). Thus, seasonal variations in the quality of pasture were not included in the model. Based on digestibility or ME and CP content, empirical equations were used to calculate some parameters (i.e. HIF, FU, NSC) from digestibility and CP, and the rest were fixed.

Experimental data on average ADG were collected from 8 studies ([Table 2](#)). Aggregated data and averages of individual animals from these experiments were used. In the experiments where animals were fasted before weighing, the fasted body weight was assumed to represent 90% of the total body weight. For the experiments by [Du Plessis et al.](#)

**Table 2**

Summary description of experimental datasets used in the study. The initial age is the age of animals at the start of an experiment.

Number simulation <sup>1</sup>	Location	Breed	Number of animals	Initial age (days)	Experiment duration (days)	References experiment
1	Bloemfontein	Composite	20	228	100	<a href="#">Esterhuizen et al., 2008</a>
2	Bloemfontein	Composite	20	228	101	<a href="#">Esterhuizen et al., 2008</a>
3	Phalaborwa	<i>Bos taurus</i>	9	237	311	<a href="#">Du Plessis et al., 2004</a>
4	Phalaborwa	Composite	9	237	311	<a href="#">Du Plessis et al., 2004</a>
5	Phalaborwa	Sanga	18	237	311	<a href="#">Du Plessis et al., 2004</a>
6	Phalaborwa	<i>Bos taurus</i>	13	237	493	<a href="#">Du Plessis et al., 2004</a>
7	Phalaborwa	Composite	17	237	493	<a href="#">Du Plessis et al., 2004</a>
8	Phalaborwa	Sanga	21	237	493	<a href="#">Du Plessis et al., 2004</a>
9	Phalaborwa	<i>Bos taurus</i>	16	237	675	<a href="#">Du Plessis et al., 2004</a>
10	Phalaborwa	Composite	17	237	675	<a href="#">Du Plessis et al., 2004</a>
11	Phalaborwa	Sanga	30	237	675	<a href="#">Du Plessis et al., 2004</a>
12	Buffalo Berlin	<i>Bos taurus</i>	15	205	342	<a href="#">Muchenje et al., 2008</a>
13	Buffalo Berlin	Composite	15	205	342	<a href="#">Muchenje et al., 2008</a>
14	Buffalo Berlin	Sanga	15	205	342	<a href="#">Muchenje et al., 2008</a>
15	Bloemfontein	<i>Bos taurus</i>	15	212	182	<a href="#">Cilliers et al., 1995</a>
16	Bloemfontein	<i>Bos taurus</i>	15	212	182	<a href="#">Cilliers et al., 1995</a>
17	Phalaborwa	Composite	354	355	210	<a href="#">Mashiloane et al., 2012</a>
18	Phalaborwa	Sanga	345	372	205	<a href="#">Mashiloane et al., 2012</a>
19	Phalaborwa	<i>Bos taurus</i>	50	237	493	<a href="#">Du Plessis et al., 2007</a>
20	Phalaborwa	Composite	50	237	493	<a href="#">Du Plessis et al., 2007</a>
21	Phalaborwa	Sanga	50	237	493	<a href="#">Du Plessis et al., 2007</a>
22	Buffalo Berlin	Sanga	10	578	60	<a href="#">Mapiye et al., 2010</a>
23	Buffalo Berlin	Sanga	10	578	60	<a href="#">Mapiye et al., 2010</a>
24	Buffalo Berlin	Sanga	10	578	60	<a href="#">Mapiye et al., 2010</a>
25	Buffalo Berlin	<i>Bos taurus</i>	14	205	342	<a href="#">Muchenje et al., 2009</a>
26	Buffalo Berlin	Composite	29	205	342	<a href="#">Muchenje et al., 2009</a>
27	Buffalo Berlin	Sanga	34	205	342	<a href="#">Muchenje et al., 2009</a>

<sup>1</sup> Simulations 1–14 were used for model calibration and simulations 15–27 were used for model validation.

(2007), it was assumed that the average of data for slaughter at 18 and 30 months represented a slaughter age of 24 months. The eight studies resulted in a total of 27 experimental treatments (combinations of location and breed), which allowed the authors to conduct 27 simulations (Table 2). All animals in the experiments were bull calves or steers. Animals grazed on pasture and were not kept in stables or confinements during parts of the day. Animals in experiments 1, 2, 23 and 24 were provided small amounts of supplements and this was also factored into the model during simulations.

## 2.4. Model calibration and validation

Based on the low stocking rate range of 10 to 12 hectares per livestock unit reported in the experiments, pasture biomass was assumed to allow ad libitum feed consumption in all experiments. Furthermore, the effects of reducing factors, livestock diseases and stress, were assumed to be minor. Given these assumptions, the measured ADGs in the experiments corresponded to simulated ADGs under feed quality limited production. The model was calibrated, therefore, at animal level under feed quality limited conditions. The calibration dataset contained the measured data associated with simulations 1–14 (55.5% all experimental treatments). When we split the experiments to have 55.5% of combinations in calibration, it is where the authors could have maximum number of experiments represented both on calibration and on validation. The calibration dataset contained all combinations of breed types and agro-ecological regions, except for the Sanga and *Bos taurus* breed type in Bloemfontein (Table 2). The breed type, climate, and pasture-based diet in the individual experiments were used as model inputs for the individual simulations.

The LiGAPS-Beef model was adjusted in such a way that the simulated TBW at the start of an experiment corresponded with the measured TBW at the start of the experiment. The simulated and measured ADG (kg per day) were calculated as the difference in simulated and measured TBW (kg) between the start and end of the experiment, divided by duration of the experiment (days). The root mean square error (RMSE) between simulated and measured ADGs was used as an indicator for model accuracy. The model was also parameterised to produce a table indicating the percentage time that a factor defined or limited ADG for all simulations. During calibration, the RMSE was minimized by adjusting breed-specific parameters. Parameters adjusted for the exotic breed type were maintenance correction factor, maximum carcass fraction, lipid bone parameter, maximum muscle to bone ratio and maximum latent heat release (Table 3). Those adjusted for the Sanga breed type were maximum latent heat release, maximum muscle to bone ratio and Gompertz curve parameters except birth weight (Table 3). Only minimum conduction body core and latent heat release were adjusted for the composite breed type (Table 3). The parameter for feed intake capacity was decreased from 0.12 fill units per kg metabolic body weight per day by 0.02 for all breeds. The model was calibrated until adjusting the parameters did not reduce the RMSE further. After model

calibration, the model was validated with an independent dataset that contained the measured data associated with simulations 15–27 (Table 2).

## 2.5. Model accuracy and statistical analysis

Model accuracy during validation was described by various statistical indicators, namely the correlation coefficient (*r*), mean absolute error (MAE), mean absolute percentage error (MAPE), root mean square error (RMSE), relative RMSE and index of agreement (*d*).

The MAE and RMSE were calculated from the measured (i.e. observed) values (*O*), the simulated values (*S*) and the sample size (*n*) Eqs. (1) and (2). These indicators reflect the deviation of simulated performance values from the measured values in absolute terms. The MAPE and relative RMSE reflect the deviation of simulated values from the measured values in relative terms. The index of agreement (*d*) is a standardized measure of the degree of model prediction error, which varies between 0 and 1 (Eq. (3)). It represents the ratio of the mean square error (MSE) and the potential error. A *d* value of 1 indicates a perfect match, whereas 0 indicates no agreement at all. The index of agreement can detect additive and proportional differences in the observed and simulated means and variances, but it is sensitive to extreme values because of the squared differences.

Eq. (1):

$$MAE = \frac{\sum |O - S|}{n} \quad (1)$$

Eq. (2):

$$RMSE = \sqrt{\frac{\sum |O - S|^2}{n}} \quad (2)$$

Eq. (3):

$$d = 1 - \frac{\sum |O - S|^2}{\sum (|O - \bar{S}| + |O - \bar{O}|)^2} \quad (3)$$

## 2.6. Sensitivity analysis

The establishment of model inputs that most affect the simulated parameters provides insights into inputs that need to be prioritized to increase the accuracy of the model (Zuidema et al., 2005; Van der Linden et al., 2019b). It is important to prioritize parameters with high uncertainty and high variability across the conditions under investigation. For instance, the CP contents of grasses in the grass-based diet vary significantly across species and seasons.

Diet quality in the simulations was the most uncertain factor because the simulations were performed on pasture-based extensive systems with high temporal variation. Sensitivity analysis (expressed as percentage change in ADG from the baseline ADG) was used to assess the effect on model outputs (ADG) of changing ME and CP contents. These

**Table 3**

Adjustments made to the input parameters for the LiGAPS-Beef model during model calibration.

Parameter <sup>1</sup>	<i>Bos taurus</i>		Composite		Sanga	
	Before calibration	After calibration	Before calibration	After calibration	Before calibration	After calibration
Maximum adult TBW (kg) (Gompertz curve)	–	–	–	–	781.46	917.44
Constant of integration (Gompertz curve)	–	–	–	–	4.20	1.80
Rate constant (Gompertz curve)	–	–	–	–	1.50	1.10
Gompertz reduction (Kg TBW)	–	–	–	–	11.46	147.44
Maintenance correction factor	1.00	0.97	–	–	–	–
Lipid bone parameter	11.00	11.10	–	–	–	–
Maximum carcass fraction%	0.58	0.61	–	–	–	–
Maximum muscle: bone ratio	4.50	4.40	–	–	4.30	4.10
Minimum conduction body core skin	–	–	1.225	1.10	–	–
Maximum latent heat release	3.08	4.00	3.985	4.50	4.89	7.50

<sup>1</sup> Detailed description of LiGAPS-Beef input parameters are found in a paper by Van der Linden et al. (2019a).



selected nutrition parameters have wide variability across ecological regions (Villalba et al., 2021) and this justified their selection for sensitivity analysis. Each of the selected parameters was decreased and increased by 10%, whereas all other parameters were kept at their original values according to the one-at-a-time approach (Pianosi et al., 2016). All simulations 1–27 (Table 2) were used for sensitivity analysis. The aggregated ADG for each breed type in an ecological region was used to calculate the percentage change from the baseline ADG.

### 3. Results and discussion

#### 3.1. Model calibration

The relative RMSE and MAPE for the calibrated model were 16.6% and 12.2% of the measured ADG, respectively. Fig. 1 shows the residuals, regression and 1:1 line for the simulated and measured ADGs of breed types for calibration across the agro-ecological regions. Calibration results in this study were comparable to calibration results of the LiGAPS-Beef model for a study in Australia where RMSE and MAPE were 14.4% and 11.3%, respectively (Van der Linden et al., 2019c). Based on these results, the model was considered to be well calibrated.

#### 3.2. Model validation

When all datasets for model validation (Simulations 15–27, Table 2) were used, the RMSE was 0.306 kg TBW per day, or 65.9% of the

measured ADG while the MAPE was 0.181 kg TBW per day, or 39% of the measured ADG. This represented a model accuracy of 61%. This low model performance was caused by large deviations between ADGs in the experiment from Cilliers et al. (1995) (Simulations 15–16). The two simulated ADGs for the experiment by Cilliers et al. (1995) (0.19 and 0.61 kg TBW per day) were significantly lower than the measured ADGs (0.93 and 1.37 kg TBW per day). In this experiment, the measured feed intake was 4.5 kg DM per head per day on unfertilized veld. The CP content was 7.7% and the ME content was 8 MJ ME per kg DM, resulting in a total intake of 36 MJ ME per head per day. It is therefore not clear how the animals could have met the requirements for maintenance and grazing and in addition grow more than 0.9 kg per day with this level of ME intake. It is postulated that either the ADG was overestimated, or the feed intake and/or quality was underestimated. Alternatively, other factors that influenced ADG were not described in the original paper. For this reason, the results for model validation are reported without the two simulated ADGs from the experiment by Cilliers et al. (1995).

When the remaining independent data sets (Simulations 17–27) were used for model validation, simulated and measured ADG values generally corresponded to each other (Fig. 2). Residuals did not significantly deviate from zero ( $P > 0.05$ ) and did not show an increasing or decreasing trend (Fig. 2). This means that there was no significant systematic bias in the calibration results, and that LiGAPS-Beef was able to capture the variability in the measured ADGs.

After exclusion of the two simulated ADGs from the experiment of

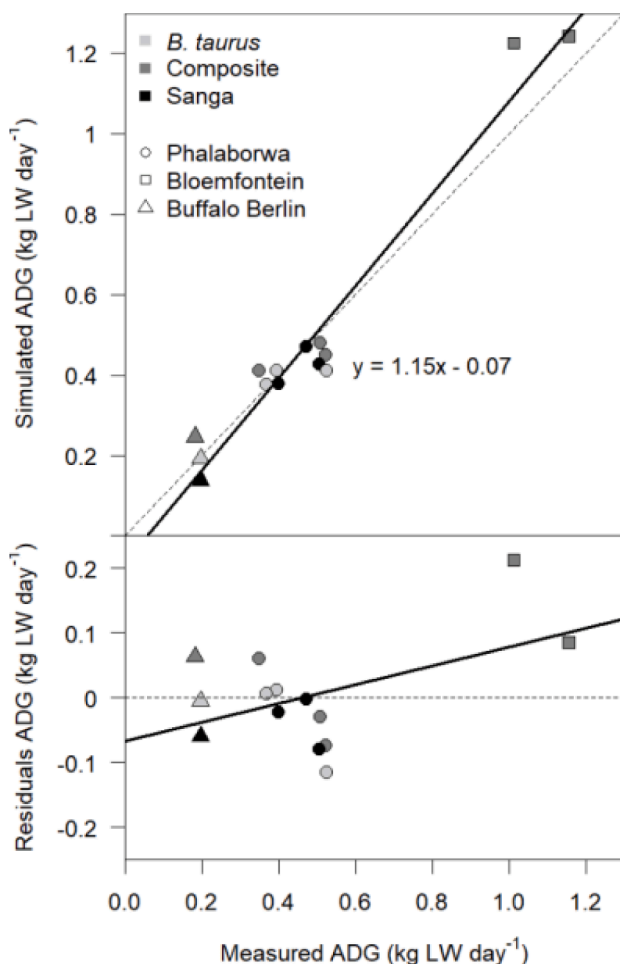


Fig. 1. Simulated and measured ADGs of breed types for calibration (experiments 1–14 in Table 2). The solid line indicates the regression line and the dashed line indicates the 1:1 line.

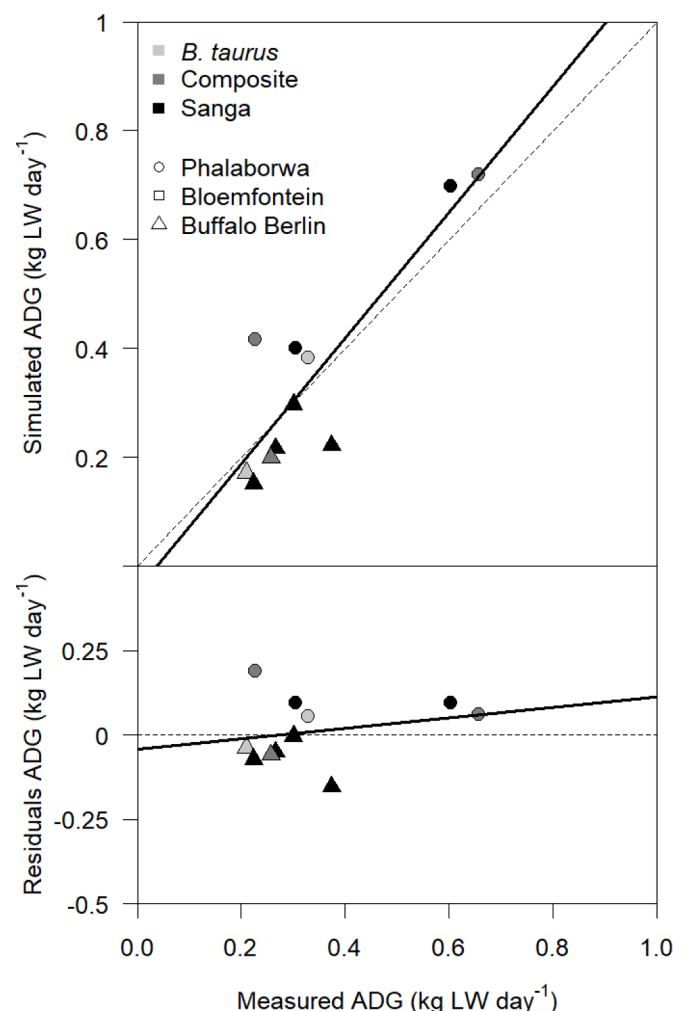


Fig. 2. Simulated and measured ADG of breed types for validation (experiments 17–27 in Table 2). The solid line indicates the regression line, and the dashed line indicates the 1:1 line.

Cilliers et al. (1995), the RMSE was 0.092 kg TBW per day, or 27% of the measured ADG. The MAPE was 0.078 kg TBW per day, or 23% of the measured ADG. As expected, the RMSE and MAE were lower under calibration than under validation, as parameters were adjusted to minimise the RMSE during calibration. Nevertheless, based on simulations 17–27, the MAPE for validation in this study represented an accuracy rate of 77%. This was comparable with levels of model accuracy reported in a study with datasets from Europe, Australia, and Uruguay, which reported MAPE values of 10% to 25% (Van der Linden et al., 2019c).

Simulated and measured values were highly positively correlated for simulations 17–27 ( $r = 0.88$ ). The accuracy of the LiGAPS-Beef model in simulating ADG was further corroborated by strong agreement between simulated and measured values, as shown by an index of agreement of 0.92. According to the aim of this paper, the simulated ADGs showed an acceptable level of representation of measured ADGs from experiments across all breed types based on all statistical indicators used to evaluate the model. The validation dataset contained contrasting breed types, agro-ecological regions and feed quality levels such that any bias associated with the model would have been reflected in the results. There are no universally fixed criteria for judging MAPE and relative RMSE (Van der Linden et al., 2019c), because of practical implications of accuracy levels. Whether a model's accuracy is sufficient depends on the aim for which it has been developed. Considering that the study was performed under data constrained conditions (limited data availability), a MAPE of 23% was considered acceptable for simulation of beef production in South Africa.

Several factors present challenges when simulating performance in natural ecosystems (Svinurai et al., 2021), such as minor climatic variations, even in the same region (Ovando et al., 2018), seasonal fluctuations in vegetation structure (Kumar et al., 2016), and the presence of non-dominant grass species that are not fully accounted for. In this study, the exact weather data for most experiments was unknown, and we used data from the nearest weather station. Some of the experiments were conducted before 2008, whereas complete weather data from nearby weather stations were only available from 2008 onwards.

Although this was addressed by using climate data of the closest years and for the same months, a part of the MAPE and relative RMSE thus might be caused by the use of weather data for different years. Additionally, the clustering of cattle breeds into three major breed types could introduce non-random errors, which have a bearing on differences between simulated and observed results. Some steers might also have received hormone implants, although this was not reported in the literature on the experiments. If so, they could have induced differences between animals of the same breed (type) with and without implants.

Feed quantity could be another source of bias since the study assumed that production was feed quality limited, and feed (pasture biomass) was available ad libitum. Nevertheless, feed quantity limitation was not expected due to low stocking rates which ranged from 10 to 12 hectares per livestock unit for the calibration and validation experiments. Furthermore, the effects of other limiting factors which include vitamins, minerals, drinking water and the reducing factors diseases and stress were not fully accounted for in the study and could have contributed to the MAPE of 23%. However, the extent to which these factors may have affected performance of the model seems limited given the low MAPE, high positive correlation and high index of agreement between measured and simulated ADGs.

Overall, the model was successfully validated with an accuracy of 77% an index of agreement of 0.92. These results indicate that LiGAPS-Beef could be used to simulate ADGs of different beef cattle breeds in extensive pasture-based farming systems in South Africa.

### 3.2. Evaluation of defining and limiting factors

The output of LiGAPS-Beef indicates the factors that defined and limited growth during the experiments. The percentage time that a factor defined or limited ADG for simulations (1–27) is shown in Table 4 and the visualisations are shown in Figures S1–S27. As expected, the growth of Sanga cattle breed types was less influenced by heat stress than that of the other two breed types, while the growth of composite cattle was less influenced by heat stress than the growth of *Bos taurus* breed type (Table 4). This corresponds to literature reporting that *Bos*

**Table 4**

Defining and limiting factors for growth and beef production of the breed types in the three ecological regions (simulations 1–27) expressed as a percentage of the experimental period.

Simulation	location	Breed	%Genotype	%Heat stress	%Cold stress <sup>1</sup>	%Digestion capacity <sup>1</sup>
1	Bloemfontein	Composite	47.0	40.0	0.0	13.0
2	Bloemfontein	Composite	41.6	40.6	0.0	17.8
3	Phalaborwa	<i>Bos taurus</i>	1.6	58.0	0.0	40.4
4	Phalaborwa	Composite	1.0	42.9	0.0	56.1
5	Phalaborwa	Sanga	1.9	25.6	0.6	72.4
6	Phalaborwa	<i>Bos taurus</i>	0.0	45.5	0.0	54.5
7	Phalaborwa	Composite	0.4	28.1	0.0	71.5
8	Phalaborwa	Sanga	0.8	16.0	0.4	83.2
9	Phalaborwa	<i>Bos taurus</i>	11.8	59.8	0.0	28.4
10	Phalaborwa	Composite	7.0	46.0	0.0	47.0
11	Phalaborwa	Sanga	5.9	32.0	0.3	62.1
12	Buffalo Berlin	<i>Bos taurus</i>	0.0	0.0	2.3	100.0
13	Buffalo Berlin	Composite	0.0	0.0	9.9	100.0
14	Buffalo Berlin	Sanga	0.0	0.0	75.4	100.0
15	Bloemfontein	<i>Bos taurus</i>	0.0	0.0	0.0	100.0
16	Bloemfontein	<i>Bos taurus</i>	0.0	1.2	0.0	98.8
17	Phalaborwa	Composite	39.5	49.1	0.0	11.4
18	Phalaborwa	Sanga	28.3	49.1	2.4	18.5
19	Phalaborwa	<i>Bos taurus</i>	0.4	40.1	0.0	59.5
20	Phalaborwa	Composite	0.4	26.1	0.0	73.5
21	Phalaborwa	Sanga	2.0	17.0	0.4	81.0
22	Buffalo Berlin	Sanga	0.0	0.0	59.0	100.0
23	Buffalo Berlin	Sanga	0.0	0.0	54.2	100.0
24	Buffalo Berlin	Sanga	0.0	0.0	42.6	100.0
25	Buffalo Berlin	<i>Bos taurus</i>	0.0	0.0	5.0	100.0
26	Buffalo Berlin	Composite	0.0	0.0	24.9	100.0
27	Buffalo Berlin	Sanga	0.0	0.0	73.7	100.0

<sup>1</sup> Cold stress and digestion capacity constraints can occur simultaneously and in such cases the sum of the percentages can be above 100%.

*taurus* cattle are less capable in coping with high temperatures than native tropical breeds (Mwai et al., 2015; Rocha et al., 2019; Cooke et al., 2020). Heat stress is often used as a measure of cattle adaptability to an ecological region. Low heat stress in composite breed types corresponded with studies by Scholtz et al. (2008), Webb et al. (2017) and Van Marle-Köster et al. (2021), which reported that the Bonsmara, a composite breed developed specifically for South African arid and semi-arid conditions, was well adapted to the main South African beef production regions.

The highest occurrence of heat stress was expected and simulated for Phalaborwa (Table 4) as the region has the highest average temperatures (Table 1). The differences in the occurrence of heat stress across three regions in this study agreed with earlier results (Mpofu et al., 2017; Webb et al. (2017). Mpofu et al. (2017) indicated that South African agro-ecological regions had a significant influence ( $P < 0.01$ ) on feed efficiency and ADG of Nguni cattle. They reported that heat stress affected feed efficiency and ADG significantly and adversely in arid regions. ADG of Nguni cattle raised in the humid region was 9% higher than that of Nguni cattle raised in the arid region (Mpofu et al., 2017).

Cold stress occurred in Buffalo Berlin (the region with the lowest average temperature), and the *Bos taurus* cattle breed had the lowest percentages of time it suffered from cold stress. The occurrence of cold stress in Buffalo Berlin agrees with reported cold stress in beef cattle in winter (Toghiani et al., 2020). While all breeds suffered from cold stress in Buffalo Berlin, the *Bos taurus* breed group had the lowest percentages of cold stress. This was expected as *Bos taurus* breed types are known to be more adapted to temperate climates and colder conditions (DAWE, 2021).

Energy and protein limitation due to feed availability did not occur since feed was available ad libitum. However, energy and protein did limit growth when maximum digestion capacity was reached. If an animal cannot consume more feed for this reason, energy or protein will limit growth as a consequence. The limitation in digestion capacity that occurred (Table 4) thus indirectly reflected a limitation in energy and protein due to digestion capacity limitation. This was more pronounced in Buffalo Berlin and in all experiments where animals were not supplemented (Table 4). The differences in the extent to which digestion capacity limited production is explained by the differences in the pasture quality in the experiments. For instance, simulations 1 and 2 in Bloemfontein included supplementation resulting in a relatively high feed ME and CP content (Table S2). In all experiments in Phalaborwa, the animals grazed on sweet veld. Sweet veld is known to have high CP values during the summer season and high digestibility during the summer and winter seasons (Nqeno, 2008; Ndlovu et al., 2009). Energy

and protein limitations were thus minimal in Phalaborwa. This explains the low observed digestion capacity limitation compared to Buffalo Berlin. The vegetation in Buffalo Berlin is mixed and sour veld which significantly loses its nutritive quality (CP can decline to 7%) during the winter season (Muchenje et al., 2009). Thus, improving digestibility of the pasture is expected to decrease digestion limitation and increase ADG considerably in Buffalo Berlin. The defining and limiting biophysical factors identified by LiGAPS-Beef were thus generally in line with expectations and literature.

#### 4. Sensitivity analysis

The one-at-a-time approach used during sensitivity analysis is a structured procedure that is normally used if standard deviations are not known, as in this study. Sensitivity results of changing ME and CP by  $\pm 10\%$  are presented in Table 5. There was no simulation for the Sanga breed type in Bloemfontein on sensitivity analysis because the experimental data sets used for calibration and validation (Table 2) did not have Sanga breed type in Bloemfontein.

For Buffalo Berlin, simulations 12, 14, 25, 26 and 27 did not contribute to the average ADG results when ME was changed by  $-10\%$  because the model did not generate results. These simulations had low baseline pasture quality such that the resulting diet energy after decreasing ME by 10% was below the minimum threshold to maintain and support growth of animals. Hence, the animals lost too much weight (ran out of fat reserves) and would not survive up to the end of the experiments. Simulated baseline ADG was significantly different ( $P = 0.0028$ ) from simulated ADG when ME was changed by  $\pm 10\%$ . The ADG was generally more sensitive to a 10% increase or decrease in ME across agro-ecological zones and breed types (Table 5). This suggested that users of LiGAPS-Beef should prioritize the accuracy of the ME content when collecting nutrition data in South African agro-ecological regions.

Simulated ADG significantly differed across breeds ( $P = 0.017$ ) and across agro-ecological zones ( $P = 0.0016$ ) during sensitivity analysis. The sensitivity of the model to changes in ME was highest in Buffalo Berlin and in the *Bos taurus* breed type across all ecological regions. Based on the simulations, different breeds within the same agro-ecological zone showed similar ADG trends to an increase or decrease in ME by 10%. Overall, ADG response to changes in ME was more pronounced amongst breeds: With an increase in ME by 10% (5.6% (Composite) vs. 42.1% (*Bos Taurus*) in Bloemfontein; 48.4% (Sanga) vs 64.5% (*Bos Taurus*) in Phalaborwa; and 229.9% (Sanga) vs 292.0% (*Bos Taurus*) in Buffalo Berlin). This could imply that the sensitivity of ADG

**Table 5**

Changes in ADG (kg/day) of breed types after changing ME and CP by  $\pm 10\%$  across Bloemfontein, Phalaborwa and Buffalo Berlin.

Location	Parameter	Baseline ADG (kg/day)	<i>Bos taurus</i>		Baseline ADG (kg/day)	Composite		Baseline ADG (kg/day)	Sanga	
			$-10\%$ ADG (kg/day)	$+10\%$ ADG (kg/day)		$-10\%$ ADG (kg/day)	$+10\%$ ADG (kg/day)		$-10\%$ ADG (kg/day)	$+10\%$ ADG (kg/day)
Bloemfontein	ME	0.401	0.221	0.566	1.233	0.710	1.303	–	–	–
	% change		–44.9%	41.2%		–42.4%	5.6%	–	–	–
Bloemfontein	CP	0.401	0.385	0.414	1.233	1.229	1.236	–	–	–
	% change		–4.0%	3.1%		–0.3%	0.2%	–	–	–
Phalaborwa	ME	0.394	0.114	0.649	0.495	0.203	0.751	0.475	0.187	0.705
	% change		–71.0%	64.5%		–59.0%	51.6%		–60.7%	48.4%
Phalaborwa	CP	0.394	0.382	0.403	0.495	0.480	0.508	0.475	0.456	0.492
	% change		–3.1%	2.1%		–3.0%	2.6%		–4.0%	3.7%
Buffalo Berlin	ME	0.183	<sup>1</sup>	0.717	0.223	–0.060 <sup>2</sup>	0.754	0.206	–0.046 <sup>2</sup>	0.679
	% change		<sup>1</sup>	292.0%		–127.0% <sup>2</sup>	237.6%		–122.4% <sup>2</sup>	229.9%
Buffalo Berlin	CP	0.183	0.171	0.190	0.223	0.212	0.232	0.206	0.195	0.214
	% change		–6.2%	3.9		–4.9	3.7		–5.4	4.2

<sup>1</sup> No results because simulations 12 and 25 did not contribute to the average ADG.

<sup>2</sup> Fewer ADGs because simulations 14, 26 and 27 did not contribute to the average ADG.

to changes in ME is breed-dependant. Furthermore, ADG responses to changes in ME (+/−10%) followed similar trends across agro-ecological zones, though they varied considerably. ADG response to a 10% increase and 10% decrease in ME was respectively 4.5 to 52.4 and 1.9 to 3.0 times higher in Buffalo Berlin than in the other two sites. This means that the sensitivity of ADG to change in ME varies across agro-ecological zones.

As with ME, ADG was generally sensitive to a 10% increase or decrease in CP across agro-ecological zones and breed types (Table 5). Simulated ADG differed significantly across agro-ecological zones ( $P = 0.00006$ ) and across breed types ( $P = 0.0028$ ). A change in CP content of feed is expected to influence the ADG of beef cattle (Chipa et al., 2012; Nyambali et al., 2022). Changes in ADG were, however, smaller with a change in CP than with a change in ME (Table 5). This was expected since CP content due to feed availability was not a limiting factor for growth, whereas ME content affects the occurrence of heat stress, cold stress and digestion capacity. Moreover, changing the CP content resulted in a slight change in total feed digestibility and consequently in ME content. Changes in ADG due to changes in CP content in this study are therefore related to changes in ME content.

The results suggest that factors that affect pasture quality such as climate change are likely to affect beef production more in Buffalo Berlin while *Bos taurus* breed type is likely to be affected the most across the three ecological regions. The one-at-a-time approach used in this study has limitations, as the joint effects of changing a combination of parameters are not investigated. It also assumes linearity of parameters (Saltelli and Annoni, 2010), which is not always the case as LiGAPS-Beef model has non-linear equations in its configuration (Van der Linden et al., 2019a). It is thus imperative to incorporate methods that fully account for non-linearity and non-additivity.

Overall, based on the accuracies of all statistical parameters used to evaluate it, LiGAPS-Beef can be used to simulate ADG of *Bos taurus*, composite and Sanga breed types in temperate, arid and semi-arid ecological regions of South Africa. Possible future applications of LiGAPS-Beef model could be simulating the effects of climate change and breeding interventions on beef production. Although not discussed in this paper, extra carcass parameter outputs generated by the model also pointed to potential by LiGAPS-Beef model to simulate carcass percentages and meat quality characteristics. It was not the objective of the study to evaluate the model on carcass traits. This was highlighted to indicate potential scope to use the model to assess carcass traits maybe in future studies. Again, carcass traits were only given for some of the studies and the carcass traits given differed per study, so there could not be a strong case to validate and report the results.

## 5. Conclusion

After calibration, the model LiGAPS-Beef simulated ADG with acceptable accuracy across all breed types in the ecological regions included in this study. The model also identified biophysical factors that define and limit the growth of beef cattle in line with expectations and literature. The accuracy of ME should be prioritized when using LiGAPS-Beef in South Africa. There is scope in using the LiGAPS-Beef model to explore the effects of climate change and breeding strategies in future studies in South African ecological regions.

## CRedit authorship contribution statement

**Christopher Magona:** Investigation, Formal analysis, Data curation, Methodology, Validation, Writing – original draft, Visualization. **Abubeker Hassen:** Conceptualization, Supervision, Writing – review & editing. **Eyob Tesfamariam:** Conceptualization, Supervision, Writing – review & editing. **Carina Visser:** Conceptualization, Supervision, Project administration, Funding acquisition, Writing – review & editing. **Simon Oosting:** Supervision, Writing – review & editing. **A. van der Linden:** Methodology, Software, Formal analysis, Resources, Data

curation, Supervision, Writing – review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Carina Visser reports financial support was provided by Red Meat Research and Development South Africa.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.livsci.2023.105231](https://doi.org/10.1016/j.livsci.2023.105231).

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