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A comparison of growth models for cross- and purebred lambs in precision livestock farming systems

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Abstract

Implementation of precision livestock farming requires extensive information to be gathered on the production cycle of slaughter lambs. Constructing accurate growth models for crossbred sheep from the South African flock would provide valuable information towards this goal. Two dam lines, Dohne Merino and Merino, were mated to rams of their own breeds and to three sire lines, namely Dorper, Dormer and Ile de France. Four ram and four ewe lambs from each group were grown out until maturity at one year of age and weighed weekly. The age–weight data thus gathered were fitted to four growth models (Brody, Gompertz, Logistic, and von Bertalanffy) and the accuracy of fit was determined. All four models were deemed to provide a good fit for the data ($R^2 > 0.86$). Comparison of predicted and observed weights showed that the Gompertz model was the best suited to predicting lifetime growth and therefore it was deemed the best model for this purpose. Crossbred animals generally achieved higher mature weights relative to the pure lines, although Dorper cross ewes were an exception. Rams also gained more benefit from heterosis for mature weights than ewes.

Keywords: age–weight data, Brody, Gompertz, heterosis, logistic, von Bertalanffy

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Introduction

Precision livestock farming (PLF) is the practice of applying the principles and technology of process engineering to managing livestock production (Wathes *et al.*, 2008). This is done to improve the economic, environmental, and social sustainability of livestock production (Tullo *et al.*, 2019) by gathering information to be used in a decision making system, which adds value by improving production yield, animal health and welfare, and decreasing environmental impact (Berckmans, 2014).

Given the challenges currently faced by the South African mutton-producing industry, which include climate change (Meissner *et al.*, 2013; Ziervogel *et al.*, 2014), growing population numbers (DALRRD, 2021), changing consumer demands (Conner *et al.*, 2005), and the decreasing market share and increasing price of red meat (Delport *et al.*, 2017; DALRRD, 2021), implementation of any measures that could increase production output and improve sustainability of the industry would be beneficial.

Wathes *et al*. (2008) identified four requirements for implementation of a PLF system, namely continual monitoring of animal responses (production outputs); a compact, predictive mathematical model to predict outputs given changes in input; a target value for each output; and a model-based predictive controller for the inputs. Creation of an accurate predictive model based on measurements of a certain input will allow for the comparison of actual and predicted animal performance, thereby allowing model-based control to be exercised over that input to modify animal performance (Berckmans, 2014).

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Animal growth, and therefore meat production, was identified as a process particularly suited to PLF (Wathes *et al*., 2008) since mammals follow a set growth pattern known as a growth curve (Fitzhugh, 1976). These curves follow a sigmoid pattern where self-acceleration of growth occurs before puberty and growth deceleration occurs after puberty (Fitzhugh, 1976; Owens *et al.*, 1993). Growth curves can be mathematically described as a function of mature mass, fractional growth rate, and age (Owens *et al.*, 1993) and are considered an effective method of describing animal development, modelling weight–age relationships, and predicting growth rate (Sieklicki *et al.*, 2018). Fitting of a growth curve to a mathematical model allows for the prediction of, among other things, feeding strategy and slaughter age (Blasco & Gomez, 1993; Malhado *et al.*, 2009). Given that growth curve parameters are associated with some production traits, estimates of these parameters can be included in selection programs as well (Blasco & Gomez, 1993; Kopuzlu *et al.*, 2014). This fitting also satisfies the requirement of Wathes *et al.* (2008), that being a compact, mathematical model with predictive capabilities. The chosen model or algorithm must be evaluated for accuracy (Tullo *et al.*, 2019) since a model with low predictive accuracy will not allow for the successful implementation of a PLF system.

Although implementation of PLF systems would likely maximize production output, regardless of the animals used in the system, selection of animals with high growth and production potential is still an essential part of ensuring profitability. Maximum growth potential is genetically fixed and differs between breeds (Brand & Franck, 2000). Different breeds also exhibit differing abilities to adapt to their production environment (Van der Merwe, 2020) and sometimes breeds exhibiting favourable growth rates may be less suited to a certain production system or vice versa. Crossbreeding offers a way of combining desirable traits from two pure breeds. It also allows for the utilization of breed dimorphism between the parental breeds to improve production (Roux, 1992; Cloete *et al*., 2004). Globally it is a common practice (Kremer *et al.*, 2004), but, according to Cloete *et al.* (2008), little research had been conducted on crossbreeding with South African breeds. As far as the authors have been able to determine, this is still the case. According to numerous researchers and studies, crossbreeding offers advantages when compared to purebred animals (Sidwell & Miller, 1962; Scales *et al.*, 2000; Özcan *et al.*, 2001; Kiyanzad, 2002; Kremer *et al.*, 2004; Cloete *et al.*, 2007, 2008; Malhado *et al.*, 2009; Duddy *et al.*, 2016).

Implementing crossbreeding on a large scale in South African flocks, which are already rich in genetic diversity (SA Stud Book, 2015), could therefore substantially improve production output. Coupling the superiority of crossbred animals with the benefits associated with PLF systems offers the possibility of further improving the profitability and sustainability of the South African mutton-producing industry. This study therefore aimed to evaluate various growth models to determine which was the most suitable for modelling the growth and production responses of several groups of crossbred sheep raised under optimal growth conditions.

Materials and methods

Ethical clearance for this study was granted by Stellenbosch University's Research and Ethics Committee: Animal Care and Use under project number ACU-2020-14574. The animals used in this trial were obtained from Langgewens Research Farm (33.28' S, 18.70' E) in the Swartland region of South Africa. The farm lies in the winter rainfall area and available grazing on the farm consists of mixed medic pastures and wheat stubble.

A flock of approximately 160 Dohne Merino and Merino ewes (80 of each breed) were divided into groups of 20 during early summer (December). Each of these groups were then mated to either rams of their own breed (Dohne Merino or Merino) or Dorper, Dormer, or Ile de France rams to create two purebred control groups and six crossbred trial groups. Offspring from these matings therefore made up eight genotypic groups, namely, Dohne Merino, Dohne × Dorper, Dohne × Dormer, Dohne × Ile de France, Merino, Merino × Dorper, Merino × Dormer, and Merino × Ile de France. The dam lines were chosen due to their popularity within the South African industry (Cloete *et al*., 2014) and suitability as terminal dams (Cloete *et al.*, 2004) while the sire lines are recognized as popular terminal sires in South Africa (Zishiri *et al.*, 2014).

Lambing took place in May and June (late autumn and early winter) and lambs remained with their dams until they reached 100 days of age, whereupon they were weaned. All lambs were weighed and tagged within 24 hours of birth and received their first dosage of oral anthelmintic medication at 28 days. Lambs received creep feed from 14 days of age (Table 1) until weaning while ewes also received supplementation. At weaning, lambs received a further dosage of anthelminthic medication and a broad spectrum anti-clostridial vaccination (Multivax P Plus; Reg. No. G3694 (Act 36/1947).

Table 1 Physical and chemical composition, on an as fed basis, of the creep feed provided to lambs prior to weaning.

Physical Composition	Content (g/kg)	Chemical Composition*	Content (%)
Maize	666.00	Dry matter	89.96
Cottonseed oilcake	233.00	Ash	7.90
Molasses powder	25.00	Crude protein	15.43
Lime	18.00	Crude fibre	7.02
Monocalcium phosphate	10.30	Fat	2.40
Bentonite	10.00	Calcium	1.91
Common salt	10.00	Phosphorous	0.69
Urea	10.00	Total digestible nutrients	71.50
Sodium bicarbonate	10.00		
Slaked lime	5.00		
Sulphur	0.50		
Commercial growth promoters and coccidiostat premix	1.20		
Vitamin and mineral premix	1.00		

*Values derived from proximate analysis of feed (AOAC International, 2002)

The first four rams and ewes born for each genotype were selected and transported to Elsenburg Research Farm after weaning, where they were placed in individual pens (1.5 m × 2 m) in a barn with slatted floors. Spatial constraints did not allow for more than 64 animals to be used. These lambs were adapted to a feedlot diet (Table 2) of lucerne hay over a seven-day period, whereafter they had *ad libitum* access to the pelleted diet for the remainder of the trial. Unrestricted access to clean water was provided throughout the trial period. Lambs were kept until they were one year old and were assumed to have reached maturity.

Lambs were weighed on a weekly basis using a Gallagher scale accurate to 200 g. The first weighing occurred at tail docking, i.e., 28 days of age and thereafter continued until the trial concluded when the animals reached one year of age. Forty-five consecutive weighings were made for each animal. Three of the lambs were unable to complete the trial, but all three had at least 35 weighings and therefore were deemed to have generated enough data to allow for accurate fitting of growth models and were not removed from the dataset.

Table 2 Physical and chemical composition, on an as fed basis, of the pelleted feedlot diet lambs received during the trial.

Physical Composition	Content (g/kg)	Chemical Composition*	Content (%)
Maize meal	500.00	Dry matter	88.86
Lucerne hay	361.00	Ash	4.92
Cottonseed oilcake meal	50.00	Crude protein	16.38
Molasses powder	25.00	Crude fibre	7.96
Ammonium chloride	5.00	Fat	2.48
Ammonium sulphate	5.00	Acid detergent fibre	9.01
Lime	5.00	Neutral detergent fibre	18.98
Monocalcium phosphate	5.00	Total digestible nutrients	75.71
Common salt	10.00		
Urea	5.00		
Sodium bicarbonate	10.00		
Slaked lime	5.00		
Sulphur	2.00		
Commercial growth promoters and coccidiostat premix	1.20		
Vitamin and mineral premix	1.50		

*Values derived from proximate analysis of feed (AOAC International, 2002)

Statistical analysis was carried out using Statistica 14 (Tibco Statistica, 2020). Differences between groups were regarded as significant at a level of $P < 0.05$ while $P < 0.1$ was seen as a tendency to differ.

Using the non-linear estimation procedure, various growth models (Table 3) were fitted to the growth data. The Levenberg–Marquardt iteration method was used with the maximum number of iterations set to 50 and a convergence criterion of 10^{-6}. Increasing the maximum number of iterations did not improve the fit of the data and therefore the default of the software, which was 50, was used. Individual curves that failed to converge within these criteria were discarded by the program. These models were evaluated and compared for goodness of fit using the R^2 and root mean square error (RMSE) statistics. This procedure generated values for each of the growth model parameters. These parameter values were then compared using a two-way analysis of variance (ANOVA) with genotype and sex set as main effects, while interactions between main effects were also considered. In the case of significant differences ($P < 0.05$) between groups, Fisher's least significant difference (LSD) multiple comparison tests were performed *post hoc*.

Table 3 Equations of the selected growth models fitted to the growth data from this trial

$W = A(1 - Be^{-kt})W = Ae^{-e^{-k(t-C)}}W = A/(1 - Be^{-kt})W = A(1 - Be^{-kt})^3$**Model**	**Function**	
Brody	$W = A(1 - Be^{-kt})$	(Brody, 1945)
Gompertz	$W = Ae^{-e^{-k(t-C)}}$	(Emmans, 1965)
Logistic	$W = A/(1 - Be^{-kt})$	(Nelder, 1961)
Von Bertalanffy	$W = A(1 - Be^{-kt})^3$	(Von Bertalanffy, 1957)

W is the live weight of the animal at time *t* (in days); *A* is the asymptotic mature weight of the animal; *B* the proportion of live weight to be gained after birth; *k* represents the maturation rate; *C* parameter of the Gompertz curve represents age in days at the inflection point

Results

After the selected models were fitted to the growth data, these models were evaluated for relative and absolute accuracy of fit using the R^2 and RMSE statistics to determine which models would provide the best fit (Table 4). All models were deemed to provide a good fit for the data, with R^2 values of 0.86 and higher. The lowest R^2 values were obtained for Merino rams, where the Gompertz, Logistic, and von Bertalanffy models all had a value of ~0.87. The best fit was obtained from the growth data of Dohne x Dormer rams, where the Brody, Gompertz, and von Bertalanffy models all had values of 0.98. The RMSE values could only be compared within production groups (genotype × sex interactions) and were therefore mainly applied to indicate extreme unsuitability of a specific model for a production group. Within genotype groups, the RMSE values were all similar, indicating that no statistically unsuitable models were present for any production group. Thus, all the models were deemed to fit the data well enough to allow for accurate predictions of growth to be made, and as a result no models were discarded at this step.

Table 3 Goodness of fit statistics for the fitting of four growth models to the various sex × genotype production groups

Genotype	Sex	Model	R^2	RMSE
Dohne Merino	Ram	Brody	0.911	7.583
		Gompertz	0.915	7.409
		Logistic	0.915	7.424
		von Bertalanffy	0.914	7.436
	Ewe	Brody	0.946	4.694
		Gompertz	0.945	4.747
		Logistic	0.942	4.890
		von Bertalanffy	0.946	4.714
Dohne × Dorper	Ram	Brody	0.970	5.060
		Gompertz	0.975	4.695
		Logistic	0.974	4.757
		von Bertalanffy	0.974	4.748
	Ewe	Brody	0.949	5.067
		Gompertz	0.950	5.007
		Logistic	0.949	5.091
		von Bertalanffy	0.950	5.003
Dohne × Dormer	Ram	Brody	0.982	3.932
		Gompertz	0.982	3.922
		Logistic	0.980	4.174
		von Bertalanffy	0.982	3.879
	Ewe	Brody	0.966	4.860
		Gompertz	0.967	4.851
		Logistic	0.965	4.992
		von Bertalanffy	0.967	4.829
Dohne × Ile de France	Ram	Brody	0.880	10.167
		Gompertz	0.877	10.294
		Logistic	0.872	10.471
		von Bertalanffy	0.878	10.240
	Ewe	Brody	0.979	3.597
		Gompertz	0.977	3.739
		Logistic	0.974	4.034
		von Bertalanffy	0.978	3.658
Merino	Ram	Brody	0.870	8.105
		Gompertz	0.869	8.136
		Logistic	0.866	8.213
		von Bertalanffy	0.869	8.118
	Ewe	Brody	0.871	7.395
		Gompertz	0.872	7.372
		Logistic	0.870	7.402
		von Bertalanffy	0.872	7.371
Merino × Dorper	Ram	Brody	0.977	4.132
		Gompertz	0.979	3.996
		Logistic	0.977	4.201
		von Bertalanffy	0.979	3.983
	Ewe	Brody	0.957	4.144
		Gompertz	0.959	4.070
		Logistic	0.958	4.141
		von Bertalanffy	0.959	4.072
Merino × Dormer	Ram	Brody	0.966	4.889
		Gompertz	0.966	4.918
		Logistic	0.963	5.110
		von Bertalanffy	0.966	4.878
	Ewe	Brody	0.904	6.602
		Gompertz	0.906	6.531
		Logistic	0.905	6.573
		von Bertalanffy	0.906	6.535
Merino × Ile de France	Ram	Brody	0.976	4.430
		Gompertz	0.976	4.471
		Logistic	0.973	4.702
		von Bertalanffy	0.976	4.422
	Ewe	Brody	0.940	5.511
		Gompertz	0.937	5.620
		Logistic	0.934	5.789
		von Bertalanffy	0.939	5.572

Since all models were deemed acceptable, parameter estimates were compiled for the models. The parameter estimates for each model are presented below in Tables 5–8. The parameter estimates were determined for each genotype × sex production group, even when no interaction was present. This was done to allow for the most accurate prediction of growth model parameters by decreasing the size of contemporary groups as far as possible. Parameter values are presented to a minimum of three decimal places throughout in order to allow for the most accurate predictions possible. The Brody model was the only model where data points were discarded due to a failure to converge within the set criteria.

Table 4 Model parameters (± standard error, SE) of the Brody growth model $[W = A(1 - Be^{-kt})]$ as determined for cross- and purebred lambs of both sexes

		Parameter		
Genotype	**Sex**	***A***	***k***	***B***
Dohne Merino	Ram	134.022^{de} ± 39.069	0.0032^{abcde} ±0.0006	1.040±0.017
	Ewe	121.200^{e} ± 39.069	0.0036^{ae} ±0.0006	1.002±0.017
Dohne × Dorper	Ram	232.673^{bcd} ± 33.835	0.0024^{abcdf} ±0.0005	1.048±0.014
	Ewe	120.598^{e} ± 39.069	0.0036^{ae} ±0.0005	1.029±0.014
Dohne × Dormer	Ram	258.287^{abc} ± 33.835	0.0020^{bcdf} ±0.0005	1.020±0.014
	Ewe	293.140^{ab} ± 33.835	0.0014^{f} ±0.0005	1.014±0.014
Dohne × Ile de France	Ram	212.474^{bcde}± 39.069	0.0020^{abcdf} ±0.0006	1.001±0.017
	Ewe	191.047^{cde} ± 33.835	0.0019^{bdf} ±0.0005	1.009±0.014
Merino	Ram	131.393^{de} ± 39.069	0.0040^{e} ±0.0006	1.042±0.017
	Ewe	116.016^{e} ± 33.835	0.0035^{abce} ±0.0006	1.024±0.017
Merino × Dorper	Ram	202.368^{bcde}± 33.835	0.0022^{abcdf} ±0.0005	1.026±0.014
	Ewe	110.156^{e} ± 33.835	0.0035^{ace} ±0.0005	1.032±0.014
Merino × Dormer	Ram	202.587^{bcde}± 39.069	0.0018^{df} ±0.0006	1.033±0.017
	Ewe	129.225^{e} ± 33.835	0.0030^{abcde} ±0.0005	1.057±0.014
Merino × Ile de France	Ram	337.950^{a} ± 33.835	0.0012^{f} ±0.0005	1.007±0.014
	Ewe	146.760^{de} ± 33.835	0.0024^{abcdf} ±0.0005	1.011±0.014
	Genotype	*<0.001*	*0.002*	*0.118*
P-value	Sex	*0.001*	*0.068*	*0.53*
	Interaction	*0.059*	*0.289*	*0.615*

Means with different superscripts ($^{a-f}$) in the same column differ significantly (P <0.05)
A = asymptotic mature weight (kg) of the animal, *B* = proportion of live weight to be gained after birth, *k* = maturation rate

None of the Brody model parameters (*A, B,* or *k*) displayed interactions between sex and genotype, although the *A* parameter tended towards it (P = 0.059). No differences were observed between groups for the *B* parameter, but both the *A* and *k* parameters showed differences between groups.

Both genotype and sex had a substantial influence on the *A* parameter with rams having a higher value than ewes (214.095 vs. 153.518) and Dohne × Dormer (275.713) having the highest value among genotypes (not shown here). For the production groups, Merino × Ile de France rams (337.950) had a substantially higher value than all other groups except the Dohne × Dormer genotype of both sexes. The lowest values were obtained by ewes from the Dohne Merino, Dohne × Dorper, Merino, Merino × Dorper, and Merino × Dormer groups (<129.225). These were not substantially lower than Dohne Merino, Merino, Merino × Dorper, and Merino × Dormer rams and Dohne × Ile de France rams and ewes, and Merino × Ile de France ewes. Dohne × Ile de France, Merino × Dorper and Merino × Dormer rams were similar. The asymptotic *A* parameter values were unrealistically high with many exceeding 200 kg and, when comparing the estimates to the observed live weights at one year of age (Table 9), it can be seen that the Brody model overestimated the weight of all groups. The average overestimation over all groups at this point was ~8.9 kg.

The *k* parameter was only influenced by genotype (P = 0.002) although sex tended towards significance (P = 0.068). The lowest values were obtained from Dohne × Dormer ewes and Merino × Ile de France rams (~0.0013), which were substantially lower than Dohne Merinos of both sexes, Dohne × Dorper ewes, Merinos of both sexes, Merino × Dorper, Merino × Dormer, and Merino × Ile de France ewes. The highest *k* parameter value was found in Merino rams (0.0040), although it was not markedly higher than either sex of Dohne Merino or Dohne × Dorper, Merino, Merino × Dorper or Merino × Dormer ewes.

Table 5 Model parameters (± standard error, SE) of the Gompertz growth model $\left[W = Ae^{-e^{-k(t-C)}}\right]$ as determined for cross- and purebred lambs of both sexes

		Parameter		
Genotype	**Sex**	***A***	***C***	***k***
Dohne Merino	Ram	110.070 ^{bcde} ±7.265	126.341±13.871	0.0083±0.0007
	Ewe	101.233 ^{cdef} ±7.265	135.675±13.871	0.0075±0.0007
Dohne × Dorper	Ram	122.021 ^{ab} ±7.265	132.597±13.871	0.0088±0.0007
	Ewe	93.754 ^{ef} ±7.265	108.545±13.871	0.0088±0.0007
Dohne × Dormer	Ram	132.072 ^{a} ±7.265	139.940±13.871	0.0074±0.0007
	Ewe	121.839 ^{abc} ±7.265	155.053±13.871	0.0067±0.0007
Dohne × Ile de France	Ram	124.616 ^{ab} ±7.265	146.588±13.871	0.0070±0.0007
	Ewe	107.983 ^{bcde}±7.265	135.075±13.871	0.0075±0.0007
Merino	Ram	100.557 ^{def} ±7.265	127.556±13.871	0.0083±0.0007
	Ewe	91.447 ^{ef} ±7.265	128.826±13.871	0.0077±0.0007
Merino × Dorper	Ram	120.091 ^{abcd} ±7.265	132.827±13.871	0.0081±0.0007
	Ewe	85.079 ^{f} ±7.265	111.627±13.871	0.0086±0.0007
Merino × Dormer	Ram	117.207 ^{abcd} ±7.265	159.885±13.871	0.0072±0.0007
	Ewe	87.080 ^{f} ±7.265	128.013±13.871	0.0086±0.0007
Merino × Ile de France	Ram	132.171 ^{a} ±7.265	154.325±13.871	0.0067±0.0007
	Ewe	95.960 ^{ef} ±7.265	128.152±13.871	0.0074±.00007
P-value	Genotype	*0.003*	*0.378*	*0.204*
	Sex	*<0.001*	*0.115*	*0.721*
	Interaction	*0.257*	*0.581*	*0.757*

Means with different superscripts ($^{a\text{-}f}$) in the same column differ significantly (P <0.05)
A = asymptotic mature weight (kg) of the animal, C = age (days) at inflection point, k = maturation rate

Only the *A* parameter of the Gompertz model showed differences between production groups and this was due to the nested effects of both sex (*P* <0.001) and genotype (*P* =0.003), since no statistically significant interaction between the main effects took place. For sex, rams had the highest parameter value (119.851 vs. 98.047), whereas the genotypic group of the greatest value was Dohne × Dormer (126.955) (not shown).

The highest *A* values from production groups were found for Dohne × Dormer and Merino × Ile de France rams (~132) although they were not substantially higher than Dohne × Dorper rams, Dohne × Dormer ewes, Dohne × Ile de France rams, Merino × Dorper, and Merino × Dormer rams. Dohne Merino rams and Dohne × Ile de France ewes did not differ from each other but were substantially different from both the highest and the lowest groups. The groups with the lowest values were Merino × Dorper and Merino × Dormer ewes (~86). They were not however, substantially lower than Dohne × Dorper ewes, either sex of Merino, or Merino × Ile de France ewes.

The Gompertz *A* parameter estimates were more realistic, with none exceeding 133 kg. The yearling weight estimates in Table 9 are also closer to the observed weights, the average overestimation only being 1.2 kg.

Table 6 Model parameters (± standard error, SE) of the logistic growth model $[W = A/(1 - Be^{-kt})]$ as determined for cross- and purebred lambs of both sexes; means with different superscripts ($^{a-f}$) in the same column differ significantly (P <0.05); A = asymptotic mature weight (kg) of the animal, B = proportion of live weight to be gained after birth, k = maturation rate

		Parameter		
Genotype	**Sex**	***A***	***B***	***k***
Dohne Merino	Ram	97.284 ^{cde} ±4.76	8.648 ^{cd} ±0.784	0.0140±0.0008
	Ewe	86.735 ^{ef} ±4.76	7.120 ^{cd} ±0.784	0.0123±0.0008
Dohne × Dorper	Ram	108.668 ^{abc}±4.76	10.946 ^{ab} ±0.784	0.0150±0.0008
	Ewe	86.959 ^{ef} ±4.76	7.286 ^{cd} ±0.784	0.0139±0.0008
Dohne × Dormer	Ram	116.291 ^{a} ±4.76	8.514 ^{cd} ±0784	0.0127±0.0008
	Ewe	105.020 ^{abc} ±4.76	9.308 ^{abc} ±0.784	0.1230±0.0008
Dohne × Ile de France	Ram	107.585 ^{abc} ±4.76	8.845 ^{bcd} ±0.784	0.1230±0.0008
	Ewe	95.370 ^{cde} ±4.76	8.281 ^{cd} ±0.784	0.0130±0.0008
Merino	Ram	89.505 ^{def} ±4.76	7.304 ^{cd} ±0.784	0.0133±0.0008
	Ewe	80.620 ^{f} ±4.76	6.847 ^{d} ±0.784	0.0126±0.0008
Merino × Dorper	Ram	106.773 ^{abc}±4.76	9.087 ^{abc} ±0.784	0.0137±0.0008
	Ewe	78.635 ^{f} ±4.76	7.274 ^{cd} ±0.784	0.0137±0.0008
Merino × Dormer	Ram	101.247 ^{bcd}±4.76	11.261^{a} ±0.784	0.0129±0.0008
	Ewe	79.162 ^{f} ±4.76	8.978 ^{bcd} ±0.784	0.0139±0.0008
Merino × Ile de France	Ram	113.325 ^{ab} ±4.76	9.280 ^{abc} ±0.784	0.0123±0.0008
	Ewe	86.0490 ^{ef} ±4.76	7.238 ^{cd} ±0.784	0.0123±0.0008
P-value	Genotype	*<0.001*	*0.02*	*0.131*
	Sex	*<0.001*	*<0.001*	*0.422*
	Interaction	*0.237*	*0.191*	*0.677*

For the logistic model (Table 7), as for the Brody model, differences existed for both the *A* and *B* parameters. In both cases, this was due to differences between genotypes (*P* <0.001), as well as sex (*P* <0.001).

With regards to the *A* parameter, rams again had a higher value than ewes (105.085 vs. 87.320) and Dohne × Dormer had the highest *A* parameter estimate among genotypes (110.660) (not shown). As expected, Dohne × Dormer rams were the production group with the highest *A* parameter (116.291), substantially higher than both sexes of Dohne Merino, Merino and Merino × Dormer; and Dohne × Dorper, Dohne × Ile de France, Merino × Dorper and Merino × Ile de France ewes. The lowest values were held by Merino, Merino × Dorper, and Merino × Dormer ewes (~79), which were similar. These groups were not substantially different from Dohne Merino, Dohne × Dorper, and Merino × Ile de France ewes, which also did not differ from one another, or from Merino rams.

For the *B* parameter, rams again had a higher value than ewes (9.236), whereas the genotype with the highest value was Merino × Dormer (10.120) (not shown). Merino × Dormer rams displayed the highest *B* value of 11.261, which was not markedly greater than Dohne × Dorper rams, Dohne × Dormer ewes, Merino × Dorper rams or Merino × Ile de France rams. Merino ewes (6.847) had the lowest value although this was not substantially lower than that of any groups except the five mentioned above. No differences existed between Dohne Merinos of both sexes, Dohne × Dorper ewes, Dohne × Dormer rams, Dohne × Ile de France ewes, Merino rams, Merino × Dorper ewes, and Merino × Ile de France ewes.

Table 7 Model parameters (± standard error, SE) for the von Bertalanffy growth model $[W = A(1 - Be^{-kt})^3]$ as estimated for cross- and purebred lambs of both sexes

		Parameter		
Genotype	**Sex**	***A***	***B***	***k***
Dohne Merino	Ram	120.629 ^{abcde} ±10.455	0.664 ^{abcdef} ±0.021	0.0064±0.0007
	Ewe	115.175 ^{bcdef} ±10.455	0.611 ^{f} ±0.021	0.0059±0.0007
Dohne × Dorper	Ram	132.654 ^{abcd} ±10.455	0.752 ^{d} ±0.021	0.0067±0.0007
	Ewe	98.295 ^{ef} ±10.455	0.631 ^{bcef} ±0.021	0.0071±0.0007
Dohne × Dormer	Ram	144.419 ^{ab} ±10.455	0.656 ^{abcef} ±0.021	0.0057±0.0007
	Ewe	135.620 ^{abc} ±10.455	0.670 ^{abcde} ±0.021	0.0051±0.0007
Dohne × Ile de France	Ram	139.471 ^{ab} ±10.455	0.648 ^{bcef} ±0.021	0.0052±0.0007
	Ewe	117.646 ^{bcdef} ±10.455	0.645 ^{bcef} ±0.021	0.0057±0.0007
Merino	Ram	109.568 ^{cdef} ±10.455	0.632 ^{bcef} ±0.021	0.0066±0.0007
	Ewe	100.318 ^{ef} ±10.455	0.613 ^{bcef} ±0.021	0.0060±0.0007
Merino × Dorper	Ram	130.243 ^{abcd} ±10.455	0.673 ^{abde} ±0.021	0.0061±0.0007
	Ewe	89.381 ^{f} ±10.455	0.633 ^{bcef} ±0.021	0.0069±0.0007
Merino × Dormer	Ram	130.759 ^{abcd} ±10.455	0.715 ^{ad} ±0.021	0.0053±0.0007
	Ewe	92.861 ^{ef} ±10.455	0.688 ^{ade} ±0.021	0.0068±0.0007
Merino × Ile de France	Ram	147.904 ^{a} ±10.455	0.666 ^{abcdef} ±0.021	0.0050±0.0007
	Ewe	103.096 ^{def} ±10.455	0.623 ^{bcf} ±0.021	0.0058±0.0007
P-value	Genotype	*0.034*	*0.016*	*0.238*
	Sex	*<0.001*	*0.003*	*0.421*
	Interaction	*0.334*	*0.321*	*0.735*

Means with different superscripts ($^{a\text{-}f}$) in the same column differ significantly ($P < 0.05$)
A = asymptotic mature weight (kg) of the animal, *B* = proportion of live weight to be gained after birth, *k* = maturation rate

In the von Bertalanffy model, both the *A* and *B* parameters differed substantially between production groups. As before, in both cases, this was due to differences between sexes and genotypes rather than interactions between main effects. Rams had higher *A* (131.956) and *B* (0.672) parameter values than ewes (106.549 and 0.639) ($P < 0.05$). Once again, the Dohne × Dormer was the genotype with the highest *A* value (140.020), whereas Merino × Dormers had the largest *B* parameter value of 0.702 and the Dohne Merino, the lowest parameter value of 0.638 (not shown).

As for production groups, Merino × Ile de France rams (147.904) had the highest *A* parameter, albeit not substantially greater than rams from Dohne Merino, Dohne × Dorper, Dohne × Dormer, Dohne × Ile de France, Merino × Dorper or Merino × Dormer genotypes, or Dohne × Dormer ewes. The lowest *A* parameter value came from Merino × Dorper ewes (89.381), which was similar to Merino rams and any other group of ewes except Dohne × Dormer. The von Bertalanffy model overestimated the yearling weights of the animals by approximately 3.1 kg (Table 9).

The lowest *B* parameter value was found for Dohne Merino ewes (0.611) and the highest for Dohne × Dorper rams (0.752). Dohne Merino ewes did not differ substantially from Dohne Merino rams, Dohne × Dorper ewes, Dohne × Dormer rams, either sex of Dohne × Ile de France and Merino, Merino × Dorper ewes and both Merino × Ile de France sexes. Dohne Merino and Merino × Ile de France rams did not differ from any other group. In addition to these two groups, Dohne × Dormer ewes, Merino × Dorper rams, and Merino × Dormer rams and ewes were not substantially different from Dohne × Dorper rams. No differences existed between Dohne × Dorper ewes, Dohne × Ile de France ewes and rams, Merino rams, and Merino × Dorper ewes.

Table 8 Observed live weight in kg (± standard error, SE) of the lambs at one year of age compared to predictions from the various growth models

Genotype	Sex	Observed	Brody	Gompertz	Logistic	von Bertalanffy
Dohne Merino	Ram	88.33^{defg} ±4.85	88.86	94.30	91.39	97.04
	Ewe	78.83^{ghi} ±4.20	87.09	82.85	79.04	90.33
Dohne x Dorper	Ram	102.83^{abc}±4.85	126.26	105.22	102.66	106.94
	Ewe	84.60^{efgh} ±4.20	85.39	83.19	82.25	83.57
Dohne x Dormer	Ram	110.05^{a} ±4.20	128.12	107.12	105.73	108.68
	Ewe	95.40^{bcde} ±4.20	110.91	93.97	93.15	94.92
Dohne x Ile de France	Ram	98.83^{abcd} ±4.20	108.74	98.05	96.12	100.25
	Ewe	91.55^{cdef} ±4.20	93.46	88.51	87.37	89.34
Merino	Ram	78.85^{fghi} ±4.20	98.93	85.91	83.76	90.29
	Ewe	71.40^{i} ±4.20	81.03	76.17	74.43	79.55
Merino x Dorper	Ram	101.33^{abcd}±4.85	104.78	100.94	99.35	101.84
	Ewe	76.13^{ghi} ±4.20	76.24	74.87	74.14	75.20
Merino x Dormer	Ram	93.18^{bcdef} ±4.20	90.21	91.06	89.97	92.01
	Ewe	75.13^{hi} ±4.20	81.97	75.02	73.99	76.04
Merino x Ile de France	Ram	105.08^{ab} ±4.20	115.84	101.82	100.71	102.60
	Ewe	84.35^{ghi} ±4.20	82.76	79.22	78.40	79.79
P-value	Genotype	*<0.001*				
	Sex	*<0.001*				
	Interaction	*0.271*				

Means with different superscripts ($^{a-i}$) in the same column differ significantly (*P* <0.05)

Looking at the observed live weights at one year of age, it can be seen that, as predicted by the *A* parameter of the Brody, Gompertz, and Logistic models, Dohne × Dormer rams were the heaviest. The von Bertalanffy model indicated that Merino × Ile de France rams would be the heaviest. Merino ewes were the lightest group. In contrast to the heaviest group, the *A* values were not indicative of the lightest group, as all models indicated that Merino × Dorper ewes had the lowest *A* parameter value and could therefore be expected to be the lightest group.

Discussion

The main purpose of this study was to determine which of the four models evaluated, namely Brody, Gompertz, logistic, and von Bertalanffy, would best serve to model the growth of crossbred lambs raised under optimal growth conditions.

Judging by the goodness of fit statistics (R^2 and RMSE), all of the models show good fit of the data, with R^2 values for any particular production group lying within one percent of each other and all being higher than 0.86. The RMSE values for the different models were also extremely close within each production group and therefore no models were statistically inaccurate. On average though, the Gompertz model was found to have the highest R^2 and lowest RMSE values over all production groups, making it the best-fitting model.

When the model parameters were examined, it was found that the Brody model had unrealistically high *A* parameter values. The *A* parameter estimate, which in all the models represents asymptotic mature weight, varied between 110 kg for Merino × Dorper ewes and 337 kg for Merino × Ile de France rams and the average value across all groups was 187 kg. Since this is unrealistic and exceeded *A* parameter values for different breeds found in literature (Bathaei & Leroy, 1996; Malhado *et al*., 2009; Kopuzlu *et al*., 2014; Hossein-Zadeh, 2015; Moreira *et al*., 2016; Sieklicki *et al*., 2018; Van der Merwe *et al*., 2019), the Brody model was not considered further.

In comparing the *A* parameter estimates of the various models, a trend emerged that is also seen in previous studies on the subject (Keskin *et al*., 2009; Malhado *et al*., 2009; Kopuzlu *et al*., 2014; Hossein-Zadeh, 2015; Moreira *et al*., 2016; Sieklicki *et al*., 2018; Van der Merwe *et al*., 2019). The Brody model tends to predict the highest *A* parameter values, followed by the von Bertalanffy, the Gompertz, and finally the logistic model.

Although this does not necessarily mean that the Brody and von Bertalanffy models will overestimate mature weight, it is nevertheless an indication that the Brody model might be less accurate in predicting mature weight.

The Gompertz model has been widely used to describe the growth of different species (Najari *et al*., 2007; Takeda *et al*., 2018) and numerous sheep breeds and crosses (Keskin *et al.*, 2009; Malhado *et al.*, 2009; Kopuzlu *et al.*, 2014; Hossein-Zadeh, 2015; Schiller *et al.*, 2015; Moreira *et al.*, 2016; Sieklicki *et al.*, 2018; Van der Merwe *et al.*, 2019). In the current study, it was also found to fit the growth data well. When comparing the *A* parameter values for Dohne Merino and Merino in this study to the values obtained by van der Merwe *et al*. (2019), who reared lambs from the same resource flock as was used in this study under similar conditions, it can be seen that the *A* values from this study are slightly higher. This was also found to be the case with the logistic and von Bertalanffy models. The difference is likely due to environmental variation.

As was expected, rams had higher *A* values than ewes due to sexual dimorphism (Butterfield, 1988; Van der Merwe *et al*., 2019). This held true for all the models. Comparison of maternal lines showed that Dohne Merino crosses had higher values than their Merino counterparts. This is likely due to the Dohne Merino being a dual-purpose breed, with focus on both wool and meat production, whereas the Merino is more focused on wool production, meaning that the Dohne Merino generally has higher mature weights (van der Merwe, 2020). An exception occurred where Merino × Ile de France rams outweighed Dohne × Ile de France rams. It could be speculated that this occurred due to a greater heterosis effect or the greater degree of breed dimorphism present between the Merino and Ile de France breeds.

The *C* parameter from the Gompertz model indicates the age of the animal at the inflection point of its growth curve. Given that animals with higher mature weights generally achieve maturity at a later age (Owens *et al*., 1993), it is to be expected that a positive correlation will exist between the *A* and *C* parameters of the Gompertz curve. This was found to be the case, with a correlation of 0.69 existing between the two parameters. Since animals generally show a decline in growth rate (ADG) after the inflection point in their growth curves, selecting animals with higher mature weights will allow the animals in a feedlot to maintain a higher growth rate for a longer time. Caution should however be exercised, since animals with higher mature weights reach maturity later (Owens *et al.*, 1993), and fat deposition, which determines carcass classification (Government Notice R. 863, 2006) and price, are influenced by stage of maturity (Brand *et al.*, 2018).

As expected, given the relationship between maturity and growth rate, a negative correlation (-0.54) existed between the *A* and *k* parameters, simply meaning that animals with higher mature weights exhibit lower maturation rates. This same negative correlation has been found in other studies (Kopuzlu *et al*., 2014; Hossein-Zadeh, 2015), although the strength of the correlation varies. Sieklicki *et al*. (2018) found a correlation of -0.925, Moreira *et al*. (2016) one of -0.873 and Malhado *et al.* (2009) values between -0.38 and -0.58. The relationship between *A* and *k* holds true, regardless of which model is being evaluated.

Since maturation rate (*k*) will influence age at inflection point (*C*), the correlation for these parameters was also determined and was found to be -0.85, thus confirming that animals that mature faster will be younger when they reach the inflection point of their growth curve. It should be noted that in none of the three models deemed biologically accurate, any significant differences in maturation rates were observed. This was somewhat unexpected as the difference in maturation rate between sexes (Butterfield, 1988) was expected to be significant even if genotype had no influence.

The logistic model has also been widely used to model growth in sheep (Carneiro *et al*., 2007; Keskin *et al*., 2009; Malhado *et al*., 2009; Kopuzlu *et al*., 2014; Hossein-Zadeh, 2015; Moreira *et al*., 2016; Sieklicki *et al*., 2018; Van der Merwe *et al*., 2019). It was found to be the most accurate of the four models for estimating yearling weight. A previous study (van der Merwe *et al.*, 2019) found that the logistic model tended to overestimate growth in the first 50 days. The same held true for this study, with the logistic model overestimating 50-day weight by 2.66 kg, on average.

As was the case for the Gompertz model, Dohne Merino crossbreds outperformed Merino crossbreds with regards to predicted mature weight, the exception being Merino × Ile de France rams. The correlation between the *A* and *k* parameters was only -0.16, much less than the -0.49 to -0.99 (Hossein-Zadeh, 2015), -0.9 (Sieklicki *et al*., 2018), and -0.84 (Moreira *et al.*, 2016) reported elsewhere. According to Fitzhugh (1976), the negative correlation between these parameters could be altered by crossbreeding, which may explain the low negative correlation in this case. However, both the Gompertz and von Bertalanffy *A* and *k* parameters still exhibit strong negative correlations and therefore this explanation may be lacking.

The von Bertalanffy model is not as widely used as the previous two models, although it is not uncommon in literature (Malhado *et al*., 2009; da Silveira *et al*., 2012; Hossein-Zadeh, 2015; Sieklicki *et al*., 2018; Van der Merwe *et al*., 2019). Like the Gompertz model, it also overestimated yearling weight, but the error was greater than that of the Gompertz (3.1 kg vs. 1.21 kg), although both values fell within the expected standard deviation in yearling weight. The *A* parameter estimates for the von Bertalanffy model was also higher than those of the Gompertz and logistic models, with the highest *A* value belonging to Merino × Ile de France rams, in contrast to the other models. As in the other models, with the exception of Merino × Ile de France rams, Dohne Merino crosses outperformed Merino crosses of the same paternal line. Thus, the von Bertalanffy model was the only model to correctly predict that Merino × Ile de France rams would outperform Dohne × Ile de France rams. A strong negative correlation (-0.703) existed between the *A* and *k* parameters for the von Bertalanffy model. Correlations of -0.952 (Sieklicki *et al*., 2018) and a range of -0.49 to -0.99 (Hossein-Zadeh, 2015) have been reported elsewhere.

Comparing all aspects of the Gompertz, logistic, and von Bertalanffy models, the Gompertz model appears to be the most suitable for modelling the growth of crossbred lambs. While the logistic model is the most accurate in predicting yearling weight, it considerably overestimates 50-day weight (~18% too heavy). In turn, the von Bertalanffy model overestimated both 50-day and yearling weight and was the least accurate of the three models in predicting yearling weight. The Gompertz model overestimated yearling weight by approximately one kilogram (~2%) and was the most accurate of the models in predicting 50-day weight and therefore is the most suitable model to predict lifetime growth of the lambs in this study.

Considering all three models together, several conclusions can be drawn based on the predicted mature weights (*A* parameters) of the models. Firstly, all three models indicate that crossbred animals generally outperform their purebred counterparts with regards to growth rate and mature weight. Thus, crossbreeding would be beneficial in the production of slaughter lambs. This supports the findings of numerous previous studies (Sidwell & Miller, 1962; Fahmy *et al*., 1972; Scales *et al*., 2000; Özcan *et al*., 2001; Kiyanzad, 2002; Cloete *et al*., 2007, 2008; Malhado *et al*., 2009; Schiller *et al*., 2015).

Secondly, an exception to the improvement in crossbred performance exists for crossbred Dorper ewes. All three models indicated that Dohne × Dorper and Merino × Dorper ewes would have mature weights lower than, or very similar to, purebred Dohne Merino and Merino ewes. The reason for this is unclear, although it could be speculated that it may be due to the Dorper being a relatively early-maturing breed (Cloete *et al*., 2007), when compared to the other sire breeds. It could be argued that, due to the Dorper crosses maturing earlier, their growth curves would plateau sooner and therefore the models would underestimate the asymptote of the curve. However, it would then be expected that Dorper cross rams would exhibit the same effect, which was not evident. Furthermore, when the yearling weights of the ewes were compared, it was found that Dorper-cross ewes were heavier than the purebreds. It is therefore likely that it is simply an inaccuracy in the models rather than a genetic quirk.

Finally, it appears that rams derive more benefit from heterosis than ewes, with crossbred rams generally displaying a larger increase in mature weight than crossbred ewes. This phenomenon might be attributable to a scale effect, i.e., rams being heavier than ewes. If both sexes displayed the same degree of heterosis for mature weight, i.e., both sexes showed the same percentage increase in mature weight, the heavier animals would, in terms of absolute weight, benefit more.

Conclusion

Of the four models evaluated, the Brody model was found to be unsuitable to model the growth of crossbred sheep in this study. The Gompertz, logistic, and von Bertalanffy models are all suitable and provide statistically good fits of the data. When comparing the observed body weights to predicted values, the Gompertz model was found to be the most biologically accurate overall while, on average, it also had the highest R^2 and lowest RMSE values. It is therefore deemed to be best suited to this purpose. It also emerged that crossbreeding with South African sheep breeds will likely improve production and that rams benefitted more from the heterosis associated with such crossbreeding than ewes.

Confirmation of the results from this trial, using more replications could be useful, while further work could also be done on more crosses. The phenomenon of the Dorper-cross ewes having lower mature weights than purebreds also warrants further investigation.

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Authors' contributions

PGT was responsible for execution of the trial, data collection, statistical analysis, and initial write-up. The study was conceptualized, designed, and funding obtained by TSB and SWPC. They, along with JHCvZ, were responsible for supervision of the trial and finalization of the manuscript. All authors have read and approved the final manuscript.

Declaration of competing interest

No conflicts of interest have been identified with this study. The opinions, findings, and conclusions in this study are that of the authors and do not necessarily reflect that of any of the funders.

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