Title

Sustainable lamb production: Evaluation of factors affecting lamb growth using hierarchical, cross classified and multiple memberships models

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Highlights

- Acute ewe lameness cases at pregnancy had a short, negative impact on lamb growth
- Pneumonia and bacterial arthritis cases had a long-lasting impact on lamb weight
- Lambs tended to be heavier prior to a disease case compared to unaffected lambs
- Results suggest a possible trade-off between growth and immune system
- Multiple membership provided better estimates than other mixed model structures

Abstract

In light of current concerns about the sustainability of red meat production in a world with increasing global demand for food from animal origin there is a need for a better understanding of factors that influence the growth rate and feed conversion efficiency of animals on commercial farms. The primary objective of this observational study was to use longitudinal data to quantify the simultaneous effects of multiple ewe and lamb factors on lamb growth rate. A secondary aim was to evaluate model structures that specifically account for lamb grouping effects during the growth period and compare these to classical hierarchical growth rate models.

A total of 4172 weight recordings from 805 lambs and data on disease events were collected over a 6-month period from a commercial pedigree sheep flock. Three mixed model structures were compared, hierarchical, cross classified and multiple membership, and final estimates determined within a Bayesian framework. The multiple membership structure provided the best model fit and was used for final inference; taking account of the effect of lamb grouping over time provided the best estimates of lamb growth rate.

Ewe lameness and mastitis cases had a deleterious impact on lamb growth. Lambs from ewes identified with mastitis during lactation were on average 3.0 (standard error (SE) 1.6) kg lighter during the four month growth period than lambs from unaffected ewes. Lambs from ewes that were not lame during pregnancy were 3.0 (SE 1.2) kg heavier at eight weeks of age than lambs from ewes with a least one lameness case during the same period. Lambs from ewes lame either during the first 4 weeks or between 4-8 weeks of a lamb’s life (but not lame during pregnancy) were also significantly heavier at 56 days of age, than lambs reared by ewes that were lame during pregnancy (2.8 (SE 1.2) and 3.4 (SE 1.2) kg respectively).

Cases of pneumonia and bacterial arthritis in lambs had a significant negative impact on lamb growth with affected lambs being on average 5.5 (SE 1.1) kg and 2.2 (SE 1.2) kg less than non-affected lambs respectively after the disease event. Prior to a case of lameness or pneumonia, lambs were significantly heavier than unaffected lambs suggesting a possible trade-off between growth and immune function.

Overall, the study provides evidence that that a combination of ewe and lamb characteristics and disease events play an important role in determining lamb growth rate and that heavier lambs may be more susceptible to disease.

Keywords

sheep; growth rate; lameness; pneumonia; multiple membership model; mixed model

1. Introduction

The underlying aim of sustainable agriculture is to provide agricultural systems that meet the needs and demands of today's society without jeopardising those of tomorrow. The three key elements of sustainability are 'environment', 'society' and 'economy' (Giddings et al., 2002) and in terms of the food supply chain, producers, processors, distributors, retailers, consumers, and waste handlers all have a role to play.

In light of current concerns about the sustainability of red meat production in a world with increasing global demand for food from animal origin (Chaudhary et al., 2018; Cobiac and Scarborough, 2019; Delgado et al., 1999; Tilman et al., 2002), there is a need for a better understanding of factors that influence the growth rate and feed conversion efficiency of animals on commercial farms. In terms of lamb production, growth rate is influenced by genotype, with a heritability of approximately 10-15% (Lôbo et al., 2009), but non-genetic factors account the majority of variability in growth rate. Therefore, understanding and optimising environmental effects will be vital to maximise the efficiency and sustainability of lamb production.

Previous research has identified a variety of non-genetic factors associated with lamb growth. Individual factors reported to be positively associated with lamb growth include greater litter size, (single lambs in contrast to twins or triplets) (Dimsoski et al., 1999), gender (Arnold and Meyer, 1988), greater ewe milk production (Snowder and Glimp, 1991) and diets with higher concentration of protein (Kellaway, 1973). In contrast, presence of disease (Coop et al., 1982;

Grant et al., 2016; Green et al., 1998) and dam age (Dickerson and Laster, 1975) were associated with lower growth rates.

There remain substantial uncertainties, however, around these non-genetic influences on lamb growth rate. Many previous studies have examined one environmental factor at a time, despite the fact that these effects tend to occur simultaneously, meaning that inevitable complex and confounding relationships can be missed. The few studies that have integrated limited information on more than one factor have reported that there can be multiple simultaneous influences on lamb growth (Green et al., 1998; Huntley et al., 2012; Juengel et al., 2018). Moreover, while several studies have looked at the effects of lamb-related factors on lamb growth, few have concurrently evaluated ewe health-related information, such as disease cases during pregnancy and lactation. The effect of mastitis on lamb growth was estimated by Huntley et al. (2012) and Grant et al. (2016) but no studies have yet evaluated the effect of lameness cases in the ewe on lamb growth, despite this being a common condition in sheep flocks (Kaler and Green, 2008; Winter et al., 2015)

In current literature, there is also very sparse information of the temporal effects of factors that impact on individual lamb growth rate. Previous research include case-control studies and a randomised clinical trial that assessed the impact of disease in groups of lambs, however longitudinal studies are necessary to capture changes in growth curves over time and are generally recommended for inference on between-subject predictors (Dohoo et al., 2003). For instance, with regards to impact of disease in lambs, previous studies have assessed the average differences in weights/growth rates of groups of lambs affected and unaffected with pneumonia (Alley, 1987; Jones et al., 1982), lameness (Marshall et al., 1991; Wassink et al., 2010), orf (Lovatt et al., 2012) and endoparasites (Coop et al., 1982). In contrast, only a few studies have followed up individual lambs in order to quantify the impact of disease cases on lamb growth e.g. diarrhoea (Green et al., 1998; Huntley et al., 2012), endoparasites (Broughan and Wall,

2007) and ewe mastitis (Grant et al., 2016). Therefore, there is limited robust evidence on the impact of endemic diseases on individual lamb growth rates.

Previous studies have modelled lamb growth using hierarchical, multilevel structures to account for repeated weight observations clustered at lamb, ewe and farm level (Grant et al., 2016; Green et al., 1998; Huntley et al., 2012) and this approach has been widely used for general livestock growth rate models (Aggrey, 2009; Bahreini Behzadi et al., 2014; Strathe et al., 2010). However, one challenge in studying growth rates on farms is the added complexity of animals changing groups over time. Previous studies on animal growth have not accounted for time-dependent grouping effects resulting from animals being moved to different locations within a farm and hence being exposed to different environments and planes of nutrition. In commercial sheep farms, lambs tend to be managed in groups and each group allocated to paddocks/fields until finishing for slaughter. Ignoring these differences is a significant limitation because group location could be an important confounding or effect-modifying factor when estimating influencers of growth rate. There have been various modelling approaches developed such as Cross-classified and Multiple Membership mixed models in educational and social science research that account for grouping effects (Goldstein et al., 2007; Grady and Beretvas, 2010). Such methods however, are yet to be employed in animal growth modelling. Exploration of alternative model structures that account for the effects of animal grouping would be beneficial to evaluate the extent to which hierarchical models can be improved upon.

The primary objective of this study was to use longitudinal data to quantify the simultaneous effects of multiple ewe and lamb factors on lamb growth rate, while accounting for correlation structures within the data. A secondary aim was to evaluate model structures that specifically account for lamb grouping effects during the growth period and compare these to a classical hierarchical growth rate model.

2. Materials and methods

The study was carried out in accordance with the STROBE-Vet recommendations (Sargeant et al., 2016), and methodological details are provided on study design, setting, participants, variables, data sources, bias, study size, and statistical methods.

2.1. **Flock information**

The data for this study originated from a 1400 ewe flock located in west Wales (UK) at an altitude between 60 and 360 metres, specialised in the production of high quality breeding animals. The breeding flock comprised several pure and stabilised composite breeds (Aberfield, Abermax, Charollais, Primera, Highlander, Texel) and F1 hybrids (Texel X Primera, Primera X Abermax, Texel X Charollais, Texel X Bluefaced Leicester and Texel X Hartline). The ewes were managed on a rotational grass-based system with minimal supplementary feeding in 2016 and 2017. An ultrasound scan to determine lamb numbers was carried out in all ewes in January 2017. The study period was January to October 2017 following an outdoor lambing between mid-April and mid-May 2017 with lambs weaned at around 12 weeks of age. From May to September lambs were kept in grass paddocks with no supplementary feeding.

The lambs and ewes in this flock were a convenience sample known to have the necessary detailed recording of health and production information for the intended analysis. Therefore, this flock represented both the target and source population for the study.

2.2. **Sample size calculation**

Since the approximate size of the available study population was known (800 lambs), the effect sizes likely to be detectable were estimated. Assumptions used to make the estimates were; power of 0.8, significance probability of 0.05, mean lamb weight in an unexposed group of 30 kg, age-specific variance in lamb weight of 20 kg. Given that the final model structure was not known in advance and that power analyses for complex mixed effect models involves assumptions around random effect variances that can be difficult to make (Johnson et al., 2015), estimates were made using a conservative assumption of only one weight recording being available per lamb. On this basis, for a sample size of 800 lambs and a balanced covariate (with an event that occurred equally in two groups), it was estimated that a difference in weight of ≥ 0.9 kg would be detectable. For a condition that occurred in 1 in 10 lambs, a difference of ≥ 1.5 kg would be detectable and for a condition that occurred in 1 in 20 lambs, ≥ 2.1 kg would be detectable. These effect sizes were deemed plausible and of biologically importance and therefore a sample size of 800 lambs was considered sufficient for this study.

2.3. **Weight recording and lamb grouping**

Lambs were weighed for the first time when they reached approximately eight weeks of age. Since the birth date of lambs varied, the first weighing (T1) took place either on the 13th of June or 12th of July 2017 (T1). The second weighing (T2) occurred at the time of weaning and took place either on the 13th or 31st of July (T2). The third weighing occasion (T3) took place on the 24th of July, the fourth (T4) on the 7th of August, the fifth (T5) either on the 18th, 22nd, 25th or 29th of August, and finally the sixth (T6) and the seventh (T7) occurred on 4th and 18th September respectively. Not all lambs were weighed on all occasions. Weighing of lambs was carried out by the farm staff using an IAE Lamb Weigh Crate True Test ® electronic weight scale and recorded in kilograms to one decimal place. Lamb weight (kg) and weighing date (DD/MM/YYYY) were recorded in an excel spreadsheet.

After each weighing, lambs were reallocated to a group. Since the flock management strategy at regrouping was to maximise lamb growth by homogenising the characteristics of each lamb group, the group allocation decision was based on a combination of lamb characteristics (birth date, ewe breed, litter size or sex) and weight. Lambs were allocated to one of five groups between birth and time T1, one of four groups between T1 and T2 (weaning), one of three groups between T3 and T4, one of four groups between T4 and T5, one of three groups between T5 and T6 and one of two groups between T6 and T7. Group allocation was recorded in an excel spreadsheet with weighing information. Additional information on grazing quality or stocking rates was not available.

2.4. **Management of flock health and recording of treatments**

Breeding ewes had been vaccinated against toxoplasma and enzootic abortion prior to their first pregnancy. Lambs and ewes were vaccinated against clostridial diseases and pasteurellosis. Ewes were vaccinated 4 weeks prior to the start of the lambing period and lambs were vaccinated at 3 and 8 weeks of age. Severely lame sheep were culled following an annual inspection of all ewe feet and no vaccine for footrot was used. Anthelmintic treatment (Albendazole) was administrated to all lambs in May 2017 for *Nematodirus battus* control and from July 2017 it was administered to lambs based on Faecal Egg Count group results (according to the "Sustainable Control of Parasites in Sheep" (SCOPS) protocol (Abbott et al., 2012).

Shepherds were trained by veterinary surgeon members of the research team (Peers Davies and Isobel Lees) on the correct identification, recording and treatment of common diseases in sheep (e.g. mastitis, pneumonia, bacterial arthritis, lameness). All stock were inspected daily for the presence of signs compatible with disease by the shepherds with an additional visual assessment approximately every three days when the lambs were moved between fields. Lameness cases were identified based on clinical signs by the farm shepherd. The animal identification number, treatment date, reason for treatment and active substance used were recorded with a mobile phone application (Shearwell ®). Treatment data were collated in an excel spreadsheet at the end of the study period (September 2017).

2.5. **Data processing**

Lamb growth data and ewe and lamb treatment records were linked using Access ® software (Microsoft Corp, 2013) and comprised information on lamb ID, ewe ID, ewe breed, ewe age, date of birth, lamb breed, lamb sex, estimated litter size at ultrasound scanning, actual litter size at birth, weighing dates, lamb weight at each weighing occasion, lamb group allocation and ewe and lamb health events.

Stata software (StataCorp, 2017) was used for data cleaning, preliminary data analysis and to explore frequency distributions of the variables.

Observations with missing data in any of the relevant variables (n=45) were excluded from the dataset. A total of 4217 weight observations were recorded but data were not present for all relevant variables (ewe ID, lamb rearing type, lamb sex or management groups) resulting in 4172 weight observations within the final dataset.

2.6. **Categorisation of ewe and lamb variables**

Ewe breeds were grouped into "maternal" (Aberfield and Highlander), "terminal" (Abermax, Primera, Charollais and Texel), and "hybrid" (Texel X Primera, Primera X Abermax, Texel X Charollais, Texel X Bluefaced Leicester, and Texel X Hartline). Seven and 8-year old ewes were merged into a single age category due the low number of observations (n=13) within the latter category. "Litter size during pregnancy" reflected the number of lambs present during pregnancy as identified at scanning. Litter sizes at scanning of three and four lambs were merged into a single category due to the low number of quadruplet lambs identified (n= 12 lambs). "Rearing type" was defined in the context of this study as the number of lambs alive immediately after lambing and was categorised as "single", "twin" or "triplet" (none of the quadruplets identified at scanning were alive after lambing). All types of ewe lameness (e.g. CODD, footrot and scald)(Aitken, 2007) were grouped into a single category due to the low total number of lameness cases (n=15).

Preliminary phenotypic lamb classification decisions were made by the farm management team according to lamb suitability for breeding purposes. Criteria were bodyweight, foot conformation and breed-specific phenotypic characteristics when lambs reached approximately twelve weeks. In the context of this study, this categorisation was defined as "high quality pedigree females", "high quality pedigree males", "low quality pedigree females" and "low quality pedigree males". This classification influenced subsequent lamb management and was therefore taken into account as a potential confounder during the statistical modelling.

2.7. **Coding of disease events**

The dates of occurrence of bacterial arthritis, pneumonia and lameness cases in lambs were taken into account when coding new variables representing disease events. To capture the possible effect of disease occurrence on lamb growth rates over time, categorical disease variables were created such that lamb weights recorded before a disease event were differentiated from those recorded afterwards. Disease events corresponding to lamb weight recordings taken before a specified disease event were classified as “1”, those corresponding to weight recordings taken after the disease event were classified as “2” and those corresponding to weight recordings from lambs never affected by the disease were classified as “0”.

For ewes, only disease events occurring before the date of weaning were included in analysis because from this point onwards ewes were separated from lambs and it was considered that further ewe disease cases would not affect lamb growth.

Mastitis in sheep causes chronic structural damage to the mammary tissue of diseased ewes and can cause a considerable reduction in milk yield (De Olives et al., 2013; Gonzalo et al., 2002) which affects lamb growth (Grant et al., 2016). To capture the potential long-term impact of the condition on lamb weight, a categorical variable for ewe mastitis was set as “1” against all lamb weights in ewes that had a case of mastitis at any time before weaning and as “0” for weight recordings of lambs from ewes unaffected by mastitis. The impact of ewe lameness on lamb growth is less well understood and therefore we hypothesised that a short-term impact of the condition on lamb weight could occur. A categorical indicator variable for lameness in ewes was created to reflect the time that lameness occurred between mating and the weaning; the indicator variable was aligned to lamb weight recordings taken at specific time points as follows. The indicator variable aligned with lamb weight recordings at time T1 (8 weeks of age) were classified as “0” if the ewe had not been affected by lameness between mating and 8 weeks after lamb birth, as “1” if the ewe was lame during pregnancy, as “2” if a ewe had been lame between lamb birth and 4 weeks of lamb age and as “3” if a ewe had been lame between 4 and 8 weeks of lamb age. At other weight recordings (T2- T7) the indicator variable was classified as “4” if a ewe had ever been affected by lameness between mating and T1, and as “5” if a ewe had not been affected by lameness between mating and T1.

2.8. **Statistical models**

For statistical modelling purposes the effects of lamb groupings over time were explored. Both the combination of individual groups a lamb was allocated to during the study period and the number of days spent in each group were determined for exploration using cross-classified and multiple membership structures.

The outcome variable for all models was defined as lamb weight (kg) at each recording between 8 and 26 weeks of age and explanatory variables considered were ewe breed, ewe age at lambing, litter size during pregnancy (at scanning), litter size after birth, lamb sex, and ewe and lamb disease events. Due to the non-independence of observations a mixed modelling approach was implemented using the software package MLwIN (version 3.0)(Charlton et al., 2017). In order to facilitate interpretation of results, lamb age was rescaled to (age-56) such that the model intercept corresponded to lamb weight at the first weighing occasion (i.e. 56 days) rather than at birth.

Initial model exploration was carried out using iterative generalised least squares and final estimates for all models parameters were made in a Bayesian framework using Markov chain Monte Carlo (MCMC), appropriate for cross classified and multiple membership models (Browne, 2017). Models were built using a forward stepwise approach and Bayesian p-values (BPv) (the posterior probability of a true parameter value being either greater or less than zero) were used to select the final model (BPv<0.05 was deemed “significant”). Non-linear effects of continuous covariates were tested by adding polynomial terms (to power 4) and interactions between final covariates were retained when BPv<0.05.

Three models were built and compared using the Deviance Information Criterion (Kuhn and Johnson, 2013; Spiegelhalter et al., 2002) to evaluate best model fit. The first model, Model 1, was a 3-level hierarchical model with repeated measures of lamb weight nested within lambs within ewes and represented a conventional growth curve model (Craig and Schinckel, 2001; Green et al., 1998; Leeden, 1998; Strenio et al., 1983) (Figure 1, A). This model contained a random slope term for "age" to allow between-lamb variation for the influence of age on growth; this improved model fit. Model 1 therefore took the form;

$$Y_{ijk} = \beta_0 + \beta_1 \mathrm{X}_{ijk} + \beta_2 \mathrm{X}_{jk} + \beta_3 \mathrm{X}_k + u.age_{jk} + v_k + u_{jk} + e_{ijk} \qquad (1)$$

Where Y_{ijk} was weight *i* of lamb *j* from ewe k, β_0 was the model intercept, $\beta_1 X_{ijk}$ represented weight measurement level covariates for weight *i* from lamb *j* from ewe k, (such as lamb age), $\beta_2 X_{jk}$ represented lamb level covariates from lamb j from ewe k, (such as litter size and lamb sex), $\beta_3 X_k$ represented ewe level covariates from ewe k, (such as ewe breed and ewe age), $u.age_{jk}$ represented a set of random variables one for each lamb, allowing between lamb variation for the effect of age on lamb weight, v_k was a random effect to reflect variation between ewes, u_{jk} was a random effect to reflect variation between lambs, and e_{ijk} reflected residual model error. Polynomial terms up to power four for the fixed effect "age" were tested in the model to account for possible non-linearity in lamb growth rate over time. The random effects and residual errors were assumed independent and normally distributed with 0 mean and variances σ^2 as follows:

$$v_k \sim N\left(0, \sigma_v^2 \quad \right)$$

$$u_{jk} \sim N(0, \sigma_u{}^2), \begin{bmatrix} \sigma_{u_0}^2 & \\ \sigma_{u_{01}} & \sigma_{u_{02}}^2 \end{bmatrix}$$

$$e_{ijk} \sim N\left(0, \sigma_e^2\right)$$

Two additional models were built to include parameters to account for the effect of lamb grouping over time. Model 2 was specified as a cross-classified model with an additional random effect representing the entire combination of groups a lamb belonged to over time. Therefore, the model contained lamb repeated weight measurements nested within lambs within ewes but lambs were also cross-classified at group level as illustrated in Figure 1, B. The model accounted for the entire combination of groups to which a lamb was allocated over time but not the time spent in each specific group. The same fixed effects were tested in the cross classified and multiple membership models. A random slope term to model variation in the effect of age between lambs was not included since model convergence did not occur because the additional random effect for lamb grouping was closely correlated to the random slope term for age. Model 2 (cross classified model) was defined as:

$$Y_{ijkh} = \beta_0 + \beta_1 X_{ijk} + \beta_2 X_{jk} + \beta_3 X_k + w_h + v_k + u_{jk} + e_{ijk} \qquad (2)$$

Where Y_{ijkh}, represented the weight *i* of lamb *j* from ewe *k* in cross classified group h, β_0, $\beta_1 X_{ijk} + \beta_2 X_{jk} + \beta_3 X_k$, and the random error terms v_k, u_{jk} and e_{ijk} were as defined in Model 1 and w_h represented a random effect at group level for lambs, in the h$_{th}$ group, that were assumed independent and normally distributed with 0 mean and variance ${\sigma_w}^2$.

The third model was specified as a multiple membership model which accounted for the time lambs spent in each management group. In the multiple membership structure, all lowest units were not assigned to a single classification, as occurred in the cross classified model but it was assumed that the effect of each grouping was a fraction of the total amount of time spent in each group by each lamb (Rasbash et al., 2017) (Figure 1,C). A weighting factor representing the number of days each lamb spent in each group was assigned to the appropriate lamb weight and weighting factors were scaled such their sum equalled to 1 for each lamb. Lambs weights were aligned to the last day a lamb had been in a membership group and therefore reflected the impact of weight of a lamb having been present in that group.

Model 3 (multiple membership model) was defined as:

$$Y_{ijkf} = \beta_0 + \beta_1 \mathrm{X}_{ijk} + \beta_2 \mathrm{X}_{jk} + \beta_3 \mathrm{X}_k + \sum_{f=1}^{f} mm_{i,f} w + v_k + u_{jk} + e_{ijk} \qquad (3)$$

Where $\mathrm{Y}_{\mathrm{ijkf}}$, represented the weight i of lamb j from ewe k in multiple membership group f, β_0, $\beta_1 \mathrm{X}_{\mathrm{ijk}} + \beta_2 \mathrm{X}_{\mathrm{jk}} + \beta_3 \mathrm{X}_{\mathrm{k}}$, and the random error terms v_k, u_{jk} and e_{ijk} were as defined in Model 1, $mm_{i,f}$ was a random effect representing the weight recording of the i_{th} lamb in f_{th} management group and w was the weighing factor for group mm representing the time a lamb spent in that group.

The higher level grouping residual errors *mm* were assumed independent and normally distributed with 0 mean and variance, $\sigma_{mm}{}^2$.

Figure 1. Schematic representation of the three hierarchical structures tested. The first figure (A) represents a structure used in conventional growth models (repeated measures of weight nested within lambs within ewes). Figure B represents a cross-classified structure of the data, with lambs nested within a combination of groups. Figure C represents a multiple membership structure, with repeated measures of weight nested within groups. The latter structure allows to account for the effect of time spent in each group.

2.9. **MCMC specification**

All models were set up within a Bayesian framework and used MCMC for parameter estimation (Browne, 2017). Diffuse, flat priors were used for fixed and random effect terms and a Wishart prior for the variance-covariance matrices, as described by Browne (2017). A burn-in of 1000 iterations was used, and all chains converged prior to the end of the burn-in. An additional 500,000 iterations were run for determination of final model parameter estimates. Model convergence was evaluated based on the Raftery-Lewis diagnostic (Raftery and Lewis, 1992) and a calculation of the chain effective sample size (Spiegelhalter et al., 2002) as well as a visual assessment of the MCMC chains.

2.10. **Comparison between models and evaluation of model fit**

The Deviance Information Criterion (Spiegelhalter et al., 2002) was used to compare fit between models and a full model assessment was conducted on the multiple membership model which was identified as the best model and used for final inference.

Initially, model assumptions were checked visually using histograms and q-q plots of error terms at each model level. To check the influence of outlying points, the final model was re-run with the omission of points with residuals falling outside two standard deviations from the mean; changes in coefficients and BPv evaluated.

To further assess model fit and explore possible overfitting, full additional model checks were conducted using model posterior predictions, both with the full dataset (internal predictions) and by implementing a 10-fold cross validation (cross validation predictions). Predictions were made without the inclusion of random effects; they were based on the fixed effects only. For both full internal and cross validation predictions, model predicted values were graphically compared to observed values and the r-squared (R_2), root mean squared error (RMSE), and mean absolute error (MAE) were computed and compared between internal and cross validation predictions.

3. **Results**

3.1. Descriptive statistics

The final dataset comprised 4172 lamb weight recordings (median number recordings per lamb = 6, interquartile range (IQR = 4- 6)) from 805 lambs. The median lamb weight across the 4 month study period was 30 kg (IQR 24.5 – 35), with a median weight of 22.5 kg (19 – 25.5) and 34.5 kg (31 – 38.5) in T1 and T7 respectively.

Out of 559 ewes, 40%, 29% and 31% were from maternal, terminal and hybrid ewes respectively. Based on ultrasound scanning during pregnancy, it was estimated that in utero, 31% (252/808) of the lambs were singletons, 58% twins and 11% triplets or quadruplets. Due to in utero losses, stillbirths or scanning error, 17% of the lambs scanned as twins were reared as single lambs and 22% and 48% of the multiples were reared as singles and twins respectively. Male and female lambs classified as poor quality (based on preliminary phenotypic selection) and not suitable for breeding represented 12% and 3% of the lambs respectively. Three per cent (15/559 ewes, corresponding to 123/4172 lamb weight recordings) of the ewes were affected by lameness and <1% were affected by mastitis (4/559 ewes, corresponding to 32/4172 lamb weight recordings). Two per cent of the lambs were affected by lameness (14/805 lambs, corresponding to 65/4172 weight recordings), 1% (10/805 lambs, corresponding to 48 weight recordings) by bacterial arthritis and <1% (4/805 lambs, corresponding to 14 weight recordings) by pneumonia.

3.2. **Comparison between models**

The final hierarchical, cross classified and multiple membership models all contained the same fixed effects terms and had DIC of 19154.6, 19130.3 and 17756.4 respectively (Supplementary materials - Table 1). The model with clearly the lowest DIC was the multiple membership model (Model 3, Table 4), and hence final results and inferences were taken from this model. Final estimates of the variance components of Models 1-3 are provided in Supplementary materials - Table 1. These indicated that residual variation between lambs was the largest variance component in the hierarchical and multiple membership models, whilst variation between groups was responsible for most residual variation in the cross classified model. The variance partitioning at each model level indicates that the levels with the greatest and smallest amount of unexplained variability were respectively at the lamb and multiple membership levels (Supplementary materials - Table 1).

3.3. **Final multiple membership model – posterior estimates**

Parameter estimates from the final multiple membership model are provided in Table 4. In terms of the impact of ewe disease on lamb growth, both mastitis and lameness during pregnancy were found to have a deleterious effect. Lambs from ewes that were identified with mastitis during lactation were on average 3.0 (SE 1.6) kg lighter at each weighing than lambs from unaffected ewes. The relationship between ewe lameness and lamb growth was more complicated and is illustrated in Figure 2. Lambs from ewes that were not lame during pregnancy were on average 3.0 (SE 1.2) kg heavier at T1 (median age 56 days) compared to lambs from ewes with a least one lameness case during the same period. Lambs from ewes lame during either the first 4 weeks or between 4-8 weeks of a lamb's life (but not lame during pregnancy) were also significantly heavier at T1 than lambs reared by ewes that were lame during pregnancy (2.8 (SE 1.2) and 3.4 (SE 1.2) kg respectively). No difference was identified in lamb weight from T2-T7 between lambs that were the offspring of lame or non-lame ewes. Cases of bacterial arthritis, pneumonia and lameness had a negative impact on lamb growth. Lambs affected by bacterial arthritis were on average 2.2 (SE 1.2) kg lighter at each weighing after the disease event than lambs that did not suffer from the disease. After a lameness case, lambs had a mean weight reduction of 1.3 (SE 0.8) kg. Despite this loss, lame lambs remained heavier, on average, than non-lame lambs, although this difference was non-significant (Figure 3). Following a pneumonia case, lambs were on average 5.5 (SE 1.1) kg lighter at each weighing than lambs unaffected with pneumonia. Lambs affected by pneumonia or lameness during the study period were heavier prior to the disease event than unaffected lambs. Specifically, prior to a pneumonia case lambs were on average 3.5 (SE 1.9) kg heavier at each weighing than unaffected lambs, and 3.1 (SE 1.0) kg heavier prior to a lameness case than non-lame lambs.

Ewe age at lambing, ewe breed and litter size also influenced lamb growth. While hybrid-breed ewes produced lambs 1.7 (SE 0.4) kg heavier on average at each weighing than ewes from maternal breeds, there was no significant difference between terminal and maternal ewe breeds with regards to lamb weight. Lambs from four-year old ewes were on average 3.1 (SE 0.4) kg heavier than lambs from compared to 2-year old ewes but no significant differences were observed between two-year old and six or seven year old ewes in terms of lamb weight.

Both "litter size" at pregnancy (assessed through ultra sound scanning) and "rearing litter size" (i.e., actual number of lambs reared per litter, after accounting for abortion cases and mortality during lambing) had a significant effect on lamb growth. Lambs from litter sizes during pregnancy of 2 and 3 lambs were on average 3.1 (SE 0.5) and 3.3 (SE 0.7) kg lighter at each weighing than single lambs. Lambs reared as singles post-birth were on average 2.1 (SE 0.4) and 3.7 (SE 1.0) kg heavier at each weighing than twins or multiples respectively (after accounting for the effect of litter size during pregnancy). Sex also influenced growth, with male lambs ("high-quality" pedigree category") being on average 2.3 (SE 0.3) kg heavier at each weighing than females. There were no significant terms identified in the final model.

Table 4. Final posterior estimates for Model 3 (multiple membership model) for the outcome lamb weight (kg) between T1 (median age = 56 days) and T7 (median age = 162 days).

		n (weight records)	**n (lambs)**	**Coefficient**	**S.E.**	**Bayesian-p**
Ewe health	Weight records of lambs descendant from ewes *not treated for mastitis* during lactation	4140	798	*Reference*		

	Weight records of lambs descendant from ewes *treated for mastitis* during lactation	32	7	-3.0	1.6	0.03
	Weight records at T1₁ for lambs descendant from ewes *treated for lameness during pregnancy*	5	5	*Reference*		
	Weight records at T1₁ for lambs descendant from ewes *not treated for lameness* during pregnancy or lactation	774	774	3.0	1.2	<0.01
	Weight records at T1₁ for lambs descendant from ewes *treated for lameness during the first 4 weeks* of lamb life	8	8	2.8	1.2	0.01

	Weight records at T1[1] descendant from ewes *treated for lameness between 4 and 8 weeks* of lamb life	11	11	3.4	1.2	<0.01
	Weight records between T2[3] and T7[4] for lambs descendant from *ewes not treated for lameness* during pregnancy or lactation	3281	764	2.3	1.6	0.08
	Weight records between T2[3] and T7[4] for lambs descendant from *ewes treated for lameness* during pregnancy or lactation	92	24	1.9	1.4	0.09
Lamb health	Weight records prior to a case of lamb lameness	52	10	*Reference*		

	Weight records for lambs not treated for lameness	4107	596	-3.1	1.0	<0.01
	Weight records for lambs after a case of lameness	13	4	-1.3	0.8	0.07
	Weight records for lambs prior to a case of pneumonia	7	3	*Reference*		
	Weight records for lambs not treated for pneumonia	4158	607	-3.5	1.9	0.04
	Weight records for lambs after a case for pneumonia	7	4	-5.5	1.1	<0.01
	Weight records for lambs not treated for bacterial arthritis	4124	598	*Reference*		
	Weight records for lambs after a case of bacterial arthritis	48	10	-2.2	1.2	0.02
Lamb characteristics	Litter size at pregnancy$_4$- Single lamb	1334	255	*Reference*		

	Litter size at pregnancy[4] - twin lamb	2375	463	-3.1	0.5	<0.01
	Litter size at pregnancy[4] - triplet lamb	463	87	-3.3	0.7	<0.01
	Rearing type[5] – single lamb	1810	341	*Reference*		
	Rearing type[5] – twin lamb	2224	435	-2.1	0.4	<0.01
	Rearing type[5] – triplet lamb	138	29	-3.7	1.0	<0.01
	Sex - High quality pedigree female lambs	2197	366	*Reference*		
	Sex - High quality pedigree male lambs	1510	281	2.3	0.3	<0.01
	Sex - Poor quality female pedigree lambs (“slaughter” lambs)	159	66	-5.4	0.5	<0.01
	Sex - Poor quality male pedigree lambs (“slaughter” lambs)	306	93	-3.5	0.4	<0.01

Ewe characteristics	Ewe breed type - Maternal	1704	319	*Reference*		
	Ewe breed type - Terminal	1144	234	0.2	0.4	0.23
	Ewe breed type - Hybrid	1324	252	1.7	0.4	<0.01
	2-year old ewe	1185	247	*Reference*		
	1-year old ewe	57	15	-4.1	1.0	<0.01
	3-year old ewe	895	160	1.5	0.4	<0.01
	4-year old ewe	1072	201	3.1	0.4	<0.01
	5-year old ewe	410	79	1.0	0.5	0.02
	6-year old ewe	453	83	-0.2	0.5	0.33
	7-year old ewe	100	20	-0.4	0.9	0.31
	Lamb age (centred at 56 days)	4172	805	0.1	<0.1	<0.01
	Lamb age (centred at 56 days)[2]	4172	805	<0.1	<0.1	0.02
	Cons	4172	805	27.5		

[1] Median age at T1 was 56 days.

[2] Median age at T2 was 92 days.

[3] Median age at T7 was 162 days.

[4] Litter size during pregnancy - number of lambs present during pregnancy as identified at scanning.

[5] Rearing type- number of lambs alive immediately after lambing.

Figure 2. Illustration of results from the multiple membership model (Model 3) for the difference in lamb weights based on the timing of ewe lameness. Lambs from ewes that were lame during pregnancy were significantly lighter at the time of first recording (~56 days of age) compared to lambs descendant from non-lame ewes during pregnancy and also compared to ewes that were lame between parturition and 56 days into lactation. There was no effect on lamb weight after weaning (from T2 onwards) between offspring of ewes that were or were not lame.

Figure 3. Illustration of results from the multiple membership model (Model 3) for the difference in lamb weight based on the timing on (A) lamb lameness, for an hypothetical lameness event that occurred at 140 days of age, and (B) lamb pneumonia for an hypothetical event that occurred at 108 days of age (Plot B). Plot A - Lambs prior to a case of acute lameness were heavier than non-lame lambs. Although there was a drop in weight after a lameness case, lame lambs remained heavier, on average, than non-lame lambs. Plot B - Prior to a pneumonia case lambs were heavier than unaffected lambs and lost weight after a case, becoming lighter, on average, than healthy lambs.

3.4. **Model fit**

Graphical observation of the residual plots at each level indicated that residuals were normally distributed. All data points with standardized residuals <-2 and >2 were excluded from the dataset, and the model re-run. There were no substantive differences in the model coefficients (<5% of change) or BPv, indicating that the outliers did not have an important influence on final model results. Assessment of the observed versus model full internal predicted values (Figure 4A), suggested a good model fit with RMSE = 4.2, r_2 = 0.68 and MAE =3.3. The 10-fold cross validation had very similar fit statistics (RMSE, r^2, and MAE values 4.4, 0.67 and 3.5 respectively, Figure 4B), indicating that overfitting was not a feature of the final model.

Figure 4. Model fit assessment for the final multiple membership model (Model 3). Observed and model-predicted lamb weights: A – Predictions using all data available to the model (full internal predictions) and B- Predictions using 10-fold cross validation. The r^2 were 0.68 (A) and 0.67 (B).

3.5. **MCMC diagnostics**

Visual assessment of MCMC chains indicated good mixing and that chains had reached a stationary distribution within 10,000 iteractions. The Effective Sample Size (ESS) ranged from a minimum of 3050 (ewe-level variance) to 49877 (lamb pneumonia). The Raftery-Lewis diagnostic indicated that a minimum 28,101 iteractions were required to estimate the upper and lower 95% credible interval (CI) of all model parameters (± 0.005) with a probability of 95%. The number of iteractions used (500,000) greatly exceeded this.

4. **Discussion**

The primary aim of this study was to quantify the effect of concurrent ewe and lamb disease events on lamb growth, while accounting for correlation structures within the data. To the authors' knowledge, this is the first longitudinal study to estimate the simultaneous effects of both ewe and lamb health events on lamb growth and the first to account for the impact of lamb grouping on growth rate.

Mastitis and lameness in ewes are relatively common conditions (Arsenault et al., 2008; Winter et al., 2015) and in this study both were found to have an important impact on lamb growth. Lambs that were offspring of ewes diagnosed with mastitis during the study period were on average 3.0 (SE 1.6) kg lighter during the growth phase (56-162 days of age) than lambs from ewes that did not have mastitis. These results are in broad agreement with previous studies

(Arsenault et al., 2008; Grant et al., 2016) that reported a negative impact of ewe mastitis cases on lamb growth. One of these studies specifically looked at the relationship between lamb growth and milk somatic cell count (SCC) (as an indicator of mastitis) and reported a less pronounced effect of mastitis on growth compared to the current study (-1.3 kg) (Huntley et al., 2012). Differences in the estimates may result from the use of different indicators of mastitis (SCC as opposed to clinical presentation of the disease) and from the longer study period of the current study. A reduced lamb growth rate is likely to result from a reduced milk production observed in ewes with mastitis (De Olives et al., 2013; Gonzalo et al., 2002). Interestingly, previous research reported the deleterious impact of mastitis was negated when lambs were given supplementary feeding (Keisler et al., 1992) which suggests that provision of additional sources of feed could have decreased the impact of mastitis on lamb growth in this study.

The impact of ewe lameness on lamb growth was explored in detail, in particular the extent to which the timing of ewe lameness affected growth rates. It was notable that only ewe lameness during pregnancy was associated with a reduction in lamb growth, and this was only for a limited time period since from the second recording onwards there were no significant weight differences between lambs descendant from lame and non-lame ewes during pregnancy. Lambs from ewes that were lame during pregnancy were lighter at the first weight recording (~56 days of age) compared to lambs from ewes that were never lame and also compared to lambs from ewes that were lame between parturition and 56 days into lactation. Although caution is needed because of the small numbers of observations of ewe lameness during pregnancy, the pattern is worthy of note because biologically the pathway is plausible and of potential importance. To the authors’ knowledge no published studies have directly looked at the effect of sheep clinical lameness on feed intake but a previous experimental study reported that limb-induced pain led to a marked drop in feed intake in ewes (Colditz et al., 2011). It has also been reported that a drop in maternal glucose concentrations during pregnancy (which could result from a period of reduced intake) caused reduced placental growth and reduced lamb growth rate (Mellor, 1983; Mellor and Murray, 1981). A reduced food intake by ewes during pregnancy could explain why, in this study, cases of lameness during pregnancy had a marked effect on early lamb growth.

Previous research reported that lame dairy ewes produced significantly lower milk compared to a control group (approximately 47 kg less milk per ewe) (Gelasakis et al., 2010) but interestingly in the current study there was no clear effect on lamb weight after weaning (>56 days of age) between offspring of ewes that were or were not lame after parturition. Therefore, ewe lameness during lactation did not appear to have subsequent deliterious effects on lamb growth. This could either be due to a neglegible effect of lameness on milk production because of prompt treatment of lameness cases, due to lambs obtaining an alternative additional nutrient supply (e.g. from increased grazing) or be resultant from a compensatory growth effect after an impact of lameness. Compensatory growth has been observed in sheep, with lambs fully recovering their weight after an energy restriction period (Fan et al., 2018; Turgeon et al., 1986). Despite there appearing to be no clear influence of ewe lameness during lactation on lamb growth, undoubtedly prompt treatment of lameness in ewes remains essential (Kaler et al., 2010).

In terms of the effect of lamb health on lamb growth rates, a deleterious impact was identified from lameness, pneumonia and bacterial arthritis. For cases of pneumonia, a significant weight reduction was observed after the disease event and this is in agreement with a recent study investigating exposure to *Mycoplasma ovipneumonie*, which concluded that exposed lambs had significantly lower daily weight gains than non-exposed lambs (Besser et al., 2019). In terms of lamb lameness in the current study, a non-significant weight reduction was observed after the disease event. A previous study examined differences between average weights of case (high lameness prevalence) and control groups (very low lameness prevalence) of lambs over a two year period and concluded that the group with untreated lameness cases had significantly lower average body weights (Marshall et al., 1991). In a further randomised control clinical trial comparing lameness treatment options, Wassink et al. (2010) observed that the group of lambs promptly treated with parenteral antibiotics had a greater proportion of lambs finished compared to the control group (Wassink et al., 2010). Nieuwhof et al. (2008) projected the growth trajectories of non-lame lambs to estimate weight differences due to a lameness case and concluded that a weight reduction between 0.5 and 2.5 kg could be expected. Although previous work reported a negative impact of lameness, none of these studies has incorporated the timing of lameness at the individual lamb level. Therefore this is the first study reporting differences in growth rate before and after a lameness case and identifying weight changes with respect to the timing of lameness. Differences in the average effect of lameness in this study compared to previous research is possibly be due to differences in type of lameness, speed of treatment and the length of the study period.

Of particular interest in this study was the finding that lambs in weight recordings prior to a case of lameness or pneumonia were significantly heavier than healthy lambs. For lamb pneumonia, our results are in broad agreement with previous research (McRae et al., 2016) that reported that lambs with pneumonic lesions at slaughter grew faster from birth to weaning and slower from weaning to slaughter compared to animals with no lesions. In this study lambs remained heavier after a lameness event than lambs that had never been lame. Previous studies also showed a similar important effect of lameness in dairy cows with respect to milk yield; higher yield cows were more likely to be lame and produced more milk throughout lactation than cows that were never lame, even though the amount of milk produced decreased after a lameness case (Green et al., 2002). Although the underlying physiological mechanism behind this effect has not yet been studied in sheep, previous research in other species suggests it may result from a trade-off between performance and immune function. An inverse relationship between growth and immune function has been observed in poultry (Van Der Most et al., 2011), cattle (Foote et al., 2007; Frisch and Vercoe, 1984) and humans (McDade et al., 2016; Urlacher et al., 2018). The high energy cost associated with the maintenace of immune cells (Mangel and Stamps, 2001) suggests that high performing animals might benefit from additional nutrient sources. It is possible that a negative relationship between immunity and growth could be more prononced in this sheep flock, where heavier, high performing animals have been selected for breeding. The results of this study pose important questions regarding breeding strategies in sheep. From the perspective of sustainable production, animal welfare and medicines usage, the selection of livestock for breeding should take into account resistance to disease and not focus solely in high growth rates which itself might lead to a predisposition to disease. Use of breedlines of poultry with slower growth rates but greater resistance to disease are currently being tested by the Dutch broiler industry as part of a strategy to reduce medicines usage (Avined, 2018). To the authors' knowledge such selection strategies are not currently used in sheep or beef production.

In contrast to lameness and pneumonia, there are no published studies that have evaluated the impact of bacterial polyarthritis ("bacterial arthritis") in live lambs. It has been reported that most causes of polyarthritis in sheep are of bacterial origin (Watkins and Sharp, 1998). The size of the effect of a case on lamb weight (2.2 kg weight reduction,) was comparable to the estimate of a recent abattoir study (2.7 kg weight difference) that evaluated deadweight of carcasses with and without lesions of bacterial polyarthritis (Lloyd et al., 2019). Results of the current study indicated that after a case, lambs did not recover their weight and remained lighter than healthy lambs. This also aligns with previous research that reported that age at slaughter increased in lambs affected by arthritis (Green et al., 1995). The relative economic importance of the condition in the UK is unknown (Watkins and Sharp, 1998), but these results confirm that it has a long-lasting impact on lamb growth as well as being an important welfare concern.

The estimate of scanning percentage information in this study allowed an estimate of the number of lambs carried by the ewe during pregnancy to be included as a predictor of lamb growth as well as the number actually born alive. Inclusion of this parameter provided a novel insight into the influence of pregnancy as opposed to lactation on subsequent lamb growth; both effects (pre-natal litter size and number of suckling lambs) had an important and separate relationship with growth. For instance, a lamb reared as a singleton was on average 3.1 kg (SE 0.5) lighter at each recording if it was scanned as a twin, compared to a lamb both scanned and reared as a singleton. Similarly, of lambs scanned as a twin, those then reared as a singleton were on average 2.1 (SE 0.4) kg heavier at each recording than those reared as twins. Previous studies that evaluated in-utero growth in multiple-size litter gestations, reported that lamb growth is regulated by restriction of placental size (Gootwine et al., 2007; Horton et al., 2016)) resulting in heavier singletons compared to twins and triplets. Additional research showed that after birth lamb growth rate was less closely correlated with milk production in twins compared to singles possibly because ewes with twins produced only 13 to 17% more milk compared to ewes with a single suckling lamb (Snowder and Glimp, 1991). Variations in placental space and quantities of milk available per lamb after birth may explain why in this study both postnatal and prenatal factors had an important effect on lamb growth.

Results of this study confirm previously reported non-disease related factors associated with lamb growth, such as ewe breed (hybrid breed individuals were associated with greater weights than animals from pure breeds (Sidwell et al., 1964)), ewe age (ewes aged between 3 and 6 years produced significant heavier lambs than yearlings (Dickerson and Laster, 1975)), and sex (males lambs grew faster than females (Fourie et al., 1970).

A secondary aim of this research was to compare and evaluate statistical models with different random effect structures (hierarchical, cross classified and multiple membership) for modelling growth curves. The results demonstrated that the multiple membership model structure provided a better model fit than the competing structures (Supplementary materials - Table 1A) and hence should provide most reliable parameter estimates. The multiple membership model performed better than the classical, hierachical alternative that included a random slope term in the *age* term. Traditional animal growth models commonly include a random slope for the time variable (Mølbak et al., 1997; Suzuki et al., 2012) to allow the relationship between age and growth to vary between individuals (Leeden, 1998), generally improving model fit. In this study, the multiple membership groups effectively incorporated the growth trajectories of individual lambs over time allowing weighing of the time spent in a group and hence accounted for variation in lamb growth at different ages. Interestingly, the multiple membership model provided a better model fit than the hierachical alternative which suggests the grouping variable provided a better representation of variation between lambs over time than a random effect for the interaction between lamb and age. This may be because the multiple membership model accounted for an effect of time spent in each group, and that growth rate differences between lambs were highy dependent on the environmental circumstances within these groups. Multiple membership structures have previously been shown to be important to optimise model fit (Grady, 2010), and since animals are commonly grouped within agricultural systems, such model structures should perhaps be investigated more commonly. One limitation of these models is that despite allowing for the effects of re-grouping over time, there is no additional historic effect captured. For example, if presence in new group resulted in a prolonged reduction in growth rate, whilst lambs entered different groups, the effect will not be identified. Whilst further modelling approaches could explore such effect it appears from the study that the inclusion of lamb group is worthwhile when estimating parameters in growth models.

In the current study the final model explained a considerable proportion of the total variability in lamb weight observations (68%), but there was still some variation that remained unexplained. Variation between lamb within ewe (which is not therefore a consequence of genetic variation) represented the greatest proportion of unexplained variability (Supplementary materials - Table 1) and this could be due to a variety of differences including colostral intake, subclinical disease, and additional unrecorded disease events, such as diahorrea (Green et al., 1998; Huntley et al., 2012) or endoparasitism (Kyriazakis et al., 1996; Mavrot et al., 2015). Collection of further data at the individual animal level could potentially reduce the proportion of unexplained variance and identify other important factors associated with lamb growth rates.

A limitation of this study was low incidence rate of some diseases and this is possibly explained by the fact that the data were collected in an intensively-managed, pro-active commercial breeding flock where disease management may be better than is typical farms in the UK. The small number of disease cases in this study could lead to an increased uncertainty in the estimation of the model parameters and result in model overfitting. In order to investigate possible overfitting, a 10-fold cross validation was carried out. The cross validation results indicated that the internal and CV model fit parameters were very similar thus suggesting that the model had a good balance between model variance and bias with no overfitting (Kuhn and Johnson, 2013). Despite the fact that this study only included data from one farm, the results from the cross validation suggest that the model results may be generalizable to other similar sheep flocks. However, the generalisability of these findings to other types of sheep flocks has yet to be assessed and requires further research. Further research would also be useful to test and validate the hypotheses generated in this study in particular the possibility that heavier lambs are more susceptible to some diseases and that in sheep the trade-off between growth and immune function exists as in other species.

5. Conclusion

This is the first longitudinal study to estimate the concurrent impact of ewe and lamb characteristics and disease events on lamb growth rate and provides evidence that that a combination of these factors play an important role in determining lamb growth rate. In addition the data suggest that faster growing lambs may be more susceptible to disease. Use of a multiple membership mixed model structure better model fit than hierarchical and cross classified alternatives, suggesting that this type of model can be useful to model growth of livestock where multiple regrouping occurs.

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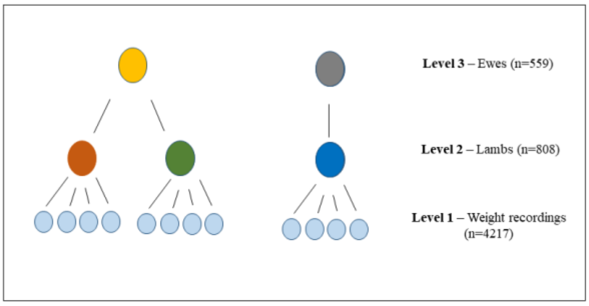
Supplementary Materials

Table 1. Variance partitioning and deviance Information Criterion of the three models compared in this study (hierarchical, cross classified and multiple membership models). The multiple membership model showed the best fit (lowest DIC).

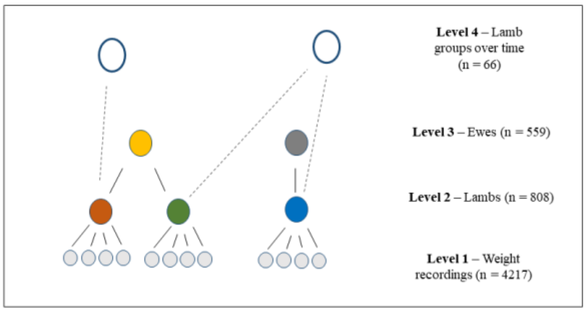
	Model 1	**Model 2**	**Model 3**	
	Hierarchical structure	Cross classified structure	Multiple Membership structure	Proportion of total variance (%)
Variance level 4 (cross classification / multiple membership level)		9.0	2.4	12%
Variance level 3 (ewe-level)	3.9	2.7	4.0	21%
Variance level 2 (lamb-level)	9.2	5.8	8.7	49%
Variance level 1 (weight repeated measures-level)	4.8	4.8	3.4	18%
Deviance Information Criterion (DIC)	19154.6	19130.3	17756.4	

Figure 1

A. Hierarchical model



B. Cross-classified model



C. Multiple membership model

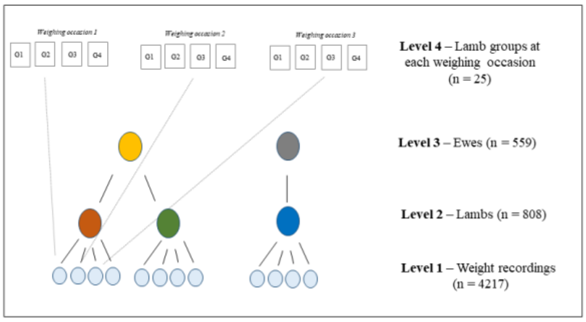


Figure 2

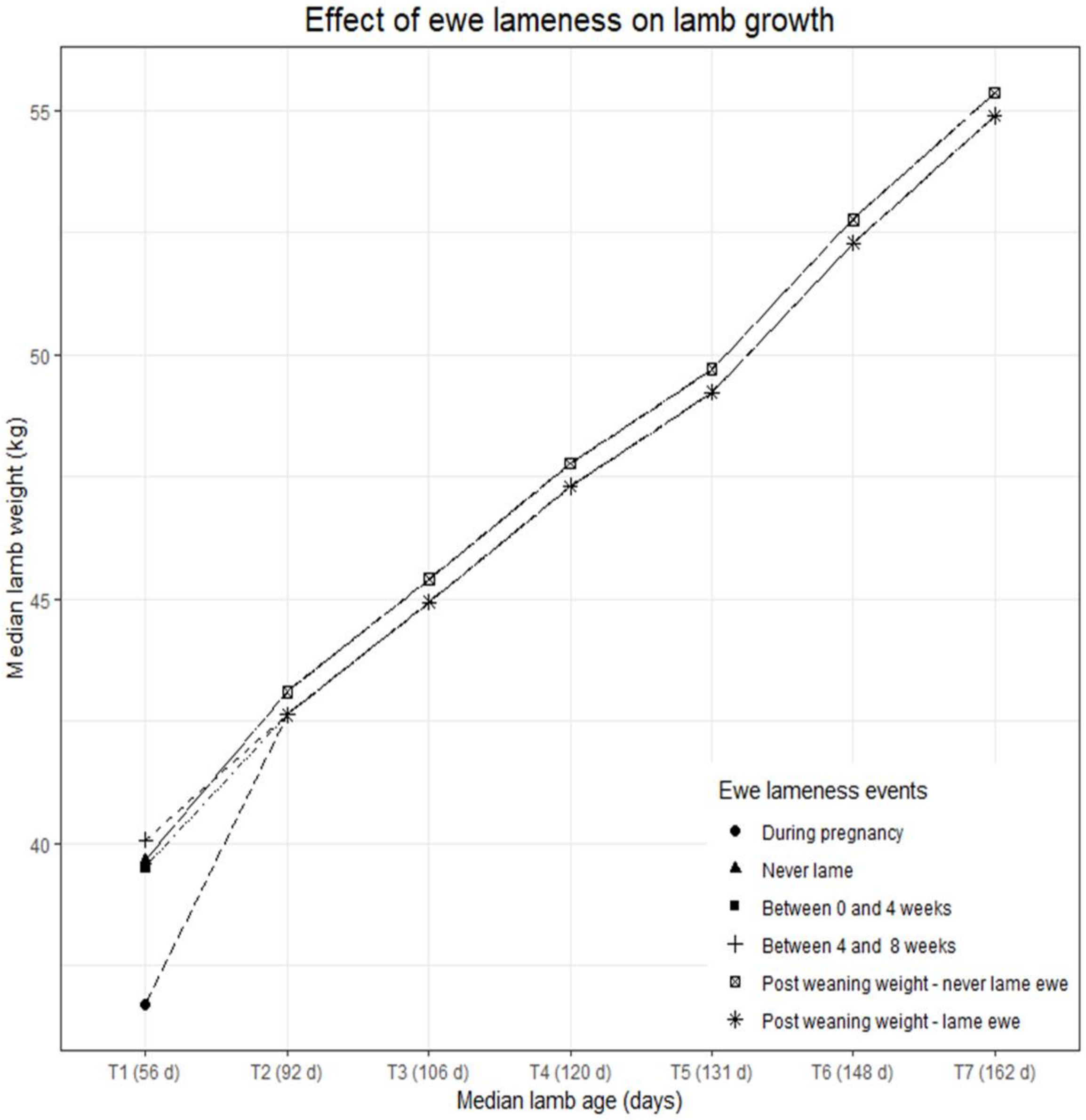
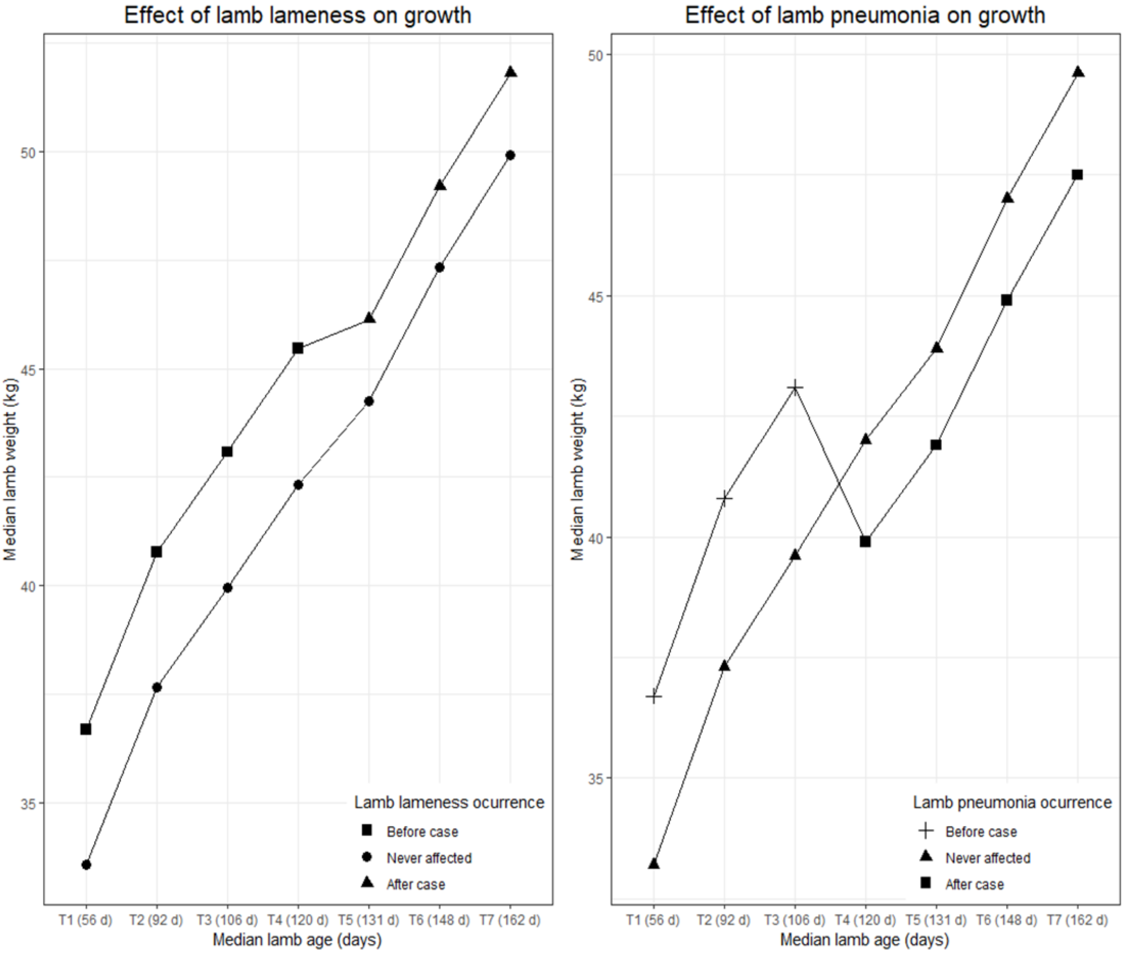
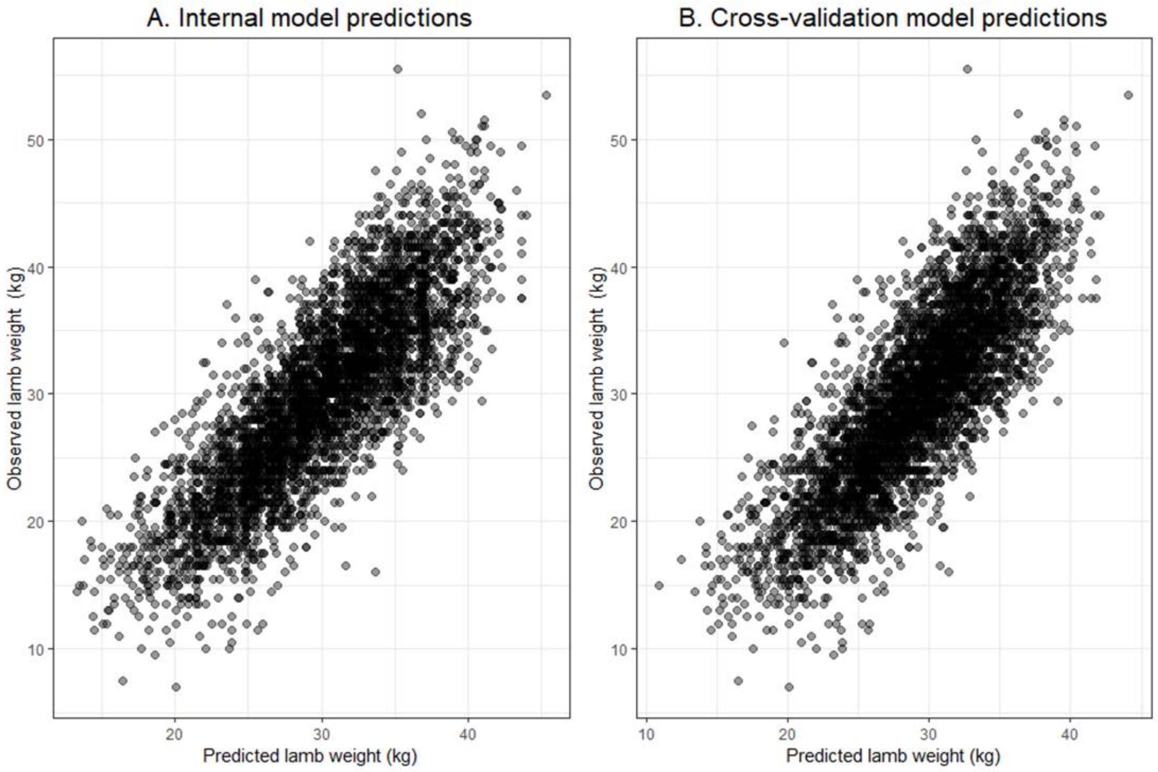

Effect of ewe lameness on lamb growth
Median lamb weight (kg)
55
50
45
40
T1 (56 d)
T2 (92 d)
T3 (106 d)
T4 (120 d)
T5 (131 d)
T6 (148 d)
T7 (162 d)
Median lamb age (days)
Ewe lameness events
● During pregnancy
▲ Never lame
■ Between 0 and 4 weeks
+ Between 4 and 8 weeks
⊠ Post weaning weight - never lame ewe
✳ Post weaning weight - lame ewe

Figure 3



Effect of lamb lameness on growth
Median lamb weight (kg)
35
40
45
50
T1 (56 d)
T2 (92 d)
T3 (106 d)
T4 (120 d)
T5 (131 d)
T6 (148 d)
T7 (162 d)
Median lamb age (days)
Lamb lameness ocurrence
■ Before case
● Never affected
▲ After case
Effect of lamb pneumonia on growth
Median lamb weight (kg)
35
40
45
50
T1 (56 d)
T2 (92 d)
T3 (106 d)
T4 (120 d)
T5 (131 d)
T6 (148 d)
T7 (162 d)
Median lamb age (days)
Lamb pneumonia ocurrence
+ Before case
▲ Never affected
■ After case

Figure 4



A. Internal model predictions

B. Cross-validation model predictions