ORIGINAL ARTICLE

Calving date and its variability as a potential trait in the breeding objective to account for reproductive seasonality in alpacas

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Abstract

The low fertility and offspring survival indicators in alpacas can be partially due to their particularity seasonal reproduction that reduces the opportunities of the females to become pregnant within a season, with the survival of the offspring concerned by the availability of food and exposure to diseases that depends on the calving date. Optimizing the date of delivery and reducing its variability are shown as eligible criteria that could be used as selection criteria within the genetic improvement programmes in alpacas, the calving date being a much more appropriate trait to measure and optimize fertility unlike of age at first calving and the calving interval, this due to the reproductive seasonality in camelids. For this study, 6,533 birth date records were taken between 2001 and 2018 of Peruvian alpacas, to estimate the genetic parameters. Models assuming heterogeneity in the residuals were fitted besides classical homogeneous models to address, not only the possibility of forwarding or delaying the calving date, but also the trend to have parturitions in similar dates. The heritability and repeatability ranged from 0.07 to 0.20 for a homogeneity model and from 0.08 to 0.23 for a heterogeneity model, and suggest the possibility of advancing or delaying the calving date. It should be taken into account that the gestation length of camelids makes it difficult to adapt many reproductive traits, and trying to centre the calving date could delay it. It was concluded the feasibility to genetically select the calving date, also in the production of camels and dromedaries, which have the same reproductive characteristics as alpacas. This selection can be combined with other traits. The heterogeneity model was shown to provide a better fit.

KEYWORDS

alpaca, calving date, genetic parameters, reproduction, seasonality

1 | INTRODUCTION

Pacomarca is an experimental ranch founded by the Inca group to act as a selection nucleus from which genetic improvement of alpaca fibre can be spread throughout the rural communities in the Peruvian Altiplano (Morante et al., 2009). Research at the farm in the last decades has importantly collaborated to increase the useful knowledge for breeding programmes, starting by the determination the most economically important selection objective and confirming that mean fibre of a staple would be the best criterion of selection for the goal of increasing the textile value of the animals (Gutiérrez, Goyache, Burgos, & Cervantes, 2009). These traits have

been complemented with other studies related to reproduction such as the effect of the milking and pregnant status on the fibre quality (Cruz, Morante, Cervantes, Burgos, & Gutiérrez, 2017) and the relationship with reproductive traits (Cruz, Cervantes, Burgos, Morante, & Gutierrez, 2015).

Managing the calving date is of special importance in alpacas as they have a particular reproductive profiling in Peru, with a marked mating seasonality, which is reduced to the summer months, in a period called campaign (Cruz et al., 2015). This seasonality is of major concern as females not getting pregnant in the campaign will remain open until next year.

Particularly, reproductive performance may dramatically affect livestock productivity (Cervantes, Gutierrez, Fernandez, & Goyache, 2010; Phocas et al., 1998), and in addition, reproductive trait heritability is known to be very low ranging between 0.03 and 0.05 (Freeman, 1984). Mating in Pacomarca has been designed according to selection criteria for twenty years, avoiding close relationship between animals to be mated. Calving date is partially defined by reproductive management decisions, but also partially due to the ability of the female to become pregnant under particular environmental conditions. Given that those females becoming open after an early mating will have a new chance within the campaign, there is a trend in the management to mate animals close to the beginning of the campaign. Then, there will be differences between animals in fertility, partly under genetic control, that will originate differences in calving date.

Cruz et al. (2015) studied several reproductive traits to be included in selection indexes of alpacas breeding programmes. They concluded that the age at first calving and the calving interval would be those to choose. Age at first calving in cattle was reported to be eligible under analyses involving both productive and reproductive traits (Tonhati, Vasconcellos, & Albuquerque, 2000), while calving rate and calving day were eligible against others (Ponzoni, 1992). The first one would be preferable over the second one in alpacas because of its higher heritability and its favourable genetic correlations with other productive and reproductive traits (Cruz et al., 2015). Traditional animal husbandry in alpacas has managed this scenario focusing on the age at first calving and calving interval traits (Cruz et al., 2015), but these traits do not account with the search of the optimal date. Calving interval, with a lower heritability, can be externally conditioned by the date the dam gave birth in the previous campaign, as animals calving early in the campaign will have more chances of becoming pregnant the next one. Lower ages at first calving will bring about more chances of pregnant for the second calving.

However, not always advancing births will be preferable. In fact, calving is preferred to occur in the middle of the reproductive season, as there will not be sufficient food resources if they are too early, and the animals will lose the opportunity of becoming pregnant for a year if they calve too late. In addition, the offspring of late calving increases the risk of becoming infected with enterotoxemia under the high humidity conditions which are common at the end of the reproductive season. Although there are vaccines against *Clostridium perfringes*, the cross-immune resistance is still deficient due to the large variability of strains of this infectious agent (Pérez, Maturrano, & Rosadio, 2012). Summarizing, optimally births would have to occur in the middle of the season, if not possible, it will be better to birth in the second half of the reproductive season than the first one.

Bourdon and Brinks (1982) proposed the use of calving date (CD) as a better measure of fertility in beef cattle than calving interval, because of its clearer economic significance and higher heritability; however, there are other criteria to increase reproductive and economic genetic gain, such as conception, calving rate or CD (called calving day), agreeing that at least some of these traits should be considered among the improvement objectives (Ponzoni, 1992). The beef scenario is not comparable to alpacas as these are seasonal and have a restricted reproductive period. However, CD has an important role to maximize economic and genetic yield in cows with seasonal pastures (Horn, Steinwidder, Starz, Pfister, & Zollitsch, 2014). CD has an additional effect on the development and body condition of newborns (McCarthy, Delaby, Pierce, Brennan, & Horan, 2013), and it was considered a less biased method to evaluate reproductive performance than calving interval; particularly, if cows were mated during a restricted breeding season (MacGregor & Casey, 1999), this extremely occurs in Alpacas. Gutiérrez et al. (2002) concluded that calving interval limits its use for selection because it is only available after a dam has calved for a second time, on the other hand, calving date can be collected from the first calving. This is still more remarkable as there is usually a strong selection for calving interval because the least fertile cows do not have much opportunities to calve for a second time (Pryce, Coffey, & Brotherstone, 2000).

The analysis of the calving date as useful trait candidate to select was promising, and not only by itself, but also its variability. The objective of this work was to estimate genetic parameters for the calving date trait and its variability to be considered as candidates to selection objective themselves as unique traits or combined.

2 | MATERIALS AND METHODS

To determinate the calving date (CD), the middle point between two consecutive calving seasons was firstly defined, which resulted in August the 8th for this data and it was considered as day 1. Then, calving date was defined as the days passed from the previous middle point (August the 8th). This definition takes as reference the middle point between two campaigns instead of the day with the highest probability of calving as usually (Gutiérrez et al., 2002). This different reference did not affect the results, but allowed to visualize the standard deviation magnitude regarding the mean, obtaining a coefficient of variation, very informative for studies of variability as the present. It also allowed to manage only positive values of the trait. Animals not becoming pregnant in a reproductive season did not have a record for the trait in this season, but the number of females not becoming pregnant each season was low (Cruz et al., 2019), and it is expected that will minimally affect the estimations. An artificial

inclusion of these animals as penalized records would skew the distribution of the records, which is a major concern for variability analyses (Gutiérrez, Nieto, Piqueras, Ibáñez, & Salgado, 2006).

The information used in this article comes from the routine registration of livestock activity and strictly complies with international legislation on animal ethics. The data were obtained from PacoPro v5.10, software of the Pacomarca experimental farm that has been proved to be more than suitable for genetic analyses (Cruz et al., 2019; Pinares et al., 2018). Data from complete reproductive campaigns from Pacomarca experimental farm from August the 8th of 2001 to August the 7th of 2018 were used, counting with 6,533 records of calving date from 1,611 females of Huacaya genetic type. Up to 282 females had more than 6 repeated records with a maximum of 16. There were 3,372 males and 3,161 females born in the calvings, with three different groups of coat colours, 4,399 being white, 1,108 cream and 1,026 black.

There were 8,383 animals in the pedigree file, with 671 different dams and 110 different sires. From the 1,611 females with own record, 641 had offspring in the data out of a total of 644 different dams in the pedigree file. There were 110 sires in the pedigree file, all of them with progeny in the data. There were 27.4 daughters on average per sire and 5.4 per dam.

Note that for this trait, it is very important to gather the information of complete campaigns to avoid skewness in the distribution of the data. Mean ± standard deviation of calving date trait as defined resulted in 171.8 ± 33.7 with 13.0 and 349.0 as minimum and maximum values, counted in days from August the 8th, with a symmetric distribution as shown in Figure 1, and with a reasonable coefficient of variation of 0.20 to carry out heterogeneity analyses (Tatliyer, Cervantes, Formoso-Rafferty, & Gutiérrez, 2019). Calving dates far from the mean value were exceptional as drawn in Figure 1.

Models assuming heterogeneity (HE) in the residuals were fitted besides classical homogeneity (HO) models to address, not only the possibility of forwarding or delaying deliveries under the HO model, but also the trend to have parturitions in similar or different dates under the HE model. It is important to note that under a reproductive scenario organized in short periods within a year, reducing the variability of birth dates would accommodate a higher number of
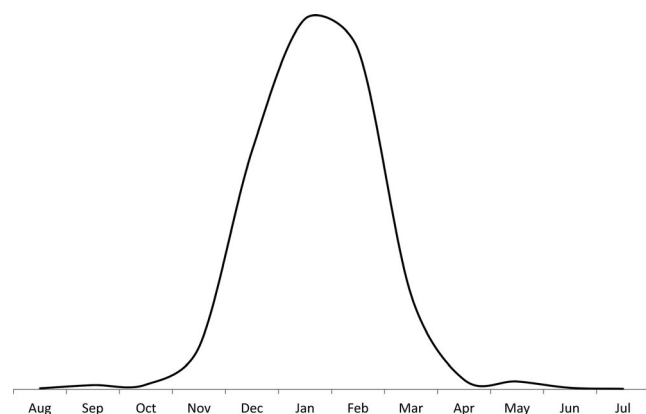

FIGURE 1 Distribution of calving date trait frequency across days in the calendar in Huacaya ecotype

calvings within those periods, making heterogeneity models interesting to deal with this. HO and HE models were fitted both including sex of the calf (2 levels), year as contemporary group (17 levels), coat colour as systematic effects (3 levels), age of the female as a covariate (in days), and genetic and permanent environmental as random effects. As females reduce the fertility with age, those animals older will need more tries to become pregnant. This was the assumption that led to fit the age effect as a covariate in the model.

Equation of the HO model was as follows:

$$y_i = x_i b + z_i a + w_i p + e_i$$

and,

$$\begin{pmatrix} a \\ p \\ e \end{pmatrix} \sim N \left(\begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & I_p\sigma_p^2 & 0 \\ 0 & 0 & I_e\sigma_e^2 \end{bmatrix} \right).$$

where y_i is the ith calving date, **b** is the vector for systematic effects listed above, **a** is the vector of the 8,383 additive genetic effects, **p** corresponds to the vector of the 1,611 permanent environments, e_i is the ith residual grouped in a vector **e**, x_i, z_i and w_i are the incidence vectors for systematic, animal and permanent environmental effects, respectively, I_e the identity matrix of equal order to the number of records (6,533), I_p the identity matrix of equal order to the number of permanent environmental subclasses (1,611), **A** the numerator relationship matrix, σ_a^2 the additive genetic variance, σ_p^2 the permanent environmental variance and σ_e^2 the residual variance.

HE model definition was as follows:

$$y_i = x_i b + z_i a + w_i p + e^{1/2(x_i b_* + z_i a_*)} \varepsilon_i$$

and,

$$\begin{pmatrix} a \\ a^* \\ p \\ e \end{pmatrix} \sim N \left(\begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} A\sigma_a^2 & A\rho\sigma_a\sigma_{a*} & 0 & 0 \\ A\rho\sigma_a\sigma_{a*} & A\sigma_{a*}^2 & 0 & 0 \\ 0 & 0 & I_p\sigma_p^2 & 0 \\ 0 & 0 & 0 & I_e\sigma_e^2 \end{bmatrix} \right).$$

where all is as in the HO model, and in addition with **a*** being the vector with the additive genetic values affecting the environmental variance of the CD, σ_{a*}^2 the additive genetic variance affecting the environmental variance of the CD and ρ the genetic correlation between the trait and the variability.

In order to compare some genetic parameters between HO and HE models, a residual variance in an average scenario was computed as follows:

$$\sigma_e^2 = e^{\sum_{i=1, systematic} \left(\sum_{j=1, n_s} \frac{\hat{b}_{ij}}{n_s} \right) + \sigma_{u*}^2/2}$$

Similarly, residual variances in the specific levels l of the campaign systematic effect c were computed as follows:

$$\sigma_{e_l}^2 = e^{\sum\limits_{i=1,systematic}^{i\neq c}\left(\sum\limits_{j=1,n_s}\frac{\hat{b}_{ij}^*}{n_s}\right)+\hat{b}_{cl}^*+\sigma_{u*}^2/2},$$

and were used jointly with the solutions for the calving date itself to estimate the period gathering 95% of the calvings each campaign. These expressions are extensions of the methodology by Formoso-Rafferty et al. (Formoso-Rafferty, Cervantes, Ibañez-Escriche, & Gutiérrez, 2017) to estimate heritabilities in particular levels of systematic effects. Predicted breeding values in **a** and **a*** were averaged within year of birth to assess the corresponding correlated genetic trends. All runs were carried out using the GSEVM program (Ibañez-Escriche, García, & Sorensen, 2010), for both HO and HE models in order to count with a deviance information criterion (DIC) value (Spiegelhalter, Best, Carlin, & van der Linde, 2002) to decide which model had better fit.

3 | RESULTS

The mean (± standard deviation) of the marginal posterior distribution of all the variances and genetic parameters is provided as estimates in Table 1. The estimate for the calving date heritability and repeatability becomes, respectively, 0.07 (± 0.02) and 0.20 (± 0.01) under the Model HO and 0.08 (± 0.03) and 0.23 (± 0.02) under the model HE. All the variances and genetic parameters were highly similar with the exception of the permanent environmental variance (and derived parameters) that was 34% higher in the model HE, and the standard deviation of the residual variance (and that of derived parameters) that was fourfold in the model HE. The estimate for the additive genetic variance affecting the residual variance (σ_{a*}^2) resulted

TABLE 1 Deviance information criterion (DIC) value and mean ± standard deviations of the marginal posterior distributions of the variances and genetic parameters estimated under homogeneous (HO) and heterogeneous (HE) models

	Model HO	Model HE
σ_a^2	86.18 ± 22.83	86.04 ± 28.15
σ_p^2	130.18 ± 22.43	174.06 ± 27.28
σ_e^2	860.75 ± 17.29	856.01 ± 81.58
σ^2	1,076.97 ± 21.04	1,111.85 ± 82.24
h^2	0.07 ± 0.02	0.08 ± 0.03
R	0.20 ± 0.01	0.23 ± 0.02
σ_{a*}^2	–	0.51 ± 0.06
r	–	−0.61 ± 0.11
DIC	51,412	49,615

Note: σ_e^2, R and σ^2 for model HE are expressed in the average of the levels of each systematic effect.
Abbreviations: σ^2, phenotypic variance; σ_{a*}^2, additive genetic variance affecting the residual variance; σ_a^2, additive genetic variance; σ_e^2, residual variance; σ_p^2, permanent environmental variance; r, genetic correlation between the trait and its residual variance; R, repeatability.

0.51 (± 0.06), with its square root as an approximate genetic coefficient of the variance for the variability of 0.71 (± 0.04), with a genetic correlation between the mean and the variability of −0.61 (± 0.11).

There was a great consistency between the mean values of calving dates found in the data and the solutions obtained for the systematic effects with both models. Mean phenotypic calving date within years of recording and those estimated with both HO and HE models are shown in Figure 2. Earliest and latest mean were 15 January and 11 February in 2008 and 2013, respectively, showing discrepancies across years with apparent tendency increasing from 2008 to 2013 and decreasing from 2013 to 2017. Mean phenotypic calving date within coat colour and those estimated with both HO and HE models are shown in Figure 3. Cream animals trended to delay the parturition 2 or 3 days, and black animals 1 or 2 days with regard to white animals. These differences concerning colours can be attributed to reproductive management within the campaign, mating first white animals as they are those with the fibre having the highest commercial value. The estimated regression coefficient for the age in days was 0.005295, in such an extent that a three-year-old female would have a parturition by 15 January delaying linearly the date up to 3 February when it becomes 10 years old, and up to 21 February if it became 20 years old.

Solutions for the fixed effects both affecting the trait and the variability allowed estimating the calving date each year. Figure 4 shows the intervals estimating the period in which 95% of the calvings were performed. The two most variable campaigns concerning calving date coincided with those which delayed the mean period of calving among campaign neighbours. The greatest extreme dates of calving were found in the year 2005 going from 18 December to 27 June. The last four campaigns were found to be shorter than the others, revealing there were changes in management. A small progressive delay in the mean calving date was also found in these years.

Genetic values for the trait under both HO and HE models and for its variability under model HE were averaged and drawn to check the genetic trends of the calving date trait and its variability, and are shown in Figure 5. A sharp genetic trend was found from 2007 to 2009 and continued keeping stable to 2018, whatever HO and HE models are considered, while the estimated genetic correlation between the trait and its variability led to a decrease in the variability in those 2007 to 2009 years, increasing later smoother. Apparently, animals have been indirectly selected to delay their parturitions decreasing at that point the variability around a date, and increasing slowly later.

4 | DISCUSSION

Modulating the calving date by artificial selection in alpacas is an interesting issue in the context of the usual reproductive management in which reproductive campaign is narrow to take in, two consecutive reproductive events for the same female, as they are the calving and a new effective mating event. A gestation length of eleven months leaves a very short period to accomplish both

FIGURE 2 Mean phenotypic calving date within years of recording as well as those estimated with both HO and HE models
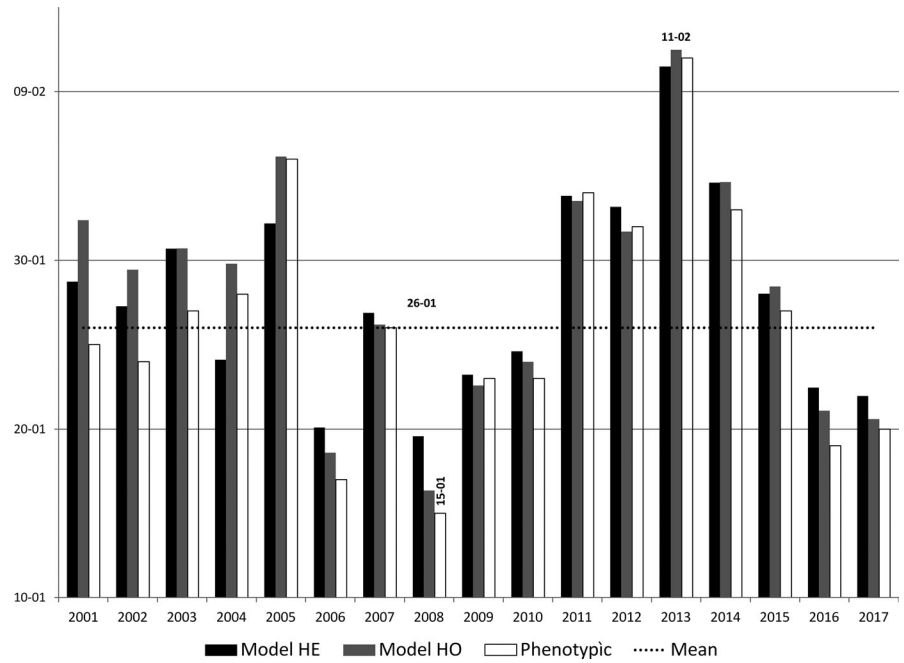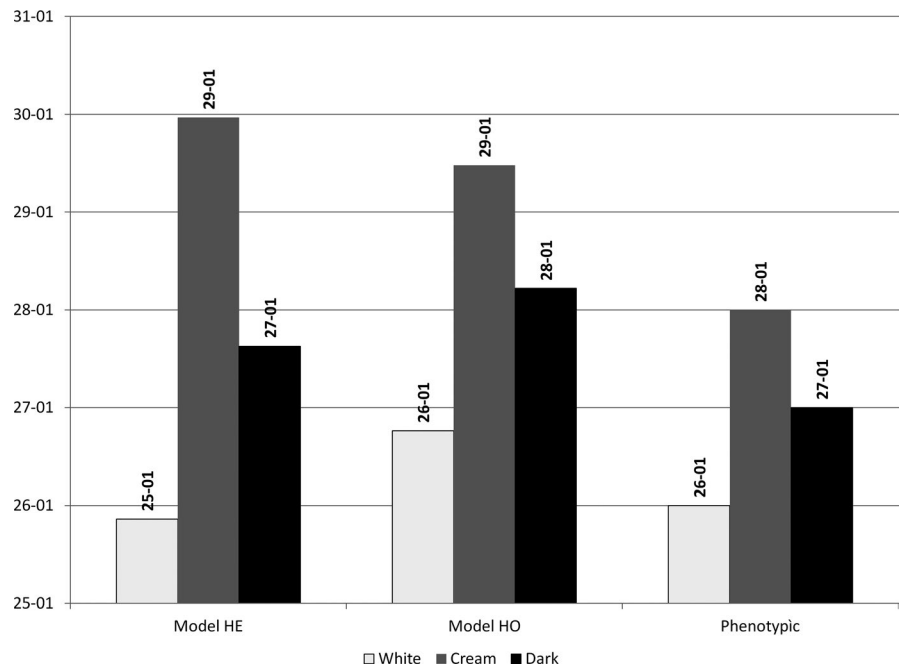

FIGURE 3 Mean phenotypic calving date within colour coat as well as those estimated with both HO and HE models

events, each consecutive year to optimize the reproductive life of a female alpaca. Calving would have to be early in this sense, but feeding resources can be scarce at the beginning of the period. On the other hand, too late calving will shorten the effective period for the next mating compromising a new gestation, in addition to having a calf in a period in which enterotoxaemia is more frequent due to higher humidity at the end of the rainy period. Moreover, the tuis could affect their growth due to the low temperatures if they are born too late in the campaign. Therefore, two are the combined objectives concerning the calving date. First, calvings around the middle of the campaign are preferred, and second, advanced calving is preferred within those close to the centre of the period. Therefore, both reducing the trait and its variability are

objectives of concern. The selection on age at first calving or on calving interval traits would be concerned as the first one can determine the second one. In beef cattle, the females with a shorter calving interval are often those whose first calves were born late (Gutiérrez et al., 2002). Selecting these animals could alter his growth curve in the future (Bourdon & Brinks, 1982). Also, animals having an undesirable performance by calving too late would be forced to have an immediate second parturition, shortening the next calving interval. This explanation is of general validity in many species, but it is particularly critical in alpacas due to the reproductive seasonality. The same need to accommodate the calving date, to optimize the fertility and survival of offspring was evidenced in the production of camels and dromedaries, which
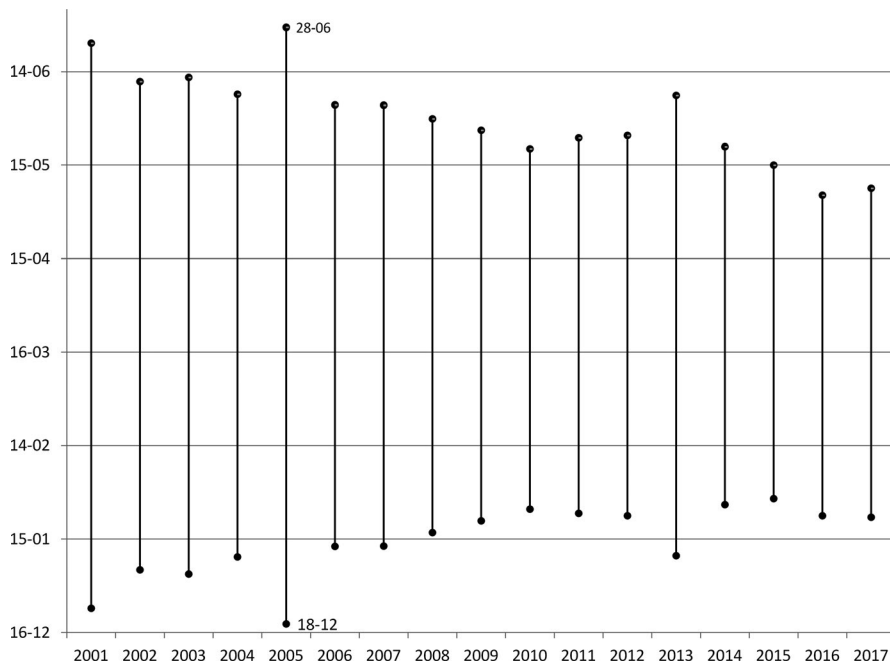
FIGURE 4 Intervals estimating the period in which 95% of the calvings were performed within campaign
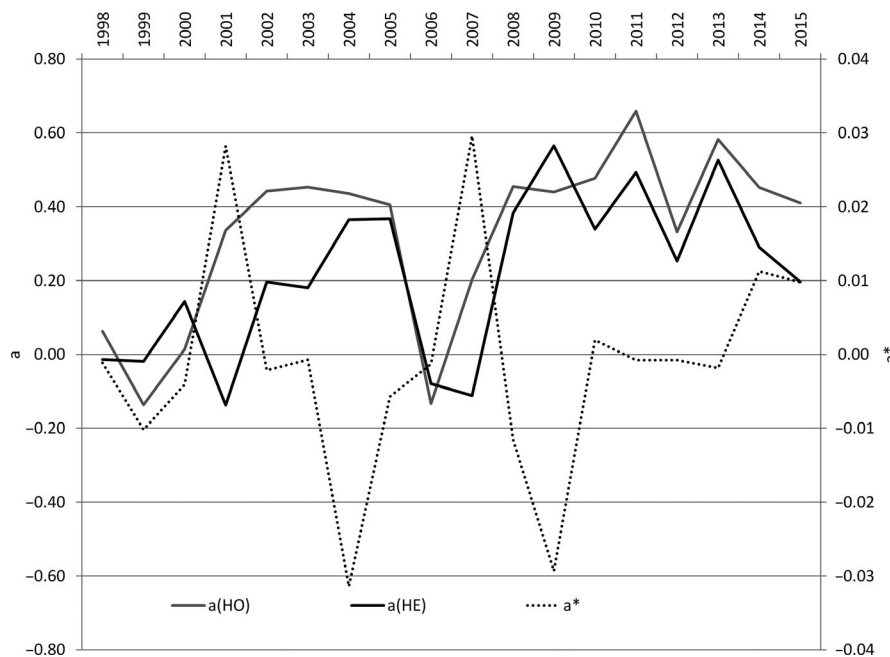

FIGURE 5 Genetic trends for the calving date (a) and its variability (a*) fitting homogeneity (HO) and heterogeneity (HE) models

have the same reproductive characteristics as that of camelids (Fernández-Baca, 1993; Musa et al., 1993), so exploring the calving date as alternative seems worthy.

Estimated genetic parameters suggest the possibility of breeding animals to delay or advance the date by selection, with the usual limitation of the low heritability of reproductive traits for this and other species (Cruz et al., 2015; Ray, Itulya, Roubicek, & Benson, 1989). The genetic coefficient of the variance for the variability, in the upper extreme of those reported in several species and traits (Hill & Mulder, 2010), suggests also the possibility of selecting animals performing the birth preferably close to the middle of the season. And finally, genetic correlation between the mean and the variability suggests that concentrating births would delay them within the

season. In addition, this genetic correlation seems to be free of the mathematical artefact sometimes appearing because of the skewness of the distribution (Yang, Christensen, & Sorensen, 2011) as it does not seem to exist (Figure 1). Positive genetic correlations between the mean and the variability have been sometimes attributed to a statistical scale effect (Tatliyer et al., 2019), as increasing the magnitude of a trait would simultaneously increase both mean and variability. However, this was not the case here, as the calving date trait was defined in such a way it does not depend on a real magnitude of the trait.

With regard to the goodness of the model, according to the deviance information criterion value, HE model performed a better fit. Apparently there were no important discrepancies in the

parameters having been estimated in both models such as heritability and repeatability. Model HE would then be preferred as in addition it offers other parameters of interest, and particularly in this trait in which reducing variability can have important economic effects. Furthermore, model HE had been experimentally shown to have a good practical performance in selection (Formoso-Rafferty, Cervantes, Ibanez-Escriche, & Gutierrez, 2016), and it has also been shown to provide interesting estimates in many other traits and species including alpacas (Gutierrez et al., 2011).

The models used here have allowed to monitor how this rather unusual trait has evolved in this population. Thus, it can be shown how calving concentration has moved from one campaign to another, being the earliest in 2008 by 15 January, and the latest in 2013 by 11 February. This was a consequence of possible eventualities that have occurred or due to unknown managing decisions, being the global mean date the 26 January with a wide range of dates across different years (Figure 2). If focusing after 2006, on the period after BLUP (Best Linear Unbiased Predictor) being implemented as selection criterion (Gutierrez, Cervantes, Perez-Cabal, Burgos, & Morante, 2014), there was a delaying of the reproductive season until 2013 maybe conditioned by the difficulties in adapting to new selection techniques, decreasing later after these practices were routine, advancing this date from 2013 to 2017 (Figure 2). Figure 4 illustrates also this, but it shows simultaneously the evolution of the variability. The first consequence of the change in the selection method is the reduction in the variability, probably because having delayed the mating, most of them have to be performed urgently before finishing the campaign, thus decreasing the variability. After a decade of BLUP selection, mating has been advanced and variability reduced, but only as a consequence of changes in management. Genetic trends (Figure 5) show the immediate and sharp correlated genetic increase in the date of calving; that is, animals are selected to delay the calving, jointly with decreasing the variability, that is, tending to have calving close to the middle of the season. After this initial effect, it seems that animals are slowly regressing to the values in the year 2007. Anyway, these trends are not really important on average, as the range in mean genetic values represent less than one day (from −0.1 to 0.6 days), while the phenotypic range of mean calving date (Figure 2) reaches almost one month (from 15 January to 11 February). However, as the range in the predicted breeding values was from −20 to +18 days, there seems exist animals tending to have a too early or too late calving within the season.

The research presented is the first analysis of the potential usefulness of CD in alpaca breeding programmes. It has been shown that there is a genetic background of the trait, also to improve (reduce) its variability. The heterogeneity model has also been shown to perform properly to manage it, and variations have been found in the calving date across time, not only as a consequence of management decisions, but also because of a correlated genetic response when selecting for other traits. The seasonality of the reproduction in Peru advices a follow-up of this issue.

CONFLICT OF INTEREST

None of the authors have any conflict of interest to declare.

AUTHOR CONTRIBUTION

All the authors have contributed in a similar percentage to the publication, with those more involved in first, second and last position of the list of authors.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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