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Genetic profile of milk production traits and analysis of correlations with reproductive performance in the Azawak Zebu in Niger

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ABSTRACT

The effects of genetic factors on the lactation traits of the Azawak cattle breed are estimated from 11,998 monthly milk records from 1275 complete lactations from 471 Azawak cows bred at the Toukounous experimental centre (Niger), using a multi-trait animal model based on the REML method. The results show that heritability was moderate for persistency ($h^2 = 0.23$), peak lactation ($h^2 = 0.34$), milk yield at 305 days ($h^2 = 0.30$), daily milk yield ($h^2 = 0.33$) and total milk yield ($h^2 = 0.35$). In addition, very high repeatability estimates ranging from 0.50 to 0.58 were associated with the last four traits. Significant phenotypic correlations varying from 0.23 to 0.40 existed between the two reproductive traits (age at first calving and calving interval) and the lactation traits. Similarly, the significant genetic correlations between the traits of milk production and reproduction traits were unfavorable, varying according to the lactation traits considered from 0.32 to 0.87 for age at first calving and from 0.48 to 0.97 for calving interval, indicating that selection for milk yield only should result in a longer calving interval and a later age at first calving. Estimates of the heritability of lactation traits are moderate, as are those of many functional reproductive traits, so the genetic gain from selection on milk production traits alone would be rapid, but antagonistic with reproductive performance.

1. Introduction

Livestock farming plays a key role in Niger, where demand from urban consumers for milk is constantly increasing (Marichatou et al., 2005b). Unfortunately, this demand is essentially met by imports (Nariindu project, 2019). The majority of industrial dairy units are still not very interested in local milk, when imported powder is more competitive than local milk whose availability in quantity and quality was limited (Yahouza & Malam Maman, 2018). According to national statistics, milk production is 1 billion litres per year, including 486 million litres of bovine milk (Nariindu Project, 2019). Overall consumption is increasing in line with population growth, hence the need for imports. The structure of milk imports remains dominated by milk powder, which accounts for 81 % of imports in terms of quantity and 93 % in terms of value. In 2017, Niger imported more than 6 million kg of dairy products, equivalent to over 40 million liters of raw milk (Nariindu Project, 2019).

Despite significant imports of dairy products, access to them has become more difficult for some sections of the population (Veillardp, 2011). The supply of milk to both towns and rural centres has become critical. Despite its size, Niger's cattle herd is unable to meet the country's milk requirements. The government has defined a strategy for the sustainable development of livestock farming, in which the dairy sector is one of the priorities, and its development is included in national programmes (Kilcher & Sani, 2020).

One of the cattle breeds used in Niger (Gagara et al., 2017; K.I. Adamou et al., 2017b) is the Azawak Zebu, named after the Azawak region. It was chosen by the government, on the basis of its dairy performance, to improve the production potential of other local breeds in farming areas (Marichatou, 2010). Taking its name from the region it comes from, the Azawak is a short-horned animal with rectilinear, mediolinear and eumetric horns (Siddo, 2017). Indeed, the Azawak cow is the most suitable of all Sahelian cows for milk production (Kassa et al., 2016).

At the Toukounous experimental center, the government and its partners had set themselves the goal, since 1936, of selecting an animal with a tawny phenotype and dark extremities, combining beef and dairy qualities, and disseminating the Azawak Zebu among traditional herds

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(Siddo, 2017).

Thus, after this long phenotypic selection, the milk production of Azawak females was evaluated at 800–3000 kg of milk per cow per lactation of 270 to 300 days. The average age at first calving for the heifers was 1108 days. The average calving interval for cows was 424 days. The average fecundity rate was 78 % (Achard & Chanono, 1997). Thanks to these performances, the Azawak is the most coveted of the cattle breeds used not only in Niger, but also in the sub-region. Studies have been undertaken for several years to characterise this breed in its cradle (the Azawak region) and in other environments (Moussa et al., 2014; Saidou, 2004), with the aim of improving its milk production performance.

Several livestock development programmes in the Sudano-Sahelian zone have therefore focused on this breed. However, its implementation is hampered by the lack of precise data on the genetic parameters of reproduction and milk production.

The heritability of weight at different ages and the genetic and phenotypic correlations between these weights have already been estimated for this Azawak cattle breed (Siddo et al., 2018). The present study is a contribution to this work and has the advantage of evaluating the effectiveness of a long phenotypic selection carried out on this Zebu breed, by estimating the genetic parameters linked to its dairy performance.

2. Materials and methods

2.1. Touknous experimental station

The animals were reared at the Touknous experimental station located 200 km north of Niamey at 14° 31 North latitude and 3° 18 East longitudes (Fig. 1). The climate was arid, Sahelian, with a rainy season from June to October (5 months) and a dry season from November to May. The average temperature was 34 °C (lows of 10 °C to 20 °C in December/January and highs of 34 °C to 40 °C in March/April). The station covers an area of 4474 ha and is divided into 31 plots to allow rotational grazing.

The farming system practised was extensive, using minimal inputs. Herbaceous cover (80.9 %) and pastoral value (87.5 %) were generally satisfactory (Saidou et al., 2010, 2013). The herbaceous vegetation was dominated by annual grasses: *Schoenefeldia gracilis, Aristida mutabilus, Cenchrus biflorus*. There was a relative abundance of woody plants (210 individuals per ha on average) consisting mainly of *Maerua crassifolia* and *Balanites aegyptiaca*. The animals, divided according to age, sex and physiological state (lactating females, pregnant females) into 8 to 12 groups, were grazed year-round on natural pasture. For most of the animals, this was their sole source of food (Achard & Chanono, 1997). Supplementary feeding (cotton cake, bran) took place in the dry season and only concerned lactating cows. The animals are watered from boreholes equipped with pumping systems. In terms of health, external and internal deworming is carried out twice a year. Animals are vaccinated against contagious bovine pleuropneumonia, symptomatic and bacterial anthrax and bovine pasteurellosis.

2.2. Data

The data used comes from the archives of the Toukounous Experimental Station. The animals were monitored using a system of individual cards on which, in addition to the registration number and date of birth, details of the sire and dam, and monthly records of lactations and successive calving were recorded. Abortions were rarely recorded (Achard & Chanono, 1997).

The data file used contains records of 11,998 monthly milk controls from 1275 complete lactations from 471 Azawak cows, daughters of 47 bulls. These cows, of which both parents are known, were born at the Toukounous station between 1981 and 2004 and calved between 1988 and 2007.

Initial data configuration in pedigree (where each individual was already associated with its dam, its sire and its phenotypes relative to the traits studied) was carried out using the pedigree package in R. The pedigree is thus made up of 678 animals belonging to four generations. The number of founders (starting parental population), considered as the first generation, was 207 animals. The 2nd, 3rd and 4th generations

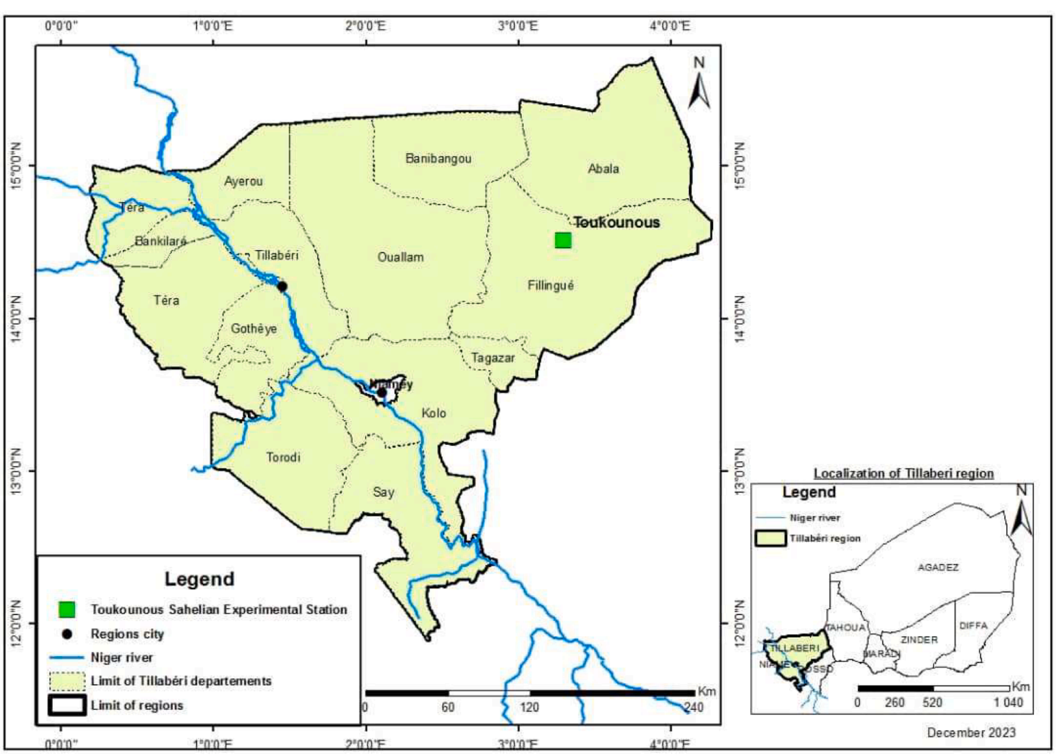

Fig. 1. Geographical location of the Toukounous Sahelian Experimental Station.

were 213, 177 and 81 animals respectively.

Milk production was assessed for each cow every month, on the morning and evening of the same fixed day. Only the quantity of milk milked was recorded; the quantity drunk by the calf was not assessed. Drying off is generally carried out when the cows start to reach low yield levels. The average age at weaning was thus 10 months (Siddo et al., 2018). Based on the milk recording performed, two groups of lactation traits were calculated (Adamou et al., 2021). The first group of traits relates to the quantification of milk production, including peak lactation, total milk yield, milk yield at 305 days and daily milk yield. The second group of traits evaluated concerns the evolution of this production. These include the lactation persistency and the lactation length. The reproductive traits considered in the study were age at first calving and calving interval (Table 1).

2.3. Statistical analysis

2.3.1. Evaluation of the effects of non-genetic factors on lactation traits

The effects of lactation rank, calving season, calving year and their interactions on lactation traits were analysed using the following fixed-effect linear model with the R software (R Core Team, 2013):

Yijkl=μ +Li +Sj +Yk+Li*Sj +Li*Yk +Sj*Yk +Li*Sj*Yk +e_{ijkl}, where

Yijkl = Performance l for a given lactation trait, of a cow of lactation rank i having calved during season j of year k,

μ = overall average;

Li = fixed effect of lactation rank; $i = 1\ldots5$;

Sj = fixed effect of calving season; $j = 1\ldots3$;

Yk = fixed effect of calving year; $k = 1\ldots12$ (Years with low calving numbers were merged, reducing the number of years from 19 to 12);

Li* Sj = interaction between lactation rank and calving season;

Li* Yk = interaction between lactation rank and calving year;

Sj* Yk = interaction between calving season and calving year;

Li*Sj*Yk = interaction between lactation rank, calving season and calving year. e_{ijpl} = residual error.

Least squares means of variable modalities were calculated using package (emmeans). The "T" test was used to test the significance of the model coefficients in relation to the reference modalities of each of the three variables (lactation rank, calving season and calving year).

Table 1
Description of traits and their abbreviations.

Trait group	Traits	Abbreviation	Trait description
reproductive traits	Age at first calving	**AFC**	Time interval in days between the birth of the cow and her first calving
	Calving interval	CI	Time interval in days between two successive calvings
Lactation production traits	Total milk yield	TMy	Total quantity of milk per lactation calculated using the Fleishman method (Meyer & Denis, 1999) for the total duration of lactation
	Peak lactation	Peak	Maximum production level determined from individual lactation curves.
	Initial milk yield	IMy	Daily production on the first day of milk control.
	Daily milk yield	DMy	Average of all daily milk production during the lactation period
	Milk yield at 305 days	My 305-d	Total quantity of milk for 305 days of lactation
Lactation evolution traits	lactation length	LL	Interval between calving and 14 days after the last check (Meyer & Denis, 1999).
	Lactation persistency	Pers	Ratio of one month's production to the previous month's production after the lactation peak.

Next, the Azawak Zebu's lactation curve was adjusted by averaging the individual curves for all the cows in the herd, then for each of the five lactation rank levels, so that all curves started lactation together. The relationship between total milk yield and peak lactation was fitted using a simple linear regression model. This model was selected on the basis of the Akaike criterion within various mixed regression models, where calving season and lactation rank were introduced as random factors. Seven models with different intercepts and random slopes were built a priori, then compared with each other and with the basic linear model (with no random effects) using the Akaike Information Criterion (AIC). The base model with the lowest AIC was selected. Its validity was based on the conditions of application and the various validity tests of the model (Chesneau, 2016): The Durbin Watson test was used to check the auto-correlation of the residuals. The distribution of these residuals was analysed after a Shapiro Wilk test. The mean conformity test was used to check whether the residual mean is zero. The Breush-Pagan test was used to analyse the heteroscedasticity of the residuals. The 'T' test was used to test the significance of the coefficients and the overall model. These analyses were performed at the 5 % level using the R software.

2.3.2. Estimation of genetic parameters

The variance and covariance components were estimated simultaneously for all nine traits studied in a multi-trait animal model, using the Monte Carlo Markov chain simulation method and Bayesian inference based on restricted maximum likelihood and an a priori distribution of the parameters to be estimated, using the MCMCglmm package under R software (R Core Team, 2013). For the analysis, chains of 100 thousand iterations were generated with samples every 10 cycles (nitt=100,000, burnin=10,000, thin=10). Calving year and lactation rank, whose effects on lactation traits have previously been shown to be highly significant, which showed better convergence and low autocorrelation in the sample chain, have been retained in this model as fixed factors. The cow was introduced into the model as a random factor in order to assess the effect of the permanent environment. The behavior of the MCMC algorithm was verified on the basis of the convergence and auto-correlation of the two main components of the sample chain of the output model, namely the "$Sol model" for the fixed effects and the "$VCV model" for the random effect. Convergence was diagnosed by a graphical check (Fig. 2) using the trace of variance as proposed by Pierre (2023) and after a Heidelberg stationary test (Table 2).

AFC: Age at first calving; CI: Calving interval; TMy: Total milk yield; Peak: Peak lactation; IMy: Initial milk yield; My: Daily milk yield; Myd: Milk yield at 305 days; LL: Lactation length, Pers: Lactation persistency

Variance-covariance components were estimated according to the following equation (Ayalew et al., 2017; Sellem et al., 2024): y = Xb + Za + Wp + e, with design matrices X, Z and W given by:

$$X = \begin{bmatrix} X_1 & 0 & \cdots & 0 \\ 0 & X_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \ldots & X_9 \end{bmatrix}; Z = \begin{bmatrix} Z_1 & 0 & \cdots & 0 \\ 0 & Z_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \ldots & Z_9 \end{bmatrix}; W = \begin{bmatrix} W_1 & 0 & \cdots & 0 \\ 0 & W_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \ldots & W_9 \end{bmatrix}$$

where y is the vector of observations for each reproductive and milk production trait; b is the vector of fixed effects (year of calving and the lactation rank); a is the vector of additive animal genetic effects; p is the vector of random effects of the cow's permanent environment; e is the vector of random residual effects; and X, Z and W are incidence matrices relating phenotypic records to fixed effects, additive animal genetic effects and the cow's permanent environment, respectively.

After obtaining the correctly converged variances and covariances, the heritability and repeatability of the lactation and reproduction traits

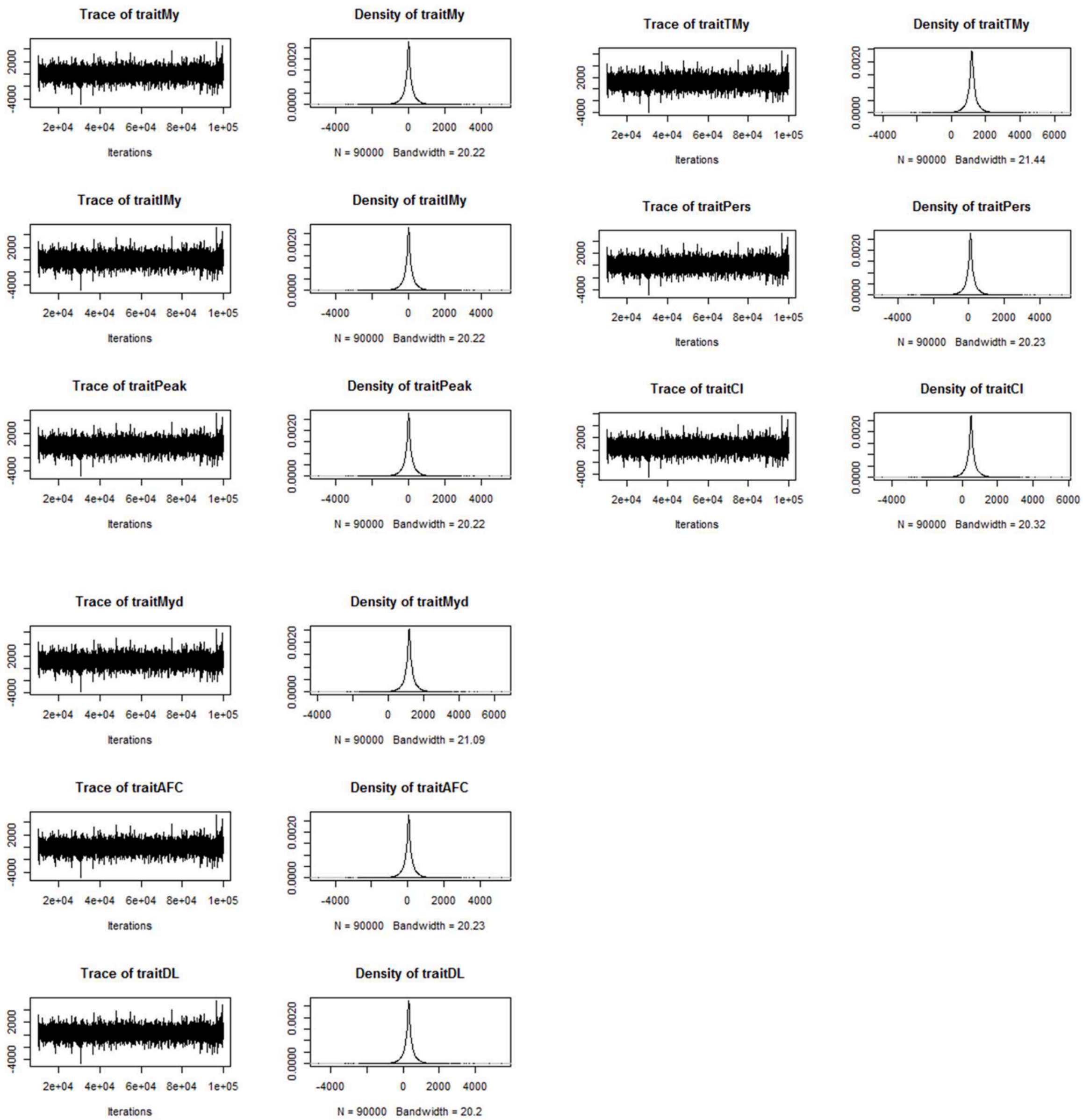

Fig. 2. Traces of variance (left) and posterior density of heritability (right) of nine reproductive and milk production traits in Azawak cattle.

Table 2
Model convergence diagnostics using the Heidelberg stationary test.

Traits	Halfwidth	p-value	Stationary test
My 305-d	3.971	0.0783	passed
AFC	3.781	0.0909	passed
LL	3.783	0.0828	passed
DMy	3.780	0.0918	passed
IMy	3.780	0.0919	passed
Peak	3.780	0.0918	passed
TMy	3.981	0.0555	passed
Pers	3.782	0.0909	passed
CI	3.806	0.0744	passed

AFC: Age at first calving; CI: Calving interval; TMy: Total milk yield; Peak: Peak lactation; IMy: Initial milk yield; DMy: Daily milk yield; Myd: Milk yield at 305 days; LL: lactation length; Pers: Lactation persistency.

and the genetic, residual and phenotypic correlations between these traits were estimated as follows:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2};\ \mathrm{r} = \frac{\sigma_a^2 +\ \sigma_e^2}{\sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2};\ r_r = \frac{\sigma_{rij}}{\sqrt{\sigma_{ri}^2\sigma_{rj}^2}};\ r_g = \frac{\sigma_{aij}}{\sqrt{\sigma_{ai}^2\sigma_{aj}^2}};\ r_p = \frac{\sigma_{pij}}{\sqrt{\sigma_{pi}^2\sigma_{pj}^2}}$$

Where: h^2 is heritability; r is repeatability; r_r is residual correlations; r_g is genetic correlations*;* r_p is phenotypic correlation; σ_a^2 is additive genetic variance; σ_e^2 is permanent environmental, σ_e^2 is residual variance;. σ_{ri}^2 is additive residual variance for trait *i;* σ_{rj}^2 is additive residual variance for trait *j;* σ_{ai}^2 is additive genetic variance for trait *i*; $\sigma_{aj}^2$is additive genetic variance for trait j; σ_{pi}^2 is phenotypic variance for trait *i*; $\sigma_{pj}^2$is phenotypic variance for trait j; σ_{rij} is additive residual covariance between trait *i* and *j*; σ_{aij} is additive genetic covariance between trait *i* and *j*; and σ_{pij} is phenotypic covariance between trait *i* and *j*.

3. Results

3.1. Variability of lactation traits

Lactation traits of Zebu Azawak show a high variability for the lactation traits studied (Fig. 3). The daily milk yield of all 471 suckler cows varied from 1.3 to 8.9 kg/day, with an average of 4.01±0.03 kg/day. The distribution of daily milk yield is not normal ($p > 0.05$), although it is more symmetrical than a normal distribution (Fig. 3a). More than half the cows (51.5 %) produced 3.5 to 5 kg of milk per day. Record daily milk yields of over 7 kg were recorded in 1.3 % of the lactations studied.

Also, the distribution of peak production was not normal ($p < 0.05$), despite being less asymmetrical than a normal distribution (Fig. 3b). It was one of the traits with the highest variability (1.5 to 15.2 kg). The average peak production of all cows observed was 5.71±0.05 kg. The most frequent lactation peaks, observed in 58.4 % of lactations, were between 5 and 8 kg. Peak production records of over 8 kg were only observed in 3.1 % of the lactations studied.

Lactation lenght was distributed more or less symmetrically around a mean of 312.1 ± 1.5 days according to a non-normal distribution (Fig. 3c). This trait fluctuated less than total milk yield. In fact, 8.9 % of lactations in the sample were limited to 250 days, while 51.9 % were longer than 305 days. The distribution of this trait is very asymmetrical, with the maximum frequency being between 250 and 300 days (36.2 % of lactations), while the average was 312 days. A similar distribution was observed for total milk yield (Fig. 3d), where individual variations ranged from 367 to 3378 kg with an average of 1252.3 ± 11.5 kg. The maximum frequency (40 % of lactations) was between 800 and 1200 kg.

3.2. Lactation curve of Azawak zebu

The Azawak lactation curve conforms to the typical standard shape (Fig. 4a). The curve shows an initial milk yield of 3.97 kg two weeks after calving. Daily milk yield increases during the first weeks following calving, reaching a peak of 4.26 kg, reached two months after calving. Daily milk yield then decreases more or less regularly until it dries up. The average persistence coefficient in the decreasing phase of the first 6 months after the peak was 86.4 %, which implies a drop in production of 13.6 % from one month to another. However, a dietary supplement is provided when the evolution of lactation indicates a very low level of milk secretion. What is evident here is a rise in the curves from the 7th month of lactation. A significant part of the irregularities observed in the lactation curve is attributed to the installation of richer feeding conditions with the return of the rainy season. Finally, a fairly marked variation in the parameters of the lactation curve (initial milk yield and peak production), greater in multiparous than primiparous cows, was observed depending on the lactation rank of the cows.

The regression model (Fig. 4b) expressing total milk yield per lactation (T-My) as a function of peak lactation (Peak) has the equation $\ln(TMy) = 0.91 * \ln(Peak) + 5.54$ (i.e. $TMy = 254 * Peak^{0,91}$). This model was highly significant (p-value: < 2.2e-16) and is therefore relevant. The model validity tests (Shapiro-Wilk p-value = 0.219, Durbin-Watson p-value = 0.227 and Breusch-Pagan p-value = 0.117) show that the residuals are normally distributed, independent and of constant variance. Moreover, the adjusted R-squared value of 0.642 indicates that the relationship between the two traits is very strong.

3.3. Effects of non-genetic factors

Analysis of variance shows highly significant effects of lactation

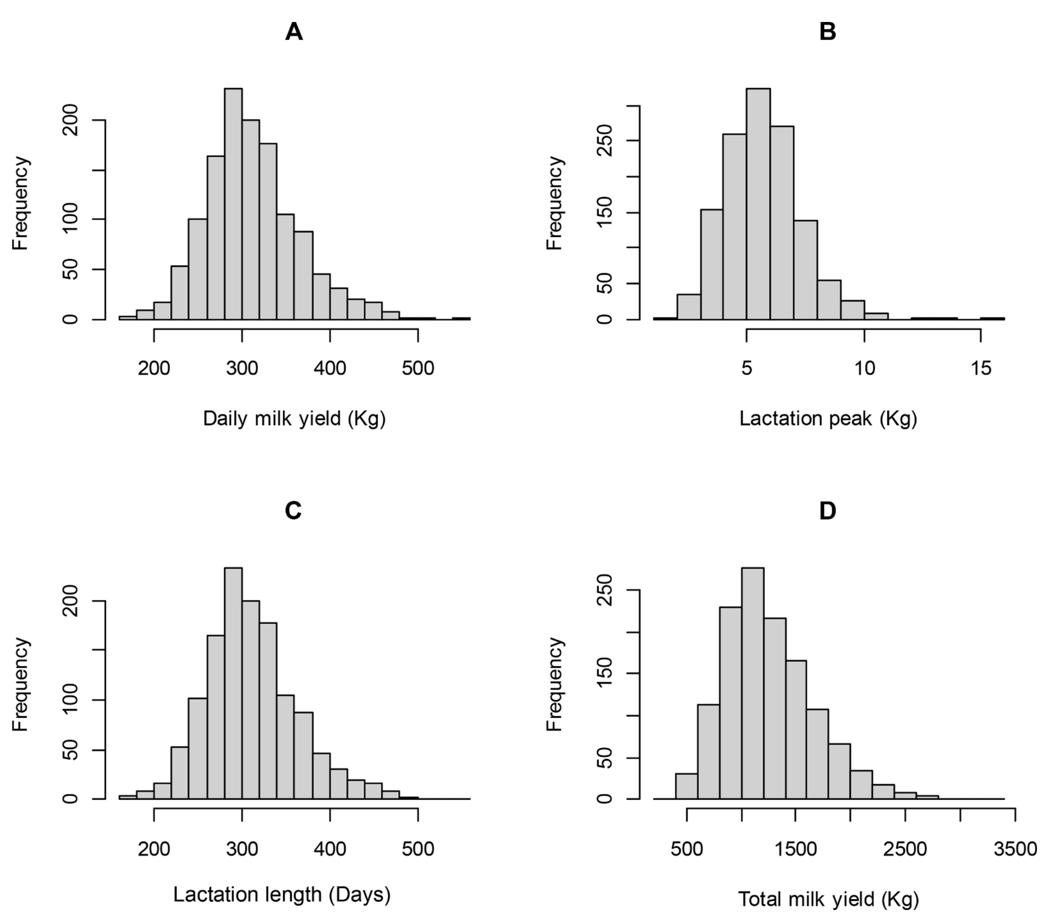

Fig. 3. Variability of milk production traits in Azawak cows.

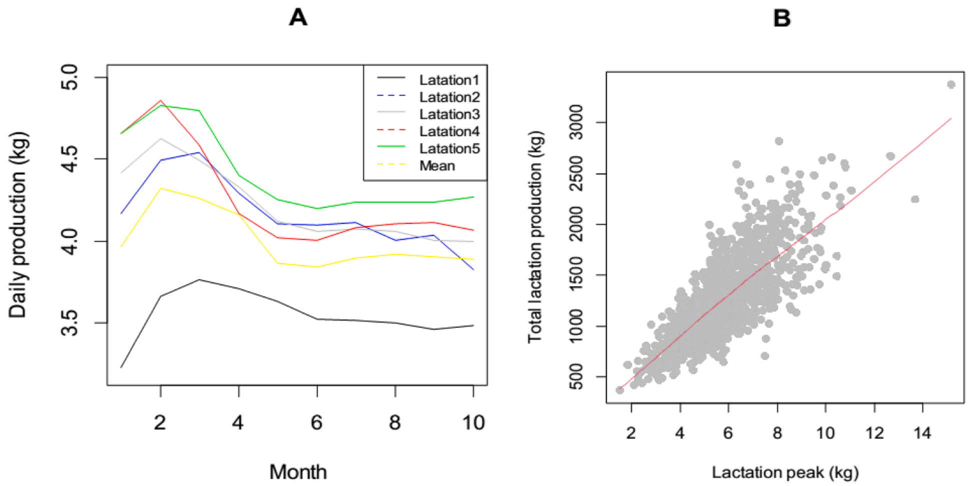

Fig. 4. Lactation curve (A) and total milk yield versus peak lactation (B).

rank, calving season and year of calving on both evolution traits and lactation quantification traits (Table 3). Calving in the rainy season, in contrast to the two dry seasons, results in lower total milk yield, due to reduced lactation duration and peak (Table 4). Similarly, lactation rank was a determining factor in variations in both lactation evolution and production traits (Table 3). Milk production was better in multiparous cows, and increased up to the 5th lactation rank, whereas primiparous cows performed the worst (Table 4). The influence of the calving season on the milk production performance of the cows shows highly significant inter-annual differences in production. Over a period of 19 years, milk production increased until around 2002, after which it showed a stable trend.

3.4. Genetic parameters

Mean values for heritability and repeatability, as well as variance components, are reported in Table 5. Heritabilities for lactation evolution traits were low, ranging from 0.007 to 0.234. It was lower for Lactation lenght and lactation persistency. Low estimates of repeatability (ranging from 0.03 to 0.25) were also associated with these traits. On the other hand, moderate heritability (0.30 to 0.35) was observed for lactation production traits, with the exception of initial milk yield, for which heritability was lower. Moderate to high repeatability estimates, varying from 0.25 to 0.58, were recorded for these characters. The variance components indicate that for all the traits studied, the residual variance was larger than the variance of the effect of the permanent environment.

There are moderate to high genetic and phenotypic correlations, all positive, between all lactation production traits on the one hand, and between milk production traits and lactation lenght on the other (Table 6). Also, genetics significantly ($p < 0.05$) controlled the influence of two reproductive traits (age at first calving and calving interval) on the dairy performance of the Azawak Zebu. In fact, analysis of genetic and residual correlations showed that an early first calving was associated with reduced total milk yield and peak lactation, and shorter lactation. Similarly, the shorter time between calvings reduced the duration of milk secretion and milk yield. Thus, simultaneous selection of milk production traits could lead to improvements in overall total milk production performance, but could reduce the animals' reproductive performance. A positive genotypic correlation preponderant over a negative residual correlation was observed between production at 305 days of lactation and lactation length. Lactation lenght was also linked to peak lactation, initial milk yield and daily milk yield by positive genetic correlations and significant negative residual correlations ($p < 0.05$).

Table 3
Effects of non-genetic factors on Azawak cow lactation traits.

Traits	Source	Lactation rank	Calving season	Calving year	Lactation rank*Calving season	Lactation rank*Calving year	Calving Season*calving year	Lactation rank*calving season*calving year
DL	DF	4	2	11	8	42	22	72
	F	37.2***	3.3*	8.0***	4.6***	1.1	0.9	1.0
My 305-d	DF	4	2	11	8	42	22	72
	F	6.6***	24.2***	1.6	1.3	1.5*	1.3	1.4*
Pers	DF	4	2	11	8	42	22	
	F	66.9	871.2***	85.9	186.8*	46.5	107.0	89.6
TMy	DF	4	2	11	8	42	22	72
	F	5.0***	3.5*	4.0***	1.5	1.7**	1.9**	1.4*
Peak	DF	4	2	11	8	42	22	72
	F	32.0***	17.4***	2.8***	1.3	1.4	1.3	1.2
IMy	DF	4	2	11	8	42	22	72
	F	49.9***	19.1***	8.5***	2.1*	2.6***	4.2***	1.5**
DMy	DF	4	2	11	8	42	22	72
	F	42.3***	1.7	3.8***	0.9	2.1***	2.4***	1.3

DF: Degrees of Freedom; F: F-value from the ANOVA; *$P < 0.05$; ** $P < 0.01$; ***$P < 0.001$; TMy: Total milk yield; Peak: Peak lactation; IMy: Initial milk yield; DMy: Daily milk yield; My 305-d: Milk yield at 305 days; LL: Lactation length; Pers: Lactation persistency.

Table 4
LSMean ± standard deviation of lactation traits of the Azawak cow according to non-genetic variation factors.

Traits	Modality	n	Lactation evolution traits		Lactation production traits				
			LL	Pers	TMy	My 305-d	Peak	IMy	DMy
Total sample		1275	300 ± 2	86 ± 0.3	1256 ± 14	1273 ± 10	5.9 ± 0.1	4.2 ± 0.1	4.2 ± 0.1
Calving season	Dry season	341	301 ± 3^{R}	85 ± 0.4^{R}	1290 ± 23^{R}	1298 ± 18^{R}	6.1 ± 0.1^{R}	3.9 ± 0.1^{R}	4.3 ± 0.1^{R}
	Rainly season	359	306 ± 2 ^{ns}	85 ± 0.5ns	1269 ± 18ns	1268 ± 14ns	6.0 ± 0.1ns	4.3 ± 0.1ns	4.2 ± 0.1ns
	Cold season	575	292 ± 3ns	88 ± 0.4***	1208 ± 23ns	1253 ± 17ns	5.6 ± 0.1ns	4.3 ± 0.1ns	4.1 ± 0.1ns
Lactation rank	Rank1	471	334 ± 2^{R}	87 ± 0.4^{R}	1181 ± 19^{R}	1067 ± 14^{R}	4.9 ± 0.1^{R}	3.2 ± 0.1^{R}	3.5 ± 0.1^{R}
	Rank2	310	298 ± 3**	86 ± 0.5ns	1258 ± 23**	1280 ± 18***	5.9 ± 0.1***	4.2 ± 0.1***	4.2 ± 0.1***
	Rank3	230	293 ± 3**	87 ± 0.6ns	1284 ± 27**	1325 ± 20***	6.1 ± 0.1***	4.5 ± 0.1***	4.3 ± 0.1***
	Rank4	168	291 ± 4**	85 ± 0.7**	1279 ± 32**	13,126 ± 24***	6.1 ± 0.1***	4.6 ± 0.1***	4.4 ± 0.1***
	Rank5	96	282 ± 5*	85 ± 1.0*	1276 ± 42*	1367 ± 32***	6.3 ± 0.2***	4.6 ± 0.2***	4.5 ± 0.1***
Calving year	1988–1991	76	272 ± 6^{R}	86 ± 1.1ns	1165 ± 47^{R}	1285 ± 36^{R}	5.7 ± 0.2^{R}	4.5 ± 0.2^{R}	4.2 ± 0.2^{R}
	1992–1993	70	291 ± 6ns	85 ± 1.2ns	1024 ± 49*	1081 ± 37***	4.7 ± 0.2ns	4.0 ± 0.1*	3.4 ± 0.1***
	1994–1995	105	280± 5ns	85 ± 1.0ns	1093 ± 41ns	1185 ± 31*	5.6 ± 0.1ns	4.2 ± 0.1	3.9 ± 0.1*
	1996–1997	109	287 ± 5ns	84 ± 0.9ns	1194 ± 39ns	1265 ± 29ns	6.1 ± 0.1ns	4.5 ± 0.1	4.2 ± 0.1ns
	1998–1999	117	295 ± 4ns	87 ± 0.9ns	1277 ± 38ns	1318 ± 28ns	6.0 ± 0.1ns	4.6 ± 0.1	4.3 ± 0.1ns
	2000	86	308 ± 5ns	87 ± 1.0ns	1411 ± 43*	1392 ± 33*	6.4 ± 0.1**	4.7 ± 0.2	4.6 ± 0.1*
	2001	97	294± 5ns	87 ± 1.0ns	1240 ± 41ns	1292 ± 31ns	6.1 ± 0.2ns	4.7 ± 0.1	4.2 ± 0.1ns
	2002	82	288 ± 5ns	86 ± 1.2ns	1365 ± 45**	1440 ± 34**	5.9 ± 0.2ns	4.3 ± 0.2	4.7 ± 0.2**
	2003	117	322 ± 4***	87 ± 0.9ns	1296 ± 38*	1219 ± 29ns	6.1 ± 0.2ns	3.5 ± 0.1***	4.0 ± 0.1ns
	2004	156	327 ± 4***	85 ± 0.8ns	1362 ± 33***	1267 ± 25ns	5.9 ± 0.1ns	3.9 ± 0.1**	4.2 ± 0.1ns
	2005	167	313 ± 4ns	87 ± 0.7ns	1334 ± 32**	1287 ± 24ns	6.1 ± 0.1*	3.9 ± 0.1***	4.2 ± 0.1 ^{ns}
	2006–2007	93	318 ± 5***	86 ± 1.0ns	1306 ± 42*	1249 ± 32ns	6.0 ± 0.2ns	3.9 ± 0.1**	4.1 ± 0.1ns

R: Reference modality for each variable to which the other modalities are compared, *$P < 0.05$; ** $P < 0.01$; ***$P < 0.001$; TMy: Total milk yield; Peak: Peak lactation; IMy: Initial milk yield; DMy: Daily milk yield; My 305-d: Milk yield at 305 days; LL: Lactation length, Pers: Lactation persistency.

Table 5
Descriptive statistics for posterior density of variance components, heritability (h^2) and repeatability estimates (r).

Parameters	σ^2_a	σ^2_e	σ^2_{pe}	σ^2_p	$h^2 \pm$ sd	h^2_{CI}	$r \pm$ sd
Age at first calving	2.20	17.25	0.0	19.45	0.11±0.04	0.04–0.20	
Calving interval	8449	19,640	764	19,474	0.29±0.06	0.19–0.39	0.47±0.05
Lactation lenght	504.1	2040.0	269.7	2954.9	0.18±0.03	0.21–0.33	0.26±0.04
Persistency	0.003	0.007	0.0024	0.0122	0.23±0.02	0.20–0.28	0.44±0.03
Milk yield at 305-d	33,490	56,780	23,253	113,523	0.30±0.05	0.20–0.39	0.50±0.02
Total milk yield	60,620	70,690.0	43,330	176,350	0.35±0.06	0.27- 0.49	0.59±0.03
Peak kactation	0.903	1.3300	0.4311	2.66	0.34±0.05	0.22- 0.45	0.50±0.03
Initial milk yield	0.391	1.9140	0.2355	2.57	0.15±0.04	0.09- 0.21	0.24±0.03
Daily milk yield	0.397	0.6110	0.209	1.22	0.33±0.05	0.25 −0.42	0.50±0.03

σ^2_a additive genetic variance; σ^2_{pe} permanent environmental variance; σ^2_e residual variance; sd standard deviation, σ^2_p phenotypic variance; CI confidence interval, sd: standard deviation.

Table 6
Estimates (mean ± standard deviation) of genetic correlations (below the diagonal), residual correlations (above the diagonal) and phenotypic correlations (in brackets) between lactation and reproduction traits in Azawak cows.

	AFC	CI	Pers	LL	My 305-d	TMy	Peak	IMy	DMy
AFC		0.31±0.09* (−0.06±0.08)	0.09±0.08 (0.27±0.14)	0.31±0.09* (−0.02±0.04)	0.22±0.13 (0.02±0.04)	0.35±0.14* (−0.01±0.04)	0.39±0.15* (0.01±0.04)	0.20±0.14 (0.01±0.03)	0.37±0.16* (0.01±0.04)
CI	0.83±0.06*		0.15 ± 0.11	0.27±0.04* (−0.04±0.05)	0.29±0.04* (0.06±0.05)	0.40±0.04* (0.004±0.05)	0.26±0.07* (0.04±0.05)	0.09±0.06 (0.002±0.04)	0.23±0.08* (0.06±0.05)
Pers	−0.02±0.11*	0.08±0.04* (−0.03±0.05		0.13±0.03* (0.05±0.03)	0.03±0.04 (0.02±0.03)	0.10±0.04* (0.06±0.05*)	−0.06±0.05 (−0.19±0.04*)	0.04±0.05 (0.01±0.04)	0.07±0.05 (0.02±0.04)
LL	0.82±0.07*	0.97±0.01*	0.15±0.11		0.02±0.04* (0.25±0.03*)	0.59±0.02* (0.45±0.03*)	0.10±0.06 (0.18±0.03*)	−0.04±0.06 (−0.16±0.03*)	0.04±0.07 (−0.26±0.03*)
My 305-d	0.37±0.22	0.73±0.07*	0.09±0.21	0.60±0.09*		0.81±0.02* (0.73±0.02*)	0.72±0.06** (0.77±0.01*)	0.56±0.06* (0.61±0.02*)	0.76±0.10* (0.75±0.02*)
TMy	0.47±0.09*	0.48±0.05*	0.05±0.11	0.66±0.09*	0.94±0.02*		0.63±0.07* (0.58±0.02*)	0.43±0.07* (0.44±0.02*)	0.62±0.09* (0.73±0.02*)
Peak	0.32±0.11*	0.22±0.15	−0.012±0.10	0.42±0.11*	0.70±0.12*	0.93±0.03*		0.65±0.05* (0.48±0.02*)	0.88±0.02* (0.77±0.01*)
IMy	−0.03 ± 0.16	−0.18±0.19	−0.07±0.11	0.03±0.15	0.50±0.15*	0.70±0.07*	0.80±0.05*		0.74±0.04* (0.61±0.02*)
DMY	0.22±0.12	0.16 ± 0.11	0.01±0.11	0.37±0.12*	0.58±0.14*	0.93±0.03*	0.95±0.02*	0.86±0.03*	

*Correlations significantly different from 0 ($P < 0.05$); AFC: Age at first calving; CI: Calving interval; TMy: Total milk yield; Peak: Peak lactation; IMy: Initial milk yield; DMy: Daily milk yield; My 305-d: Milk yield at 305 days; LL: Lactation length, Pers: Lactation persistency.

4. Discussion

4.1. Average performance and variation factors

Unlike European breeds, for which total milk yield is calculated for 305 days of lactation, indigenous breeds used in West African ranching systems (extensive) are standardised for only a limited fraction of dairy cows (Halidou et al., 2021; Adamou et al., 2021). At the Toukounouss experimental centre, only 51.9 % of lactations lasted more than 305 days. The Management system, in particular the feeding of herds based essentially on natural grazing, the quantity and quality of which depend on rainfall (Siddo, 2017), coupled with a Sahelian breeding environment that is very stressful for the animals, could be at the root of this limited performance.

The dairy performance of the Azawak Zebu has been studied for several decades (Oumarou, 2004). Historical data from the Toukounous experimental station for the period 1987 to 1992 showed an lactation duration of 278 ± 5 days and total milk yield 1215 litres for 272 cows (Siddo, 2017). The performances reported in the present study (lactation length of 312.1 ± 1.5 days, daily milk yield of 4.01±0.03 kg and total milk yield of 1252.3 ± 11.5 kg per lactation) concern the period from 1988 to 2007. On the basis of these results, it would be safe to say that there is a likely insignificant improvement in the dairy performance of this breed, even after these decades of progeny-test selection (Siddo, 2017). The daily milk yield of 4.84 kg/day with an total milk yield of 1350 kg in 332 days of lactation, recently reported by Halidou et al. (2021) and the data of Oumarou (2004) on the performance of 300 lactations in station (daily milk yield of 3.56 kg with an total milk yield of 995 kg) seem to confirm this hypothesis. Achard et Chanono (1997) had nevertheless observed a clear improvement in the reproductive performance of azawak, following the modification of the breeding system initiated at the time of the 1984 drought, in particular the reduction in the grazing load. Genetic parameters need to be estimated in order to assess more accurately the effectiveness of the phenotypic selection long carried out on this zebu, and to decide, if necessary, on the causes of the phenotypic progress achieved.

With a daily milk yield of 4.01±0.03 kg/day, Azawak cows confirmed their position as the best milk producers among the local breeds reared in the country and in the sub-region (Ouédraogo, 2013; Youssao, 2016; Adamou et al., 2021). It also had a longer lactation period than several traditional African breeds (Bayemi et al., 2005) and some of the products of their crosses with exotic breeds such as Holstein-Friesian, Montpelier and Holstein Demeke et al. (2000); Marichatou et al. (2005a).

The significant influence of lactation rank on milk production, demonstrated in the Azawak cow, is consistent with many results from West African cattle breeds (Kassa et al., 2016). The daily milk yield of multiparous cows was significantly higher than that of primiparous cows in essentially all these cattle breed. On the other hand, in Azawak, lactation lasted significantly longer in primiparous cows than in multiparous cows. This result has been confirmed in numerous research studies on the Azawak cow, such as those by Oumarou (2004), Saidou (2004) and Halidou et al. (2021). It is known from the physiology of milk secretion that well-developed mammary glands in multiparous cows give them a higher production capacity than multiparous cows. This mammary development is also coupled with a higher intake capacity during grazing in multiparous cows than in primiparous cows (Johnson al., 2005). Multiparous cows are less stressed during milking and therefore produce more milk than primiparous cows (Gloria et al., 2012).

At the Toukounous station, Azawak dairy performance (lactation length, peak lactation, daily and total milk yield) varied with the year and calving season so that it was minimal for calving in the rainy season and maximal for calving in the dry season. Similar year- and calving-season-dependent variations in reproductive performance and milk production have been reported in local breeds of cattle in Sahelian ranching environments (Adamou et al., 2021). This result, confirmed by a number of authors (El-Awadyl, 2013; Gebreyohannes et al., 2013), is explained by the inter-annual variation and seasonal dynamics of the food available from natural pastures. Females calving during the rainy season spend most of their lactation during the dry season, with a drop in production linked to the quantity and quality of feed. On the other hand, females that give birth during the dry season continue to produce during the rainy season, thanks to the favourable grazing conditions and good feed. Adequate supplementation in extensive farming tends to eliminate the influence of the season on milk production (Kamga et al., 2001).

4.2. Lactation curve

The average profile of the Azawak lactation curve is similar to the standard curve described for the dairy cow (Jingar et al., 2014; Nishiura et al., 2015; Buaban et al., 2016; Puangdee et al., 2017; Bangar & Verma, 2017). Differences between studies are reflected in terms of lactation peak and persistence. In intensive management systems, peak lactation occurs between 6 and 8 weeks after calving, depending on the breed (Jingar et al., 2014; Bangar & Verma, 2017), and between 2 and 9 weeks in African production systems (Marichatou et al., 2005; Gbodjo et al., 2013). In the present study, the peak was reached two months after parturition (36.5 ± 0.5 days), which is consistent with that reported by Oumarou (2004), Saidou (2004) and Halidou et al. (2021) for the same breed. The lactogenetic phase is therefore in the same range as that reported in extensive systems with low inputs. The irregularities observed in relation to the standard form are comparable to those observed, in a controlled environment, in females of the N'Damance genetic type (Gbodjo et al., 2013), in primiparous Goudali heifers (Marichatou et al., 2005a) and in Ankole cattle and Ankole crossbreds in Rwanda (Maximillian et al., 2020). This might be an effect of the very low yield in these systems.

In general, the milk production rate falls to around 7 % (Val-Arreola et al., 2004). Azawak's average lactation persistency coefficient (86 %) remains relatively low compared with the 85–95 % range accepted for breeds in African production systems (Saidou, 2004; Marichatou et al., 2005a).

Finally, one of the aims of analysing the effects of environmental factors on milk production is to take them into account for a more accurate assessment of genetic parameters. In this way, a model for predicting the genetic values of improving sires can be developed (Siddo et al., 2018).

4.3. Genetic parameters

4.3.1. Heritability and repeatability

There are very few studies concerning estimates of the heritability and repeatability of milk production traits in West African cattle breeds, and even fewer concerning local breeds in Niger. Generally, traits associated with reproduction have low heritability; some traits related to milk production have moderate heritability; on the other hand, others affecting production quality have high heritability (Salifou et al., 2012).

The heritability of daily milk yield in the Azawak Zebu (0.33±0.05) is higher than that of the Polish Holstein-Friesian cow, which varies from 0.12 to 0.20 depending on the first three lactations (Satoła & Ptak, 2019). Also, the heritability of the total milk yield of the Azawak Zebu (0.35±0.06), obtained for this study, corresponds practically to the maximum of what is generally observed. Indeed, for milk yield at 305 days, heritability is between 0.19 and 0.37 in cattle breeds in tropical regions (Lobo et al., 2000), in Brazilian *Bos taurus* and *Bos indicus* dairy crossbred females (Vercesi Filho et al., 2007), in Holstein-Friesian dairy cows (Pritchard et al., 2012) and in Girolando cows (Canaza-Cayo et al., 2018).

Differences from estimates reported in the literature can be attributed to several factors such as production levels, population size, analysis model, measure evaluated, environmental effects and others that affect genetics and environmental variations (Canaza-cayo et al., 2018). At the Toukounous experimental centre, the very wide phenotypic variances observed, which would be related to the effects of a very heterogeneous rearing environment, therefore suggest that the heritability obtained in this study is low for initial milk yield (h2=0.15), lactation lenght (h2=0.18), lactation persistency (h2=0.23) and is moderate for peak lactation (h2=0.34), daily milk yield (h2=0.33) and total milk yield (h2=0.35). This suggests considerable additive genetic variance, which offers the possibility of selecting the Azawak Zebu for these last three milk production traits.

On the other hand, improvements in initial milk yield, persistency and lactation duration of Azawak zebu cattle were due to environmental factors in the breeding system, not genetic factors. Emphasis should therefore be placed on improving the energy balance of dairy cows through feed management, animal health and welfare practices, etc.

4.3.2. Genetic and residual correlations

Correlations are important for assessing the feasibility of joint selection between two or more traits (K.I. Adamou et al., 2017a). At the Toukounous experimental station, significant genetic correlations between the functional traits of lactation and reproduction were wider and contrasted with residual correlations. A moderate positive genetic correlations between peak lactation and lactation lenght (0.42±0.11*) was opposed by weaker unfavourable residual correlations (−0.18±0.03*). This implies that selecting cows for milk production could improve lactation length and lead to standardised production at 305 days, like European dairy cows.

The positive genetic correlations between milk production and reproduction traits were unfavourable. In fact, the significant correlations varied according to the lactation traits considered from 0.32 to 0.82 for age at first calving and from 0.48 to 0.97 for calving interval, indicating that selection for milk should result in a longer calving interval and a later age at first calving.

In the literature, reported genetic correlations between milk yield and calving interval ranged from 0.22 to 0.59 (Pryce et al., 2004; Wall et al., 2003; Pritchard et al., 2012). The antagonistic relationships observed in this study between milk production traits and fertility in Azawak cows may be partly explained by the negative energy balance of the animals (Pritchard et al., 2012). In order to mitigate the negative effects on milk production of certain additive genes that favour an increase in the age at first calving and the time between calvings, it is necessary to act effectively on the energy component through a very balanced and regular feed intake, capable of shortening the age at puberty (Bhatti et al., 2007).

These high and positive genetic correlations between milk production traits and age at first calving imply that some of the additive genes that positively influence milk production act to increase age at first calving. This result, which is consistent with that reported by Wenceslau et al. (2000) on Gyr dairy cattle (0.49), suggests that daughters from genetic sires of high value for milk production have lower sexual precocity. Consequently, the selection process aimed at increasing milk production would result in lower heifer precocity. In the bovine species (Holstein cows, Mantiqueira) the genetic correlations reported between milk yield at 305 days and age at first calving are negative and lie in the range −0.65 to −0.29 (Balieiro et al., 2003; Silva et al., 1998, 2001). The residual correlation between these two traits (−0.01±0.04) in Azawak is as negative as that (−0.11) reported by Canaza-cayo et al. (2018), although in most cattle breeds, authors report low to high positive values with a range from 0.02 to 0.71 (Balieiro et al., 2003; Silva et al., 1998, 2001).

Genetic correlations between total milk yield and calving interval in the Azawak cow were significant (0.48±0.05*) and positive, suggesting a genetic antagonism between these two functional traits. Similar unfavourable associations have been reported at first calving (Balieiro et al. 2003; Lobo et al., 2000; Silva et al. 1998). Pryce et al. (2004) and Pritchard et al. (2012) examined estimates of the genetic correlation between milk yield and calving interval, and these ranged from 0.22 to 0.59. However, other authors did not find such correlations. However, other authors found no adverse genetic associations between these two functional traits (Montaldo et al. 2010; Ojango & Pollot 2001; Val-Arreola et al. 2004).

4.3.3. Optimal regression model for milk production

The coefficients of the genetic and residual correlations between total milk yield and peak production were 0.93 and 0.58 respectively. This genetic correlation, which is as high as the residual correlation, reflects a strong phenotypic link between these two traits. Therefore, an early estimate of total milk yield can be obtained from peak production (i.e. $TMy = 254 * Peak^{0,91}$). Peak production can therefore be considered a good estimate of the milk value of an Azawak cow. Using it to estimate the milk value of daughters of bulls in test would simplify calculations and save at least 10 months. Peak production also shows an unfavorable genetic correlation with age at first calving (0.32±0.11*). However, this link is not strong enough for selecting cows according to their peak production to seriously increase age at first calving. However, it would be more prudent to take it into account when developing a selection index.

4.3.4. Implications of the results

As part of the policy adopted in 2000 to revive the livestock sector, one of the strategic options of the Niger government was to improve the genetics of local livestock. The Azawak breed was targeted among Niger's local breeds for a selection programme at the Toukounous experimental Sahelian station. The genetic successes achieved were limited to meet milk requirements. With this in mind, a national genetic improvement programme for local cattle was launched in 2009 by the Ministry of Livestock. It focused on cross-breeding foreign cattle breeds with high dairy potential with local breeds. The Brune des Alpes, a dairy breed adapted to hot tropical climates, was chosen for its hardiness as an improver breed.

Crossing between purebred lines or populations is known to produce offspring with better economic and phenotypic capacities than their parent breeds. This is the case with Holstein-Frise x Polish crosses, in which hybrid vigour has led to production records of 27.8 to 34.5 kg/day (Nishiura et al., 2015; Satoła & Ptak, 2019). After the Azawak breed underwent selection among cattle, the milk yield at 305 days of Azawak Alpine Brown crosses was estimated at 2398 kg for primiparous and 3445 kg in multiparous (Halidou et al., 2021). It should be noted that the selection of the Azawak Zebu in question was entirely phenotypic and based on progeny testing (Siddo, 2017). The main selection traits were the fawn coat with black tips, and dairy and meat aptitudes. This was done without any prior analysis of the genetic correlations between dairy performance, coat phaneroptics and meat performance. The relationship between these traits can be unfavourable, like the one just described in the present study between functional traits for milk production and those for reproduction.

Furthermore, analysis of the evolution of Azawak dairy performance, coupled with genetic parameters, indicates random genetic progress and low selection pressure on this Zebu. The very high heritability and repeatability of milk production traits show that additive genetic factors are still important in the variation of trait expression within the population. This suggests that there is still considerable room for improvement. In view of the high heritability values, the dairy performance of the Azawak should be sufficiently improved by selection, with crossbreeding with the Brune des Alpes to follow in order to hope for an optimal heterotic response. In fact, when heritability is high, selection is the best route to genetic improvement.

The response to selection would be faster if it were based on genotypic improvement on progeny according to an open selection scheme with a nucleus and breeding herd using a monitoring system adapted to the Toukounous experimental station, but extended to the other stations in the country (Fako and Ibecetan experimental centres) where the breed is currently bred. In this national programme for the genetic improvement of local breeds, intensive peri-urban farms should be used to speed up the creation and exploitation of genetic progress. It would be wiser to improve the breed on its best performance, that of milk, and then possibly improve meat. The genetic evaluation of animals, as a decision-making tool for selecting breeding stock, should be based on the standard method of restricted maximum likelihood applied to the 'animal model'.

5. Conclusion

High variability with record milk production (peak lactation and total milk yield) shows the milk production potential of this Azawak cattle breed. The study also showed the high importance of environmental factors. These factors include lactation rank, calving year and calving season, as well as excessive heat, which clearly reduce potential production, and climatic hazards, more pronounced in the Sahel, where interannual rainfall variability is a determining factor in the variability of available resources. More comprehensive monitoring under good feeding conditions would be needed to quantify the breed's full potential more accurately.

Given the high importance of the effects of unfavourable environmental factors, the study also reported moderate estimates of heritability and repeatability of lactation traits in the Azawak breed, showing that there is considerable scope for improving dairy performance through selection.

Dairy breed improvement programmes, in which the Azawak plays a central role, must continue to place greater emphasis on selecting animals for milk performance before cross-breeding. Estimates of the heritability of lactation traits are moderate, as are many functional reproductive traits, so genetic gain through selection for milk production traits alone would be rapid, but antagonistic with reproductive performance. This antagonism shows the importance of selecting animals on the basis of a selection index that takes into account both milk production traits and reproductive traits, including age at first calving and calving interval. The importance of extending the selection programme to other farms and experimental centres must be stressed to avoid too much inbreeding and loss of genetic variation in the final products. Standardised recording protocols need to be established to improve the accuracy of genetic evaluations and facilitate selection response.

CRediT authorship contribution statement

Adamou Karimou Ibrahim: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Issa Moumouni:** Writing – review & editing, Writing – original draft, Conceptualization. **Chanono Mogueza:** Writing – review & editing, Data curation, Conceptualization.

Declaration of competing interest

The authors certify that they have no known competing financial interests or personal relationships that might appear to influence the work reported in this article.

Ethical statement

The authors certify that the present work did not involve any use of human subjects, and that all animal experiments were ARRIVE-compliant and were carried out in accordance with the UK Animals (Scientific Procedures) Act 1986 and associated guidance, the EU Animal Experiments Directive 2010/63/EU, or the National Research Council Guide for the Care and Use of Laboratory Animals and the authors.

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