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Original article

Genetic variability of the length of *postpartum anoestrus* in Charolais cows and its relationship with age at puberty

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Abstract – Fertility records ($n = 1802$) were collected from 615 Charolais primiparous and multiparous cows managed in an experimental herd over an 11-year period. The objectives of the study were to describe the genetic variability of the re-establishment of *postpartum* reproductive activity and the relationship with body weight (BW) and body condition score (BCS) at calving and age at puberty. The length of *postpartum anoestrus* was estimated based on weekly blood progesterone assays and on twice daily detection of *oestrus* behaviour. The first *oestrus* behaviour was observed 69 days (± 25 days s.d.) post-calving and the first positive progesterone measurement ($\geq 1 \text{ ng mL}^{-1}$) was observed at 66 days (± 22 days s.d.) for the group of easy-calving multiparous suckling cows. Estimates of heritability and repeatability were $h^2 = 0.12$ and $r = 0.38$ respectively, for the interval from calving to first *oestrus* (ICO). Corresponding values were $h^2 = 0.35$ and $r = 0.60$ for the interval from calving to the first positive progesterone test (ICP). The genetic correlation between both criteria was high ($r_g = 0.98$). The genetic relationships between *postpartum* intervals and BW and BCS of the female at calving were negative: the genetic aptitude to be heavier at calving and to have high body reserves was related to shorter *postpartum* intervals. A favourable genetic correlation between age at puberty and *postpartum* intervals was found (r_g between 0.45 and 0.70). The heifers which were genetically younger at puberty also had shorter *postpartum* intervals

beef cattle / *postpartum* / puberty / body weight / genetic parameter

Résumé – Variabilité génétique de la durée d'*anoestrus postpartum* chez la vache Charolaise et relation avec l'âge à la puberté. Des données ont été collectées pendant 11 ans en troupeau expérimental ($n = 1802$) sur 615 vaches Charolaises primipares et multipares. Les objectifs de cette étude étaient de décrire

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la variabilité génétique du rétablissement de l'activité ovarienne après vêlage et sa relation avec le poids (BW) et l'état au vêlage (BCS) et l'âge à la puberté. La durée d'*anoestrus postpartum* a été estimée par des dosages hebdomadaires de progestérone plasmatique et une détection biquotidienne des comportements de chaleurs. Les premières chaleurs ont été détectées 69 jours (± 25 jours) après vêlage et le premier test positif de progestérone ($\geq 1 \text{ ng} \cdot \text{mL}^{-1}$) a été observé 66 jours (± 22 jours) pour le groupe des vaches multipares allaitantes avec vêlage facile. Les estimations d'héritabilité et de répétabilité ont été $h^2 = 0,12$ et $r = 0,38$ respectivement pour l'intervalle vêlage–premières chaleurs (ICO) et $h^2 = 0,35$ et $r = 0,60$ pour l'intervalle vêlage–premier test positif de progestérone (ICP). La corrélation génétique entre ces deux critères était élevée ($r_g = 0,98$). La relation génétique entre intervalles *postpartum*, note d'état corporel et poids vif des femelles au vêlage était négative. Un potentiel génétique pour être lourde au vêlage et avoir d'importantes réserves corporelles allait de pair avec des intervalles *postpartum* courts. Une relation génétique favorable entre les mesures de l'âge à la puberté et les intervalles *postpartum* a été trouvée (r_g entre 0,45 et 0,70). Les génisses génétiquement jeunes à la puberté avaient un potentiel génétique pour des intervalles courts.

vache à viande / *postpartum* / puberté / poids vif / paramètre génétique

1. INTRODUCTION

High rates of reproduction are directly related to the profitability of beef cattle herds [20], so the reproductive traits should be considered with more importance in breeding programs. The low heritability generally associated to conventional fertility measurements [8,12,15] makes it difficult to detect the more fertile genotypes. This limits the development of selection aimed at obtaining a significant genetic gain in reproductive efficiency. An alternative approach may be the identification of physiological parameters, like endocrine factors, that are related to fertility and are heritable [4].

In beef production, several studies have illustrated that the length of *postpartum anoestrus* might be a limiting factor, particularly in extreme situations such as underfed primiparous suckling cows, and might compromise the objective of producing one calf per year [10,23]. This is all the more true as the breeding period is short. It would therefore be interesting to reduce the length of the *postpartum anoestrus* in order to increase the number of opportunities for a cow to conceive during the breeding period. To our knowledge, the genetic variability of this trait has only been explored in a few studies, mainly performed on dairy cattle, [2,18,26]. Indeed, it is difficult to obtain sufficient numbers of observation using non invasive techniques in order to quantify the additive genetic variability. The use of routine progesterone measurements has provided a practical means of achieving this result. The heritability coefficients obtained in previously cited studies were significantly different from 0 (between 0.13 and 0.28). In dairy cattle, a selection for shorter *postpartum anoestrus* periods might be feasible.

In beef suckling Charolais cows, the *postpartum anoestrus* period is also a major component of the biological rhythm of the females (Mialon *et al.*, unpublished results). The objective of the present study was to describe the genetic

variation of two measurements of this *anoestrus* period, *i.e.* the *postpartum* intervals (i) from calving to the first observed *oestrus* (ICO) (ii) from calving to the first positive progesterone test (ICP). Since the females were controlled for several other aptitudes, we were also interested in quantifying the genetic and environmental associations between these two measurements and other traits such as body weight and body condition at calving and age at puberty.

2. MATERIALS AND METHODS

2.1. Data set

The data used in this study were collected from an INRA experimental herd located in Bourges (centre of France).

Animals

At the beginning of this experiment between 1985 and 1987, Charolais females (breed representative) were bought at weaning from farms in order to establish the foundation of the experimental herd (generation G_0). After rearing, 300 of these females were first mated at two years of age and were inseminated for seven years with semen from 60 Charolais bulls which were performance-tested in stations. These matings produced 351 heifers born between 1988 and 1994 (generation G_1), the progeny of 192 of the G_0 females and of the 60 sires. These 351 heifers were also first mated at two years of age, and then during four consecutive years. For all the females involved in this study, the breeding period was from the end of April to early July (10 weeks), and the females were inseminated during their natural *oestrus*.

Management

After weaning at 32 weeks of age, the heifers were reared in free stall barns and fed a roughage ration [16]. During the calving period, whatever the year and the date, the females were managed according to normal practices used in French farms but with no grazing. The management system included a period of underfeeding before and after calving in order to induce mobilisation and recovery of body reserves.

Data and trait definition

For the analysis of the *postpartum* period, all the calving information collected from 1988 to 1998 was used ($n = 1802$). This information came from 615 Charolais females: 289 from generation G_0 and 326 from generation G_1 . These data were recorded after first calvings ($n = 568$) or posterior calvings ($n = 1234$). The average number of records per female was 2.9 (1 to 7). The *postpartum anoestrus* period was recorded from the fourth week after calving onwards. *Oestrus* was detected twice daily with vasectomised bulls. Ovarian function was examined by measuring, once per week, blood progesterone concentration according to the radioimmunoassay procedure described by Terqui

and Thimonier [25]. Blood samples were collected from the caudal vein into heparinised vacutainers. Plasma was separated by centrifuging within 1 h of sampling and was stored at -20°C until analysis. Intra- and inter-assay coefficients of variation were 2.5% and 6%, respectively, when estimated with a reference plasma of $1\text{ ng}\cdot\text{mL}^{-1}$. The progesterone test was declared positive when progesterone concentration was higher or equal to $1\text{ ng}\cdot\text{mL}^{-1}$. With this experimental design of one test per week, the length of the *postpartum* period might be overestimated by 6 days for some females. But on the average, the precision of the progesterone test was about 3.5 days.

Body weight (BW) was measured within 48 h after calving. Body condition score (BCS) at calving was recorded on a 6-point scale, according to Agabriel *et al.* [1]: *i.e.*, from the very thin (0) to the very fat (5).

For studying age at puberty, the available data were collected only on the 351 G_1 heifers born in the experimental herd between 1988 and 1994. Age at puberty was also estimated between 10 and 20 months of age by detecting *oestrus* twice a day and by two progesterone tests every month at alternating intervals of 10 or 20 days. The precision of the measurement method was discussed in detail in a previous paper [16].

The traits studied were two *postpartum* intervals (ICO and ICP), two body traits at calving (BW and BCS) and two estimations of age at puberty: age at first observed *oestrus* (AFO) and age at the first positive progesterone test (AFP). A preliminary analysis (non-published) indicated that a high genetic correlation did exist between *anoestrus* intervals of different parities; therefore, we were able to consider them as the same trait with repeated measures.

2.2. Statistical analysis

Preliminary analyses were performed using the MIXED procedure of SAS[®] [14] for *postpartum* intervals and body traits, with a female random effect, and the GLM procedure of SAS[®] [22] for age at puberty in order to determine the fixed effects which should be taken into account in the following analyses. In addition to the residual effects, the random effects were the cow permanent effect and the cow additive genetic effect. The genetic model was therefore an animal model.

- The linear model describing ICO, ICP, BW and BCS is:

$$y_{ijklmn} = \text{Year}_i + \text{Period}_j + \text{Calving difficulty}_k \\ + (\text{Lactation} * \text{Age})_l + p_m + a_m + e_{ijklmn}$$

where:

- Year_{*i*} = fixed effect of year of calving *i* (11 levels);
- Period_{*j*} = fixed effect of period of calving *j* (6 levels: end of January, 4 two-week periods in February and March, early April);
- Calving difficulty_{*k*} = fixed effect of calving difficulty score (2 levels: natural parturition, assisted or not, and caesarean delivery);

- (Lactation * Age)_{*l*} = interaction between 2 fixed effects: lactation status (2 levels suckling or not (loss of the calf, 5%)) and age (2 levels: 3 years, called primiparous and 4 years and more, called multiparous);
- p_m = random permanent environmental effect related to cow m ;
- a_m = random additive genetic effect of cow m ;
- e_{ijklmn} = random residual effect.

- The model describing AFO and AFP is:

$$y_{ijklm} = \text{Year}_i + \text{Period}_j + \text{Dam Age}_k + \text{Twinning}_l + a_m + e_{ijklm}$$

where:

- Year_i = fixed effect of year of birth i (7 levels);
- Period_j = fixed effect of period of birth j (6 levels: end of January, 4 two-week periods in February and March, early April);
- Dam Age_k = fixed effect of dam age k (3 levels: 3–4; 5–6 and 7+ years);
- Twinning_l = fixed effect of type of birth l (2 levels: single or twin);
- a_m = random additive genetic effect of heifer m ;
- e_{ijklm} = random residual effect.

Heifers with a male twin were not included in the puberty study

Variance and covariance components were estimated using a restricted maximum likelihood (REML) procedure applied to a multiple-trait individual animal model using the VCE 4.0 software developed by Groeneveld [7]. The complete available pedigree information over two to seven generations of ancestors were taken into account in the pedigree file.

For the *postpartum anoestrus*, heritability (h^2) and repeatability (r) were obtained from the estimated variance components σ_a^2 (additive genetic), σ_p^2 (permanent environment) and σ_e^2 (residual) as follows:

$$h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_p^2 + \sigma_e^2) \quad \text{and} \quad r = (\sigma_a^2 + \sigma_p^2) / (\sigma_a^2 + \sigma_p^2 + \sigma_e^2).$$

For age at puberty, heritability (h^2) was obtained from the estimated variance components σ_a^2 (additive genetic) and σ_e^2 (residual) as follows:

$$h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_e^2).$$

3. RESULTS

3.1. Genetic variability of the different traits (Tab. I)

In this experiment, the rough means for ICO and ICP were 72 ± 27 days and 68 ± 25 days respectively. Since these rough values included females in different situations (primiparous, multiparous, suckling or not...), the adjusted averages for a given group of females were 69 and 66 days for ICO and ICP respectively for multiparous suckling cows with easy calving. The phenotypic

Table I. Estimates of heritability (h^2), proportion of variance due to permanent environment ($c^2 = \sigma_p^2 / (\sigma_a^2 + \sigma_p^2 + \sigma_e^2)$) and repeatability ($r = h^2 + c^2$) for reproductive traits, body weight and body condition score at calving of beef Charolais cows.

		No records	Trait mean $\pm$ SD ^(b)	Parameter estimates		
				$h^2 \pm$ SE	c^2	r
Postpartum interval to first observed oestrus (days)	ICO	1 765	69 ^(a) $\pm$ 25	0.12 $\pm$ 0.04	0.26	0.38
Postpartum interval to first positive progesterone test (days)	ICP	1 757	66 ^(a) $\pm$ 22	0.35 $\pm$ 0.06	0.25	0.60
Body weight at calving (kg)	BW	1 782	671 ^(a) $\pm$ 65	0.58 $\pm$ 0.06	0.14	0.72
Body condition score at calving	BCS	1 538	2.7 ^(a) $\pm$ 0.6	0.19 $\pm$ 0.03	0.03	0.22
Age at first observed oestrus (days)	AFO	344	426 $\pm$ 42	0.33 $\pm$ 0.09	–	0.33
Age at first positive progesterone test (days)	AFP	335	445 $\pm$ 43	0.34 $\pm$ 0.09	–	0.34

^(a) Adjusted for an easy calving and suckling multiparous cow.

^(b) Phenotypic standard deviation.

standard deviation was higher for ICO than for ICP: 25 days (CV = 36%) *vs.* 22 days (CV = 33%), respectively. At calving, the mean BW of these cows was 671 ± 65 kg (CV = 9.7%) with a mean BCS of 2.7 ± 0.6 (CV = 22%).

The proportion of phenotypic variance of *postpartum* intervals due to the cow effects (permanent and additive) expressed through the repeatability coefficient was relatively important, especially for ICP ($r = 0.60$). For ICO, repeatability was only 0.38. The proportion of phenotypic variance due to the permanent environmental effect was similar (0.25) for both *postpartum* intervals. In contrast, the proportion due to the additive genetic variance was lower for ICO ($h^2 = 0.12$), than for ICP ($h^2 = 0.35$).

The heritability estimates for BW and BCS at calving were $h^2 = 0.58$ and $h^2 = 0.19$ respectively. For BCS, the proportion of variance related to the permanent environment was low (3%). The heritability estimates for age at puberty were $h^2 = 0.33$ when measured by AFO and $h^2 = 0.34$ when measured by AFP.

3.2. Relationship between ICO, ICP, BW and BCS (Tab. II)

Although phenotypically different ($r_p = 0.65$), the two *postpartum* intervals could be considered to be under the control of virtually the same genes since the genetic correlation was as high as +0.98. The correlation between the environmental effects (permanent plus residual) was also positive: $r_e = +0.59$.

Table II. Genetic ($G \pm SE^a$), Environmental (E^b) and Phenotypic (P) correlations among *postpartum* intervals to resumption of cyclicity and body weight and body condition score at calving in beef Charolais cows.

Traits and correlates	ICP	BW	BCS
ICO			
G	$0.98 \pm 0.01^{(a)}$	$-0.19 \pm 0.14^{(a)}$	$-0.49 \pm 0.16^{(a)}$
$E^{(b)}$	0.59	-0.14	-0.02
P	0.65	-0.14	-0.10
ICP			
G		$-0.17 \pm 0.11^{(a)}$	$-0.25 \pm 0.13^{(a)}$
$E^{(b)}$		-0.22	-0.08
P		-0.19	-0.12

^(a) SE = Standard Error.

^(b) E = permanent environment and residual.

Phenotypically, these two *postpartum* intervals were correlated with BW and BCS at calving.

For BW, the phenotypic correlation was $r_p = -0.14$ for ICO and $r_p = -0.19$ for ICP. This phenotypic relationship between *postpartum* intervals and BW was a consequence of both a favourable genetic ($r_g = -0.19$ for ICO and $r_g = -0.17$ for ICP) and environmental ($r_e = -0.14$ for ICO and $r_e = -0.22$ for ICP) relationship in similar proportions.

The phenotypic correlation between the two *postpartum* intervals and BCS at calving was also negative: $r_p = -0.10$ for ICO and $r_p = -0.12$ for ICP. The cows in better condition at calving had shorter *postpartum* intervals. This phenotypic relationship between *postpartum* intervals and BCS at calving was mainly due to a negative genetic relationship ($r_g = -0.49$ for ICO and $r_g = -0.25$ for ICP), the environmental correlation being as low as $r_e = -0.02$ for ICO and $r_e = -0.08$ for ICP.

3.3. Relationship between age at puberty and ICO and ICP (Tab. III)

The phenotypic relationship between both measures of age at puberty and both measures of the *postpartum anoestrus* period were low ($r_p = +0.20$ to $r_p = +0.31$). The females that were pubertal at younger ages also tended to have shorter *postpartum* intervals during their reproductive life. This relationship was mainly due to a positive genetic relationship ($r_p = +0.45$ to $r_p = +0.70$) between these two groups of traits. The environmental correlations were only slightly positive ($r_e = +0.08$ to $r_e = +0.21$): the environmental factors that had a favourable influence on the establishment of reproductive activity at puberty also had a favourable influence on the resumption of reproductive *postpartum* activity.

Table III. Genetic ($G \pm SE^a$), Environmental (E) and Phenotypic (P) correlations among *postpartum* intervals and age at puberty.

Traits and correlates	<i>Postpartum</i> intervals	
	ICO	ICP
AFO		
G	$0.64 \pm 0.12^{(a)}$	$0.45 \pm 0.11^{(a)}$
E	0.08	0.13
P	0.20	0.24
AFP		
G	$0.70 \pm 0.09^{(a)}$	$0.50 \pm 0.09^{(a)}$
E	0.08	0.21
P	0.21	0.31

^(a) SE = Standard Error.

4. DISCUSSION

In the past, several studies have already described the environmental factors that influence the length of *postpartum anoestrus* and have particularly underlined the deleterious effect of suckling on resumption of cyclic ovarian activity [10,23,24]. For this reason, the mean length of *postpartum anoestrus* was generally lower in dairy cattle studies than in beef cattle studies. However, only a few studies, mainly in dairy cattle, examined the genetic variation of *postpartum* resumption of ovarian activity [2,18,26]. Darwash *et al.* [2] quantified the extent of genetic variation within a dairy breed and obtained heritability estimates significantly different from 0 (between 0.13 and 0.28 according to the method of transformation of data) for the interval from calving to the onset of luteal *postpartum* activity. The present study is the first one to our knowledge illustrating that, in a beef cattle breed, a substantial proportion of variation of *postpartum* intervals among individuals is genetically additive. The model of analysis of our data and the available information allow us to use both the relationship between dam and daughters and between paternal half-sisters. This maximum utilisation of information balanced the relatively limited number of sires ($n = 60$). The heritability of the *postpartum* interval to first observed *oestrus* was relatively low ($h^2 = 0.12$) whereas the heritability of the *postpartum* interval to the first positive progesterone test ($h^2 = 0.35$) was higher than the estimation of Darwash *et al.* [2]. For ICO, the heritability estimate was lower, essentially because of a greater incidence of nonidentified environmental factors (like errors of detection). In fact, our method of *oestrus* detection might have been relatively subjective, and influenced by behavioural interactions between cows and vasectomised bulls and finally by human motivation translated by the time and effort devoted to observation. Therefore, this method led to less accurate information than the progesterone test, which is an objective measurement. The measurement of *postpartum anoestrus* by a progesterone test is directly related to a physiological function and then, is less subject to interpretation.

The measurement of ICP appears to be a good criterion since it is relatively heritable although errors exist due to the blood sampling design and easier to practice than *oestrus* detection. However, it remains a heavy test requiring weekly blood sampling from calving to the beginning of the luteal phase. If selection on *postpartum* cyclic activity should be considered in the future, the most appropriate method would probably be a test of cyclicity at fixed intervals after calving, including 2 or 3 weeks of controls. The information recorded would not be a continuous trait like an interval but a categorical trait (cycled or not) the analysis of which would need adequate statistical methods. Veerkamp *et al.* [26] pointed out that monthly progesterone tests on large progeny groups may be sufficient to rank bulls according to their daughter's mean progesterone profile.

Another important result of the present experiment was the study of the genetic relationship between the variability of *postpartum* intervals and the variability of body condition score and body weight at calving for females always managed in the same conditions, whatever the year and the period of calving.

In the literature, several experiments [9,13,21] or analyses of field records [5,6,11] showed that the amount of body fat stores at calving is the factor most influencing the length of *postpartum anoestrus*. In situations of underfeeding, an important part of these body fat stores are mobilised to compensate for the insufficient level of energy intake. That level of body fat stores depends on both environment and genetic aptitude. In a preliminary study, Mialon *et al.* (unpublished results) illustrated that in a standardised environment, the way the females use their body stores has a significant influence on the re-establishment of reproductive activity after calving. In the present study, the phenotypic, genetic and environmental relationships between *postpartum* intervals and BCS at calving were quantified. Firstly, not surprisingly, the results indicated a negative phenotypic correlation between BCS and *postpartum* interval length. Secondly, the genetic relationship between these two types of traits was also negative. The genetic aptitude of being in good condition at calving, *i.e.* of being fit to a given management system, was linked to the aptitude of rapidly resuming ovarian activity after calving.

The second body trait studied was body weight at calving which represents the growth capacity of the female. The phenotypic relationship between BW and *postpartum* intervals was negative: the heavier females at calving tended to have shorter *anoestrus* periods. The genetic relationship was also negative and moderate. This important result shows that, in the Charolais breed, a selection mainly aimed at improving growth traits and consequently the female adult weight would not have a deleterious effect on the *postpartum* cyclicity of the females. In a precedent paper dealing with the same experiment [17], we also presented a favourable genetic correlation between the growth rates of the young females and their ages at puberty.

The greatest value of the present experiment was the possibility to study age at puberty and *postpartum anoestrus* on the same females and on related females. Physiological similarities exist between puberty for heifers and resumption of *oestrus* cycles for cows after parturition. Therefore, it is interesting to investigate whether age at puberty allows one to predict the length

of *postpartum* intervals in cows. Numerous studies have described factors that influence these two traits, but rarely evaluated relationship between these two reproductive traits. Patterson *et al.* [19] illustrated the phenotypic relationship between these two traits in a limited number of crossbred heifers first calving at two years of age. In their study, a negative relationship between age at puberty and length of *postpartum* interval to *oestrus* seemed to exist among Angus $\times$ Hereford cows, but not among Brahman $\times$ Hereford ones. In the present study, the phenotypic relationship was favourable (*i.e.* positive) but low whatever the criterion retained for measuring age at puberty and *postpartum* interval. However, the genetic relationship was much higher: the heifers which were genetically younger at puberty also had a genetic aptitude for shorter *postpartum* intervals during their reproductive life. Some common genes may be involved in both traits. The genetic parameters found in the present study showed that the genetic ability to recover a sexual activity after calving can be indirectly improved if age at puberty is decreased by selection. This correlated response would, however, be about half of the direct response to selection for decreasing the ICP.

The respective interest of direct selection on the length of *postpartum anoestrus* or indirect selection on the age at puberty has to be discussed according to the relationship between these two traits and more traditional measures of fertility. Darwash *et al.* [3] illustrated a favourable phenotypic association between the interval to *postpartum* ovulation and fertility in dairy cattle: females cycling early after calving have shorter intervals to conception, higher conception rates and a reduced number of services per conception than those with prolonged *postpartum* anovulatory periods. Conception rate increased significantly with a higher number of 21-day periods observed between the first ovulation and the first *postpartum* insemination, because recovery of luteal function was found to be progressive. In the present experiment, females were also controlled for their fertility during several breeding seasons and further analyses should allow one to quantify the relationship between the different components of the reproductive aptitude of a cow during its reproductive life. Then, it would be possible to determine all the implications of a given selection.

5. CONCLUSION

The *postpartum* intervals to first observed *oestrus* and to the first positive progesterone test in a French population of Charolais cows were heritable and repeatable. The progesterone measurement appeared to be a more precise measure directly related to physiology and the corresponding interval was more heritable than the calving to *oestrus* interval.

A genetic aptitude for high body stores, or for a high body weight is related to a rapid resumption of ovarian activity after calving.

The relationship between age at puberty and length of *postpartum anoestrus* showed that heifers which were genetically younger at puberty also had a genetic aptitude for shorter *postpartum* intervals. These results indicate that selection for shorter *postpartum* intervals might be feasible indirectly through selection on age at puberty. However, further studies are needed to measure

the genetic and environmental association between these two reproductive traits and more traditional measures of fertility.

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