Ann. Zootech. 48 (1999) 427–434

Original article

Puberty in Charolais heifers in relation to growth rate. 2. Genetic variability

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(Received 18 December 1998; accepted 30 July 1999)

Abstract — The genetic variability of age at puberty estimated by the age at the first observed oestrus and the age at the first positive progesterone test was described for 351 Charolais heifers, the progeny of 60 sires. The relationship between age at puberty and growth rate of the heifers was also studied. Estimates of heritability were 0.34 for the age at the first observed oestrus and 0.27 for the age at the first positive progesterone test. The genetic correlation between these two criteria was high ($r_g = 0.94$). Negative environmental relations existed between age at puberty and growth rate of the heifers until 1 year of age and with mature weight. The genetic relationship between puberty criteria and growth rate was also negative. Heifers with a high genetic potential for growth also had a high potential for an early puberty. Puberty age criteria were, however, independent of the degree of weight maturity at 1 year of age but negatively related to adult weight. Weight maturity at the first oestrus was highly correlated ($r_g = 0.70$) with age at the first oestrus. (© Elsevier / Inra)

beef cattle / puberty / heritabilities / genetic correlations / growth

Résumé — **Âge à la puberté chez la génisse Charolaise en relation avec la croissance. 2. Variabilité génétique.** La variabilité génétique de l'âge à la puberté estimé par l'âge au 1[er] comportement de chaleurs et par l'âge au 1[er] dosage positif de progestérone a été décrite pour 351 génisses Charolaises filles de 60 pères. La relation entre l'âge à la puberté et la croissance pondérale a également été étudiée. L'héritabilité de l'âge aux 1[res] chaleurs et de l'âge au 1[er] dosage positif de progestérone étaient respectivement de 0,34 et 0,27. La relation génétique était forte ($r_g = 0{,}94$) entre ces deux âges. La relation environnementale entre critères de puberté et de croissance était négative et favorable. Une relation génétique favorable existait entre l'âge à la puberté et la vitesse de croissance de la génisse jusqu'à un an et avec son poids adulte. Les génisses à fort potentiel de croissance avaient également une bonne capacité à avoir une puberté précoce. Par contre les critères d'âge à la puberté apparaissaient indépendants du degré de maturité pondérale à 1 an mais reliés négativement au poids adulte. La maturité pondérale aux 1[res] chaleurs était fortement corrélée ($r_g = 0{,}70$) avec l'âge aux 1[res] chaleurs. (© Elsevier / Inra)

génisse à viande / puberté / héritabilités / corrélations génétiques / croissance

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1. INTRODUCTION

Age at puberty of heifers can be an important limiting factor for the improvement of reproductive efficiency. This age has a significant effect on beef production when heifers are bred to calve at 2 years of age, particularly in production systems that use a restricted breeding season. Even if heifers are bred at 2 years of age, as in most French production systems, it may be useful to know the genetic variability of age at puberty as an indicator of the inherent ability of breeding in a poor environment. Age at puberty is the first fertility trait expressed in the life of a female; it is sensitive to the nutritional regimen but not affected by milking unlike other cow fertility traits [10]. It is, however, necessary to make certain that the selection realised for improving production traits within a beef cattle breed has no detrimental effect on the age of the females at puberty.

In most studies reported in the literature, age at puberty was assessed by the observation of the first oestrus. Several studies realised on different breeds showed that faster-gaining breeds of larger mature size reach puberty at a later age than do slower-gaining breeds of smaller mature size [10]. Within breed, Martin et al. [10] reviewed several heritability estimates for age at first oestrus in beef heifers. They were included between 0.10 and 0.67 with most of them above 0.40. A reproductive tract score (RTS) was proposed by Andersen et al. [1] to estimate the pubertal status of heifers. This score, determined 1 month before the start of the breeding season of heifers, was shown to have an intermediate heritability value ($h^2 = 0.32$). In all these studies both puberty measurements, age at first oestrus and RTS, had favourable genetic correlations with growth of heifers from birth to 1 year of age [10]. Smith et al. [15] and Gregory et al. [5] were interested in the relationships between the age at puberty, maturing pattern and mature weight.

The objective of this paper was to estimate the genetic variability of two measurements of puberty: the age at the first observed oestrus and age at the first positive progesterone test, and to describe the relationship between these ages and the growth capacity of Charolais heifers managed in a controlled environment.

2. MATERIAL AND METHODS

2.1. Data source

The experiment took place on the Inra experimental farm of Galle (Bourges, Centre of France). The 351 heifers born during seven calving seasons (1988–1994) were progeny of a sample of 60 Charolais bulls used by artificial insemination and a sample of 192 Charolais females representative of the breed. The experimental design, management and trait measurements are described in detail in Mialon et al. [11].

The traits analysed included puberty measurements (age and weight at the first observed oestrus, and age and weight at the first positive progesterone test); body weights at birth (BW), at weaning (WW), at 12 months of age (W12) and at 54 months of age (W54); average daily gains (ADG from birth to weaning and from weaning to 12 months of age); and degree of body weight maturity at 12 months of age and at the first observed oestrus. For birth to weaning growth traits, the performance of contemporary male half sibs were analysed simultaneously to female performance, assuming the same genetic determinism in males and females. In order to study the relationship between puberty and maturing pattern (mature weight, degree of maturity for weight), the weight at 54 months of age (4.5 years) was calculated by interpolation between the two nearest weights for the 299 females that had already reached that age. Up until now, only 209 females have actually reached the culling age of about 6.5 years (80 months), for which they are considered as fully mature. The weight at 54 months of age of these 209 culled females represented 95 % of their weight at 80 months of age. In the present study, the weight at 54 months of age was therefore close to the true mature weight of these 299 females. The degree of maturity in body weight at 12 months of age and at the first observed oestrus was taken as a proportion of the mature weight attained at these events.

2.2. Statistical analyses

The data were analysed in a mixed model including the fixed effects described in the previous paper [11]. The model describing age at puberty was:

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

where Year_i = fixed effect of year of birth i ($1 \leq i \leq 7$); Period_j = fixed effect of period of birth j ($1 \leq j \leq 6$); Dam Age_k = fixed effect of dam age k ($1 \leq k \leq 3$); Twinning_l = fixed effect of type of birth l ($1 \leq l \leq 2$); a_{ijklm} = random additive genetic effect of heifer m; e_{ijklm} = random residual effect.

For postweaning traits, two random effects were similarly considered in the model: the animal and residual effects. The complete available pedigree information of two to seven generations of ancestors of the calves were taken into account. For growth traits of males and females from birth to weaning, a fixed effect of sex was included in the model, and the random dam effect took the significant maternal influence on these preweaning growth traits into account.

The animal and residual (co)variances were estimated with the restricted maximum likelihood (REML) method applied to multiple trait animal models using the VCE 4.0 software developed by Groeneveld [6]. Genetic parameters were calculated directly from these (co)variance estimates. In order to estimate genetic correlation coefficients among and between puberty and growth traits, several three or four trait analyses were performed successively.

3. RESULTS AND DISCUSSION

3.1. Phenotypic variability

As shown in the preceding paper [11], both puberty age criteria had similar phenotypic variations of 42–43 days when corrected for environmental factors, with coefficients of variation of 10 %. Sapa et al. [14] found a similar coefficient of phenotypic variation (CV = 12 %) for age at the first oestrus in the Charolais breed, while he found coefficients of variation of only 6 and 8 %, respectively, in the Limousine and Blonde d'Aquitaine breeds. In the literature, coefficients of variation of age at puberty are relatively low, between 6 and 8 % [3, 5, 13, 16]. In this study, the magnitude of the variation in body weights was equivalent to that of the variation in ages, with coefficients of variation decreasing from 11 % at birth to 9 % at 54 months of age. Daily gains were more variable (CV = 11 and 19 %, respectively), especially after weaning. This suggested compensatory growth effects. At 12 months of age, the coefficient of variation of the degree of body weight maturity was 8 %, similar to the results of Fitzhugh and Taylor [4] and slightly higher than the 7 % related by Smith et al. [15] for British breeds. Although a true mature weight of females was not used in this study, the relative variability of the degree of maturity, calculated as a proportion of the weight at 54 months of age was comparable to those results where a true mature weight was used. When measured at puberty, the degree of maturity presented a phenotypic coefficient of variation slightly larger (CV = 9 %) than that at 12 months of age.

3.2. Heritability estimates and correlations between the puberty traits (*table I*)

The heritability estimate of age at the first observed oestrus ($h^2 = 0.34$) was similar to the first value estimated by Sapa et al. [14] for Charolais heifers tested in French stations ($h^2 = 0.33$), and close to coefficients estimated by Morris et al. [12] and Gregory et al. [5]: $h^2 = 0.31$ in both studies. In the literature, higher heritability coefficients ($h^2 = 0.64$; 0.41; 0.48; 0.61; 0.67) were found respectively by Smith et al. [15], Laster et al. [8], King et al. [7], MacNeil et al. [9], Werre and Brinks [18] and some lower coefficients ($h^2 = 0.20$; 0.10) by Arije and Wiltbank [3] and Smith et al. [16]. In the Limousine and Blonde d'Aquitaine breeds, moderate heritabilities ($h^2 = 0.21$; 0.13) were found in French testing stations by Sapa et al. [14]. Andersen et al. [1] used the Reproductive Tract Scoring system to estimate the pubertal status by rectal palpa-

Table I. Estimates of heritability, genetic and environmental correlation coefficients between puberty measurements.

Variable	Heritability ± SE	Genetic correlation ± SE Environmental correlation: Age at first observed oestrus	Age at first positive progesterone test	Weight at first observed oestrus
Age at first observed oestrus	0.34 ± 0.09	1.00		
Age at first positive progesterone test	0.27 ± 0.08	0.94 ± 0.10 0.53	1.00	
Weight at first observed oestrus	0.28 ± 0.10	0.35 ± 0.20 0.54	0.24 ± 0.28 0.16	1.00
Weight at first positive progesterone test	0.33 ± 0.10	0.39 ± 0.19 0.28	0.31 ± 0.25 0.51	0.97 ± 0.05 0.77

SE: standard error.

tion of uterine horns and ovaries. These authors found a heritability estimate of $h^2 = 0.31$ for that trait. In the present study, there was a slightly lower heritability ($h^2 = 0.27$) for the age at the first positive progesterone test than the age at the first oestrus. These traits were, however, closely related. Although these two ages were phenotypically slightly different ($r_p = +0.64$ and a mean difference of 19 days), they could be considered to be under the control of almost the same genes since the genetic correlation was as high as $r_g = +0.94$.

Heritability estimates of weights at the first oestrus and at the first positive progesterone test were close to estimates obtained for these ages: $h^2 = 0.28$ and 0.33. In the literature [8, 9, 12, 14, 15, 18], most of the estimates of heritability of weight at puberty were close to the estimates of age at puberty in a given study. Weights were also closely related ($r_g = +0.97$) as were the ages at these two events. The genetic correlations between ages and weights at puberty were positive: +0.35 and +0.31. These estimates were close to those given by Arije and Wiltbank [3] ($r_g = +0.36$). While Werre and Brinks [18] found a surprisingly negative correlation ($r_g = -0.41$) between age and weight at puberty, other authors found a genetic relationship that was even more positive: $r_g = +0.67$ [15]; $r_g = +0.87$ [12].

All these estimates showed that genetic variability of age and weight at puberty was relatively high, in the present study as well as in most other cattle populations, while most other fertility trait estimates of heritability were much lower. This puberty genetic variability could, therefore, eventually be exploited by selection.

3.3. Genetic and environmental correlations between puberty-related traits and growth traits (*tables II* and *III*)

Both puberty age criteria were little related to birth weight: $r_g = +0.15$ for age at the first oestrus and $r_g = -0.11$ for age at the first positive progesterone test (*table II*). In the literature, this genetic correlation was not homogeneous across different studies. Smith et al. [15] and Werre and Brinks [18] found low negative correlations: $r_g = -0.07$

Table II. Genetic and environmental correlations between reproduction traits and growth traits.

	BW	ADG birth-weaning	WW	ADG weaning –12 months	W12	Maturity in weight at 12 months	W54
Age at first observed oestrus	+0.15 ± 0.17 0.10	–0.42 ± 0.30 –0.22	–0.25 ± 0.27 –0.20	–0.36 ± 0.16 –0.07	–0.30 ± 0.17 –0.17	+0.02 ± 0.21 –0.35	– 0.38 ± 0.24 0.18
Age at first positive progesterone test	–0.11 ± 0.20 0.17	–0.56 ± 0.28 –0.39	–0.44 ± 0.29 –0.33	–0.39 ± 0.18 –0.16	–0.34 ± 0.17 –0.31	+0.05 ± 0.24 –0.31	–0.46 ± 0.24 0.03

First line: genetic correlation coefficients ± standard error.
Second line: environmental correlation coefficients.
BW: body weight at birth; ADG: average daily gains; WW: body weight at weaning; W12: body weight at 12 months of age; W54: body weight at 54 months of age.

Table III. Genetic and environmental correlations between growth rate and maturity at first observed oestrus.*

	W12	W54	Maturity at 12 months	Age at first observed oestrus	Weight at first observed oestrus
Weight at first observed oestrus	0.74 ± 0.12 0.72	0.27 ± 0.20 0.65	0.40 ± 0.22 0.15	0.35 ± 0.20 0.54	1.00
Maturity at first observed oestrus	0.13 ± 0.14 0.25	–0.65 ± 0.12 –0.30	0.78 ± 0.09 0.60	0.70 ± 0.14 0.43	0.51 ± 0.15 0.56

First line: genetic correlation coefficients ± standard error.
Second line: environmental correlation coefficient.
* Results related to age at first positive progesterone were not reported since they gave the same conclusions.
W12: body weight at 12 months of age; W54: body weight at 54 months of age.

and –0.16, respectively, while Smith et al. [16] and Gregory et al. [5] found positive correlations: r_g = +0.58 and +0.03, respectively. Andersen et al. [1] obtained a negative correlation between the Reproductive Tract Score and birth weight: r_g = –0.37.

The age at the first observed oestrus had a negative genetic correlation with the growth rate of heifers: r_g = –0.25 to –0.42 for daily gain until weaning, weaning weight, postweaning daily gain to 1 year of age and weight at 12 months of age *(table II)*. The genetic correlations between the age at the first positive progesterone test and growth rate parameters were even more negative: r_g = –0.34 to –0.56. These negative coefficients indicated that faster-growing heifers reached puberty at an earlier age, and that puberty was favourably related to growth capacity. In the literature, all estimates except one showed favourable genetic correlations between age at the first observed oestrus and different growth traits: with a daily gain to weaning: r_g = –0.59 and –0.31 for Smith et al. [15] and Werre and Brinks [18], respectively; with weaning weight: r_g = –0.52; –0.04; –0.14; for Smith et al. [15]; Smith et al. [16] and Gregory et al. [5], respectively; with postweaning daily gain to 1 year of age: r_g = +0.80; –0.25; –0.21; for Smith et al. [15]; Werre and Brinks [18] and Smith et al. [16], respectively; and with yearling weight: r_g = –0.29; –0.37; –0.14; –0.05; for Smith et al. [15]; Morris et al. [12]; Smith et al. [16] and Gregory et al. [5], respectively. In French studies, Sapa et al. [14] also found similar correlations for weaning weight (–0.45, Charolais breed; –0.17, Blonde d'Aquitaine) and yearling weight (–0.46, Limousine breed; –0.07, Blonde d'Aquitaine). The Reproductive Tract Score of Andersen et al. [1] was also favourably related for weaning and yearling weights of heifers: r_g = +0.20 and +0.31, respectively.

This favourable genetic relationship of age at puberty of heifers with their growth performance might not be the same with growth performance of males. MacNeil et al. [9] estimated that age at puberty of heifers was slightly positively, unfavourably, correlated with daily gain and carcass weight of male half sibs, r_g = +0.16 and +0.17, respectively. Some selection experiments were conducted to examine the realised response to selection on growth rate particularly for reproductive performance, since growth rate remains the primary selection criterion for most beef cattle breeders around the world. In three Hereford lines, selected either for weaning weight, yearling weight or yearling weight combined with muscling score, Wolfe et al. [19] observed a favourable response, although not significant, for age at puberty (–13, –18 and –30 days) and for the percent of heifers attaining puberty at approximately 14 months of age (+1, +1 and +7 %). In two Angus lines selected either for yearling weight or weight at 18 months of age, Morris et al. [13] observed a very small increase of age at puberty (+4 days in both lines) and a favourable increase in the percent of observed oestrus at about 14 months of age (+14 % and +11 %). In a divergent selection program for yearling growth rate in Angus cattle, Archer et al. [2] showed that heifers from a high growth rate line were younger at puberty (mean of 324 days) than control line heifers (mean of 336 days), whereas heifers from a low growth rate line were older (mean of 355 days). In these three situations, there were no adverse effects of selection for high growth rate on age of heifers at puberty.

Although weight at the first oestrus was positively correlated with age at the first oestrus (r_g = +0.35, *table I*), a selection to improve the weight of females at 12 months of age would increase the weight at the first oestrus (r_g = +0.74, *table III*) and simultaneously decrease the age at the first oestrus (r_g = –0.30, *table II*).

Growth performances in early ages depend on two components that reflect the growth curve: the mature weight and the degree of maturity. It was interesting to study the relationship between the age at puberty and both of these growth components. On one hand, the genetic relationship between age at the first oestrus and adult weight clearly appeared to be favourable ($r_g = -0.38$, *table II*). On the other hand, age at the first observed oestrus was independent of the degree of maturity for weight at 1 year of age ($r_g = +0.02$, *table II*). The favourable genetic relationship between puberty and growth performance of heifers was therefore not mediated by a higher degree of body weight maturity in early ages but by a higher growth capacity linked to mature weight. Smith et al. [15] also estimated a negative genetic correlation coefficient ($r_g = -0.20$) between age at puberty and mature weight but found a negative correlation between age at puberty and maturity at 1 year of age ($r_g = -0.18$) in contrast to our results. In the cattle population that they studied, the favourable genetic relationship between early growth and puberty was mediated almost equally by the degree of maturity and mature weight. For Gregory et al. [5], there was no relationship of age at puberty with mature weight ($r_g = -0.05$). From their results, we may conclude that there was also no relationship with maturity for weight at 1 year of age.

Smith et al. [15] studied the degree of maturity at puberty and found a high positive genetic correlation with age at puberty ($r_g = +0.89$). In the present study, we also found a high positive genetic correlation of $r_g = +0.70$ (*table III*) between both traits. In both studies, these genetic correlations show that heifers that are older at puberty are not only heavier at puberty but also then reach a higher degree of maturity.

Estimates of environmental correlations showed trends very similar to those exhibited by genetic correlations for weaning and 12-month weights, and average daily gain for the periods birth-to-weaning and weaning-to-12 months of age. Any residual or environmental factor that would promote a rather high growth rate mainly during the birth-to-weaning period would have a favourable (negative) influence on age at puberty of the heifers. In the accompanying paper, Mialon et al. [11] showed that when a year effect was favourable for a high growth rate, it was also favourable for puberty at a young age. When all the identified environmental effects were corrected, the analyses revealed a negative phenotypic correlation between growth rate and age at puberty [11]. This favourable phenotypic correlation resulted from both favourable genetic ($r_g = -0.30$ and -0.34) and environmental ($r_e = -0.17$ and -0.31) correlations between growth and ages at puberty. The positive environmental correlations between ages at the first observed oestrus and at the first positive progesterone test and birth weight were, however, surprising. There should have been some environmental factors that increased birth weight and consequently delayed the puberty of the heifers. Dystocia may eventually be evoked for this unfavourable environmental factor. For the relationship between age at puberty and the degree of weight maturity at 1 year of age, if there was independence from a genetic point of view we could notice a favourable moderate environmental relationship $r_e = -0.31$ and -0.35). Any residual or environmental factor that would lead to a higher degree of maturity at 1 year of age would also induce the onset of puberty at a younger age.

4. CONCLUSION

In our Charolais population, age at puberty appeared relatively heritable and favourably (negatively) correlated with the growth rate of heifers as previously reported for several other cattle populations in the literature. Some selection experiments conducted to examine realised genetic correlations have also shown that a selection based on a high growth rate does not affect age at puberty.

For the beef cattle breeder, reproductive efficiency is an important economical component of total beef cattle production. Selection in order to improve the fertility of the females is, however, particularly challenging because of the strong environmental influence on this trait that may prevent the expression of the genetic merit. Age at puberty as the first reproduction trait expressed before a cow is in production, is relatively independent of interactions with other traits. The previous information related to age at puberty is very important when considering a selection objective which includes production and reproduction traits. Before deciding to select for this trait in order to improve fertility, the genetic relationship between age at puberty and subsequent reproduction of the females and between age at puberty and production traits in our cattle population should be studied.

ACKNOWLEDGEMENTS

The authors wish to thank the staff at the Inra experimental herd of Galle for help with oestrus detection, blood sampling and data collection, A. Neau for writing the relevant computer programmes used in data collection, D. André (Inra, Laboratory of Hormonal Assays) for performing progesterone assays, and W. Brand-Williams for English revision of the manuscript.

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