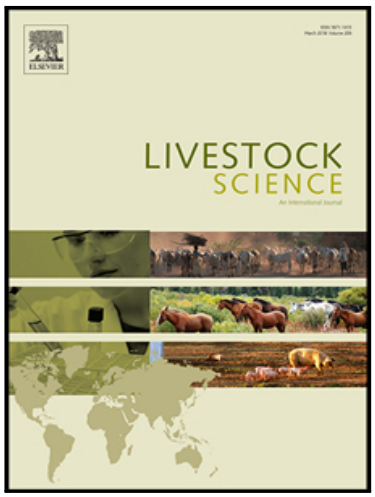

Early rather than late scrotal circumference measurements better reflect female precocity in beef cattle.

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PII: S1871-1413(18)30602-4
DOI: https://doi.org/10.1016/j.livsci.2018.10.019
Reference: LIVSCI 3563

To appear in: *Livestock Science*

Received date: 30 April 2018
Revised date: 26 August 2018
Accepted date: 30 October 2018

Please cite this article as: Bonamy Martin , de Iraola Julieta Josefina , Baldo Andrés , Prando Alberto , Giovambattista Guillermo , Munilla Sebastián , Early rather than late scrotal circumference measurements better reflect female precocity in beef cattle., *Livestock Science* (2018), doi: https://doi.org/10.1016/j.livsci.2018.10.019

Highlights

- We estimated genetic parameters for male and female reproductive traits.
- Our focus was on genetic correlations with scrotal circumference at different ages.
- Age at first calving correlated strongly with earlier scrotal circumference measurements.
- In turn, adult scrotal circumference was poorly correlated with age at first calving.
- We conclude scrotal circumference should be recorded earlier in breeding programs.

Early rather than late scrotal circumference measurements better reflect female precocity in beef cattle.

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Authors declare no conflicts of interest.

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ABSTRACT

In cow-calf operations the moment the heifer achieves her first pregnancy set up her future productivity. Although puberty itself is a yes-or-no condition, time to the event has a quantitative genetic basis and thus is suitable for genetic selection. However, the trait is difficult to measure directly and proxies such as age at first calving (AFC), or scrotal circumference (SC), are typically used. In genetic evaluations, the age at which SC is measured usually corresponds to last part of pubertal development phase. But given that initiation of puberty in both sexes is controlled by the same neuroendocrine mechanisms, we argue that an earlier measurement, taken instead at the start of the pubertal development phase, is probably a better indicator of female precocity. To support the hypothesis, we fitted a multiple-trait animal model on AFC records and SC measurements taken at 300, 400, and 630 days of age and estimated heritabilities and genetic correlations by REML. Importantly, usually AFC data is afflicted by the problem that when breeding season starts most heifers are already cyclying (which is, of course, the desired condition) and thus the record poorly reflects precocity. To avoid the problem, in this study we used records collected from an Angus herd in which heifers receive an early natural first service at 375 days of age. Genetic correlation between AFC and SC300 was twice as large as the one

corresponding to SC400 (–0.478±0.13 vs –0.244±0.11) and three times larger than to SC630 (–0.478±0.13 vs –0.152±0.12), a result that supports our hypothesis. Heritabilities for SC300, SC400 and SC630 were 0.429±0.07, 0.704±0.07 and 0.576±0.08, respectively, and 0.371±0.05 for AFC. Our results have an important implication in the age at which SC, as an indirect trait for improving precocity, is typically measured in beef cattle breeding programs. Indeed, they indicate that measurements should be taken earlier.

Keywords: Scrotal Circumference; Age at first calving; Heifer; Angus; Puberty.

INTRODUCTION

Females are much more numerous in cow-calf operations and thus responsible for the largest proportion of costs and profits. Usually the condition for a cow to remain in the herd is weaning a calf per year (Carrillo, 1997; Mathews and Short, 2001). In addition, this calf should be as heavy as possible. In any given herd, heavier calves are produced if they born early in the calving season simply because older calves are on average heavier than younger ones (Funston et al., 2012; Lesmeister et al., 1973), regardless their individual genetic merit or the mothering ability of the cow.

Given that gestation length is very consistent, early calving is manageable by achieving early pregnancy in the previous mating season. In turn, early pregnancies are more probable in cows that had a larger puerperium (Perry and Cushman, 2013; Short et al., 1990; Yavas and Walton, 2000), which depend on how early the previous calving occurred and, eventually, on how early the cow, as a heifer, first calved. Indeed, heifers that calved early in their first parity tend to calve earlier throughout their productive life (Lesmeister et al., 1973), and remain longer in the herd (Cushman et al., 2013).

The reasoning is quite straight forward for herds with restricted breeding season: the earlier the first calving, the largest the subsequent puerperium, a more probable early pregnancy, and

an earlier subsequent calving. As the cycle repeats itself, the moment the heifer achieves her first pregnancy set her future productivity (Day and Nogueira, 2013). Furthermore, as heifers on average wean lighter calves than mature cows, early pregnancies within this category will somehow compensate by more days up to weaning (Cushman et al., 2013; Funston et al., 2012).

The *sine qua non* condition to obtain pregnancy for the first time is to achieve puberty before the start of the breeding season. Although puberty itself is a yes-or-no condition, time to the event (say, age at puberty) has a quantitative genetic basis and thus is suitable for standard genetic selection (Morris and Wilson, 1997). However, is difficult to measure age at puberty directly, as the gold standard requires repeated echography measurements or serum progesterone determinations taken in short periods of time (e.g. Honaramooz et al., 2004; Johnston et al., 2009). Consequently, traits such as age at first calving (AFC), calving date, days to calving and heifer pregnancy are usually found in the literature (cf. Cammack et al., 2009) as proxies, as they help to identify heifers that have calved early in the calving season. In addition, they usually show larger heritabilities than other fertility traits. In particular, estimates of heritability for AFC average around 0.2 – 0.3 in beef cattle (cf. Cammack et al., 2009).

On the other hand, given that growth and reproductive development share common metabolic pathways in both sexes (Evans and Rawlings, 2010), genetic improvement for early puberty in females could also be accomplished by selecting for precocity in males. The classical trait used in beef cattle is scrotal circumference (SC). Easy to measure, SC has an average estimated heritability of about 0.50, with estimates ranging between 0.30 and 0.78 (e.g. Martinez-Velazquez et al., 2003; Corbet et al., 2009), and has been positively correlated with live spermatozoa per ejaculation and sperm motility and concentration (Gipson et al., 1985; Knights et al., 1984). It has also been negatively correlated with age at puberty in males (Lunstra et al., 1988, 1978; Lunstra and Cundiff, 2003) and age at first calving in females, both in taurine (Toelle and Robison, 1985) and indicine breeds (Fortes et al., 2012).

Testicular growth in cattle is known to follow a sigmoid function: initially slow, it next shows a rapid growth phase, known as pubertal development (Rawlings et al., 2008), and finally it slows down to a stable *plateau* (Coulter et al., 1975). Scrotal circumference records used in genetic evaluations are usually taken as a single trait at yearling (BIF, 2010) or 18 mo in most Argentinean genetic evaluations (Foro Argentino de Genética Bovina, 2010, p57). Notice that the recommended age at

measurement corresponds to last part of pubertal development phase according to the review published by Rawlings et al. (2008). Now, studying sexual hormones secretion patterns Schams et al. (1981) concluded that the "initiation of puberty in both sexes is controlled by the same neuroendocrine mechanisms". This leads to the idea that a scrotal circumference measurement taken at the start of the testis growth exponential phase will probably be a better indicator of female puberty. Consequently, AFC should genetically correlate strongly to earlier measures of SC.

To gain support for the hypothesis, the objective of the present study was to estimate genetic correlations between age at first calving and scrotal circumference measured at different ages: 300, 400, and 630 days. Importantly, we fitted data collected from an Angus cattle herd where first service heifers are early bred by natural service, so age at first calving should better reflect precocity.

MATERIALS AND METHODS

Herd management

In this study we used records collected between 2004 and 2013 from "Flores chicas" Angus herd, located at Buenos Aires Province, Argentina (58° 28' 36.17" W; 38° 06' 45" S). The reproductive management is next described. Multiparous cows are inseminated with a FTAI protocol in November. Next, after five days of a second AI (now, watching heat), females are located with bulls until January. Calves are born between August and October and weaned at around six months of age. After weaning, heifers and young bulls are separated and raised on *Avena sativa* and *Lollium multiflorum* pastures.

This herd has been under selection for functionality, fertility and sexual precocity since the year 2002. Heifers are first mated by natural service and selected for fertility. Yearling females begin their first service with an average age of 375 days in September without hormonal supplement or any stimulation by contemporary bulls. Pregnancy diagnosis is performed 60 days after the end of the breeding season. Only pregnant heifers are retained in the herd. After a second pregnancy, primiparous cows receive de same management than multiparous cows.

Young males, in turn, are evaluated for seminal quality between 270 to 330 days of age. Specifically, a single sample of semen is obtained by electroejaculation and puberty is defined as a yes-or-no condition when the ejaculate presents a concentration of 50×10^6 sperms/ml and 10% of progressive linear motility, following Wolf et al. (1965) criterion. With this information, sires are selected for sexual precocity as assessed by the proportion of pubertal yearlings.

Measurements and data files build-up

The herd is intensively recorded for fertility traits. In particular, scrotal circumference (SC, cm) is measured in young bulls at different ages. For this study we grouped SC according to three well-defined age classes: scrotal circumference at 300 days (SC300, n = 2,476), with measurements taken between 250 and 349 days of age, scrotal circumference at 400 days (SC400, n = 2,120), including records between 370 and 430 days of age, and scrotal circumference at 630 days (SC630, n = 2,066), with records between 580 and 679 days of age. Most young bulls included in the data set were recorded for the three SC traits. In turn, age at first calving (AFC, n = 2,463) was computed for females using the data available by subtracting birth date to first calving date. Figure 1 summarizes the phenotypic data used in this study.

In every case, animals with unknown parents or with records beyond three standard deviations from the mean contemporary group were deleted. A pedigree was constructed using the information available from the herd for up to three generations. The entire pedigree file contained 26,302 individuals. The number of sires and dams of the 5,984 recorded animals was 47 and 3,051, respectively. Database elaboration was performed using Microsoft Access and R (R Core Team, 2017).

Statistical analysis

Data was analyzed by fitting a multiple-trait animal model (cf. Mrode and Thompson, 2005, ch. 5) and genetic parameters were estimated via a restricted maximum likelihood (REML, cf. Searle et al., 2006) algorithm, implemented through AIREMLF90 program from BLUPF90 package (Misztal et al., 2002). Details are next presented. The model equation in matrix notation is:

$$\begin{bmatrix} \boldsymbol{y_{AFC}} \\ \boldsymbol{y_{SC300}} \\ \boldsymbol{y_{SC400}} \\ \boldsymbol{y_{SC630}} \end{bmatrix} =$$

$$\begin{bmatrix} \boldsymbol{X_1} & 0 & 0 & 0 \\ 0 & \boldsymbol{X_2} & 0 & 0 \\ 0 & 0 & \boldsymbol{X_3} & 0 \\ 0 & 0 & 0 & \boldsymbol{X_4} \end{bmatrix} \begin{bmatrix} \boldsymbol{b_1} \\ \boldsymbol{b_2} \\ \boldsymbol{b_3} \\ \boldsymbol{b_4} \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z_1} & 0 & 0 & 0 \\ 0 & \boldsymbol{Z_2} & 0 & 0 \\ 0 & 0 & \boldsymbol{Z_3} & 0 \\ 0 & 0 & 0 & \boldsymbol{Z_4} \end{bmatrix} \begin{bmatrix} \boldsymbol{a_{AFC}} \\ \boldsymbol{a_{SC300}} \\ \boldsymbol{a_{SC400}} \\ \boldsymbol{a_{SC630}} \end{bmatrix} +$$

$$\begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \\ \boldsymbol{e_3} \\ \boldsymbol{e_4} \end{bmatrix},$$

where vector $\boldsymbol{y_{trait}}$ contains records for each trait, $\boldsymbol{b_i}$ (i maps to the set {AFC, SC300, SC400, SC630}) is the fixed effects vector for the corresponding trait, and includes contemporary group effects and age at measurement for SC traits and only CG effects for AFC, $\boldsymbol{a_{trait}}$ is the breeding value vector for each trait, and $\boldsymbol{e_i}$ represents model error vectors. Matrices $\boldsymbol{X_i}$ and $\boldsymbol{Z_i}$ relate records to fixed and random effects in the model, respectively.

The model is complemented by the following definition of the covariance structure for random effects:

$$\text{Cov} \begin{bmatrix} \boldsymbol{a_{AFC}} \\ \boldsymbol{a_{SC300}} \\ \boldsymbol{a_{SC400}} \\ \boldsymbol{a_{SC630}} \end{bmatrix} = \mathbf{G}_0 \otimes \boldsymbol{A},$$

where $\mathbf{G}_0$ is the additive genetic (co)variance matrix,

$$\mathbf{G}_0 = \begin{bmatrix} \sigma^2_{aAFC} & \sigma_{AFC,SC300} & \sigma_{AFC,SC400} & \sigma_{AFC,SC630} \\ & \sigma^2_{aSC300} & \sigma_{SC300,SC400} & \sigma_{SC300,SC630} \\ & & \sigma^2_{aSC400} & \sigma_{SC400,SC630} \\ sym & & & \sigma^2_{aSC630} \end{bmatrix},$$

A is the numerator relationship matrix and $\otimes$ is the Kronecker operator. In turn,

$$\text{Cov} \begin{bmatrix} \boldsymbol{e_1} \\ \boldsymbol{e_2} \\ \boldsymbol{e_3} \\ \boldsymbol{e_4} \end{bmatrix} = \begin{bmatrix} \sigma^2_{e1}\boldsymbol{I} & \mathbf{0} \\ \mathbf{0} & \mathbf{R}_0 \otimes \boldsymbol{I} \end{bmatrix},$$

where $\mathbf{R}_0$ is

$$\mathbf{R}_0 = \begin{bmatrix} \sigma^2_{e2} & \sigma_{e_2,e_3} & \sigma_{e_2,e_4} \\ & \sigma^2_{e3} & \sigma_{e_3,e_4} \\ sym & & \sigma^2_{e4} \end{bmatrix}.$$

Here, the diagonals entries correspond to scrotal circumferences error variances (σ^2_{ei}, i = 2, 3, 4) and the off-diagonals represent error covariances ($\sigma_{e_i e_j}$, i, j = 2, 3, 4, $i \neq j$) between SC measurements. Notice that this particular error covariance structure arises because AFC is only measured in females whereas SC traits are only measured in males and thus, by definition, there are no error covariances between them (Schaeffer et al., 1978). (A note on notation: the Kronecker product $\mathbf{R}_0 \otimes \boldsymbol{I}$ is a slight simplification that we believe helps to better understand the error covariance structure; formally, it will apply exactly only if every bull was measured for the three SC traits).

Reporting

Our main focus was on the estimation of the genetic correlations between female fertility traits (AFC and DFC) and scrotal circumferences at different ages. As usual, genetic correlation was computed as the standardized covariance (based on the estimates delivered by the AIREMLF90 program). For example, genetic correlation between AFC and SC300 was computed as:

$$r_{G(AFC,SC300)} = \frac{\hat{\sigma}_{AFC,SC300}}{(\hat{\sigma}^2_{aAFC} \times \hat{\sigma}^2_{aSC300})^{\frac{1}{2}}}.$$

In addition, we calculated heritabilities for every trait as the quotient between estimated additive genetic variance and phenotypic variance. Asymptotic standard errors for the estimates were also available from BLUPF90 package (Misztal et al., 2002). Finally, we obtained the expected progeny differences (EPDs) of the bulls for each trait, rank the latter by this criterion, and computed Spearman rank correlations between all pairs of traits.

RESULTS

Variance components estimates and standard errors are presented in Table 1. In turn, estimated heritabilities and correlations are displayed in Table 2. Heritability for age at first calving was large, with a low standard error (0.371±0.05). Among scrotal circumference traits, SC400 presented the greatest heritability (0.704±0.07), followed by SC630 (0.576±0.08) and SC300 (0.429±0.07). All SC heritability estimates showed low standard errors. Genetic correlations among SC traits were quite large, particularly between SC400 and SC630 (0.983±0.02). Phenotypic correlations were sensitively lower (e.g., phenotypic correlation between SC400 and SC630 was 0.726±0.05). Estimates also showed low standard errors.

Genetic correlations between AFC and SC were always negative, with magnitudes decreasing with the age at measurement from –0.478±0.13 (SC300) to –0.152±0.12 (SC630) (Table 2). Genetic correlations estimates showed greater standard errors than heritabilities. The period evaluated in this research covered from somewhere at the beginning of the pubertal development up to some months before the growth plateau is reached. The estimated linear regression coefficients for age at measurement were 0.052±0.002, 0.031±0.003, and 0.009±0.002 for SC300, SC400, and SC630, respectively. These values reflect the actual decreasing

of the testicle growth rate across ages at which measurements were taken.

Bulls EPDs rank correlations are presented in Table 3. Overall, results followed the same pattern than genetic correlations. Although this is somehow expected, as EPDs are functions of the estimated genetic parameters, bulls are evaluated with large amount of data, with records from both sons and daughters, and differences may arise. Importantly, rank correlation between AFC and SC300 was almost twice than the corresponding correlation to SC400 (–0.243 vs –0.109). In turn, rank correlation between AFC and SC630 was not significantly different from zero (–0.028). In these analyses, the hypothesis that is being tested is whether the observed correlation could not be distinguished from the case in which the two EPDs ranks are unrelated.

DISCUSSION

In this study we jointly estimated genetic parameters for age at first calving and scrotal circumference measured at different ages using a multiple-trait approach. The hypothesis we sustain is that larger EPDs for SC measured in early pubertal development, when testicles growth curve starts the exponential phase, will better reflect a genetically driven early starting of the hormonal signaling system that triggers reproductive function and, by analogue physiology, female precocity genetic merit. It is important to emphasize that we have not formally put this hypothesis under consideration, but instead followed a correlational inference approach to support the idea. Indeed, we were particularly interested in the genetic correlations between AFC and SC traits. If the hypothesis holds, it has an important implication in the age at which scrotal circumference is typically measured in beef cattle breeding programs.

As a proxy for female precocity, age at first calving is an economically relevant trait in beef cattle herds as it usually shows large heritability compared to other fertility traits (cf. Cammack et al., 2009). There are many reports of heritabilities for AFC in the literature. In comparison, the estimate in our study was similar to the one reported by Minick Bormann and Wilson (2010), but larger than other reports (Gutiérrez et al., 2002; Martinez-Velazquez et

al., 2003). Heritability is a population-specific parameter and estimates are expected to vary across studies. A more homogenous management, for instance, may induce lower environmental variances and thus relatively larger heritabilities (see a related discussion in Bourdon, 2000, ch. 9).

On the other hand, as it happens with other female fertility traits, AFC is challenging to deal with in breeding programs (Rust and Groeneveld, 2001). Usually, by the time the breeding season starts most of the heifers are already cycling and the trait actually do not reflect differences in precocity. But, of course, starting the breeding season when most of the heifers are cycling is the recommended practice (BIF, 2010, p.86) when the focus is not placed in the selection program for precocity. Furthermore, as first service heifers are generally more fertile than multiparous cows (Pursley et al., 1997), the category is more probably managed under FTAI programs. In that case, estrus synchronization protocols induce cyclicity in heifers that naturally will take longer to get pregnant (Anderson et al., 1996; Lucy et al., 2001; Short et al., 1976) and consequently the datum becomes inadequate. At this point, it is important to emphasize that the AFC data we fitted in this study was alleviated from these problems as it was collected from an Angus cattle herd phenotypically selected for female

sexual precocity, where heifers are early bred (at 375 days of age on average) by natural service without any hormonal stimulation.

Probably to avoid the issues just mentioned, the most common approach in genetic evaluations is to report EPDs for scrotal circumference as an indirect trait for female precocity. The trait is easy to record, usually shows large heritability and correlates negatively to AFC (e.g. Thompson et al., 1992; Pires et al., 2016). A seminal paper about the relationship between SC and precocity in beef cattle is the one produced by Lunstra et al. (1978). Analyzing USMARC data from several taurine breeds, they estimated that puberty, defined by 50×10^6 sperm count per millimeter with a minimum 10% of progressive motility, is reached on average when SC is about 27.9±0.2 cm. Importantly, as SC was the least variable among several factors studied they suggested this threshold can be used to assess puberty in males. In their 1978 paper, Angus bulls achieved this SC at about 300 days of age. Twenty five years later, Lunstra and Cundiff (2003) reported that at this age 100% of bulls studied were already pubertal, but the threshold remained in 27.9 cm. This implies that bulls that grow faster reach puberty earlier. Stated the other way around, large scrotal circumferences measured at a younger age are good indicators of male precocity.

In this study we estimated heritabilities for SC measured at 300, 400 and 630 days of ages fitting a multiple-trait animal model (cf. Mrode, 2005, ch. 5.). Estimates showed differences in magnitude across ages, being SC400 the trait that showed the largest heritability. These results were similar to the ones reported by Corbet et al. (2013), who described an increase in SC heritability from 6 to 18 mo in Brahman bulls, but not in tropical composite breed, and Gargantini et al. (2005), who found larger heritability for SC measured at 15 mo than at yearling in British crossbreeds. In contrast, Morris et al. (1992) estimated a steadily decreasing heritability when SC records were taken at 8, 11 and 13 mo of age.

In our study, genetic correlations estimates between AFC and SC measured at different ages were always negative, as has been consistently reported for these two traits in the literature since the paper by Toelle and Robinson (1985). The largest correlation was obtained when SC was measured at 300 days of age, a result that supports the hypothesis that earlier measurements better reflect precocity.

In addition, EPDs rank correlation among the bulls in this population followed the same pattern: correlations were greater for AFC and SC300 than for other SC traits. In contrast, the estimates we obtained differ from those reported by Morris et al. (1992). In

that study, authors estimated genetic correlations for SC measured at 8, 11, and 13 mo with age at first estrus (and other female fertility related measures) and reported an increasing genetic correlation with age at measurement. Notice that 11 and 13 mo measurements approximately relates to our SC300 and SC400 traits. Certainly, Morris et al. (1992) paper is an important reference as their objectives were similar to ours. Both analyses are different in several ways: the population, the data collected, the model fitted and the estimation procedure undertaken, and thus hard to compare. More research is certainly needed to better understand the relationships between male and female pubertal traits, and we believe it should be particularly focused on uncovering the mechanisms underlying the response.

In any case, we argue that the age at which SC is measured is important when the trait is used as an indirect way to select for female precocity. This idea can be supported in both taurine and indicine cattle breeds, although the specific time at which they attain sexual maturation may differ: indicine cattle breeds are in general less precocious than taurine ones (Lunstra and Cundiff, 2003; Rodrigues et al., 2002).

In this study we followed a quantitative approach to assess the relationship between male and female precocity traits. However, we must acknowledge that several authors have explored

the genetic architecture and, in general, biological processes regarding this relationship. Schams et al. (1981) concluded that the mechanisms underlying sexual development between sexes are basically the same. This idea was reinforced by studies based on molecular markers. For example, Fortes et al. (2012) performed a GWAS and found 32 SNPs in common between age at *corpum luteum* and age at 26 cm of SC, a trait related to puberty in Brahman bulls. Interesting enough, many of these SNPs are located in BTA 14. On the other hand, from an animal breeding perspective this understanding has not yet brought about any new way to better select for precocity: we still rely on selecting under the "black-box" approach (van der Werf, 2007).

At present, in Argentina none of the most important beef cattle breeds include female fertility traits in their genetic evaluation programs. So producers rely at best on 18 month scrotal circumference EPDs or, more frequently, they select based on phenotypic observations (for example, a common practice is to cull heifers that have a low reproductive tract scoring). Given the increasing use of computerized herd recording systems, some EPDs for at least one time-to-event trait will certainly be delivered in the near future. However, the way herds are typically managed puts a constraint in the amount and/or adequacy of data to be collected. Hence, if scrotal circumference would still be the

standard trait for improving precocity in beef cattle breeding programs, our results indicate that recording early measurements is the best practice to follow.

ACKNOWLEDGEMENTS

We especially thank to Ing. Agr. Alberto Areco, owner of Flores Chicas cow-calf operation for providing the data used in this study. MB and JJdI were supported by a doctoral scholarship from SCyT-UNLP and CONICET, respectively. This research was founded by CONICET and MINCyT (Argentina).

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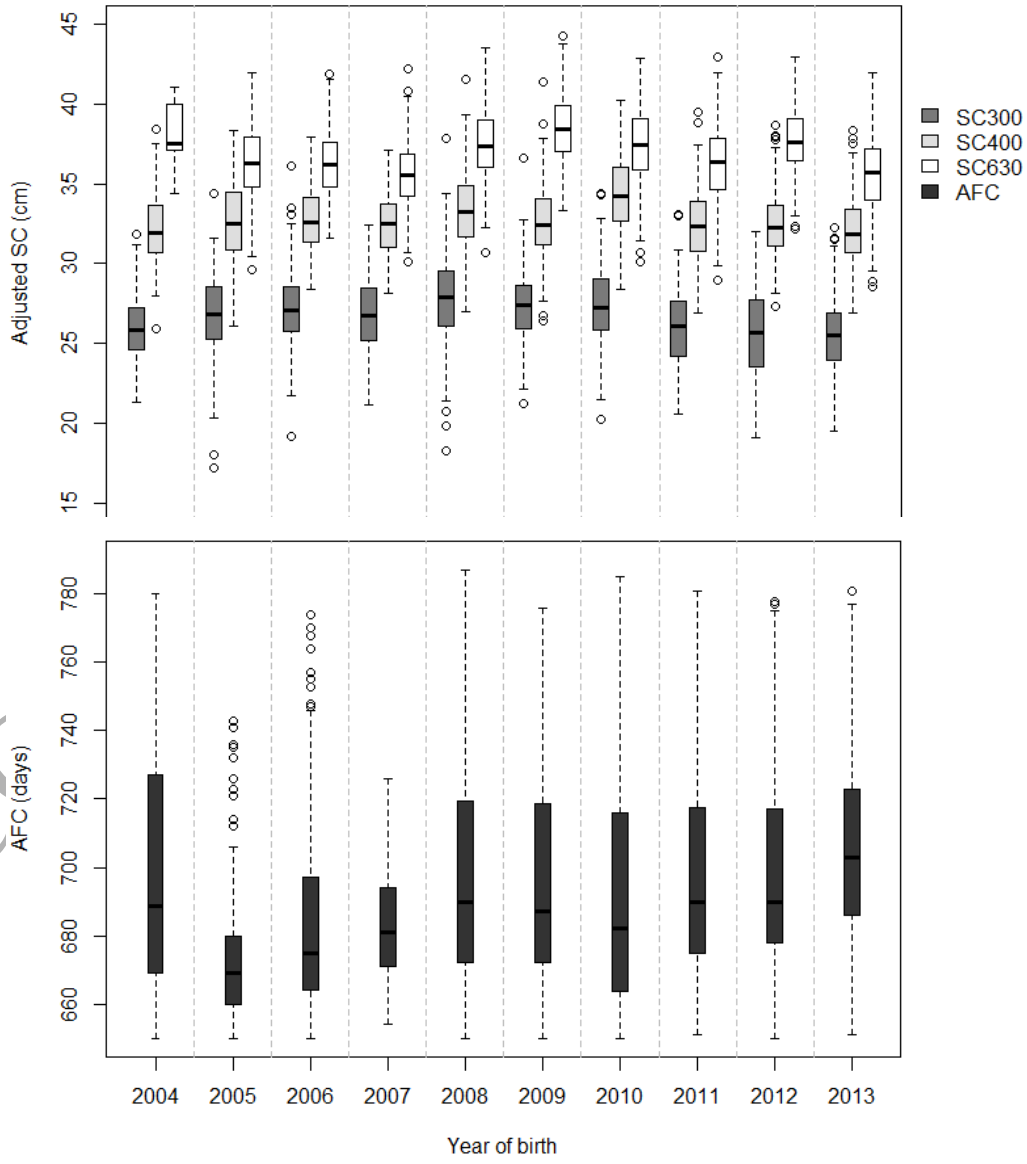
FIGURE CAPTIONS

Figure 1. Boxplots depicting age-adjusted scrotal circumference measurements (top) and age at first calving (bottom) across years of birth (contemporary groups).

FIGURE 1

Figure 1



TABLES

Table 1. Additive genetic variance (σ_a^2) and error variance (σ_e^2) for age to first calving (AFC) and scrotal circumference at 300, 400 and 630 days of age (SC300, SC400, SC630).

	$\sigma_a^2 \pm$ SE	$\sigma_e^2 \pm$ SE
AFC	316.53±46.64	536.15±41.623
SC300	1.994±0.342	2.649±0.288
SC400	3.416±0.423	1.436±0.337
SC630	2.560±0.384	1.886±0.318

Table 2. Heritabilities (diagonal), genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for age to first calving (AFC) and scrotal circumference at 300, 400 and 630 days of age (SC300, SC400, SC630).

	AFC	SC300	SC400	SC630
AFC	**0.371±0.05**	-0.478±0.13	-0.244±0.11	-0.152±0.12
SC300	-0.191±0.14	**0.429±0.07**	0.770±0.07	0.737±0.08
SC400	-0.125±0.13	0.524±0.09	**0.704±0.07**	0.983±0.02
SC630	-0.070±0.15	0.466±0.08	0.726±0.05	**0.576±0.08**

Table 3. Spearman rank correlation of bulls' expected progeny differences.

	AFC	CE300	CE400	CE630
AFC	---	-0.243	-0.109	-0.028
CE300	< 0.0001	---	0.418	0.291
CE400	< 0.0001	<0.0001	---	0.522
CE630	NS	<0.0001	<0.0001	---

Above diagonal: correlations; Below diagonal: p-values. NS: not significant at 0.05 level.