



Characterization of biological types of cattle: indicator traits of fertility in beef cows

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ABSTRACT:

Genetic diversity among breeds of cattle allows producers to select animals for specific environments or market conditions. Reproductive efficiency is a multi-component trait that is largely influenced by environmental influences such as health and nutritional status; however, there are clearly genetic components to reproductive efficiency, and breed differences in a number of indicator traits associated with fertility and cow productivity have been identified. Historical indicators of fertility include scrotal circumference, age at puberty, and postpartum interval. Both age at puberty and postpartum interval are laborious traits to collect in heifers and cows because they require many days of detection of behavioral estrus. In recent years, the addition of ultrasonography to management practices has allowed for the collection of female traits such as follicle diameter, antral follicle counts, and fetal age that are not as labor intensive. These additional diagnostic traits provide novel phenotypes for the identification of genetic markers of fertility and cow productivity, which would be the ultimate goal. Genetic markers of the number of follicles in the bovine ovary have the potential to identify heifers that will be highly productive cows. Furthermore, identifying and understanding the genes that control various reproductive traits and the response to stressors, such as temperature and nutrient availability, could improve production efficiency by improving management and breeding decisions in a wide range of production environments.

Key words: beef, biodiversity, germplasm preservation, reproductive efficiency

Introduction

Approximately 70% of the world's rural poor depend upon livestock as a component of their livelihoods (Pattison et al., 2007), and genetic diversity allows farmers to select stock or develop new breed characteristics in response to environmental changes, disease threats, changes in market conditions and changes of societal needs. However, an estimated 16% of unique breeds adapted to a wide range of environments have been lost over the last century (Hall and Ruane, 1993; Taberlet et al., 2008). Preservation of diverse germplasm and understanding of the unique genes involved in this diversity are critical for sustaining and improving production efficiency. Specifically, reproductive efficiency is a trait with a large impact on profitability (Melton, 1995; Renquist et al., 2006), because the primary reason that beef cows are removed from the production herd is failure to become pregnant, and a cow that fails to produce

enough calves to recoup her development costs is a financial loss.

A number of reproductive traits have been linked to fertility in cattle, including scrotal circumference (Willett and Ohms, 1957; Gargantini et al., 2005), age at puberty (Lesmeister et al., 1973; Ferrell, 1982; Martin et al., 1992; Gargantini et al., 2005), postpartum interval (Short et al., 1990), length of the estrous cycle immediately prior to breeding (Ahmad et al., 1997; Townson et al., 2002; Cushman et al., 2007), size of the ovulatory follicle (Perry et al., 2005; Robinson et al., 2005; MacNeil et al., 2006; Perry et al., 2007), the total number of follicles in the ovary (Maurer and Echterkamp, 1985; Cushman et al., 1999; Oliveira et al., 2002), and days to calving (Urioste et al., 2007a, b). The first three traits have a long history of evaluation as indicator traits of fertility in cattle. The latter four traits have a more recent history as possible indicators of fertility in cattle. The objectives of research in beef cattle reproductive physiology at the U.S. Meat Animal Research Center (USMARC) are: 1) to evaluate novel

indicators of fertility; and 2) to understand how breed differences in these indicator traits and the genes controlling these differences can be harnessed to improve reproductive efficiency and cow productivity.

Scrotal Circumference

The positive relationship between scrotal circumference and spermatozoa production in bulls has been studied for over fifty years (Willett and Ohms, 1957). The heritability of scrotal circumference was moderate in a number of studies, ranging from 0.26 to 0.78, and yearling scrotal circumference had favorable genetic correlations with daughter age at puberty and heifer pregnancy rate (Martin et al., 1992; Gargantini et al., 2005). Therefore, scrotal circumference may provide a means for measuring daughter reproductive capacity that is easier and less expensive to measure than many female traits that include daily detection of behavioral estrus.

Lunstra and Cundiff (2003) reported sire breed effects on age at puberty in bulls from Cycle V (Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli) of the Germplasm Evaluation Project. Brahman sired bulls were older at puberty than all other sire breeds except Boran. Yearling scrotal circumference was smaller in bulls from Brahman, Boran and Tuli sires. In Cycle VI, bulls sired by Wagyu or Swedish Red and White bulls had an older age at puberty than those sired by Hereford, Angus, Norwegian Red or Friesian bulls (Casas et al., 2007). There was no difference in testes size at puberty due to sire breed in either study, and the average scrotal circumference at puberty was 28 cm, suggesting that a threshold of testes size is required to attain puberty across all breeds of cattle.

Age at Puberty

Age at puberty for heifers and bulls was another moderately heritable reproductive trait with heritability ranging from 0.10 to 0.67 (Martin et al., 1992). Laster et al. (1979) reported favorable correlations among breed means for the age at puberty in heifers and the percent giving birth in the first 25 days of the calving season, and Werre and Brinks (1986) reported a favorable correlation between age at puberty and the estrous cycle of conception (1st, 2nd, 3rd,

etc.) during a 60 day breeding season. Due to the intense labor requirements to collect age at puberty in heifers, a five point reproductive tract score which assessed the development of the uterus and ovary by rectal palpation was proposed (Martin et al., 1992). Reproductive tract score had a heritability of 0.24 and was predictive of reproductive performance in yearling heifers, because heifers with higher reproductive tract scores (more mature) had higher pregnancy rates and calved earlier. Age at puberty was reported to have a favorable genetic correlation with postpartum interval in Charolais cows (Mialon et al., 2000), suggesting that there are common genes involved with the initiation of estrous cycles at puberty and resumption of estrous cycles in the postpartum interval.

Age at puberty has been reported throughout the history of the Germplasm Evaluation Project at USMARC. Thallman et al. (1999) reported sire breed effects in Cycle IV of the Germplasm Evaluation Project with Nellore sired heifers having an older age at puberty (405 days of age) than heifers from the other sire breeds (Piedmontese, Shorthorn, Charolais, Hereford, Galloway, Salers, and Longhorn). They suggested that the lower proportion of Nellore-sired heifers detected in estrus might be due to difficulty observing behavioral estrus. However, a recent study from Brazil using serum progesterone concentrations instead of behavioral estrus to identify first ovulation in Nellore heifers reported age at puberty at 510 – 540 days of age (Romano et al., 2007). Accounting for differences due to location, management practices and heterosis in the Germplasm Evaluation Project, these data support an advanced age at puberty in the Nellore breed. In Cycle V, heifers sired by Tuli, Boran, or Brahman bulls reached puberty at a later age than heifers sired by Piedmontese, Belgian Blue, Angus, or Hereford bulls (Freetly and Cundiff, 1997), in good agreement with the later age of puberty reported in the bulls by Lunstra and Cundiff (2003).

Postpartum Interval

Mialon et al. (Mialon et al., 2000) reported the heritability for postpartum interval to be between 0.12 and 0.38, respectively, depending upon whether behavioral estrus or serum progesterone concentrations were used to determine the initiation of estrous cycles;

however, the genetic correlation between the two phenotypes was high ($r_g = 0.98$). This would suggest that even if some cows had a silent first ovulation that was not associated with behavioral estrus, the temporal relationship of the first behavioral estrus to the time of first ovulation was strong.

A number of studies in the Germplasm Evaluation Project have reported sire breed effects on postpartum interval to estrus. Freetly and Cundiff (1998) reported that heifers sired by Brahman, Boran or Tuli bulls had longer postpartum intervals than heifers sired by Angus or Hereford bulls. The longer postpartum intervals in heifers from these sire breeds agreed well with the older age at puberty reported for these sire breeds (Freetly and Cundiff, 1997; Lunstra and Cundiff, 2003). Similarly, Roberts et al. (2005) reported longer postpartum intervals in Nellore sired cows from Cycle IV in agreement with the older age at puberty of heifers from this population reported by Thallman et al. (1999). In Cycle VII of the Germplasm Evaluation Project, Cushman et al. (2007) reported that Simmental and Gelbvieh sired cows had shorter postpartum intervals than Angus or Limousin sired cows and that Hereford, Charolais, and Red Angus sired cows had intermediate postpartum intervals. To date, age at puberty has not been reported in Cycle VII of the Germplasm Evaluation Project, but the general trend in Cycle IV and Cycle V suggests that breeds with an older age at puberty also had longer postpartum intervals as cows.

Estrous Cycle Length

Heritability for the length of the bovine estrous cycle has not been reported to our knowledge; most likely due to the intensity of labor required to collect the phenotype. However, breed differences in the length of the estrous cycle have been reported (Lamond et al., 1971; Cushman et al., 2007). Lamond et al. (1971) collected daily blood samples from Angus and Hereford cows to evaluate serum progesterone concentrations. They reported that the estrous cycle of the Hereford cows was 1.5 days shorter than that of the Angus cows, and that this was mainly due to a difference in the length of the follicular phase. In a larger study involving only detection of mating behavior, Cushman et al. (2007) found that the estrous cycle immediately

before natural breeding was one day shorter for cows from Hereford dams than cows from Angus dams in Cycle VII of the Germplasm Evaluation Project.

Landaeta-Hernandez et al. (2002) examined differences in the length of the follicular phase of Angus, Brahman and Senepol cows using prostaglandin F_{2α} to promote luteal regression and induce the follicular phase. The interval from treatment to the onset of estrus was shorter in Angus cows (31 ± 5 h) than in Brahman (53 ± 7 h) or Senepol (53 ± 4 h) cows; however, Alvarez et al. (2000) identified no differences in estrous cycle length or in the growth rate of the ovulatory follicle between these three breeds during a natural estrous cycle. Although there was no difference in the length of the estrous cycle, a greater ovulatory follicle diameter at an equivalent rate of growth would imply a longer follicular phase in the Brahman cows.

Because there is large variation among subjects (animal or human) in the dose of hormones required in assisted reproductive technologies, there may be genetic markers associated with the required dosage that would help to increase efficacy of treatments by tailoring hormone doses to the individual (Greb et al., 2005; Marrer and Dieterle, 2007; Moron et al., 2007). For example, in humans, a polymorphism in the FSH receptor has been associated with a decreased rate of follicle growth, resulting in a longer follicular phase of the menstrual cycle and decreased fertility. Breed differences for length of the follicular phase in cows suggest that similar pharmacogenetic approaches might be useful to improve assisted reproductive technologies.

Follicle Diameter

Ovulatory follicle diameter has increased in prominence as an indicator of fertility in cattle in the last several years. Unlike the previously discussed reproductive traits, follicle diameter does not require extensive detection of behavioral estrus, although it does require knowing that a cow is in estrus. Perry et al. (2005) reported a decreased pregnancy rate in cows induced to ovulate with gonadotropin releasing hormone when follicle diameter was less than 11 mm; however, they observed no influence of follicle diameter on pregnancy rates in spontaneously ovulating cows. In a subsequent study with heifers, Perry et al.

(2007) observed decreased pregnancy rates in both heifers induced to ovulate with gonadotropin releasing hormone and spontaneously ovulating heifers when follicle diameter was less than 10.7 mm or greater than 15.7 mm. The maximum pregnancy rate occurred when the diameter of the ovulatory follicle was 12.8 mm.

The heritability estimated for follicle diameter was 0.16 ± 0.03 (MacNeil et al., 2007), and breed effects on ovulatory follicle diameter were identified between Brahman, Senepol, and Angus cows (Alvarez et al., 2000). The maximum diameter of the dominant follicle from the first follicular wave was greater in Brahman and Senepol cows compared to Angus cows; however, the maximum diameter of the ovulatory follicle was greater in Brahman cows than Angus or Senepol cows. Combined with the results from Perry et al. (2007), this may suggest that there is an optimal follicle diameter, even in spontaneously ovulating cows, and that the Angus cows with the smaller average follicle diameter, as a breed, may come closer to the optimal follicle diameter. This would explain higher fertility rates in Angus than Brahman or Senepol cows.

Antral Follicle Count

Hereford heifers are born with approximately 100,000 follicles in their combined ovaries, and there was large variation among heifers in the number of follicles present at birth (Erickson, 1966). Heifers born with less than 100,000 primordial follicles (i.e. the ovarian reserve) had fewer growing secondary and antral follicles than heifers born with more than 100,000 primordial follicles, and the number of primordial follicles correlated positively with the number of growing follicles. Cushman et al. (1999) confirmed this positive correlation between the number of primordial follicles and the number of growing follicles in the bovine ovary, and reported that the number of primordial follicles and the number of antral follicles in one ovary was predictive of ovulatory response to exogenous gonadotropins in the contra-lateral ovary, suggesting a link between the ovarian reserve and reproductive capacity. When Brangus Ibage cows having a one year calving interval were compared to contemporary cows having a two year calving interval, the cows with the shorter calving intervals had more antral follicles detectable by ultrasonography than cows

with longer calving intervals during the fifteen days after weaning (Oliveira et al., 2002). While the investigators did not report postpartum intervals in this study, this would imply a shorter postpartum interval in the cows with shorter calving intervals and greater antral follicle counts. Furthermore, Maurer and Echternkamp (1985) reported that repeater breeder cows had fewer small antral follicles than contemporary controls. Taken together, these results suggested that antral follicle counts by ultrasound may be an indicator of fertility and of the size of the ovarian reserve in cows. Because depletion of the ovarian reserve is associated with reproductive senescence in mammalian females, antral follicle counts in heifers could be an indicator of life time productivity.

Alvarez et al. (2000) reported breed differences in the number of antral follicles detected by ultrasonography. Brahman cows had a greater number of antral follicles detectable by ultrasound than did Senepol cows, and Senepol cows had a greater number of antral follicles than Angus cows. These results suggest a difference in the ovarian reserve due to biological type that may be due, in part, to genetic differences.

Although performing antral follicle counts by ultrasonography on heifers and cows focuses on the ovary, it provides results very similar to the reproductive tract score when, along with the total number of follicles observed, the presence of corpora lutea and the presence of medium and large follicles are recorded. Reproductive tract score had a heritability of 0.28, and heifers with higher reproductive tract scores prior to the breeding season calved earlier in the subsequent calving season (Martin et al., 1992). Therefore, evaluating the reproductive tract and counting antral follicles in heifers prior to their first breeding season has the potential to identify highly fertile heifers that will produce large numbers of calves.

Calving Day

Calving day, defined as the number of days from the start of calving to the cow's calving day, provides a phenotype that is extremely easy to collect. Calving day provides a better estimate of fertility than calving interval, because in the US beef industry, a majority of producers use a defined breeding season with natural

service in a pasture setting and do not know the exact day of conception. Heritability estimates for first, second, and third calving day were 0.23 ± 0.03 , 0.21 ± 0.03 , and 0.19 ± 0.03 , respectively (Urioste et al., 2007a, b); however, to our knowledge, no study has reported breed effects of calving day. Calving day will be affected by where a cow is in her estrous cycle at the start of breeding and variation in the length of the estrous cycle. Therefore, first service conception, as diagnosed by calving day or by ultrasonography, may be the more important clinical endpoint than actual calving day.

There are issues with handling of data from cows that fail to produce a calf when working with this phenotype. There is no way to know whether this is simply a product of cows being anestrous, true first service conception failure or pregnancy loss between breeding and calving. The first two are difficult to resolve, but pregnancy diagnosis by ultrasonography approximately 35 days after the end of the breeding season allows for the estimation of fetal age in naturally bred cows (Hughes and Davies, 1989; Lamb et al., 2003). Therefore, conception day can be estimated and used for those cows that fail to calve (approximately 3 % between ultrasonography at day 70 of pregnancy and calving). From a management stand point, using ultrasonography to estimate day of conception and predict day of calving may have benefits for calf survival, because cows that are due to calve earliest can be moved closer to the barn and observed more closely at the start of the calving season. From a research standpoint, estimation of conception day by ultrasound in cattle breeds at USMARC provides another potential phenotype to include in models to analyze calving day data.

Conclusions

Historically, the Germplasm Evaluation Project at UMARC has identified differences among biological types of cattle in traits of economic importance to the producer. Breed differences in reproductive traits suggest that there are underlying genetic components to these traits, and in most cases genetic parameters have been calculated. Reproductive phenotyping is costly and laborious. Novel phenotypes that can be collected in large numbers with a minimum of effort continue to be needed. The use of ultrasonography to collect these phenotypes can be beneficial because relatively large

numbers of phenotypes can be collected in short time as compared to the extended periods required to detect behavioral estrus. The majority of the presented traits are being collected in one or more populations at USMARC that will be genotyped, potentially providing novel genetic markers for reproductive efficiency in cattle. However, awareness of scrotal circumference, age at puberty, postpartum interval, follicle number, and calving day measurements within the herd, allows producers to make better informed management decisions as well.

References

- Ahmad, N.; Townsend E. C.; Dailey, R.A. et al. Relationships of hormonal patterns and fertility to occurrence of two or three waves of ovarian follicles, before and after breeding, in beef cows and heifers. *Animal Reproduction Science*, v. 49, n.1, p.13-28, 1997.
- Alvarez, P.; Spicer, L.J.; Chase, C.C. Jr. et al. Ovarian and endocrine characteristics during an estrous cycle in Angus, Brahman, and Senepol cows in a subtropical environment. *Journal of Animal Science* v. 78, n. 5, p.1291-1302, 2000.
- Casas, E.; Lunstra, D.D.; Cundiff, L.V. et al. Growth and pubertal development of F1 bulls from Hereford, Angus, Norwegian Red, Swedish Red and White, Friesian, and Wagyu sires. *Journal of Animal Science* v. 85, n.11, p.2904-2909, 2007.
- Cushman, R.A.; Allan, M.F.; Thallman, R. M. et al. Characterization of biological types of cattle (Cycle VII): Influence of postpartum interval and estrous cycle length on fertility. *Journal of Animal Science* v. 85, n. 9, p.2156-2162, 2007.
- Cushman, R.A.; DeSouza, J.C.; Hedgpeth, V.S. et al. Superovulatory response of one ovary is related to the micro- and macroscopic population of follicles in the contralateral ovary of the cow. *Biology of Reproduction* v. 60, n. 2, p. 349-354, 1999.
- Erickson, B.H. Development and senescence of the postnatal bovine ovary. *Journal of Animal Science* v. 25, n. 3, p. 800-805, 1966.
- Ferrell, C.L. Effects of postweaning rate of gain on onset of puberty and productive performance of heifers of different breeds. *Journal of Animal Science* v. 55, n. 6, p. 1272-1283, 1982.
- Freetly, H.C.; and Cundiff, L.V. Postweaning growth and reproduction characteristics of heifers sired by bulls of seven breeds and raised on different levels of nutrition. *Journal of Animal Science* v. 75, n. 11, p. 2841-2851, 1997.
- Freetly, H.C.; and Cundiff, L.V. Reproductive performance, calf growth, and milk production of first-calf heifers sired by seven breeds and raised on different levels of nutrition. *Journal of Animal Science* v.76, n. , p. 1513-1522, 1998.
- Gargantini, G.; Cundiff, L.V.; Lunstra, D.D. et al. Genetic relationships between male and female reproductive traits in beef cattle. *The Professional Animal Scientist* v. 21, p. 195 - 199, 2005.
- Greb, R.R.; Behre, H.M.; and Simoni, M. Pharmacogenetics in ovarian stimulation - current concepts and future options. *Reproductive Biomedicine Online* v. 11, n. 5, p. 589-600, 2005.

- Hall, S.J.G.; and Ruane, J. Livestock breeds and their conservation: A global overview. *Conservation Biology* v. 7, n. 4, p. 815-825, 1993.
- Hughes, E.A.; and Davies, D.A. Practical uses of ultrasound in early pregnancy in cattle. *Veterinary Record* v. 124, n. , p. 456-458, 1989.
- Lamb, G.C.; Dahlen, C.R. and Brown, D.R. Reproductive ultrasonography for monitoring ovarian structure development, fetal development, embryo survival, and twins in beef cows. *The Professional Animal Scientist* v. 19, p. 135 - 143, 2003.
- Lamond, D.R., D. M. Henricks, D.M.; Hill, J.R. Jr. et al. Breed differences in plasma progesterone concentration in the bovine during proestrus. *Biology of Reproduction* v. 5, n. 3, p. 258-261, 1971.
- Landaeta-Hernandez, A.J.; Yelich, J.V.; Lemaster, J.W. et al. Environmental, genetic and social factors affecting the expression of estrus in beef cows. *Theriogenology* v. 57, n. 4, p. 1357-1370, 2002.
- Laster, D.B.; Smith, G.M.; Cundiff, L.V. et al. Characterization of biological types of cattle (Cycle II) . II. Postweaning growth and puberty of heifers. *Journal of Animal Science* v. 48, n. 3, p. 500-508, 1979.
- Lesmeister, J. L.; Burfening, P.J.; and Blackwell, R.L. Date of first calving in beef cows and subsequent calf production. *Journal of Animal Science* v. 73, n. 1, p. 1-6, 1973.
- Lunstra, D.D.; and Cundiff, L.V. Growth and pubertal development in Brahman-, Boran-, Tuli-, Belgian Blue-, Hereford- and Angus-sired F1 bulls. *Journal of Animal Science* v. 81, n. 6, p. 1414-1426, 2003.
- MacNeil, M.D.; Geary, T.W.; Perry, G.A. et al. Genetic partitioning of variation in ovulatory follicle size and probability of pregnancy in beef cattle. *Journal of Animal Science* v. 84, n. 7, p. 1646-1650, 2006.
- Marrer, E.; and Dieterle, F. Promises of biomarkers in drug development—a reality check. *Chemistry of Biological Drug Design* v. 69, n. 6, p. 381-394, 2007.
- Martin, L.C.; Brinks, J.S.; Bourdon, R.M. et al. 1992. Genetic effects on beef heifer puberty and subsequent reproduction. *Journal of Animal Science* v. 70, n. 12, p. 4006-4017, 1992.
- Maurer, R.R.; and Echterkamp, S.E. Repeat-breeder females in beef cattle: Influences and causes. *Journal of Animal Science* v. 61, n. , p. 624 - 636, 1985.
- Melton, B.F. Conception to consumption: The economics of genetic improvement. In: *The Proceedings of the Beef Improvement Federation 27th Research Symposium and Annual Meeting*, Sheridan, Wyoming: 40-47, 1995.
- Mialon, M.M.; Renand, G.; Krauss, D. et al. Genetic variability of the length of postpartum anoestrus in Charolais cows and its relationship with age at puberty. *Genetics Selection and Evolution* v. 32, n. 4, p. 403-414, 2000.
- Moron, F. J.; Galan, J.J. and Ruiz, A. Controlled ovarian hyperstimulation pharmacogenetics: A simplified model to genetically dissect estrogen-related diseases. *Pharmacogenomics* v. 8, n.7 . p. 775-785, 2007.
- Oliveira, J.F.; Neves, J.P.; Moraes, J.C. et al. Follicular development and steroid concentrations in cows with different levels of fertility raised under nutritional stress. *Animal Reproduction Science* v. 73, n. 1, p.1-10, 2002.
- Pattison, J.; Drucker, A.G.; and Anderson, S. The cost of conserving livestock diversity? Incentive measures and conservation options for maintaining indigenous Pelon pigs in Yucatan, Mexico. *Tropical Animal Health and Production* v. 39, n. 5, p. 339-353, 2007.
- Perry, G.A.; Smith, M.F.; Lucy, M.C. et al. Relationship between follicle size at insemination and pregnancy success. *Proceedings of the National Academy of Sciences, USA* v. 102, n. 14, p. 5268-5273, 2005.
- Perry, G.A.; Smith, M.F.; Roberts, A.J. et al. Relationship between size of the ovulatory follicle and pregnancy success in beef heifers. *Journal of Animal Science* v. 85, n. 3, p. 684-689, 2007.
- Renquist, B.J.; Oltjen, J.W.; Sainz, R.D. et al. Effects of age on body condition and production parameters of multiparous beef cows. *Journal of Animal Science* v. 84, n. 7, p. 1890-1895, 2006.
- Roberts, A.J.; Klindt, J.; and Jenkins, T.G. Effects of varying energy intake and sire breed on duration of postpartum anestrus, Insulin Like Growth Factor-I, and Growth Hormone in mature crossbred cows. *Journal of Animal Science* v. 83, n. 7, p. 1705-1714, 2005.
- Robinson, R.S.; Hammond, A.J.; Hunter, M.G. et al. The induction of a delayed post-ovulatory progesterone rise in dairy cows: A novel model. *Domestic Animal Endocrinology* v. 28, n. 3, p. 285-295, 2005.
- Romano, M.A.; Barnabe, V.H.; Kastelic, J.P. et al. Follicular dynamics in heifers during pre-pubertal and pubertal period kept under two levels of dietary energy intake. *Reproduction in Domestic Animals* v. 42, n. 6, p. 616-622, 2007.
- Short, R.E.; Bellows, R.A.; Staigmiller, R.B. et al. Physiological mechanisms controlling anestrus and infertility in postpartum beef cattle. *Journal of Animal Science* v. 68, n. 3, p. 799-816, 1990.
- Taberlet, P.; Valentini, A.; Rezaei, H.R. et al. Are cattle, sheep, and goats endangered species? *Molecular Ecology* v. 17, n. 1, p. 275-284, 2008.
- Thallman, R.M.; Cundiff, L.V.; K. E. Gregory, K.E. et al. Germplasm evaluation in beef cattle—Cycle IV: Postweaning growth and puberty of heifers. *Journal of Animal Science* v.77, n. 10, p. 2651-2659, 1999.
- Townson, D.H.; Tsang, P.C.W.; Butler, W.R. et al. Relationship of fertility to ovarian follicular waves before breeding in dairy cows. *Journal of Animal Science* v. 80, n. 4, p. 1053-1058, 2002.
- Urioste, J.I.; Misztal, I.; and Bertrand, J.K. 2007a. Fertility traits in spring-calving Aberdeen Angus cattle. 1. Model development and genetic parameters. *Journal of Animal Science* v. 85, n. 11, p. 2854-2860, 2007a.
- Urioste, J.I.; Misztal, I.; and Bertrand, J.K. 2007b. Fertility traits in spring-calving Aberdeen Angus cattle. 2. Model comparison. *Journal of Animal Science* v. 85, n. 11, p. 2861-2865, 2007b.
- Werre, J.F.; and Brinks, J.S. Relationship of age at puberty with growth and subsequent productivity in beef heifers. *Proceedings of the Western Section of the American Society of Animal Science* v. 37, p. 300, 1986.
- Willett, E.L.; and Ohms, J.I. Measurement of testicular size and its relation to production of spermatozoa by bulls. *Journal of Dairy Science* v. 40, n. 12, p. 1559-1569, 1957.