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Genetic partitioning of variation in ovulatory follicle size and probability of pregnancy in beef cattle[1]

M. D. MacNeil,[2]* T. W. Geary,* G. A. Perry,[3] A. J. Roberts,* and L. J. Alexander*

*USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT 59301

ABSTRACT: The objectives of this research were to partition variation in ovulatory follicle size into genetic and nongenetic components and to assess the utility of ovulatory follicle size as an indicator trait associated with reproductive success in beef cattle. Data were collected during the years 2002 to 2005 from 780 beef females that ranged in age from 1 to 12 yr (mean of 2.4 observations per female). Data were analyzed with a multiple trait Gibbs sampler for animal models to make Bayesian inferences from flat priors. A chain of 500,000 Gibbs samples was thinned to every 200th sample to produce a posterior distribution composed of 2,500 samples. Heritability estimates (posterior mean ± SD) were 0.16 ± 0.03 for follicle size and 0.07 ± 0.02 and 0.02 ± 0.01 for pregnancy rate as a trait of the female and service sire, respectively. Posterior means of genetic correlations were all <0.10, with 0.00 contained within the respective 90% probability density posterior intervals. Results indicate that whereas follicle size is of greater heritability than pregnancy rate, its usefulness to improve reproductive rate is greatest as an ancillary phenotype in multiple trait selection.

Key words: cattle, fertility, follicle, ovulation

INTRODUCTION

Successful reproduction is the single largest determinant of biological and economical efficiencies of cow-calf production (Dickerson, 1970). Failure to establish pregnancy has a major effect on pounds of calf produced per cow (Wiltbank et al., 1961). Genetic improvement in reproductive efficiency through selection has been slow because of the all or none nature of many reproductive traits, their low heritability, and occurrence relatively late in life (Morris et al., 1993). In general, quantitative traits associated with puberty are moderately heritable (MacNeil et al., 1984; Morris et al., 1992b) and positively correlated (Brinks et al., 1978; Morris et al., 1992a), and selection based on these traits may increase lifetime pregnancy rate (Morris and Cullen, 1994; Morris et al., 2000). Qualitative traits, like pregnancy rates of yearling heifers and 2-yr-old cows, appear to be less heritable (Koots et al., 1994; Snelling et al., 1995; Doyle et al., 2000). However, size of the ovulatory follicle is a quantitative trait that has recently been phenotypically associated with pregnancy rate (Perry et al., 2005). Thus, objectives of this research were to partition phenotypic variation of follicle size into genetic and nongenetic components and to assess genetic and environmental covariation between follicle size and the probability of successfully establishing pregnancy.

MATERIALS AND METHODS

A stable composite population composed of 50% Red Angus, 25% Charolais, and 25% Tarentaise germplasm (CGC) was used in this research. Currently, all animals in CGC result from 4 or more generations of inter se mating. Pedigree information traces the ancestry of each individual in the population (n = 7,105) to the founding Red Angus dams and Charolais and Tarentaise sires. This composite population was previously characterized over an 11-yr period under management

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typical of current practices in commercial beef production on the Northern Great Plains and found to achieve relatively high rates of reproductive success (Newman et al., 1993). This germplasm is also well accepted by commercial producers in the region (Roybal, 1998).

Cows were stratified by age and assigned at random to 1 of 2 protocols for providing supplemental feed during winter and coincident with late gestation. As is typical in the region, supplemental feed was provided as a pellet or cake beginning about December 1, or earlier if the weather, grazing conditions, or both warranted. One group of control-fed (**CF**) cows was provided 1.8 kg·head^{-1}·d^{-1} of a 20% protein cake as supplement to native forages. The second group of restricted-fed (**RF**) cows was provided 1.1 kg·head^{-1}·d^{-1} of the same feedstuff. Hay was fed when the snow cover precluded grazing. The RF group was fed 80% of the hay given the CF group. The amount of supplemental feed provided varied between years because of variations in range conditions and forage quality. Cows were maintained as a single herd during the last 30 d of gestation and from calving (late March through mid May) until approximately 8 mo postpartum (2 mo after weaning).

After weaning at approximately 6 mo of age, heifer calves were randomly assigned to 1 of 2 development systems. Like CF and RF, these development systems differed in the amount of energy provided from harvested feeds. Calves assigned to the conventional development system (CF) were fed to appetite diets based on NRC (1996) to meet requirements for heifer calves to gain 0.5 kg/d. Calves assigned to receive the reduced level of harvested feed inputs (RF) were provided the same diet at the rate of 80% per unit BW of CF calves.

Data used in this study were collected from 2002 to 2005, and the females (n = 780) ranged in age from 1 to 12 yr. Synchronization of estrus, induction of ovulation, and artificial insemination were used to facilitate data collection. Blood samples were collected from each female on d −16 and −9 (d 0 = day of insemination). Blood was allowed to clot for 1 h at room temperature, stored at 4°C for 24 h, and centrifuged at 1,200 × *g* for 30 min. Serum was harvested and stored at −20°C until assayed for progesterone by RIA (Diagnostic Products Corp., Los Angeles, CA; Bellows et al., 1991). Intra- and interassay CV were 6 and 9%, respectively. Females were considered anestrus if the serum concentration of progesterone was <1 ng/mL in each sample and considered to be exhibiting luteal activity if the serum concentration of progesterone was ≥1 ng/mL in either sample (Wheeler et al., 1982).

Ovaries of all females were examined by transrectal ultrasonography using a 7.5-MHz linear probe and Aloka 500V ultrasound (Aloka Co. Ltd., Tokyo, Japan) to characterize follicular development and measure diameter of the ovulatory follicle at the time of insemination. Pregnancy status was determined by transrectal ultrasonography approximately 28 d after insemination, with confirmation of a fetal heartbeat. Forty females had a missing observation for either follicle size

or the corresponding assessment of pregnancy status. Follicle sizes were measured in 760 females, and on average 2.3 measurements were collected per female over the course of the study. Similarly, pregnancy establishment was determined for 760 females, and there were on average 2.4 determinations per female.

Preliminary analyses of these data were conducted using PROC MIXED of SAS (version 9.1, SAS Inst. Inc., Cary, NC) to assess the importance of year, age of female (1, 2, or 3+ yr), nutritional paradigm, protocol used for synchronization, and induction of estrus [Natural occurring estrus, CO-Synch (Geary and Whittier, 1998), controlled internal drug-releasing (**CIDR**) device, CO-Synch + CIDR, CO-Synch + CIDR + estradiol cypionate 24 h after PG, CO-Synch + CIDR + Flunixin Meglumine (1.1 mg/kg of BW, i.m.) approximately 13 d after AI, and CO-Synch + CIDR + estradiol cypionate 24 h after PGF + Flunixin Meglumine (1.1 mg/kg of BW, i.m.) approximately 13 d after AI], cycling or anestrus, whether ovulation was induced, and all 2- and 3-factor interactions among these effects.

Based on results from these analyses, macro effects of the year-age-nutritional paradigm and of the estrous management protocol-cycling status-ovulation type were formed in a manner analogous to the formation of contemporary groups. These macro effects account for the important interactions affecting follicle size or establishment of pregnancy and simplify subsequent analysis. Estimable contrasts of the protocols used for synchronization and induction of estrus have been reported elsewhere (Geary et al., 2005; Larson et al., 2005). Random effects of the female and service sire (pregnancy establishment only) were simultaneously considered in these analyses.

Final data analyses were conducted using a multiple-trait Gibbs sampler for animal models (VanTassell and Van Vleck, 1996). Linear models used for both traits included the macro effects described previously, an additive direct effect of the female, an independent permanent environmental effect for repeated observations on the female and for pregnancy establishment only, and an additive direct effect of service sire. Thus, the multiple-trait model expressed in matrix notation was

$$y = X\beta + Zu + Z_a a + Wc + e,$$

where y is a vector of phenotypes, β is the vector of systematic macro-effects, u is a vector of animal effects associated with females, a is a second vector of animal effects associated with service sires and affecting only pregnancy rate, c is a vector of permanent environmental effects for repeated records of the phenotypes of each female, e is a vector of temporary environmental effects on the phenotypes, and X, Z, Z_a, and W are incidence matrices of appropriate dimensions associating the effects with the phenotypes. Assumed (co)variances of u, a, c, and e are as follows:

Table 1. Estimates of posterior means of the variance (Var) and covariance (Cov) components for follicle size (FS, mm) and pregnancy rate (PR, 0 = not pregnant and 1 = pregnant) due to females (f) and service sires (s)

Component	Additive genetic	Permanent environmental	Temporary environmental
Var (FS)	0.7765	0.0513	3.9757
Var (PR_f)	0.0171	0.0046	0.2096
Var (PR_s)	0.0057		
Cov (FS, PR_f)	0.0095	0.0048	0.0892
Cov (FS, PR_s)	0.0091		
Cov (PR_f, PR_s)	0.0079		

$$
\begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{a}_1 \\ \mathbf{c}_1 \\ \mathbf{c}_2 \\ \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{u1}^2 & \mathbf{A}\sigma_{u1u2} & \mathbf{A}\sigma_{u1a1} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ & \mathbf{A}\sigma_{u2}^2 & \mathbf{A}\sigma_{u2a1} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ & & \mathbf{A}\sigma_{a1}^2 & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ & & & \mathbf{I}\sigma_{c1}^2 & \mathbf{I}\sigma_{c1c2} & \mathbf{0} & \mathbf{0} \\ & & & & \mathbf{I}\sigma_{c2}^2 & \mathbf{0} & \mathbf{0} \\ & & & & & \mathbf{I}\sigma_{e1}^2 & \mathbf{I}\sigma_{e1e2} \\ & & & & & & \mathbf{I}\sigma_{e2}^2 \end{bmatrix},
$$

where A is the additive relationship matrix among all animals in the pedigree file (n = 7,105).

Initial Gibbs samples from flat prior distributions were obtained for a chain of 30,000, saving every 30th sample round, and without discarding earlier rounds for burn-in. The Gibbsit program of Raftery and Lewis (1995) was used to evaluate the length of the burn-in period and the thinning interval needed to obtain stationary chains of independent samples and also to estimate the total number of Gibbs samples required for the cumulative distribution function of the 0.025 quantile to be estimated within ± 0.0125 with a probability of 0.95 for all genetic parameters. The recommended burn-in periods were ≤12,960 rounds. The thinning interval recommended by Gibbsit was consistently ≤120 rounds. However, it has been shown that the thinning intervals recommended by Gibbsit are not sufficiently large (Van Tassell and Van Vleck, 1996). Thus, final analyses were conducted using a conservative burn-in of 15,000 rounds, 500,000 rounds of post burn-in Gibbs sampling, and a thinning interval of 200 rounds. In summarizing the Gibbs samples, results are reported as means ± SD of the posterior Gibbs samples.

RESULTS AND DISCUSSION

Follicle size and pregnancy rate to a single service averaged 13.4 mm and 0.55, respectively. Mean estimates of variances and covariances for components of follicle size and pregnancy rate from the posterior distribution are shown in Table 1. No similar partitioning of phenotypic variation in follicle size was found in the literature. Based on these estimates, phenotypic vari-
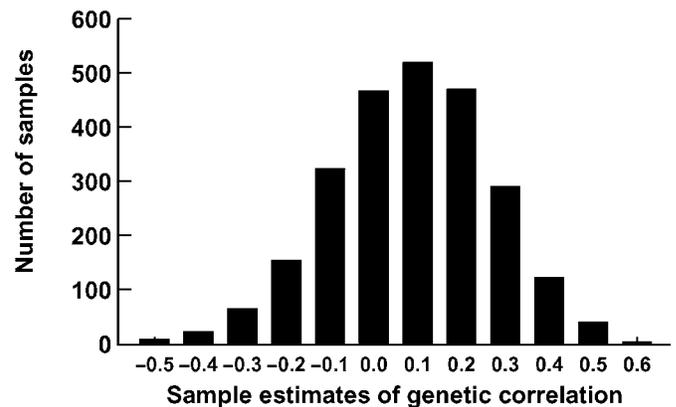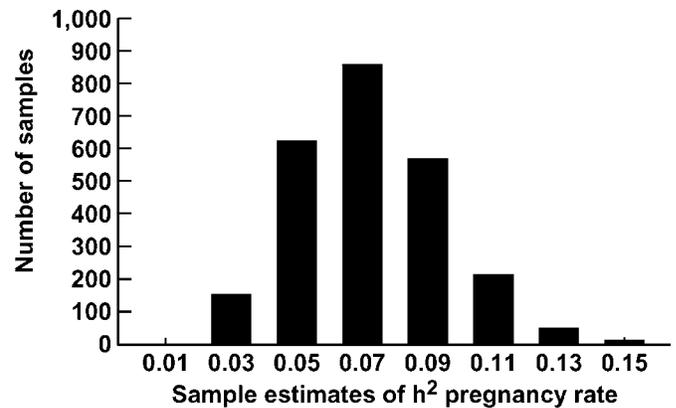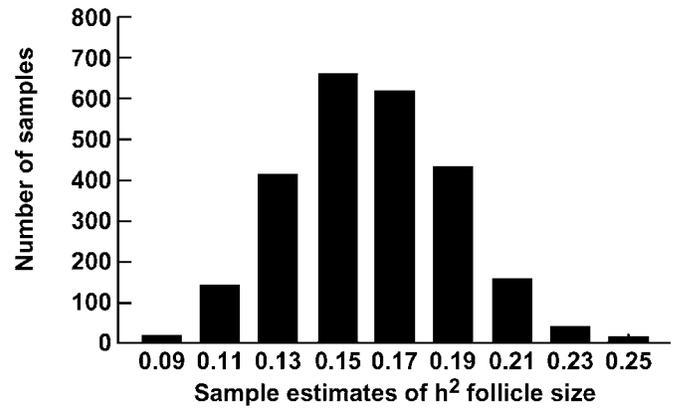

Figure 1. Marginal posterior distributions of Gibbs sample estimates of heritability for follicle size and the probability of pregnancy establishment as a trait of the female and their genetic correlation.

ances of follicle size and pregnancy rate were 4.80 mm^2 and 0.24, respectively. The posterior distributions of estimates of heritability for follicle size and pregnancy rate as a trait of the female and their genetic correlation are shown in Figure 1. Posterior distributions of all genetic parameters were approximately symmetric and had practically coincident means, medians, and modes. Thus, mean estimates are presented here. The mean estimate of heritability of follicle size was 0.16 ± 0.03. Mean estimates of heritability of pregnancy rate as a trait of the female and service sire were 0.07 ± 0.02 and 0.02 ± 0.01, respectively. The mean of the posterior

distribution of the genetic correlation between follicle size and pregnancy rate as a trait of the female was 0.08 ± 0.18. Genetic correlations of follicle size and pregnancy rate as a trait of the female with pregnancy rate as a trait of the service sire were 0.08 ± 0.28 and 0.07 ± 0.30, respectively. Interpretation of the (co)variances associated with service sire should be qualified in that only those sires producing sufficient qualities of semen with >30% postthaw progressive motility of normal spermatozoa were used for AI. Based on these estimates, selection for follicle size would produce essentially no correlated response in pregnancy rate, being, on average, only 12% as efficient as direct selection for pregnancy rate. However, joint use of follicle size and pregnancy rate in a selection index context would, on average, be 19% more efficient in improving pregnancy rate than selection for pregnancy rate alone.

Fractions of the variances of follicle size and pregnancy rate attributable to repeated observations were <2% with 0.00 contained within the respective 90% probability density posterior intervals. The posterior mean estimate of the correlation between repeated observations of follicle size and pregnancy rate was 0.31 ± 0.44. Posterior mean estimates of repeatability of follicle size and pregnancy rate were 0.17 ± 0.03 and 0.09 ± 0.02, respectively.

Despite being a continuous trait that can be accurately measured using synchronization to time estrus/ovulation and ultrasonography, the vast majority of variation in follicle size was attributed to temporary environmental effects with $83 \pm 3\%$ of the phenotypic variance unaccounted for. Likewise, other phenotypes associated with successful reproduction also have low heritability and substantial temporary environmental components of variance (Koots et al., 1994). Similarly, in the present data, $88 \pm 3\%$ of the phenotypic variance in pregnancy rate was due to temporary environmental effects. The posterior mean correlation among temporary environmental effects on pregnancy rate and follicle size was 0.10 ± 0.03.

Successful establishment of pregnancy requires ovulation of a viable oocyte, adequate progesterone production by the corpus luteum, and an adequate uterine environment. Data presented by Domínguez (1995) indicate an inverse relationship between follicle size and proportion of normal oocytes in cows slaughtered at abattoirs in Northeastern Mexico. In contrast, follicle size has been positively associated with serum progesterone concentration (Vasconcelos et al., 2001; Perry et al., 2005). These conflicting effects of follicle size on factors that influence successful establishment of pregnancy may partially explain the weak positive association between follicle size and pregnancy rate observed in the current study. Also, the relationship between follicle size and pregnancy rate may be nonlinear (Perry et al., 2005). However, comparison of the coefficients of determination from the logistical regression analyses of Perry et al. (2005) with the phenotypic correlation

from the present analysis (0.10 ± 0.02) suggests the linear statistics explain most of the covariation.

IMPLICATIONS

In a population of beef cattle with a relatively high rate of reproductive success overall, heritability of follicle size was low. Despite a finding of significant logistic regression of pregnancy rate on follicle size, genetic and nongenetic associations of follicle size with pregnancy rate found here were weak. However, follicle size may be of some benefit as an ancillary phenotype for use in multiple trait selection to improve reproductive rate.

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