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THRESHOLD SIRE MODELS FOR ESTIMATING GENETIC PARAMETERS FOR STAYABILITY IN BEEF COWS

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Abstract

Stayability is the ability of a beef cow to remain in production to a specified age. In this study, the interest was in determining the genetic relationship between stayability to an early age with stayability to a later age. A nested threshold sire model for stayability was used here to estimate the genetic relationship between stayability to different ages. Genetic correlations were estimated among six different stayability traits using records from 1,868 Hereford cows. The model included period and year of birth as fixed factors and sire as a random factor. The numerator relationship matrix accounted for all known relationships among sires. Penalized quasi-likelihood estimates were obtained using a probit link function. Estimates of heritability on the original scale were small and ranged from 0.09 to 0.17. Estimates of genetic correlations were low to moderate and variable in sign. Results indicate that selection for stayability to an early age would have a limited impact on stayability to later ages.

1. Introduction

The longevity of a beef cow is a complex trait that reflects performance over her total herd life and is determined principally by her fertility, maternal ability, and health (ability to avoid involuntary culling). For livestock production, longevity is a trait that affects overall profitability

One problem with working with longevity is that longevity can only be measured after the cows have been culled or have died (actual length of life). An alternative measure of herd life is the use of stayability traits. Stayability is defined as the probability of surviving to a specific age, given the opportunity to reach that age (Hudson and Van Vleck, 1981). Stayability can be measured at any time in the cow's life, but such a measure contains less information than traits that measure the entire life span of the animal (Hudson and Van Vleck, 1981). Cows are evaluated in opportunity groups where the score of an animal with the opportunity to survive to a given age is recorded as one (1) if she survives and zero (0) if she fails to survive to the given age (Famula, 1981). Foulley and Gianola (1984) discussed the possibility of analyzing bivariate "all or none" responses.

Analyses assuming a threshold model for discrete traits such as stayability and fertility in beef cattle have not been common. Previous studies have generally used threshold sire models for single trait analyses (Snelling *et al.*, 1994; Snelling *et al.*, 1995; Vega, 1999). Still, knowledge of genetic relationships among stayability traits is important for designing economically optimum recording and selection programs.

The objectives of this study were to estimate heritability and to determine the genetic correlations between a stayability trait measured at an early age and stayability traits measured at older ages.

2. Materials and Methods

2.1 The Project

Data were from the Nebraska Agricultural Experiment Station project 40-002 entitled "Effect of selection for weaning weight, yearling weight, and muscling in beef cattle" in cooperation with the Roman L. Hruska U.S. Meat Animal Research Center ARS, USDA (USMARC) (Koch *et al.*, 1974a, b; Koch *et al.*, 1994). Data used were from animals born in years 1964 through 1980.

2.2 The Population

Three selection lines were established in 1960 by randomly allocating 325 cows from 14 private Hereford herds to a weaning weight line (WWL), a yearling weight line (YWL), and an index line based on yearling weight and muscle score (IXL). The 42 foundation sires used from 1957 to 1963 were from 11 of the same 14 herds as the cows and from two other herds (Koch *et al.*, 1974a, b; Koch *et al.*, 1994).

The cattle were at Fort Robinson Beef Cattle Research Station, Crawford, Nebraska until 1971, when they were moved to USMARC, near Clay Center, Nebraska. The projected herd size of 150 breeding females per line was reached by 1964 and maintained until the end of the experiment. Approximately 225 foundation cows and other cows from the three selection lines that had been replaced were artificially inseminated with semen from seven of the foundation sires from 1968 through 1971 to provide the basis for a control line. In 1971 the control line (CTL) was established from 20 representative sons and heifer calves from matings with the 225 cows (Koch *et al.*, 1974a, b; Koch *et al.*, 1994).

Bulls were selected at two years of age. Through 1970, two bulls were chosen from each year of birth and used to sire calves when three, four, and five years old. After 1970, three two-year old bulls were selected each year to be used for two years, i.e., they sired calves when three and four years of age. Bulls were removed from service early only because of breeding unsoundness. To minimize inbreeding no more than two sons of a given sire or dam were selected (Koch *et al.*, 1974a, b; Koch *et al.*, 1994). Heifers born in 1964 and later were bred to calve at two years of age. All heifers were exposed to bulls. Selection was practiced only among those that were pregnant. Through 1970 the top 25 heifers from each line were selected. After 1970, the top 35 heifers from each line were selected. After 1973 essentially all pregnant heifers were kept in the herd. Cows were removed without regard to progeny performance based on the following criteria (Koch *et al.*, 1974a, b; Koch *et al.*, 1994):

1) not pregnant at weaning time,
2) serious unsoundness,
3) failure to raise a live calf for two consecutive years, and
4) old age.

For each breeding season, mating sires were randomly assigned to females within each age and line, except that half sib or more closely related matings were avoided.

All lines were maintained as one herd except during the breeding season. The herd calved only in the spring. Calves were weaned together each year when the average age was about 200 days (Koch *et al.*, 1974a, b; Koch *et al.*, 1994).

2.3 Selection Objectives in the Original Project

Selection in WWL was based on weight adjusted to 200 days of age. Selection in YWL was based on weight at 452 days (approximately 15 months of age) for bulls and at 550 days (approximately 18 months of age) for heifers. Selection in IXL was based on an index giving equal emphasis to muscle score and yearling weight when both were expressed in standard measure. Selection of heifers in IXL from birth years of 1960 through 1965 was based on yearling weight alone. Originally, only bulls were evaluated for muscle score, but beginning in the 1966 birth year, heifers were also evaluated for muscle score and were also selected for an index of muscle score and yearling weight until the end of the experiment (Koch *et al.*, 1974a, b; Koch *et al.*, 1994). Selection continued through matings to produce the 1982 calf crop.

2.4 Analysis of Stayability

Stayability to a specific age was defined as whether or not the cow survived to a specific age, given the opportunity (date of birth) to reach that age. Six age-specific conditional stayability traits were defined as whether or not 1) a cow survived another year of life after first calving given that she became a dam as a two year old (ST1|0), 2) she survived another 2 years (ST2|1) after first calving given that she was alive one year after first calving (i.e., score for ST1|0 was 1), 3) she survived another 3 years (ST3|1) after first calving given that she was alive one year after first calving, 4) she survived another 4 years (ST4|1) after first calving given that she was alive one year after first calving, 5) she survived another 5 years (ST5|1) after first calving given that she was alive one year after first calving , and 6) she survived another 6 years (ST6|1) after first calving given that she was alive one year after first calving. Observations were binary with a 1 indicating that a cow survived from first calving to a specific age and otherwise a 0. The measures of stayability to the specific number of years after first calving were considered different traits. Numbers of observations and frequencies of success for measures of stayability to the specific number of years are presented in Table 1.

The software package, MATVEC (Wang *et al.*, 2001), based on a penalized quasi-likelihood function (Breslow and Clayton, 1993) as showed by Kachman (2001) was used with a two-trait

threshold sire model to estimate genetic parameters for stayability. An example of the data and pedigree files and MATVEC statements for this analysis are given in the appendix.

Conditional on the fixed and random effects, stayability traits were assumed to follow a Bernoulli distribution. The mixed linear predictor used was:

$$\eta = Xb + Zs$$

where:

$$\eta = \begin{bmatrix} \eta_1 \\ \eta_2 \end{bmatrix},$$

η_1 = is a n_1 x 1 vector of linear predictors, which is related to predictions on the observational scale through the inverse link function for ST1|0,

η_2 = is a n_2 x 1 vector of linear predictors, which is related to predictions on the observational scale through the inverse link function for STk|1 (k = 2, 3. 4.5 or 6),

$$b = \begin{bmatrix} b_1 \\ b_2 \end{bmatrix},$$

b_1 = is a p x 1 vector of fixed effects for ST1|0,
b_2 = is a q x 1 vector of fixed effects for the other definition of stayability,
s_1 = is a r x 1 vector of random sire transmitting abilities for ST1|0,
s_2 = is a s x 1 vector of random sire transmitting abilities for the other definition of stayability (STk|1, k = 2, 3, 4, 5 or 6),

$$X = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix}, \quad Z = \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix},$$

X_1, X_2, Z_1, and Z_2 = are known incidence matrices relating the observations in y_1 and y_2, the n_1 x 1 and n_2 x 1 vectors of observations, or its conditional expectation, $E[y_i \mid \eta_i] = h(\eta_i) = p_i$, to fixed and random effects, respectively.

The residual variance on the underlying scale is assumed to be 1.

The link function was the probit function: $\eta = \Phi^{-1}(p_i)$, with inverse link $p_i = \Phi(\eta) = $

$\int_{-\infty}^{\eta} \frac{1}{\sqrt{2\pi}} e^{-x^2/2} dx$, where Φ is the cumulative standard normal density function and p_i denotes the

probability of survival (success) for cow **i**. The Bernoulli distribution for defined stayability traits for cow i, with $y_i = 1$ denoting success and $y_i = 0$ denoting failure, is the probability

$$\left(y_i \mid p_i\right) = \left(p_i\right)^{y_i}\left(1 - p_i\right)^{1-y_i}.$$

The estimating equations for the fixed and random effects are:

$$\begin{bmatrix} X'H'R^{-1}HX & X'H'R^{-1}HZ \\ Z'H'R^{-1}HX & Z'H'R^{-1}HZ + \left[G_0 \otimes A^{-1}\right] \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{s} \end{bmatrix} = \begin{bmatrix} X'H'R^{-1}(y^*) \\ Z'H'R^{-1}(y^*) \end{bmatrix}$$

where:

$$H = \mathrm{Diag}\left(H_{ij} = \frac{\partial \mu_{ij}}{\partial \eta_{ij}} \right) = \mathrm{Diag}\left(\frac{1}{\sqrt{2\pi}} e^{-\eta_{ij}^2/2} \right),$$

$$R = \mathrm{Diag}\left(\mathrm{var}\left(y_{ij} \mid \eta_{ij}\right)\right) = \mathrm{Diag}\left(p_{ij}\left(1 - p_{ij}\right)\right),$$

$$y_{ij}^* = y_{ij} - \phi\left(\eta_{ij}\right) + H_{ij}\eta_{ij},$$

A = is the Wright's numerator relationship matrix among sires,

$$G_0 = \begin{bmatrix} \sigma_{s1}^2 & \sigma_{s1s2} \\ \sigma_{s1s2} & \sigma_{s2}^2 \end{bmatrix},$$

σ_{s1}^2 = is the variance of sire transmitting ability for ST1|0,

σ_{s2}^2 = is the variance of sire transmitting ability for STk|1 (k = 2, 3, 4, 5 or 6),

σ_{s1s2} = covariance between transmitting ability for ST1|0 and sire transmitting ability for STk|1.

Estimates of heritability for the underlying normal distribution were obtained as:

$$\hat{h}_t^2 = \frac{4\hat{\sigma}_s^2}{\left(1 + \hat{\sigma}_s^2\right)}$$

Estimates of heritability were transformed to a binomial scale using the formula described by Robertson and Lerner (1949) as follows:

$$h_b^2 = \frac{h_t^2 * z^2}{p * (1 - p)}$$

where

h_t^2 = is the estimate of heritability on the underlying normal scale (from threshold model),

h_b^2 = is the estimate of heritability on the binomial scale,

p = is the fraction of cows with observations of 1, and

z = is the height of the ordinate at the truncation point for an area of p under the normal curve.

The standard errors for estimates of heritability and genetic correlations were calculated using the delta method and the information matrix at convergence from estimating the variance components (Searle et al., 1992).

3. Results and Discussion

Estimates of heritability and genetic correlations are summarized in Table 2. In general, estimates of heritability ranged from 0.18 ± 0.11 for ST5|1 to 0.30 ± 0.14 for ST6|1 on the underlying scale. Estimates of heritability transformed to a binomial scale (observed) ranged from 0.07 to 0.17 for ST2|1, ST3|1 and ST6|1, respectively.

Estimates of genetic correlations (underlying scale) were variable in magnitude as well as in sign. Estimates of genetic correlations ranged from -0.22 ± 0.57 between ST1|0 and ST3|1 and 0.54 ± 0.49 between ST1|0 and ST6|1.

Estimates of heritability for ST1|0 were consistent with those reported by Martinez (2002) working with the same data set who reported an estimate of heritability of 0.23 ± 0.12. Estimates of heritability were slightly higher at early ages but in agreement at latter ages with estimates reported in the literature.

Estimates of genetic correlations on the underlying scale were variable in magnitude as well as in sign. Estimates of genetic correlations ranged from -0.22 ± 0.57 between ST1|0 and ST3|1 and 0.54 ± 0.49 between ST1|0 and ST6|1.

Vega (1999) using a sire model with measurements from an experimental herd of beef cattle reported estimates of heritability with a threshold model of 0.00, 0.08, 0.02, 0.22, 0.24, 0.28, and 0.00 for stayability to 2, 3, 4, 5, 6, 7, and 8 years of age. Estimates of heritability by van der Westhuizen et al. (2001), with a sire model were 0.06, 0.10, 0.06, 0.03, and 0.11, for stayability to 3, 4, 5, 6, and 7 years of age.

Reports of genetic correlations among stayability traits with threshold models were not found in the literature.

4. Summary

Two-trait threshold models can be used to estimate heritability and genetic relationships between stayability measured at an early and at later ages.

Selection for stayability would be possible but would be expected to be slow due to low estimates of heritability on the observed (binomial) scale.

Estimates of genetic correlations indicate that selection for stayability to an early age would have limited impact on improvement for stayability to later ages. More research is needed in this area especially with other definitions of stayability such as stayability to calving and stayability to weaning.

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Table 1. Numbers of observations, frequencies of success and standard deviations for measures of stayability to the specific ages

Trait	n	Mean	sd
ST1|0	1868	0.87	0.36
ST2|1	1460	0.91	0.29
ST3|1	1333	0.81	0.40
ST4|1	1214	0.69	0.46
ST5|1	1133	0.54	0.49
ST6|1	1016	0.30	0.50

Table 2. Estimates (and standard errors) of heritability and genetic correlations for stayability to different specified ages

Trait 1	Trait 2	σ_{s1}^2	σ_{s2}^2	σ_{12}	h_{1u}^2	h_{2u}^2	r_g	h_{1b}^2	h_{2b}^2
ST1|0	ST2|1	0.057	0.054	-0.0086	0.22 ± 0.12	0.20 ± 0.15	-0.16 ± 0.52	0.09	0.07
ST1|0	ST3|1	0.057	0.035	-0.0100	0.22 ± 0.12	0.14 ± 0.12	-0.22 ± 0.57	0.09	0.07
ST1|0	ST4|1	0.058	0.070	0.0080	0.22 ± 0.12	0.26 ± 0.13	0.13 ± 0.46	0.09	0.15
ST1|0	ST5|1	0.059	0.046	0.0120	0.22 ± 0.12	0.18 ± 0.11	0.22 ± 0.57	0.09	0.11
ST1|0	ST6|1	0.061	0.082	0.0380	0.23 ± 0.12	0.30 ± 0.14	0.54 ± 0.49	0.09	0.17

σ_{s1}^2 = sire variance for ST1\|0 (trait 1);

σ_{s2}^2 = sire variance for trait 2 (STk\|1, k = 2, 3, 4, 5 or 6);

σ_{12} = genetic covariance;

h_{1u}^2 = estimate of heritability for ST1\|0;

h_{2u}^2 = estimate of heritability for STk\|1;

r_g = genetic correlation;

h_{1b}^2 = estimate of heritability transformed to a binomial scale for ST1\|0;

h_{2b}^2 = estimate of heritability transformed to a binomial scale for STk\|1;

ST1\|0 = survived another year after first calving given that she became a dam as a two year old;
ST2\|1 = survived another 2 years after first calving given that she was alive one year after first calving;
ST3\|1 = survived another 3 years after first calving given that she was alive one year after calving;
ST4\|1 = survived another 4 years after first calving given that she was alive one year after calving;
ST5\|1 = survived another 5 years after first calving given that she was alive one year after calving;
ST6\|1 = survived another 6 years after first calving given that she was alive one year after calving.

Appendix example: data file, pedigree file and MATVEC statements

An annotated example of the data:
    Data file ("st1224.dat")

Sire 1	Sire 2	Line	(Y)ear	(Trait) (P)eriod	PxY	Obs
For P = 1	2000			1		0 or 1
2000	For P = 2			2		
700049	2000	21	74	1	174	1
2000	700049	21	74	2	274	1
700049	2000	21	74	1	174	1
2000	700049	21	74	2	274	0
700049	2000	21	74	1	174	0
700049	2000	21	74	1	174	0

Line 1:   Progeny 1 of 700049 is present in period 1   (obs = 1)
Line 2:   Progeny 1 of 700049 is present in period 2   (obs = 1)

Line 3:   Progeny 2 of 700049 is present in period 1   (obs = 1)
Line 4:   Progeny 2 of 700049 is absent in period 2   (obs = 0)

Line 5:   Progeny 3 of 700049 is absent in period 1   (obs = 0)
           (Progeny 3 was absent in period 1, so no observation
           in period 2; conditional on being present in period 1)
Line 6:   Progeny 4 of 700049 is absent in period 1   (obs = 0)

Example of the pedigree:
    Pedigree file ("sire.dat")

Sire	Sire of sire	Dam of sire
2000	0	0
390689	310982	0
430015	390689	0
450117	0	0
470018	0	0
481657	0	0
490355	450117	0
500368	430015	0
500373	470018	420122

Line 1:   Dummy sire 2000 with unknown parents (0 and 0)
Line 2:   Sire 390689 with parents (310982 and unknown, 0)
Line 4:   Sire 450117 with unknown parents (0 and 0)
Line 9:   Sire 500373 with parents (470018 and 420122)

MATVEC statements:

```
this.parameter("EPSILON",1.e-8);
start=time();
D=Data();
D.input("st1224.dat","sire1 sire2 line yob per pyob st1224");
P=Pedigree();
P.input("sire.dat","individual father mother");
M=Model();
M.equation("st1224=pyob sire1 sire2");
M.variance("residual",1);
M.variance("sire1",P,1);
M.variance("sire2",P,1)
M.variance("sire1","sire2",.001);
M.link("probit",0);
M.fitdata(D);
M.glim(5);
M.save("st1224b_1.out","out");
M.num_glmm(5);
vce=M.vce_aireml(20,0);
M.info("st1224b1.infout","out");
M.save("st1224b1.out","out");
difftime(time(),start)
```