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J ANIM SCI 1995, 73:993-1001.

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Within-Herd Genetic Analyses of Stayability of Beef Females

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ABSTRACT: Nonlinear mixed-model procedures for analysis of binary data were used to estimate heritability (h^2), predict individual genetic merit, and determine genetic and environmental trends for four measures of stayability of beef females. Traits considered were probabilities of a female having 2 [S(2|1)], 5 [S(5|1)], 8 [S(8|1)] and 11 [S(11|1)] calves, given that she calved once. Colorado State University Beef Improvement Center (BIC) and Beckton Stock Farm (BSF) provided data for the analyses. Heritability was estimated using animal model marginal maximum likelihood (AM MML), sire model marginal maximum likelihood (SM MML), and animal model Method R (AM MR). Individual genetic merit was predicted using single-trait animal models with each

h^2 estimate. Birth year was treated as fixed in all analyses. Only AM MML yielded h^2 estimates for all traits in both herds. The AM MML h^2 estimates for S(2|1), S(5|1), S(8|1), and S(11|1) were .09, .11, .07, and .20, respectively, for BSF data and .02, .14, .09, and .07, respectively, for BIC data. Differing h^2 estimates did not substantially influence rank of individual predictions. Genetic trends in stayability were positive in both herds, although birth year solutions indicated variable or negative environmental trends. Genetic improvement of stayability may be accelerated by incorporating predictions of genetic merit for stayability in selection criteria. S(5|1) may be the most useful trait for consideration in national cattle evaluations.

Key Words: Sire Evaluation, Threshold Models, Reproductive Traits, Survival

J. Anim. Sci. 1995. 73:993-1001

Introduction

Under typical market conditions, a beef cow must remain in production for several years to generate revenue sufficient to offset development and maintenance costs. With \$50 to \$100 annual net return per cow and \$100 to \$200 difference between heifer development costs and cow salvage value, two to eight calves are required to break even (Table 1; Dalsted and Gutierrez, 1989). For a herd to be profitable, the number of cows remaining in production past their breakeven age must compensate for those cows that were culled before that age.

Stayability is the probability of surviving to a specific age, given the opportunity to reach that age (Hudson and Van Vleck, 1981). Provided sufficient genetic variation exists, predictions of genetic merit for stayability may allow selection of parents whose daughters are most likely to remain in production long enough to be profitable. Objectives of this initial

investigation of stayability in beef cattle were to estimate heritability, predict genetic merit, and determine genetic and environmental trends for stayability in seedstock herds. Different threshold model procedures and age-specific measures were evaluated to determine which procedures and age-specific measures might merit consideration in further analyses, such as national cattle evaluations for stayability.

Materials and Methods

Data

Four age-specific conditional stayability traits were analyzed (Table 2). Necessary pedigree and birth date information were obtained from the Colorado State University Beef Improvement Center (BIC), Saratoga, WY and Beckton Stock Farm (BSF), Sheridan, WY. Data were available for the years 1958 through 1992 from BIC and for the years 1950 through 1989 from BSF. History and management of the BIC herd was documented by Schons et al. (1985), Schafer (1987), and Schafer et al. (1990). The purebred Angus BIC herd was founded by John E. Rouse in 1953, and management of the herd was assumed by Colorado State University in 1986.

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Received July 29, 1994.

Accepted December 6, 1994.

Table 1. Breakeven ownership period of a cow (years)^a

Replacement heifer value	Salvage value	Net return/cow ^b		
		\$50	\$100	\$150
\$500	\$400	4	2	1
	450	2	1	1
	500	1	1	1
\$600	\$400	8	3	2
	450	6	2	2
	500	5	2	1
\$700	\$400	14	5	3
	450	12	4	3
	500	10	3	2

^aDalsted and Gutierrez, 1989.^b90% weaning rate and 5% discount rate.

Artificial insemination has been used since 1958. The AI breeding season for cows started in June, with heifers bred approximately 3 wk before cows. In the AI mating, semen from bulls selected from within the herd as well as from outside Angus bulls was used. Following AI mating, females were exposed to natural mating in single- and multiple-sire pastures with bulls selected from within the herd. Replacement heifers were selected from within the herd, based on weaning weight, yearling weight, and the record of their dam. Cows were culled on results of a fall pregnancy examination, progeny weaning weight, health, and structural soundness.

Schafer (1991) documented the Red Angus BSF herd. In 1945, Waldo Forbes began collecting red progeny of black Angus parents, leading to the formation of the Red Angus Association of America. Selection emphasis in the BSF herd has changed over time. In the 1950s, the primary emphasis was to increase growth. Since then, birth weight, maternal ability, and reproduction have received attention at different times. Cow culling criteria included progeny performance and failure to rebreed. Structural soundness of cows greater than 11 yr old was also considered.

Because both herds had a policy of culling nonpregnant cows, stayability of a dam to a given age and the potential number of calves produced by that age were essentially the same measure. The number of calves born to each dam was used to assign binary stayability observations. Twins were counted as a single calf. Binary observations, with 0 indicating failure and 1 indicating success, were assigned to dams old enough to have had the required number of calves. Observations of failure on culled cows not yet old enough to have had the required number of calves were not used. These cows had contemporaries remaining in production so the observations would not be informative until the birth year contemporary group could be completely observed (Schons et al., 1985). For S(2|1), two calves were required for success. Dams with two or more calves were assigned a 1 and those with only one calf

were assigned a 0. Observations on dams that were 2 yr old in the last year of available data were considered unknown. For S(5|1), dams with at least five calves received a 1 and dams with fewer than five calves received a 0. The phenotype of dams 6 yr old and younger was not observed. Records for S(8|1) and S(11|1) were coded in a similar manner. Males and females not recorded as dams were not assigned observations.

Analyses

All analyses included year of birth contemporary groups as the only fixed effect and either animal or sire as a random effect. With animal model analyses, the inverse numerator relationship matrix accounted for all known relationships among animals in each herd (Golden et al., 1991). With sire model analyses, the inverse numerator relationship matrix accounted for known relationships among sires and maternal grandsires. All analyses were conducted using the Animal Breeder's Toolkit (Golden et al., 1992). Some procedures required elements of the inverse of the coefficient matrix. These were obtained with routines based on FSPAK (Misztal and Perez-Enciso, 1992).

Heritability estimates and predictions of genetic merit for each trait were obtained from within-herd analyses. Heritability was estimated using three variations of nonlinear procedures for mixed-model

Table 2. Definitions of traits measuring stayability of dams

Trait	Definition
S(2 1)	Probability of a female having two calves, given she becomes a dam
S(5 1)	Probability of a female having five calves, given she becomes a dam
S(8 1)	Probability of a female having eight calves, given she becomes a dam
S(11 1)	Probability of a female having 11 calves, given she becomes a dam

Table 3. Frequency of successful observations for stayability of dams

Trait	BSF		BIC	
	n	% Success	n	% Success
S(2 1)	2,130	75	3,105	79
S(5 1)	1,722	39	2,803	38
S(8 1)	1,393	21	2,594	18
S(11 1)	1,081	10	2,276	9

analysis of binary data (Gianola and Foulley, 1983; Harville and Mee, 1984). Only single-trait analyses were conducted. Although these procedures allow multiple-trait analysis of independently observed traits, the complete dependency of stayability to a late age on stayability to earlier ages did not allow simultaneous consideration of more than one stayability trait.

Animal model marginal maximum likelihood (**AM MML**) included the random effect of animal using the MML procedure of Hoeschele et al. (1987) to estimate heritability. Sire model MML (**SM MML**) was the same procedure as AM MML, except sire, instead of animal, was the random effect. Animal model Method R (**AM MR**, Reverter et al., 1994) used regression of high accuracy maximum *a posteriori* (**MAP**) predictions on lower accuracy MAP predictions to estimate heritability.

For AM MR estimates of heritability, high accuracy predictions used all available observations. Low accuracy predictions were obtained with random 50% subsamples of observations. The AM MR estimates were obtained from the mean estimate of Method R applied to five usable subsamples. Six rounds, with linear extrapolation of the reciprocal of estimated genetic variance between rounds, were used to estimate heritability with each subsample. Subsamples were not used if there was no variation in binary observations within a birth year. Subsamples yielding heritability estimates less than zero were discarded. Subsamples were also discarded if regression values from all six rounds of Method R iteration were greater than the expected value of 1 or all six regression values were less than 1. Heritability estimates from these subsamples were not used because they resulted from extrapolation outside the range of available data.

Predictions of genetic merit of all animals were obtained with animal model MAP procedures using AM MML, SM MML, and AM MR estimates of heritability. The MAP solutions on the underlying standard normal scale were transformed to a probability scale with the following equation:

$$\text{MAP}_{pi} = \Phi(\text{MAP}_{ui})$$

where MAP_{pi} is the i^{th} MAP fixed or random effect solution on the probability scale and $\Phi(\text{MAP}_{ui})$ is the standard normal integral of the i^{th} MAP solution on

the underlying scale. Rank and simple correlations among all predictions, predictions of sires, and predictions of sires with daughters observed were calculated within each trait to assess the impact of heritability estimated with different methods.

Accuracies (r) of these predictions were calculated as follows:

$$r_i = \left[1 - \frac{\text{PEV}_i}{(1 + F_i) \hat{\sigma}_a^2} \right]^{.5}$$

where r_i is the accuracy of the i^{th} individual's prediction, PEV_i is the error variance of the i^{th} individual's prediction, $\hat{\sigma}_a^2$ is the estimate of genetic variance, and F_i is the i^{th} individual's inbreeding coefficient. Prediction error variances (**PEV**) were obtained from diagonal elements of the inverse of the coefficient matrix assembled in the final round of Newton-Raphson iteration. Mean accuracies of all predictions, predictions of sires, and predictions of sires with daughters observed were determined.

Changes in environment and genotype over time were determined from MAP solutions transformed to the probability scale. Fluctuations in environment were determined from the birth year fixed effect solutions and changes in genotype over time were determined from means by birth year of estimated breeding values (**EBV**) obtained from MAP solutions transformed to the probability scale. Only MAP solutions using AM MML heritability estimates were used for these trends because SM MML and AM MR procedures did not result in complete sets of heritability estimates for all traits in both herds.

Results and Discussion

Estimates of Heritability

Number of observations and frequency of success for each trait measured in the BSF and BIC data sets are presented in Table 3. Heritability estimates on the underlying scale for stayability to various ages are presented in Table 4. Estimates using AM MML ranged from .09 for S(2|1) to .20 for S(11|1) in the BSF herd and from .02 for S(2|1) to .14 for S(5|1) in BIC. The .02 estimate for S(2|1) in BIC and the .20

Table 4. Heritability estimates for measures of stayability of dams

Trait	BSF	BIC
	AM MML ^a	
S(2 1)	.093	.019
S(5 1)	.105	.143
S(8 1)	.070	.091
S(11 1)	.195	.068
Trait	SM MML ^b	
	BSF	BIC
S(2 1)	.080	.072
S(5 1)	.121	.708
S(8 1)	—	.628
S(11 1)	—	.680
Trait	AM MR ^c	
	BSF	BIC
S(2 1)	.208 ± .044	.025 ± .007
S(5 1)	.123 ± .028	.227 ± .010
S(8 1)	.163 ± .018	.188 ± .044
S(11 1)	—	.192 ± .022

^aAnimal model marginal maximum likelihood.

^bSire model marginal maximum likelihood.

^cAnimal model Method R. Mean and SE of five 50% samples.

for S(11|1) in BSF seem somewhat unusual compared to the remaining estimates, which ranged from .07 to .14. The expectation maximization-like procedure used to obtain these estimates, however, did not provide a mechanism to establish confidence intervals about these estimates.

Transformed to the binary scale of observation, the AM MML heritability estimates ranged from .04 to .07 for BSF and from .01 to .09 for BIC. These estimates are within the .01 to .15 range of heritability estimates for stayability in dairy cows (Schaeffer and Burnside, 1974; Hudson and Van Vleck, 1981; Van Doormaal et al., 1985; DeLorenzo and Everett, 1986).

The SM MML estimates for S(2|1) and S(5|1) in BSF are the only SM MML estimates obtained that are within the range of AM MML and AM MR estimates. No solution was obtained from SM MML procedures when implemented with S(8|1) and S(11|1) using BSF data. With the BIC data set, SM MML resulted in heritability estimates 4 to 10 times greater than the AM MML estimate for the same trait. These estimates may be due to a lack of sire information in the BIC herd, because 60% of sires of dams were unknown and known sires were confounded with birth year. Using only observations of dams with known sires resulted in SM MML estimates of .08 for S(2|1), .59 for S(5|1), .46 for S(8|1), and .56 for S(11|1).

The results from BIC and lack of results from BSF indicate sire models can be problematic for estimating heritability of stayability traits. Even though sire models accounted for relationships among sires through maternal grandsires, information about relationships was incomplete. The limited information had different effects in the two herds. In BSF, sire

differences for S(8|1) and S(11|1) could not be resolved, so no heritability estimate could be obtained. In BIC, sire effects could not be separated from birth year effects, resulting in an apparent overestimation of heritability.

The AM MR heritability estimates presented are the mean and SE of estimates from five random 50% subsamples of binary observations. Consistent with results of a comparison of AM MML and AM MR estimation procedures using simulated data (Snelling, 1994), AM MR resulted in higher estimates than AM MML. An AM MR heritability estimate for BSF S(11|1) was not obtained. In 50 attempts using a 50% sampling rate, no subsamples were obtained that contained variation within all levels of birth year. A 90% sampling rate with only 10% of observations discarded yielded subsamples containing variation in all birth years. Within each of 50 90% subsamples, all regression values were either greater than or less than 1, resulting in extrapolation of the heritability estimate beyond the range of regression values for that subsample.

These results suggest AM MML may be preferred to estimate heritability of stayability and other binary traits. Computational demands, particularly inversion of the coefficient matrix, may make AM MML infeasible to implement on much larger data sets. One alternative to implementing AM MML on larger data sets may be to obtain AM MML estimates from several subsets. The AM MR is more feasible with larger data sets, but different sampling strategies to obtain low accuracy predictions may be necessary. Alternatives to randomly deleting individual observations, such as deleting all observations from randomly selected levels of a fixed effect, should be evaluated. The SM MML results from this study could not be considered reliable.

Predictions of Genetic Merit

The effect of heritability estimates on EBV of stayability on the probability scale is indicated by differences in mean, SD, and range of EBV of sires (Table 5). For both data sets, within each trait the SD and range of EBV are greater with higher estimates of heritability. Mean EBV were also greater with higher heritabilities. Compared with EBV of all animals, sire EBV had greater SD with the same or smaller range. The SD of sires with observations on daughters were somewhat greater than SD of all sires.

Rank and simple correlations between predictions of genetic merit for age-specific stayability traits using heritability estimates derived from different methods indicate the potential influence of variation in heritability estimates on selection decisions. Correlations between solutions obtained with AM MML and AM MR heritabilities were .98 or greater, even though some AM MR heritability estimates were more than two times greater than corresponding AM MML

Table 5. Mean, standard deviation, and range of predicted genetic merit^a of sires for stayability using heritability (h^2) estimated by different methods

Trait	h^2 Estimate		Mean	SD	Minimum	Maximum
	Method	Value				
BSF data						
S(2 1)	AM MML ^b	.093	.511	.041	.371	.677
	SM MML ^c	.080	.509	.036	.384	.662
	AM MR ^d	.208	.521	.071	.282	.758
S(5 1)	AM MML	.105	.543	.052	.378	.689
	SM MML	.121	.548	.058	.369	.711
	AM MR	.123	.549	.058	.368	.713
S(8 1)	AM MML	.070	.518	.028	.437	.603
	SM MML	—	—	—	—	—
	AM MR	.163	.536	.056	.393	.686
S(11 1)	AM MML	.195	.593	.074	.433	.756
	SM MML	—	—	—	—	—
	AM MR	—	—	—	—	—
BIC data						
S(2 1)	AM MML	.019	.505	.011	.477	.538
	SM MML	.072	.513	.034	.421	.618
	AM MR	.025	.506	.014	.471	.548
S(5 1)	AM MML	.143	.545	.085	.330	.836
	SM MML	.708	.624	.230	.123	.992
	AM MR	.227	.563	.114	.289	.894
S(8 1)	AM MML	.091	.528	.049	.398	.680
	SM MML	.628	.618	.194	.186	.987
	AM MR	.188	.549	.085	.334	.796
S(11 1)	AM MML	.068	.513	.028	.464	.639
	SM MML	.680	.585	.169	.199	.991
	AM MR	.192	.531	.065	.404	.799

^aEstimated breeding values on probability scale.

^bAnimal model marginal maximum likelihood.

^cSire model marginal maximum likelihood.

^dAnimal model Method R.

estimates. Heritability estimates most different from AM MML were for S(11|1) in BIC, with the SM MML estimate 10 times greater than the AM MML estimate and the AM MR estimate 2.8 times greater than the AM MML estimate. Resulting correlations between predictions of all animals were .87 between AM MML and SM MML predictions and .98 between AM MML and AM MR predictions. Of 18 BIC sires selected in the top 10% using the AM MML estimate, 13 were selected using the SM MML estimate and 15 using the AM MR estimate. One of the 180 BIC sires differed by 103 places; the EBV of .51 was derived using the AM MML heritability and the EBV of .25 was derived using the SM MML heritability estimate. This sire differed by 81 places between AM MML and AM MR rankings; the EBV of .48 was calculated using the AM MR heritability.

The most similar heritability estimates were for S(5|1) in BSF, with all correlations among animal solutions greater than .99. In the 293 BSF sires, 28 of 29 were common to the top 10% selected using AM MML, SM MML, and AM MR. The greatest difference in rank among these sires was 29 places. The sire with the greatest difference in rank had EBV of .501 with the AM MML heritability estimate and .499 with the SM MML and AM MR estimates.

Within each trait and data set, calculated accuracies of prediction were scaled according to the estimate of heritability. The highest mean accuracies resulted from the highest heritability estimates (Table 6). For BSF, correlations were .99 or greater among accuracies for each trait computed with different heritability estimates. In BIC, correlations between accuracies using AM MML and AM MR heritabilities were .99 or greater and were .92 or greater between accuracies obtained with SM MML and animal model heritability estimates.

Comparing accuracies computed using AM MML heritabilities, S(5|1) predictions had the highest mean accuracy in both data sets. Higher heritability estimates for S(5|1) offset the greater number of observations for S(2|1). Disregarding the apparently inflated accuracies from the SM MML heritability estimates in BIC, mean accuracies of all animals and all sires were higher for BSF than for BIC. Sires with daughters observed had similar levels of accuracy in both herds.

Differences between MAP predictions for the same trait made with different levels of heritability suggest that the exact value of the heritability estimate may not have a large impact on selection decisions. Except

Table 6. Mean, standard deviation, and range of accuracies of predicted genetic merit^a of sires for stayability using heritability (h^2) estimated by different methods

Trait	h^2 Estimate		Mean	SD	Minimum	Maximum
	Method	Value				
BSF data						
S(2 1)	AM MML ^b	.093	.360	.151	.003	.680
	SM MML ^c	.080	.342	.145	.003	.653
	AM MR ^d	.208	.462	.182	.002	.803
S(5 1)	AM MML	.105	.362	.168	.000	.740
	SM MML	.121	.379	.175	.000	.764
	AM MR	.123	.381	.175	.000	.764
S(8 1)	AM MLL	.070	.271	.136	.002	.630
	SM MML	—	—	—	—	—
	AM MR	.163	.363	.175	.000	.768
S(11 1)	AM MML	.195	.289	.161	.000	.716
	SM MML	—	—	—	—	—
	AM MR	—	—	—	—	—
BIC data						
S(2 1)	AM MML	.019	.144	.100	.005	.506
	SM MML	.072	.252	.165	.000	.745
	AM MR	.025	.161	.111	.006	.553
S(5 1)	AM MML	.143	.292	.214	.003	.865
	SM MML	.708	.475	.303	.000	.971
	AM MR	.227	.341	.239	.000	.971
S(8 1)	AM MML	.091	.207	.165	.002	.775
	SM MML	.628	.398	.286	.003	.958
	AM MR	.188	.267	.210	.000	.869
S(11 1)	AM MML	.068	.142	.130	.002	.630
	SM MML	.680	.329	.276	.000	.940
	AM MR	.192	.210	.190	.000	.807

^aEstimated breeding values on probability scale.

^bAnimal model marginal maximum likelihood.

^cSire model marginal maximum likelihood.

^dAnimal model Method R.

for vastly different estimates, such as those obtained for S(11|1) in BIC with AM MML and SM MML, the estimate used to predict genetic merit had more influence on the scale of predictions and accuracy values than on the relative merit of an individual compared with other animals in the evaluation.

Genetic and Environmental Trends

Figures 1 and 2 depict estimated birth year effects and mean EBV by year of birth with solutions obtained using AM MML heritability estimates. These figures clearly indicate separation of genetic and environmental effects. The decrease in general level of environment from S(2|1) to S(11|1) corresponds to the decrease in frequency of successful observation as the age considered increases (Table 3). Mean EBV for all traits increased over time in both herds, with the average change per year ranging from .018%/yr for S(2|1) in BSF to .305%/yr for S(5|1) in BIC. Because nonpregnant cows were culled in these herds, the stayability traits measure continuous fertility to each age. The increasing genetic trends suggest that the culling policies may have had a favorable genetic influence on underlying fertility.

The decreasing environmental trends from 1963 to the last year of available data for S(5|1), S(8|1) and S(11|1) in BSF correspond to declining nutritional conditions for the BSF herd. The size of the herd increased from nearly 100 cows in 1960 until it stabilized at approximately 450 cows in the 1980s. Increases in land available for grazing did not match increases in herd size, resulting in increased competition for available forage.

A steady environmental trend is not readily apparent in the BIC herd. The low birth year solutions for S(2|1) in 1965 and 1983 correspond to herd reductions in 1967 and 1985 when relatively large portions of the heifers that calved as 2-yr-olds were sold. The effect of these reductions is also noticeable in the environmental trend for S(5|1) but is less apparent in the S(8|1) and S(11|1) trends. The dilution of the effect of herd reduction in S(8|1) and S(11|1) may be explained by the lag between the time a cow is born and when she qualifies for a stayability observation. The first reduction affected all cows born prior to 1966 for both S(8|1) and S(11|1). Changes in environment for S(8|1) and S(11|1) since the second reduction cannot be determined until several more

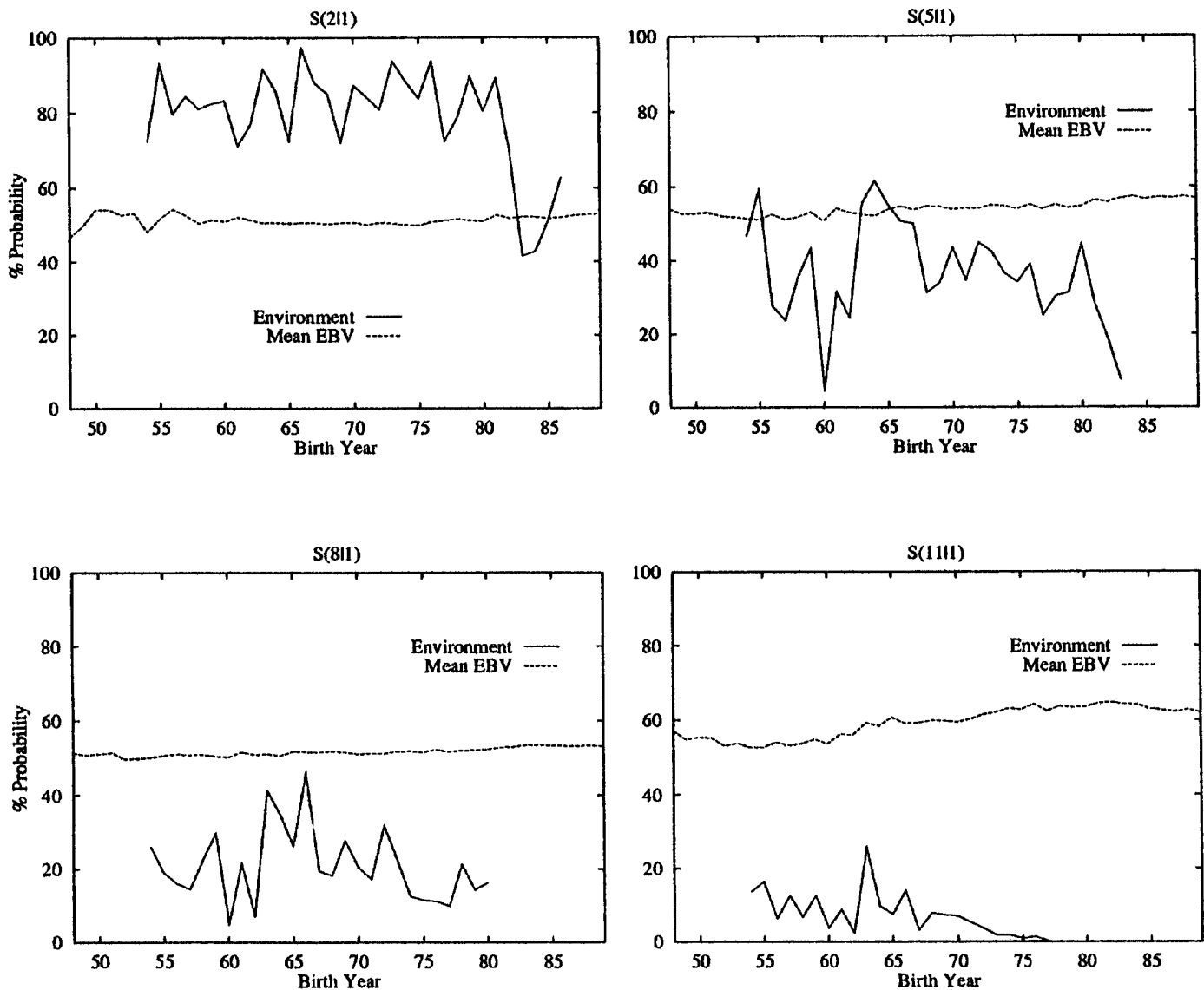


Figure 1. Environmental effects and mean estimated breeding values (EBV) by birth year for stayability of dams to have 2, 5, 8, and 11 calves (Beckton Stock Farm data).

years of data are available. In analyses of S(8|1) and S(11|1), observations on females born after the latest reduction were not available.

For stayability evaluations to be most useful, the trait considered should reflect the age that has the greatest economic impact, weighted by the amount of information available to make the predictions. Although extremely old cows may be the most profitable, genetic predictions for the probability of surviving to an extremely old age may be meaningless without sufficient information to make reliable predictions. Further study to identify the most valuable stayability trait for given situations is needed.

If a single trait were to be chosen from those considered in this study, S(5|1) may be preferred. In many situations, five calves may be close to the

number required for a cow to break even. The heritability of S(5|1) seems sufficiently high to overcome the loss of available information relative to S(2|1). Evaluations for S(5|1) include more information than evaluations for later ages. Due to the serial nature of stayability to a specific age, selection for S(5|1) should have favorable influence on stayability to later ages.

Implications

This study estimated heritability and predicted genetic merit for the probability of cows staying in production to different ages. Additional study is needed to quantify the value of different age-specific

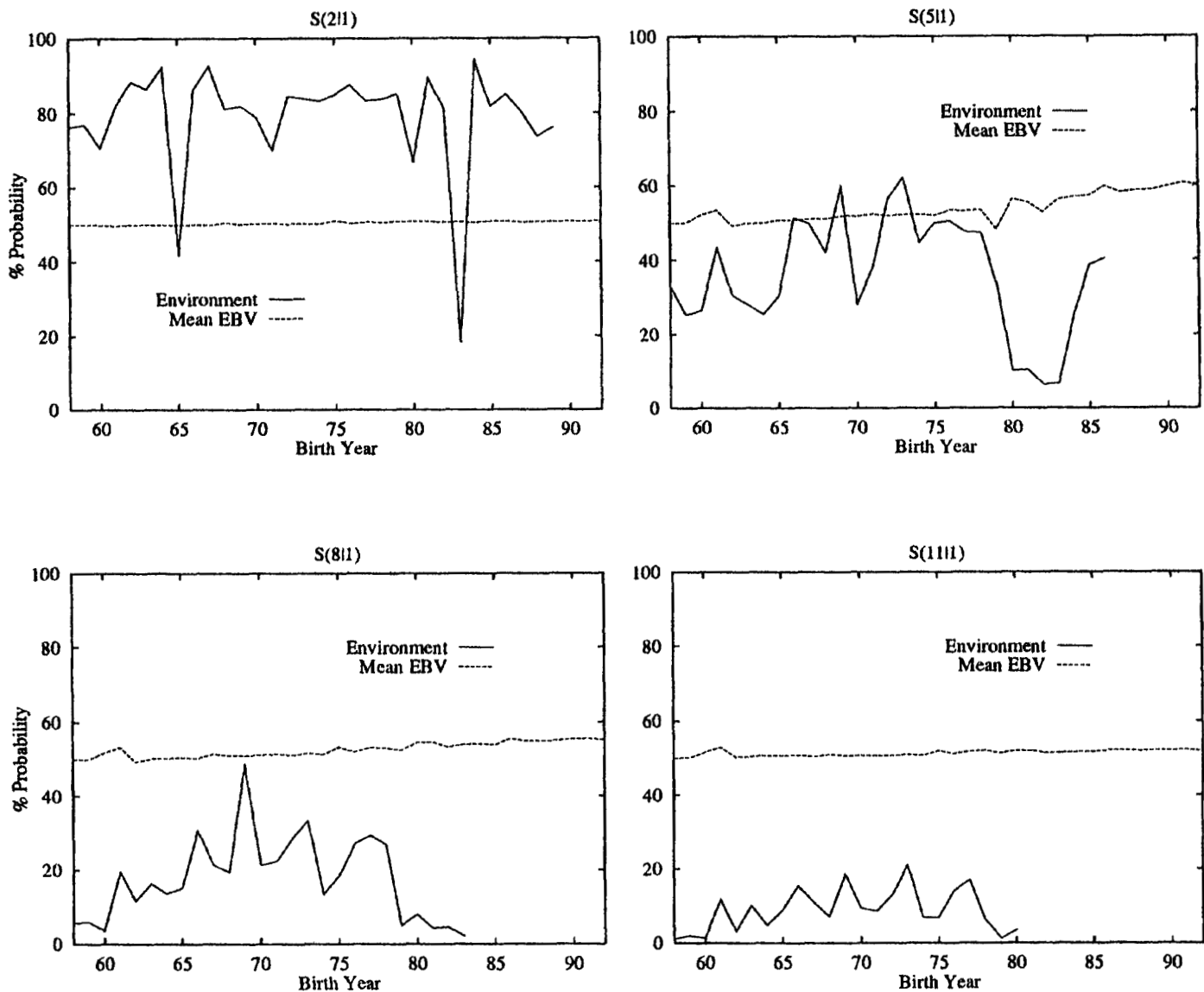


Figure 2. Environmental effects and mean estimated breeding values (EBV) by birth year for stayability of dams to have 2, 5, 8, and 11 calves (Beef Improvement Center data).

stayability measures and the relationships with other economically important traits. Age-specific stayability predictions could be most useful to identify which bulls are most likely to have daughters remain in production until that age. They can also be useful in replacement heifer selection, but they should not be considered when culling nonpregnant cows. As with any prediction of genetic merit, the decisions of exactly how to use or not use them are left to the individual.

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