It has been suggested that traits of fertility have the single largest economic impact for cow-calf producers. Many traits of fertility are threshold traits, which are observed on a discrete scale. Stayability has been reported as a measure of sustained reproductive ability which is measured on a discrete basis. For reproductive traits, several analyses with field data have shown very small differences between the threshold and the linear model. Therefore, the objective of this study was to investigate the use of linear and threshold models to estimate heritability and trends for Stayability in beef cattle. Data reported to the American Hereford Association were used in this study.

INDEX WORDS: Beef, Fertility, Reproduction, Threshold, Linear
LINEAR AND THRESHOLD MODELS TO ESTIMATE HERITABILITY AND TRENDS FOR STAYABILITY IN BEEF CATTLE

by

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LINEAR AND THRESHOLD MODELS TO ESTIMATE HERITABILITY AND TRENDS FOR STAYABILITY IN BEEF CATTLE

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This document represents the sacrifice, encouragement and support of the author’s friends, peers, colleagues, graduate faculty and family. There have been many unexpected trials and obstacles to overcome and it is sincere appreciation this author has for those that made this possible. I am reminded of the poem “Footprints in the Sand”.

One night I dreamed I was walking
Along the beach with the Lord.
Many scenes from my life flashed across the sky.
In each scene I noticed footprints in the sand.
Sometimes there were two sets of footprints.
Other times there were one set of footprints.
This bothered me because I noticed that
During the low periods of my life when I was Suffering from anguish, sorrow, or defeat
I could see only one set of footprints,
So I said to the Lord, “You promised me, Lord, that if I followed You,
You would walk with me always.
But I noticed that during the most trying periods
Of my life there have only been
One set of prints in the sand.
Why, when I have needed You most,
You have not been there for me?”
The Lord replied,
“The times when you have seen only one set of footprints
Is when I carried you.”

By Mary Stevenson
(Born 11/8/22 Died 1/6/99)

Although this document carries my name it was many times that the footprints belonged to someone else.
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Melton, (1995, BIF) indicated that weaning rate is the trait having the largest single economic impact for cow-calf producers. In a recent evaluation of the Limousin breed, infertility was identified as the primary reason Limousin cows are culled, accounting for fewer than 25% of all identified cullings (Anderson, 1996). However, reproductive traits of the beef cow are generally perceived to have low heritabilities and are difficult to record and interpret and therefore have not been included in National Cattle Evaluations (NCE) to the extent as growth traits. While most producers recognize the value of reproductive efficiency, little emphasis is traditionally placed on reproductive efficiency when selecting replacements. This is likely because fertility is expressed later in life, and most selection schemes for fertility are based on phenotypic indicator traits expressed at the time of selection. Furthermore, because of the perception of low heritability for reproductive traits, most producers feel that little can be accomplished by selecting for fertility traits. Therefore, and unfortunately, many traits that have been shown to be important to the overall financial health of the enterprise have been left to the producers best judgment based upon some knowledge of the trait, how it interacts with the environment, and limited within herd observations. This type of selection scheme in many cases can place emphasis on traits unrelated or perhaps even antagonistic to reproductive
efficiency. Expected Progeny Differences (EPD) for traits that influence reproductive performances of the beef cowherd need to be reported. In fact, many breed organizations are beginning to collect and report reproductive performance and are beginning to build databases for reporting fertility trait EPD.
Literature Cited


CHAPTER 2
LITERATURE REVIEW

Reproduction in Beef Females

The measure of reproduction for most producers is usually expressed only as success or failure, while in fact this may not be the most suitable measure for the genetic improvement for reproduction because these binary traits are not easily modeled and because of possible interactions (Snelling, 1994b). Production and environmental effects may easily mask expression of many reproductive traits. For example, an evaluation of the Limousin breed showed that, in general, cows that were culled because they were open, had the highest average Expected Progeny Differences (EPD) for birth weight, weaning weight, yearling weight and total maternal as compared to the average EPD for groups of cows culled for other reasons. This suggests that genetics for increased levels of growth and maternal performance may increase the percentage of cows that are culled for reproductive failure (Anderson, 1996). Furthermore, all else being equal, differences in inherent fertility are more pronounced in poor environments than in good environments. Heavy milking cows with high inherent fertility may calve regularly in good environments, but in poor environments they may have worse reproductive performance than inherently less fertile, but lighter milking cows (Martin, 1992). This could also be true for growth traits; lack of adequate nutrition for those cows with genetics for
high growth and/or high milk production may mask the genetics of fertility in many cows.

Traits that influence lifetime reproductive performance of the beef cow need to be identified and measured. Age at puberty (AP), when defined as the age at first behavioral estrus, has been shown to be desirably associated with reproductive performance in the beef cow (Morris et al. 1994, Laster et al. 1979). Economic efficiency can be improved when cows calve first at 2 years of age rather than 3 years of age or older (Nunez-Dominguez et al., 1991). Cows that initially calve early have been shown to be superior to their late calving cohorts in subsequent reproduction and productive performance (Rege and Famula, 1993). However, because of the difficulty in collecting data on AP, indirect selection for AP is likely to be more feasible in the current industry. Land (1973) indicated that the quantitative expression of sexual activity in males and females may be genetically correlated. Many beef cattle associations are currently reporting EPD for Scrotal Circumference (SC) in their genetic analysis. Another trait that has received considerable consideration and is reported for some breeds is Stayability (STAY) (Snelling et al., 1994a). Stayability is defined as the probability of surviving to a specific age, given the opportunity to reach that age (Hudson and Van Vleck, 1981). More specifically in beef cattle it has been defined as the probability of a cow having a calf reported at a given age or later for cows given the opportunity to reach that age. For Stayability cows are assigned a binary observation for either success (1) or failure (0). Selection practices based on these traits are only meaningful if they are associated with
increases in lifetime reproductive efficiency in the beef herd that enhances the economic viability of the beef enterprise. This paper reviews literature for the prediction of genetic values for fertility traits to increase lifetime reproductive performance in the beef herd.

Age at Puberty and Reproduction

Literature heritability estimates for Age at Puberty (AP) are listed in Table 2-1 and ranged from .10 to .67. Heritability estimates for AP are generally higher than estimates for many other reproductive traits. Various researchers have reported that individual sires influence percentage of heifers reaching puberty based on either age or weight (Laster et al., 1976; Laster et al., 1979; Wiltbank et al., 1966). This along with the relatively high heritability for AP indicates that the percentage of heifers reaching puberty by a given age or weight could be affected by selection of sires within a breed. However, such selection practices are only meaningful if they are associated with decreasing age at first calving and/or lifetime reproductive efficiency in the beef herd. Furthermore, AP is one trait that is relatively immune from interactions with other traits. This is probably because AP is expressed before a cow is in production (Martin, 1992).

MacKinnon et al. (1990) analyzed data from a tropical beef herd over three calf crops for correlated responses to selection for high and low line estimated breeding values for pregnancy rate. Scrotal circumference was significantly higher in high line bulls between 9 and 18 months of age. Pregnancy rates of heifers were 12% higher in the high line than in the low line
despite similar average live weights at mating. This study concluded that accelerated sexual maturity in both heifers and bulls has occurred as a result of selection for lifetime cow fertility and that such selection did not alter the progeny's growth rate.

In a Nebraska study (Gregory et al., 1979), Brahman crosses were significantly older and heavier at puberty than Hereford, Angus, Sahiwal, Pinzgauer and Tarentaise sire breed groups at puberty. However, pregnancy rates were significantly higher at 550 days for Brahman, Sahiwal and Pinzgauer crosses than Angus-Hereford crosses. Laster et al. (1976) reported no significant differences among sire breeds for pregnancy percentage and Dow et al. (1982) had similar results, reporting that pregnancy rates at 24 months of age were not significant among breed groups. However, the start of the breeding season in the study of Dow et al. (1982) was at 19.5 months of age which would not be acceptable in most management programs. Most heifers are mature enough at a given point during a typical breeding season to conceive so that AP does not adversely affect pregnancy rates. However, if nutrition is limiting, direct selection for AP may be more beneficial for improving pregnancy percentage. It has been shown that heifers developed more slowly on diets with lower energy density, reached puberty at significantly older ages, and had lower pregnancy rates than did heifers developed more rapidly when both were exposed to breeding as yearlings (Wiltbank et al., 1966, 1969). Thus, it appears that an increase in pregnancy from selection for AP must be assessed in relation to available levels of nutrition and management.
Morris et al. (1993) evaluated three selection herds and a control herd of Angus cattle in New Zealand. Selection was first applied to 1982 born animals; single selection objectives were scrotal circumference (SC), AGE+, and AGE-, where '+' and '-' indicate selection for greater or lesser AP. The purpose of the paper was to report on the genetic parameters for AP in heifers, weight at puberty in heifers, scrotal circumference, 13 month weight and calving day, to compare the performance of young animals in the selection and control herds, and to assess prospects of achieving a correlated response in calving rate. Heritability estimates were .15, .30, .24 and .33 for AP, weight at puberty in heifers, SC, and 13 month weight, respectively. A genetic correlation between AP and SC of -.81 +/- 0.38 was reported. The response to selection for AP after nine years of selection was 16.5 days between the AGE+ and AGE- herds. The direct response to selection for SC during the same period was 1.6 cm above the control. Lifetime cow reproduction should respond to selection for decreased AP and increased SC.

When cows calve first at two years of age rather than three years of age or older, economic efficiency can be improved (Núñez-Dominguez et al., 1991). Early initial calvers are superior to their late calving cohorts in subsequent reproduction and productive performance (Rege and Famula, 1993). Thus, producers that place a high priority on having a high proportion of their heifers pregnant early in a fixed breeding season are justified.

Morris and Cullen (1994) estimated genetic correlations between puberty traits of males and females for yearling and lifetime pregnancy rates in beef cows
up to 5 mating/calving years for each cow using 269 paternal half-sib groups. The genetic correlations between age at first estrus with yearling and lifetime pregnancy rates were -.30 and -.29, indicating favorable associations. Other studies exist, although limited, that indicate similar relationships between AP and subsequent lifetime reproduction. Laster et al. (1979) reported a correlation between AP and percentage pregnant that was relatively low \( r = .42 \), while there was a higher association \( r = .75 \) between AP and percentage calving the first 25 days of the calving season. Splan et al. (1996) found similar results in 2,936 crossbred heifers. The estimated genetic correlations in her study also indicated that selection for AP resulted in slightly increased calving rates in heifers. Lesmeister et al. (1973) reported that heifers tending to conceive early in their first breeding season tend to calve earlier throughout the remainder of their productive lives compared to later conceiving heifers. Werre and Brinks (1986) reported favorable correlations among line of sire AP means with heat cycle of conception for the first four lactations. These correlations indicate that heifers from lines of cattle with earlier puberty tended to conceive earlier each year through four breeding seasons. This same study also found favorable relationships between AP and adjusted weaning weights and most probable producing ability.

Selection for early maturity should contribute to profit in the beef herd as it relates to fertility. However, management programs have a significant effect on subsequent reproduction and must be considered in selection of replacement females. Unfortunately, direct selection for AP in females is seldom practiced.
because of the time and labor required to obtain necessary data (Anderson et al., 1991a).

Scrotal Circumference

Various possibilities exist where either direct or indirect selection may result in more rapid genetic progress. Indirect selection using an alternative trait may or may not be better than direct selection for the trait of interest. Also one alternative may be better than the other, or it may be better only when combined in an index with the trait of interest. Furthermore, two indirect traits may each not be as good as the trait of interest but may be better when combined in an index (Searle, 1965). In the beef industry indirect selection is often practiced for traits that are expensive and difficult to measure or cannot be measured until after such time that selection normally occurs in the herd, also, the desired trait may only be observed in one sex. This is the case for many reproductive traits where the trait is usually only measurable in one sex and the expression of most female reproduction occurs long after the selection of replacement females has occurred. For some traits it is possible that we might achieve more rapid progress by selecting for a correlated trait than from selection for the desired trait itself. According to Falconer (1989) the merit of indirect selection relative to that of direct selection may be expressed as the ratio of the expected responses. Bourdon (2000) gives the following equation.
\[ \frac{CR_{x/y}}{R_x} = \frac{i_y \ r^\wedge_{BVy} \ r_{BVy} \ i_x \ r^\wedge_{BVx} \ BVx}{i_x \ r_{BVx} \ BVx} \]

Where,

- \( R_x \) is the direct response of the desired trait \( X \), if selection were applied directly to it.
- \( CR_{x/y} \) is the correlated response of trait \( X \) resulting from selection applied to trait \( Y \).
- \( i_y \) is the intensity of selection for trait \( Y \).
- \( i_x \) is the intensity of selection for trait \( X \).
- \( r_{ia} \) is the genetic correlation between trait \( X \) and \( Y \).
- \( r^\wedge_{BVy} \ BVy \) is the accuracy of selection for trait \( Y \).
- \( r^\wedge_{BVx} \ BVx \) is the accuracy of selection for trait \( X \).

Let \( X \) represent the trait of interest (female reproductive trait) and \( Y \) represent the secondary trait (scrotal circumference for example) where selection is applied. Accuracy of selection in this example should easily be as high and likely higher due to ease of collecting scrotal data as compared to that of many female reproductive traits (age at puberty for example). Many sires in National Cattle Evaluation due to large numbers of progeny records reported attain accuracy levels above .90 for SC. It can readily be seen that selection for SC will be better if \( r_{ia} r^\wedge_{BVy} BVy \) is greater than \( r^\wedge_{BVx} BVx \). Toelle and Robinson (1985) has indicated that even if a low genetic relationship existed between SC and female reproductive traits indirect selection may still be more efficient than direct selection if the
selection intensity on the male trait were large enough. Furthermore, the
generation interval should be shorter in males than in females, which could also
increase the value of indirect selection schemes.

Land (1973) investigated the relationship between males and females in
two species, the mouse and the sheep. In the mouse, Land reported a .97
correlation between mean testis weight and mean ovulation rate of five mouse
lines selected for ovulation rate. In sheep, Land (1973) examined the growth rate
of the testis diameter of pure and crossbred males and reported that the testis
diameter was greater in the breed with the higher ovulation rate. Subsequently
numerous researchers have investigated the relationship between scrotal
measurements in the male and AP in the female. Koots et al. (1994) reported a
weighted mean heritability for SC of .48 across 25 studies. The favorable
relationship between SC in males and reproductive traits in females has been
documented in several studies. Morris et al. (1992) reported estimates for
heritability and genetic correlation's for SC and AP. Scrotal circumference
measurements were taken on bulls at an average age of 8, 11, and 13 months.
Puberty was recorded for heifers from ages 8 to 14 months. Heritabilities for SC
were .50, .33 and .29 for the three respective age groups, while heritability for AP
was .33. Genetic correlations between SC and AP were -.11, -.41, and -.60 for
the three age groups of bulls.

Toelle and Robinson (1985) estimated genetic correlation's between SC in
the male and female reproductive traits with data from two Hereford herds
involved in long term selection programs. In this study data from 528 male and
645 female progeny of 63 sires were used to estimate genetic correlations between female and male reproductive traits. Testicular measurements of circumference, diameter, length and volume were obtained on bulls at 205 and 365 d of age. Testicular growth measures were defined as differences between 205 and 365-d measurements. Traits utilized from females were three age-at-first-breeding traits, two age-at-first-calving traits, two pregnancy rate traits, rebreeding interval and calving interval. Testicular circumference had a less favorable correlation to female reproductive traits than length, volume or diameter. However, average correlations were similar (-.26, -.30, -.34 and -.31, respectively). Genetic correlation estimates of testicular measurements with female reproductive traits were similar for measurements taken at 205 or 365 days except correlations tended to be larger at 365 days. Selection on testicular measurements at 365 days would be more effective and likely more practical than selection at 205 days for improving female reproduction.

Swanepoel et al. (1992) estimated relationships of lifetime fertility of Bonsmara cows with growth and SC of their calves. Cows were divided into long calving interval and short calving interval groups according to their average lifetime calving interval. Scrotal circumference for calves from the short calving interval group was significantly larger than bull calves from the long calving interval group at 12 and 15 months of age. This study concluded that high lifetime fertility is not incompatible with growth and a desirable relationship exists between SC and lifetime fertility.
The most effective methodology for predicting genetic values for many traits is implementing the use of multiple trait models. Multiple trait models are useful to improve the accuracy of genetic evaluations of lowly heritable traits or to account for selection bias. Favorable relationships have been reported between SC and growth traits (Latimer et al., 1982; Bourdon and Brinks, 1986; Kriese et al., 1991). Bourdon and Brinks (1986) found that SC, adjusted for days of age and age of dam, was positively correlated genetically and phenotypically with all weights and was most highly correlated with 365-d weight. They reported a genetic correlation between adjusted SC and 365-d weight of .44 +/- .16 which is in general agreement with other studies. However in most beef cattle herds animals are culled from the breeding herd at weaning and subsequent measurements are not available. Because of this, weaning weight would be a more suitable trait than yearling weight to be included in a multiple trait model for the prediction of breeding values for SC to both increase accuracy of selection and to account for culling bias. Many breed associations are currently using multiple trait models to report EPD for SC in their genetic evaluations.

Moser et al. (1996) selected 9 pair of Limousin bulls based on phenotypic SC measurements that represented an 8 cm difference in adjusted yearling SC. Each pair of bulls originated from the same contemporary group and had similar EPD for growth traits. No significant line differences were reported in heifer progeny for AP when lines were formed based on high or low yearling phenotypic SC measures. However, when bulls were sorted into high, average and low line groups based on SC EPD, a significant difference was reported for AP between
the high line SC EPD and the other two lines. This study further reported no significant differences in pregnancy percentage when bulls were grouped based on phenotypic measures of SC or SC EPD. This is in agreement with other studies (Gregory et al., 1979; Laster et al., 1976; Dow et al., 1982), where it has been shown that AP is not always associated with increased pregnancy percentage. It appears that most heifers are mature enough at a given point during the breeding season to conceive and that AP may not adversely affect pregnancy rates in most herds once heifers have been given a chance to reach puberty.

Scrotal circumference is an easily measured trait in bulls. It has been shown that selection for increased SC is associated with decreased AP in females and increased lifetime reproductive performance of the cow herd. Furthermore, selection for SC has been shown not to be antagonist to selection for increased growth and may also result in more rapid genetic improvement for female reproduction than selection for many female reproductive traits directly due to favorable genetic relationships and the increased selection intensity on males. Scrotal circumference is a useful tool for indirect selection of female reproduction; therefore those breeds not currently reporting EPD for SC should include it in their genetic analysis for subsequent consideration in producer selection schemes. Furthermore, because of the favorable genetic relationships, selection should be implemented in both sexes to enhance genetic improvement in reproductive traits of the beef herd.
Reproductive Tract Score

Anderson et al. (1991a) summarized data from Colorado State University on Reproductive Tract Scores (RTS) as a trait that can be used to estimate pubertal status of the beef heifer by rectal palpation of the uterine horns and ovaries. There are obvious benefits from RTS for making beef heifer management decisions because of the favorable response to synchronized breeding and to breeding season pregnancy rates (Table 2-2). Heifers with more mature reproductive tracts had higher pregnancy rates and calved earlier. There also appears to be some genetic potential to using RTS as a measure of puberty in the beef female.

For RTS, heifers are assigned a value from 1 to 5. A RTS of 1 is assigned to heifers with infantile tracts and are likely the furthest from cycling at the time of examination. Heifers given a RTS of 2 are thought to be closer to cycling than those scoring 1, primarily due to the presence of small follicles and slightly larger uterine horns and ovaries. Those heifers assigned a RTS of 3 are thought to be on the verge of cycling, based on slight uterine tone, in addition to the presence of follicles. Heifers assigned a score of 4 are presumably cycling as indicated by good uterine tone, uterine size, and follicular growth. However, unlike heifers that are assigned a RTS of 5, heifers scoring a 4 lack an easily distinguished corpus luteum, due to the stage of the estrous cycle.

Anderson et al. (1991a) summarized results from his Masters Thesis at Colorado State University and reported a moderate heritability of .32 ± 0.17 for RTS. This estimate is within the range of literature estimates for AP and
indicates that RTS should respond favorably to selection pressure. This same study reported favorable genetic correlations of -0.37, 0.20, 0.31, and 0.53 between RTS and birth weight, weaning weight, yearling weight and pelvic area, respectively. Breed differences were also observed and generally breeds selected for milk also had higher reproductive tract scores, this is in agreement with the current literature for AP.

In a separate study, Anderson (1991b) reported a heritability of \(0.24 \pm 0.13\) for RTS on an age constant basis. Reproductive tract score was significant and favorably associated with pregnancy status after the first breeding season, day of first and second calving, and progeny weaning weight, but not pregnancy status after the second breeding season. This study also reported that heifers with RTS of 4 and 5 calved approximately one week, two weeks and one month earlier than heifers receiving a RTS of 3, 2, and 1, respectively.

Reproductive tract scores are a useful tool for producer to help in decision making for the replacement heifer. The poor reproductive performance of heifers with RTS of 1 indicates the importance of identifying and culling these heifers before the breeding season begins. The time or age at which heifers are examined depends on the desired use and the particular heifers to be evaluated. Variation within a group of heifers is only temporary, depending upon the age and maturity pattern of the heifers. For breeding, heifers should be evaluated sufficiently early enough to make necessary adjustments in the ration or start of the breeding season. If the primary use is to place selection pressure on AP, the best time to evaluate heifers is when about half of the heifers are believed to be
cycling. Scoring should coincide well with general processing as part of a yearling heifer evaluation and health program.

**Stayability**

To maximize the opportunity for profit the ideal beef female should cycle and conceive early in the breeding season and also calve on an annual basis, any female not conceiving and weaning a calf is a missed opportunity. Rogers (1972) indicated that retention of cows beyond 10 years of age is likely to result in reduced profits due to percent calf crop weaned, reduced weaning weight, loss in sale value of the cow, and death loss among cows. Using capital budgeting, Dalsted and Gutierrez (1989) indicated factors that determine the number of calves a beef cow must raise to break even. These include the initial investment, future returns and costs, salvage value, and the rate of inflation. When initial investment and salvage value are similar or net return per cow relatively high, a cow may pay for herself with 1 to 3 calves. With relatively large differences between initial investment and salvage value and low net return per cow, at least 10 to 14 calves may be required for a cow to break even. Therefore, the culling policy of non-pregnant cows should be given careful consideration. Under some circumstances it may be shown that a culling policy allowing some non-pregnant cows to remain in the herd may be more economically feasible than if replacing those cows with heifers. This is because non-pregnant cows may result in more calf weaning weight per cow exposed at breeding due to better conception rates and heavier weaning weights. Furthermore cows are less costly to maintain from
time of calf weaning until subsequent calving, and have fewer calving problems
than replacement heifers. Non-pregnant cows that are physically sound should
be considered for subsequent rebreeding because it may be more profitable to
retain rather than cull all non-pregnant cows (Neville et al., 1990).

In current analyses of Stayability in the U.S. reasons for being culled are
ignored and the assumption is that cows are culled exclusively (or at least
primarily) for reproductive failure. Indeed the amount and type of selection and
culling pressure that is applied to the beef herd is variable and depends upon
several factors, including the management system, pedigree, environmental
conditions in which the cow must perform, health, and for other performance
traits (perceived and real) such as growth, carcass, and reproduction.
Remember, in the Limousin study (Anderson, 1996) the number one reason
cows were culled was for fertility, 75% of the cows culled were for reasons not
related to fertility.

Threshold Traits

Selection among farm animals for economically important production traits
since the early 1980’s until present have relied heavily on the use of breeding
values estimated from mixed model procedures for those traits that are
expressed and inherited on a continuous scale with a normal distribution (i.e.
growth, birth weight, yearling weight, milk, and carcass traits). However selection
for other traits that are considered to be important for the overall financial health
of the enterprise has been left to the producer’s best judgment based upon some
knowledge of the trait, how it interacts with the environment, and the producer’s observations. Many of these traits are threshold traits, which are observed on a discrete basis but usually have an un-observable underlying variable that is usually normally distributed (Quaas, et al., 1988). Examples of such traits usually include traits of fitness and fertility, some examples are:

- Disease (or resistance to disease)
- Calving ease
- Calving vs. non-calving
- Single or multiple births
- Phenotypic traits (conformation, structure, etc.)
- Reproduction (stayability, pregnancy status, reproductive tract score)

The problem has not been entirely that we do not have the capability to estimate breeding values for these traits because, theory, knowledge of modeling and interpreting the results for these traits are expanding. Threshold traits can be more difficult and time consuming to measure. For example, a fertility trait in beef cattle might be the probability of a female having her second calf at three years of age. A female may be culled from the herd at any time before having her second calf for any number of reasons that may or may not be related to her inherent fertility. Thus, accurate and complete records of these traits are required before breeding values from which to make selection that will result in an anticipated directional change in the herd can be accomplished. With this being the case many beef cattle associations are now moving to whole herd reporting systems of recording. Beginning in 1995 the Red Angus Association of
America was the first beef breed association to require whole herd reporting for the primary purpose of recording reproductive data. Whole herd reporting should make available for the analysis information that will aid in the development of EPD for many threshold traits.

Analysis of Threshold Traits

Threshold models are more appropriate for analysis of categorical data than linear models (Thompson, 1979; Gianola, 1982). That superiority was confirmed in simulation studies (Meijering and Gianola, 1985; Hoeschele, 1988). However, in field data the results were mixed. For reproductive traits, several analyses with actual data (Olesen et al., 1994; Matos et al., 1997) have shown very small differences between the threshold and the linear model. In particular, Moreno et al. (1997) have shown that estimates of variance components in the binary models were biased.

Summary

Heritability estimates for age at puberty suggest positive response to selection. The literature, although limited, indicates that age at puberty and scrotal circumference are favorably associated with subsequent yearling and lifetime reproduction of the beef female, and selection for pubertal traits in both the male and female can effectively increase percentage of heifers calving early in their first season and subsequent lifetime production. In addition, selection for pubertal traits does not appear to be incompatible with growth traits.
Reproductive tract scores appear to be moderately heritable and favorably associated to decreased age at puberty in the beef heifer, increased pregnancy rate in the heifer, and day of first and second calving. T. E. Kiser (personal communication) suggested that a relationship may exist between the diameter of the ovaries in females and SC in males using ultrasound technology. Ultrasound is an accurate method of measuring the growth and diameter of ovaries in the beef heifer. Researchers should investigate further, the genetic value of reproductive tract scores measured either by rectal palpation or ultrasound as methods to evaluate pubertal status of the beef heifer.

Measurements of most lifetime reproductive traits become available late in a cows life and the low heritability of most reproductive traits slow the rate of genetic improvement in the beef cow herd. Researchers have indicated that lifetime cow reproduction should respond favorably to selection for decreased age at puberty in the heifer and increased scrotal circumference in the male. Selecting for pubertal traits in both the male and female may be an economical means for beef producers to genetically increase reproductive efficiency in the beef herd.
<table>
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<sup>a</sup> From Anderson et al., 1991a

<sup>b</sup> Average of four trials.

<sup>c</sup> Average of three trials and average number of days into the breeding season compared to RTS 5.
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CHAPTER 3
LINEAR AND THRESHOLD MODELS TO ESTIMATE HERITABILITY AND TRENDS FOR STAYABILITY IN THE HEREFORD BREED

ABSTRACT

Data reported to the American Hereford Association (AHA) through May 1998 were used to evaluate genetic parameters for Stayability. Included in the data were only those cows that had at least one performance record for a calf reported. Furthermore, included were only those cows born in 1970 and later, and only those sires that had at least 50 daughters in production. Contemporary groups (CG) were formed based on cows that had the same birth year, breeder, and had their first and last reported calves in the same herd. After edits the data set included 147,490 cows represented by 1,695 sires in 32,388 contemporary groups. Stayability was defined for this analysis as the probability of a cow having a calf reported at age six or later for cows given the opportunity to reach that age. Both threshold (TM) and linear model (LM) analyses were evaluated. The model included fixed sire and cow group effects and the random effects for contemporary group and sire. The SIRE and residual variance components were estimated using REML for the LM model and by the counterpart of REML for TM analysis. Sire and residual variances were estimated using three different variance ratios for the random CG effect at 5, 10 and 20%. Heritability estimates were higher for TM than for LM analysis in all cases. Heritabilities, SIRE and residual variance components for both TM and LM models increased with increasing variance ratios. Heritabilities for LM analysis were .24, .27 and .28 for the variance ratios of 5, 10 and 20%, respectively. Heritabilities for TM analysis were .39, .44 and .47 for the variance ratios of 5, 10 and 20%, respectively.
Trends for fixed effects among LM models are virtually identical to those for TM models.

Introduction

The probability of survival to a specific age, given the opportunity to reach that age has been used as the definition of stayability in dairy and beef herds (Hudson and Van Vleck, 1981; Snelling, 1994a) representing a measure of sustained reproductive ability (Snelling, 1995). In an evaluation of the Limousin breed, infertility was identified as the primary reason Limousin cows were culled, although only accounting for fewer than 25% of all identified cullings (Anderson, 1996). Greer et al. (1980) and Nunez-Dominguez et al. (1991) have reported similar results in research herds. Fertility is expressed later in life, and most selection schemes are based on phenotypic indicator traits for fertility and growth traits that are expressed at the time of selection. Tanida et al. (1988) found little or no relationship between traits measured early in life and longevity in a research Hereford population. Expected Progeny Differences (EPD) for traits that influence reproductive performance of the beef herd need to be reported. In fact, many beef breed registries are beginning to collect and report reproductive performance and are beginning to report fertility trait EPD. Stayability is one such trait. While Stayability is considered by many to be a fertility trait, the collection of data used to evaluate Stayability may not adequately address the issue of fertility. It may well be confounded with selection for traits other than those directly related to fertility. Therefore, selection for Stayability may reflect
an increase in the herd life of cows, but may not be indicative of inherent fertility. This paper investigates the use of linear and threshold models to estimate heritability and trends for Stayability in the Hereford breed.

Material and Methods

Data reported to the American Hereford Association (AHA) through May 1998 were used to evaluate genetic parameters for Stayability. Included in the data were only those females that had at least one calf performance record for a calf reported. Furthermore, included in the sample data set were only those females born in 1970 and later, and only those sires that had at least 50 daughters in production. Records were edited for missing registration numbers, date of birth, breeder, sex and pedigree (sire). Contemporary groups (CG) for Stayability were formed based on females that had the same birth year, breeder, and had their first and last reported calves in the same herd. The first and last reported calves for females in the same contemporary group, while in the same herd may have been in different years. For example, two females from the same herd and the same birth year may have both calved in their second year, however, one female may have had her last reported calf as a four year old and the other as a seven year old. After edits the sample data set included 147,490 females represented by 1,695 sires in 32,388 contemporary groups.

Stayability was defined for this analysis as the probability of a cow having a calf reported at age six or later for cows given the opportunity to reach that age. Cows were considered to be eligible to receive a record for the trait if they had a
calf reported at any age and the cow was six years or older as of May 31, 1998. Because of incomplete reporting of data it was not required that a cow have a calf reported each year (Snelling et al., 1994a). Cows not receiving observations were females not yet 6 years of age or those females that calved with their cohorts in their sixth year but were not yet six when they gave birth. Cows were assigned a binary stayability observation for either success (1) or failure (0).

Threshold models are more appropriate for analysis of categorical data than linear models (Thompson, 1979; Gianola, 1982). That superiority was confirmed in simulation studies (Meijering and Gianola, 1985; Hoeschele, 1988). However, in field data the results were mixed. For reproductive traits, several analyses with real data (Olesen et al., 1994; Matos et al., 1997) have shown very small differences between the threshold and the linear model. In particular, Moreno et al. (1997) have shown that estimates of variance components in the binary models were biased. Therefore, for comparison, in this study both threshold (TM) and linear model (LM) analyses were evaluated.

Both threshold (TM) and linear model (LM) analyses were evaluated. The following model was used for the analyses:

\[ Y_{ijklq} = CG_i + SIRE_{YR_l} + COW_{YR_j} + SIRE_{jk} + e_{ijklq}, \]

Where:

\( Y_{ijklq} = \) record on cow ijk\(iq; \)

\( CG_i = \) random effect of contemporary group i;

\( SIRE_{YR_l} = \) fixed effect of group l of sires of dams;

\( COW_{YR_j} = \) fixed effect of group j of cows;
SIRE_{jk} = \text{random effect of sire of cow k in group j};

E_{ijklq} = \text{random residual.}

Random effects were assumed to be mutually uncorrelated with diagonal dispersion matrices. Sire and residual variances were estimated using three different variances for the random CG effect at 5, 10 and 20%. Using these assumptions the CG effect could be absorbed.

Sires and cows were grouped by year of birth. After editing the data, sire groups included years 1962 through 1990 while cow groups were those years 1970 through 1991. A small number of females that meet the editing criteria were born in 1992 and were combined with those females born in 1991. Also, a small number of sires that were born prior to 1962 were combined with those born in 1962.

A program based on principles described by Misztal et al. (1989) was used for the analysis. The SIRE and residual variance components were estimated using REML for the LM model analysis and by the counterpart of REML for TM analysis (Gianola and Foulley, 1983). After absorption of CG effects, coefficient matrices were inverted at each round of iteration for both models. In TM analysis, iteration involved Fisher’s scoring and a modification of the expectation-maximization (EM) algorithm for variance components (Misztal et al., 1989). Heritability (h^2) for the TM and LM was calculated as a trait of the cow.
Results and Discussion

Figures showing the distribution and trends for number and percentage of stayability scores for the sample data sets are in Figures 3-1 and 3-2, respectively. Figures 3-3 and 3-4 show the number and percentages of stayability scores for years 1950 through 1991 and was edited exactly the same as the sample data set, except the sample data set only included daughter records from sires that had at least 50 daughters in production. Figures comparing the sample data set and the complete data set show similar trends over the same period of time. Of particular interest are the figures showing the percentages of females by stayability score. While, the average incidence for all the years included in the sample data (Figure 3-2) set was 49% and 51% for failure and success, respectively, the trend by year did not follow the same incidence rate. Approximately 65% of the females were successful in reaching the age of 6 in the year 1970. There was a decreasing pattern in those females that were successful until the year 1977 when a higher percentage of females failed to reach the age of 6 than those that succeeded. This trend continued to the years 1982 through 1986 when the incidence rate was approximately 50% for success and failure. From 1986 until 1991 there was a steady decrease in the number of females that successfully had calves reported after they reached 6 years of age. By 1991 only 31% of the females had calves reported after the age of 6 years. This same trend was also true for the complete data set (Figure 3-4) where in 1991 only 32% of the females that entered production prior to 6 years of age had a calf reported to AHA after the age of 6 years. The sharper decrease in
the last two years may be exaggerated, as many of those females may still be in production beyond the age of six but a calf was not yet reported. This may actually bias a genetic evaluation of the youngest females in the analysis and their sires more than for older females.

The trends for success and failure prior to 1970 were dissimilar to those after 1970. Between the years of 1950 to 1969 an average of 79% of females that had at least one performance record reported for a calf were successful in having a calf reported to AHA after the age of 6. The pattern peaked in the late 1950’s at over 96% and then gradually tapered to 67% by 1969. This was during a period of popularity for the Hereford breed in the United States when the AHA recorded the largest number of registrations of all beef breeds in the United States (National Pedigreed Livestock Council Annual Reports).

Of interest are the percentages of females by stayability score for each year. It has been shown that the highest amount of information in a binary trait is when incidence is approximately 50% (Abdel-Azim and Berger, 1999). While the average for this data set meets this criterion, the trend is less than desirable. The choice of 6 years has been selected because of its suggested relationship with herd profitability and higher estimates of heritability in research trials (Snelling et al., 1995) and was first reported for breeding programs in the beef industry in the 1994 Red Angus Association of America national cattle evaluation. However, several studies have shown favorable relationships between fertility traits at younger ages and lifetime reproductive efficiency (Lesmeister, 1973; Rege and Famula, 1993; Morris and Cullen, 1994). A different choice for the age
used to define stayability or perhaps indicator traits that are related to lifetime fertility may account for more information. Furthermore, other traits may be less dependent on selection and culling decisions. The current definition of stayability does not require a cow to have a calf reported each year and furthermore the trait depends on cows being culled for reproductive failure (Snelling and Golden, 1994b). As stated earlier, Anderson (1996) identified fertility as the primary reason Limousin cows are culled, accounting for fewer than 25% of all identified cullings. However, approximately 75% of all identified cullings were for traits other than those describing fertility. The current definition of stayability when based on non-inventory data collection schemes may be better described as a trait of productive herd life rather than a trait of direct fertility.

Estimates for SIRE and residual variance components and heritabilities are in Table 3-1 for all analysis. In all cases heritability estimates were higher for TM than for LM analysis. Various authors (Weller et al., 1988; Snelling et al., 1994a) have previously reported similar results. Heritabilities, SIRE and residual variance components for both TM and LM models increased with increasing contemporary group variance ratios. Heritabilities for stayability were higher in this analysis than a previous study (Snelling et al., 1994a).

Solutions for fixed sire and cow group effects for both the TM and LM models are presented in Figures 3-5 and 3-6, respectively. The SIRE and residual variances were estimated using three different variances for the random CG effect at 5, 10 and 20%; solutions are presented for the variance ratio of 5% only. Among the LM models, the trends for the fixed effects and heritability are
virtually identical as they are for TM models. In both the LM and TM models, SIREYR had a positive trend while COWYR was a negative trend. The magnitude of the differences between SIREYR and COWYR appear to be different between the TM and LM, diminishing in later years for the LM and increasing in the TM. This is explained as a scaling difference between TM and LM model analysis. The decreasing trend among females corresponds to decreasing numbers of females staying in production. Sire year corresponds to genetic trend while COWYR corresponds to both the genetic and environmental trend. Producers may be retaining daughters of popular sires in the herd for longer periods of times than non-popular sires for traits other than fertility. If antagonistic relationships existed between selection criteria for sires and reproductive efficiency for females this may account for the differences between SIRE and COW GROUPS trends.

Implications
Given the current definition of Stayability for beef herds, genetic trend can be achieved based on selection. However, stayability as described may be a more accurate description of culling and retention practices which may be more subjective than objective in many breeding programs. Also, the genetic evaluation for females born in the most recent years may be more biased than older females because they have reached the age of six, are still in production, but have not yet had a calf reported. This is unfortunate, as these females would represent females currently in production in addition to being daughters of young
and current sires available for breeding. If selection of lifetime production of the beef female is of value to the beef producer, it then appears warranted that genetic programs move to whole herd inventory based reporting procedures. Inventory based reporting procedures should place more emphasis on recording information regarding lifetime reproductive performance so that genetic values for traits more directly related to inherent fertility can be published.
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National Pedigreed Livestock Council. 272 Meetinghouse Lane, Brattleboro, VT, 05301.


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*The variances of the random contemporary group effect were tested at 5, 10, and 20% of the residual variance.
Figure 3-1  Distribution and Trends for Number of Success and Failure Stayability Scores (Sample Data Set)
Figure 3-2  Distribution and Trends for Percentage of Success and Failure Stayability Scores (Sample Data Set)
Figure 3-3  Distribution and Trends for Number of Success and Failure Stayability Scores (Complete Data Set)
Figure 3-4  Distribution and Trends for Percentage of Success and Failure Stayability Scores (Complete Data Set)
Figure 3-5  Solutions for Fixed SIRE and COW GROUP Effects for the Threshold Model (Var Ratio 5)
Figure 3-6 Solutions for Fixed SIRE and COW GROUP Effects for the Linear Model (Var Ratio 5)
Traits of fertility have a large economic impact for cow-calf producers. Most traits of fertility are threshold traits which are observed and recorded on a discrete scale. Furthermore, traits of fertility are generally perceived to have low heritabilities, are difficult to record and interpret, are generally expressed later in life and therefore have not been included in National Cattle Evaluation programs to the extent as growth and carcass traits.

Scrotal Circumference, Heifer Pregnancy, and Stayability are three reproductive traits currently being published by some beef breed registries. While stayability is generally considered by many to be a trait of fertility, the data currently used to evaluate Stayability may not adequately address the issue of inherent fertility. This research has indicated that with the given definition of Stayability genetic trend can be achieved. However, Stayability as described may be a more accurate description of culling and retention practices which may be more subjective than objective in many seedstock breeding programs.

Traits that influence lifetime reproduction of the beef female need to be identified, measured, and recorded in national beef breed databases. Many national beef breed registries have already implemented whole herd reporting strategies that should allow
for a more accurate reporting of beef herd reproduction data. Inventory based reporting schemes should place more emphasis on recording information regarding lifetime reproductive performance so that genetic values for traits directly related to inherent fertility and lifetime reproduction can be published.