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REVIEW

Review: Reproductive Traits and Their Heritabilities in Beef Cattle

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ABSTRACT

Fertility is a complex trait in beef production systems and genetic evaluation procedures, which is partly due to the numerous measures used to assess reproduction. Beyond beef cattle, fertility measures vary according to animal species, and even within beef cattle, they vary by breed, location, sex, and class. Fertility is of significant economic importance to beef cattle producers, and therefore should be included in their breeding objective. However, traits considered indicative of fertility are in general of low heritability, are expressed late in the life of an animal, or both. Complicating genetic analyses is the binary nature of many of these traits because of truncation of data from short-controlled breeding seasons (typically 60 to 90 d long). Additionally, implementation of genetic prediction of reproductive traits in beef cattle has previously been hampered by a lack of total-herd data reporting systems. This review evaluates historic and current measures of assessing fertility and the heritabilities of these traits in beef cattle. Successful implementation of fertility traits into genetic improvement programs is dependent on whole-herd reporting and improved analysis techniques.

Key words: beef cattle, reproduction, fertility, heritability

INTRODUCTION

Biological and economical efficiencies of cow-calf production are largely dependent on successful reproduction (Dickerson, 1970). Improvements in reproductive performance can be up to 4-fold more important than improvements in end-product traits in a conventional cow-calf operation selling market calves at weaning (Melton, 1995). National cattle evaluations have previously focused primarily on production traits, including growth and carcass traits, rather than on reproductive traits because of the availability of data and ease of analysis procedures (Evans et al., 1999). Consequently, effective selection tools for genetic improvement of reproductive traits are limited (Gutiérrez et al., 2002). Improvement in reproductive efficiency has generally been slow because of low heritability, the binomial nature of a short-controlled breeding season, or late expression of traits in the life of the animal (MacNeil et al., 2006). Much work has been done to improve reproductive efficiency through crossbreeding and improved management techniques (Minick Bormann et al., 2006), although less has been done through direct selection. However, recording data from direct measures of reproductive traits, along with improved methodologies to analyze such data, suggests the opportunity for improving reproduction through selection.

Fertility is a general term and not a single, easily defined trait. It instead encompasses a variety of traits important in animal reproduction. Reproduction is dependent on several factors, including species (i.e., *Bos taurus*, *Bos indicus*), breed, location, sex, and animal class (Martin et al., 1992; Patterson et al., 1992; Lopez et al., 2006). Successful reproduction is dependent on many factors that require the capability of sires and dams to achieve each critical stage of reproductive development (Foote, 2003). Whereas estimates of heritability for many reproductive traits are low, some exist that have moderate heritabilities, and there are important genetic correlations between reproductive traits and other production traits that are moderately to highly heritable. Consequently, consideration of reproductive traits in selection programs appears feasible, whether by direct or indirect selection (Meyer et al., 1990). Heritability estimates of reproductive traits are reviewed herein. However, genetic relationships of these traits with other production traits of importance, and the consequences of selection for reproductive traits, warrant further review.

Genetic prediction for fertility traits in beef cattle production systems has been hindered by the need for data

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to be collected from whole- or total-herd reporting systems (Middleton and Gibb, 1991; Rust and Groenveld, 2001; Urioste et al., 2007a,b); specifically, data must be recorded from each cow each year. Several US breed associations are now recording these data, with the objective of conducting genetic prediction of reproductive traits. Development of guidelines for these traits by the Beef Improvement Federation has been beneficial in these efforts (Bertrand, 1999; Hough, 2000; Hough and Ponder, 2001). However, in general, the US beef industry has been slow to adopt these data-recording protocols and reach a unified effort for genetic improvement of fertility.

Given the potential for genetic evaluation of fertility and the importance of reproduction to economic performance, the following review describes reproductive measures of fertility collected from beef cattle and heritability estimates for most of these traits. Some traits described herein have not had ample data collected for heritability estimates; however, they are discussed because the physiology underlying these traits is important to understanding the traits that do allow genetic parameter estimation.

REVIEW AND DISCUSSION

Heritability estimates for reproductive traits are listed in Table 1. In general, heritability estimates of reproductive traits in cattle are low because of a large, unexplainable portion of residual variation (Veerkamp and Beerda, 2007) and the considerable influence of management on many of these measures (Hoekstra et al., 1994; de Vries and Veerkamp, 2000). The residual variation is likely due to both unknown environmental effects and as yet unexplained additive and nonadditive genetic effects because of the threshold nature of pregnancy and management for high pregnancy rates. Low heritability estimates do not necessarily suggest that genetic control of reproductive traits is less economically important than management inputs or vice versa. Nonetheless, reports of the low heritable nature of reproductive traits have led to an assumption of small genetic variability, and hence ineffective selection (Hahn, 1969). However, some reproductive traits, including pregnancy rate, show evidence of substantial genetic effects (Weigel, 2006; Veerkamp and Beerda, 2007). Such genetic effects may be both additive and nonadditive, both of which are difficult to quantify given the binary nature of pregnancy and the use of a binary trait to explain underlying continuous genetic variability. Various techniques have been used to quantify that underlying genetic variability (Snelling et al., 1995). In addition, the expression of heterosis in several reproductive traits indicates that improvements in reproductive efficiency can be realized through crossbreeding strategies, which improve nonadditive genetic value. Earlier puberty (Martin et al., 1992), increased pregnancy rate (Winder et al., 1992; Olson et al., 1993), heavier birth and weaning weights (Olson et al., 1993), decreased dystocia (Weigel and Barlass, 2003), increased longevity (Weigel and Barlass, 2003), and decreased calving interval (Wall et al., 2005) have all been associated with improvement from crossbreeding. Therefore, despite a body of evidence indicating the low heritable level of reproductive traits, genetic improvement of fertility, or at least a prevention of deterioration, may be possible. This review focuses on the various measures of fertility and the additive genetic control of those measures with the goal of sustained genetic improvement by the beef industry. Although nonadditive genetic effects (i.e., crossbreeding) are not the focus of this review, these genetic components are addressed when necessary to complete this concise review.

Female Reproductive Measures

In general, domestic beef cattle are not considered highly fertile or reproductively efficient. The per-service calving rate for AI or natural service is approximately 50 to 60% (Parkinson, 2004). Although there does not appear to be substantial documentation of selection progress in reproductive traits, improvements have been achieved through management strategies to minimize infertility (Parkinson, 2004). In the dairy industry, declines in female fertility have been quite dramatic because of heavy selection pressure on milk production traits, given the unfavorable genetic correlations between milk yield and fertility (Darwash et al., 1997). Females are generally considered subfertile during lactation. With the genetic improvements in milk yield and the associated unfavorable correlations with fertility, conception rates in dairy cows have declined by 25% since 1951 (Lucy, 2001), and pregnancy rates decreased by 0.45% per annum in the United States from 1975 to 1997 (Royal et al., 2002). Improved reproduction in higher producing herds has been demonstrated (Nebel and McGilliard, 1993); however, such improvements are most likely due to better feeding and management strategies (Lucy, 2001).

Reproduction is an inherent event, but related traits are not readily measured directly on the animal itself, other than through the success or failure of conception or pregnancy. It is a function of the underlying genetic potential of the endocrine and physiological factors that contributes to overall fertility (Eler et al., 2002). Increasing efficiency of a cow-calf herd requires improvement of fertility of both cows and yearling heifers (Smith et al., 1989). Additionally, the success of a replacement heifer development program is largely dependent on fertility (Buskirk et al., 1995). Beef female fertility has been recorded and measured in a multitude of ways, including age at first calving, calving date, first insemination conception (nonreturn rate), days to first breeding (days open), pregnancy rate, calving interval, longevity, and stayability. Besides the variability in fertility measures and no agreed on trait from which to evaluate and select animals, the time interval required to record such data can be quite lengthy, reduc-

Table 1. Summary of heritability estimates (h^2) for commonly used reproduction traits in beef cattle

Trait	h^2	References
Age at first calving	<0.10	Smith et al., 1989; Martínez-Velázquez et al., 2003
	0.20 to 0.30	Morris et al., 1992, 2000; Gutiérrez et al., 2002
Age at puberty	<0.10	McInerney, 1977
	0.10 to ≤0.200.40	Arije and Wiltbank, 1971; Smith et al., 1989; Martínez-Veláquez et al.,
	to ≤0.50	2003Laster et al., 1979; Lunstra, 1982; King et al., 1983; Martin et al., 1992
	≥0.60	Smith et al., 1976; Werre and Brinks, 1986; MacNeil et al., 1984
Calving date	<0.10	Buddenberg et al., 1990; MacNeil and Newman, 1994; Morris and Cullen, 1994; Morris et al., 2000
	0.20 to ≤0.30	MacNeil et al., 1984; Buddenberg et al., 1990; Gutiérrez et al., 2002
	0.40 to ≤0.50	Cundiff et al., 1986
Calving rate	<0.10	Meyer et al., 1990
	0.10 to ≤0.20	Meyer et al., 1990
Calving success	<0.05	Meyer et al., 1990
	0.05 to ≤0.10	Meyer et al., 1990
Calving to first insemination	<0.10	Donoghue et al., 2004a,b
Days to calving	<0.10	Meyer et al., 1990; Donoghue et al., 2004b
First-service conception rate	<0.10	Minick Bormann et al., 2006
	0.20 to ≤0.30	Dearborn et al., 1973
Heifer pregnancy	<0.20	Evans et al., 1999
	0.20 to ≤0.30	Doyle et al., 2000
Number of calves	<0.10	Meyer et al., 1990; Martínez et al., 2004a
	0.10 to 0.20	Martínez et al., 2004a,b
	0.30 to ≤0.40	Meyer et al., 1990
Pregnancy rate	<0.10	Toelle and Robison, 1985; Morris and Cullen, 1994; Mathiews et al., 1995; Morris et al., 2000
	0.10 to ≤0.20	Evans et al., 1999; Morris et al., 2000; Martínez-Velázquez et al., 2003; Minick Bormann et al., 2006
	0.20 to ≤0.30	Doyle et al., 1996, 2000; Evans et al., 1999; Thallman et al., 1999
Probability of pregnancy	<0.10	Koots et al., 1994
	0.10 to ≤0.20	Evans et al., 1999
	0.20 to ≤0.30	Snelling et al., 1995; Doyle et al., 1996, 2000
	0.50 to ≤0.60	Eler et al., 2002
Scrotal circumference	0.20 to ≤0.40	Latimer et al., 1982; King et al., 1983; Knights et al., 1984
	0.40 to ≤0.50	Neely et al., 1982; Bourdon and Brinks, 1986; Nelsen et al., 1986; Lunstra et al., 1988; Smith et al., 1989; Morris et al., 1992, 2000; Martínez-Velázquez et al., 2003
	0.50 to ≤0.80	Coulter and Foote, 1979; Lunstra, 1982; Evans et al., 1999

ing the amount of available data from many populations. Often, even with sufficient data, heritability estimates of these reproductive measures are quite low (Mackinnon et al., 1990; Gutiérrez et al., 2002). Additionally, limited information on female fertility is available from pasture mating situations (Meyer et al., 1990). Subsequently, various measures used to assess female fertility, their definitions, justification for use, and the heritability of those traits are discussed. One of the goals of this review is to prepare a basis from which a concerted effort can be made by the industry to improve beef cattle fertility and improve profitability.

Age at Puberty

Age at puberty is used as a measure of heifer fertility and may influence subsequent reproductive trait performance. Other traits closely related to age at puberty that are also used as predictors of heifer fertility include age at first corpus luteum (used by the Australian Beef Cooperative Research Centre; Cooperative Research Centre for Beef Genetics Technologies, 2006), age at first estrous, and age at first breeding (Herring and Patterson, 1997). Reproductively efficient heifers reach puberty earlier, and therefore can potentially conceive earlier in the breeding season. This trait is influenced by a number of factors, including BW, nutritional status, and, in particular, breed (Martin et al., 1992). Specifically, differences in age at puberty have been attributed to differences in sire breeds. Gregory et al. (1979) compared age at puberty in heifers produced from Hereford or Angus dams crossed with Brahman, Sahiwal, Pinzgauer, and Tarentaise sires. Heifers sired by Pinzgauer or Tarentaise bulls had an earlier average age at puberty (303 ± 5.7 and 318 ± 6.3 d, respectively) than heifers sired by Brahman or Sahiwal bulls (398 ± 5.8 and 383 ± 6.4 d, respectively). Laster et al. (1972) found similar differences in age at puberty in heifers produced from Hereford or Angus dams crossed with Hereford, Angus, Charolais, Jersey, South Devon, Simmental, and Limousin sires. Purebred Hereford and purebred Angus heifers had greater ages at puberty (389.5 ± 12.9 and 372.2 ± 10.0 d, respectively) than all crossbred heifer averages, indicating that not only does heterosis contribute to an earlier age at puberty, but breed itself (purebred Hereford vs. purebred Angus) also plays an important role.

A case study of this relationship indicated that Angus heifers typically reach puberty approximately 1 mo earlier than Brangus (3/8 Brahman × 5/8 Angus), and both Angus and Brangus heifers attain puberty much earlier than purebred Brahman heifers (Lopez et al., 2006). Because of these breed differences, heifers are bred to calve as 2 yr olds in production systems using *Bos taurus* heifers and typically as 3 yr olds in some systems using *Bos indicus* heifers. Onset of puberty may also be influenced by feed intake parameters, by several metabolites and metabolic hormones indicative of nutritional status, and by various components of reproduction. For example, insulin, triiodothyronine, IGF-I, and leptin have all been shown to be positively correlated phenotypically with age at puberty (Hawkins et al., 2000; Garcia et al., 2002, 2003; Shirley et al., 2006). Reported heritability estimates of age at puberty varied from 0.10 to 0.67, but in general tended to be moderate (Table 1).

A trait associated with age at puberty is BW at first estrus. Heritability estimates for BW at first estrus ranged from 0.40 (Morris et al., 1992) to 0.70 (MacNeil et al., 1984). Cumulatively, it should be noted that age of puberty had a heritability estimate much greater than the other female reproductive traits discussed herein. However, even with extensive knowledge of the physiology of puberty, age at puberty is a difficult trait to observe in field populations. Puberty is typically defined as the time at which a heifer has exhibited 2 luteal phase progesterone values above 1 ng/mL when the samples have been collected 3 to 4 d apart. This measurement is indicative of the maintenance of a viable corpus luteum between d 5 and 15 of the estrous cycle (Day and Anderson, 1998; Lopez et al., 2006; Shirley et al., 2006). This hormone determination requires blood sampling and subsequent laboratory analyses, which can be expensive, so this process is typically only accomplished in a research setting.

Age at First Calving

Age at first calving is routinely recorded and is highly genetically correlated with age at subsequent calvings and the interval between subsequent calvings (Gutiérrez et al., 2002). Because of these relationships, this measure is often used to evaluate heifer fertility. Despite short intervals between subsequent calvings, a later age at first calving is associated with a decrease in lifetime productivity of the beef female (Wiltbank et al., 1985; Nunez-Dominguez et al., 1991; Gutiérrez et al., 2002). Age at first calving heritability estimates were low to moderate, ranging from 0.01 to 0.27.

Ovulatory Follicle Size

Ovulatory follicle size has been demonstrated as an indicator of pregnancy success in beef heifers and as a potential selection tool to improve reproduction. Ovulatory follicle size appears to be an indicator of follicle maturity, and therefore may be an indicator of female fertility at the time of AI or estrus expression. Improved pregnancy rates in heifers have been observed in breeding protocols that control follicular development and increase the probability of optimally sized follicles being ovulated (Perry et al., 2007). To our knowledge, heritability of follicle size has not been estimated.

Calving Date

Calving date is defined as the day within the calving season in which the heifer or cow calved, and is similar to measurements of days to calving (MacNeil and Newman, 1994; Gutiérrez et al., 2002). Calving date is an easily recorded trait (Buddenberg et al., 1990) and has been proposed as a strong indicator of beef cow fertility because of its economic importance (Bourdon and Brinks, 1983). Earlier calving dates are associated with higher weaning weights because weaning typically occurs on a specific day of the calendar rather than on a weight-constant or age-constant basis (Lesmeister et al., 1973), and dams that calve earlier tend to be more reproductively efficient because of the increased number of days allowed postpartum within a controlled breeding season. Conversely, cows that calve later in the season do not have sufficient time to return to estrus for the next breeding season because they are most likely still experiencing postpartum anestrous at the end of a short-controlled breeding season (Wiltbank, 1970). Calving date reflects the effects of initiation of calving by the calf, initiation of estrous cycles and fertility by the dam, and semen quality and libido of the service sire in the previous breeding season (MacNeil and Newman, 1994). Calving date is generally moderately heritable; however, estimates in the literature are variable, ranging from 0.03 to 0.21. Days to calving is a trait similar to calving date and is estimated as the interval between when the female was first exposed to the bull and calving (Meyer et al., 1990). Genetic values for days to calving should consider both AI and natural service matings (Donoghue et al., 2004b). Heritability estimates for days to calving were low, typically <0.10 (Meyer et al., 1990; Donoghue et al., 2004b).

Calving to First Insemination and First-Service Conception

Calving to first insemination is a binary trait that is typically expressed as the probability that a female will successfully produce a calf from her first AI service. A female that became pregnant and produced a calf from her first AI could theoretically be compared with a naturally bred female that successfully produced a calf from a pregnancy within the first 21 d of the breeding season (Donoghue et al., 2004a). Even though calving to first insemination could be included as a trait within a breeding objective, genetic evaluations have previously not considered or have "combined" a measure of fertility that merged data from both natural and artificial matings (Donoghue et al., 2004a,b). The heritability of this measure of fertility, calving to first insemination both by natural and artificial service, tended to be low (0.03 to 0.05). The interval of calving to conception also had low heritability, with an estimate of 0.11 in beef cows (Morris et al., 2000) and estimates of 0.01 and 0.02 in first- and second-lactation dairy cows, respectively (Grosshans et al., 1997).

First-service conception rate is a reproductive measure similar to calving to first insemination and pregnancy rate (Minick Bormann et al., 2006). However, this trait provides producers a management opportunity for separating females that become pregnant on the first AI breeding from those that require multiple breedings or that become pregnant by natural service. The economic value associated with heifers successfully bred at first AI service is associated with the cost of semen, the labor for estrus detection and breeding, and the quality and age differences between calves from AI and natural service. Additionally, heifers that became pregnant at first AI service calve earlier and tend to have high pregnancy rates in the subsequent breeding season (Minick Bormann et al., 2006). First-service conception success is also often included in dairy female selection indices. Heritability estimates for first-service conception rate were variable, ranging from 0.03 to 0.22. Conceptions per estrous cycle exposed had a greater heritability estimate (0.27; Dearborn et al., 1973) than conceptions per service (0.03; MacNeil et al., 1984). These are 2 additional traits that take into account AI efforts or breeding services of multiple estrous cycles. These traits would be more typical of dairy production systems because most beef production systems use estrus synchronization, timed AI, and then exposure to cleanup (natural service) sires; thus, most beef females typically have only a single AI opportunity.

Pregnancy Rate

Heifer pregnancy is a measure of reproduction indicative of sexual maturity and is often included in breeding objectives. Heifer pregnancy, like cow pregnancy, is a binary trait (1 = pregnant; 0 = not pregnant) defined as the probability of an exposed heifer being pregnant by the end of the yearling breeding season (Eler et al., 2002) and remaining pregnant to palpation (approximately 120 d postbreeding; Evans et al., 1999). Specifically, this means that a heifer became pubertal and subsequently pregnant at 12 to 15 mo of age so as to calve by 24 mo of age (Eler et al., 2002). Heritability estimates for heifer pregnancy ranged from 0.14 to 0.21. Greater lifetime production has been associated with heifers that conceive early in their first breeding season (Lesmeister et al., 1973).

Replacement heifers require significant time and resources; thus, having heifers bred and calved by 2 yr of age contributes to the economic success of a beef cattle operation. These females must remain in the productive herd and continue to contribute calves to sustain the economic viability of the operation (Doyle et al., 2000). Therefore, lifetime pregnancy rate is an economically relevant trait. Like heifer pregnancy, subsequent pregnancies and calving success are classified binomially after a short-controlled breeding season. Calving success had low heritability, with estimates ranging from 0.02 to 0.08. Lifetime pregnancy rate can be calculated by dividing the number of pregnancies by the number of mating years (Morris and Cullen, 1994). Overall pregnancy rate can be affected by several factors, specifically length of the breeding season. Pregnancy rate (i.e., pregnancy percentage), described binomially according to conception success, had low heritability, with estimates from 0.04 to 0.12. A longer breeding season is generally associated with higher pregnancy rates, although producing lighter calves at weaning, assuming a constant weaning date (Werth et al., 1991). Estimates of heritability for the probability of pregnancy, or the likelihood of conceiving and remaining pregnant (Evans et al., 1999), ranged from low (0.05) to high (0.57); however, the majority of estimates were moderate to low.

Pregnancy in cattle is typically determined by rectal palpation; however, a proposed indicator of pregnancy is circulating serum lactate dehydrogenase isoenzyme patterns. These patterns have been used to detect pregnancy accurately in Holstein cows as early as 36 d into gestation; however, the potential of using these patterns to determine pregnancy in nondairy breeds may be limited (Wright and Grammer, 1980). There is limited discussion regarding the use of lactate dehydrogenase isoenzyme patterns for pregnancy detection in commercial practices. Prolactin has also been suggested to play a role in pregnancy as a tissue protein (Anthony et al., 1995), but not as a hormone (Short et al., 1990). Nonetheless, pregnancy-specific protein B has been implemented in a commercial test determining pregnancy from blood samples of cattle (Bertolini et al., 2006).

Net Calf Crop and Calving Rate

Net calf crop is a measure of reproductive performance estimated by the percentage of calves weaned per cow exposed in the breeding herd (Dziuk and Bellows, 1983) and is often used as a gross measure of herd reproductive ability. To our knowledge, no heritability estimates are available for net calf crop; however, number of lifetime calves had low to moderate heritability, ranging from 0.07 to 0.36. A net calf crop of less than 100% indicates calf losses at some stage within the production cycle. Losses in the net calf crop can be attributed to females not pregnant by the end of the breeding season, fetal deaths during gestation, perinatal calf deaths, and calf deaths from birth to weaning. Pregnancy failure with a controlled breeding season accounted for the largest number of losses (Dziuk and Bellows, 1983). Related to the number of calves, calving rate is defined as the number of calves produced by a cow divided by the number of potential calves (Meyer et al., 1990). Calving rate had heritability estimates ranging from 0.02 to 0.17, with higher estimates calculated in *Bos indicus*-influenced animals. Calf survival also had low heritability, as reflected by low estimates for the number of calves born live (0.00; Dearborn et al., 1973) and calf survival (0.11; Cundiff et al., 1986).

Prolificacy

Beef cattle productivity can theoretically be improved through an increase in prolificacy or an increased frequency of twins. However, twin production is not generally considered a desirable trait in beef cattle production because of associations with calving difficulty, reduced calf survival, and retained placenta. Gestation length is shortened in twin pregnancies and likely contributes to the increased frequency of retained placentas (Echternkamp and Gregory, 1999a). In addition, subsequent pregnancy rates are lower in dams birthing twins and nursing 1 or 2 calves than in dams birthing and nursing a single calf (Echternkamp and Gregory, 1999b). The Roman L. Hruska US Meat Animal Research Center established a twinning population in which the twinning rate was initially 3.4% and exceeded 35% after a 12-yr period (Van Vleck and Gregory, 1996; Echternkamp and Gregory, 1999a). Genetic selection for twinning in replacement heifers is based on multiple observations of ovulation rate (Echternkamp and Gregory, 1999a). Heritability estimates for ovulation rates ranged from 0.11 to 0.38 for a single ovulation cycle to the mean of 8 cycles; the overall heritability for twinning rate was 0.09 (Gregory et al., 1997).

Calving Interval

Calving interval, the number of days between successive calvings, is an easily measurable trait used as an indicator of female fertility. In most US beef production systems, the target level is 365 d. Although this measure has been a principal measure of reproductive health throughout the productive life of the cow, it may not be the most appropriate measure of overall reproductive ability. A shorter calving interval can be associated with cows whose first calves were born late, and selection of these animals may result in an indirect selection for a later age at puberty (Bourdon and Brinks, 1983). Calving interval has been traditionally used as a measure of reproductive efficiency over calving date. However, more sources of bias are associated with calving interval than calving date during a fixed breeding season (Bourdon and Brinks, 1983). Another challenge associated with calving date is appropriate scoring of individuals culled for which no calving record exists, especially in terms of sire evaluation using daughter information. Calving interval is also used as a measure of dairy cow fertility, and is often incorporated into selection indices. One reported heritability of calving interval suggested this measure had low heritability, with an estimate of 0.13 (Gutiérrez et al., 2002).

Dystocia

Dystocia is a known risk factor associated with subsequent infertility (Ducrot et al., 1994; Kristula and Bartholomew, 1998). Dystocia categories may be scaled, with the lower end of the scale reflecting no or little assistance required and with the higher end reflecting substantial assistance or a caesarian operation (Meijering, 1984). Fertility is substantially lower after caesarian surgery as a result of dystocia (Dobson et al., 2001). Dystocia is often unfavorably associated with calf survival (Cundiff et al., 1986) and therefore may be reflected by other reproductive measures, including calving rate. Additionally, anestrus, the major contributor to postpartum infertility, is affected by calving difficulty (Short et al., 1990). An increased incidence of dystocia is observed among very young heifers (Dziuk and Bellows, 1983; Sheldon and Dobson, 2003) with calves having higher birth weights and with heifers have longer gestation lengths (Cundiff et al., 1986). Fetopelvic incompatibility is the major contributor to calving difficulty. This can arise from an oversized calf, an undersized pelvic area of the dam, or both (Meijering, 1984). Measures of pelvic size may include pelvic width, pelvic height, and various calculations of pelvic area. Pelvic width and dystocia are inversely related, and pelvic area is the maternal factor with the greatest impact on calving difficulty (Morrison et al., 1986). Pelvic area has been shown to negatively affect ($P < 0.05$) calving difficulty score (Bellows et al., 1971; Johnson et al., 1988). However, relationships between pelvic measurements and dystocia are too low for accurate prediction of calving difficulty (Laster, 1974)

The heritability of calving difficulty was moderate, with estimates from 0.22 to 0.42 (MacNeil et al., 1984; Cundiff et al., 1986). The influence of calving difficulty on fertility most likely is related to effects on uterine involution, which can extend postpartum anestrous. The influence of dystocia on related traits is beyond the scope of this review. However, calving difficulty has been shown to decrease subsequent milk production (McGuirk et al., 2007), increase the risk of culling (López de Maturana et al., 2007), decrease calf survival to weaning (Tarrés et al., 2005), and affect the subsequent conception date (Colburn et al., 1997). Given these relationships, any genetic improvement program for fertility should give consideration to cows that have experienced dystocia.

Longevity and Stayability

Female longevity measures the length of time a female remains in the breeding herd. Longevity is influenced by several economically important traits, including female reproduction. Increased female longevity translates to fewer replacement heifers, an increased number of high-producing mature cows, and a reduced number of involuntarily culled cows. However, the expression of this trait late in life hinders its inclusion in most genetic evaluation programs (Rogers et al., 2004). An alternate definition for longevity is stayability, which can be defined as the probability of a cow surviving or staying in a herd to a given age provided it has the opportunity (Snelling et al., 1995). Like longevity, stayability affects the profitability of a herd through several traits, including female reproduction and calf performance (mature cows tend to wean heavier calves, all else being equal). Heritability of stayability has been estimated to range from 0.02 to 0.23, depending on the age end point chosen (Snelling et al., 1995).

Selection Indices

The dairy industry frequently uses selection indices to assess female fertility, generally defined as the ability of a dairy female to conceive and produce a calf successfully after insemination (Royal et al., 2000). Fertility indices should include a measure of conception success after insemination or reproductive rate measured by intervals, or both. Such intervals may include calving interval (described previously), days to first service (the interval from parturition to first insemination), and calving to postpartum rebreeding (measure of reproductive efficiency). Other traits include nonreturn rates (reflection of pregnancy success and maintenance), BCS (indirect measure of fertility), milk progesterone (indicator of commencement of luteal activity postpartum, or reestablishment of ovarian activity), and bull fertility ratings (indicator of subsequent daughter fertility). Because these efforts have been successful for dairy cattle genetic selection programs, the beef industry should explore the implementation of similar programs.

Male Reproductive Measures

Measures of fertility need to be considered not only in the female, but also in the male. Natural service has historically been, and continues to be, used in most beef cattle operations; therefore, acceptable bull fertility is critical to the success of these operations (Boyd et al., 1989; Carpenter et al., 1992). Bull management is highly intertwined with female fertility, bull fertility, and cow management. Bull fertility may be affected by the number of cows a particular bull is expected to service and, in natural mating, the length of the mating period, as well as the serving capacity of the bulls (Neville et al., 1987; Boyd et al., 1989; Godfrey and Lunstra, 1989). Fertility measures may be superficially increased in bulls exposed to a small number of cows during a lengthy breeding season (Parkinson, 2004). However, determining the proper bull-to-cow ratio is challenging because these influences are in addition to issues of pasture size and topography, multiple water sources within a pasture, and behavior (McCosker et al., 1989; Fordyce et al., 2002; Holroyd et al., 2002).

Scrotal Circumference

Scrotal circumference is used to predict the quality and quantity of spermatozoa-producing tissue and age at puberty. A scrotal circumference measurement of 28 to 30 cm is generally associated with onset of puberty; specifically, 52 and 97% of males are pubertal when scrotal circumference is 28 and 30 cm, respectively (Parkinson, 2004). Increased scrotal circumference has been associated with increased sperm production but decreased semen quality (Brito et al., 2002). Reported heritability estimates for scrotal circumference were generally high and ranged from 0.29 to 0.78.

Because female fertility traits in general have low heritability, correlated or indicator traits that are more highly heritable are often used to produce more effective selection (Evans et al., 1999; Morris et al., 2000). Yearling bull scrotal circumference is commonly used to improve female fertility because it is genetically correlated with age at puberty in heifers (Evans et al., 1999). Although consistently favorable, the magnitude of this correlation was variable across field and experimental populations, ranging from equal to or less than −0.80 to equal to or greater than −0.15. In general, scrotal circumference as an indicator trait is easy and inexpensive to measure. However, scrotal circumference has also been shown to be positively genetically correlated with growth traits (Martínez-Velázquez et al., 2003). Because of these findings and the fact that the trait is easily recorded, genetic selection programs have been successful at improving scrotal circumference; thus, the statistical association between scrotal circumference and heifer fertility trait measures is not as easily detected in data sets from more recent times relative to data collected before 1990 (Martin et al., 1992; Martínez-Velázquez et al., 2003; Shirley et al., 2006).

Breeding Soundness

The lack of feasible methods for determining male puberty has made selection and management of young, unproven bulls difficult in regard to fertility. Currently, a breeding soundness exam, or evaluation, is the most practical means to assess bull fertility (Kennedy et al., 2002), and consists of a physical examination, scrotal circumference measurement, and semen evaluation. Sex drive and mating ability are not typically included in this evaluation, although they are obviously essential to the successful impregnation of females (Boyd et al., 1989). Guidelines for breeding soundness exams were established in 1983 by the Society for Theriogenology (Ball et al., 1983) and were revised in 1993 (Chenoweth et al., 1993). Breeding soundness exams lead to improved reproductive efficiency through identification of subfertile bulls and the assessment of current bulls previously identified as fertile (Coe, 1999). *Bos indicus*-influenced breeds have been found to have lower rates of satisfactory breeding soundness, as have younger bulls in conventional yearling bull tests (Kennedy et al., 2002). Reasons for unsatisfactory breeding soundness are numerous; however, most reasons can be grouped into broad categories of inadequate scrotal circumference or inadequate spermatozoal motility or abnormal morphology. To pass a breeding soundness exam, a bull must have a scrotal circumference of 30 cm by 365 d of age (Decker et al., 2008). To our knowledge, there have been no estimates of heritability of the probability of passing a breeding soundness exam.

Libido and Serving Capacity

Mating behavior, as reflected by measures of libido and serving capacity tests, may be used to assess the reproductive capability of bulls. Libido and serving capacity are terms that are often interchanged. However, libido typically is a more general term describing the sex drive of a bull, whereas serving capacity is a measurement of the number of times a bull mounts and copulates with a female. A libido test pairs a single bull with a restrained female. Libido scoring may include several variables, such as the number and vigor of mating attempts and a subjective assessment of overall sexual interest. A serving capacity test uses steroid-treated or nonestrous females that are sedated or restrained and exposed to a small group of bulls. This trait can be recorded in 2 ways: 1) the number of services within a specified time, or 2) as a grade, which is a subjective score assigned by those working with the bulls, and can account for serving capacity test interruptions and distractions (Morris et al., 1992). Serving capacity and libido tests are highly phenotypically correlated (Chenoweth et al., 1979), and bulls that score well on these types of tests yield increased pregnancy rates in cow herds (Carpenter et al., 1992; Chenoweth, 1997), which is of relevance to this review. No heritability estimates for these traits were found in the literature.

Genetic Analyses of Fertility Traits

It is apparent that a multitude of traits have been used as indicators of inherent fertility; however, few have been used for purposes of genetic evaluation on a breed-wide basis. The exceptions are scrotal circumference, heifer pregnancy, and stayability, which have been used to calculate EPD to varying degrees by breeds such as the American Angus Association, the American Hereford Association, and the Red Angus Association of America. Historically, genetic predictions of fertility have been problematic because of the limited amounts of data, with most US breeds having only recently implemented whole-herd reporting. Whole-herd reporting information is critical for traits such as stayability and longevity, for which cows may be culled from the productive herd for reasons unrelated to fertility. Additionally, many traditional measures of fertility have been difficult to analyze statistically because of their binary nature (i.e., 0 or 1; yes or no), but with recent advances in and applications of survival (Rogers et al., 2004) and threshold analyses, these limitations are being overcome, as illustrated by Snelling et al. (1995). Although these binary traits likely reflect a continuous underlying genetic distribution, they are expressed as a binary distribution, potentially masking genetic differences between individuals. With increasing use of whole-herd reporting, advances in computing capabilities, and improved statistical methodologies, additional consideration should be given to implementation of these evaluations and delivery to the industry.

The purpose of this review was to outline traits often used as surrogates for selection and culling purposes. Because of the extensive and diverse nature of genetic predictions used for the selection of animals with improved fertility, the genetic correlations between economically relevant fertility traits and their indicators, and the changing methodologies, they were not addressed in this review, but rather require a future review focusing on genetic prediction of fertility traits.

Summary

Fertility is a difficult physiological event to define because of the complexities of reproduction, yet it remains one of the driving factors influencing beef cow herd profitability. Definitions of reproductive traits vary across species of cattle, breeds, locations, sexes, and animal classes. Despite recognizing that measures of reproductive efficiency should be included in the breeding objective, genetic improvement of reproductive traits has generally been hindered because of the lack of information, low heritability, and delayed expression of these traits. Whole- or total-herd reporting is necessary in the beef cattle industry for implementation of genetic prediction of reproductive traits, and as these databases are improved, new methodologies will likely be developed for genetic improvement of fertility.

IMPLICATIONS

Reproduction is an economically relevant component of beef production systems, and national survey results suggest that opportunities exist to improve reproductive efficiency in many herds. However, genetic improvement programs for reproductive traits have been much slower to develop than programs for growth and carcass traits. This is due to the difficulty of developing whole-herd data collection systems, the challenges of collecting binary traits derived from short-controlled breeding systems, and the time required to collect ample data needed for genetic prediction as well as the multitude of traits identified as indicators of fertility. To implement sound and effective selection procedures for sustained genetic improvement of fertility, 3 things must occur. First, the economically relevant traits must be identified. Second, appropriate indicator traits must be identified that are suitable for field data collection. Third, breed associations must continue to compile this information for eventual use in genetic prediction and delivery to breeders.

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