Genetics and Biology of Reproduction in Cattle

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Introduction

This review of the genetics of reproduction in cattle proceeds on a trait-by-trait basis and considers twinning and ovulation rate, age at puberty, dystocia, gestation length and conception rate. In most cases, the pertinent scientific literature has been previously reviewed, and it is the intent of the author of this chapter to summarize the previous reviews and examine the subsequent work in the area.

Genetics of Twinning and Ovulation Rate

The genetics of twinning in cattle has been previously reviewed by Hendy and Bowman (1970), Rutledge (1975), Stolzenburg and Schönmuth (1979), Morris (1984) and Morris and Day (1986). The reviews of Hendy and Bowman (1970), Rutledge (1975) and Stolzenburg and Schönmuth (1979) provide rather extensive lists of studies reporting estimates for frequency of twin birth in various breeds of cattle. Hendy and Bowman report estimates, primarily from dairy cattle, that range from 0.34 to 4.50%. Rutledge provided a more comprehensive list and summarized his findings in part with a contrast of US beef and

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dairy breed differences. Dairy breed averages (1.3–8.9% twinning) were in general two to three times the level of beef breed averages (0.4–1.1%). Rutledge's survey of beef breeds primarily involved British breeds. As pointed out by Morris (1984), other European breeds, including Simmental, Charolais and Maine-Anjou, have twinning rates considerably higher than the British breeds. While nutritional and other management differences exist between beef and dairy cattle, this summary of breed differences suggests a potential genetic correlation between lactation and twinning rate.

The overwhelming majority of bovine twins are dizygotic, or fraternal, twins as opposed to monozygotic, or identical, twins. Estimates of the frequency of monozygotic twinning are derived by comparing the incidence of like- versus unlike-sex twins. Monozygotic twins are estimated to comprise less than 10% of all twin births when considering typical breed averages for twinning rate (Johansson, 1932; Bonnier, 1946; Johansson and Venge, 1951; Cady and Van Vleck, 1978), and heritability of monozygotic twinning is thought to be nil. As a consequence, twinning rate in cattle is closely related to ovulation rate.

Twinning rate is generally considered a trait with low heritability. Maijala and Syväjärvi (1977) reviewed the literature with regard to estimates of twinning-rate heritability. They report an average heritability estimate of 0.028 ± 0.0004. Subsequent studies with various cattle populations are generally consistent in reporting low heritability estimates for twinning (Table 13.1). Ovulation rate, when considered as a single observation with a binary outcome, likewise has a low heritability. Estimates of heritability for a single observation range from 0.07 to 0.11 (Echternkamp *et al.*, 1990; Van Vleck and Gregory, 1996; Gregory *et al.*, 1997). However, when ovulation rate is evaluated over multiple oestrous cycles, the effective heritability of the average of multiple observations is considerably higher. When considering average ovulation rate over eight cycles, effective heritability rises to approximately 0.38 (Echternkamp *et al.*, 1990; Van Vleck and Gregory, 1996). The genetic correlation between twinning rate and ovulation rate has been estimated to be between 0.75 and 1.00 (Van Vleck and Gregory, 1996; Gregory *et al.*, 1997).

Table 13.1. Recent heritability estimates for twinning rate in cattle, on the observed, binary scale.

Author	Estimate	Population
Cady and Van Vleck, 1978	0.03 to 0.06	US Holstein
Syrstad, 1984	0.006 ± 0.001 to 0.046 ± 0.006	Norwegian dairy cattle
Gregory *et al.*, 1990a	0.02 ± 0.07	USDA-MARC twinning population
Maijala and Osva, 1990	0.005 to 0.007	1st parity Ayrshire and Friesian
	0.023 to 0.051	2nd and later parity
Ron *et al.*, 1990	0.017 to 0.022	Israeli Holstein
Van Vleck and Gregory, 1996	0.03 to 0.08	USDA-MARC twinning population
Gregory *et al.*, 1997	0.09 to 0.10	USDA-MARC twinning population

Given this high genetic correlation, use of ovulation rate as the selection criterion for improving twinning rate makes an excellent case for the potential benefit from indirect selection on a correlated trait.

Several selection experiments aimed at increasing twinning rate are or have been conducted (reviewed by Morris and Day, 1986, 1990b). Efforts in New Zealand (Morris and Day, 1990b) and the USA (Gregory *et al.*, 1997) have used ovulation-rate data as part of the basis for selection. This approach has been particularly successful in the US Department of Agriculture (USDA)-Meat Animal Research Center (USDA-MARC) twinning herd; at the latest report, the twinning rate had reached a level exceeding 30% twin births (Gregory *et al.*, 1997). The twinning rate in this herd is increasing at a rate of approximately 2.5% per year.

Twinning rate is influenced by seasonal effects, although the nature of the seasonal effect (photoperiod, nutritional, etc.) is uncertain. Hendy and Bowman (1970) and Rutledge (1975) reviewed work from eight studies from the 1920s to mid-1960s which examined seasonal effects on twinning rate. Roughly half of these studies identified significant seasonal effects on twinning rate, with peak twinning rate generally corresponding to spring and autumn conception. Studies by Johansson *et al.* (1974) and Cady and Van Vleck (1978) likewise identified seasonal effects, with highest twinning rates corresponding to spring and autumn conception. Analysis of data from the USDA-MARC twinning population provides a more limited analysis of seasonal effects, given that mating is limited to periods corresponding to spring and autumn calving (conception in mid-June to mid-August and late October to late December, respectively). In this population, twinning rates for the October–December-conceiving cows exceed those for the June–August-bred group, with a difference of 4–6% occurrence of twin births (Gregory *et al.*, 1990a; Van Vleck and Gregory, 1996).

Twinning rate increases with age and parity of dam, with the increase continuing through 8–11 years of age in the work reviewed by Hendy and Bowman (1970) and Rutledge (1975). While this might in part be attributable to improvement in embryo survival with dam age and parity, it probably results in large part from increases in ovulation rate with age (Labhsetwar *et al.*, 1963; Morris *et al.*, 1992). These earlier findings for association of dam age and twinning rate are paralleled by more recent work. Cady and Van Vleck (1978) examined data from US Holsteins and reported twinning frequencies of 1.05, 4.32 and 6.18% for parities 1, 2 and ≥ 3, respectively. Syrstad (1984) examined data from Norwegian dairy cattle and observed twinning frequencies of 0.46, 1.64, 2.31, 3.11 and 3.57% for parities 1–5, respectively. Berry *et al.* (1994) reported twinning frequencies of 1.3, 6.0 and 9.4% for US Holstein females in parities 1, 2 and ≥ 3, respectively. In studies with the composite USDA-MARC twinning population, Gregory *et al.* (1990) observed twinning rates of 6, 8–11, 12–13 and 11–14% for cows of 2, 3, 4 or 5 years of age at calving. Morris and Day (1990) analysed data from two milking Shorthorn herds and one Holstein herd; increases in twinning rate with age were observed, with the largest increases occurring over the first five parities and the single biggest increase occurring between parities 1 and 2. Maijala and Osva (1990) examined data from a Finnish Ayrshire and Friesian population and observed increases in twinning rate of roughly 2% and 1% between first and second and second and third parities, respectively.

Twin birth is associated with a number of detriments, including lower perinatal calf survival and poorer cow reproductive performance. These associations have been previously reviewed by Hendy and Bowman (1970) and Cady and Van Vleck (1978). Additional reports of these associations published since these reviews are summarized in Table 13.2. Regarding cow performance, twinning is associated with increased dystocia (due to malpresentation),

Table 13.2. Detrimental association of twinning with calf and cow performance.

Source	Single birth	Twin birth	*P* value
Perinatal calf mortality (%)			
Cady and Van Vleck, 1978	5.9	22.4	< 0.05
Anderson *et al*., 1982, heifers	9.1	5.3	NS
Anderson *et al*., 1982, cows	0	0	NS
Gregory *et al*., 1990b	5	22	< 0.01
Guerra-Martinez *et al*., 1990, heifers	8.5	11.9	NS
Guerra-Martinez *et al*., 1990, cows	4.3	10.8	NS
Day *et al*., 1995	3.2	15.7	< 0.005
Gregory *et al*., 1996	3.5	16.5	< 0.01
Retained placenta (%)			
Anderson *et al*., 1979	0	14	NS
Anderson *et al*., 1982, heifers	2.3	27.2	< 0.05
Anderson *et al*., 1982, cows	6.7	33.3	< 0.05
Gregory *et al*., 1990b	2.8	21.5	< 0.01
Guerra-Martinez *et al*., 1990, heifers	11.9	35.2	< 0.05
Guerra-Martinez *et al*., 1990, cows	4.3	24.3	< 0.05
Eddy *et al*., 1991	2	16	< 0.001
Dystocia (%)			
Anderson *et al*., 1979	20	21	NS
Anderson *et al*., 1982, heifers	47.8	21.2	< 0.05
Anderson *et al*., 1982, cows	6.7	5.6	NS
Gregory *et al*., 1990b	23	35	< 0.01
Guerra-Martinez *et al*., 1990, heifers	37.3	21.6	NS
Guerra-Martinez *et al*., 1990, cows	8.7	10.8	NS
Eddy *et al*., 1991	5	7	NS
Berry *et al*., 1994			
lactation 1	30.6	34.5	NS
lactation 2	11.8	30.0	< 0.05
Gregory *et al*., 1996	20.4	42.2	–
Abortion frequency (%)			
Day *et al*., 1995	12.0	29.3	< 0.05
Guerra-Martinez *et al*., 1990, heifers	3.0	4.1	NS
Guerra-Martinez *et al*., 1990, cows	0	0	NS
Interval, parturition to conception (days)			
Chapin and Van Vleck, 1980	107	132	< 0.05
Gregory *et al*., 1990b	83	93	< 0.01
Eddy *et al*., 1991	92	125	< 0.001

NS, not significant.

increased incidence of retained placenta, greater frequency of abortion in twin gestation and longer interval from parturition to first oestrus. Inconsistent results for the incidence of dystocia may reflect two competing dynamics: twinning reduces the incidence of dystocia attributable to large calf size but increases the incidence of dystocia attributable to malpresentation.

After considering costs of twinning on cow and calf performance, the increased calf output is insufficient to make twinning a benefit in typical dairy operations. Recent studies in the Netherlands and the UK suggest lost income of $104 to $108 per cow producing twin calves vs. singles (Eddy *et al.*, 1991; Beerepoot *et al.*, 1992). However, when considering beef production, exploitation of twin birth in an intensive, non-traditional management scheme may provide an opportunity to dramatically increase production efficiency.

The issue of greater frequency of abortion in twin gestations deserves further discussion, as this may impose a limit on the level of twinning that is attainable in a system seeking to exploit high twinning frequency in cattle production. Previous studies of embryo survival in twin pregnancies created by embryo transfer have generally indicated greater embryo survival for bilateral than for unilateral transfers (Hanrahan, 1983). Morris and Day (1990b) report a similar trend in analysis of natural twin pregnancy in the New Zealand twinning herd; in this case, embryo survival for bilateral ovulations (69%) exceeded that for unilateral ovulations (55%). The same authors have suggested that selection based on twinning rate would be selection for increased frequency of bilateral ovulation. Interestingly, there was no difference in embryo survival between unilateral and bilateral pregnancies in the USDA-MARC herd (Echternkamp *et al.*, 1990). In a further analysis of the USDA-MARC data, Echternkamp *et al.* (1990) found the observed proportions of twin pregnancies, single pregnancies and open cows (from those shedding two eggs at ovulation) to fit well with a two-stage model of embryonic loss. In this model, the first stage corresponded to the period prior to placental anastomosis, where loss of one embryo in a twin pregnancy is independent of the other. The latter stage following placental anastomosis is one where the survival of one embryo is dependent on the survival of the second. Results from this study suggest that joint dependency of embryo survival is more the crux of the issue than differences between bilateral and unilateral ovulation. The distribution of twin, single and no pregnancy from double ovulating cows in this study (Echternkamp *et al.*, 1990) was 48%, 29% and 23%, respectively. Twinning frequency as a percentage of pregnant cows would be 62% in this case.

Numerous reports have speculated about the existence of single genes with large effects on twinning rate. Often this speculation follows from the identification of a sire or dam with an exceptional record with regard to twinning rate. Rutledge (1975) and Morris (1984) have listed a number of such reports in the literature. In few, if any, cases have single-gene hypotheses been put to a test that would either build strong support for or refute such a hypothesis, based on segregation of phenotypic classes. Syrstad (1984) and Gregory *et al.* (1990a) examined daughter twinning rates for sons of sires with exceptional twinning rates. The absence of bimodality in progeny twinning rates in both cases was taken as an indication that twinning rate within these exceptional families was not under the control of a single locus. Morris and Day (1990) and Morris and Foulley (1991) categorized sires and dams into high and low groups, based on offspring or own performance. In analysing offspring twinning rates, no evidence of sire group × dam group interaction was observed, suggesting little support for a hypothesis of a single, recessive gene responsible for twinning rate. The advent of highly polymorphic genetic markers and dense marker linkage maps now provides a more powerful tool for dissection of genetic variation in twinning and ovulation rate.

The USDA-MARC twinning population represents a unique resource for identification of ovulation-rate quantitative trait loci (QTL). Initial efforts to map QTL for ovulation rate in the USDA-MARC population have led to the identification of a QTL on bovine chromosome 7 (Blattman *et al.*, 1996). The QTL in question was identified in a Swedish Friesian sire used in the foundation of the USDA-MARC twinning population. Given the sire's ancestry this locus may eventually prove relevant to dairy cattle selection, where the focus would probably be on reducing the incidence of alleles conferring higher a twinning rate.

Identification of an ovulation-rate QTL within the USDA-MARC population may prove useful in cattle selection in two alternative ways. In one case, this information could be used to facilitate introgression of alleles conferring high twinning rate in commercially relevant beef cattle populations. Alternatively, QTL identified in the USDA-MARC herd may help to reveal the location of existing QTL in commercial populations. This information could be used to select for or against alleles conferring higher twinning rates, depending on the population and management system.

Genetics and Biology of Puberty

Martin *et al.* (1992) previously reviewed genetic aspects of puberty in cattle. Much of the information in their review comes from the extensive breed evaluation work conducted by geneticists at the USDA-MARC (Cundiff *et al.*, 1986). Breed differences in age and weight at puberty are in some cases quite dramatic. Information on breed differences previously summarized by Cundiff *et al.* (1986) and Gregory *et al.* (1993) is supplemented in Table 13.3 with additional, recent data from Freetly and Cundiff (1997). There are several relationships that become apparent when examining the data on breed differences. Dairy breeds (Brown Swiss, Holstein, Jersey) attain puberty at younger ages in general than beef breeds, suggesting perhaps that there are genes with pleiotropic effects on lactation and age at puberty. Another general relationship is that breeds with larger mature size in general attain puberty at greater weights and later ages than breeds with lesser mature size. Finally, *Bos indicus* breeds (Boran, Brahman, Sahiwal) and breeds with a major *B. indicus* component (Brangus, Santa Gertrudis) attain puberty at later ages than *Bos taurus* breeds.

Table 13.3. Breed effects on puberty in cattle.

Breed	Weight at puberty (kg)	Age at puberty (days)	Gestation length	% Calf crop born	% Calving difficulty	
					Sire	Maternal
Sire breed[*]						
Angus[†]	344	351	284.6	–	–	–
Belgian Blue	329	347	285.8	–	–	–
Boran	316	396	293.3	–	–	–
Brahman[‡]	323	429	291.7	94	1	10
Brahman[§]	358	426	292.6	–	–	–
Brangus	308	377	285.5	88	12	4
Brown Swiss	279	332	285.0	92	8	8
Charolais	319	384	287.0	88	18	15
Chianina	317	384	287.5	93	12	8
Devon	290	356	284.1	90	4	10
Gelbvieh	284	326	286.3	95	8	11
Hereford[†]	350	355	286.3	–	–	–
Hereford-Angus[‖]	282	357	284.0	91	3	13
Holstein	300	341	282.0	95	5	10
Jersey	235	308	282.9	90	3	7
Limousin	308	384	289.2	89	9	12
Maine Anjou	305	357	285.4	94	20	11
Piedmontese	300	348	289.9	–	–	–
Pinzgauer	277	334	286.0	93	6	13
Red Poll	263	337	285.2	90	4	14
Sahiwal	291	414	294.0	95	2	6
Santa Gertrudis	315	383	286.0	88	4	6
Simmental	302	358	287.3	89	15	17
South Devon	290	350	286.7	88	12	15
Tarentaise	282	349	287.1	91	6	10
Tuli	306	371	291.0	–	–	–
					As a trait of dam	
Purebred means					*Parity 1*	*Parity 2*
Angus	317	393	283	81	32	1
Braunvieh	333	350	290	82	74	13
Charolais	370	391	286	81	49	10
Gelbvieh	339	353	287	83	61	8
Hereford	316	411	288	79	49	5
Limousin	338	408	289	75	41	7
Pinzgauer	336	360	287	84	62	16
Red Poll	295	359	288	81	54	3
Simmental	345	363	287	81	49	14

[*] Offspring sired by bulls of breeds listed with dams of Hereford and Angus breeds.

[†] Offspring from Hereford and Angus sires born after 1981.

[‡] Offspring from Brahman sires born between 1964 and 1975.

[§] Offspring from original Brahman sires (born between 1964 and 1975) and a roughly equal number of sires born between 1984 and 1989.

[‖] Offspring from Hereford and Angus sires born prior to 1970.

Regarding estimates of genetic parameters, Martin *et al.* (1992) identified nine previous studies in which heritability of age at puberty (female) had been evaluated. The average heritability estimate of 0.40 was relatively high, suggesting that age at puberty is a trait which should be readily amenable to change through selection. While puberty in bulls cannot be determined directly as easily as in heifers, the correlated trait of scrotal circumference can be used as an indicator trait. Martin *et al.* (1992) cite estimates of genetic correlation between age at puberty in heifers and scrotal circumference in bulls which range between −0.71 and −1.07 (i.e. larger scrotal circumference at a constant age corresponding with earlier attainment of puberty in related females). As with age at puberty in heifers, scrotal circumference in males has a relatively high heritability. Martin *et al.* (1992) and Brinks (1994) summarized previous estimates of scrotal circumference heritability; the average of the studies listed was 0.47 and 0.49, respectively. There have been few additional reports of heritability estimates since the aforementioned reviews. Gregory *et al.* (1995) examined various purebred and composite populations and reported a heritability estimate for female age at puberty of 0.31. Keeton *et al.* (1996) examined field data from the Limousin breed and reported an estimated heritability of 0.46 for scrotal circumference. Both estimates are in reasonable agreement with previous results.

Nutritional and seasonal influences on attainment of puberty in cattle were thoroughly reviewed by Schillo *et al.* (1992). Age at puberty and nutritional level are inversely related, i.e. heifers fed a higher energy level attain puberty at younger ages than heifers fed a lower energy level. With regard to effects of season, season of birth has a significant effect on age at puberty, with autumn-born heifers reaching puberty at younger ages than spring-born heifers. Studies with controlled environments indicate that much of the seasonal effect can be attributed to the effects of photoperiod. The physiological basis for onset of puberty is thought to be related to increases in frequency of the pulsatile release of luteinizing hormone (LH) from the anterior pituitary. The hypothalamus is fully capable in the prepubertal heifer of producing the gonadotrophin-releasing hormone (GnRH) that causes secretion of LH from the anterior pituitary. However, the hypothalamus and pituitary exhibit a strong negative-feedback response to oestradiol produced in the ovary. It is a decrease in the negative-feedback response that eventually leads to an increase in LH pulse frequency, with a consequent increase in follicular development, increase in oestradiol production by the follicles and a surge of LH that triggers the initial ovulation and oestrous cycle. How nutritional and photoperiodic effects on attainment of puberty are mediated is uncertain.

At least one effort is being made to use selection in an experimental herd to create differences in age at puberty and examine correlated response to selection for pubertal traits. Morris *et al.* (1993) have created three different selection lines and one control line within an Angus population. One line was selected for increased scrotal circumference at 13 months of age, a second line was selected for reduced age at first oestrus in heifers and increased yearling weight in bulls and a third line was selected for increased age at first oestrus in heifers and increased yearling weight in bulls. The only report from this project to date indicates that both scrotal circumference and age at first oestrus have responded to direct selection after 9 years of selection. However, no correlated response in scrotal circumference was observed in the two lines divergently selected for age at first oestrus while concomitantly selecting for increased yearling weight. Several breeds of beef cattle now include scrotal circumference as a trait for which expected progeny differences (EPDs) are calculated. It is unclear to what extent scrotal circumference is used in practice as a criterion in beef cattle selection.

Genetics and Biology of Gestation Length

Unlike the other traits considered thus far, gestation length is a trait influenced by two genotypes, that of the calf and that of the cow. In most instances, effects of calf and cow genotype are somewhat confounded, given the mother's genetic contribution to the calf. Still, ample evidence exists in the literature that both genotypes are significant contributors to variation in gestation length.

The most extensive information on breed of sire effects on gestation length (through calf genotype) comes from the breed evaluation studies conducted at USDA-MARC (Cundiff *et al.*, 1986; Gregory *et al.*, 1993; Table 13.3). The breed averages listed in the first section of Table 13.3 represent gestation lengths for calves sired by bulls of the listed breeds with mothers of primarily Hereford and Angus breeding. The most pronounced difference evident in these results are the longer gestation lengths for calves sired by bulls of the *B. indicus* breeds (Brahman and Sahiwal). Williamson and Humes (1985) likewise observed gestations of 2–5 days greater length for Brahman-sired calves compared with calves sired by *B. taurus* breeds (all dams were Hereford or Angus). Comparison of Angus-sired and Santa Gertrudis-sired (Gotti *et al.*, 1985) or Brahman-sired (Reynolds *et al.*, 1980) calves also provided evidence of longer gestation lengths for calves sired by the breed (Santa Gertrudis, + 2.0 days; Brahman, + 6.8 days) with *B. indicus* influence. Differences can also be identified between *B. taurus* breeds (Table 13.3), with the most pronounced difference being the shorter gestation lengths associated with dairy sires (Jersey and Holstein). Lawlor *et al.* (1984) compared calves of 25 and 50% Simmental breeding with straightbred Hereford and 50% Angus calves, all produced from Hereford dams. The 50% Simmental group had 2–4-day longer gestation lengths than the Hereford- and Angus-sired groups in this study. The Simmental–Angus difference corresponds well with the breed differences observed in the USDA-MARC study, while the Simmental–Hereford difference is greater. Differences could be attributable to sampling or perhaps heterosis, although other studies suggest heterosis for gestation length is negligible (Sacco *et al.*, 1990; Gregory *et al.*, 1991).

Dam genotype effects on gestation length have also been documented in several cases. When mated to a variety of sire breeds (Brahman, Chianina, Maine Anjou and Simmental), Angus dams had shorter gestation lengths by approximately 2.5 days ($P < 0.001$) than did Hereford dams in a study reported by Williamson and Humes (1985). Reynolds *et al.* (1980) and Gotti *et al.* (1985) compared Santa Gertrudis or Brahman to Angus dams and found Angus dams to have gestation lengths of 4.0 and 4.2 days less, respectively.

Heritability of gestation length has been estimated in several studies since being reviewed by Andersen and Plum (1965). Andersen and Plum identified nine studies estimating heritability of gestation length, with most estimates falling between 0.25 and 0.50. More recent estimates (Table 13.4) generally fall into the same range for estimates of heritability, due to direct additive effects. Estimates of heritability associated with maternal additive effects have been lower. This and the corresponding observation of heritability exceeding estimates of repeatability (Andersen and Plum, 1965) can be taken to indicate that gestation length is under the control more of the fetus than of the dam. Perhaps the most interesting genetic parameter estimate is the negative correlation between growth and gestation length, which has been reported several times (Bourdon and Brinks, 1982; MacNeil *et al.*, 1984; Gregory *et al.*, 1995). Successful selection for reduced gestation length might be beneficial in expanding days available for post-partum reproduction. The negative genetic correlation between growth and gestation length would be favourable to their concomitant improvement.

As indicated in the review by Andersen and Plum (1965) there are non-genetic factors that have repeatedly been associated with differences in gestation length. Dam age or parity is one such factor which has been consistently identified. Mature cows typically have gestation lengths exceeding those of heifers by approximately 1–2 days. Calf gender has also been commonly reported to affect gestation length, with males being carried longer than females, again with a typical difference of 1–2 days.

Table 13.4. Heritability (h^2) estimates for gestation length in cattle.

Author	h^2_{direct}	h^2_{maternal}	Population
MacNeil *et al.*, 1984	0.30*	–	USDA-MARC populations
Cundiff *et al.*, 1986	0.64–0.77	–	USDA-MARC populations
Azzam and Nielsen, 1987	0.36–0.45	0.02–0.13	US, multiple breeds
Wray *et al.*, 1987	0.37	0.09	US Simmental
Moore *et al.*, 1990	–	0.01*	Canadian Ayrshire
	–	0.05*	Canadian Holstein
Silva *et al.*, 1992	0.22	–	US Holstein
Gregory *et al.*, 1995	–	0.45*	USDA-MARC populations

*Gestation length considered as trait of the cow.

Genetics and Biology of Dystocia

Dystocia, or calving difficulty, is the leading cause of calf mortality (Patterson *et al.*, 1987; Wittum *et al.*, 1993) and a major source of veterinary expense for cattle producers (Hird *et al.*, 1991; New, 1991; Salman *et al.*, 1991; Wittum *et al.*, 1993). Price and Wiltbank (1978a), Meijering (1984) and Rice (1994) reviewed the literature pertaining to the basis for calving difficulty and potential means for preventing it. It is generally accepted that the primary reason for calving difficulty is incompatibility in size of calf and dam; calf birth weight by itself is the single greatest predictor of calving difficulty. The genetics of dystocia is in large part the genetics of birth weight. Differences in birth weight are moderately heritable, and cattle producers are frequently admonished to choose sires with low birth-weight EPDs for use on immature females. Effects of calf genotype and effects of sire breed on incidence of dystocia have been clearly documented in breed evaluation (see Table 13.3) and other studies. More vexing is the maternal contribution to variation in dystocia.

That there is a maternal genetic component to dystocia is attested to both by breed differences in dystocia (Cundiff *et al.*, 1986; Gregory *et al.*, 1993) and by evidence for heritable differences in calving difficulty. Breed differences in the maternal component of dystocia have been characterized extensively by research conducted at the USDA-MARC (see Table 13.3). F_1 females sired by bulls of various breeds exhibited incidences of calving difficulty that varied significantly from 1% to 17%. Notable among these breed differences are the low incidence of calving difficulty for *B. indicus* breeds (Brahman, Sahiwal) and for Jersey F_1 females, the latter representing the breed cross with smallest skeletal size. The basis for the *B. indicus* superiority for calving difficulty will be addressed later.

Heritability of both direct (i.e. effect of calf genotype) and maternal effects on calving difficulty has been estimated in numerous studies, and those reported since the review of this topic by Meijering (1984) are listed in Table 13.5. In general, heritability of dystocia is higher in heifers than in cows, although heritability of both direct and maternal effects tends to be low. Direct and maternal genetic components of dystocia typically exhibit a negative genetic correlation which works against simultaneous improvement of both aspects of dystocia.

The maternal complement to calf size is pelvic area, and the influence of pelvic area on dystocia has come under considerable study. While the supposition that pelvic area might be a predictor of calving difficulty is intuitively appealing, research studies have provided relatively little support for this idea. As an illustration, one of the most favourable outcomes was reported by Price and Wiltbank (1978b), in which pelvic area accounted for only one quarter of the amount of phenotypic variation in dystocia compared with calf birth weight. After first accounting for the influence of birth weight on dystocia, pelvic area typically accounts for a very minor part of the remaining variation in dystocia. As a consequence, efforts to use pelvic area as a predictor of calving difficulty (Naazie *et al.*, 1989; Basarab *et al.*, 1993; Van Donkersgoed *et al.*,

Table 13.5. Recent genetic parameter estimates for dystocia.

Author	h^2_{direct}	h^2_{maternal}	$r_{\text{G direct.maternal}}$	Population
Meijering, 1984	0.03 to 0.20	0.03 to 0.20	–0.19 to -0.63	Heifers, review article
	0.00 to 0.08	–	–	Cows, review article
Thompson and Rege, 1984	0.24	–	–	US Holstein
Weller *et al.*, 1988	0.03 to 0.06	–	–	Heifers, Israeli Holstein
	0.00 to 0.01	–	–	Cows, Israeli Holstein
Cubas *et al.*, 1991	0.14	0.24	–0.86	US Angus
Naazie *et al.*, 1991	0.28 to 0.37	0.12 to 0.47*	–	Beef and dairy synthetic populations
Manfredi *et al.*, 1991	0.08	0.11	0.15	French Normande
	0.07	0.07	–0.09	French Holstein
Kriese *et al.*, 1994	–	0.09 to 0.11*	–	USDA-MARC purebreds and composites
Gregory *et al.*, 1995	0.18 to 0.42	–	–	USDA-MARC purebreds and composites
	0.04 to 0.29†	–	–	USDA-MARC purebreds and composites

*Calving difficulty score considered a trait of the mother.
†Percentage of difficult births, all others evaluated calving difficulty on a subjective scale.
h^2, heritability; r_G, genetic correlation.

1993) or simulation studies considering the use of pelvic area in animal selection aimed at reducing incidence of dystocia (Cook *et al.*, 1993) have suggested that this is an ineffective strategy.

Pelvic area is only one potential aspect of maternal influence on dystocia. The *B. indicus* advantage in maternal calving ease mentioned above appears to be due to the dam's ability to alter growth of the fetus *in utero*. This is accomplished through reduced placentome weight and reduced uterine blood flow (Ferrell, 1991). Undoubtedly there are other mechanisms which contribute to dam variation in calving ease as well (e.g. variation in relaxin levels or response to relaxin, etc.).

A preponderance of data document the association of two non-genetic factors with dystocia in the dam (Meijering, 1984; Rice, 1994). One of these factors is the age or parity of the dam. Incidence of dystocia is typically three to four times as frequent in females calving for the first time compared with females in second or later parity. The propensity for first-calf heifers to have calves of lighter birth weight is more than offset by the dam's lesser stage of skeletal development relative to mature females (although perhaps other factors play a role in the higher incidence of dystocia as well). The second factor with clearly documented effects on incidence of dystocia is gender of the calf. Male calves typically have greater birth weights than female calves, and there is likewise a greater incidence of dystocia associated with the birth of bull calves compared with heifers (of the order of twofold greater). Clearly, these are two non-genetic factors that need to be accounted for when performing genetic analyses, such as estimation of breeding values for dystocia.

Genetics and Biology of Conception Rate

Failure of cows to conceive is the primary factor contributing to loss of reproductive efficiency in beef and dairy cattle production (Wiltbank, 1994). There is some evidence for genetic variation in conception rate, although the proportion of phenotypic variation associated with genetic effects appears to be small.

Fertility data are more commonly recorded for dairy than for beef cattle, owing in large part to the more common use of artificial insemination in dairy cattle. As a consequence, there are numerous reports in the scientific literature of estimates of heritability for fertility traits based on dairy cattle records. The three traits for which heritability estimates are summarized here are conception rate, days open and services per conception. This list is intentionally limited to those traits most closely associated with the cycling cow's ability to conceive. Days open is the furthest removed, given that it also incorporates variation in length of the post-partum anoestrous period. Heritability estimates for these traits are routinely small (Table 13.6), with most being 5% or less. Many

Table 13.6. Recent heritability estimates for conception traits.

Author	Conception rate	Days open	Services per conception	Population
Smith and Legates, 1962	–	0.01	–	US dairy
Everett *et al.*, 1966	–	0.07	–	US Holstein and Guernsey
Janson and Andreasson, 1981	–	0.03*	–	Swedish Red and White
	–	0.04*	–	Swedish Friesian
Seykora and McDaniel, 1983	–	0.05–0.13	–	US dairy
Hansen *et al.*, 1983	–	0.03	–	US Holstein
Taylor *et al.*, 1985	0.08	–	–	US Holstein
Jansen, 1986	0.013	–	–	Swedish Friesian: Parity 0
	0.013	–	–	Parity 1
	0.029	–	–	Parity 2
	0.019	–	–	Parity 3
Jansen *et al.*, 1987	–	0.025	–	Swedish dairy: Parity 1
	–	0.021	–	Parity 2
	–	0.070	–	Parity 3
Hermas *et al.*, 1987	0.03	0.04	–	US Guernsey
Raheja *et al.*, 1989b	–	0.03–0.05	0.03–0.06	Canadian Holstein, cows
Raheja *et al.*, 1989a	–	–	0.04	Canadian Holstein, heifers
Weller, 1989	–	–	0.035[†]	Israeli Holstein, first parity
	–	–	0.022[†]	Israeli Holstein, second parity
Moore *et al.*, 1990	–	0.004	0.008	Canadian Ayrshire
	–	0.013	0.013	Canadian Holstein
Hayes *et al.*, 1992	–	0.05	0.03	Canadian Holstein
Buxadera and Dempfle, 1997	0.02	–	0.03	Cuban Holstein

*Calving interval.

[†] Conception status, similar to the inverse of services per conception.

authors cite the low estimates of heritability in arguing against devoting effort to selection for fertility. However, others have advanced the idea that the low heritability is offset by the appreciable amount of genetic variation existing for fertility traits (Philipsson, 1981; Hermas *et al.*, 1987).

Breed differences and strain differences within breed also provide some evidence for genetic variation in conception rate. Breed evaluation studies at USDA-MARC have examined differences in percentage calf crop at birth and weaning (percentage of cows exposed to a bull that produced a calf at birth or weaning) and found limited evidence for breed differences. The overall variation between breeds (see Table 13.3) is not as great as for other traits, and it is only the most extreme breed differences that were statistically significant in these studies (Cundiff *et al.*, 1986; Gregory *et al.*, 1993). Weller (1989) presented evidence of differences in fertility between strains of Holstein cattle, with Swedish and US Holsteins differing by more than 10% in conception status (roughly the inverse of services per conception).

Given the low heritability for conception rate, the most effective way to genetically exploit this trait is through utilization of heterosis by crossbreeding. Comparisons of straight and crossbreeding mating systems with beef cattle have clearly demonstrated the potential for raising conception rates. Kress *et al.* (1992) cite an average improvement of 5.5% in calving rate for eight previous studies, while their own and other recent studies show improvements in excess of 10% (Kress *et al.*, 1990; Williams *et al.*, 1990; Brown *et al.*, 1997).

Identifying Genes Responsible for Variation in Reproductive Traits

The development of highly polymorphic genetic markers and extensive linkage maps (Barendse *et al.*, 1997; Kappes *et al.*, 1997) now makes it possible to dissect genetic variation for quantitative traits and identify the chromosomal regions and genes contributing most to variation. As mentioned above, efforts to identify QTL for ovulation rate and twinning rate are already well under way (Blattman *et al.*, 1996). Other traits discussed here should also be considered. Reproductive traits are particularly good candidates for the application of marker or marker-assisted selection, given that their sex-limited phenotypes prohibit the practice of direct phenotypic selection in both genders. The alternative is progeny testing, which is both costly and time-consuming. The primary challenge to studies of this type, in many cases, will be redefining the trait (as in the focus on ovulation rate as a proxy for twinning rate) to effectively raise the heritability of the trait under evaluation.

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