Prediction of milk yield of 3-year-old Angus cows and the influence of maternal milk production on the postnatal growth of beef steers.

A thesis presented in fulfilment of the requirements for the degree,
Master of Science (Animal Science)

Massey University, Palmerston North New Zealand

Fernando Javier Roca Fraga

2013

Table of Contents

List of Tables

List of Figures

Abstract

Maternal milk production influences calf weaning weight which is the major driver for economic return in a cow-calf operation. The objective of this study was to use measures of calf milk intake to estimate milk production of Angus (AA; n=43), Angus×Friesian (AF; n=32), Angus×Jersey (AJ; n=40) and Angus×Kiwi-Cross (AK; n=21) cows, and to determine how milk yield was related to calf growth rate (n=64) from birth to one year of age. Milk production was estimated by the weigh-suckle-weigh (WSW) technique at an average 32, 49, 80, 120 and 160 days (D) post-partum. Third-order Legendre polynomials were fitted to milk data using random regression to estimate the lactation curve for each cow. Live weight of all steers was recorded at birth and thereafter accompanying every WSW measurement. Post-weaning live weight was recorded at an average D240, D330 and D350 of age. Growth curves for each steer were estimated by fitting third-order Legendre polynomials to live weight data using random regression. The average total milk production from D32 to D160 was 1337 ± 22 kg for AF cows, 1245 ± 20 kg for AJ cows, 1301 ± 32 kg for AK cows and 1017 ± 20 kg for Angus cows. The AF, AJ and AK cows produced more ($P<0.05$) milk from D32 to D160 than the AA cows. The AF cows produced more ($P<0.05$) milk than AJ cows, with AK cows being intermediate and not differing ($P>0.05$) from either AF or AJ cows. Crossbred cows produced more milk ($P<0.05$) at all stages of lactation when compared with straightbred AA cows. In the present study, as the proportion of Friesian or Jersey in the crossbreds increased from 0 to 50%, an extra 325 kg and 240 kg of milk, respectively, was expected compared to the AA cows. Total energy intake from milk was higher ($P<0.05$) for the AF-, AJ- and AK-reared steers compared to those reared by AA dams. This resulted in higher liveweight gains so that steers reared by crossbred cows were heavier ($P<0.05$) from D60 to D270 than those reared by AA cows. Results also revealed that the higher live weight at D60 in AJ-reared steers compared to AA-reared steers was due to differences in milk consumption from D32 to D60. The higher live weight of AF- and AK-reared steers at D60 compared to AA-reared steers was attributed to a maternal effect on steer size; however, from D90 until weaning at D160, any differences in live weight were due to differences in milk consumption. Estimation of the theoretical pasture consumption revealed that AA- reared steers compensated for the lower milk intake by eating more grass, however, this was not enough to support high daily gains during the pre-weaning period. The differences in live weight seen at weaning between steers were maintained post-weaning until D270 and were attributed to differences in milk consumption during the pre-weaning period. Under non-limiting nutrient availability, AF, AJ and AK cows were able to produce more milk and wean heavier calves compared to straightbred AA cows.

Key words: milk production, weaning weight, energy intake, pasture consumption

Acknowledgements

I would like to take this opportunity to acknowledge and express gratitude to my supervisors, Dr Rebecca Hickson, and Professors Paul Kenyon and Steve Morris from Massey University, for their support and advice throughout my Masters experimental work and thesis writing. Special thanks go to Associate Professor Nicolas Lopez-Villalobos for his invaluable advice and guidance regarding the statistical analysis and modelling required for this project.

Preamble

The relationship between maternal lactation performance and offspring postnatal growth is of great economic importance in animals that nurse their young, such as beef cattle. Milk production in beef cows is affected by several factors including: breed and age of the cow (Rutledge et al., 1971); the suckling capacity of the calf (Gifford, 1953); sex of the calf (Barton, 1970a, Barton, 1970b, Hickson et al., 2009b), parity (Johnson et al., 2002) and dam nutrition (Hickson et al., 2009a). Milk is the sole source of nutrients for a newborn in early postnatal life and remains a significant component of the diet until weaning, and accordingly is a major driver of calf liveweight gain from birth to weaning (Neville, 1962, Grings et al., 2007).

The assessment of the quantity of milk a beef cow is capable of producing throughout lactation is not a commonly performed practice in a cow-calf operation as it can be difficult, time-consuming and dangerous. For research purposes, various techniques have been developed which can be allocated into two categories: 1) estimation of milk yield by repeated measurements of a characteristic known to be related to milk yield (ie. calf's milk intake) and 2) direct measurement by extracting and weighing the milk produced by a cow at different time points of the lactation. Some of the most commonly used methods to estimate or measure milk yield in beef cows are: machine milking trained cows (Cole and Johansson, 1933), milking while the calf nurses (Gifford, 1953); the suckling method (Knapp and Black, 1941, Drewry et al., 1959, Neville, 1962); the use of oxytocin before machine milking (Anthony et al., 1959, Marston et al., 1992) and the use of isotope dilution or transfer techniques (Macfarlane et al., 1969, Yates et al., 1971, Auchtung et al., 2002, Holleman et al., 1975) .

Data generated by these methods are seldom easy to interpret and compare across studies. Difficulties arise when comparing milk yields using different methods and even modifications within the same method. Additionally, the diverse breeds, cow's live weight and feeding regimes across studies make comparisons challenging; and despite good experimental designs, there are also experimental factors that need to be considered such as interacting effects of stage of lactation, sampling errors and analytical procedures (Oftedal, 1984) and the diverse statistical models used to generate and explain lactation curves.

Calf weaning weight is a major driver of economic return in a cow-calf operation. Regardless of the technique used to measure milk yield, various authors (Gifford, 1953, Neville, 1962, Schwulst et al., 1966, Barton, 1970b) have concluded that milk yield influences calf weaning weights and have reported correlations to be in the range of 0.17 to 0.94. Barton (1970b) stated that the size of this correlation tends to be lower as lactation progresses, which indicates that older calves rely upon non-milk nutrient sources to maintain a desirable liveweight gain. Little is known about the influence of maternal lactational performance on the post-weaning growth of their progeny and consequently conflicting results have been reported in this area.

The first section of this review deals with the methods used to measure and estimate milk yield in beef cows, their general assumptions, inconsistencies and most commonly known sampling errors as well as their potential advantages. The purpose of this section was to determine the suitability of the various methods for experimental conditions such as those presented in New Zealand with grazing animals. Where possible, comparisons between methods were presented. A comparison of the expected milk yield of the various breeds and crossbreeds of cows used in this experiment was beyond the scope of this review. The second section of this review deals with the relationship between maternal milk production and postnatal growth of the offspring. Partial milk conversion efficiency and differences in calf growth relative to the maternal stage of lactation were also considered.

Chapter 1. Literature Review

1.1. Introduction

Determination of milk yield in beef cattle can be stressful to both cow and calf as it is disruptive of their natural behavioural activities (Oftedal, 1984). Methods designed to estimate milk yield need to be of relatively low risk to the researcher whilst at the same time minimising disruption to the animals so as to reduce sources of variation that may cause under- and/or over-estimation of milk yields. Increasing the accuracy of milk yield estimates often requires more costly procedures and therefore it is important to determine additional accuracy by greater efforts in measuring and sampling and to what extent it may be further improved by altering existing sampling procedures.

Ideally, methods used to estimate milk yield over a known period of time should allow all research animals to be tested on the same day and therefore eliminating variation in milk yield and composition between days (Oftedal, 1984). Sampling procedures should resemble the natural suckling behaviour of the animals, thus taking advantage of the stimulus caused by the suckling calf to encourage milk let down (Coward et al., 1982, Cameron, 1998). However, it is not possible to replicate this completely in experimental grazing system conditions because calves suckle several times per day, sometimes irrespective of the presence of milk (Wolff, 1968) and consequently, some disruption to the normal suckling pattern occurs during measuring and sampling. Accordingly, when designing methodology there are two major factors affecting the accuracy of milk yield estimates, that need to be taken into account: 1) frequency and timing of suckling/sampling (Totusek et al., 1973) and 2) the interval allowed for milk accumulation before suckling/sampling and/or the time that cow and calf remain separated prior to suckling/sampling (Williams et al., 1979a). Labour intensive practices that require a great deal of sampling and animal handling should be avoided because only a small number of animals can be sampled in a day and consequently the technique may not be suitable to on-farm trials with larger herd numbers (Beal et al., 1990). Ideally, the frequency and timing of sampling measurements should allow estimation of milk yield in early (post-calostral), mid- and late lactation, with special emphasis on determining peak lactation and lactation persistency.

Historically, the way researchers determined milk yield in beef cows could be categorised into two groups; (i) estimating milk production via a variable highly correlated with milk yield or, (ii) actual extraction of milk from the udder. Both methods require separation of the cow-calf pair so milk is not removed from the udder by the calf and also to allow the researcher to establish a timeframe in which milk is produced. The main difference, however, is that when extracting milk from the udder, removal of residual milk is a controlled process whilst when estimating milk yield by measuring the calf's intake, the separation time allows hunger to develop in the calf and therefore relying on the suckling ability of the calf to remove all milk. This falls into the assumption that the calf is able to remove all milk produced in that period of time; an assumption that may not necessarily be the case during early lactation when milk production surpasses the calf's appetite for milk (Barton, 1970b).

Irrespective of the method used to determine milk yield, the separation period is crucial to obtain accurate estimates. Milk estimates are often represented on a 24h basis, however, when very short periods of separation (ie. 4h) are used, more than one measurement per day is needed to increase the accuracy of milk estimates (Williams et al., 1979a). Williams et al. (1979a) explained that estimates taken after separations of only 4h were less accurate than those taken at separation periods of 8h and 16h because of a scaling effect when expressing the estimates on a 24h basis. This scaling effect was attributed to the error introduced by the scale calibration used to weigh animals and the 24h multiplier of each separation period. At 4h, a multiplier of 6 was needed to represent 24h milk yield, however this also represented a ±1.38kg of over or underestimation simply due to scale calibration; an effect that was less evident with 8h (±0.7kg) and 16h (±0.3kg). Additionally, there is an interaction between mammary evacuation and milk production, where cows suckled or milked more often produce higher levels of milk than those with less and/or infrequent mammary evacuation (Williams et al., 1979b).

Conversely, whilst a prolonged separation period may increase the accumulation of milk in the udder, it may also lead to four major consequences that will ultimately result in a less accurate estimation: a) calves may not physically be able to consume all milk in a single suckling bout; b) cows may become uncomfortable and un-cooperative due to excessive milk accumulation in the udder and may not allow the calf to suckle (Williams et al., 1979a); c) the disruption of the maternal-offspring relationship could have an adverse effect on milk output mainly due to a reduction of normal levels of suckling stimulation (Coward et al., 1982), which when combined with handling stress may lead to incomplete milk let down and consequently low or underestimated milk yield measurements (Oftedal, 1984) and; d) excessive accumulation of milk in the udder may initiate mammary involution and consequently changes in milk composition and subsequent milk yields (Lascelles and Lee, 1978). For practicality, one or two measurements are required throughout a day to maximise the number of animals to be handled in a single sampling event, which also allows separating animals in intervals from 8h to 12h prior to each measurement.

1.2. Methods for measuring milk yield

1.2.1. Hand and machine milking

Research measuring the lactational performance of beef cattle has a long history. Early in the 1900's hand or machine milking offered a way to determine milk yield differences between beef cattle breeds. Reports of total milk yield for Aberdeen Angus cows estimated a range of production from 485 kg to 1296 kg for an 8-month lactation (Gowen, 1918, Gowen, 1920). Cole and Johansson (1933) argued that the number of reports used to assess the relative milk yield of the Angus breed was scarce and that the data generated from these studies was overestimated as experiments used only high producing cows and obtained extremely variable yields. As a consequence, Cole and Johansson (1933) investigated the lactation performance of seven purebred Angus cows over four lactations. All animals were machine milked twice a day and kept on free stalls all year round with a similar diet based on hay, silage and concentrate. No procedure is described in this investigation as to how the seven Angus cows were trained to be machine milked; however, it seems that in this experiment, beef cows were kept together with eight mature dairy cows for their daily milking and feeding routines, which may had facilitated the behavioural training of the younger beef cows towards a more dairy orientated. The average fat corrected (4%) milk in 180 days (d) for the seven Angus cows were 972, 1267, 1257 and 1122 kg for first, second, third and fourth lactations respectively.

Gifford (1953) designed an experiment to measure milk yield in Hereford, Angus and Shorthorn cows, by hand milking while the calf nursed. Milk yield was measured three times per month for a total of 8 months. Cow and calf were separated for 24 hours then the calf was allowed to suckle on one side of the udder whilst the other was hand milked. On the next day, the same procedure was repeated but on opposite sides. Left and right udder half hand-milking yields were summed to estimate daily milk yield. Total milk production for the 8-month lactation across all breeds ranged from 142kg to 1117kg. Gifford (1953) found that peak milk yield occurred within the first month of lactation with a consistent decline observed in subsequent months.

A similar approach was used by Totusek et al. (1973) with measurements of milk yield made once a week for 30 weeks. On one week, one side of the udder was milked twice a day whilst the calf suckled the other. The following week the same procedure was applied to the alternate side. Daily milk yield was assumed to be twice the quantity of milk obtained from the side of the udder that was hand milked. Average daily milk yield at 210d lactation was approximately 4.54 kg. Similar studies have reported lower daily milk estimates, varying from 1.9kg to 3.9kg (Furr, 1962, Gifford, 1953, Gifford, 1949, Klett et al., 1962, Velasco, 1962, Masilo et al., 1992); however, despite the higher milk yield estimates found by Totusek et al. (1973), the weaning weights of the calves did not reflect the higher milk consumption of their study. In agreement with Gifford (1953), data from Totusek et al. (1973), suggested that peak lactation occurred at approximately 3 weeks post-parturition and that milk yield declined linearly after that.

1.2.2. Oxytocin method

Training beef cows to be machine milked or using the calf to encourage milk let down depends highly on the cooperation of the animal and this can vary greatly between days (Lamond et al., 1969). To overcome this inconvenience, the use of oxytocin to facilitate milk let-down was first reported in sheep by McCance (1959) and in beef cattle by Anthony et al. (1959). Briefly, oxytocin is a nine amino acid peptide produced by hypothalamic neurons and transported into the blood stream from the posterior pituitary lobe (Tancin and Bruckmaier, 2001). One of the actions of this hormone is to facilitate milk let-down by acting directly on the smooth muscle myoepithelial cells surrounding the mammary alveoli, stimulating contractions that force milk down the udder ducts into the cistern and further to the teat cisterns (Neville, 1998, Tancin and Bruckmaier, 2001). Additionally, oxytocin causes an increased blood flow to the teat, facilitating milk passage (Tancin and Bruckmaier, 2001).

The proposed oxytocin method for beef cattle (Anthony et al., 1959) consisted in separating the cow from its calf and immediately injecting the cow with 40 IU (international units) of oxytocin intramuscularly. Cows were then machine milked and carefully hand stripped to completely remove milk from the udder thereby effectively equilibrating all cows prior to the test-milking day. Animals remained separated for 12h and cows given access to food and water. In the test-milking day, cows were injected with 40 IU of oxytocin, machine milked until milk flow ceased from all quarters and hand stripped for 5 minutes to remove residual milk. Twelve-hour milk yield was assumed to be the weight of both collected plus residual milk.

Marston et al. (1992) used a similar approach to determine the milk yield of three Angus herds. The first herd (A1) consisted of only 2 years-old Angus heifers; the second group (A2) was a mixed age group with an age range from 2 to 10 years and the third group (A3) was also a mixed age group with an age range from 3 to 10 years. In contrast with Anthony et al. (1959), on the pre-test days, calves were separated from their dams for an average of 5h and then allowed to suckle ad libitum for 45 min to empty the udder to a similar degree. Animals were then separated from an average of 10.7±1.8h until milking started. On the test day, cows were injected with 40 IU of oxytocin intramuscularly and immediately machine milked until milk flow ceased. Hand stripping was performed to collect residual milk. Cows were milked at an average of 60, 108 and 196d postpartum for all herds. The A1 herd had two additional milkings at 35 and 145 days postpartum. Average milk production in 205d lactation was 1283±43kg, 1556±43 and 1617±77 for A1, A2 and A3 herds, respectively. The average daily milk yield for all herds was 7.09 kg. Contrary to other researchers (Gifford, 1953, Totusek et al., 1973) using only machine or hand milking without the aid of oxytocin to facilitate milk let down, Marston et al. (1992) found that peak lactation occurred at a mean of 88 days postpartum (ie. week 13) for all three herds as opposed to 3 weeks postpartum. Average milk yield at peak lactation was of 8.5±0.3, 10.7±0.5 and 10.1±0.6kg for the A1, A2 and A3 herds, respectively.

Fiss and Wilton (1992) recorded the milk yield of Angus cows (n=21) and heifers (n=21) using the oxytocin method at approximately 6-week intervals throughout the lactation. The cow and her calf were separated early in the test day. Immediately, cows were injected with 60 IU of oxytocin and then machine milked until empty. Animals remained separated for 6h and the procedure was repeated again to measure 6h milk yield and multiplied by 4 to estimate 24h milk production. Average milk production for the whole Angus herd in 200d lactation was 1436 kg with an average daily yield of 7.18±0.81kg. This is in agreement with the results by Marston et al. (1992) but much higher than those reported by other researchers (Gifford, 1953, Totusek et al., 1973, Masilo et al., 1992) using only machine or hand milking without the aid of oxytocin to facilitate milk let down.

A variation of the previously described oxytocin method was utilized by Brown et al. (1996) to investigate the milk production of 3 year-old Angus heifers grazing on either Bermuda Grass (*Cynodon dactylon*) or endophyte-infected tall fescue (*Festuca arundinacea*). Milk measurements were taken 5 times over the lactation at 61, 90, 117, 145 and 173 days, however, no pre-test day evacuation of the udder was performed. The procedure consisted on overnight separation (14h) of the animals and machine milking with a single-cow portable machine after sedation (1.5 mL of acepromazine) and injection of 20 IU units of oxytocin. Milk estimates for 14h were calibrated for 12h using the conversion factor ([milk yield/14] × 12) and doubled to estimate 24h milk yield. Table 1 show the milk yield estimates obtained with animals grazing the two types of grasses.

Table 1. Average milk yield (kg) of Angus heifers grazing on either Bermuda grass (BG) or endophyte-infected tall fescue (E+) (adapted from Brown et al., 1996).

	Days postpartum						
Grass	61	90	117	145	173	200	Average
BG	8.6±0.7	8.1±0.6	6.8±0.5	6.53±0.5	5.9±0.4	5.5±0.5	6.9±0.4
E+	5.4±0.7	3.9±0.5	3.9±0.5	3.79±0.4	3.7±0.4	3.5±0.5	3.9±0.4

Peak milk yield was reached at about 61 days postpartum (ie. week 9 postpartum) with a gradual decrease over time until its lowest at 200d (Table 1). Peak milk yield estimates were similar to those reported by Marston et al. (1992) with Angus heifers on drylot (8.5±0.3kg/d) and average milk yield estimates were also similar to those of Fiss and Wilton (1992) with a herd consisting of 50% heifer and 50% mature cows on a corn silage and haylage based diet (7.18±0.81kg/d).

In New Zealand, Peterson et al. (2007) estimated the milk yield of 17 Angus heifers kept on average quality late spring pasture and milked once during weeks 7, 9 and 11 of lactation.

Cows were separated from their offspring, injected with 50 IU of oxytocin, placed in a cattle crush and the left hind legs were roped before machine milking and hand stripping. Animals remained separated for 6h and the same procedure repeated to determine 6h milk yield and multiplied by 4 to estimate 24h milk yield. Average milk yield across animals was 5.87±0.26kg/d, which is lower than those reported by other researchers using the oxytocin method (Brown et al., 1996, Marston et al., 1992, Fiss and Wilton, 1992) but higher than those using only machine or hand milking without the aid of oxytocin to facilitate milk let down (Totusek et al., 1973, Gifford, 1953). Under grazing conditions, the results in this study suggested that peak milk yield occurred at week 9 of lactation which is in agreement with Brown et al. (1996) with Angus cows grazing Bermuda grass but earlier than the results from Marston et al. (1992); however, Peterson et al. (2007) reports an average milk yield at week 9 of 7.4kg compared to 8.6kg from Brown et al. (1996). Additionally, Marston et al., (1992) reported a higher milk yield at peak lactation (8.5±0.3kg/d) of Angus heifers. Denamur (1965) advised that large, non-physiological quantities of oxytocin are required to overcome the inhibitory effect of adrenaline on milk ejection response in stressed animals. This may explain the lower milk yield recorded by Peterson et al. (2007), since roping the left hind legs may have cause stress in the cows and consequently the dosage of oxytocin was not adequate given the circumstances. However, other factors such as diet and genetic potential for milk yield need also to be considered.

1.2.2.1. Limitations of the oxytocin method

It seems that the oxytocin method relies greatly on the efficiency and comparability of mammary evacuation, the amount and frequency of oxytocin injection and correct handling of the animals prior to the test. Additionally, large or frequently administered quantities of oxytocin may affect the rate of milk secretion causing an individual animal to produce more milk throughout lactation when is injected with oxytocin than its regular levels of production without oxytocin (Sprain et al., 1954). Also, frequent oxytocin injection decreases the lactose content of milk because it can affect the exchange of ions and small molecules (such as lactose) between the aqueous phase of milk and extracellular fluids in the intercellular junctions of the mammary alveoli (Oftedal, 1984). Coward et al. (1982) argued that the physiological relevance of milk yield estimations may be unreliable due to the excessive amounts of oxytocin required to bring them about and the effect on subsequent measurements.

Whilst machine and hand milking beef cattle may help determine milk production across breeds, it requires a behavioural adaptation of the experimental animals towards a more dairy orientated conduct. This adaptation may be difficult to achieve with a greater number of animals in large on-farm experiments, as is the case of grazing beef cattle in New Zealand. The use of oxytocin to aid milk let down provides a tool to increase the reliability of those estimates, however, it does not allow for estimations of calf milk consumption and therefore the relationship between calf growth and milk intake cannot be identified.

1.2.3. Suckling behaviour as an indicator of milk yield

Estimation of milk consumption under grazing conditions is difficult to assess without disrupting normal behavioural patterns of the experimental animals. One way to overcome this disruption was by observing the suckling behaviour of the offspring as an indicator of the maternal milk yield. The assumption was that the length and frequency of suckling determines the quantity of milk transferred from mother to offspring (Fletcher, 1971). Across species, however, there has been an increasing number of studies that have failed to show a significant positive correlation between suckling behaviour and milk production and consequently, the reliability of the technique has been questioned (Cameron, 1998).

One of the arguments against this assumption is that weaker calves may take longer to drain the udder but no extra milk is being extracted (Clutton-Brock, 1991). Additionally, with increasing age, the ability of a calf to suckle increases, therefore an increase in the amount of milk consumed per bout could occur. Nicol and Sharafeldin (1975) observed that with increasing age, frequency of suckling decreased from 5.6 times a day at 7d of age to 3.5 times a day from 24 to 120 days of age. The time spent per suckling bout increased from 6 minutes (min) in the first month of age to an average of 10.5 min at 35d of age and remained constant up to 120d of age. Despite these observations, there was no relationship between suckling time and milk yield (r^2=0.023). In cattle, milk let-down does not occur immediately after suckling is started (Whittemore, 1980) and with this, overestimation of the length of a suckling bout may occur due to an inclusion of a non-nutritive period in the estimates, which may explain the low correlation between suckling time and milk yield found by Nicol and Sharafeldin (1975). This non-nutritive period is however, necessary to stimulate milk production and in cattle, as in other species, infants often suckle irrespective of the presence of milk (Cameron, 1998).

Another explanation for the low correlation between suckling behaviour and milk yield may be related to the character of the suckling bout, meaning that some suckling events may be more social rather than nutritive (Adler et al., 1958), especially when a calf is alarmed or distressed. Suckling is therefore considered to satisfy both emotional and nutritional needs of the calf (Adler et al., 1958) suggesting that not every suckling event culminate in milk being transferred to the offspring (Cameron, 1998). In their study, Nicol and Sharafeldin (1975) noted that both cows and calves were responsible for initiating a suckling event either by the calf approaching the cow to suckle or as a response to its mother call; however, the frequency of these events was not recorded. Wagnon (1963) reported that 83% of the suckling events occurred when the calf approached the cow whilst the remaining happened as a result of a mother's call.

Another confounding effect when estimating milk yield by measuring the offspring suckling behaviour is related to the variation of the suckling ability of the calf. Nicol and Sharafeldin (1975) found that Friesian sired calves suckled slightly more often (3.83 vs. 3.37 times per day) and longer (9.98 vs. 9.69) than Angus sired calves. This resulted in a greater total suckling time for the Friesian calves (35.6 min vs. 30.9 min) when compared to the Angus bred calves. In a follow up investigation, Nicol (1976) followed the lactation of cows suckling Friesian × Angus and pure Angus calves. He found a 9% difference in milk yield; with cows suckling Friesian sired calves producing 944 kg of solid corrected milk (SCM) in 135d of lactation compared to 862 kg SCM in cows suckling pure Angus calves. This increased milk production was partly attributed to a greater suckling ability of the Friesian sired calves that led to a better emptying of the udder, which may have contributed to a greater stimulation for milk production. Lidfors et al. (1994) suggested that pre- and post-suckling stimulation occurring in beef cattle during non-nutritive periods might determine the future availability of milk to the calf. This may explain the longer suckling bouts for the Friesian bred calves and consequently the higher stimulation in the cows to produce the extra 9% of milk.

1.2.3.1. Limitations of the suckling behaviour technique

Cameron (1998) pointed that confounding factors such as: 1) the method of estimation of suckling behaviour; 2) the variation of suckling ability of the offspring; 3) motivation for suckling; 4) the mother's experience, physiology and ability for milk let-down; 5) non-nutritive suckling and; 6) variation in milk composition are just few of the experimental biases that this technique has to overcome in order to provide accurate estimations. Consequently, time spent suckling may not be indicative of milk intake but rather an indicator of the offspring's motivation for suckling.

1.2.4. Isotopic techniques for determining milk yield

Isotopic techniques are more standardized methods that minimised animal handling and provided information about maternal milk performance under normal suckling behavioural patterns. It also allows a large number of animals to be handled in a single experiment which can result in less variability and a greater reliability of the data obtained. Yates et al. (1971) explained that milk contains about 85% of water and that metabolic water formed from the oxidation of the hydrogen (H_2) present in milk solids, yields an extra 10% of the total milk volume, indicating that milk consumption can be accurately measured as the rate of water turn over estimated by the exponential decline in concentration of a given tracer in body fluids. This means that if a known concentration of tracer is injected into the bloodstream, a proportion of it leaves the body as water in physiological processes, but because of the body's necessity to be in water balance more water comes in therefore diluting the tracer. Over a period of time, more tracer leaves the body and more water comes in allowing estimation of the disappearance rate of the tracer in the blood. This relies on the assumption that the only source of water that the calf is ingesting over that time period is from milk. This method is usually referred as to the isotope dilution method and the tracers used are generally tritiated water (Howard and Macfarlane, 1967, Yates et al., 1971) and deuterium oxide (Holleman et al., 1975, Auchtung et al., 2002).

Briefly, tritiated water (HTO), also called tritium oxide, is a molecule of water where one atom of H_2 has been replaced by an atom of the radioactive isotope of H_2 called tritium (^3H or T). An isotopic relationship exists between H_2 and T, whereby they possess the same chemical properties which therefore gives HTO the same properties as regular water with a physiological half-life of 8 to14 days (Pinson, 1952). This makes HTO of practical use as a tracer in water turnover studies. Tritiated water is normally injected in a saline solution at a known and very low radioactivity, measured in Curies (Ci). Deuterium oxide (D_2O), refers to water that has been enriched with the H_2 isotope deuterium (^2H or D). This isotope is particularly important, since it's a non-radioactive isotope, which reduces the risks and waste-handling problems associated with radioactive isotopes. Additionally, deuterium is a very stable isotope and therefore crosses body barriers at the same rate as water to be uniformly distributed in total body water (Auchtung et al., 2002). Deuterium oxide is often injected diluted in a saline solution and analysed by spectrometry.

The procedure of the isotope dilution method consists of the separation of cow and calf on the test day to let any milk consumed by the calf to be equilibrated in the stomach. A blank blood sample is taken to determine a base line of body water content. This blank blood sample is also useful when D_2O is used since it allows determination of the amount of naturally D_2O present in the animal's body before the injection of the tracer. After a known concentration of tracer is injected, the cow and calf remain separated for an additional period of time to allow tracer equilibration (ie. 2h for calves) and a sample of the equilibrated blood is taken for calculations. Animals are sent back to pasture for a known time interval, normally between 7d to 15d, and returned to the facilities for blood sampling and weighing. A new dose of tracer is then injected and the same procedure is repeated at similar intervals throughout the experiment. The continuous injection of tracer over the measurement period not only allows calculation of changes in water volume and tracer disappearance but is also a direct measurement of changes in body solids (ie. muscle).

Using the isotope dilution method with HTO as the tracer, Dove and Axelsen (1979) conducted an experiment in Angus and Angus×Friesian (AF) calves fed *ad libitum* through rubber teats from self-feeders over the first 6 weeks of lactation to determine the effect of increasing pool size on estimates of water turnover. Measurements were taken every week and with every measurement, concentrations of HTO were injected to compensate for calf growth starting with 150 μCi on the first week postpartum up to 300 μCi at week 6 postpartum. Milk samples were collected every week from the cows to generate a conversion factor to which water turnover measurements can be converted into milk intake. Table 2 shows the uncorrected and corrected values of water turnover for calves during the 6 week study.

Table 2. Estimated water turnovers and estimated milk intakes of Angus (AA) and Angus×Friesian (AF) calves during the first six weeks of lactation (taken from Dove and Axelsen, 1979).

Breed/Week	Water turnover		Increase from correction (%)	Conversion factor	Milk intake (kg/day)
	Uncorrected (kg/day)	Corrected (kg/day)			
AF(1)	7.740	8.294	7.2	0.9588	8.651
A(1)	5.777	6.057	4.9	0.9601	6.309
AF(2)	6.766	7.100	4.9	0.9601	7.388
A(2)	6.120	6.445	5.3	0.9572	6.731
AF(3)	8.068	8.619	6.8	0.9605	8.974
A(3)	7.191	7.831	8.9	0.9607	8.152
AF(4)	9.592	10.341	7.8	0.9598	10.774
A(4)	8.377	8.698	3.8	0.9594	9.066
AF(5)	9.124	9.451	3.6	0.9598	9.846
A(5)	8.983	9.238	2.8	0.9591	9.631
AF(6)	10.370	10.759	3.8	0.9597	11.211
A(6)	9.026	9.620	6.6	0.9598	10.023

On average, pool size correction increased water turnover estimates and consequently milk intakes by 5.5%. Milk intake estimates are higher than those reported using other techniques (Totusek et al., 1973, Hickson et al., 2008, Hickson et al., 2009a, Hickson et al., 2009b, Peterson et al., 2007). Whilst the results shown in Table 2 cannot be readily compared to those of grazing conditions, it demonstrates that the isotope dilution technique may be a more realistic approach to determine milk intake in ruminants. Contrary to other techniques, where estimates are taken during a period of disturbance to the animals, estimates of the isotope dilution technique have the potential to be taken while the animals are grazing on the field (Macfarlane et al., 1969, Dove and Axelsen, 1979).

To overcome overestimation of milk consumption through ingestion of pasture, various isotope transfer methods have been proposed. Nicol and Irvine (1973) proposed an Iodine (I) isotope transfer method using the radioisotopes ^{131}I and ^{125}I. The procedure involves the separation of cow and calf for 6h, milk sample collection and subsequent injection of ^{131}I to the cow. Cow and calf remain separated for an additional 6h to allow accumulation of milk in the udder and isotope equilibration. During this 6h, the milk sample collected previously is incubated at 37^{o}C and ^{125}I is mixed at a rate of 1 μCi per 5kg of calf body weight and injected into the teat canal. Calves are allowed to suckle and blood samples are taken at 1h and 4h post suckling. Six hour milk production is then calculated using the formula:

$$6h\ \ milk\ yield = \frac{Total\ ^{125}I\ given}{^{131}I\ in\ 1l\ of\ milk} \times \frac{^{131}I\ in\ calf}{^{125}I}$$

To validate this technique, Nicol and Irvine (1973) compared 6h milk intake estimates obtained by the oxytocin and the isotope transfer techniques. On average, milk intake as obtained by the oxytocin technique was 1.65 kg whilst for the isotope transfer technique was 1.77kg, suggesting an overestimation of 7.4% when the isotopic methods was used; however, they found a high correlation (r=0.76) between the two techniques. Nicol and Irvine (1973) concluded that despite the high correlation found between the two techniques, estimates of milk intake obtained by isotopic transfer may change the shape of the lactation curve compared to that expected using the oxytocin method, although they conceded that the procedure of isotopic transfer is more laborious and require adequate facilities and equipment to process samples.

Figure 1 illustrates a proposed isotopic transfer method that uses both mother and offspring for determination of intake. This technique consisted in one isotope being used to assess the transfer of fluids (ie. milk) from mother to offspring and a simultaneous determination of water turnover in the offspring calculated from the disappearance of a second isotope injected directly in the young.

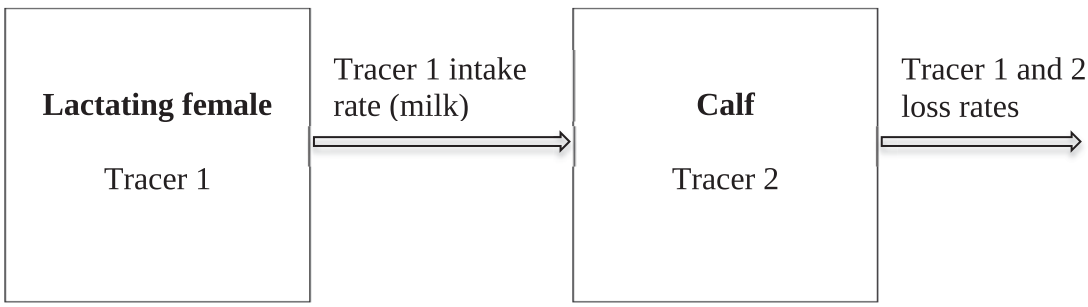

Figure 1. Diagram illustrating the proposed isotopic transfer method by Holleman et al., (1975).

Holleman et al. (1975) proposed two combinations of tracers to be used in an isotopic transfer technique: 1) HTO and D_2O and; 2) Cesium (^{134}Cs) and HTO. From Figure 2, it can be seen that in the former method, HTO is used to obtain estimates of water (from milk) coming from mother to offspring following a suckling event. In time, concentration of HTO increases in the calf as it gets diluted in the mother (Figure 2). On the other hand, D_2O is injected into the offspring to measure its concentration in plasma water after milk consumption and over a period of time its dilution rate can be calculated.

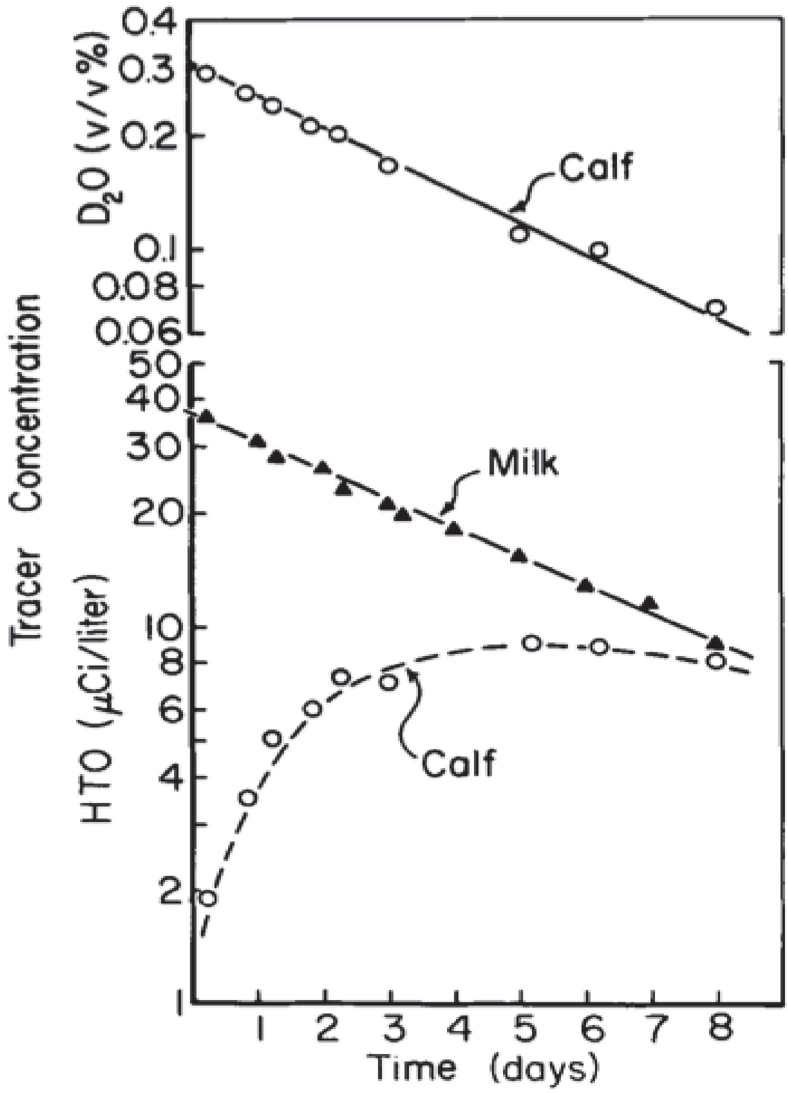

Figure 2. Illustration of the expected concentration of HTO and D_2O over an 8 day period in the calf and it mother's milk for the calculation of milk consumption estimates using isotopic transfer (taken from Holleman et al., 1975).

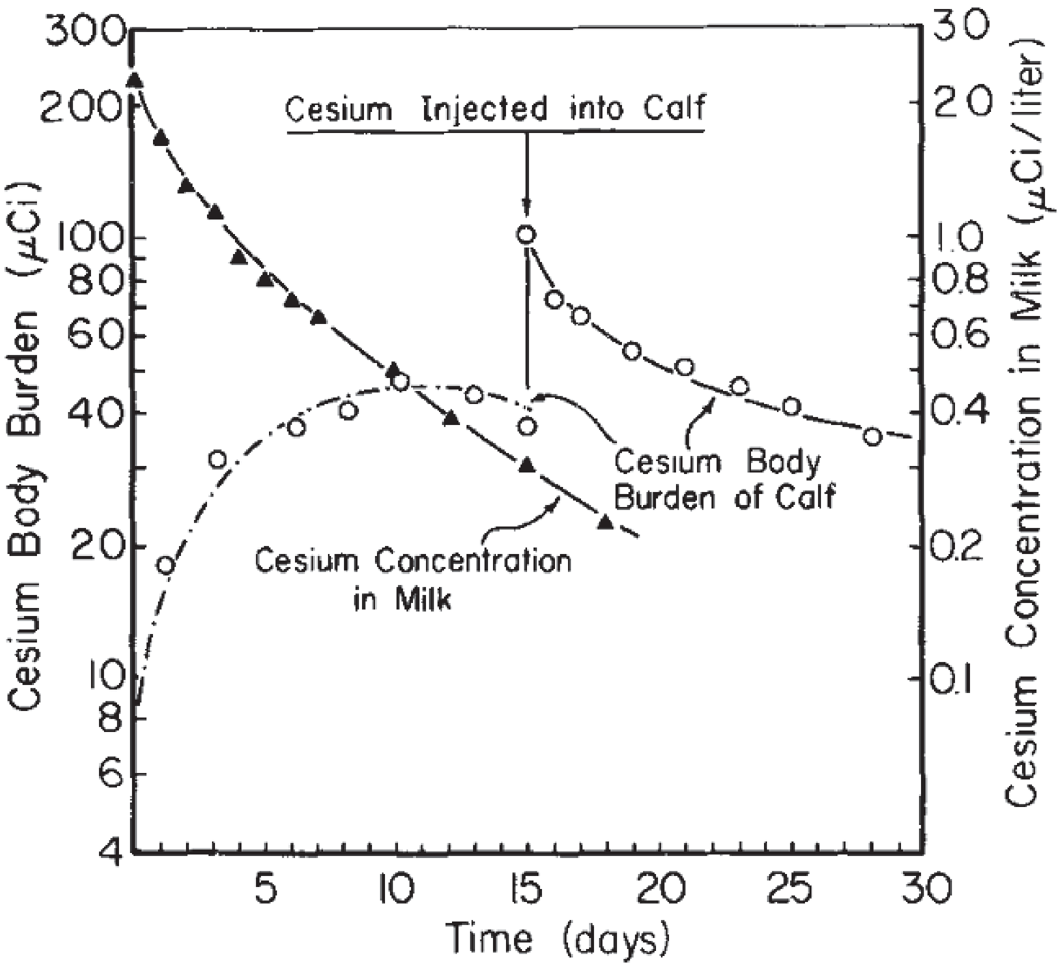

Figure 3. Caesium concentration in milk and the resulting body burden of the calf following a meal. (taken from Holleman et al., 1975).

In the latter method using ^{134}Cs, both isotopes are introduced into the mother. HTO is used to measure the transfer of water coming from milk during a meal (see ▲ in Figure 3) and the build-up of Cs concentration is monitored in the calf for around 10d to 15d for kinetics analysis (see ○ in Figure 3 from day 0 to day 15). An extra dose of Cs is then given to the calf to measure its body burden (ie. accumulation and loss of tracer) for an additional 10d to 15d (see ○ in Figure 3 from day 15 to day 30). These data is then converted to milk intake from the concentration of Cs in milk using a simulation model (Holleman et al., 1975). Table 3 shows a comparison of milk intake estimates obtained in bottle-fed dairy calves and the two isotope transfer techniques.

Table 3. Actual and calculated intakes for dairy calves in two measurements at an average of 50 and 76 days postpartum (adapted from Holland et al., 1975).

			Calculated milk intake (l/d)		
			HTO/D_2O		^{134}Cs
Calf #	Preformed[a] water (l/d)	Actual milk intake (l/d)	Calculated value	Simulation value	Simulation value
1	7.33	4.25	4.18	4.08	4.15
2	7.81	5.62	5.43	5.48	5.33
3	8.29	6.91	6.74	6.83	6.80
4	9.77	8.70	8.88	8.88	8.75
1	9.92	4.37	4.65	4.65	ND[b]
2	9.67	5.67	5.93	5.44	ND
3	9.52	6.99	7.74	7.09	ND
4	10.95	8.77	9.46	8.63	ND

[a] Drinking water + food water + milk water
[b] ND, not determined

There was a high correlation (r=0.998) between actual milk intake and intake estimates (ie. calculated) obtained by the HTO/D_2O transfer technique. The largest difference between actual and calculated milk estimates was approximately 5%, suggesting that the HTO/D_2O transfer technique is a valid method to determine milk intake in calves. Additionally, the HTO/D_2O technique was highly correlated (r=0.999) to the ^{134}Cs technique and consequently, estimates obtained by the ^{134}Cs technique were similar to the actual intake of the calves. They suggested that both methods have the advantage over the isotope dilution technique because estimates of metabolic water are not necessary to estimate milk intake since intake is estimated by the transfer of tracer from mother to offspring. Contrary to the isotope dilution method, both transfer techniques can distinguish between water obtained from milk and water obtained from other sources (ie. forage or free water). A study in reindeer calves cross-suckling reindeer cows suggested that separation of the animals may be necessary to overcome overestimation of intakes due to increased amount of tracer going into the calves (Holleman et al., 1971).

1.2.4.1. Limitations of the isotopic techniques

The theoretical milk intakes as estimated by the isotope dilution technique compared to the actual milk intake of bottle or bucket fed lambs, calves and elk fawns have been similar across studies (McFarlane et al., 1969, McEwan and Whitehead, 1971, Sekine et al., 1972, Wright et al., 1974). However, three limitations for this technique have to be underlined, firstly that the rate of water turnover can estimate milk intake only when milk is the sole source of water for the animal (Dove and Freer, 1979) or restricted to conditions where the relative proportion of ingested water derived from alternate sources can be measured (Oftedal, 1981). Both conditions may not be possible in grazing ruminants further than the first two weeks of lactation where pasture intake is negligible. Secondly, isotope concentrations can decrease if the isotope is incorporated or deposited in organic material that is produced during growth. MacFarlane et al. (1969) suggested that the exchange of T and H_2 in tissue is generally 1-2% but can reach up to 4% in ruminants. Thirdly, in a growing animal the rate of water turnover may not be a simple function of serum specific activity after HTO injection (Dove and Freer, 1979) because dilution of the isotope can be caused by an increase in total body water pool size rather than water turnover. Searle (1970) showed that total body water could change 1% during the first two months of life. Failure to include a correction for increased water pool size during the first two weeks of lactation have been reported to underestimate milk intake by 6.4% and 9.7% for Shorthorn×Brahman calves maintained in unfertilized and fertilized tropical pastures, respectively (Siebert, 1971). Additionally, Auchtung et al. (2002) pointed out that the cost of obtaining and analysing the samples may be cost prohibitive.

1.2.5. Weigh-Suckle-Weigh method

In beef cattle, suckling is essential for the future availability of milk for the calf (Lidfors et al., 1994), but also is necessary to stimulate milk let down. Techniques that rely on artificial milking such as machine or hand milking beef cattle do not take advantage of this stimulus (Dawson et al., 1960) and deprive the calf of milk that would normally be consumed. Suckling behavioural observations do not necessarily estimate the amount of milk transfer from mother to offspring (Adler et al., 1958, Cameron, 1998). One such method that uses the calf's suckling stimulus and estimates the calf's milk consumption is commonly referred as to the "weigh-suckle-weigh" (WSW) or the "plunket" method and is one of the most frequently used techniques for researching milk yield and calf consumption in beef cows and other species. The procedure is based on weighing the calf before and after a suckling event. Suckling is allowed as a controlled process after the mother and its calf are separated over a known period of time with suckling occurring at defined points. The weight differential between sucklings over a 24-hour period is considered to be the calf's appetite for milk and it is assumed that this value is equivalent to the milk production of the cow at that point in time (Barton, 1970b).

Comparison of the WSW data between studies is challenging due to three major inconsistencies that can be seen between experiments: 1) differences in the length of separation of the calf and its mother; 2) the frequency at which samples are taken throughout the lactation, and; 3) the presence or absence of a pre-nursing period prior to the day of the test, to effectively put all cows on an equal baseline. As a result, three variations of the WSW methods can be found in the literature and they are discussed below.

1.2.5.1. Weigh-suckle-weigh with continuous sampling

Research using the WSW method in beef cattle was first reported by Knapp and Black (1941). Data was collected over 5 years from Shorthorn and Hereford cows, with milk consumption of calves measured from calving to weaning (at 180 days) by weighing calves once a week before and after a controlled suckling event, however, no estimates of milk intake or milk yield are given by the authors in this study. The WSW method was first introduced to New Zealand by Walker and Pos (1963) who applied the technique to pasture-fed purebred Angus (AA), Hereford×Angus (HxA), Angus×Jersey (AxJ) and Angus×Friesian (AxF) cows. Milk consumption of calves was measured every day using the WSW technique starting at 3 days postcalving until weaning at week 29 postcalving. Calves were weighed before and after two suckling events per day with inter-suckling intervals of approximately 13h and 10h for first and second sucklings, respectively. The differences in weight were assumed to be the milk production of the cows in each particular day. Figure 4 shows the lactation curves for the four breeds based on calf consumption intakes.

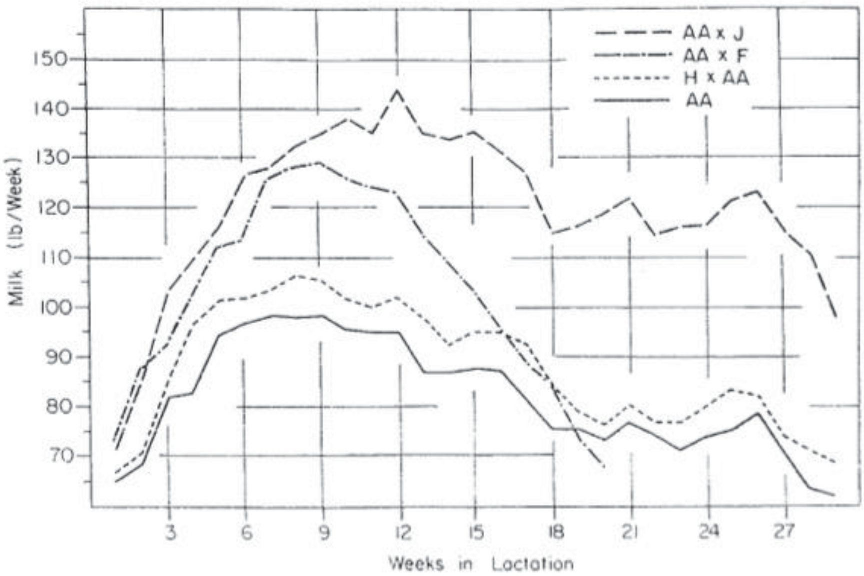

Figure 4. Milk production of four test breed groups: AAxJ, Angus x Jersey; AAxF, Angus × Friesian; HxAA, Hereford x Angus; and AA, purebred Angus (taken from Walker and Pos, 1963).

Average daily milk yield in 180 days was 5.45kg (AA), 5.83kg (HA), 7.88kg (AJ) and 5.83kg (AF). Peak lactation for the AA cows was reached at about week 7 postpartum and yield remained constant (average peak milk yield just below 6.5kg) until week 9. These results are in agreement with Totusek et al. (1973) using the WSW technique, where peak lactation was reached at week 7 but remained constant up to week 10 postpartum. However, the results differ from those of Gifford (1953) and Totusek et al. (1973) using hand milking where peak lactation of AA cows was reached close to 30 days postpartum, suggesting a possible interaction between milking technique and lactation curve shape.

Another variation of the WSW technique with continuous sampling was used by Gaskin and Anderson (1980) with Jersey×Angus, Angus×Hereford and Simmental×Angus cows bred to Shorthorn and Charolais bulls over a 3 year period. All animals were maintained in a feedlot with cows and calves separated and food and water withheld from calves during the twice-daily suckling events. Inter-suckling intervals were 6h and 12h for first and second sucklings, respectively, but only in 2-year-old cows. Milk production in older cows was only measured once daily after a 6h separation and a second measurement was calculated using a linear regression equation. Throughout the lactation until weaning, measurements in 2-year-old cows were taken every week starting on day 42 until day 91 and then every month until weaning. In older cows, monthly measurements were taken starting from day 28 until day 196. During the period of measurements in this study, on average, milk yield declined continuously as lactation progressed. Analysis of single measurements revealed that 2 and 4 years-old Jersey×Angus crossbreds reached peak lactation at an average of 56d or week 8 postpartum, which is much lower than the findings by Walker and Pos (1963) in New Zealand.

1.2.5.2. Weigh-suckle-weigh with partial sampling

A simpler variation of the WSW technique using continuous sampling was proposed by Neville (1962) using Hereford cows maintained in a feedlot. Measurements were taken only at 4 time points from day 60 postcalving until weaning at 240 days (ie. every 60 days). At every test day, the inter-suckling intervals were 14h and 8h for first and second suckling events, respectively. Average milk yield for the 240-day lactation was 3.64kg. Rutledge et al. (1972) suggested that causing minimal disturbance to the animals during the sampling period is necessary in order to achieve accurate estimates of milk yield and that ideally just 2 to 3 measures would be required to sample a whole lactation in beef cattle. To determine how many and how apart WSW measurements can be taken, they conducted an experiment with Hereford cattle where inter-suckling intervals were 8 and 16h for first and second suckling events. Measurements were taken once monthly for the 7-month lactation period and a prediction equation for total milk yield developed. Coefficients of determination and correlations between subsets of the monthly measurement were compared to determine the amount of milk consumption estimates needed to accurately measure milk yield.

They found that prediction of milk yield was more accurate (r^2=0.92) when three measurements throughout lactation were taken than when only two measurements (r^2=0.88) are used to create a prediction equation for milk yield. Therefore, four sampling schemes (of three measurements) were tested to correlate actual with predicted milk yield: 1) measurements at 2-3-4 months post calving, 2) at 1-3-5 months postcalving, 3) at 2-4-6 months postcalving and 4) at 1-4-7 months postcalving. Inclusion of measurement taken during the first month of lactation (ie. 1-3-5 and 1-4-7) tended to decrease the correlation (r=0.91) between actual and predicted milk yield when compared to those sampling schemes starting at the second month of lactation (r=0.92). This is similar to the finding of Totusek et al. (1973) where inclusion of an estimate of early lactation at day 10 of lactation, lowered the correlation between actual and total milk yield.

Additionally, Rutledge et al. (1972) found that the accuracy to represent milk yield tend also to decrease, as the interval between measurements was higher (ie. every three month compared to every two months). They concluded that bi-monthly estimates of milk consumption at 2, 4 and 6 months postcalving were more accurate than any other sampling scheme to represent total milk yield and consequently correlation between actual and predicted milk yield were also high (r=0.90). Data from both experiments (Totusek et al., 1973, Rutledge et al., 1972) suggests that no less than three, well-timed measurements are sufficient to estimate milk yield with the WSW technique in beef cattle.

1.2.5.3. Weigh-suckle-weigh with partial sampling and pre-nursing period

Drewry et al. (1959), using pasture fed purebred Angus cows, were the first researchers to incorporate a preliminary suckling period to the WSW method. This preliminary suckling was intended to empty the udder prior to the test day. This variation of the WSW technique consisted in separating the calves from their dams for 2 to 3 hours and then allowed to suckle. After this pre-nursing period, animals were separated for 12h until the first suckling event. The animals were separated again for an extra 10h and a second measurement was taken. Measurements were taken during the first, third and sixth month postcalving of two consecutive lactations. Each year, the 3 measurements were taken to represent, early, peak and the end of lactation. Average daily milk estimates for the selected periods over the two years were 6.4, 7.3 and 4.1 kg, whilst the total average milk yield was 5.9 kg. Similarly, Clutter and Nielsen (1987), using Angus-cross cows fed a mixed diet of pasture and winter feed, employed a pre-nursing period after a 4h separation followed by overnight separation. Inter-suckling intervals were 12h and 8h for first and second suckling events respectively. Three measurements were taken at an average 50, 103 and 158 days postpartum over three lactation. They found that average milk yield varied from 6.26 kg daily in heifers to an average of 7.64 kg daily in 3, 4 and 5 year-old cows.

Differences in the practice of this variation of the WSW method are minimal and generally only differ in the number of measurements taken throughout lactation and the way daily milk yield is calculated. For example, Boggs et al. (1980), using pasture fed Hereford cows, estimated milk yield monthly over a 6-month period. Each sampling period consisted of 3 days where cow and calf were separated for pre-nursing period of 12h before the daily suckling event. The 3 measurements taken each month were averaged and doubled to calculate 24h milk production in a particular month. Comparably, Le Du et al. (1979) separated cow and calf for 8h before allowing pre-nursing period, however, daily milk consumption of the calves was measured using three suckling events each day, with inter-suckling intervals of 8h. These three consecutive measurements were summed to calculate 24h milk yield.

1.2.5.4. Limitations of the weigh-suckle-weigh technique

Barton (1970b) argued that errors in the WSW technique might arise from interactions between the cow and calf that may influence milk production or consumption. Such factors are the sex of calf, its birth weight and subsequent weight changes, breed and its ability to stimulate milk let-down. In New Zealand, Anderson (1977) studied the influence of plane of nutrition pre-calving on the milk production of Angus heifers during the first 60 days of lactation using a switchover design where the switchover point was approximately 3 weeks before the onset of calving. The switchover groups were identified as: 1) High plane (HP)-Low plane (LP), 2) LP-HP and 3) HP-HP. Milk consumption estimates were taken once on an average calf age of 20, 40 and 60 days postpartum. The technique consisted in separating animals for 17h prior to the WSW procedure. Table 4 shows the average milk yield for the three planes of nutrition over a 60 day period.

Table 4. Average milk consumption estimates of calves born to heifers from three different nutrition treatments: high nutritional plane (HP) vs. low nutritional plane (LP) during the first 60 days of lactation followed by a switchover at approximately 3 weeks before the onset of calving, creating three groups: HP followed by LP (HP-LP); LP followed by HP (LP-HP); and HP followed by HP (HP-HP) (taken from Anderson, 1977).

	Milk consumption (kg)		
Treatment	20 days	40 days	60 days
HP-LP	4.13±0.21	4.03±0.34	4.06±0.58
LP-HP	4.22±0.23	3.73±0.38	4.61±0.65
HP-HP	4.05±0.22	4.15±0.36	3.74±0.62

Anderson (1977) found a close association in changes on milk consumption related to interaction between the calves and their dams. For example, the HP-LP calves showed its higher milk intake at day 20 with marginal decreases up to day 60. This effect was attributed to lighter calves in this group removing less milk than calves in the other two groups and therefore leading to a fall in production during the first 60 days of lactation. Similarly, Hickson et al., (2009a) showed that calves born to heifer in a low plane of nutrition during the first trimester of pregnancy were lighter and consumed less milk than those born in a combination of a LP and a HP of nutrition during the first trimester.

Anderson (1977) also found a close relationship between the weight changes of the heifers in the LP-HP group and the weight changes and milk consumption of their calves. During the first 20 days postpartum, the weight gain of heifers in this group was approximately 4.3kg whilst their calves grew an average of 21.8kg, hence the highest milk yield during the first 20 days for the LP-HP group. However, in the next 20 days the milk yield of this group fell significantly. This was associated with a higher weight gain of the heifers (14.2kg vs. 4.3kg) than the preceding 20 days, but also to a slower growth in the calves (11.5kg). The HP-HP calves had higher weight gains for all periods than the other two groups

Oftedal (1984) suggested that reliable results using the WSW technique can be achieved if: a) urination and defecation of the calf during the test are accounted for; b) the intervals between sucklings and the time allowed for each suckling bout resembles those of an undisturbed situation; c) the separation process is accomplished with minimal distress to both the calf and the cow, and; d) the animals have been suitably acclimatized to the facilities where the procedure is going to be performed so stress due to handling is reduced but also animals need to be acclimatized to the routine involving the technique since maternal ability and the capacity of the calf to find its mother may play a big role in the accuracy of the milk consumption estimates (Wagnon, 1963). Anderson (1977) reported increased agitation in Angus heifers that were not accustomed to the yards and the WSW procedure. This resulted in lower milk yield estimates compared to Angus heifers that were more familiar with the yards and have grown with mothers that were subjected to the WSW technique. The second not accustomed group had higher milk yields but it was associated with a greater calf appetite and a lower maternal growth during the measurement period.

Weigh-suckle-weigh variants that require continuous sampling outlined above are difficult and expensive to replicate. Their labour intensive practices make them unsuitable for on-farm experiments with a large numbers of animals. With continuous sampling, handling stress may lead to underestimation of yield by means of un-cooperative mothers not allowing the calf to suckle or by poor milk let-down. Often, increased urination and defecation can be observed in stressed calves, consequently reducing the accuracy of the weight estimates. Additionally, keeping animals penned for long periods of time is not representative of normal behavioural suckling activities.

The major disadvantage of the WSW technique is that estimates obtaining using any WSW procedure are measurements of the calf's appetite rather than the actual milk yield of the cow, especially during early lactation where calves are unable to completely evacuate the udder (Oftedal, 1984). However, if careful and well-timed measurements are taken, the accuracy and reliability of the WSW technique to estimate milk yield can be improved greatly (Totusek et al., 1973, Beal et al., 1990). Some studies have suggested that estimates taken during early lactation decreased the correlation between actual and predicted or total milk yield (Totusek et al., 1973, Rutledge et al., 1971) for reasons that have already being explained. To overcome this problem, estimation of milk yield for practical reasons start when the experimental calves are reaching a mean age of 30 days. Milk intakes of up to 13.2kg per day (Gleddie and Berg, 1968) have been reported in calves with a mean age of 30 days.

It's clear from the studies summarised above that separation intervals ranging from 4h to 16h are those most frequently used. Williams et al. (1979b) showed that separating cow and calf for an 8h period prior to the sampling produced better estimated milk yield during the first 56 days of lactation and milk yield estimates were more highly correlated with calf average daily gains than both a 4h and 16h separation. However in early lactation, it is arguable that a young calf (ie. 2-3 weeks) is capable of drinking all milk produced from an 8h and 16h separation time, and consequently a shorter separation time may resemble a more real consumption.

The problem with shorter separation times is that calves may acquire different amounts of milk in subsequent suckling events. Lampkin et al. (1961) estimated that calves consumed 54%, 21% and 25% on total milk produced in a day at the morning, noon and evening sucklings, respectively. This suggests that measurements taken only once in the morning may overestimate the average daily intake of milk compared to measurements taken at noon or evening. Consequently, more than one measurement is needed throughout a day if short separation times are used. On the other hand, long separation times (ie. 16h) do not resemble the normal suckling behaviour of cattle and are often used for practicality reasons. Williams et al. (1979b) observed irritation and discomfort behaviour in cows separated from their calves for 16h. Low or underestimated estimates of milk yield and consumption may arise from insufficient milk let-down due to stressed cows. Le Du et al. (1979) showed that three daily suckling events with separation times of 8h each, were more suitable to estimate milk consumption and yield and consequently making the WSW technique similar to the oxytocin technique than only one suckling event with 16h separation time.

The addition of a pre-nursing period when using the WSW technique is assumed to help obtaining more standardized estimates of milk yield assuming mammary evacuation during that period is comparable across cows. However, complete mammary evacuation during early lactation may not be possible if long pre-nursing periods are used and may also be dependent on the breed and sex of the calf. Although, the pre-nursing period ensures that all cows have been suckled and therefore it can be said that all cows have received a similar stimulus for milk production prior to the test. Additionally, a pre-nursing period can be accounted for as an approach to train and acclimatize animals to the technique and facilities prior to each test.

1.2.6. Comparison and validation of the weigh-suckle-weight technique with other techniques to estimate milk yield.

The reliability of milk yield estimates using the WSW technique has been confirmed in a comparison trial against hand milking (Totusek et al., 1973). Table 5 shows the average milk yield estimates for different periods of lactation and Figure 5 shows the lactation curves as estimated by using the WSW and the hand milking techniques described by Totusek et al. (1973). The hand milking technique used in this experiment has been explained previously. The WSW technique involved allowing calves to suckle twice daily with inter-suckling intervals of 12 hours (h) to determine 24h milk intake. The calves were weighed immediately before and after suckling twice daily 6 days per week throughout 30 weeks of lactation. The difference in pre- and post-suckling weight changes for the 6 day measurements were adjusted to a 7-day week and considered to be the milk yield of the cows.

Table 5. Means and standard deviations (SD) of milk yield measurements in different periods of lactation, estimated by the weigh-suckle-weigh (WSW) and hand milking (HM) techniques (adapted from Totusek et al., 1973).

	Milk yield estimation technique		Correlation with total milk yield (r)	
Period	WSW (kg)	HM (kg)	WSW	HM
D1 - D70	6.58±1.27	5.49±1.72	0.82	NA
D1 - D112	6.44±1.27	5.13±1.54	0.93	NA
D1 - D210	5.85±1.32	4.54±1.45		
D30	6.90±1.63	5.44±2.13	0.48	0.61
D112	6.08±1.90	NA*	0.81	NA
D190	4.90±1.86	NA	0.78	NA
D30, 70	6.80±1.41	5.35±1.90	0.77	0.80
D90, 180	5.85±1.54	NA	0.87	NA
D30, 70, 112	6.53±1.41	5.08±1.72	0.85	0.92
D30, 70, 112, 210	6.08±1.41	4.63±1.59	0.91	0.96
D30, 70, 112, 140 210	6.06±1.45	NA	0.93	NA
D10, 30, 70, 112, 210	6.03±1.27	4.85±1.59	0.91	0.94

* NA= not available

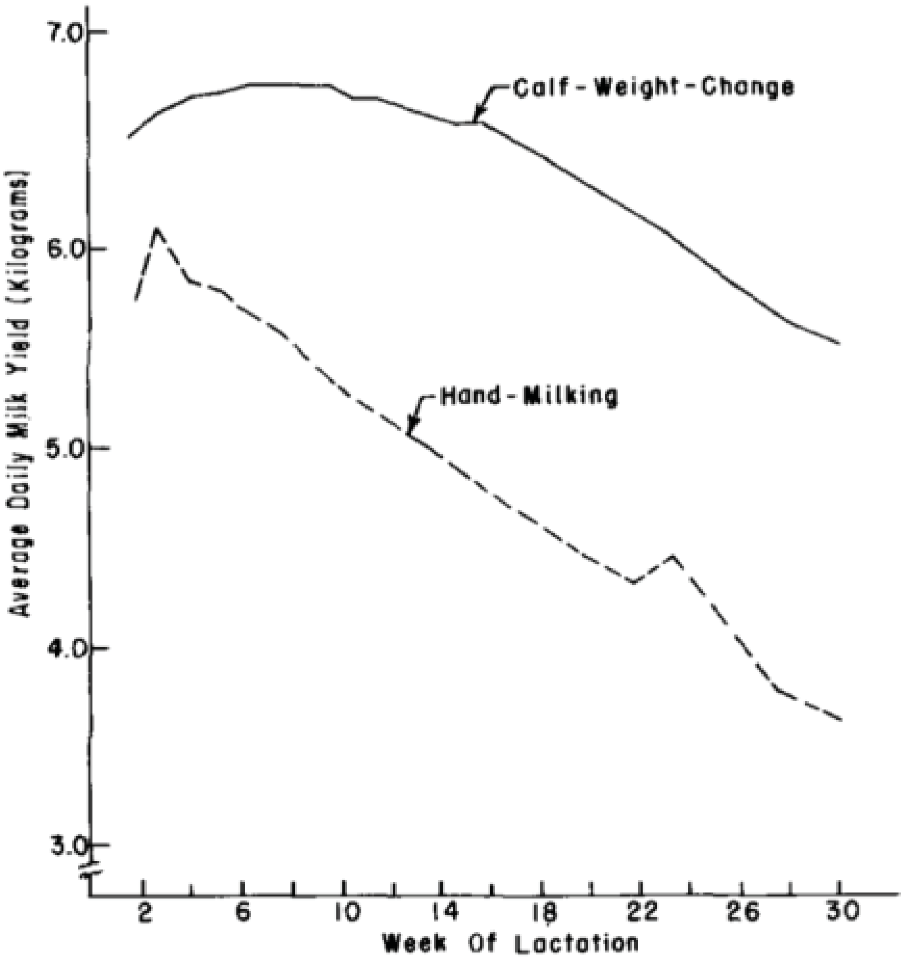

Figure 5. Lactation curves estimated using the weigh-suckle-weigh and the hand milking technique (taken from Totusek et al., 1973).

Milk yield estimates for the WSW technique were higher than the hand milking estimates at every single stage of lactation (Table 5). This resulted in lactation curves that differed in shape and persistency(Figure 5). Using the WSW technique, individual estimates from the second third of lactation (ie. D90, 180) were more correlated (0.87 vs. 0.77) than those from early lactation (ie. D30, 70). This suggests that as lactation progressed, milk yield estimates obtained with the WSW technique are less variable and more reliable than those of early lactation. This is supported with a lower coefficient of variation (CV) for mid lactation (CV=20.7) when compared to early lactation (CV=38.0). Inclusion of mid and late lactation estimates (ie. D112, 140 and 210) to calculate average daily yield for the whole lactation significantly increased the correlation with total milk yield, however, inclusion of one estimate from very early in lactation (ie. D10) did not increase the correlation (Table 5). The higher milk production obtained with the WSW technique was attributed to a greater release of oxytocin caused by the stimulus of the suckling calf; an effect that was also apparent since cows subjected to WSW tend to dry off later than those hand milked (Totusek et al., 1973). This is in agreement with the findings of Somerville and Lowman (1980) where cows subjected to machine milking tend to dry off earlier than those on WSW. In both cases (Totusek et al., 1973, Somerville and Lowman, 1980), they concluded that the WSW technique is better suited for estimating milk yield in beef cattle than hand milking or machine milking, respectively.

The average daily milk yield (5.85±1.32) in the study reported by Totusek et al. (1973) is similar to that reported by Peterson et al. (2007) using the oxytocin technique with machine milking but considerably lower than those of other researchers (Marston et al., 1992, Brown et al., 1996) using the oxytocin technique. Analysing the data from Figure 5, milk production estimated with WSW increased rapidly after parturition until about week 3 and more gradually until week 7 when peak milk yield was reached. Production is consistently maintained until about week 10 when milk production started to decrease gradually. In contrast, hand-milking data showed that peak milk yield was reached at week 3 and that production declines rapidly after this. Fiss and Wilton (1992) and Brown et al. (1996) using the oxytocin technique with machine milking found that peak milk yield was reached at about week 9 of lactation, however, these authors did not measure milk yield before week 9 and it cannot be established if peak milk yield was actually reached before this time. Marston et al. (1992) reported that peak lactation in Angus heifers was reached at about week 10 postpartum, which is later than the week 7 peak by Totusek et al. (1973), but the fact that animals remained at peak for an extra 3 weeks suggests that results are highly comparable.

In another comparison trial, Beal et al. (1990) compared the accuracy of milk yield estimates obtained by either the WSW or the oxytocin technique in Angus and Angus×Friesians cows. In the WSW procedure, measurements were taken at an average 50, 95, 136 and 179 days post calving. Calves were weighed before and after one suckling event that occurred 16h after separation. An additional suckling event was performed 3 days after the second regularly schedule procedure to estimate the precision of the WSW technique. The oxytocin technique consisted of measurements taken at an average 66, 123 and 189 days post calving. Calves were separated from their dams for 16 h. On the test-milking day, cows were injected with 20 IU of oxytocin and machine milked until milk flow ceased. An extra milking procedure was performed in 12 cows, three days after the second regularly schedule procedure to estimate the precision of the oxytocin technique. Figure 6 shows the average milk yield estimates for the two techniques. Milk yield estimates with the oxytocin technique were higher than the WSW at all stages (Beal et al., 1990). The average milk yield for the WSW technique was 5.2±0.5kg for 4 measurements compared to 5.1±0.2kg for 3 measurements with the oxytocin technique. This suggests that the WSW technique may require more measurements throughout the lactation to increase the reliability of the estimates.

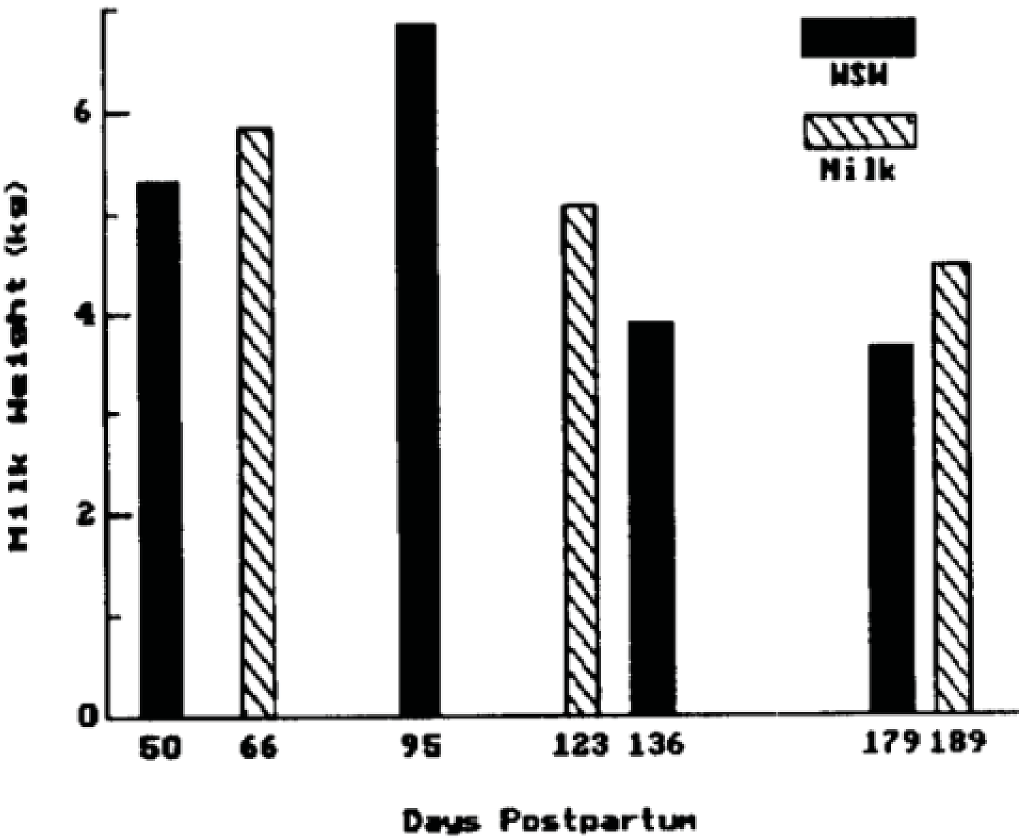

Figure 6. Average milk yield estimates (kg) for the oxytocin and the weigh-suckle weigh (WSW techniques for Angus and Angus×Friesian cows (taken from Beal et al., 1990).

This is supported by a greater correlation (r=0.96) between measurements for the oxytocin technique when compared to the WSW (r=0.35). In the oxytocin technique, all 12 cows retained their rank in the herd in consecutive milkings, suggesting a more consistent thus less variable measurements; however, when the WSW technique was used, re-ranking of animals occurred with an average change of rank of 3.5±0.3 positions in consecutive milkings. This suggests that WSW measurements are highly dependable on the vigour of the suckling calf and its ability to encourage milk let down (Barton, 1970b).

Milk yield estimates were also correlated with calf growth to determine the degree of correlation with single milk measurements. At all times, estimates obtained by the oxytocin technique had higher correlations (0.97, 0.98 and 0.94 for first second and third measurements, respectively) than those obtained with WSW (0.37, 0.45, 0.22 and 0.35 for first, second, third and fourth measurements, respectively) and it was only when the four WSW measurements were combined that the correlation increased to a level similar to those of the oxytocin technique with single measurements. Beal et al. (1990) concluded that machine milking with the aid of oxytocin to facilitate milk let down was a better estimator of differences in milk yield between cows and was more repeatable than the WSW technique, however, the results were highly comparable as the number of WSW measurements increased. In contrast, Le Du et al. (1979) found an excellent agreement (r^2=0.99) between estimates of WSW and the oxytocin technique. In their experiment, the oxytocin technique consisted of injecting 5 IU of oxytocin to the cows prior to machine milking and an extra dose of 10 IU once milk flow ceased to aid further machine milking and hand stripping. The procedure was performed twice daily with separation periods of 8h and 6h. The WSW technique consisted in weighing the calves before and after three daily suckling events with separation periods of 8h. Weights were summed to estimate 24h milk yield. Prior to the initial separation, calves were allowed to suckle to evacuate all udders to similar levels. Beal et al. (1990) argued that the WSW technique used in their experiment was simple and practical and that more controlled procedures such as those involving various suckling events per days (ie. to account for changes in intake throughout a day) or those with pre evacuation of the udder prior to the test may increase the reliability of estimates, which is the case of the WSW technique used by Le Du et al. (1979). Although, Le Du et al. (1979) suggested that the high correlation between the two techniques may not be as good in early stages of lactation.

One of the major arguments against the WSW technique is that during early lactation, milk consumption is not an accurate measurement of milk yield since the cow's milk yield and the calf's appetite are not in equilibrium and consequently a measurement of calf consumption may underestimate milk yield during this period (Schwulst et al., 1966, Le Du et al., 1979). Schwulst et al. (1966) designed an experiment that studied the effect of residual milk on WSW estimates in Angus cows with an age range from 4 to 7 years-old. The treatments were as follows: 1) estimations of milk yield using only WSW; 2) estimations milk yield using WSW followed by oxytocin facilitated collection of residual milk by machine milking and; 3) estimations of milk yield by WSW with an injection of oxytocin administered to the cow prior to the calf suckling. Measurements were taken on a single day during weeks 2, 3 and 5 post calving. Prior to the test day, all cows were separated from their calves for 3h and then the calf was allowed to suckle. Residual milk was later removed by machine milking after oxytocin injection. Calves remained separated from their mothers for 12h and then were allowed to suckle to obtain milk consumption data. Cows assigned to the second treatment were machine milked for 4 minutes after injection of 40 IU of oxytocin. Animals remained separated for another 8h and milk was withdrawn from all cows by machine milking after 40 IU of oxytocin injection. Data from this experiment is presented in Table 6.

Table 6. Average milk consumption of 45 days-old Angus calves, milk yield and chemical composition of Angus cows (adapted from Schwulst et al., 1966).

	Treatments:		
	WSW[a] (N=12)	WSW+OxMM[b] (N=12)	Ox+WSW[c] (N=12)
12h milk consumption (kg)	2.53	2.71	3.04
12h milk yield (kg)*	2.84	3.04	3.32
Protein (%)	2.97	3.00	3.03
Fat (%)	4.34	4.21	3.94
Non-fat solids (%)	8.59	8.65	8.49
Total solids (%)	12.87	12.89	12.42

* 12h adjusted milk yield was calculated as the average hourly rate of milk secretion between the morning and afternoon sampling events, multiplied by 12.

[a] =weigh-suckle-weigh, [b] = weigh-suckle-weigh followed by oxytocin facilitated collection of residual milk by machine milking and [c] =oxytocin administered prior to the weigh-suckle-weigh procedure.

There was no significant difference in estimated milk yield, calf consumption or milk composition between treatments; however, there was a trend towards an increased yield, consumption and lower fat percentage when oxytocin was used. Similarly, McCance (1959) found increased milk consumption by lambs when oxytocin was used in sheep. Schwulst et al. (1966) concluded that the use of oxytocin may not reduce variation in milk yield estimates caused by nervous cows subjected to WSW, nor was it suitable as a routine procedure to estimate calf consumption and milk yield. Data from this experiment indicates that measurements obtained by the WSW technique may lead to errors when estimating milk yield during early lactation. Schwulst et al. (1966) conceded that the use of oxytocin in combination with the WSW technique may correct underestimations of milk yield during early lactation due to insufficient consumption by the calf. It was reported that average residual milk collected very early in the lactation (weeks 2 and 3) represented 15% and 11% of total milk collected, respectively. By week 5, residual milk was only 6% of total milk yield. The decrease in residual milk collected was attributed to either a bigger and more efficient calves being able to consume more milk by week 5 or to cows becoming resistant to the oxytocin.

In a comparison study, Gleddie and Berg (1968), compare the milk yield estimates as obtained with the oxytocin method proposed by Anthony et al. (1959) and the WSW method. Measurements were taken so it coincide with the first, second, third and fifth month of lactation. On the day before the test, the cow and calf were separated after complete removal of milk by the calf. After overnight separation (12h), cows were injected intrajugularly with 20 I.U. of oxytocin and all milk was removed from one side of the udder by machine milking. The amount of milk obtained was multiplied by four to estimate 24h milk yield. On the other side of the udder, the calf was allowed to suckle at four inter-suckling intervals of 6h. Calf weights were recorded before and after each suckling and differences in weight were summed to estimate 24h milk consumption.

Estimated calf consumption at 30d post calving was 6.5±2.36kg with a range between 2.7 to 13.2kg. Machine milk estimates for the same period ranged from 3.7 to 9.9kg with an average milk yield of 7.7±2.39. In agreement with Schwulst et al. (1966), Gleddie and Berg (1968) estimates of milk yield via the oxytocin technique were higher than those of milk consumption, supporting the argument that during early lactation there is more milk available to the calf than was being consumed. Contrary to other studies using the oxytocin technique (Marston et al., 1992, Brown et al., 1996, Peterson et al., 2007) where peak milk yield was reached around week 9 post calving, the results by Gleddie and Berg (1968) showed that peak milk yield was reached during the first month of lactation, however on average, daily milk yield throughout lactation was similar to those other studies.

In a validation study, Auchtung et al. (2002) compared the estimates for milk yield/consumption between the isotope dilution method using D_2O (300 mg/kg BW) as a tracer and the WSW technique during the first 76 days of lactation in Angus calves (N=40). They found that the average estimate for milk yield/consumption for the WSW method (10.7 L/day) was 18% lower than the estimate for water turnover (13.1 L/day). This was attributed to an ineffectiveness of the WSW method recording some salivary and metabolic losses during the measurement period; although, the higher calf consumption obtained with the isotope dilution technique can also be attributed to an overestimation due to consumption of pasture (and consequently water) that was not account for. A significant relationship was found between both methods ($r^2 = 0.89$) and concluded that the isotope dilution method was preferred over other methods for estimation of milk yield since it requires less frequent contact with the animals which means less disturbance to their natural behaviour and consequently less stress to the animals, allowing for more accurate and adaptable measurements to be taken. Oftedal (1981) reviewed that milk intake of lambs obtained by the isotope dilution and the WSW techniques are comparable during the period of 2-4 weeks postpartum (ie. at peak yield). Prior to the second week of lactation, both techniques may underestimate milk intake compared to the oxytocin technique because lambs are unable to consume all the milk that ewes can produce. After 4 weeks postpartum, the isotope dilution technique overestimate milk intake due to ingestion of water from sources other than milk.

1.3. Milk yield, pasture intake and calf growth

In New Zealand, beef bred calves are typically reared by the dam and weaned at approximately 180 days of age. At birth, calves undergo a diet transition from one that is primarily based on glucose and amino acids to one that is quantitatively greater and proportionally higher in fat (Greenwood and Cafe, 2007). Milk represents the sole source of nutrients for the newborn in early postnatal life and it remains a significant component of the diet until weaning (Grings et al., 2007). Greenwood and Cafe (2007) suggested that the major nutritional factors affecting pre-weaning calf growth and body composition at weaning were the lactational performance of the dam and the availability of nutrients from pasture or supplements following birth.

1.3.1. Milk yield and calf liveweight gains

A significant positive association is generally reported in studies that relate milk production of beef cows with liveweight gain of calves. As a consequence, milk yield is considered an important factor determining liveweight gain during the pre-weaning period (Rutledge et al., 1971, Beal et al., 1990). However, there are differences in the degree of influence that dam milk production has on calf liveweight gain. Martin and Franke (1982) and Ansotegui et al. (1991) reported no correlation between dam milk production and calf liveweight gain, whilst others have found correlations that ranged from 0.14 to 0.84 (Table 7). Jeffery et al. (1971) determined that milk production of the dam explained 58% to 61% of the variation in liveweight gain in crossbred beef calves. Similarly, Pope et al. (1963) reported that the dam's milk production accounted for 36% to 49% of the variation in calf liveweight gain, whilst Koch (1972) found that 40% to 46% of the variation in calf liveweight gain was explained by milk production of the dam.

Correlations between milk yield and calf average liveweight gain (LWG) from birth to weaning are generally moderate to high with variation between breeds (Table 7). It seems that the stage of lactation affects the size of the correlation. In early lactation, the correlations tend to be high and then decrease over time as lactation progresses (Neville, 1962). Indeed, reported correlations during the first month of lactation have ranged from 0.58 to 0.73 (Melton et al., 1967; Gleddie and Berg, 1968) whilst in the last month of lactation to weaning have ranged from 0.03 to 0.41 (Melton et al., 1967; Franke et al., 1975; Daley et al., 1987). Reported correlations between milk yield in early lactation and LWG from birth until 3 month of age have ranged from 0.26 to 0.83, suggesting that on average milk intake during early lactation plays a major role in calf liveweight gains. Mid-lactation (3 to 5 months post-partum) correlations were somewhat lower than in early lactation, ranging from 0.19 to 0.56 (Melton et al., 1967; Gleddie and Berg, 1968; Reynolds et al., 1978; Franke et al., 1975; Schwulst et al., 1980; Clutter and Nielsen, 1987). During late lactation, (Melton et al., 1967; Franke et al., 1975) a low-non-significant correlations between milk yield and LWG has been reported (0.03 to 0.17) whilst others (Reynolds et al., 1978; Clutter and Nielsen, 1987; Daley et al., 1987) have found a low to moderate correlations ranging from 0.11 to 0.46.

Table 7. Correlations between average liveweight gain of calves and average milk yield of their dams.

Breed	Milk estimation technique	r	Reference
Angus	WSW	0.45*	Franke et al., (1975)
	Oxytocin	0.46	Cobb et al., (1978)
	WSW	0.50**	Drewry et al., (1959)
	WSW	0.54	Reynolds et al., (1978)
Hereford	WSW	0.36*	Carpenter et al., (1972)
	WSW	0.80	Meyer et al., (1994)
	WSW	0.41*	Franke et al., (1975)
	WSW	0.52**	Knapp and Black (1941)
	Oxytocin	0.67	Cobb et al., (1978)
Crossbreds	WSW	0.60**	Clutter and Nielsen (1987)
	Oxytocin	0.14*	Todd et al., (1968)
	Oxytocin	0.29*	Chenette and Frahm (1981)
	WSW	0.36*	Carpenter et al., (1972)
	WSW	0.46	Wilson et al., (1968)
	WSW	0.49*	Wilson et al., (1969)
	Oxytocin	0.84**	Gleddie and Berg (1968)
	Oxytocin	0.29*	Belcher et al., (1979)
	Oxytocin	0.78	Jeffery et al., (1971)

Where significance was stated by author: * P<0.05; ** P<0.01
Lack of superscript: significance was not stated by the author (s).

1.3.2. Milk yield and calf weaning weight

In a cow-calf operation, net income is dependent on calf weaning weights and the percentage of calves weaned (Lindholn and Stonaker, 1957, Wiltbank, 1970). Thus, research has typically focused on the factors that may affect weaning weight of calves and ultimately, the expected economic return of beef cattle systems. Various authors (Gifford, 1953, Neville, 1962, Totusek et al., 1973, Mondragon et al., 1983) have concluded that milk production exerts a major influence on calf weaning weight. However, some disagreement exists on how important this relationship is and estimated correlations have ranged from 0.17 to 0.94 (Table 8). Neville (1962) found that 66% of the variation in weaning weight could be explained by the milk production of the dam. Similarly, Rutledge et al. (1971) reported that milk yield accounts for 60% of the variation in weaning weight. In crossbred cows and calves, Jeffery et al. (1971) found that total milk yield accounted from 42% to 57% of the variation in weaning weight, whilst Butson et al. (1980) determined that average daily milk yield explained 38.4% of the variation in weaning weight.

Table 8. Correlations between milk yield and weaning weight by various authors.

Breed	Milk estimation technique	Creep feeding	r	Reference
Angus	Oxytocin	Yes	0.30^{***}	Marston et al., (1992)
	Oxytocin	Yes	0.40	Marston et al., (1990)
	Oxytocin	No	0.62	Marston et al., (1989)
	Oxytocin	No	0.17^{ns}	Belcher et al., (1979)
Simmental	WSW	No	0.36	Mallinckrodt et al., (1993)
	Oxytocin	Yes	0.47^{***}	Marston et al., (1992)
	Oxytocin	Yes	0.61	Marston et al., (1990)
	Oxytocin	No	0.62	Marston et al., (1989)
Hereford	WSW	No	0.40	Mallinckrodt et al., (1993)
	WSW	No	0.63^{**}	Robinson et al., (1978)
	Oxytocin	No	0.64^{***}	Diaz et al., (1992)
Crossbreds	Oxytocin	No	0.20^{+}	Chenette and Frahm (1981)
	WSW	Yes	0.52^{***}	Marshall and Long (1993)
	Oxytocin	No	0.60^{**}	Butson et al., (1980)
	Oxytocin	No	0.69	Belcher and Frahm (1979)
	WSW	No	0.94	Nelson et al., (1985)
Various breeds	Hand milking / WSW	No	0.81-0.88	Totusek et al., (1973)

^{ns} not significant; $^{+}$ P<0.1; * P<0.05; ** P<0.01; *** P<0.001
Lack of superscript: significance was not stated by the author (s).

It seems that the correlation between milk yield and calf weaning weight may be affected by the method of milk collection. Apart from the studies reported by Belcher et al. (1979) and Chenette and Frahm (1981), where the correlation between milk yield and calf weaning weight were not significant or low, respectively; studies using the oxytocin technique tend to repeatedly report a moderate correlation of approximately 60% (Table 8). On the contrary, studies using the WSW technique tend to be more variable and correlations have ranged from moderate (Mallinckrodt et al., 1993; Robinson et al., 1978; Marshall and Long 1993) to high (Nelson et al., 1985; Totusek et al., 1973). Creep fed calves may be less dependent on milk nutrients; however, this could vary depending on the quality and quantity of feed available. As a consequence, from Table 8, it appears that the level of creep feeding tends to decrease the correlation between milk yield and calf weaning weigh compared to studies were creep feeding was not practiced. Marston et al. (1990) found an overall correlation between milk yield and calf weaning weight of 0.40 and 0.61 for Angus and Simmental calves, respectively. The majority of cow-calf pairs grazed together on pasture and creep feeding was not practiced. Only a small group of calves were exposed to a high energy ration because they were born in a period of low pasture availability for their dams. The correlations for Angus and Simmental calves found by Marston et al. (1990) were higher than those reported later by Marston et al. (1992). In this second study the reported correlation between dam milk yield and calf weaning weight was 0.30 and 0.47 for Angus and Simmental calves, respectively. Cows were maintained in drylot from early to mid-lactation and then allowed to graze on fresh pasture. In some calves, creep feeding was not practiced, however, a large proportion of calves were fed a high energy diet and others had access to alfalfa hay. The differences in the overall level of creep feeding in these studies may explain the changes in the reported correlations.

The correlation between milk yield and calf weaning weight also varies depending on breed and the stage of lactation when the measurements were taken. Rutledge et al. (1971) designed an experiment to determine the influence of milk yield of Hereford dams on the weaning weight of their calf. No creep feeding was practiced in this experiment. They found a correlation between milk yield and calf weaning weight of 0.49 during the first month of lactation; however, no correlation was found between milk yield during the last month of lactation and the weaning weight of calves. Another study with Hereford cows (Robison et al., 1978) reported that correlations between milk yield and weaning weight decreased from 0.48 in the first 60 days of lactation to 0.44 in the last 60 days of lactation. In Angus cows and calves, Baker (1997) reported correlations of 0.35, 0.16, 0.44 and 0.37 between calf weaning weight and milk production of the dam at 40, 100, 150 and 205 days in milk, respectively.

The regression of total milk yield on weaning weight is essential to understand the efficiency at which extra milk produced by the dam is used by the calf to grow, although values for these coefficients have varied across studies. Neville (1962) reported that an extra kg of milk at the end of lactation was associated with an increase in live weight at weaning of 0.028 kg in Hereford calves nursing from dams allocated to different nutritional treatments. Marston et al. (1992) suggested that an additional 1 kg of milk produced by the end of lactation was associated with 0.014±0.006 and 0.032±0.009 kg of weaning weight in Angus and Simmental calves, respectively. Clutter and Nielsen (1987) reported regression coefficients of 0.032, 0.032 and 0.053 for calves reared by high, medium and low producing crossbred cows, respectively; suggesting that the partial efficiency of milk utilization is higher for calves reared by low producing compared to calves reared by high producing cows.

The relationship between milk production of the dam and calf weaning weight suggests that heavier calves could be weaned if milk production of the dam could be increased (Ansotegui et al., 1991). Dairy breeds have been often used in crossbreeding systems for beef production, with the general assumption that the resultant crossbred cows would produce more milk and, therefore, wean a heavier calf (Arthur et al., 1997). Totusek et al. (1971) reported the weaning weight of calves reared by either a Hereford (HH), Hereford×Holstein (HF) and Holstein (FF) dam. Average daily milk production at weaning was 5.54 kg, 9.8 kg and 12.9 kg for HH, HF and FF cows, respectively. Weaning occurred at 205 days of age and recorded weaning weights were 177 kg, 207 kg and 229 kg for HH-, HF- and FF reared steers. In another study involving HH and HF cows, Arthur et al. (1997) determined that HF cows produced on average 2.8 kg of milk more than HH cows (8.3 kg vs. 5.5 kg respectively) when grazing high quality pasture. This resulted in HF-reared calves being on average 35 kg heavier at weaning (210 days of age) than HH-reared calves. Average milk production when grazing medium and low quality pasture was 6.2 kg and 3.7 kg for HF cows, respectively and 4.5 kg and 2.7 kg for HH and HF cows. Hereford×Holstein calves were 27 and 44 kg heavier than HH calves on medium and low quality pasture, respectively. These results indicate that persistency of lactation is affected by the level of nutrition; crossbred cows are able to support higher calf liveweight gains by producing more milk than straightbred cows, although this may be done at the expense of body reserves.

Deutscher and Whiteman (1971) conducted an experiment were milk production was measured in Angus (AA) and Angus×Holstein(AF) cows to determine the influence of the milk production throughout lactation on their calves weaning weights. They found that AF cows significantly produced (P<0.05) more milk than AA cows during lactation and this was also reflected in the weaning weight of their calves. Steers and heifers reared by AF dams were weaned at 195.5 kg and 190.5 kg, respectively, whilst those reared by AA dams weighed 175.2 kg and 156.0 kg at weaning. In crossbred cows of high (HI, Angus×Milking Shorthorn), medium (ME, Angus×Red Poll) and low (LO, Angus×Hereford) milk production potential, Clutter and Nielsen (1987) found that the estimated milk production of the HI group exceeded that of the ME and LO groups by 186 kg and 561 kg, respectively. The differences in milk production and by assumption the calf's milk intake resulted in heavier calves in the HI group compared to the ME (8.2 kg differences) and LO group (16.9 kg difference).

1.3.3. Milk yield and post-weaning calf growth

Increasing milk yield in beef cows can increase calf weaning weights and efficiency of growth to weaning (Lewis et al., 1990). However, limited literature and often conflicting results have been reported regarding the effect that maternal milk yield may have on the post-weaning growth of calves. A low and negative relationship has been reported by Clutter and Nielsen (1987), and Montano-Bermudez and Nielsen (1990). Clutter and Nielsen (1987) reported that progeny of high yielding dams were significantly heavier at weaning than those from low yielding dams, however, progeny of high yielding dams gained 6.3 kg less than those from low yielding dams post-weaning in a 280 day feedlot period. Similarly, Montano-Bermudez and Nielsen (1990) reported that steers reared by medium and high yielding cows had lower LWG in a 272 day feedlot period post-weaning when compared to steers reared by low yielding dams. On the contrary, Jones et al. (1982) and Fiss and Wilton (1992) found that milk yield was positively associated with LWG during the post-weaning period when steers were placed in a feedlot situation.

Various authors (Richardson et al., 1978; Lewis et al., 1990; Miller et al., 1999) have reported that differences in maternal milk yield had no relationship with post-weaning growth of beef calves. Richardson et al. (1978) reported that calves reared by high producing dams were heavier at 91 and 180 days when compared to calves reared by low yielding dams. However, during the post-weaning period from 180 days until 330 days of age, LWG did not differ between groups and almost the same margin of live weight difference seen at weaning was seen at 330 days. Miller et al. (1999) showed that maternal milk production influenced pre-weaning growth but not post-weaning growth. They showed no compensatory growth in the feedlot period for calves reared by low producing dams and any differences in live weight at the end of the post-weaning period was largely due to differences in live weight obtained during the pre-weaning period.

Wang et al. (2009) reported positive, negative and equivalent relationships between maternal milk production and post-weaning calf growth among different breeds of steers and two post-weaning management systems (feedlot and grazing). They concluded that an interaction exists between maternal milk yield, sire breed of calf and post-weaning management system. They found that under a drylot post-weaning system, greater levels of milk production were associated with lower gains in Gelbvieh-sired calves, whereas higher levels of milk production benefited Brangus- and Charolais-sired calves. Additionally, the post-weaning ADG for Romosinuano- and Hereford-sired calves was unaffected by the level of maternal milk production. In the grazing system, the effect of maternal milk production on calf post-weaning weight was less apparent. This was attributed to calves requiring a period of adaptation to the wheat pasture diet, therefore resulting in lower liveweight gains under grazing conditions. However, Romosinuano-sired calves and Gelbvieh-sired calves appeared to benefit from an increased maternal milk yield.

1.3.4. Milk intake and pasture consumption

With increasing age, an increase in nutrient uptake is necessary to maintain a desirable rate of gain. The typical mammalian lactation curve shape increases with increasing requirements of the offspring up to a peak and then decreases as lactation progresses. This suggests that at some point during the pre-weaning period, energy intake solely from milk is inadequate to fully sustain continued growth and, therefore, calves become dependent upon non-milk nutrient sources. Indeed, Boggs et al. (1980) found that forage dry matter (DM) intake represented 0.62, 1.46, 1.51, 1.75 and 2.2% of calf body weight from the second until the sixth month of lactation, indicating an increased dependence on non-milk nutrients as lactation progresses. Bailey and Lawson (1981) explained that young calves consume small amounts of forage early in life as they imitate their mother's behaviour, however, a significant increase in forage intake in their diet is unlikely until a fully functional reticulo-rumen is developed. As a consequence, they designed an experiment to determine the water and forage intake of Angus calves on pasture, based on estimations of total water intake, milk intake and digestible energy (DE) requirements. They found that water intake from milk increased from 8.3 kg/day at 44 days of age to 17.5 kg/day at weaning. Milk supplied 90% of the water at 44 days whilst only 25% at weaning. Average DE requirements increased from 26.3 MJ at 44 days to 56.0 MJ at weaning. This suggested that milk supplied around 86% of the requirements at 44 days and only 25% at weaning. Estimated pasture intake to compensate for the extra requirements increased from 0.5 kg DM/day at 44 days to 5.5 kg DM/day at weaning. They noticed that as the proportion of faecal DM from forage increased with age, while milk intake decreased proportionally. Bartle et al. (1984) determined that by week 9 of lactation, milk production from the dam was inadequate to support calf growth, whilst Richardson et al. (1978) found that by week 13 post-partum, beef bred calves not receiving solid food required a nutritional supplement to milk to sustain the growth rates of their counterparts receiving *ad libitum* or restricted amounts of solid foods.

There is evidence to suggest that if adequate forage is available, calves receiving less milk during lactation may increase their forage intake to compensate for the reduced milk consumption (Boggs et al., 1980) thereby gaining similar weight to those calves consuming higher quantities of milk (Baker et al., 1976; Le Du et al., 1976). Baker et al. (1976) designed an experiment to determine how different levels of milk intake affect herbage consumption. Eighteen Hereford×Holstein steers were fed reconstituted milk replacements to simulate a lactation curve with peak lactation occurring at week 5 post-partum and allocated to 3 different levels of total milk production: High (HI) 2101 kg, Medium (ME) 1635 kg and Low (LO) 1165 kg. At day 59, calves were offered a herbage allowance of 0.06 kg DM/kg calf live weight and fed their milk allowance twice a day in individual pens. Herbage intake was estimated six times starting 4 days after calves were introduced to pasture. For the HI group, herbage intake ranged from 0.04 kg to 3.71 kg, whereas for the ME and LO groups herbage intake ranged from 0.38 kg and 0.63 kg to 4.62 kg and 3.8, respectively. Live weight at 240 days (weaning) did not differ between the HI and ME group (292 kg vs. 287 kg) but calves from the HI and ME group were significantly heavier at weaning than those in the LO group. This suggests that if pasture quality and availability is not limiting, calves under a medium milk diet may be able to compensate for the reduced milk supply and grow at a similar rate to those in a high milk diet. The authors concluded that consumption of milk reduced herbage intake and that calves growing under a high milk diet will grow faster than those on very low milk diets.

In a follow up experiment, Le Du et al. (1976) utilised forty-eight Hereford×Friesian calves, approximately 1 week of age, which were allocated to eight treatments in a 2×4 factorial design involving two milk levels and four weaning weights. The milk treatments were intended to provide low (LO) 1000 kg or high (HI) 2000 kg levels of milk over 240 days. In the four weaning treatments, calves were weaned at 86, 128, 170 or 212 days of age. Calves were fed only reconstituted milk replacement indoors until day 63, thereafter in addition to reconstituted milk replacement they were also allowed to graze perennial ryegrass. The authors found that during the indoor period (day 0 to day 63), daily liveweight gain in calves on the HI group was higher than those in the LO group (0.68 kg/day vs. 0.49 kg/day). They also found a linear increase in herbage intake with time within the milk-fed groups. On average and irrespective of the weaning treatment, no difference was found in daily liveweight gain from day 63 to day 231 when pasture was introduced (0.87 kg/day vs. 0.83kg/day) confirming that calves under a low milk diet can compensate for the restricted nutrient intake from milk by consuming more pasture, therefore growing at a similar rates to those fed high levels of milk. Similarly, Boggs et al. (1980) reported a negative relationship between milk intake and forage consumption. They found that two-month-old calves consumed 0.03 kg/day less grass for every extra 1 kg of milk consumed. This negative relationship increased with increased age resulting in 6-month old calves consuming 0.07 kg/day less grass per extra kg of milk consumed. Although, Baker et al. (1976) and Le Du et al. (1976) reported calf growth was not enhanced by consumption of non-milk nutrients. Grass intake was poorly related to calf performance when the entire pre-weaning period was considered. They found that during the first two months of lactation, grass intake was negatively related to LWG and this was attributed to calves not receiving enough nutrients from milk and trying unsuccessfully to increase their nutrient intake by consuming more grass, however, during the following months, grass intake tended to increase calf gain.

1.4. Summary

Regular assessment of the lactation performance of beef cattle breeds is not a commonly performed on-farm routine and has only been possible due to the development and improvement of the techniques here reviewed; however, despite the great efforts in minimising sampling errors through complex experimental designs, to date, no unbiased technique to measure milk yield in beef cattle has been developed.

Machine-milking trained animals or machine milking whilst the calf is suckling may not reflect the behavioural characteristics of beef cattle. Milk data obtained from these procedures tends to be low, mostly from underestimation of milk consumption due to insufficient milk let down. The techniques can be laborious in terms of animal training and constant sampling which may become expensive, hard to replicate and of limited biological use because of the overexposure of animals to extensive handling practices that will further limit the number of animals that can be handled within a certain time frame.

The oxytocin method has the disadvantage that by itself it is only useful to measure the amount of milk produced in the cow. When using this method, estimation of calf consumption cannot be determined. Also it's questionable that the amount of oxytocin needed to extract milk from animals may not be of biological usefulness other than giving a rough estimate of milk production of a particular animal in a certain population. However, when combined with the WSW method, it may offer the advantage of overcoming the problem of underestimation of calf consumption during early lactation and, therefore, better estimates at this stage can improve later correlation with the calf's growth.

Newer methods such as those using isotope dilution and/or transfer techniques may offer advantages. Stress caused by over handling animals and separating cows and calves for several hours and the variation in milk yield estimates due to disturbance of behavioural patterns is almost completely removed. Suckling occurs normally without disturbance over long periods of time ranging from 7d to 15d and handling is only required during short periods for blood sampling, weighing and isotope injection and equilibration. This allows an even greater number of animals to be tested over the sampling period and could also increase the number of measurements possible for a whole lactation which may lead to increased accuracy and reliability of estimates. The disadvantage of the isotope dilution technique is that it relies on the assumption that the animals are only ingesting water coming from milk and consequently it may only be possible to use this technique during the first two weeks of lactation. Once corrections for changing pool size, isotope recycling and sources of water other than milk are made, the isotope transfer technique offers great practicality and biological significance to the research worker. However, isotopes are expensive to obtain and in the case of radioactive isotopes, there are also waste handling costs involved. They require specialised equipment and in some cases great computational and mathematical analysis. As a consequence, the large capital investment required when using these techniques may over shadow their advantages.

It seems that the most suitable and cost-effective method to determine milk intake is the WSW technique, however it has two major disadvantages, firstly, during early lactation when milk production of the cow exceeds calf intake, WSW may result in an underestimation of milk consumption. Measurements of milk consumption prior to 28-30 days postpartum tend only to decrease the accuracy and reliability of the estimates. Secondly, long periods of separation between the calf and its mother may not reflect actual suckling behavioural patterns showed under normal, undisturbed conditions, indeed infrequent suckling stimulation may reduce milk output. It is questionable that measurements taken during a period of stress to the animal may not be of any biological usefulness when extrapolated to the field. However if careful, well-timed and detailed measurements are taken, the reliability of the technique can increase considerably. The WSW method is undemanding for both the researcher and the experimental animals, and offers the greatest practicality for grazing systems where animals are handled relatively few times a year. After a period of acclimatization to the facilities and procedures, animals are comfortable if adequate handling is provided and pose minimal risk to the researcher. Financially, it is the most affordable method since it makes no use of external inputs to the systems and only requires labour and good facilities.

Milk production influences calf liveweight gain, however, the importance of this relationship has varied across studies Some authors have reported no correlation between milk production and liveweight gain, whilst other have reported correlations that ranged from 0.14 to 0.84. Similarly, research has shown that a relationship exists between milk production and calf weaning weight, the hypothesis being that high producing cows would be able to wean heavier calves. The size of this relationship has varied between authors and consequently, reported correlations have ranged from 0.17 to 0.94. The differences between authors are attributed to differences in the breeds studied, methods of estimation of milk yield and particularly the herd management. Correlations tend to be lower for pure breed studies compared to crossbred studies. Estimation of milk yield by the oxytocin technique resulted in more consistent correlations between milk yield and calf liveweight gain and calf weaning weight across studies when compared to the WSW technique, however, reported correlation were on average lower when obtained by the oxytocin technique compared to the WSW.

Milk consumption is important during the first months of lactation as it supplies the animals with enough water and nutrients for their development. Research has shown that milk supplied about 86% of the nutrients needed to grow in 44 days-old calves. However, at some point during the pre-weaning period, calf growth may be limited by the consumption of a diet consisting solely in milk. Some authors have reported that by week 9 to 13, milk production is inadequate to support calf growth. As calves grow in age, pasture consumption becomes important to maintain a desirable daily gain. Pasture intake is therefore, inversely correlated with milk consumption. Research has demonstrated that calves receiving less milk can compensate by consuming more pasture and therefore gaining similar weight to those receiving more milk. However, consumption of nutrients from sources other than milk not always resulted in increased liveweight gains and some authors have reported that the increased pasture consumption seen in calves consuming low levels of milk may not be sufficient to support high daily gains.

In the study reported in the remainder of this thesis, the WSW technique was used to estimate calf consumption of beef bred calves. The objective was to determine the suitability of a random regression methodology to predict the milk yield of beef cows based on a limited number of test-day records obtained by the WSW technique. A secondary objective of this experiment was to identify the most significant sampling time point throughout lactation to optimise future WSW sampling schemes. Research has demonstrated that dairy breed crossbreeding in beef production systems have resulted in increased milk yield, and consequently a second objective of the first experiment was to determine and quantify the lactational performance of straightbred Angus cows and Angus×Friesian, Angus×Jersey and Angus×Kiwi-Cross cows. In the study reported here, calves were reared by dams of different milk production potential and their lactation curves were estimated in the first experiment; consequently, the objective of the second experiment was to determine to what extend any differences in milk yield, and by assumption calf intake, may affect the growth trajectory of calves up to a year of age. Estimation of the theoretical metabolizable energy requirements and the estimated energy consumption from milk were necessary to determine differences in pasture consumption between beef steers.

Chapter 2. Lactational performance of straightbred Angus cows and three Angus-dairy cross genotypes.

2.1. Introduction

In beef cattle systems, maternal milk production is one of the most important factors affecting weaning weight of calves (Totusek et al., 1973, Neville, 1962) and the production costs associated with the maternal metabolisable energy requirements for production (Montano Bermudez et al., 1990). Therefore, the profitability of the cow-calf producer is directly affected by changes in the lactational performance of the beef herd (Minick et al., 2001). Introduction of dairy genetics into a beef cattle herd can result in increased milk yield (Walker and Pos, 1963, Deutscher and Whiteman, 1971), calf liveweight gain (Baker et al., 1990, Baker et al., 1981) and both biological and economic efficiencies (Morris et al., 1994). Examples of this include: Angus×Friesian cows produced more milk but required higher levels of nutrition (Deutscher and Whiteman, 1971, Hendrix, 1971, Kropp et al., 1973), had a larger mature size (Cundiff, 2007) and a superior maternal ability (Nicoll et al., 1978) relative to straightbred Angus cows. Angus×Jersey cows offered reproductive advantages such as early puberty and fewer calving difficulties (Morris et al., 1986, Morris et al., 1993b), higher milk production and remarkable biological productivity and efficiency (Morris et al., 1993a) compared to straightbred Angus cows. Morris (2008) suggested that both Friesian- and Jersey- crosses are highly adapted to New Zealand's pastoral conditions and consequently have high potential for use as suckler cows.

Milk yield is affected by numerous factors: the interaction between dam genotype and age (Rutledge et al., 1971); parity (Johnson et al., 2002); nutrient availability (Hickson et al., 2008); body condition and liveweight of the dam (Greenwood and Cafe, 2007); the calf's capacity to grow (ie. sex, genotype) and consume milk (Barton, 1970b); and interactions between the cow and calf during the pre-weaning period (Anderson, 1977). Assessment of milk yield in beef cows is challenging as they are maintained on pasture with the calf consuming all of the milk. To measure the relative milk yield of different breed groups or to estimate the influence of milk yield on calf pre-weaning growth, the weigh-suckle-weigh (WSW) technique has been commonly used (Neville, 1962, Walker and Pos, 1963, Totusek et al., 1973, Gaskins and Anderson, 1980, Hickson et al., 2008). Few studies have reported lactation curves of beef-cross-dairy cows or attempted to mathematically study the properties of these lactation curves (Deutscher and Whiteman, 1971, Chenette and Frahm, 1981, Kropp et al., 1973, Gaskins and Anderson, 1980, Hohenboken et al., 1992). Understanding and validating the research tools used to estimate beef cow milk yield would provide fundamental information of the beef cow herd and their milk production pattern, which could be used for on-farm management decision making.

One of the main limitations when measuring milk yield in beef cattle is related to the limited number of "test-day records" or measurements that can be taken throughout the lactation without disrupting the natural behaviour of the animals (ie. suckling patterns). Jenkins and Ferrell (1984) proposed an equation that allowed researchers to estimate lactation curve parameters with a minimum number of data points. This equation has been largely used in beef cattle research, however it has been criticised because it may produce lactation curves that are inconsistent with the collected data (Hohenboken et al., 1992) or is unable to predict continuously decreasing curves (Landete-Castillejos and Gallego, 2000). More recently, a random regression methodology consisting of fitting an average lactation curve for a subgroup of animals and estimating individual lactation curves based on the deviation from the average, has been used to describe the properties of lactation curves in dairy cattle. This method appears to outperform traditional lactation equations such as the Wood or Ali and Schaeffer models (Silvestre et al., 2006).

The primary objectives of this study were: 1) to test the suitability of a random regression methodology to predict lactation curves of straightbred Angus cows and three F1 Angus-cross-dairy genotypes; 2) identify differences in the shape and parameters of the predicted lactation curves and 3) to determine a relationship between individual measurements with predicted milk yield for future reference in designing sampling schemes for this group of animals.

2.2. Materials and methods

2.2.1. Animals

One hundred and thirty six second-lactation 3-year-old Angus (AA; n=43), Angus×Friesian (AF; n=32), Angus×Jersey (AJ; n=40) and Angus×Kiwi-Cross (AK; n=21) cows rearing calves sired by Angus (n=4) or Simmental (n=4) bulls were used in this study. Cows with live singleton calves were allocated into one of three groups (A, B and C) based on their calving date, with early, mid- and late calving cows assigned to either group A, B or C, respectively. Groups were intended to have at least two calves of each sex of every combination of breeds. Allocation into the three groups was done for ease of management during the milk test days. Calving commenced on the 12th September 2011 and continued until the 1st December 2011 (80 days). Overall mean calving date was the 9th October 2011. Mean calving date for groups A, B and C were 23rd September, 6th October and 28th October respectively. All calves were tagged, weighed and sex recorded at birth. Nineteen cows were removed from the study due to: fetal loss/abortion (n=7), disease (n=1), twinning (n=3), death of the calf (n=4) and other cow/calf complications (n=4). A total of 117 cow-calf pairs were used in the study.

Cows were managed under commercial conditions throughout the experiment at Massey University's Tuapaka Beef Research Farm, located 20 kilometres east of Palmerston North, New Zealand (latitude 40.33° S and longitude 175.73° E). The farm is subdivided into two units: a) a predominantly flat ground unit, where perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) are the main pasture species; and b) a typical hill country unit where browntop (*Agorstis capillaris*), crested dogstail (*Cynosurus cristatus*), ryegrass and white clover are predominantly present. During winter, cows were maintained on the hill country unit, whilst during lactation, cows rotationally grazed both flat and hill pastures. Average pre-grazing mass offered to the animals during the calving period was approximately 4610±389 kg DM/ha with an average post grazing residual for the same period of 1809±56 kg DM/ha. Pasture mass was assessed by rising plate meter (Jenquip, Fielding, New Zealand) using the formula: Pasture mass (KgDM/Ha) = Plate meter reading × 158 + 200. Following calving and until weaning, the average pre-grazing mass offered was 2715±102 kg DM/ha with an average post-grazing residual of 1541±113 kg DM/ha. Pasture quality ranged from 12.5±0.2 MJ ME/kg DM in early- to late-spring (ie. during calving) to 10.5±0.2 MJ ME/kg DM in mid- to late-summer and early-autumn (ie. end of calving through weaning). Body condition score (BCS 1-10 scale; Law et al., 2013) prior to parturition was 6 for AA, and 5 for AF, AJ and AK. Calves remained with their dams until weaning at an average of 148±18.69 days post-partum.

2.2.2. Milk measurements

Milk production was estimated by using the weigh-suckle-weight technique (WSW) on 6 occasions for groups A and B at an average of 16, 32, 49, 80, 120 and 148 days postpartum (D16, D32, D49, D80, D120 and D148, respectively) and on 4 occasions for group C at D49, D80, D120 and D148. Calves were separated from their dams on the test day starting at 0800 and separation time recorded for each animal. Average separation times at D16 and D32 were 6.12±0.84 h and 5.6 ± 0.90 h respectively. Following the separation time, the first calves were allowed to suckle beginning at 1200 and calf live weights were recorded before and after the suckling event at a scale resolution of 0.1 kg (True-Test ® XR 3000 Auckland, New Zealand). The difference between the live weight of the calves pre- and post-suckling (ie. milk intake) was assumed to be the milk production of the cow during that period and converted to a 24-h milk yield.

Milk yield measurements taken after D32 for all groups started with an initial pre-separation period of 2 hours. The day prior to the test day, calves were brought to the yards and separated from their dams for roughly 2h beginning at 1200 and then allowed to suckle. Following suckling, calves were separated overnight starting at 1600 and separation times recorded for each animal. Average separation time for all groups at D49, D80, D120 and D149 was 17.4 ± 1.10 h, 17.28±1.09 h, 16.88±0.80 h and 18.12±1.15 h, respectively. Following the overnight separation, calves were allowed to suckle beginning at 0900 and calf live weights recorded before and after the suckling event at a scale resolution of 0.1 kg, except on D149 where scale resolution was 0.5 kg due to restrictions on the scale's capability at the greater live weights of the calves. The difference between the live weight of the calves pre- and post-suckling was assumed to be the milk production of the cow during that period and converted to 24-h milk yield.

2.2.3. Data set constraints

Measurements at D16 were intended to provide reliable data so lactation curves can be modelled from early lactation until weaning. Calves as young as 3 days of age were tested during D16 and various difficulties completing the WSW procedures with such young calves were experienced. These included unsettled cows not allowing their calves to suckle or calves uninterested in suckling during the WSW procedures. Consequently, since such undesirable observable behaviours may have led to unreliable estimates, measurements of D16 were removed from the data set.

Due to the complications encountered with young calves during WSW procedures and the excessive variability in their intake measurements, the data set was constrained so only calves older than a month of age were included. These constraints guaranteed that the data used for this study were collected from cow-calf pairs that had already experienced WSW procedures at least once and were more accustomed to the procedure. Additionally, cow-calf pairs were required to have at least 2 or more measurements throughout the lactation to be considered in the experiment. The average age of the calves at weaning was estimated at 158 day post-partum and consequently, intake measurements later than day 160 were removed from the data set. Table 9 shows the number of observations used to predict the individual lactation curves from D32 to D160. Five cow-calf pairs (AA, n=2; AF, n=1; AJ, n=1; AK, n=1) were removed from the study due to failing to meet the minimum constraints required to be included in the data set.

Table 9. Number of observations used to predict lactation curves for Angus (AA), Angus×Friesian (AF), Angus×Jersey (AJ) and Angus×Kiwi-Cross (AK) at different time intervals from day 32 until day 160 of lactation.

	Day of lactation					
	D32-D50	D51-D70	D71-D90	D91-D110	D111-D130	D131-D160
AA	23	15	21	17	25	33
AF	16	19	13	17	17	16
AJ	24	15	23	16	29	21
AK	10	7	11	6	11	8

2.2.4. Statistical methods

All statistical analyses were carried out using the Statistical Analysis System (SAS version 9.2, SAS Institute Inc., Cary, NC, USA, 2009). A third-order Legendre polynomial was fitted to lactation data using a random regression to obtain an average lactation curve for the population and for each cow with the following model:

$$y_{tm} = \sum_{i=0}^{3} b_i \, P(x)_t^i + \sum_{i=1}^{3} \alpha_{im} P(x)_{tm}^i + e_{tm}$$

where y_{tm} is the observation at time t in cow m for daily milk yield, b_i are fixed regression coefficients of days in milk on variable y (b_0 = intercept, b_1 = linear effect, b_2 = quadratic effect and b_3 = cubic effect); α_{im} are random regression coefficients of days in milk on variable y in cow m (α_{0m} = intercept, α_{1m}=linear effect, α_{2m}= quadratic effect and α_{3m} = cubic effect), x_{tm}^{i} is the observation of standardized days in milk at time t in cow m at the power 0, 1, 2, and 3; e_{tm} is the residual error associated with observation y_{tm}. The standardized unit of time x ranges from -1 to +1, and was calculated as:

$$x = 2\left(\frac{t - t_{min}}{t_{max} - t_{min}}\right) - 1$$

where t is days in milk (DIM), t_{min} is the earliest DIM, and t_{max} is the latest DIM. In this study, t_{min} was 32 DIM and t_{max} was 160 DIM. The first four Legendre polynomial functions of standardized units of time (x) are defined as below:

$$P(x)^0 = 1$$

$$P(x)^1 = x$$

$$P(x)^2 = \frac{1}{2}(3x^2 - 1)$$

$$P(x)^3 = \frac{1}{2}(5x^3 - 3x)$$

Random coefficients for each cow were obtained using the MIXED procedure assuming an unstructured covariance structure between the variance and covariances of the random regression coefficients of the model. Using the estimated random regression coefficients for each cow, parameters of the lactation curve (ie. peak milk yield, days in milk at peak lactation, milk yield at D160 and total milk yield from D32 to D160) for each cow were estimated.

Analysis of variance for each of these parameters was performed with the MIXED procedure with a linear model that included the fixed effects of breed of the dam, group, calf sex, and the interaction between calf sex and breed of the dam. The breed effects for Friesian and Jersey proportions in the dam compared to the Angus breed were determined with the MIXED procedure using a model that included the fixed effects of group and calf sex, and the covariates for proportion of Friesian and Jersey. Differences in lactation shape due to differences in suckling capacity of the calf was determined with the MIXED procedure using a model that included the fixed effects of group, breed of dam, calf sex, calf birth weight and the different proportions of maternal and paternal breeds in the calves.

The goodness of fit achieved with the model and for each lactation curve per breed was evaluated by standard procedures obtaining the coefficient of correlation (r) and determination (r^2), the relative prediction error (RPE) and the Linn's concordance correlation coefficient (CCC). Agreement between actual and predicted milk yield was examined by regression analyses using the REG procedure. Test-day correlations between individual measurement days and their individual relationship with total milk yield were evaluated using the CORR procedure.

2.3. Results

2.3.1. Lactation curves – goodness of fit

Periodic milk yield records were fitted with the random regression methodology and individual lactation curves for each animal were estimated. Figure 7 illustrates the uncorrected average lactation curves for AA, AF, AJ and AK cows. Table 10 shows the criteria used in assessing the goodness of fit of the random regression methodology for the Angus breed and the three beef-cross-dairy genotypes and the general model used to predict them.

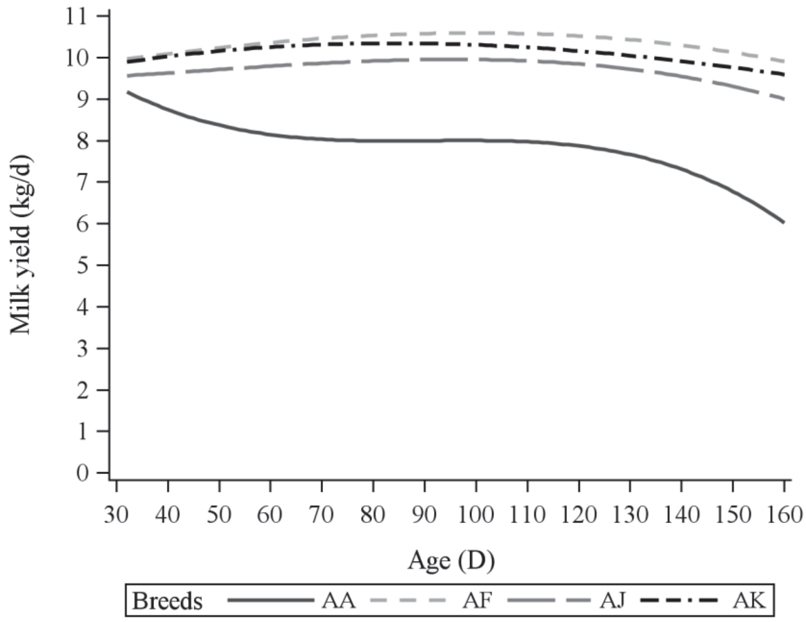

Figure 7. Lactation curves of straightbred Angus (AA), Angus×Friesian (AF), Angus×Jersey (AJ) and Angus×Kiwi-Cross (AK) crossbreds from D32 to D160 of lactation.

Table 10. Goodness of fit indicators of the lactation curves corresponding to each genotype: straightbred Angus, Angus×Friesian, Angus×Jersey and Angus×Kiwi-Cross crossbreds; and the model used to predict them.

	Goodness of fit		
	RPE§	r^{2}†	CCC‡
Genotypes:			
Angus	0.15	0.74	0.72
Angus×Friesian	0.13	0.72	0.65
Angus×Jersey	0.14	0.66	0.63
Angus×Kiwi-Cross	0.16	0.58	0.56
Model	0.14	0.77	0.76

§ Relative prediction error
† Coefficient of variation
‡ Linn's concordance correlation coefficient

Assessment of the goodness of fit of the model (ie. all cows included independent of genotype) suggested that prediction estimates were highly correlated (r=0.86, P<0.01) to actual measurements of milk yield (Figure 8). Almost 80% of the variation in milk yield between cows was explained by the model, with an average 14% variation between predicted and actual measurements. Reproducibility of the prediction between the animals in this study, based on lactation curves calculated with Legendre polynomials fitted with random regression, was from moderate to high with a CCC of 76%, therefore explaining the high correlation between actual and predicted measurements.

When each lactation curve corresponding to each breed were evaluated separately, predicted milk estimates for AA ($r=0.82$, $P<0.01$), AF ($r=0.84$, $P<0.01$) and AJ ($r=0.80$, $P<0.01$) cows were highly correlated with actual measurements of milk yield but only moderately correlated in the AK group ($r=0.73$, $P<0.01$). On average, 71% of the variation in milk yield in the AA, AF and AJ groups was explained by the predicted lactation curve with only 14% variation between predicted and actual measurements. However, only 58% of the variation in milk yield in the AK group was explained by the predicted lactation curve. This was due to the lower number of animals in the AK group compared to the AA, AF and AJ groups and is reflected by a higher RPE in the AK group, showing a greater dispersion of the records from the mean, therefore resulting in a lower r^2 and CCC compared to the other groups of cows.

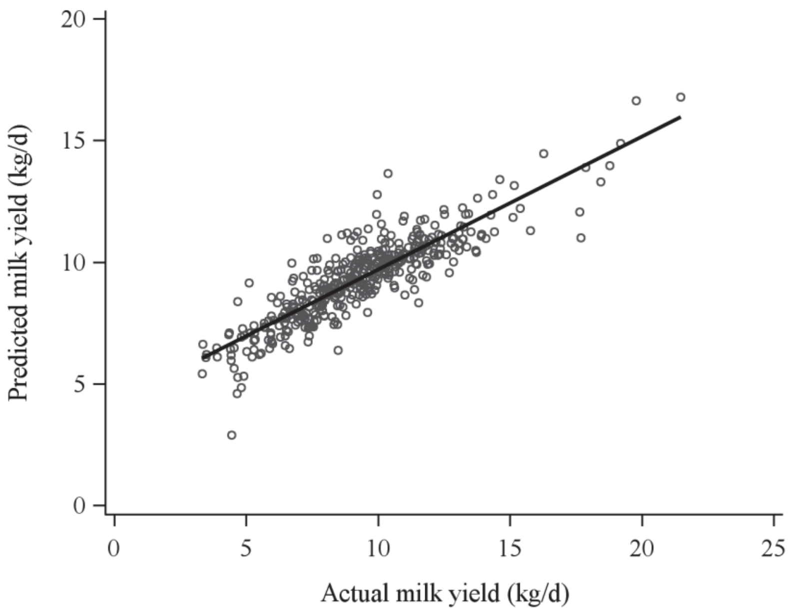

Figure 8. Predicted milk yield estimated by third order Legendre polynomials and fitted to lactation data using a random regression versus actual observations of milk yield.

2.3.2. Lactation curves – shape and curve parameters

Predicted lactation curves based on test-day records varied across genotypes and the shapes can be classified into three types according to the pattern of milk production from D32 to D160. Type 1 (AA group): peak milk production is reached during the first month of lactation and slowly decreases until D83, thereafter it remained fairly constant until approximately D115 when it finally decreased more dramatically towards weaning; Type 2 (AF, AJ and AK groups): milk production increased continuously from the beginning of the lactation period, reached a peak around D80 and then decreased until the end of the lactation.

The effect of birth weight and differing breed proportions in the calf on lactation curve shape were investigated, however no effect for bull breed ($P>0.05$), proportion of maternal genotype in the calf ($P>0.05$) or birth weight of the calves ($P>0.05$) was observed. This indicates that it was primarily the breed of the cow that determined milk production in this study.

The corrected "Best Linear Unbiased Estimates" and SE for total milk yield from D32 to D160, milk yield at peak lactation, days in milk at peak lactation and milk yield at weaning are shown in Table 11. The AF, AK and AJ cows reached peak lactation at a similar ($P>0.05$) day of lactation; around D75 days post-partum but they differed ($P<0.05$) from the AA group which reached peak lactation at D46 days post-partum. Angus×Friesian cows produced more milk ($P<0.05$) during peak lactation than AJ and AA cows but did not differ ($P>0.05$) from AK cows. Angus×Jersey and AK cows produced more milk at peak ($P<0.05$) than AA cows. On average, beef-cross-dairy crossbreds produced approximately 2kg per day more milk during peak lactation than AA cows. The sex of calf affected milk production at peak lactation, such that dams nursing female calves ($P=0.05$) produced less milk (approximately 0.8 kg per day) than those nursing male calves.

Angus×Friesian cows produced more milk at weaning ($P<0.05$) than AJ and AA cows but not AK cows. The AA cows had the lowest milk yield at weaning with an average difference compared to the other genotypes of 3.4 kg per day. The range of total milk production was from 1067 kg to 1599 kg for AF cows, 1077 kg to 1510 kg for AJ cows, 1093 kg to 1471 kg for AK cows and from 760 kg to 1306 kg for the Angus cows. The AF, AJ and AK cows produced more ($P<0.05$) milk from D32 to D160 than the AA cows. The AF cows produced more ($P<0.05$) milk from D32 to D160 than AJ cows, with AK cows being intermediate and not differing ($P>0.05$) from either AF or AJ cows. In the present study, as the proportion of Friesian or Jersey in the crossbreds increased from 0 to 50%, an extra 325 kg and 240 kg of milk, respectively, was expected compared to the AA cows. Given that a Kiwi-Cross is a Friesian-Jersey hybrid, it was expected that AK cows would have production intermediate between AF and AJ cows, and produce an extra 282.5 kg of milk compared to the AA cows.

Table 11. Best linear unbiased estimates and standard error for the lactation curve parameters of Angus (AA), Angus-Friesian (AF), Angus-Jersey (AJ) and Angus-Kiwi Cross (AK) cows.

Breeds	Lactation curve parameters							
	Random regression coefficient				Milk yield (kg/d)			DIM‡ at peak lactation (d)
	α0	α1	α2	α3	Peak	D160	Total†	
AA	8.43±0.23[c]	-2.01±0.49[a]	0.86±0.51	-1.23±0.26[b]	9.82±0.31[c]	6.06±0.25[c]	1017.48±19.98[c]	46±6[b]
AF	10.47±0.26[a]	-0.33±0.55[b]	0.13±0.57	-0.45±0.28[a]	12.07±0.35[a]	9.82±0.28[a]	1337.34±22.25[a]	71±7[a]
AJ	9.70±0.23[b]	-0.29±0.49[b]	-0.21±0.51	-0.32±0.25[a]	10.87±0.31[b]	8.88±0.25[b]	1244.51±19.89[b]	74±6[a]
AK	10.03±0.37[ab]	0.20±0.78[b]	-0.66±0.81	-0.06±0.40[a]	11.41±0.49[ab]	9.50±0.40[ab]	1307.76±31.64[ab]	82±9[a]

† Total milk yield from day 32 to day160 postpartum.

‡ Days in milk

abc Values within columns with different superscripts differ at the $P<0.05$ level.

2.3.3. Test-day correlations

Measurements taken at D32 were highly correlated with D49 measurements; however, as lactation progressed the correlations with later days decreased considerably and were not significant until the end of the lactation. Compared to D32, D49 measurements had higher correlations with D80, D120 and D160. Measurements at D120 and D160 were highly correlated with each other (Table 12). There was a poor, but significant, correlation between D32 measurements and total milk yield, the relationship was greater for measurements taken late in lactation.

Table 12. Correlation between test-day measurements and their individual correlation with total milk yield.

	Day of measurement				Total milk yield†
	D49	D80	D120	D160	
D32	0.82***	0.04	0.16	0.30**	0.41*
D49		0.59***	0.59***	0.78***	0.82***
D80			0.92***	0.95***	0.92***
D120				0.88***	0.94***
D160					0.97***

†Total milk yield from D32 to D160.

* indicates a significance of P<0.05; ** P<0.01 and *** P<0.001.

2.4. Discussion

2.4.1. Lactation curves - goodness of fit

Random regression models are highly applicable when a relationship between variables and time exists and have been recommended for the analysis of test day records of dairy cattle (Schaeffer, 2004). However, overestimation of the variance prediction at the extremes of the lactation curves are expected in random regression models (Pool et al., 2000) and this perhaps explain to some extent the dramatic drop in milk yield at the end of the lactation curve from AA cows. Results of the goodness of fit from this study suggested that the random regression methodology used to estimate the lactation curves of straightbred Angus cows and three beef-cross-dairy genotypes was effective in predicting the variance of test day records between animals in the population and within animals of a particular genotype. Whilst the primary objective of the study reported here was to determine the suitability of a random regression on Legendre polynomials model to predict milk yield, it may be of value to compare or examine the suitability of other published equations to fit lactation curves to limited test-day milk yield records.

2.4.2. Lactation curves – shape and curve parameters

The lactation curves for beef-cross-dairy cows are of similar shape and resemble a typical mammalian lactation curve, where milk production increases with increasing requirements of the offspring up to a peak and then decreases as lactation progresses. The findings in the present study are similar to those of Walker and Pos (1963) in New Zealand, where AF and AJ cows reached peak lactation at an average D74 postpartum; and with those reported by Chennete and Frahm (1981) whereby peak lactation in JA cows was detected at approximately D70 of lactation followed by a steady decrease as lactation progressed.

Post peak lactation, milk production levels tended to be maintained until approximately D120 when a decrease in milk production occurred for all three crossbred genotypes. Gaskins and Anderson (1980) reported peak lactation in AJ cows during the first month of lactation, which is earlier than reported in the present study, however, milk yield remained constant until D84 in 2-year-old cows and until D112 in 3-year-old cows. These results suggest that lactation curve persistency in beef cows can be greatly improved by the introduction of genes from dairy animals.

Contrary to the beef-cross-dairy crossbreds, the milk yield of AA cows started at its maximum during early lactation, decreased slightly close to D80 and thereafter remained relatively constant until approximately D115, before decreasing more drastically towards weaning. The results reported here for AA cows are in contrast with the findings of Jenkins and Ferrell (1984), Hohenboken et al. (1992), Sawyer et al. (1994) and Minick et al. (2001), where the “Jenkins” equation was used and peak milk yield was reached between approximately D60 to D70 postpartum. However, the “Jenkins” equation repeatedly produced curves that peaked around D70 and underestimated milk yield during the first month of lactation since it forces the curve through the origin (Hohenboken et al., 1992; Sawyer et al., 1994). Although, the variance accounted for by their equations were 77% and 88% respectively, compared to 74% accounted for by the model used in this study. Other lactation equations such as the Wood and weighted Wood equations (Hohenboken et al., 1992; Sawyer et al., 1994), Morant equation (Hohenboken et al., 1992), or other simple polynomials (Holloway et al., 1985) have shown peak milk yields relatively early in the lactation (ie. around day 30 postpartum). This is earlier than those found in the present AA cows.

There is evidence (Oftedal, 1984) that the calf’s ability to withdraw milk may be reduced in early lactation and that the residual milk left in the udder would stimulate mammary involution. An interaction exists between mammary evacuation and milk production, where cows suckled or milked more often produce higher levels of milk than those with infrequent mammary evacuation (Williams et al., 1979b). Angus cows may be more sensitive to changes in mammary evacuation during early and late-lactation than the crossbred cows. The first drop in production seen in AA cows may be explained by the calf not being physically capable to fully evacuate the udder due to physical consumption constraints and consequently, the residual milk left in the udder would stimulate the dam to reduce her milk production (Oftedal, 1981). Then, as the calf grows and its ability to suckle increases, milk production stabilises at a lower level to provide nutrients to the calf. Indeed, Blaxter (1961) suggested that milk yield is motivated towards the maximum possible growth rate of the offspring. Thus it is likely that a dams milk production would respond to the stimulus from her calf, although as a non-dairy animal, AA cows would not have the capacity to produce more milk.

Energy requirements increase with increasing age (Nicol and Brookes, 2007) and there is evidence (Baker et al., 1976) that if forage availability is adequate, calves receiving less milk during lactation could increase their pasture intake to compensate for the low energy intake from milk. In this study during late-lactation, calves reared by AA cows may have not been receiving enough nutrients from a suckling event; therefore losing interest in consuming milk in favour of consuming more pasture. This may explain the second drop in milk production observed towards the end of the lactation of AA cows.

As expected, differences between crossbred cow groups followed patterns found in their dairy counterparts, where Friesians are ranked first, followed by Kiwi-cross cows and finally the Jerseys (Holmes et al. 2002). In this study, crossbred cows produced significantly more milk at all stages of lactation compared to AA cows. The average estimates of calf milk intake and by assumption, the milk yield of the dams in this study were high relative to reports with AA, AF and AJ using the WSW technique under different feeding regimes (Walker and Pos, 1963, Wilson et al., 1969, Deutscher and Whiteman, 1971, Gaskins and Anderson, 1980, Sacco et al., 1987). Results for AA cows only were comparable with those obtained using the WSW technique with mature (ie 5 to 12 years-old) Angus cows on a fescue-legume diet (Holloway and Worley, 1983) and with the oxytocin method in a drylot study with Angus heifers (Marston et al., 1992) and with another study involving a mixed heifer/mature cow herd on a corn silage and haylage-based diet (Fiss and Wilton, 1992). Whilst the data is not reported here, it's interesting to note that the lower production of milk in AA cows was accompanied by almost one unit of body condition score (BCS) gain throughout the lactation period, whilst the crossbreds remained unchanged during the lactation and had a similar BCS between groups; however the desired mean BCS of at least 5/10 was achieved by all groups by the end of lactation (Law et al., 2013). This indicates that the feeding level in this study was adequate not only to maintain the lactation of a high-producing crossbred but also to maintain condition of the dam. Since milk yield is a major determinant of calf postnatal growth further work should be done to determine the effect of the extra milk produced by the crossbreds on the weaning weight of the calves and its longer term effects on the calf growth.

2.4.3. Test-day records

Frequent WSW measurements under grazing conditions are often not feasible due to the laborious practices involved in the technique and consequently only few measurements throughout lactation are taken to represent the different stages of lactation. Therefore, it is useful to identify how individual measurements are correlated with each other and their ability to individually predict total milk yield. In this study, measurements of calf intake prior to one month of age were relatively difficult to obtain because of complications surrounding the necessity of achieving a normal suckling event during the test, however, it seems that after one month of age, more consistent estimates can be obtained. As lactation progressed the correlation between individual test-day records with total milk yield increased significantly. Totusek et al. (1973) found that the correlation of a measurement taken at D30 postpartum and total milk yield was 0.48, which is similar to that obtained in this study at D32 (r=0.41). This relatively low correlation was probably a reflection of the limited capacity of the calf to fully evacuate the udder and therefore limiting the ability of the model to predict milk yield at this stage. However, in the Totusek et al. (1973) study, the correlation increased from 0.77 to almost 1.0 when test-day records where obtained after D70. Similarly, in this study, correlations between individual test-day records and total milk yield increased as lactation progressed. With WSW measurements, an underestimation is expected during the first month of lactation (Totusek et al., 1973) meaning data collected during this period may not be useful and it would be advantageous to begin measurements later in lactation when estimations are likely to be more accurate. The present study demonstrated that D49 measurements can accurately predict milk yield earlier in lactation. Delaying sampling until after the first month of lactation may be preferred for studies under pastoral systems where samplings are logistically difficult.

2.5. Conclusion

Results reported here suggest that the random regression methodology used in this experiment can accurately predict milk yield from test-day records obtained with the WSW technique, and can satisfactorily be used for the modelling of lactation curves in beef cattle. Additionally, the relationship of individual test-day records to predicted milk yield should be taken into account when designing sampling schemes during early lactation in beef cattle, in particular those within pastoral systems. Results from this experiment also confirmed the hypothesis that increasing the proportion of dairy genetics in the beef herd is accompanied with an increase in milk production. Under a non-limiting pasture quality and availability, AF, AJ and AK cows produce more milk throughout lactation than AA cows.

Chapter 3. Effect of maternal milk production on postnatal growth of male steers.

3.1. Introduction

In a cow-calf operation net income is dependent on both, calf weaning weights and the percentage of calves weaned (Lindholn and Stonaker, 1957, Wiltbank, 1970). Thus research has typically focused on the factors that may affect weaning weight of calves and ultimately, the expected economic return of beef cattle systems. It has been suggested that the major nutritional factors affecting pre-weaning calf growth are the lactational performance of the dam and the quality and availability of nutrients from pasture and/or supplements prior to parturition to the dam, and following parturition to both the dam and calf (Neville, 1962, Totusek et al., 1973, Greenwood and Cafe, 2007)

In New Zealand, beef calves are typically reared by the dam and weaned at approximately 180 days postpartum. Milk represents the sole source of nutrients for the newborn in early postnatal life and it remains a significant component of the diet until weaning (Grings et al., 2007). Observations of calf growth demonstrate a growth trajectory that tends to be curvilinear (Boggs et al., 1980, Ahunu and Makarechian, 1987, Woodward et al., 1989), suggesting that as calves grow, nutrient intake from milk becomes limiting and they become increasingly dependent upon non-milk nutrient sources such as pasture. Estimated correlations between milk intake and calf weaning weight have ranged from 0.12 to 0.90 (Neville, 1962, Furr, 1962, Totusek et al., 1973, Chenette and Frahm, 1981). Milk production during the first few months of lactation explains a significant proportion of the variation in calf weaning weight and that this relationship decreases as lactation progresses (Barton, 1970b, Rutledge et al., 1971). Bailey and Lawson (1981) found that at 44 days of age, milk supplied 86% of the digestible energy intake (DEI) of Angus calves on pasture but dropped drastically towards weaning at 139 days to approximately 19% of DEI. If the relationship between milk intake and growth is purely nutritional and milk yield is increased, then by assumption, the weaning weight of calves should also increase (Ansotegui et al., 1991).

In Chapter 2 it was demonstrated that crossbreeding between three dairy breeds (ie. Friesian, Jersey and Kiwi-Cross) and Angus cows, significantly increased milk output of the resulting crossbred cows compared to straightbred Angus cows. Morris et al. (1993b) demonstrated that these crosses were suitable for the demanding conditions of pastoral beef farming in New Zealand, where nutrient quantity and quality fluctuates throughout the year. The objective of the experiment reported in this Chapter, was to determine to what extent differences in the lactational performance of the dam may affect the pre- and post-weaning growth of steers up to one year of age.

3.2. Materials and methods

3.2.1. Animals

Sixty four male calves resulting from a terminal cross between Angus (AA), Angus×Friesian (AF), Angus×Jersey (AJ) and Angus×Kiwi-Cross (AK) cows with Angus (AA) or Simmental (SS) bulls were selected for use in this study (Hickson et al., 2012). The growth trajectory of these calves was examined from birth to one year of age. The study was conducted using commercial beef cattle management practices at Massey University's Tuapaka Beef Research Farm, located 20 kilometres east of Palmerston North, New Zealand (latitude 40.33° S and longitude 175.73° E). Management practices and feed allowances were the same as that described in Chapter two.

Calves were castrated at an average age of 46 days (D) by application of a rubber ring (Elastrator. Heiniger, Industrieweg, Switzerland). Milk intake was recorded postpartum using the weigh-suckle-weigh (WSW) technique as explained in Chapter two, on D32, D49, D80, D120 and D160 (weaning). For the purpose of this chapter, the estimated milk production of the dams in Chapter two was assumed to be the milk intake of their calves. Live weight of all calves was recorded at birth (D0) and accompanying every WSW measurement on D32, D49, D80, D120 and D160. Post-weaning liveweight measurements were taken on D240, D330 and D350. At an average D270, groups of steers balanced for genotype were allocated to one of the following three winter feeding treatments: 1) set stock grazing; 2) break fed grazing or; 3) break fed grazing with feedpad option.

3.2.2. Statistical methods

All statistical analyses were carried out using the Statistical Analysis System (SAS version 9.2, SAS Institute Inc., Cary, NC, USA, 2009). A third order Legendre polynomial was fitted to growth data using a random regression to obtain an average growth curve for the population and for each calf with the following model:

$$y_{tm} = \sum_{i=0}^{3} b_i\, P(x)_t^i + \sum_{i=1}^{3} \alpha_{im} P(x)_{tm}^i + e_{tm}$$

where y_{tm} is the observation at time t in calf m for live weight, b_i are fixed regression coefficients of days of age on variable y (b_0 = intercept, b_1 = linear effect, b_2 = quadratic effect and b_3 = cubic effect); α_{im} are random regression coefficients of age on variable y in calf m (α_{0m} = intercept, α_{1m}=linear effect, α_{2m}= quadratic effect and α_{3m} = cubic effect), x_{tm}^i is the observation of standardized age at time t in calf m at the power 0, 1, 2, and 3; e_{tm} is the residual error associated with observation y_{tm}. The standardized unit of time x ranges from -1 to +1, and was calculated as:

$$x = 2\left(\frac{t - t_{min}}{t_{max} - t_{min}}\right) - 1$$

where t is age, t_{min} is the youngest age, and t_{max} is the eldest age. In this study, t_{min} was 0 days of age (birth) and t_{max} was 365 days of age. The first four Legendre polynomial functions of standardized units of time (x) are defined as below:

$$P(x)^0 = 1$$

$$P(x)^1 = x$$

$$P(x)^2 = \frac{1}{2}(3x^2 - 1)$$

$$P(x)^3 = \frac{1}{2}(5x^3 - 3x)$$

The goodness of fit achieved with the model and for each growth curve per calf genotype was evaluated by standard procedures obtaining the coefficient of correlation (r) and determination (r^2), the relative prediction error (RPE) and the Linn's concordance correlation coefficient (CCC). Agreement between actual and predicted live weight was examined by regression analyses using the REG procedure.

Differences in live weight at different ages were estimated by analysis of variance using the MIXED procedure with a model that included mob, dam's genotype, sire breed, and the interaction between dam's genotype and sire breed. Beyond D270, the model included the fixed effect of winter treatment.

A second analysis was performed to determine the effect of milk intake on the live weight of the steers with a model that included mob, dam's genotype, sire breed, the interactions between dam's genotype and sire breed as fixed effects; and, cumulative milk intake was used as a covariate for the model. Beyond D270, the model included the fixed effect of winter treatment. Regression coefficients of cumulative milk intakes (or total milk yield) at D40, D60, D90, D160 on weaning and yearling weights were estimated by analysis of variance using the MIXED procedure with a linear model that included mob, dam breed, sire breed, the interactions between dam and sire breed and cumulative milk intake at the selected days as a covariate for this model. Beyond D270 the model included the fixed effect of winter treatment. Differences between regression coefficients were detected using the equation proposed by Paternoster et al. (1998).

Individual steer metabolisable energy requirements were calculated using the methods used by Freer et al. (2007) and Nicol and Brookes (2007). Since composition of milk was not tested in this study, estimated milk composition values for the Friesian, Jersey and Kiwi-Cross breeds were taken from New Zealand averages reported by Holmes et al. (2002) and for the Angus breed from Peterson et al. (2010). Energy intake from pasture consumption was estimated as the difference between energy requirements and energy provided by milk for each individual animal. Differences in calf metabolisable energy requirements, and energy intake from milk and from pasture were estimated by analysis of variance with the MIXED procedure, using a linear model that included the fixed effects of mob, dam breed, sire breed and the interaction between dam and sire breed.

3.3. Results

3.3.1. Growth curves – goodness of fit

Figure 9 illustrates the average growth curves for each particular genotype and Table 13 shows the criteria used in assessing the goodness of fit of the random regression model for the different steer genotypes and for the model used to predict the growth curves.

Assessment of the goodness of fit of the model (ie. all calves included independent of the genotype) suggested that prediction estimates were highly correlated (r=0.99, P<0.0001) to actual measurements of growth (Figure 10). Almost 100% of the variation in growth between steers was explained by the model, with an average 6% variation between predicted and actual measurements. Reproducibility of the model, based on growth curves calculated with Legendre polynomials fitted with random regression, was high with a CCC of 89%, therefore, explaining the high correlation between actual and predicted measurements.

When each growth curve corresponding to each genotype was evaluated separately, predicted growth estimates for all genotypes were highly correlated (r=0.99, P<0.0001) with actual measurements of growth. On average, 99% of the variation in growth was explained by the growth curves in Table 13, with only 6.3% variation between predicted and actual measurements. The CCC of individual growth curves ranged from 0.85 to 0.93 suggesting a high reproducibility of the model when growth data is fitted with Legendre polynomials on random regression.

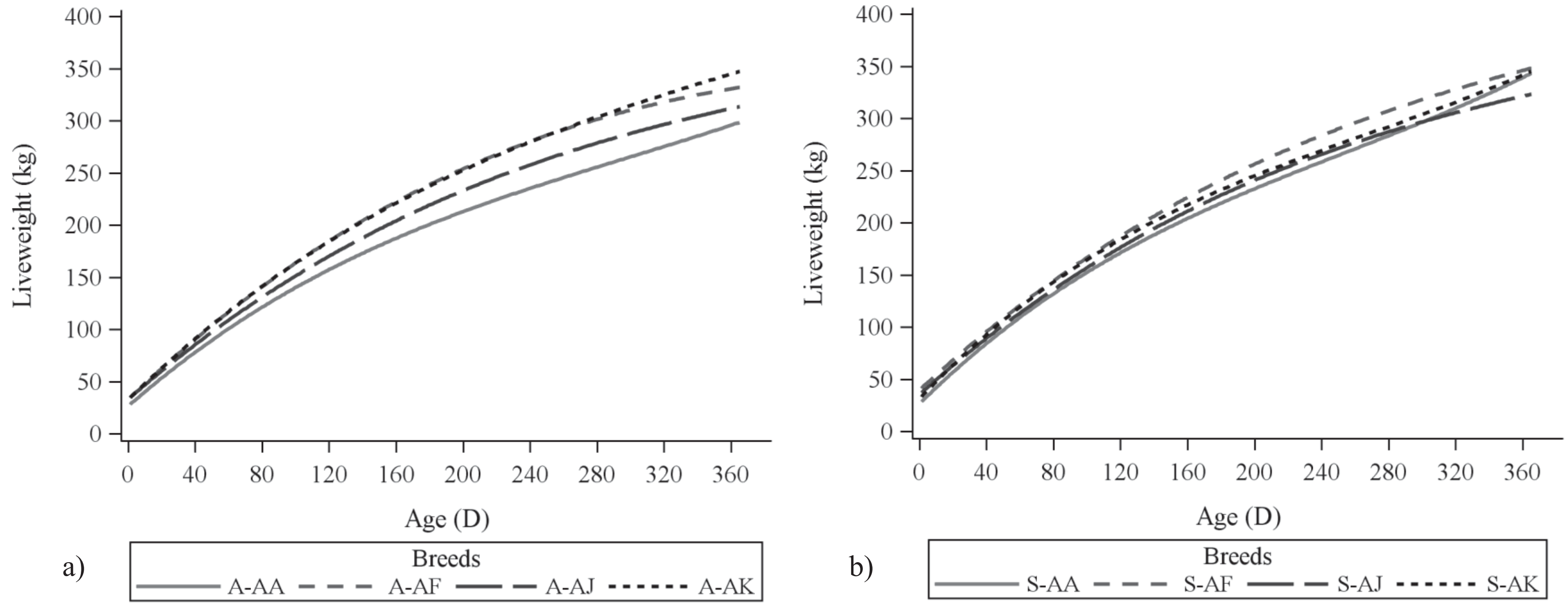

Figure 9. Predicted live weight of a) Angus-sired and b) Simmental-sired steers using third order Legendre polynomials fitted to liveweight data with random regression. Steers genotypes represented by the sire breed-dam breed abbreviation: Straightbred Angus (A-AA), Angus-Angus×Friesian (A-AF), Angus-Angus×Jersey (A-AJ), Angus-Angus×Kiwi-cross (A-AK), Simmental-Angus×Angus (S-AA), Simmental-Angus×Friesian (S-AF), Simmental-Angus×Jersey (S-AJ) and Simmental-Angus×Kiwi-cross (S-AK).

Table 13. Goodness of fit for the predicted growth curves of the different beef steers genotypes and the model used to predict them.

Genotypes[§]	$r^{2\dagger}$	RPE[‡]	CCC[*]
A-AA	0.99	6.48	0.88
A-AF	0.99	5.19	0.89
A-AJ	0.99	5.70	0.90
A-AK	0.99	5.22	0.85
S-AA	0.99	6.40	0.93
S-AF	0.98	7.95	0.86
S-AJ	0.99	6.05	0.87
S-AK	0.98	7.56	0.91
Model	0.99	6.20	0.89

[§] A-AA = Pure Angus, A-AF = Angus-Angus×Friesian, A-AJ = Angus-Angus×Jersey, A-AK = Angus-Angus×Kiwi-cross, S-AA = Simmental-Angus×Angus, S-AF = Simmental-Angus×Friesian, S-AJ = Simmental-Angus×Jersey and S-AK = Simmental-Angus×Kiwi-cross.

[†]Coefficient of determination

[‡]Relative prediction error

[*]Lin's concordance correlation coefficient

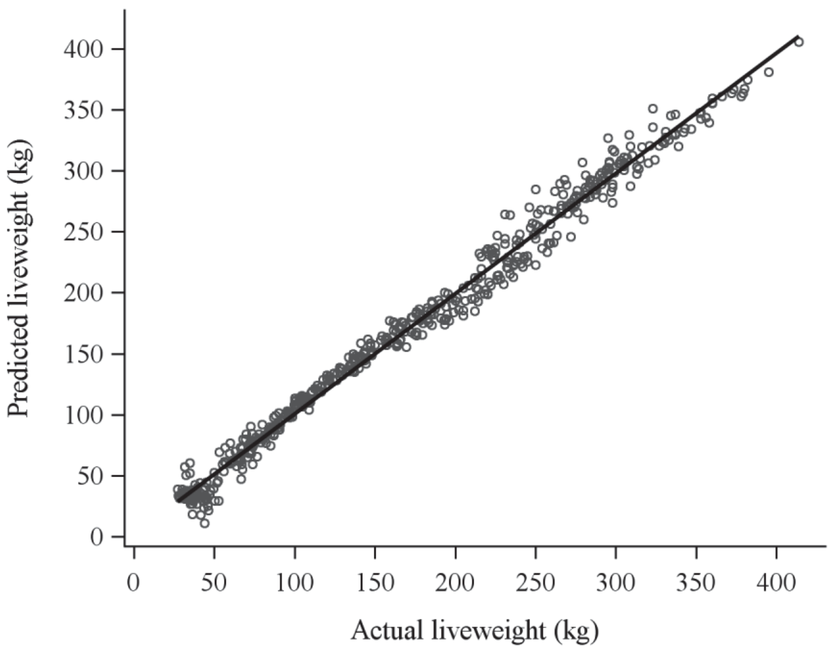

Figure 10. Regression plot of actual versus predicted beef steer live weight.

3.3.2. Growth curves – genotype differences

The maternal and paternal effect on average steer live weight at D60, D90, D120, D160, D270 and D365, without and with cumulative calf milk intake included as a covariate, are shown in Table 14 (i) and (ii), respectively. The covariate value included for each measurement of steer live weight is the cumulative calf milk consumption to that day of measurement.

Analysis of variance of steer live weight without the inclusion of milk intake as a covariate (Table 14 (i)) shows that there was a maternal genotype effect, whereby all steers reared by crossbred cows were heavier (P<0.05) from D60 to D270 than those reared by AA cows, however, the live weight of AA-reared steers increased significantly towards D365 to reach a yearling weight that was similar (P>0.05) AJ-reared steers but remained lower than AF- and AK-reared steers. Steers reared by AJ cows were lighter from D60 to D356 than AF- and AK-reared steers. At D365, AK-reared steers were heavier (P<0.05) than those reared by AJ and AA cows, but did not differ (P>0.05) from AF-reared steers. There was no interaction (P>0.05) between dam and sire breed on live weight of steers from D60 to D365.

Due to the differences in maternal lactational performance, reported in Chapter two, the cumulative milk yield (and by assumption the progeny's cumulative milk intake for the purpose of this chapter) was included as a covariate in the model to determine the response in live weight to different levels of milk intake (Table 14 (ii)). At D60, steers reared by AF and AK cows were heavier (P<0.05) than steers reared by AA and AJ cows. At D90, steers reared by AA, AF and AK cows did not differ (P>0.05) in live weight but were heavier (P<0.05) than those reared by AJ cows. By D120, there were no differences (P>0.05) in live weight between steers reared by AA, AF and AJ cows, however, the latter steers were lighter than those reared by AK cows. The effect of maternal genotype on steer live weight was no longer apparent at weaning and steers remained of a similar live weight from D160 until D270. At D365, the live weight of steers reared by AK cows was higher (P<0.05) than those reared by AJ cows, but did not differ (P>0.05) from those reared by AA and AF cows. For duration of this study, in both models (Table 14 (i) and Table 14 (ii)), steers sired by SS bulls were significantly (P<0.05) heavier than those sired by AA bulls.

Table 14. The maternal and paternal effect on average steer live weight at day (D) 60, D90, D120, D160, D270 and D365 postpartum, (i) without calf milk intake included in the model as a covariate and (ii) with calf milk intake included in the model as a covariate*.

(i)	Live weight (kg)					
	D60	D90	D120	D160	D270	D365
Dam genotype effect						
AA	105.3±1.7[c]	137.3±2.2[c]	165.3±2.8[c]	197.6±3.3[c]	265.0±4.4[c]	316.1±5.4[b]
AF	119.1±2.5[a]	154.5±3.4[a]	186.3±4.1[a]	225.3±4.4[a]	299.3±6.5[a]	340.1±7.9[a]
AJ	111.4±1.6[b]	144.4±2.3[b]	173.9±2.8[b]	208.8±3.3[b]	279.1±4.3[b]	317.5±5.3[b]
AK	118.9±2.3[a]	154.3±3.2[a]	185.3±4.0[a]	220.8±4.7[a]	293.8±6.2[a]	344.6±7.6[a]
P value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Sire breed effect						
A	111.3±1.3[b]	144.8±1.8[b]	174.2±2.1[b]	208.6±2.6[b]	279.5±3.4	321.4±4.2[b]
S	116.0±1.6[a]	150.5±2.3[a]	182.9±2.5[a]	217.6±3.1[a]	289.1±4.3	337.8±5.3[a]
P value	0.03	0.05	0.08	0.03	0.09	0.02
(ii)	Live weight (kg)					
	D60	D90	D120	D160	D270	D365
Dam genotype effect						
AA	106.7±1.9[b]	143.1±3.0[ab]	174.6±3.9[ab]	208.2±4.7	275.7±6.3	328.2±7.8[ab]
AF	118.8±2.5[a]	151.7±3.4[a]	180.4±4.3[ab]	216.0±5.2	291.2±7.0	330.8±8.6[ab]
AJ	111.4±1.73[b]	143.0±2.3[b]	171.5±2.8[b]	205.6±3.4	276.1±4.6	314.4±5.6[b]
AK	118.5±2.4[a]	151.9±3.2[a]	181.4±3.9[a]	216.1±4.7	288.8±6.3	338.8±7.7[a]
P value	<0.001	0.05	0.12	0.17	0.16	0.05
Sire breed effect						
A	110.6±1.4[b]	143.1±1.8[b]	172.5±2.2[b]	206.7±2.6[b]	276.5±3.5[b]	317.8±4.2[b]
S	117.1±1.8[a]	151.7±2.2[a]	181.4±2.6[a]	216.2±3.1[a]	289.4±4.2[a]	338.3±5.2[a]
P value	<0.001	<0.001	0.01	0.02	0.02	<0.001

[ab] Different superscripts within main effect and column indicate values that are significantly different (P<0.05).

* The covariate value included for each measurement of steer liveweight is the cumulative calf milk consumption to that day of measurement.

Regression coefficients of cumulative calf milk consumption on live weight at weaning are presented in Table 15. This represents the proportion of live weight at weaning that was associated with the consumption of an additional 1 kg of milk at different stages of lactation. Overall and independently of the genotypes of the steers, there was no effect ($P>0.05$) of cumulative milk intake at D40 and D60 on the weaning weight of the steers in this study;

however, as lactation progressed, the effect of milk yield on live weight was more evident. Cumulative milk intake from D32-D90, D32-D120 and D32-D160 significantly ($P<0.01$) affected live weight at weaning. An extra kg of milk consumed from D32 to D90 was associated with an increase in weaning weight of 0.09 kg ($P<0.01$). This relationship continued to be significant ($P<0.01$) as lactation progressed such that an extra kg of milk consumed from D32 to D120 was associated with an increase in live weight at weaning of approximately 0.08 kg ($P<0.01$). A relationship existed between total milk intake and live weight at weaning (D160) such that, for every extra kg of milk consumed by the end of lactation (D32-D160) an increase in live weight of 0.05 kg ($P<0.01$) was expected in all steers irrespective of their genotype.

When steers were evaluated based on their proportion of maternal genotype, a relationship existed only for the AK-reared steers between the cumulative milk intake from D40 to D160 and their growth. At D40, an additional kg of milk consumed from D32 to D40 was associated with an increase in 0.44 kg ($P<0.05$) of live weight at weaning. As lactation progressed (D60), the relationship between milk intake and weaning weight became significant also for AA-reared steers. At D60, a kg of milk was associated with 0.38 kg ($P<0.05$) and 0.23 kg ($P<0.05$) of live weight at weaning for AA- and AK-reared steers respectively. As lactation progressed, pasture consumption increased relative to milk intake; at D120 a kg of milk was associated with an additional 0.26 kg ($P<0.05$) and 0.18 kg ($P<0.01$) of live weight at weaning for AA- and AK-reared steers respectively. At weaning (D160) an extra kg milk consumed was associated with 0.10 kg of live weight for both AA- ($P<0.05$) and AK- ($P<0.01$) reared steers. From D60 to D160 the expected conversion of milk to live weight did not differ ($P>0.05$) between AA and AK groups. Interestingly, cumulative milk yield became a significant ($P<0.05$) factor in the live weight at weaning of AF reared steers, only from D120 until weaning (D160). An extra kg of milk produced from D32 to D120 was associated with an increase in live weight at weaning of 0.08 kg ($P<0.05$) for AF-reared steers, whilst at weaning (D160) the expected conversion of milk to live weight of AF-reared steers was similar ($P>0.05$) to that of AA- and AK-reared steers (Table 15). There was no significant interaction between dam genotype and sire breed seen in the growth trajectory of these steers.

Regression coefficients of cumulative calf milk consumption on yearling live weight are presented in Table 16. Overall and independently of the genotypes of the steers, there was no effect ($P>0.05$) of cumulative milk intake up to D90 on the yearling weight of the steers in this study; however, the effect of milk intake on live weight became more apparent when cumulative milk intake up to D120 and D160 was regressed on yearling weight. An extra kg of milk consumed by D120 was associated with an increase in yearling weight of 0.09 kg ($P<0.05$). This relationship continued to be significant ($P<0.01$) at D160, where an extra kg of milk consumed was associated with an increase in yearling weight of approximately 0.06 kg ($P<0.01$).

When steers were evaluated based on their proportion of maternal breed, a relationship existed only for AK-reared steers between the cumulative milk intake from D60 to D120 and their live weight at D365. From D32 to D60, an additional kg of milk was associated with an increase in yearling weight of 0.38 kg ($P<0.05$), whilst a kg of milk at D120 was associated with an increase in live weight at D365 of 0.19 kg ($P<0.05$). When steers were evaluated based on their proportion of paternal breed, a relationship existed between milk intake and the growth of SS-sired steers. From D32 to D120, an additional kg of milk was associated with an increase in yearling weight of 0.16 kg ($P<0.05$) and this expected conversion from milk to live weight decreased towards weaning to approximately 0.10 kg ($P<0.05$) per kg of total milk consumed by D160. As with weaning weight, there was no significant interaction between dam genotype and sire breed for the post-weaning growth trajectory of these steers.

Table 15. Regression coefficients of cumulative milk intake from day (D)32 to D40, D60, D90, D120 and D160 of lactation on the weaning (D160) live weight of steers.

Maternal Genotype	Paternal breed	β40	β60	β90	β120	β160
Overall[§]		0.07(0.1)	0.07(0.05)	0.09(0.03)**	0.08(0.03)**	0.05(0.02)**
AA		0.55(0.4)	0.38(0.2)*	0.26(0.10)*	0.14(0.06)*	0.10(0.04)*
AF		-0.11(0.2)	0.006(0.08)	0.07(0.06)	0.08(0.04)*	0.10(0.03)*
AJ		-0.10(0.2)	-0.03(0.07)	-0.01(0.05)	0.01(0.05)	-0.01(0.03)
AK		0.44(0.2)*	0.23(0.09)*	0.18(0.06)**	0.14(0.05)**	0.10(0.04)*
	A	0.12(0.1)	0.06(0.05)	0.06(0.04)	0.04(0.03)	0.03(0.02)
	S	-0.37(0.3)	0.11(0.2)	0.23(0.08)**	0.17(0.05)***	0.11(0.03)***
AA	A	0.74(0.4)	0.43(0.22)	0.25(0.16)	0.09(0.1)	0.04(0.1)
AA	S	0.30(0.7)	0.33(0.3)	0.26(0.14)	0.18(0.1)*	0.11(0.05)*
AF	A	0.05(0.2)	0.05(0.09)	0.05(0.06)	0.05(0.05)	0.04(0.03)
AF	S	-1.22(0.6)*	-0.40(0.3)	0.14(0.16)	0.20(0.1)*	0.13(0.1)*
AJ	A	-0.10(0.2)	-0.04(0.07)	-0.03(0.06)	-0.04(0.05)	-0.03(0.03)
AJ	S	0.50(0.8)	0.30(0.3)	0.24(0.20)	0.16(0.1)	0.10(0.1)
AK	A	0.50(0.2)*	0.22(0.1)*	0.16(0.07)	0.13(0.06)*	0.08(0.04)
AK	S	-0.40(0.8)	0.45(0.4)	0.27(0.16)	0.14(0.1)	0.10(0.01)

[§] "Overall" refers to the overall effect of milk intake of a particular day on calf weaning weights.

[*] superscript indicates $\beta \neq 0$ at $P<0.05$; ** superscript indicates $\beta \neq 0$ at $P<0.01$; *** superscript indicates $\beta \neq 0$ at $P<0.0001$

Table 16. Regression coefficients of cumulative milk intake from day (D)32 to D40, D60, D90, D120 and D160 of lactation on the yearling (D365) live weight of the calves.

Maternal Genotype	Paternal Genotype	β40	β60	β90	β120	β160
Overall[§]		0.06(0.2)	0.07(0.08)	0.10(0.1)	0.09(0.04)*	0.06(0.03)*
AA		0.21(0.6)	0.22(0.3)	0.18(0.2)	0.09(0.1)	0.06(0.07)
AF		-0.07(0.3)	0.04(0.01)	0.11(0.1)	0.12(0.1)	0.09(0.05)
AJ		-0.33(0.2)	-0.10(0.1)	-0.03(0.1)	0.00(0.1)	0.01(0.05)
AK		0.82(0.3)	0.38(0.1)*	0.27(0.1)*	0.19(0.1)*	0.11(0.06)
	A	0.14(0.2)	0.08(0.08)	0.08(0.1)	0.06(0.1)	0.04(0.03)
	S	-0.62(0.6)	0.01(0.3)	0.21(0.1)	0.16(0.1)*	0.10(0.04)*
AA	A	-0.07(0.7)	-0.11(0.4)	-0.18(0.3)	-0.14(0.2)	-0.09(0.1)
AA	S	1.64(1.1)	0.86(0.5)	0.44(0.23)	0.25(0.1)	0.14(0.1)
AF	A	0.19(0.3)*	0.11(0.1)	0.12(0.1)	0.12(0.1)	0.08(0.01)
AF	S	-1.83(0.9)*	-0.59(0.4)	0.00(0.3)	0.13(0.2)	0.10(0.1)
AJ	A	-0.22(0.2)	-0.08(0.1)	-0.03(0.1)	-0.01(0.1)	-0.00(0.1)
AJ	S	-1.28(1.3)	-0.34(0.6)	-0.02(0.4)	0.06(0.2)	0.04(0.1)
AK	A	0.85(0.3)*	0.37(0.1)*	0.27(0.1)*	0.20(0.1)	0.12(0.1)
AK	S	-0.68(1.2)	0.35(0.06)	0.25(0.3)	0.13(0.2)	0.07(0.1)

[§] "Overall" refers to the overall effect of milk intake of a particular day on calf weaning weights.

* superscript indicates $\beta \neq 0$ at $P<0.05$; ** superscript indicates $\beta \neq 0$ at $P<0.01$; *** superscript indicates $\beta \neq 0$ at $P<0.0001$

Figure 11 shows the trajectory from D32 to D160 of the predicted metabolisable energy (ME) requirements, milk energy intake and assumed pasture energy consumption for AA-, AF-, AJ- and AK-reared steers. Daily energy requirements for AA-reared steers increased from 43 MJ at D32 to 56 MJ at weaning; whilst AF-, AJ- and AK-reared steers required 48 MJ, 44 MJ and 49 MJ, respectively, at D32 and increased towards weaning to 67 MJ, 62 MJ and 64 MJ, respectively. Steers reared by AF, AJ and AK dams had significantly greater ($P<0.05$) total ME requirements for growth compared to those reared by AA dams but did not differ ($P>0.05$) from each other (Table 17). Despite not differing at a $P=0.05$ level, total ME requirements for AF- and AK-reared steers tended ($P=0.06$ for AF and $P=0.06$ for AK) to be higher than those of AJ-reared steers.

Energy intake from milk for AA-reared steers provided about 27 MJ of daily energy intake at D32 and dropped rapidly towards weaning to provide approximately 17 MJ. For AF-, AJ- and AK-reared steers, more than 35 MJ of daily energy intake were provided solely by milk at D32 and remained constant towards weaning to provide around 30 MJ of energy. This resulted in a total energy intake from milk that was higher ($P<0.05$) for the crossbred-reared steers compared to those reared by AA dams. Estimated daily energy intake from pasture ranged from 16 MJ at D32 to 38 MJ at weaning for AA-reared steers; from 10 MJ at D32 to 35 MJ at weaning for AF-reared steers, from 8 MJ at D32 to 29 MJ at weaning for AJ-reared steers, and; from 15 MJ at D32 to 31 MJ at weaning for AK-reared steers. This resulted in a total pasture energy intake that did not differ between AA-, AF- and AK-reared steers but that was significantly higher ($P<0.05$) than the total energy intake from pasture of steers reared by AJ dams (Table 17).

Table 17. Least square means for predicted total energy requirements, energy intakes from milk and pasture from day 32 to day 160 of steers from dams that were Angus×Angus (AA), Angus×Friesian (AF), Angus×Jersey (AJ) and Angus×Kiwi-Cross (AK).

Maternal genotypes	Total energy requirements (MJ)	Energy intake from milk (MJ)	Energy intake from pasture (MJ)
AA	6573.4±148.8^{b}	2974.1±156.3^{b}	3565.9.9±166.1^{a}
AF	7539.61±213.7^{a}	4330.4±224.6^{a}	3241.0±238.7^{a}
AJ	7047.4±143.5^{a}	4224.2±150.8^{a}	2443.4±160.3^{b}
AK	7518.6±204.4^{a}	4290.3±214.7^{a}	3206.5±228.2^{a}

^{ab} different superscripts within column indicate values that significantly differ ($P<0.05$)

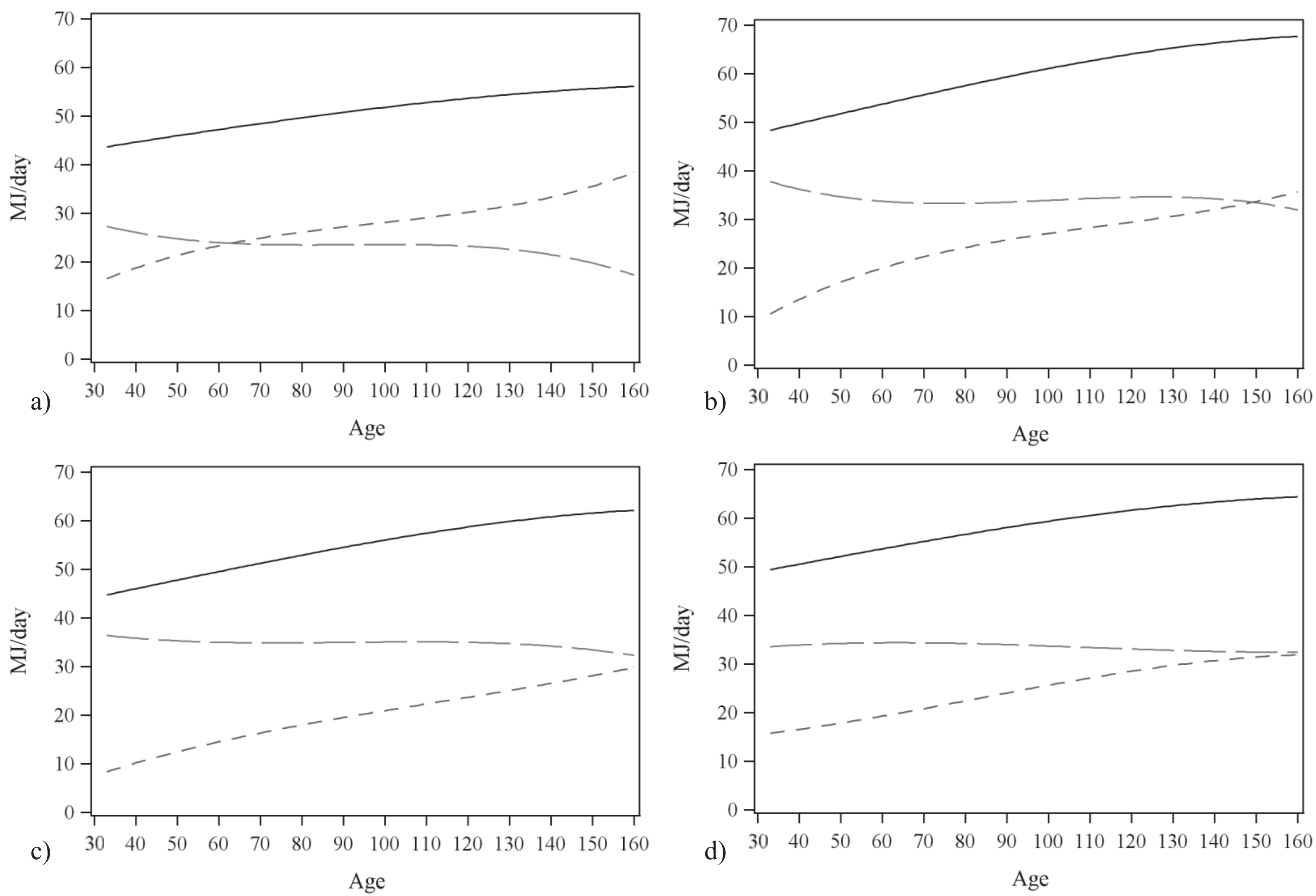

Figure 11. Daily total net energy requirements (——), net energy intake from milk (— —) and implied energy intake from pasture (- - -) of steers from dams that were a) Angus×Angus (AA), b) Angus×Friesian (AF), c) Angus×Jersey (AJ) and d) Angus×Kiwi-Cross (AK).

3.4. Discussion

Numerous previous studies have reported positive correlations between milk yield and calf weaning weights (Neville, 1962; Gleddie and Berg, 1968; Totusek et al., 1973; Mondragon et al., 1983). There is evidence in the literature that indicates increased dam milk production through the use of crossbreeding beef breeds with dairy breeds can increase calf milk consumption and, therefore, significantly increase calf weaning weights (Deutscher and Whiteman, 1971, Morris et al., 1993b, Arthur et al., 1997). The objective of the present experiment was to determine to what extent differences in the lactational performance of the dam may affect the pre- and post-weaning growth of steers up to one year of age.

3.4.1. Relationship between milk intake and steer live weight

When the live weight of steers from D60 to weaning (D160) was examined, without milk intake included as a covariate, the results indicated that there were differences in weaning weight between steers reared by cows differing in genotype such that steers reared by AF and AK cows were heavier than steers reared by AJ cows, and all steers reared by beef-cross-dairy cows were heavier than AA-reared steers. Additionally steers sired by SS-bulls were heavier than those sired by AA-bulls. This suggests that there were both, maternal and paternal genotype may have an influence on steer weaning weight. Inclusion of the predicted cumulative milk intake as a covariate in the analysis of steer weaning weight, helped to remove some of the phenotypic variation that would otherwise appear as noise, and consequently revealed that the higher live weight at D60 in AJ-reared steers compared to AA-reared steers was due to differences in milk consumption from D32 to D60. When cumulative milk intake was included in the model as a covariate, differences in live weight between AA-, AF- and AK-reared steers were less apparent at D90, suggesting that from D90 until weaning, any differences in live weight between the steers were due to differences in milk consumption rather than a maternal effect on steer size. Steers that were reared by dams with higher milk potential (ie. AF, AJ and AK cows) compared to those reared by AA cows were able to consume more energy from milk throughout the lactation period and consequently were able to support greater daily gains, thus reaching greater weaning weights. This is similar to the results reported by Arthur et al. (1997), Morris et al. (1993b) and Deutscher and Whiteman, (1971). Differences in weaning weight between AF-, AJ- and AK-reared steers were mainly due to differences in size rather than differences in milk consumption.

The advantage in liveweight at weaning achieved by the steers reared by beef-cross-dairy cows was maintained until D270 and was attributed to the greater milk consumption of the calves rather than their growth potential. At one year of age, differences in liveweight between steers due to milk consumption were less apparent, however, differences in milk consumption in the pre-weaning period may have, in part, played a role in the liveweight differences seen between AF- and AA-reared steers later in life. Paternal genotype influenced steers growth but further analysis is needed to determine the extent of this effect.

Morris et al. (1994) suggested that beef-cross-dairy cows have a higher productivity and efficiency compared to straightbred beef animals. Estimation of the biological efficiency of the different genotypes used in this study was not within the scope of this work, however, it seems that on average, AJ-reared steers have similar ME requirements and milk energy intakes to AF- and AK-reared steers, but had significantly lower apparent pasture intakes. If efficiency is measured as the ratio between output and input, and assuming AJ dams were lighter than AF and AK dams, then by assumption the biological efficiency may be higher in AJ animals, although further analysis and more research would be needed to determine if this is the case.

3.4.2. Cumulative milk intake and steer weaning and yearling weight

The regression coefficients in Table 15 showed a rather difficult scenario to interpret since significance of regression coefficients was only achieved by two groups of animals (AA- and AK-reared steers) whilst the other groups were not different from zero, however, in most cases all groups did not differ from each other. It is possible that the number of animals in this study limited the power of the analysis; therefore the model was not able to determine differences between groups. Despite this limitation, some logical assumptions can be taken from the experiment reported here. It seems that the regression coefficients varied depending on the stage of lactation when the measurements were taken. Extra milk produced during the first two months of lactation (from D32 to D40 and D32 to D60) was associated with a higher increase in weaning weight compared to the other three periods: D32-D90, D32-D120 and D32-D160. This suggests that high energy consumption from milk during the early pre-weaning period is crucial to maintain high daily gains and therefore to achieve a high weaning weight. This is because during the early pre-weaning period, nutrient intake from milk represents a greater proportion of the diet (Bailey and Lawson, 1981) compared to the diet at weaning where pasture intake is necessary to maintain a desirable rate of gain (Richardson et al., 1978, Bartle et al., 1984). Indeed, Bailey and Lawson (1981), demonstrated that milk supplied 86% of the total digestible energy requirements for 44 day-old Angus calves, but only 19% at weaning. In the experiment reported here, energy intake from milk supplied 62% of total ME requirements in AA-reared steers at D32 and this decreased towards weaning to around 30%. Milk energy intake in AF-, AJ- and AK-reared steers supplied 74% of total ME requirements at D32 but only 47% at weaning.

There is evidence that if adequate forage is available, calves receiving less milk during lactation may increase their forage intake to compensate for the reduced milk intake, thereby gaining similar weight to those calves under a high milk diet (Baker et al., 1976, Le Du et al., 1976, Boggs et al., 1980). Indeed, Bailey and Lawson (1981), demonstrated that calves consuming low levels of milk, still consumed a total digestible energy similar to that of calves consuming high levels of milk, with this additional digestible energy coming from increased pasture consumption. In the experiment reported in this Chapter, pasture availability was not limiting throughout the lactation period. The theoretical energy intake from pasture of AA-reared steers increased more rapidly towards weaning than for AF-, AJ- and AK-reared steers and was higher compared to AJ-reared steers. In contrast to Baker et al. (1976) and Le Du et al. (1976), this increased pasture consumption of AA-reared steers was not enough to supply enough nutrients to achieve high weaning weights. More research is needed to determine how forage consumption of the cow-calf pair may be affected the fluctuation in pasture availability and the consequences in weaning weight.

Steers that were reared by dams with higher milk potential (ie. AF, AJ and AK cows) compared to the AA cows were able to maintain the liveweight differences seen at weaning (D160) until D270. These differences in D270 liveweight were mainly due to differences in total milk intake from D32 to D160. This is similar to the results of Clutter and Nielsen (1987) where progeny of high producing dams maintained 63% of the advantage in weaning weight through the post-weaning period. At D365, differences in live weight among AA-, AF- and AK-reared steers were less apparent, although a major proportion of the liveweight differences between AF- and AA-reared steers were due to differences in milk consumption. It should be noted that the greater nutrient requirements of the AF-reared steers necessitated increased nutrient intake to achieve a yearling weight greater than the AA-reared steers, and this would need to be taken into account when evaluating their use on hill country beef farms.

The AJ-reared steers, whilst not significantly different in live weight from AA-reared steers at D365, were lighter than AF- and AK-reared steers. Despite balancing the different genotypes across the nutritional treatments that steers were exposed to during winter, the introduction of these nutritional treatments may have obscured changes in live weight between steer genotypes beyond 270 days of age and additional research would be required to determine the longer-term effects of total milk intake on yearling weight.

3.5. Conclusion

Results from this experiment confirmed the hypothesis than increased maternal milk production is associated with increased calf weaning weights. Under a non-limiting pasture quality and availability, steers reared by AF, AJ and AK cows consumed more milk and consequently, gain more weight from birth to weaning compared to steers reared by AA cows. The advantage in steer live weight due to increased milk intake seen at weaning was maintained until D270. In this experiment, the increased pasture consumption seen in AA-reared steers was not sufficient to support high daily gains throughout the pre-weaning period, resulting in lower daily gains and lower live weight from birth until D270 compared to steers reared by high-producing crossbred cows. This is of particular importance for beef cattle enterprises where calves are sold as weaners rather than later in life.

Chapter 4. General Discussion

4.1. Summary of findings

Estimation of the lactation curves of crossbred cows (AF, AJ and AK) and straightbred AA cows using a random regression methodology provided evidence of differences in daily and total milk production between the different genotypes used in this study. Additionally, it provided the necessary information to compare the shape of milk production curves between genotypes. Average daily milk production from crossbred cows (AF, AJ and AK) was higher compared with straightbred AA cows, and it was demonstrated that crossbred cows produced greater total milk yield over the entire lactation period. There was also evidence of greater persistence in milk yield from crossbred cows compared to straightbred AA cows. Early in the lactation, milk production from crossbred dams provided enough nutrients to support high daily liveweight gains of their steer calves. As steers aged and their requirements for growth increased, milk yield from the crossbred dams also increased to a peak at about D74 and was maintained at reasonably similar levels until about D120. On the contrary, peak lactation in AA cows was reached early in the second month of lactation at a lower level than for the crossbred cows. Milk consumption during this period was not sufficient to support high daily gains in AA-reared steers and consequently, despite calves having similar birth weights (Law et al., 2013), differences in live weight became apparent at D60. Milk yield in AA cows decreased toward mid-lactation and was maintained at a similar level until approximately D115 but decreased drastically towards weaning (D160). Increased estimated pasture consumption in AA-reared steers indicates that they were compensating for the low nutrient intake from milk by consuming more pasture; however, this was not enough to sustain a constant high growth rate until weaning, resulting in AA-reared steers being lighter than AF-, AJ-, and AK-reared steers.

Increased milk production was associated with a lower BCS in the cows used in the present study (Law et al., 2013). This was somewhat expected because crossbreed cows should partition available nutrients to milk production rather than maintenance of body fat stores, more so than AA cows. However, the feeding level in this experiment was adequate not only to maintain lactation of high-producing crossbreds but also to maintain an average BCS of 5 on a 1 to 10 scale, at the end of lactation.

4.2. Potential limitations of the current study

The WSW technique is the most suitable and cost-effective method to determine calf milk intake and by assumption, the milk production of beef cows under pastoral conditions. However, the major disadvantage of this technique can be seen in early lactation when milk production exceeds calf appetite, typically resulting in underestimation of milk yield and low correlations between early lactation milk production and calf growth. In the experiment reported here, when completing the first WSW procedure in early lactation (at approximately D16) it was apparent that the procedure was challenging to both the calves and their dams. Dams were observed as being agitated and refusing to allow calves to suckle normally, and calves themselves were observed as refusing to suckle when reunited with their dams, thereby requiring measurement periods to be restarted in some cases. This led to unreliable milk intake data that was not included in later analysis. Indeed, Oftedal (1984) stated that WSW measurements taken during a period of stress may be of any questionable biological usefulness when extrapolated to the field. The cow-calf pairs used in the present experiment appeared to become less stressed and more cooperative as they became accustomed to the yards and the WSW measurement procedures. Hence, it may be advantageous to consider a period of acclimatization of the cow-calf pair to the WSW procedures and handling prior to the first measurement.

The general method for random regression models consists of fitting an average lactation curve for a subpopulation of animals and to describe an animal specific curve based on the deviation from the average curve (Bohmanova et al., 2008). Legendre polynomials have replaced parametric or lactational functions such as Ali and Schaeffer (1987) and Wilmink (1987) because by being orthogonal have better convergence properties but also because the former models have been unable to properly model peak lactation in the resulting lactation curves (Schaeffer, 2004). In the study reported here, the random regression methodology used to predict lactation and growth curves was effective in predicting the variance between animals in a population and within animals of a particular genotype. The use of a random regression model in the present study, in the absence of other lactational models did not allow any comparison of goodness of fit results. It may be of value for future research to compare between random regression models using different parametric, lactational or piecewise (ie. splines) functions to perhaps better predict the lactation characteristics of beef cattle.

The results reported in this study showed that a significant proportion of the weight advantage seen at weaning (D160) in steers reared by crossbred cows was due to increased milk consumption during this period, and this advantage was maintained until D270 post-weaning. This live weight advantage due to increase milk consumption is no longer apparent at D365, although, that was not the case for AF-reared steers where a great proportion of the increased live weight at weaning compared to AA-reared steers were due to differences in milk consumption early in life. Further research would be required to clarify the post-weaning persistency of the advantage in live weight at weaning. The results from this research indicate that increased milk production arising from crossbreeding between dairy and beef genotypes may be desirable if calves are sold as weaners or soon after weaning (ie. D270). Further research is needed to identify differences in carcass composition and quality grade between steers than were reared by AA, AF, AJ and AK cows.

4.3. Future studies

Rainfall and forage availability can be highly variable across New Zealand and often, beef cows have a complementary role in mixed sheep and beef livestock farming systems. Beef cows in these systems are required to be highly productive under potentially limited pasture supply. In this study, the level of nutrition was not limiting and it may be of value to investigate the lactational performance of crossbreds under limited feed supply. Additionally, research also indicates that increased milk production may be detrimental to subsequent reproductive performance (Deutscher and Whiteman, 1971). Thus, investigation of the interaction between nutrient intake, milk production and the rebreeding performance of crossbreds would be of interest to determine how crossbred cows would respond to varying levels of pasture intake and/or quality during lactation, especially during the pre-mating period in regards to their lactational performance and growth of their offspring, and their subsequent reproductive performance.

4.4. Conclusions and implications

The experiments reported here demonstrate that under non-limiting nutrient availability, AF, AJ and AK cows are able to produce more milk than AA cows. This increased milk production allowed AF, AJ and AK cows to wean heavier steers when compared to steers reared by straightbred AA cows, however, this may be done at the expense of body condition (Law et al., 2013).

Results reported here also suggest that when designing a sampling scheme for the WSW technique care must be taken in the first month of lactation to avoid collection of unreliable milk yield estimates. It may be beneficial to perform a series of sequential measurements (ie, sample on D16 and again on D17) or a series of multiple measurements with shorter separation periods over a 24h period (ie, 2 measurements each with a separation period of only 8h, rather than a single measurement with a separation of 12h) in the first month of lactation to validate the data collected. This would allow better estimation of calf consumption during this early lactation period and using shorter separation periods for the first WSW measurements may facilitate more natural cow-calf suckling behaviour thus alleviating problems associated with agitated cows and reluctant calves. Additionally, frequent WSW measurements under grazing conditions are often not feasible due to the laborious practices involved in the technique and consequently the sampling scheme needs to be strategically designed to take the minimum number of samples that best represent the different stages of lactation and lead to good predictions of total milk yield. The present study took samples at both D32 and D49, however, results indicated that the D49 measurement was more highly correlated to total milk yield. This suggests that the D32 sample could be removed from the sampling scheme without significantly impacting the results of the study, thereby reducing the number of sampling events required.

Collectively the results reported in this thesis suggest that inclusion of dairy breeds in beef cattle crossbreeding programs may be a means by which producers can increased the milk production potential of their beef herd, thereby potentially increasing calf weaning weights and ultimately, increasing the economic return of the cow-calf operation. The economic value of milk is likely to decline beyond 270 days of age as liveweight differences become less apparent, therefore, consideration is required at the individual farm level.

References

ADLER, J., LINN, L. & MOORE, A. U. 1958. Pushing in cattle: its relation to instinctive grasping in humans. *Animal Behaviour,* 1**,** 85-86.

AHUNU, B. & MAKARECHIAN, M. 1987. Preweaning patterns of growth in three breed groups of range beef calves. *Canadian Journal of Animal Science,* 67**,** 653-661.

ALI, T. E. & SCHAEFFER, L. R. 1987. Accounting for covariances among test day milk yields in dairy cows. *Canadian Journal of Animal Science,* 67**,** 637-644.

ANDERSON, W. J. 1977. *Influence of plane of nutrition on the productivity of Angus heifers*. M.Sc.. Massey University.

ANSOTEGUI, R. P., HAVSTAD, K. M., WALLACE, J. D. & HALLFORD, D. M. 1991. Effects of milk intake on forage intake and performance of suckling range calves. *Journal of Animal Science,* 69**,** 899-904.

ANTHONY, W. B., PARKS, P. F., MAYTON, E. L., BROWN, L. V., STARLING, J. G. & PATTERSON, T. B. 1959. A new technique for securing milk production data for beef cows nursing calves in nutrition studies. *Journal of Animal Science,* 18**,** 1541(Abstr.).

ARTHUR, P. F., HEARNSHAW, H., BARLOW, J., WILLIAMSON, P. J., STEPHENSON, P. D. & DIBLEY, K. 1997. Evaluation of Hereford and first-cross cows on three pasture systems. III. Milk yield and its influence on calf performance. *Journal of Agricultural Science,* 129**,** 91-98.

AUCHTUNG, T. L., BAER, D. J., ERDMAN, R. A., BARAO, S. M. & DAHL, G. E. 2002. Relation of growth hormone response to growth hormone-releasing hormone to estimation of milk production via deuterium oxide dilution in beef cattle. *Journal of Animal Science,* 80**,** 1270-1274.

BAILEY, C. B. & LAWSON, J. E. 1981. Estimated water and forage intake in nursing beef calves. *Canadian Journal of Animal Science,* 61**,** 415-421.

BAKER, B. L., CARTER, A. H. & MULLER, J. P. 1981. Performance of crossbreds cows in the Ruakura beef breed evaluation trial. *Proceedings of the New Zealand Society of Animal Production,* 41**,** 254-266.

BAKER, J. F. 1997. Evaluation of maternl EPD selection line, weaning weights and measured milk production in first lactation Angus cows. *Journal of Animal Science,* 75 (Suppl. 1)**,** 148 (Abstr).

BAKER, R. D., LE DU, Y. L. P. & BARKET, J. M. 1976. Milk-fed calves. 1. The effect of milk intake upon the herbage intake and performance of grazing calves. *Journal of Agricultural Science,* 87**,** 187-196.

BAKER, R. L., CARTER, A. H., MORRIS, C. A. & JOHNSON, D. L. 1990. Evaluation of eleven cattle breeds for crossbred beef production: Performance of progeny up to 13 months of age. *Proceedings of the New Zealand Society of Animal Production,* 50**,** 63-77.

BARTLE, S. J., MALES, J. R. & PRESTON, R. L. 1984. Effect of energy intake on the portpartum interval in beef cows and the adequacy of the cow's milk production for calf growth. *Journal of Animal Science,* 58**,** 1068-1074.

BARTON, R. A. 1970a. Dairy Beef Production .1. Prospects Are Bright. *New Zealand Journal of Agriculture,* 121**,** 20-&.

BARTON, R. A. 1970b. The yield and composition of milk of suckled beef cows and their relation to calf liveweight gains. *In:* CAMPBELL, A. G. (ed.) *New Zealand beef production, processing and marketing.* Petone: New Zealand Institute of Agricultural Science (Inc.).

BEAL, W. E., NOTTER, D. R. & AKERS, R. M. 1990. Techniques for estimation of milk-yield in beef cows and relationships of milk yield to calf weight gain and postpartum reproduction. *Journal of Animal Science,* 68**,** 937-943.

BELCHER, C. G. & FRAHM, R. R. 1979. Productivity of two-year-old cows producing three-breed cross calves. *Journal of Animal Science,* 49**,** 1195-1206.

BELCHER, C. G., FRAHM, R. R., BELCHER, D. R. & BENNET, E. N. 1979. Comparison of lactational performance among various four-year-old crossbred cow groups. *Animal Science Research Report* Oklahoma: Oklahoma Agricultural Experimental Station.

BLAXTER, K. L. 1961. Lactation and the growth of the young. *In*: KON, S. K. & COWIE, A. T. (eds.) Milk: the mammary gland and its secretion. New York: Academic Press.

BOGGS, D. L., SMITH, E. F., SCHALLES, R. R., BRENT, B. E., CORAH, L. R. & PRUITT, R. J. 1980. Effects of milk and forage intake on calf performance. *Journal of Animal Science,* 51**,** 550-553.

BOHMANOVA, J., MIGLIOR, F., JAMROSIK, J., MISZTAL, I. & SULLIVAN, P. G. 2008. Comparison of random regression models with Legendre polynomials and linear splines for production traits and somatic cell score of Canadian Holstein cows. *Journal of Dairy Science,* 91**,** 3627-3638.

BROWN, M. A., BROWN, A. H., JACKSON, W. G. & MIESNER, J. R. 1996. Milk production in Angus, Brahman, and reciprocal-cross cows grazing common bermudagrass or endophyte-infected tall fescue. *Journal of Animal Science,* 74**,** 2058-2066.

BUTSON, S., BERG, R. T. & HARDIN, R. T. 1980. Factors influencing weaning weights of range beef and dairy-beef calves. *Canadian Journal of Animal Science,* 60.

CAMERON, E. Z. 1998. Is suckling behaviour a useful predictor of milk intake? A review. *Animal Behaviour,* 56**,** 521-532.

CARPENTER, J. A., FITZHUGH, T. C., CARTWRIGHT, T. C. & THOMAS, R. C. 1972. Relationships between calf performance and mature size of beef cows. *Program Report.* Texas Agricultural Experimental Station.

CHENETTE, C. G. & FRAHM, R. R. 1981. Yield and composition of milk from various two-breed cross cows. *Journal of Animal Science,* 52**,** 483-492.

CLUTTER, A. C. & NIELSEN, M. K. 1987. Effect of level of beef cow milk-production on preweaning and postweaning calf growth. *Journal of Animal Science,* 64**,** 1313-1322.

CLUTTON-BROCK, T. H. 1991. *The evolution of parental care.*, Princetone, New Jersey, Princetone University Press. 368 pp.

COBB, A. B., FRAHM, R. R. & BOYD, M. E. 1978. Lactation performance of Hereford and Angus cows. *Journal of Animal Science,* 47 (Supple. 1)**,** 67 (Abstr.).

COLE, L. J. & JOHANSSON, I. 1933. The yield and composition of milk from Aberdeen-Angus cows. *Journal of Dairy Science,* 16**,** 565-580.

COWARD, W. A., COLE, T. J., GERBER, H., ROBERTS, S. B. & FLEET, I. 1982. Water turnover and the measurement of milk intake. *Pflugers Archiv-European Journal of Physiology,* 393**,** 344-347.

CUNDIFF, L. V. 2007. Cattle breed evaluation at the U.S. Meat Animal Research Centre and implications for commercial beef farmers. *Proceeding of the New Zealand Society of Animal Production,* 67**,** 9-17.

DALEY, D. R., MCCUSKEY, A. & BAILEY, C. M. 1987. Composition and yield of milk from beef-type *bos taurus* and *bos indicus* x *bos tarus* dams. Journal of Animal Science, 64, 373.-383.

DAWSON, W. M., COOK, A. C. & KNAPP, B. 1960. Milk production of beef shorthorn cows. *Journal of Animal Science,* 19**,** 502-508.

DENAMUR, R. 1965. The hypothalamo-neurohypophysial system and the milk ejection reflex. *Dairy Science Abstracts,* 27**,** 193 (Abstr.).

DEUTSCHER, G. H. & WHITEMAN, J. V. 1971. Productivity as two-year-olds of Angus-Holstein crossbreds compared to Angus heifers under range condition. *Journal of Animal Sience,* 33**,** 337-342.

DIAZ, C., NOTTER, D. R. & BEAL, W. E. 1992. Relationship between milk expected progeny differences of Polled Hereford sires and actual milk production of their crossbreds dughters. *Journal of Animal Science,* 70**,** 396-402.

DOVE, H. & AXELSEN, A. 1979. Estimation of milk consumption in beef-calves using a tritiated-water dilution technique. *Australian Journal of Experimental Agriculture,* 19**,** 666-672.

DOVE, H. & FREER, M. 1979. Accuracy of tritiated-water turnover rate as an estimate of milk intake in lambs. *Australian Journal of Agricultural Research,* 30**,** 725-739.

DREWRY, K. J., BROWN, C. J. & HONEA, R. S. 1959. Relationships among factors associated with mothering ability in beef cattle. *Journal of Animal Science,* 18**,** 938-946.

FISS, C. F. & WILTON, J. W. 1992. Contribution of breed, cow weight, and milk yield to the traits of heifers and cows in four beef breeding systems. *Journal of Animal Science,* 70**,** 3686-3696.

FLETCHER, I. C. 1971. Relationships between frequency of suckling, lamb growth and post-partum oestrous behaviour in ewes. *Animal Behaviour,* 19**,** 108-111.

FRANKE, D. E., BURNS, W. C., & KOGER, M. 1975. Milk yield and preweaning growth in beef cattle. *Journal of Animal Science,* 41**,** 267 (Abstr.).

FREER, M., DOVE, H. & NOLAN, J. V. 2007. *Nutrient requirements of domesticated ruminants,* Melbourne, CSIRO Publishing. 270 pp.

FURR, R. D. 1962. *Effect of different levels of supplemental winter feed upon the production of fall-calving beef cows.* Ph.D., Oklahoma State University.

GASKINS, C. T. & ANDERSON, D. C. 1980. Comparison of lactation curves in Angus-Hereford, Jersey-Angus and Simmental-Angus cows. *Journal of Animal Science,* 50**,** 828-832.

GIFFORD, W. 1949. Importance of high milk production in beef cows found over-estimated. *Journal of Animal Science,* 8**,** 605-606.

GIFFORD, W. 1953. Records of performance tests for beef cattle in breeding herds. Milk production of dams and growth of calves. *Arkansas Agricultural Experimental Station Bulletins***,** 531.

GLEDDIE, V. M. & BERG, R. T. 1968. Milk production in range beef cows and its relationship to calf gains. *Canadian Journal of Animal Science,* 48**,** 323-333.

GOWEN, J. W. 1918. Studies in inheritance of certain characters of crosses between dairy and beef breeds of cattle. *Journal of Agricultural Research,* 15**,** 1-58.

GOWEN, J. W. 1920. Inheritance on crosses of dairy and beef breeds of cattle. *Journal of Heredity,* 11**,** 365-377.

GREENWOOD, P. L. & CAFE, L. M. 2007. Prenatal and pre-weaning growth and nutrition of cattle: long-term consequences for beef production. *Animal,* 1**,** 1283-1296.

GRINGS, E. E., ROBERTS, A. J., GEARY, T. W. & MACNEIL, M. D. 2007. Milk yield of primiparous beef cows from three calving systems and varied weaning ages. *Journal of Animal Science,* 86**,** 768-779.

HENDRIX, K. S. 1971. *A study of methods for estimating milk production in range beef cows and factors associated with the milk production estimate*. M.S. , Oklahoma State University.

HICKSON, R. E., KENYON, P. R., LOPEZ-VILLALOBOS, N. & MORRIS, S. T. 2008. Effects of liveweight gain during pregnancy of 15-month-old Angus heifers on dystocia and birth weight, body dimensions, estimated milk intake and weaning weight of the calves. *New Zealand Journal of Agricultural Research,* 51**,** 171-180.

HICKSON, R. E., KENYON, P. R., LOPEZ-VILLALOBOS, N. & MORRIS, S. T. 2009a. Effects of liveweight gain of 15-month-old Angus heifers during the first trimester of pregnancy on liveweight and milk intake of their calves. *New Zealand Journal of Agricultural Research,* 52**,** 39-46.

HICKSON, R. E., LOPEZ-VILLALOBOS, N., KENYON, P. R. & MORRIS, S. T. 2009b. Effect of liveweight gain of pregnant 15-month-old Angus heifers on the milk intake of their first calves and the liveweight of their first and second calves. *Animal Production Science,* 49**,** 112-120.

HICKSON, R. E., LAVEN, R. L., LOPEZ-VILLALOBOS, N., KENYON, P. R. & MORRIS, S. T. 2012. Postpartum anoestrous interval in first-lactation beef and dairy-beef crossbred cows. *Animal Production Science,* 52**,** 478-482.

HOHENBOKEN, W. D., DUDLEY, A. & MOODY, D. E. 1992. A comparison among equations to characterize lactation curves in beef cows. *Animal Production,* 55**,** 23-28.

HOLLEMAN, D. F., LUICK, J. R. & WHITE, R. G. 1971. Transfer of radiocesium in milk from reindeer cow to calf. *In:* NELSON, D. J. (ed.) *Proceedings of the 3rd National Symposium of Radioecology*. Oak Ridge, TN.

HOLLEMAN, D. F., WHITE, R. G. & LUICK, J. R. 1975. New Isotope Methods for Estimating Milk Intake and Yield. *Journal of Dairy Science,* 58**,** 1814-1821.

HOLLOWAY, J. W. & WORLEY, T. L. 1983. Pattern of milk intake as related to weaning traits of Angus calves grazing fescue-legume or fescue pastures. *Livestock Production Science,* 10**,** 351-364.

HOLLOWAY, J. W., BUTTS, J., W. T., MCCURLEY, J. R., BEAVER, E. E., PEELER, H. L. & BACKUS, W. L. 1985. Breed × nutritional environment interactions for beef female weight and fatness, milk production and calf growth. *Journal of Animal Science,* 61**,** 1354-1363.

HOLMES, C. W., BROOKES, I. M., GARRICK, D. J., MACKENSIE, D. D. S., PARKINSON, T. J. & WILSON, G. F. 2002. *Milk production from pasture: principles and practices,* Palmerston North, Massey University.

HOWARD, B. & MACFARLANE, W. V. 1967. Use of tritiated water in estimating milk intake and efficiency of growth processes in sheep at pasture. *Australian Journal of Experimental Biology and Medical Science,* 45**,** P11 (Abstr.).

JEFFERY, H. B., BERG, R. T. & HARDIN, R. T. 1971. Factors affecting preweaning performance in beef calves. *Canadian Journal of Animal Science* 51**,** 561-577.

JENKINS, T. G. & FERRELL, C. L. 1984. A note on lactation curves of crossbred cows. *Animal Production,* 39**,** 479-482.

JONES, S.D.M., WILTON, J. W. & SONG, H. 1982. The effect of cow size, milk yield and cow fatness on the carcass characteristics and meat quality of their progeny. *Canadian Institute of Food Science and Technology Journal* 15**,** 170-173.

JOHNSON, C. R., LALMAN, D. L., APPEDDU, L. A., BROWN, M. A., WETTEMANN, R. P. & BUCHANAN, D. S. 2002. *Effect of parity and milk production potential on forage intake of beef cows during late gestation.* [Online]. TEKRAN United States Department of Agriculture, Agricultural Research Services.

KLETT, R. H., MASON, T. R. & RIGGS, J. K. 1962. Preliminary studies on milk production of beef cows. Miscelaneous Publication, 591:79.

KNAPP, B. & BLACK, W. H. 1941. Factors influencing rate of gain of beef calves during the suckling period. *Journal of Agricultural Research,* 63**,** 249-254.

KOCH, R. M. 1972. The role of maternal effects in animal breeding: VI. Maternal efects in beef cattle. *Journal of Animal Science,* 35**,** 1316-1323.

KROPP, J. R., STEPHENS, D. F., HOLLOWAY, J. W., WHITEMAN, J. V., KNORI, L. & TOTUSEK, R. 1973. Performance on range and drylot of two-year-old Hereford,

Hereford x Holstein and Holstein females as influenced by level of winter supplementation. *Journal of Animal Science,* 37**,** 1222-1232.

LAMOND, D. R., HOLMES, J. H. G. & HAYDOCK, K. P. 1969. Estimation of yield and composition of milk produced by grazing beef cows. *Journal of Animal Science,* 29**,** 606-611.

LAMPKIN, G. H., HOWARD, D. A. & BURDIN, M. L. 1961. Studies on Production of Beef from Zebu Cattle in East Africa .3. Value of Feeding a Phosphatic Supplement. *Journal of Agricultural Science,* 57**,** 39-47.

LANDETE-CASTILLEJOS, T. & GALLEGO, L. 2000. Technical note: The ability of mathematical models to describe the shape of lactation curves. *Journal of Animal Science,* 78**,** 3010-3013.

LASCELLES, A. K. & LEE, C. S. 1978. Involution of the mammary gland. *In:* LARSON, B. L. (ed.) *Lactation: A comprehensive treatise.* New York, NY: Academic Press.

LAW, N. L., HICKSON, R. E., LOPEZ-VILLALOBOS, N., KENYON, P. R. & MORRIS, S. T. 2013. Efficiency of beef breeding cows that vary in live weight and milk potential. *Proceedings of the New Zealand Society of Animal Production,*73**,** 11-16.

LE DU, Y. L. P., BAKER, R. D. & BARKER, J. M. 1976. Milk-fed calves. 2.The effect of length of milk feeding period and milk intake upon herbage intake and performance of grazing calves. *Journal of Agricultural Science,* 87**,** 197-204.

LE DU, Y. L. P., MACDONALD, A. J. & PEART, J. N. 1979. Comparison of 2 techniques for estimating the milk-production of suckler cows. *Livestock Production Science,* 6**,** 277-281.

LEWIS, J. M , KLOPFENSTEIN, T. J., STOCK,, R. A. & NIELSEN, M. K. 1990. Evaluation of intensive vs extensive systems of beef production and the effect of level of beef cow milk production on postweaning performance. *Journal of Agricultural Science,* 68**,** 2517-2524.

LIDFORS, L. M., JENSEN, P. & ALGERS, B. 1994. Suckling in free-ranging beef-cattle - temporal patterning of suckling bouts and effects of age and sex. *Ethology,* 98**,** 321-332.

LINDHOLN, H. B. & STONAKER, H. H. 1957. Economic importance of traits and selection indexes for beef cattle. *Journal of Animal Science,* 16**,** 998-1006.

MACFARLANE, W. V., HOWARD, B. & SIEBERT, B. D. 1969. Tritiated water in measurement of milk intake and tissue growth of ruminants in the field. *Nature,* 221**,** 578-579.

MALLINCKRODT, C. H., BOURDON, R. M., GORDON, B. L., SHALLES, R. R. & ODDE, K. G. 1993. Relationship of milk expected progeny differences to actual milk production and calf weaning weight. *Journal of Animal Science,* 71**,** 355-362.

MARSHALL, D. M. & LONG, M. B. 1993. Relationship of beef sire expected progeny difference to maternal performance of crossbred daughters. *Journal of Animal Science,* 71**,** 2371-2374.

MARSTON, T. T., SIMMS, D. D., SCHALLES, R. R., CLARKE, L. S. & ZOELLNER, K. O. 1989. Relationship of milk expected progeny differences to total milk production and calf weaning weight. *Journal of Animal Science,* 67 (Suppl. 1)**,** 466-467 (Abstr.).

MARSTON, T. T., SIMMS, D. D., SCHALLES, R. R., ZOELLNER, K. O. & MARTIN, L. C. 1990. Relationship of milk expected progeny difference to total milk production and calf weaning weight in Angus and Simmental cows. *Journal of Animal Science,* 68 (Suppl. 1)**,** 488 (Abstr.).

MARSTON, T. T., SIMMS, D. D., SCHALLES, R. R., ZOELLNER, K. O., MARTIN, L. C. & FINK, G. M. 1992. Relationship of milk production, milk expected progeny difference, and calf weaning weight in angus and simmental cow-calf pairs. *Journal of Animal Science,* 70**,** 3304-3310.

MARTIN, S. E. & FRANKE, D. E. 1982. Milk yields, composition and production effects in straighbred and crossbred beef cows. *Journal of Animal Science,* 55 (Suppl.)**,** 3 (Abstr.).

MASILO, B. S., STEVENSON, J. S., SCHALLES, R. R. & SHIRLEY, J. E. 1992. Influence of genotype and yield and composition of milk on interval to first postpartum ovulation in milked beef and dairy cows. *Journal of Animal Science,* 70**,** 379-85.

MCCANCE, I. 1959. The determination of milk yield in the merino ewe. *Australian Journal of Agricultural Research,* 10**,** 839-853.

MCEWAN, E. H. & WHITEHEAD, P. E. 1971. Measurement of milk intake of reindeer and caribou calves using tritiated water. *Canadian Journal of Zoology,* 49**,** 443-447.

MELTON, A. A., CARTWRIGHT, T. C. & NELSON, L. A. 1967. Milk production, composition and calf gains in Angus, Charolais and Hereford cows. *Journal of Animal Science,* 26**,** 804-809.

MEYER, K., CARRICK, M. J. & DONNELLY, B. J. P. 1994. Genetic parameters for milk production of Australian beef cows and weaning weight of their calves. *Journal of Animal Science,* 72**,** 1155-1165.

MILLER, S.P., WILTON, J. W. & PFEIFFER, W. C. 1999. Effects of milk yield on biological efficiency and profit of beef production from birth to slaughter. *Journal of Animal Science,* 77**,** 344-352.

MINICK, J. A., BUCHANAN, D. S. & RUPERT, S. D. 2001. Milk production of crossbred daughters of high- and low-milk EPD Angus and Hereford bulls. *Journal of Animal Science,* 79**,** 1386-1393.

MONDRAGON, I., WILTON, J. W., ALLEN, O. B. & SONG, H. 1983. Stage of lactation effects, repeatabilities and influences on weaning weights of yield and composition of milk in beef cattle. *Canadian Journal of Animal Science,* 63**,** 751-761.

MONTAÑO-BERMUDEZ, M., NIELSEN, M. K. & DEUTSCHER, G. H. 1990. Energy requirements for maintenance of crossbred beef cattle with different genetic potential for milk. *Journal of Animal Science,* 68**,** 2279-2288.

MONTAÑO-BERMUDEZ, M & NIELSEN, M. K. 1990. Biological efficiency to weaning and to slaughter of crossbred beef cattle with different genetic potential for milk. *Journal of Animal Science,* 68**,** 2297-2309.

MORRIS, C. A., BAKER, B. L. & BENNET, G. L. 1986. Some genetic and non-genetic efects on the first oestrous and pregnancy rates of beef heifers. *Proceeding of the New Zealand Society of Animal Production,* 46**,** 71-75.

MORRIS, C. A., BAKER, B. L., HICKEY, S. M., JOHNSON, D. L., CULLEN, N. G. & WILSON, J. A. 1993a. Genetic analysis of cow lifetime production up to 12 mating years in crossbred beef cattle. *Animal Production,* 57**,** 29-36.

MORRIS, C. A., BAKER, R. L., HICKEY, S. M., JOHNSON, D. L., CULLEN, N. G. & WILSON, J. A. 1993b. Evidence of genotype by enviroment interaction for reproductive and maternal traits in beef cattle. *Animal Production* 56**,** 69-83.

MORRIS, S. T. 2008. A review of beef cross dairy bred cattle as breeding cows. Unpublished review for Beef&Lamb, NZ.

MORRIS, S. T., BROOKES, I. M., PARKER, W. J. & MCCUTCHEON, S. N. 1994. Biological efficiency: how relevant is this concept to beef cows in a mixed livestock seasonal pasture supply context? *Proceeding of the New Zealand Society of Animal Production,* 54**,** 333-336.

NELSON, L. A., MARTIN, T.G. & SANDHAGE, C. J. 1985. Influence of breeding system and breed type of cow on milk yield and calf weaning weight. Indiana Agricultural Experimental Station. Indian Beef Report. 15-17.

NEVILLE, M. C. 1998. *Oxytocin and milk ejection* [Online]. Available: http://mammary.nih.gov/reviews/lactation/Neville002/index.html [Accessed 12 March 2012].

NEVILLE, W. E. 1962. Influence of dams milk production and other factors on 120-day weight and 240-day weight of Hereford calves. *Journal of Animal Science,* 21**,** 315-320.

NICOL, A. M. & BROOKES, I. M. 2007 The metabolisable energy requirements of grazing livestock. *In:* RATTRAY, P. V., BROOKES, I. M. & NICOL, A. M. (eds.) *Pasture and supplements for grazing animals.* Hamilton, New Zealand: New Zealand Society of Animal Production.

NICOL, A. M. & IRVINE, C. H. G. 1973. Measurement of the milk consumption of suckling beef calves by an isotope dilution method. *Proceeding of the New Zealand Society of Animal Production,* 33**,** 176-183.

NICOL, A. M. & SHARAFELDIN, M. A. 1975. Observation of the behaviour of single-suckled calves from birth to 120 days. *Proceeding of the New Zealand Society of Animal Production,* 35**,** 221-230.

NICOL, A. M. 1976. The influence of breed of calf on the milk production of beef cows. *Proceeding of the New Zealand Society of Animal Production,* 36.

NICOLL, G. B., HIGHT, G. K. & EVERITT, G. C. 1978. Some components of improved beef cow productivity on hill country. *Proceeding of the New Zealand Society of Animal Production,* 38**,** 151-160.

OFTEDAL, O. T. 1981. *Milk, protein and energy intakes of suckling mammalian young: a comparative study.* Ph.D., Cornell University.

OFTEDAL, O. T. 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symposia of the Zoological Society of London,* 51**,** 33-85.

PATERNOSTER, R., BRAME, R., MAZEROLLE, P. & PIQUERO, A. 1998. Using the correct statistical test for the equality of regression coefficients. *Criminology,* 36**,** 859-866.

PETERSON, S. W., JENKINSON, C. M. C., HICKSON, R. E., MORRIS, S. T., BLAIR, H. & KENYON, P. R. 2010. Preliminary investigation of milk production in Angus heifers exposed to different nutrition *in utero. Proceeding of the New Zealand Society of Animal Production,* 70**,** 194-198.

PINSON, E. A. 1952. Water exchanges and barriers as studied by the use of hydrogen isotopes. *Physiological Reviews,* 32**,** 123-134.

POOL, M. H., JANSS, L. L. G. & MEUWISSEN, T. H. E. 2000. Genetic parameters of Legendre Polynomials for first parity lactation curves. *Journal of Dairy Science,* 83**,** 2640-2649.

POPE, L. S., SMITHSON, L., STEPHEN, D. F., PINNEY, D. O. & VELASCO, M. 1963. Factors affecting milk production of range beef cows. *Miscelaneous publication.* Oklahoma Agricultural experimental station.

REYNOLDS, W. L., DEROUEN, T. M. & BELLOWS, R. A. 1978. Relationship of milk yield of dam to early growth rate of straighbred and crossbred calves. *Journal of Animal Science,* 47**,** 584-594.

RICHARDSON, F. D., OLIVER, J. & CLARKE, G. P. 1978. The pre-weaning and post-weaning growth of beef calves in relation to the amounts of milk and solid food consumed during the suckling period. *Rhodesian Journal of Agricultural Research,* 16**,** 97-108.

ROBINSON, O. W., YUSUFF, M. K. M. & DILLARD, E. U. 1978. Milk production in Hereford cows I. Means and correlations. *Journal of Animal Science,* 47**,** 131-136.

RUTLEDGE, J. J., ROBISON, O. W., AHLSCHWE.WT & LEGATES, J. E. 1971. Milk yield and its influence on 205-day weight of beef calves. *Journal of Animal Science,* 33**,** 563-567.

RUTLEDGE, J. J., ROBISON, O. W., AHLSCHWE.WT & LEGATES, J. E. 1972. Estimating milk yield of beef cows. *Journal of Animal Science,* 34**,** 9-13.

SACCO, R. E., BAKER, J. F. & CARTWRIGHT, T. C. 1987. Production characters of primiparous females of a five-breed diallele. *Journal of Animal Science,* 64**,** 612-1618.

SAWYER, G. J., SPEIJERS, E. J., MORRIS, R. J. & COUPAR, F. J. 1994. Characterising lactation curves in heifers of different breeds first calved in moderate or low condition. *Proceedings of the Australian Society of Animal Production,* 20**,** 128-131.

SCHAEFFER, L. R. 2004. Application of random regression models in animals breeding. *Livestock Production Science,* 86**,** 35-45.

SCHWULST, F. J., SUMPTION, L. J., SWIGER, L. A. & ARTHAUD, V. H. 1966. Use of oxytocin for estimating milk production of beef cows. *Journal of Animal Science,* 25**,** 1045-1047.

SEARLE, T.W. 1970. Body composition of lambs and young sheep and its prediction in vivo from tritiated water space and bodyweight. Journal of Agricultural Science, 74**,** 357-362.

SEKINE, J., ASAHIDA, Y. & HIROSE, Y. 1972. Water in ruminants. 1. Water consumption and water turnover in growing calves. *Journal of the Faculty of Agriculture, Hokkaido University,* 57**,** 51-60.

SIEBERT, B. D. 1971. Growth and Water Metabolism of Cows and Progeny on Fertilized and Unfertilized Tropical Pastures. *Australian Journal of Agricultural Research,* 22**,** 415-428.

SILVESTRE, A. M., PETIM-BATISTA, F. & COLACO, J. 2006. The accuracy of seven mathematical finctions in modeling dairy cattle lactation curves based on test-day records from varying sample schemes. *Journal of Dairy Science,* 89**,** 1813-1821.

SOMERVILLE, S. H. & LOWMAN, B. G. 1980. A comparison of machine-milking and the calf-suckling technique as methods of measuring the milk yield of beef cows. *Animal Production,* 30**,** 365-372.

SPRAIN, D. G., SMITH, V. R., TYLER, W. J. & FOSGATE, O. T. 1954. The effect on milk and fat production of injections of oxytocin at alternate 14-day periods during lactation. *Journal of Dairy Science,* 37**,** 195-201.

TANCIN, V. & BRUCKMAIER, R. M. 2001. Factors affecting milk ejection and removal during milking and suckling of dairy cows. *Veterinarni Medicina,* 46**,** 108-118.

TODD, J. C., RIGGS, J. K. & SMITH, J. C. 1968. Milk yields and calf weights from Brahman, Hereford and crossbreds cows in the Gulf Coast prairie. *Journal of Animal Science,* 27**,** 286 (Abstr.).

TOTUSEK, R., ARNETT, D. W., HOLLAND, G. L. & WHITEMAN, J. V. 1973. Relation of estimation method, sampling interval and milk composition to milk yield of beef cows and calf gain. *Journal of Animal Science,* 37**,** 153-158.

VELASCO, M. 1962. *Level of winter feeding on range beef cows.* M.Sc., Oklahoma State University.

WAGNON, K. A. 1963. Behaviour of beef cows on a California range.: California Agricultural Experimental Station.

WALKER, D. E. K. & POS, H. G. 1963. Milk production in beef heifers. *New Zealand Journal of Agriculture,* 107**,** 277-280.

WANG, X. Z, BROWN, M. A., GAO, F. Q., WU, J. P., LALMAN, D .L & LIU, W. J. 2009. Relationship of milk production of beef cows to postweaning gain of the calves. *The Professional Animal Scientist,* 25**,** 226-272.

WHITTEMORE, C. T. 1980. *Lactation of the dairy cow,* London ; New York, Longman.

WILLIAMS, J. H., ANDERSON, D. C. & KRESS, D. D. 1979a. Milk production in Hereford cattle .1. Effects of separation interval on weigh-suckle-weigh milk production estimates. *Journal of Animal Science,* 49**,** 1438-1442.

WILLIAMS, J. H., ANDERSON, D. C. & KRESS, D. D. 1979b. Milk production in Hereford cattle .2. Physical measurements - repeatabilities and relationships with milk production. *Journal of Animal Science,* 49**,** 1443-1448.

WILMINK, J. B. M. 1987. Adjustment of lactation yield for age at calving in relation to level of production. *Livestock Production Science,* 16**,** 335-345.

WILSON, L. L., GILLOLY, J. E., RUGH, M. C., THOMSON, C. E. & PURDY, H. R. 1968. Relation of milk and progeny growth traits of Angus x Holstein cows. *Journal of Animal Science,* 27**,** 1512(Abstr.).

WILSON, L. L., GILLOLY, J. E., RUGH, M. C., THOMSON, C. E. & PURDY, H. R. 1969. Effects of energy intake, cow body size and calf sex on composition and yield of milk by Angus-Holstein cows and pre-weaning growth rate of progeny. *Journal of Animal Science,* 28**,** 789-796.

WILTBANK, J. N. 1970. Research needs in beef cattle production. *Journal of Animal Science,* 31**,** 755-762.

WOLFF, P. H. 1968. Sucking patterns of infant mammals. *Brain Behavior and Evolution,* 1**,** 354-367.

WOODWARD, B. W., POLLAK, E. J. & QUASS, R. L. 1989. Adjusting weaning weights of Simmental calves to an age-constant basis. *Journal of Animal Science,* 67**,** 20-27.

WRIGHT, D. E., JONES, B. A. & GEENTY, K. G. 1974. Measurement of milk consumption in young ruminants using tritiated water. *Proceedings of the New Zealand Society of Animal Production,* 34**,** 145-150.

YATES, N. G., MACFARLA.W.V. & ELLIS, R. 1971. Estimation of milk intake and growth of beef calves in field by using tritiated water. *Australian Journal of Agricultural Research,* 22**,** 291-306.