

Integrating Concepts Mammary Development, Growth and Nutrient Requirements to Describe Productivity Outcomes in Dairy Heifers

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■ Take Home Messages

- Growth objectives and nutrient requirements are a function of mature body weight, thus each herd has slightly different requirements as mature weight is a phenotypic expression of both genetics and environment.
- Mammary development is positively responsive to level of nutrient intake before weaning and slows post-weaning through puberty and then accelerates once the heifer becomes pregnant.
- Mammary develop is not negatively impacted by pre-pubertal nutrition and appears to be a function of time because reproductive organs grow in proportion to the body and not in response to nutrient intake.
- The inability to achieve pregnancy by 55-60% of mature weight will generally result in heifers calving at heavier weights, likely with greater fat content, resulting in reduced milk yields in the 1st and possibly subsequent lactations.
- Body composition at calving can have a significant impact on first lactation milk yield, especially if body condition score and greater body fat make up a larger percent of the additional weight.
- Within the management system available, adhering to specific growth targets throughout the rearing period and calving as early as feasible are essential to ensure optimum economic returns during the first lactation.

■ Introduction

The growth of dairy replacement animals has several objectives: low cost, a low number of days of non-productive life, adequate body weight, appropriate body composition, and capacity for optimum milk yield over the heifers' lifetimes associated with a long productive life. The actual growth objectives are a function of several factors such as mature body weight (MBW), body weight (BW) at calving and calving age that optimizes raising cost and nutrients partitioned to growth during lactation thus allowing for optimum milk yield and a prospective decision concerning the age at first calving (Hoffman, 1996; Fox et al., 1999). The integration of those factors provides the target growth rate necessary to meet the BW goal for first parturition within the stated amount of time and this then determines the nutrient supply required daily to meet the objectives.

Overall, changes in body chemical composition are affected either by growth, or by an altered level of nutrient intake above maintenance nutrient requirements, or both, which results in dilution of empty body ash, water, and protein (CP) by fat (Reid, 1972; Garrett, 1987) because the chemical composition of the fat-free matter is largely unresponsive to BW or level of nutrient intake (Reid, 1972; Fortin et al., 1980; Garrett, 1987; Waldo et al., 1997). Furthermore, the retention rate of body CP relative to body fat decreases

with increasing BW and increasing level of nutrient intake, which limits CP composition of the empty body. Data suggest that the rate of protein synthesis becomes limiting in cattle beyond a certain energy intake and growth rate; therefore, energy not deposited as protein is deposited as fat and this breakpoint appears to be at approximately 1.0 to 1.1 kg/d gain and is most likely MBW dependent (Byers, 1982).

The current Dairy NRC (2001) recommendations for nutrient requirements of growing Holstein heifers are based largely upon a data set collected from beef breeds (Garrett, 1980). With the exception of data collected in the 1950s and 1960s (Fortin et al., 1980), little serial harvest data existed that described the composition of retained tissue in the growing Holstein heifer. Since the NRC's publication, the chemical growth of both pre-weaned and pre-pubertal Byers breed heifers has received considerable research interest (Diaz et al., 2001; 2001; Meyer, 2005; Bartlett et al., 2006; Bascom et al., 2007; Stamey et al. 2012). Further, research has been conducted to evaluate the effects of diet, nutrient intake, or both, on the composition of retained tissue between approximately 100 kg BW (Moallem et al., 2004) or 180 kg BW (Waldo et al., 1997) and puberty in Holstein heifers. The data of Waldo et al. (1997) suggested that the composition of the Holstein heifers in that study contained less body fat than previously described, possibly due to changes in MBW associated with selection for milk yield.

Further, data published over 40 years suggested that milk yield was reduced as pre-pubertal ADG increased, especially if the associated energy intake allowed for increased adipose deposition in the animal. Swanson (1960) was the first to publish data demonstrating that as energy intake increased, fat deposition increased in the heifer, milk yield was reduced and 'fatty infiltration' of the mammary gland was likely the causative factor. This observation led to much more work investigating mammary development and growth rate with the objective of understanding why high growth rate reduced mammary parenchymal development (Sejrsen et al., 1982; Peticlerc et al., 1984; Mantysaari et al., 1995). Capuco et al. (1995) and Waldo et al. (1997, 1998) were the first to quantitatively integrate body growth, mammary development and milk yield; their observations were not consistent with the previously held perspective that decreased pre-pubertal mammary development negatively impacted milk yield. However this information was largely ignored.

The goals for raising replacement heifers go beyond achieving a specific weight gain. Given that they are future dairy cows, the final goal of heifer rearing should be to optimize their future milk production potential. Body composition is directly related to growth rate, diet composition and stage of maturity at the time the growth occurred. With this in mind, it is vital to remember the effects of body condition or body composition at calving on milk yield. The effect of greater body condition on performance of dairy cattle was reported as a linear decrease in milk yield (Garnsworthy and Topps, 1982). More contemporary data have refined this observation and associated it with reduced dry matter intake (DMI); this is the focus of much research into transition cow metabolism, insulin resistance and the interaction between obesity and milk yield (Ingvarstsen and Andersen, 2000; Douglas et al. 2006; Allen et al., 2009; Overton, 2011). Thus, when evaluating the data integrating pre-pubertal growth rates, mammary development and milk yield, the composition of growth, and therefore the final body composition of the heifer at calving are essential when comparing studies related to milk production.

This paper will integrate concepts of body growth and composition, and nutrient requirements along with mammary development and first lactation milk yield to provide a systems-based approach to describe the effects of incorrect body growth on first lactation milk production that has been associated primarily with mammary development. The purpose of this review is to describe nutrient requirements and body composition and discuss how the stage of maturity and the rate of gain at each stage of physiological development can result in changes in body composition that help explain the milk yield observed in previously published studies. This information can be used to reduce total replacement raising cost and improve lactation performance by promoting growth at each stage of maturity while considering the final body composition of the animals. For a more thorough evaluation of body composition and energy and protein content of tissues over time, please see Van Amburgh et al. (2019).

■ Mammary Development and Milk Yield

Traditionally, body composition has been overlooked when analyzing the effects of pre-pubertal growth rates on first lactation performance. However, just as body composition and obesity influence the performance of mature dairy cattle, those factors are also a crucial determinant of first lactation heifer performance. As reported by Swanson (1960), when heifers were fattened and bred to calve at the same age as their non-fattened twins, the fattened heifers produced considerably less milk during their first lactation. Although the goals of that study were to compare fattened vs. non-fattened heifers and their corresponding lactation performance, the data were associated with the concept that something other than body composition was impacting the lactation performance.

Subsequently, the seminal work by Sejrsen et al. (1982; 1983) describing the effect of high energy intake on mammary development and the relationship with circulating growth hormone linked the relationship between pre-pubertal growth, mammary development, and future milk yield. The primary outcome of this work was to provide an intuitive mechanism to explain why rapid growth during the pre-pubertal phase resulted in reduced milk production in the first lactation. The observation of reduced mammary development could be repeated in almost every experiment (Pritchard et al., 1972; Petitclerc et al., 1984; Mäntysaari et al., 1995; Capuco et al., 1995; Meyer et al., 2006ab). These repeatable observations led to the conclusion that high energy intakes reduced mammary development through altered hormone status or signaling processes. However, Meyer et al. (2006ab) were the first to recognize that mammary development was not reduced by high energy intake, but instead, the time to reach puberty and the associated signals to change allometric mammary growth were altered. The mammary gland, like all other reproductive organs, grows in proportion to the size of the body and not in proportion to nutrient intake during the post-weaning, pre-pubertal phase.

To evaluate whether the time effect associated with the mammary development observed in Meyer et al. (2006ab) was similar to previous studies, the amount of mammary development (measured in milligrams of DNA accumulation per day) was determined. Meyer (2005) hypothesized that if the observation was consistent among studies, mammary development should be predictable based on days on treatment. The daily DNA accumulation from Meyer et al. (2006b) was compared to five other studies with adequate descriptions of the experimental design (Figure 1). In that comparison, a majority ($R^2=0.83$) of the difference in mammary development could be explained by time on study, suggesting that in all of these studies, energy intake hastened the time to puberty, and earlier puberty and the hormonal changes associated with puberty were responsible for the decreased mammary development.

Tissue harvest was the endpoint in most of these studies of mammary development so milk yield could not be evaluated. There are a few studies where tissue harvest and pregnancy and milk yield data were collected under similar feeding conditions to be able to measure heifers in a 'pair-fed' experimental design. The studies with direct comparisons are those of Capuco et al. (1995), Waldo et al. (1998) and Smith (2002). Other studies with similar but sequential study data are from Radcliff et al. (1997; 2000). In each of these studies, the authors observed significant changes in mammary development without significant changes in first lactation milk yield.

Capuco et al. (1995) observed a 52% decrease in mammary development at puberty in heifers fed for higher rates of pre-pubertal gain, but in the pair-fed animals, there was no significant difference in milk yield (Waldo et al., 1998). Smith (2002) fed a calcium salt of conjugated linoleic acid (Ca-CLA) and measured differences in body composition and pre-pubertal mammary development, and in pair-fed animals, measured milk yield. In this study, mammary development was reduced by approximately 60% in heifers fed Ca-CL; however, there was no significant difference in milk yield of the pair-fed heifers.

In the studies by Radcliff et al. (1997; 2000), bST (growth hormone) was administered from 125 to 336 kg BW to enhance pre-pubertal mammary development. In the tissue harvest study, mammary development was enhanced approximately 48% by the use of bST (Radcliff et al., 1997). Milk yield from the heifers treated with bST before puberty increased by approximately 5.9%, but that was not significant and not

highly correlated with the increase in mammary parenchyma development (Radcliff et al., 2000). Thus, mammary development, measured as DNA content of the parenchyma at puberty, varied by about 100% (+48 to -60%) with no significant difference in milk yield. This strongly suggests that mammary development, when measured as DNA content at puberty, is not a good indicator of future milk yield. This is not to dismiss the concept that mammary development is important, but rather to provide opportunity to consider specific cell types instead of gross measurements using DNA as a proxy for cell number (Sinha and Tucker, 1969; Ballagh et al., 2008).

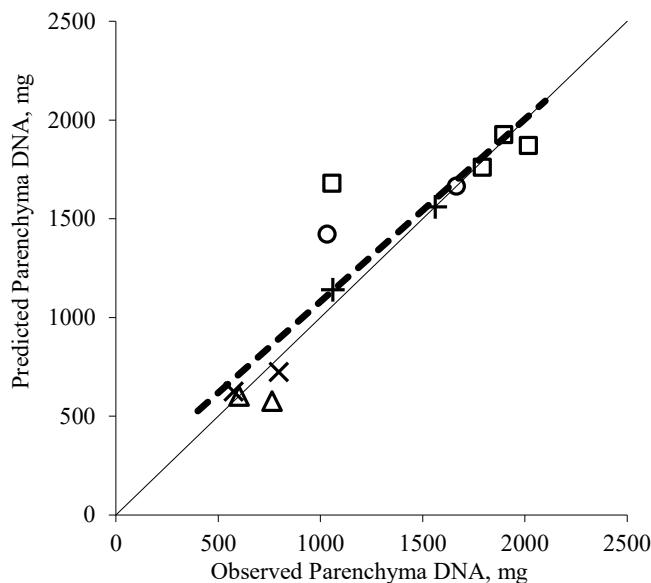


Figure 1. Evaluation of the prediction of ‘normal’ and ‘diet impaired’ pre-pubertal parenchyma development in Holstein heifers. The data points are predicted versus observed. Observed data are from previously published papers [Pritchard et al., 1972, (Δ); Sejrsen et al., 1982, (+); Petitclerc et al., 1984, (X); Capucco et al., 1995, (\square) and Mäntysaari et al., (1995), (\circ)]. Predicted values were generated using the mean daily DNA accretion rate determined in the current study and the average age at harvest as published in the respective papers. Slope of predicted versus observed (dotted line) is 0.95, $r^2 = 82\%$ ($P < 0.01$). The solid line represents unity ($X = Y$). Van Amburgh et al. (2019).

■ Body Composition and Milk Yield

One aspect that is difficult to quantify is the difference in body composition among heifers at calving in studies investigating the effect of age at first calving (AFC) on milk yield. For example, Swanson (1960) compared the milk yield of fat versus moderately conditioned heifers and observed that the fatter heifers did not perform as well. Based on data describing the productivity of dairy cows calving at higher than desired body condition scores, DMI, milk yield and post-partum health are usually at greater risk of being compromised (Grummer et al. 2004; Allen et al 2005; Douglas et al., 2006; Ospina et al. 2010). Thus, body composition at calving, as it relates to energy balance, is as important for first lactation cattle as multiparous cattle. Further, any difference in body composition of heifers at puberty or pregnancy will most likely be maintained or enhanced since, under most conditions, the animals remain in positive energy balance from puberty to calving. Thus, experiments evaluating rapid growth before puberty are potentially measuring the long-term effect of altered body composition at calving.

There are data available to make accurate predictions of the maintenance and growth requirements of dairy heifers, as well as to model growth and body composition while taking into consideration stage of maturity of the heifer. In this paper, we used published equations describing energy and protein requirements and body composition to predict body composition at various stages of growth up to calving. Predictions were made using the current NRC (2001) publication and from optimizations of requirements calculated from data generated after the publication of the NRC (Van Amburgh and Drackley, 2005). Equations from Fox et al. (1999) and the Nutrient Requirements of Beef Cattle (NRC, 1996) were also used to predict nutrient requirements or body composition. The predictions for body fat percent were evaluated using data from Meyer (2005) and resulted in a R^2 of 0.94 (Figure 2). Protein and lean tissue composition were also considered and the body composition of the protein content was also predicted by the model.

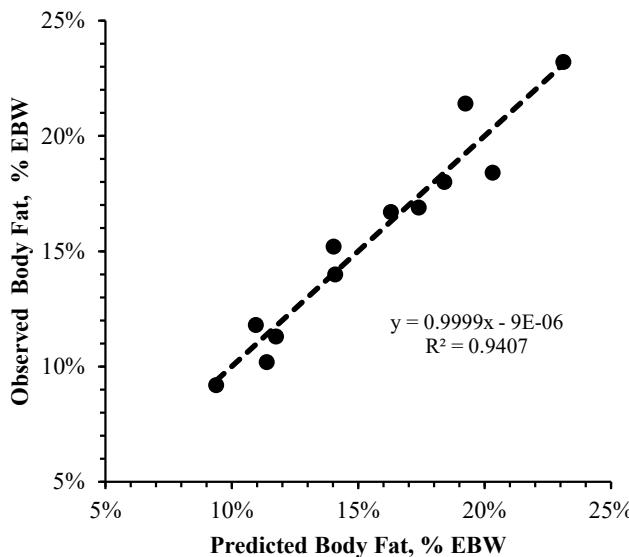


Figure 2. Regression of predicted and observed empty body fat content of dairy calves and heifers at different weights for calves grown at two different rates of gain. Measured body compositions taken from Meyer et al. (2005).

The model was evaluated with data from Gibb et al. (1992), where post-calving body composition was available for cows fed to grow at three different ADG pre-calving. A distinctive characteristic of this study was that the MBW of the cattle was approximately 700 kg because the study used cows with three and greater lactations. The body fat content of the cows grown at the three different pre-calving body growth rates was 18.6%, 19.4% and 21.2%. When accounting for the MBW of the population, the estimates from our model for post-calving body fat content were 18.5%, 19.5% and 20.8% for each of the respective ADG.

To better understand the relationship between rate of gain, composition of gain and AFC, the model was used to develop estimates of the body composition at calving of heifers who were grown at different rates of gain, bred when they had achieved 55% of their MBW and had calved at 82% of their mature body weight as per current recommendations (Fox et al. 1999; NRC, 2001). In the base scenario, all animals were assumed to double their birth weight by 60 days and have an ADG of 0.6 kg during pregnancy, excluding the weight of the gravid uterus. Three different pre-pubertal growth rates were used: 0.75 kg/d, 0.64 kg/d and 0.56 kg/d that allowed for AFC of 22, 24 and 26 mo., respectively. Given these growth

rates, the three groups of animals were estimated to calve at 25% body fat and 15% protein, and would not be expected to have differences in milk production, although the animals that calve at 22 months would be producing milk four months sooner than those set to calve at 26 months.

Subsequently, several different scenarios were created based on published data to represent studies and potential on-farm conditions that describe various management approaches to decision making for AFC and BW at or post-calving. When pre-pubertal growth rates were adjusted but heifers were bred by age, the predicted body composition of heifers in each group changed significantly. Using similar assumptions, if calves double their birth weight by 60 days and grow at 0.7 kg/d during pregnancy (without the weight of pregnancy), and all heifers are bred at 16 months for an expected AFC of 25 months, but during pre-puberty had ADG of 1.0 kg, 0.8 kg or 0.6 kg, they would calve at 30%, 27% or 23% body fat and 14%, 15% and 16% protein, respectively. Data are not available to fully characterize the body composition at calving that provides the most optimum energy balance for first lactation cattle; however, the difference in body fat from 23 to 30% would be enough to increase the BCS by at least one score, equivalent to 40 kg body fat in a 560 kg Holstein heifer. These calculations are consistent with data where heifers were bred to calve at the same age but at different BW; consequently, heavier (fatter) heifers produced less milk during first lactation (Swanson, 1978).

To better understand the effects of pre-pubertal ADG on future milk production, we estimated the body composition at calving for heifers from published studies where milk yield was evaluated.

Valentine et al. (1987) reported that actual growth rates varied from 0.18 kg/d to 0.94 kg/d, where AFC ranged from 26.9 months for the slowest treatment to 22.4 months for the treatment gaining over 0.9 kg/d. After calving, the estimated body fat percent for all groups was 22% and researchers reported no difference in milk production among any of the groups. These data suggest that if little difference exists in body composition at calving, and BW are reasonably similar, DMI, energy balance and milk yield will not be negatively impacted.

Hohenboken et al. (1995) compared three different growth rates from 6 weeks of life to 300 kg. All heifers were bred at the same weight resulting in AFC of 29, 26 and 23 months for heifers raised at ADG of 0.6 kg/d, 0.7 kg/d or 0.9 kg/d, respectively. These treatments resulted in a predicted body composition of 17% and 25% body fat and 18% and 16% protein for calves raised at ADG of 0.6 kg/d and 0.9 kg/d respectively. The treatment heifers with 17% predicted body fat produced 500 kg more milk than the heifers with higher body fat percent. This is consistent with the data describing the potential impact of greater body condition score on DMI, energy balance and milk yield (Garnsworthy and Jones, 1987; Allen et al., 2005; Janovick and Drackley, 2010)

In agreement with these calculations are the results from Hoffman et al. (1996), who reported the effects of different growth rates post-puberty (~45% of MBW) and during pregnancy on first lactation milk yield. Heifers on this study were fed to achieve an ADG of 0.97 or 0.79 kg from 10 months of age until calving. The group fed for higher gain was bred at 10 months while the control group was bred at 14 months. At calving, both groups had similar BW but researchers reported that the group with higher gains had lower wither height and pelvic area. The interpretation of these results suggests that calves with higher ADG during pregnancy had a higher fat composition given that they were smaller framed animals but had similar weights to the control animals. Furthermore, milk production of the calves with higher ADG during pregnancy was 2 kg/d lower than control calves but their milk fat yield was higher during the first 2 months of lactation. These observations are consistent with the lactation performance of over-conditioned cattle.

One of the most crucial and overlooked variables in the effects of growth rate on future performance is MBW. As previously mentioned, the composition of the gain is dependent on the stage of maturity, therefore, when evaluating growth rates pre-puberty, it is important to characterize the growth rates within the stage of physiological maturity. This concept was described for dairy cattle by Fox et al. (1999), where they described the percent of MBW at pregnancy (55%) and post-calving BW (minimum 82%) necessary to optimize first lactation milk yield. The key factor in this approach is using the MBW of the herd to adjust

for stage of maturity for nutrient requirements instead of using a population value. In all the studies conducted on heifers prior to the publication of the Dairy NRC (2001), no consideration was given to the MBW of the cattle, thus most data were not adjusted for stage of growth and under those conditions, energy intake is almost always greater than required for dairy replacements (Van Amburgh and Meyer, 2005).

Foldager and Sejrsen (1987) concluded that the optimal growth rate of dairy calves between 90 and 350 kg live weight should be 0.6 kg/d. Representative animals from that data set are shown in Figure 3. From this picture, over-conditioning of the fastest growing heifers was not included in the analysis and was probably a confounding factor in milk production. To better describe this, the growth data from Foldager and Sejrsen (1987) were used to predict body composition at calving; however, we had to make assumptions about the MBW of the animals represented and chose a range of mature weights for comparison. Predicted body composition at calving for cattle with mature body weights from 500 to 700 kg are presented in Table 1. As mature weight increased, body fat decreased at similar calving weights.

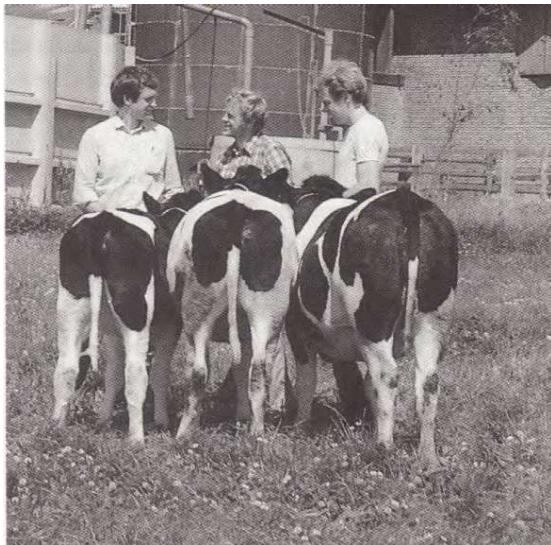


Figure 3. Three 18 month-old heifers grown at ADG of 400, 600 and 800 g/d. Live weights were 250, 402 and 540 kg, respectively (Foldager and Sejrsen, 1987; used with permission of the publisher).

The cattle represented in the study appear to be small framed cattle with MBW between 500 and 550 kg. If this study had been performed with larger framed cattle, conclusions on the effects of growth rate on milk performance might have been different because of the composition of the gain of the animals. Again, depending on the MBW of the cattle, the differences in fat percent translate into differences in BCS of at least 1 unit and this would have a significant effect on post-partum DMI, and milk yield. Milk production on this study differed by 500 kg in the first 250 days of lactation where heifers grown at 0.6 kg/d produced 5,100 kg of milk compared with 4,600 kg produced by heifers grown at 0.8 kg/d during the pre-pubertal period.

Table 1. Calculated body composition at calving of heifers grown at different pre-pubertal rates with different mature body weights.

Mature body weight, kg (lbs)	ADG from 90 to 350 kg, g/d	Calculated body fat, %	Calculated body protein, %
700 (1,544)	400	18.5%	18.0%
700 (1,544)	600	19.5%	17.7%
700 (1,544)	800	20.8%	17.4%
600 (1,323)	400	20.8%	17.3%
600 (1,323)	600	22.0%	17.0%
600 (1,323)	800	23.6%	16.6%
550 (1,213)	400	22.2%	16.9%
550 (1,213)	600	23.6%	16.5%
550 (1,213)	800	25.3%	16.1%
500 (1,103)	400	23.9%	16.4%
500 (1,103)	600	25.4%	16.0%
500 (1,103)	800	27.2%	15.5%

The overall goal of heifer rearing is to provide the management and nutrition that allows for optimum milk yield in the first and subsequent lactations. Research has evaluated many aspects of heifer rearing. However, most of the focus has been on pre-pubertal growth rate and its effects on mammary development. Little to no attention has been placed on the effects of such growth rates on body composition at calving. Transition cow research has unequivocally shown the negative effects of over-conditioned cattle at the time of calving on DMI, metabolic problems and milk yield. These findings also apply to first lactation heifers. When accounting for predicted body composition at calving, we are able to explain most of the variation in milk production observed in different studies. Body composition explains both the lack of differences in production observed in some studies (Valentine et al., 1987; Waldo et al., 1998) and the differences in milk production observed in others (Swanson, 1978; Foldager and Sejrsen, 1987; Hohenboken et al., 1995). Thus, in many studies evaluating mammary development and milk yield, directly or indirectly, the outcome was most likely better predicted by body composition at calving and not mammary development.

Moreover, body composition during growth is greatly influenced by MBW. When MBW is not accounted for in diet formulation, energy is often over-fed, resulting in greater fat deposition in growing heifers in subtle but significant outcomes.

■ Summary

Data presented in this paper support the current growth benchmarks for heifer rearing (Fox et al., 1999; NRC, 2001) to achieve a body composition by calving that does not compromise post-partum energy balance or milk yield and allows for earlier AFC. Heifers should be bred between 55 and 60% of their MBW to achieve a post-calving weight of 82 to 85% of the MBW of the herd. When these targets are attained, heifers can successfully calve earlier without a negative impact on milk production, with the added benefit of having reduced the length of the non-productive stage.

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