A 100-Year Review: A century of dairy heifer research^{1,2}

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ABSTRACT

The years 1917 to 2017 saw many advances in research related to the dairy heifer, and the *Journal of Dairy Science* currently publishes more than 20 articles per year focused on heifers. In general, nutrition and management changes made in rearing the dairy heifer have been tremendous in the past century. The earliest literature on the growing heifer identified costs of feeding and implications of growth on future productivity as major concepts requiring further study to improve the overall sustainability of the dairy herd. Research into growth rates and standards for body size and stature have been instrumental in developing rearing programs that provide heifers with adequate nutrients to support growth and improve milk production in first lactation. Nutrient requirements, most notably for protein but also for energy, minerals, and vitamins, have been researched extensively. Scientific evaluation of heifer programs also encouraged a dramatic shift toward a lower average age at first calving over the past 30 yr. Calving at 22 to 24 mo best balances the cost of growing heifers with their production and lifetime income potential. Increasingly, farms have become more progressive in adopting management practices based on the physiology and nutrient needs of the heifer while refining key economic strategies to be successful. Research published in the *Journal of Dairy Science* has an integral role in the progress of dairy heifer programs around the world.

Key words: dairy heifer, growth, age at first calving, heifer nutrition

INTRODUCTION

The years 1917 to 2017 saw many great advances in research related to the dairy heifer, and in this time the industry has made many improvements to the way we grow and manage heifers (Appendix Table A1). In the earliest years of the century, the *Journal of Dairy Science* (JDS) had very few heifer publications—sometimes <1 or 2 per year related to the growing heifer. However, the later years, notably the past 20 yr, have seen a dramatic increase in heifer research publications, with 20 or more per year. This review includes publications appearing in JDS since its beginning that had the term *dairy heifer* in the title or key words. Papers focusing on preweaned calves and treatments applied to heifers after their first calving were excluded. Topics related to breeding and reproduction, welfare, disease, and housing and facilities are not covered to limit duplication with other articles in this issue of JDS.

In the earliest literature on the growing heifer, researchers identified costs of feeding and implications of growth on future productivity as major concepts requiring further study to improve the overall sustainability of the dairy herd. The status of knowledge of the practical feeding of dairy heifers at the time JDS was established was well summarized by Henry and Morrison (1915; page 426): “The rearing of the heifer after 6 to 8 months of age is an easy task, and perhaps because of this many are stunted for lack of suitable feed.” The authors subsequently described the feeding of heifers in approximately half a page, clearly indicating opportunity for conducting and reporting additional research on growth, nutrition, and management.

GROWTH

Growth has been a fundamental outcome of interest in heifer nutrition and management research over the years. Eckles (1920) and Ragsdale (1934) published the first growth standards for dairy heifers at the University of Missouri; standards from USDA Beltsville (Matthews and Fohrman, 1954) and the University of Nebraska (Davis and Hathaway, 1956) followed. Most were derived from a single experiment station herd over

Received April 7, 2017.

Accepted August 4, 2017.

¹This review is part of a special issue of the *Journal of Dairy Science* commissioned to celebrate 100 years of publishing (1917–2017).

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a period of years, yet all were quite similar in their outcome. In many early heifer studies, researchers characterized growth relative to a “standard” or “normal” heifer using 1 of these reports. There are even instances in which a control group was not included in an experiment because comparisons could be made with such a standard (Maynard and Norris, 1923). Also of interest, in this early period of research many articles contained pictures of the animals on study to supplement growth data with a visual representation of the form of growth. These practices emphasize 2 important concepts of this early work: experiments consistently contained a very small number of animals, and appropriate controls rarely were included.

In one of the earliest reports of growth, McCandlish published measurements from birth to production age and showed that BW consistently increased proportionally to the product of height, depth, and width (McCandlish, 1922). Likewise, height:weight ratio was suggested to maintain a constant proportionality independent of age (Brody and Ragsdale, 1922). Much later, Swanson et al. (1967) published an estimate of optimal growth patterns for dairy heifers. Twenty years after this, Heinrichs and Hargrove (1987) published Holstein heifer weight and height growth standards derived from population studies that showed that heifers were larger than previously published standards, which likely represented changes in breeding programs over time. In addition, they published population growth studies of other dairy breeds from 2 to 24 mo of age (Heinrichs and Hargrove, 1991, 1994). These were (and still are) the most comprehensive publications of growth standards for these breeds.

Summaries of data by Kertz et al. (1998) provided descriptions of Holstein growth through the heifer development phase. Growth rate was fastest in the first 6 mo of life, and feed cost per unit of BW or withers height was lowest during this time. Heinrichs et al. (1992) showed equations predicting BW from other body measurements and published a modified heart girth to BW equation, likely reflecting changes in conformation from early standards (Ragsdale, 1934; USDA/Matthews and Fohrman, 1954). Taking this concept further, Oliveira et al. (2013) developed an equation using heart girth to estimate BW for crossbred Holstein-zebu heifers in Brazil.

Early studies began to relate growth to production and later to economics. Growth from birth to 2 yr was uncorrelated with first-lactation or lifetime-lactation performance (Davis and Willett, 1938). In contrast, Plum et al. (1952) documented a positive relationship between growth of chest girth and butterfat production; however, this relationship was suggested to have been attributable to environmental factors instead of

genetics. This same study reported a positive genetic correlation between growth in withers height and butterfat production. Touchberry (1951) and Blackmore et al. (1958) reported a negative genetic association between body size measurements and milk production, with the exception of a positive correlation between withers height and production in the latter study. With the limited data available, it was noted that there was a correlation (44 comparisons, $r = +0.40$) between BW gain during the last 2 mo of pregnancy and subsequent lactation performance regardless of season of calving (Blackmore et al., 1958).

Further studies on growth looked at the genetic relationships of growth and production. Koenen and Groen (1996) estimated the genetic relationship between BW at first calving and other growth patterns and found that estimated mature BW was negatively correlated with rate of maturation, whereas BW at first calving had a strong correlation with mature BW and a negative correlation with maturation rate. Coffey et al. (2006) studied growth of dairy heifers from 2 genetic lines in the United Kingdom: selection for maximum production of fat and protein (select) or average production (control). Under the same management, heifers from the select line grew faster and were heavier at first calving. However, Van de Stroet et al. (2016) showed that larger heifers were not superior in production compared with average-sized animals.

Swanson published a series of papers in the 1960s reporting heifer growth and its relationship to future production (Swanson and Hinton, 1964; Swanson et al., 1967; Swanson, 1971). This helped support his definition that an optimal growth pattern for dairy heifers will develop their full lactation potential at the desired age with minimum expense. Many of these early growth studies used twins to minimize genetic differences, and many of these studies were done with a limited number of animals, often with a variety of breeds. Swanson and Hinton (1964) restricted growth of twin heifers by 25%, and although first-lactation production was 78 to 95% that of the normal-growth heifers, in second and third lactations the pairmates produced almost alike, showing no harmful effect of subnormal growth after the first lactation. However, size of the restricted-growth animals was smaller through maturity. Swanson et al. (1967) studied slowly grown heifers versus those grown at normal rates of gain. Their results showed that prepartum supplementation of the slowly grown heifers allowed them to attain, if not exceed, normal lactation performance. On this basis, liberal prepartum feeding for 9 to 12 wk before expected calving was recommended for heifers if they were substandard in size.

Gardner et al. (1977) published the first work on accelerated growth and early breeding of heifers. They in-

creased ADG from weaning to breeding and accelerated heifers calved at 19.7 mo, 7.2 mo earlier than control heifers. Accelerated heifers produced significantly less milk in first lactation and numerically less in following lactations. Interestingly, the authors provided little to no discussion of the results. Kertz et al. (1987) showed that growth of Holstein heifers can be accelerated up to 1 kg of ADG from 3 to 12 mo of age without excessive fattening. Several studies evaluated prepubertal ADG and first-lactation milk production, often with differing conclusions. Zanton and Heinrichs (2005) conducted a meta-analysis of heifer growth and production studies and found a quadratic relationship, which demonstrated that the conclusions of each study were tied to the ADG chosen. The reported optimal ADG was 799 g/d before puberty.

AGE AT CALVING

In reference to growth and management effects on age at first calving (AFC), a progression of research has demonstrated the economic importance of this aspect of heifer raising. In the first year of JDS, cows calving at later than 30 mo of age were shown to have produced more milk in 2 lactations than cows calving earlier than 30 mo did in 3 lactations (White, 1917). This was shown by following 10 cows that calved for the first time over an 8.3-yr period and were not randomly assigned to early or late treatments. In an observational study, Plum and Lush (1934) reported that average AFC in the Iowa Cow Testing Association registry was 27.1 mo, with a median age of 25.33 mo. These data also showed that half of the purebred calves in this analysis were born to dams that were <52 mo of age. Similarly, the average age of a cow was reported to be 56.4 mo in the Iowa Cow Testing Association using broader inclusion criteria than were used previously (Cannon and Hansen, 1939). These data indicated that an average cow spends a substantial proportion of her life in the unproductive state. Thus, management factors that reduced the time or increased the efficiency of raising heifers from weaning to first calving without negatively affecting future productivity could positively influence profitability of dairy farms. It should be noted that much of the research in the area of age at calving does not take into account the length or number of lactations or age of animal life.

In a review of heifer growth and production research, Schultz (1969) stated that there appeared to be a trend in more recent publications to revise the breeding age downward. Schultz discussed research on the effects of alterations in the rearing system from the “standard” or “normal” procedures to make recommendations for lowering AFC. Powell (1985) published a review of AFC

trends covering 1960 to 1982. Means and distributions were similar for all breeds, and the distribution of AFC was skewed toward higher AFC for all breeds. Ayrshires had the highest mean AFC, and Jerseys had the lowest. Mean AFC changed little from the early 1960s to the early 1980s, although it peaked slightly around 1976. Powell's (1985) data showed that AFC decreased about 3 d/yr from the mid 1970s through 1982. Later work showed that trend (AFC decreasing 3 d/yr) continuing in the Holstein breed from 1985 to 1990 (Heinrichs and Vazquez-Anon, 1993).

Breeding heifers at a younger age coupled with a proper rearing program offers a promising approach to increase profit for the dairy industry. Lin et al. (1986) showed that breeding heifers as early as 350 d of age had no adverse effects on calving ease or retained placenta but did result in calves that were 1.2 kg lighter at birth. Heifers of the 350-d breeding group had lower milk production but were the same size at all points as heifers bred at 462 d. When lactation performance was analyzed, a reduction of 1 mo in AFC increased 3-parity and 61-mo total milk by 427 and 554 kg, respectively (Lin et al., 1988). Gardner et al. (1988) observed no differences in reproduction or production in heifers managed to achieve early or late AFC. Results from these studies suggested that early breeding was a viable and practical approach to improving profitability. The industry responded with a strong trend in reducing AFC from this point onward. However, Mohd Nor et al. (2013) showed that calving earlier on Dutch farms resulted in less milk in first lactation, indicating that management changes must accompany breeding at earlier ages.

Heinrichs et al. (1994) reported results of the National Dairy Heifer Evaluation Project, the first epidemiological study of the national dairy industry conducted by USDA. In this survey, operations with mean BW >545 kg at first calving and AFC ≤27 mo had higher milk production. Hare et al. (2006) examined AFC from 1980 through 2004 and found that it declined progressively with time for all 5 breeds studied. Jerseys had the lowest AFC, and it declined from 26.5 mo in 1980 to 24 mo in 2004. Ayrshires had the highest AFC at 29 mo in 1980 and 28.5 mo in 2004. Holstein AFC was 28 mo in 1980 and decreased to 25.5 mo by 2004. The distribution also shifted to the left during this period, with almost 20% of heifers calving at 24 mo in 2004 compared with approximately 8% in 1980.

Results of studies conducted in multiple states and countries investigating optimum AFC are remarkably consistent. Gill and Allaire (1976) using Ohio data showed that optimal AFC for total lifetime production was 22.5 to 23.5 mo. Hoffman and Funk (1992) proposed that 22 to 24 mo was the best AFC; calving ear-

lier resulted in reduced milk yield. In Italian Holstein-Friesians, an AFC between 23 and 24 mo was found to best balance rearing costs and milk yield (Pirlo et al., 2000). In California Holsteins, the highest economic return was generated for AFC from 23 to 24.5 mo when considering milk production, stillbirths, reproduction, and health (Ettema and Santos, 2004). Nilforooshan and Edriss (2004) observed that milk yield in Iranian Holsteins increased as AFC increased from 21 to 24 mo but decreased as AFC extended past 24 mo; they determined that the optimum AFC was 24 mo. In Pennsylvania the most efficient heifer-raising programs had AFC of 23.7 mo and first-lactation animals producing 88.42% of the milk produced by multiparous cows (Heinrichs et al., 2013).

Simerl et al. (1991) showed that Florida herds were calving at 22.2 mo of age without issues at parturition. Bach et al. (2008) compared 47 dairy herds in Spain that fed the same lactation ration but were under individual management and had a range of 13 kg/d in average milk production. Four factors, including AFC of heifers, accounted for more than 50% of the variation in milk production observed between these herds. Mohd Nor et al. (2013) introduced relative AFC (the difference between AFC of an individual and median AFC of the herd) as a new way of evaluating the effect of AFC. Dutch heifers calving 1 mo earlier than the median AFC produced 90 kg less milk per 305 d; those calving 1 mo later produced 86 kg more. This measurement assumed that heifers had the same management within a herd, and a heifer's deviation from the median reflected her development. Thus, earlier breeding without adjusting management to ensure adequate development was shown to reduce first-lactation production. Krpálková et al. (2014) reported that AFC <23 mo did not negatively affect milk yield or reproduction parameters during the first 3 lactations. Other than the normal known factors, AFC in heifers and level of milk production during gestation in cows were indicated as decisive determinants of calf birth size (Kamal et al., 2014). Thus, we can see the progression of a downward trend in AFC worldwide. Current genetics of the Holstein breed and management of commercial farms will allow the breed to reach at least 22 mo AFC on average.

NUTRIENT REQUIREMENTS

Determining nutrient requirements of heifers was the subject of much research throughout the first 100 yr of JDS. Early on, the maintenance energy requirement of young growing Holsteins was determined to be approximately 90% of that previously reported by Armsby (Eckles et al., 1927). Eckles suggested that this discrepancy was attributable to Armsby's (1917) use

of beef cattle in deriving maintenance values. Mixed diets marginally improved heifer growth and improved first- and second-lactation production compared with alfalfa-only diets when heifers were fed the test diets starting at about 315 kg of BW (Woll, 1918). Supplementing a winter ration of alfalfa hay with barley grain increased winter growth compared with heifers fed alfalfa hay only (Willard, 1932). In this study, growth was compared with Eckles' "normal." Further study at the Wyoming station demonstrated that increased consumption of alfalfa hay was obtainable by increasing the hay allowance and decreasing the grain allowance (Willard, 1938).

Feedstuff digestibility for Holstein heifers fed diets that contained no roughage (Mead and Goss, 1935) was shown to be consistent with what would be calculated from ingredient digestibility coefficients determined from the book values of Henry and Morrison (1923), which had been determined when forage was fed. Differing hay quality grades affected gains and feed efficiency (Kelkar and Gullickson, 1950; Gordon et al., 1954, 1956); however, it was noted that the current chemical and physical analyses were insufficient to completely characterize the value of hays for heifer growth (Gordon et al., 1952). Donker et al. (1968) published a method for evaluating forage energy production formulas by comparing various published energy intake estimates with heifer requirements. They reported that of the 9 equations used to estimate forage energy, all were inadequate for differentiating the ability of hay qualities to stimulate heifer growth. Corn silage was found to be inferior to grass silage as the sole source of forage, although heifer growth was improved if a small amount of grass hay was added to either ration (Keener et al., 1958).

Reid and Robb (1971) evaluated the relationship of body composition to energy intake and energetic efficiency. Their work showed that body protein and fat were linearly related to empty BW; furthermore, body protein and fat explained 99.7 and 96.1% of the variation in empty BW, respectively. They used 61 heifers from 1 d to 14 mo of age and provided a wide range of body composition data covering 4 different breeds and crosses fed a variety of nutritional regimens. In the same year, Swanson (1971) investigated feed energy requirements of heifers under different rates of growth. Data for this meta-analysis came from 16 experiments involving more than 900 heifers in 267 experimental groups, within which heifers had been fed to produce different growth rates. He published a prediction equation based on diet TDN and BW that was reported to apply to all dairy breeds from 4 to 22 mo of age. Fox et al. (1999) evaluated the applicability of the beef NRC (1996) equations for predicting growth requirements,

target weights based on mature size, and energy reserves in dairy cattle. Coefficients of the equations were modified, but the methods were accurate when predictions were compared with actual observations for heifers >100 kg. With slight modifications, this system was adopted by the next edition of the dairy NRC (2001).

Protein

Early research evaluated using homegrown protein supplements to reduce costs of providing protein to growing heifers. Hilton et al. (1932) demonstrated that raw soybeans could effectively replace linseed oil meal when fed for approximately 1 yr in a diet containing alfalfa hay as the source of forage. Subsequently, heifers were found to grow equally well on diets containing either steam-dried or flame-dried fish meal (Berry and Manning, 1936). Results based on weight gains alone provide little insight into the nutritional mechanisms affecting an increased ADG or the effect of protein quality on ADG. Hart et al. (1939) initiated studies that evaluated the ability of the growing ruminant animal to use NPN supplements to increase the CP content of a CP-deficient diet. In one of the first studies of its kind, a rumen-fistulated Holstein heifer was used to demonstrate the conversion of dietary urea to protein in the rumen (Wegner et al., 1941a). Further work with the fistulated Holstein heifer demonstrated that conversion of urea to protein was affected by the protein (Wegner et al., 1941b), starch (Mills et al., 1942), and soluble sugar (molasses; Mills et al., 1944) contents of the basal diet. Growth studies showed that although urea could be used as a source of CP, the N from urea was not used as effectively as the N from soybean meal (Bohman et al., 1954; Lassiter et al., 1958) or when urea was included in a molasses-containing diet compared with a corn-containing diet (Bohman et al., 1954; King et al., 1957). In heifers fed low-protein diets, feeding high energy markedly increased the retention of N that was available for growth (Lofgreen et al., 1951). Later researchers from New Hampshire also studied urea utilization. Using 3 sets of twins in a respiration chamber, Colovos et al. (1963) showed that including urea in limited amounts was beneficial in higher forage rations.

Some interesting work from the late 1970s and early 1980s evaluated unusual alternative protein and energy sources. Johnson and McCormick (1975) fed municipal waste with sorghum silage, and Cross and Jenny (1976) fed turkey litter silage. Block and Shellenberger (1980) fed wood fines, and Keys and Smith (1981) fed poultry litter. All found adequate growth when diets were balanced; however, this line of research did not seem to

go further, likely because of the questionable welfare of heifers fed these types of alternative feedstuffs.

Since the 1990s a great deal of dairy heifer nutrition research has been conducted, much of it related to updating protein requirements with little emphasis on energy. In general, these studies had reasonably large numbers of animals and adequate controls, unlike some of the earlier work. A variety of research groups studied total protein intake as it relates to diet energy. Lammers and Heinrichs (2000) used a CP:ME ratio of 46:1, 54:1, or 61:1 g/Mcal and found a linear increase in ADG, feed efficiency, and structural growth with increasing CP:ME ratio. Hoffman et al. (2001) investigated 8, 11, 13, or 15% CP in similar energy diets; structural growth, N retention, and diet digestibility were maximized at 13% CP. Gabler and Heinrichs (2003) fed a CP:ME ratio of 48.3, 59.1, 67.5, or 76.5 g/Mcal at DMI allowing an ADG of 800 g/d; feed efficiency and height improved linearly with increasing CP:ME ratio. Marini and Van Amburgh (2005) observed that low-N diets reduced urine excretion of N, whereas growth rates were maintained. These studies showed that altering the CP:energy ratio of heifer diets improved growth and feed efficiency.

Research on the effects of protein degradability on growth has begun relatively recently. Petit and Yu (1993) fed heifers fresh grass (timothy-clover mix) *ad libitum* with no supplemental N, a high-NPN molasses block, or high-RUP block containing animal proteins. Protein supplementation increased ADG, but no difference was observed between blocks, so the authors concluded that RUP was not the limiting factor. Casper et al. (1994), using 3-mo-old Holstein heifers, found that ADG improved in diets with extruded soybean meal, with greater improvement in diets containing barley versus corn. They recommended 35 to 40% RUP for heifers 3 to 6 mo of age. Bethard et al. (1997) used 32 heifers fed rations formulated for an ADG of 0.6 or 0.9 kg/d with 30 or 50% of CP as RUP from age 6 to 13 mo and found improved feed efficiency for high-energy and high-RUP diets. However, Steen et al. (1992) and Swartz et al. (1991) found no growth advantage to increasing the undegradable protein intake of heifers, as was noted in the 1989 NRC (NRC, 1989). Daccarett et al. (1993) fed Holstein heifers 107 or 124% of NRC requirements for CP and ME from 3 to 6 mo of age and 100 or 115% from 6 to 24 mo and demonstrated that feeding in excess of NRC (1989) recommendations increased BW and height without fattening. Van Amburgh et al. (1998) evaluated NRC (1989) and Cornell Net Carbohydrate and Protein System recommendations using 273 Holsteins with ADG treatments of 0.6, 0.8, or 1.0 kg/d from 90 to 320 kg of BW. Actual ADG

were 0.68, 0.83, and 0.94 kg/d and were not affected by feeding plant and animal or plant and urea protein sources. They also showed, consistent with several previous studies, that NRC underestimated RDP and overestimated RUP requirements. Zanton and Heinrichs (2008a) published a meta-analysis of N utilization and excretion in weaned dairy calves that summarized 10 experiments with 57 different treatments. True N digestibility was estimated at 96.4%, and endogenous, nondietary fecal N excretion was 6.51 g of N/kg of DMI. Diet CP of 14.2% and N intake of 1.84 g/kg of metabolic BW maximized gross N efficiency. They concluded that reductions in fecal N excretion would be most achievable through reduced DMI while feeding a high enough concentration of energy to meet the needs of the animal. Reducing urinary N excretion is best accomplished by decreasing N intake. In a follow-up study (Zanton and Heinrichs, 2009), Holsteins of 362 kg of BW and 12.3 mo of age were fed 25 or 75% forage diets with 0.94, 1.62, 2.30, or 2.96 g of N/kg of metabolic BW and equal energy intakes. Their results suggested that feeding 1.67 g of N/kg of metabolic BW optimized N efficiency regardless of the forage level in the ration. Lascano et al. (2012) used those levels of N to evaluate starch digestibility and found that high starch decreased ADF and increased hemicellulose digestibility. Lascano et al. (2016) concluded that low fiber levels in low- and high-forage diets increased utilization of nutrients under limit-feeding conditions when provided with high RDP. Furthermore, Zanton and Heinrichs (2016) reported that heifers limit-fed high-energy diets had increased digestibility and N retention and that younger animals were more responsive to this feeding strategy.

Vitamins and Minerals

The early research on vitamins for dairy heifers occurred closely in parallel with the development of the understanding of the importance of vitamins in overall nutrition. The first evidence that the knowledge of the chemical composition of feeds was incomplete was determined when researchers fed rations comprising a single plant source (corn, wheat, or oats) to dairy heifers, resulting in differences in offspring vigor and milk production capacity even though the chemical compositions of the rations were, in all known respects, identical (Hart et al., 1911). Several studies were subsequently reported detailing vitamin requirements of heifers. Vitamin A was shown to be indispensable for the normal growth and development of calves (Jones et al., 1926). However, calves could grow and reproduce normally on a ration that contained vitamin B insufficient to support the growth and well-being of

rats; the deficit in dietary vitamin B was proposed to be synthesized by the rumen bacteria (Bechdel et al., 1926). Likewise, heifers were shown to grow normally for 1 yr on a ration that resulted in death from scurvy of guinea pigs in less than 30 d (Thurston et al., 1926), indicating that heifers can synthesize sufficient vitamin C. Calves grown from birth to first calving in the dark grew normally (Gullickson and Eckles, 1927). However, these calves were provided with ad libitum access to timothy hay, which was subsequently shown to prevent rickets when sun cured but not when cured in the dark (Huffman et al., 1935). The forage component of the heifer diet was suggested to be a significant contributor to the vitamin and mineral requirements of heifers when a diet devoid of roughage was able to support normal growth when supplemented with cod liver oil and alfalfa ash (Mead and Regan, 1931; Wise et al., 1939). Previously, it was unclear whether the deficiency in a roughage-free diet was attributable to a lack of bulk in the diet or a vitamin or mineral deficiency (McCandlish, 1923). More recently, biotin supplementation of heifers precalving and during first lactation did not affect incidence of lameness (though it did for cows of greater parity; Hedges et al., 2001), and no improvement in immune function was detected in heifers fed a source of vitamin C after being transported for 2.3 h (Tyler and Cummins, 2003). In addition, studies showed that vitamin D could be administered effectively using mucosal absorption (Okura et al., 2004; Rivera et al., 2005).

As bone diseases were not uncommon in developing dairy heifers, a description was made of normal bone from 60 to 180 d (Kruger and Bechdel, 1928). Bone meal supplemented to heifers for approximately 18 mo was said to be without effect compared with when heifers were supplemented with common salt (Salmon and Eaton, 1925). Diets low in P (0.2% DM) resulted in reduced ADG; however, reproduction was not compromised compared with a group fed a diet with adequate P (0.4% DM; Huffman et al., 1933). Noller et al. (1977) evaluated the ability to meet P requirements from natural feedstuffs and the adequacy of minimums for P recommended by NRC (1971) and determined that those requirements (0.22%) were adequate based on mineral status of the heifers and conception rates. Subsequently, Esser et al. (2009) fed diets with (0.39% P) or without (0.29% P) supplemental P from 4 to 21 mo of age and found no effect of supplementation on frame measurements, bone density, or markers of bone metabolism. Similarly, Bjelland et al. (2011) found similar ADG and body measurements at 22 mo with or without supplemental P (0.4 or 0.3% DM) from 4 to 22 mo of age. No difference was observed in heifer reproductive performance (services per conception, age

at conception, or dystocia) or in first-lactation milk production and reproduction; however, heifers fed supplemental P excreted more P (29.9 vs. 24.2 g/d). Ray et al. (2012) evaluated disappearance of phytate from the large intestine using heifers with ruminal and ileal cannulas using ileal infusions of 0, 5, 15, or 25 g of phytate/d. Ileally infused phytate was degraded in the large intestine, but degradability was not dependent on the amount of phytate.

Studies showed little difference in the absorption of Cu from sulfate, proteinate, carbonate, or Cu-AA complex (Du et al., 1996; Ward et al., 1996; Yost et al., 2002); however, when S and Mo were included in the diet, the proteinate form had better absorption than sulfate and was stored more efficiently than carbonate (Ward et al., 1996). Supplementing Cu in the form of sulfate or Lys also made little difference in growth, though Cu-Lys enhanced liver and plasma Cu concentrations in heifers with low Cu status (Rabiansky et al., 1999). Holstein heifers supplemented with Cu sulfate or proteinate prepartum and in early lactation had improved plasma and liver Cu status and a less severe response to an *Escherichia coli* mastitis challenge in one study (Scaletti et al., 2003) and lower bacteria count in their milk in another study (Scaletti and Harmon, 2012). Sumner et al. (2007) fed 0, 5, 10, or 15 mg of Cr/d from 11 to 14 mo of age; increasing Cr increased glucose concentration and utilization and decreased insulin and nonesterified fatty acid (NEFA) concentration. Spears et al. (2012) reported that feeding Cr propionate increased tissue sensitivity to insulin and recommended providing 3 mg/d or 0.47 mg/kg of DM.

In a survey of 22 herds in Finland, Jukola et al. (1996) found that serum Se and vitamin E were adequate in heifers and that supplementation was not needed. However, supplementing vitamin E at 3,000 IU/d beginning 2 mo before calving increased blood, liver, milk, and follicular fluid levels of vitamin E in other reports (Bouwstra et al., 2008; Dobbelaar et al., 2010). In addition, Ceballos-Marquez et al. (2010) found that supplementing Se to Chilean Holstein-Friesian heifers precalving via a single barium selenite injection or Se yeast at 3 mg/head daily for 45 d increased blood glutathione peroxidase activity and tended to reduce IMI and quarters with high SCC at calving.

Kincaid et al. (1997) fed weaned calves (6–12 wk of age) starter containing Zn at various concentrations from Zn-Met, Zn-Lys, or ZnO. No effects were observed on BW, DMI, or immune functions, but Met or Lys forms were absorbed and retained better than oxide. Feeding vitamin E, Zn, and Fe for 42 d before calving had no effect on the incidence of retained fetal membranes, but supplementing Zn or vitamin E before calving reduced days to first estrus (Campbell and Miller,

1998). Beef heifers fed a basal diet containing 15.8 mg of Mn/kg of DM or supplemented with 50 mg of Mn/kg of DM had no difference in blood concentration of Mn and grew similarly; calves born to unsupplemented heifers had lower blood Mn and presented signs of Mn deficiency (Hansen et al., 2006). Weiss et al. (2010) reported that feeding supplemental Fe for 60 d before calving resulted in no differences in measures of Fe status or in milk production, but SCC was reduced with supplemental Fe.

Nennich et al. (2005) compiled data from 4 universities to update prediction equations for nutrient excretion by dairy heifers, including total manure, total DM, N, P, and K. Current accurate predictions are important because farms use these equations to comply with environmental regulations. Manure excretion for heifers was predicted based on BW and DMI using previously published data sets. Lascano et al. (2015) reported that dietary fiber modulated ammonia emissions differently on diets extremely high (~80%) and low (~20%) in forage and that methane concentration was correlated with odor intensity. Methane emissions were not reduced when corn silage with differing NDF and starch concentrations was used or when oil from extruded linseed meal was incorporated into heifer diets (Hammond et al., 2015).

MANAGEMENT

Management systems and alterations in management have long been a topic of heifer research, as reviewed by Clark et al. (1984), who summarized much of the early feeding and management research in a review of the NC-119 cooperative research group that studies dairy heifers.

Feeding

Stair-step compensatory growth strategies have fed above or below recommendations for 2 to 3 mo and then reversed, supporting lower growth and then allowing feed-efficient, compensatory growth when animals were on a higher plane of nutrition (Choi et al., 1997; Park et al., 1998). Feed efficiency with the stair-step program was improved compared with controls (Park et al., 1998) and enhanced by including lasalocid in the diet (Ford and Park, 2001). Heifers on a compensatory program also had greater milk yield in first and second lactation (Ford and Park, 2001).

Some interest was focused on the proposal that more frequent feeding of the growing ruminant would produce faster weight gains. Clark and Keener (1962) suggested that as a result of frequent feeding, specific enzyme pathways for the metabolism of end products

of rumination may be altered because of a change in the concentration ratios of these metabolites. In Missouri, Campbell et al. (1963) used 40 Guernsey heifers to study urea feeding and indicated that rumen adaptation to urea may be related to increased frequency of feeding. Later work (Swanson and Hinton, 1964) showed no advantage of feeding more than once a day.

Montgomery and Baumgardt (1965a, b) used heifers as a model for feed intake studies. Quigley et al. (1986a,b) evaluated factors affecting intake of heifers in intensive management and developed an equation to predict daily DMI of heifers weighing 100 to 400 kg. Intake of DM and digestible energy was affected by BW, BW gain, ration ADF, NDF, bulk density, and ambient temperature. Hoffman et al. (2008) evaluated previously published DMI prediction equations (Quigley et al., 1986b; NRC, 2001) using observed daily pen DMI over 28 mo ($n = 9,275$) and found that both equations predicted DMI reasonably well in the middle of the growth period, but both were less precise for lighter and heavier heifers. Alternative prediction equations were derived, and greatest precision was obtained with an exponential equation that included adjustment for diet NDF.

Lammers et al. (1999) adopted a concept from the beef industry and fed heifers a high-energy diet but limited DMI to meet their requirements for growth. This began a long series of studies evaluating limit feeding of heifers in Pennsylvania and Wisconsin, with additional work done in Ontario and South Dakota. Limit feeding offers a way to improve feed efficiency and reduce nutrient losses while meeting the nutrient needs of the growing heifer. Hoffman et al. (2007) fed an ad libitum (control) diet or more nutrient-dense diets at 80 or 90% of ad libitum DMI and found no difference in weight gain, structural growth, or 150-d milk production. Limit-fed heifers had higher feed efficiency and lower manure DM excretion. Zanton and Heinrichs (2008b) fed 14.5-mo-old heifers a high-forage diet at 1.25, 1.50, 1.75, or 2.00% BW and concluded that limit feeding increased nutrient utilization efficiency but that DMI below 1.5% of BW reduced efficiency. Green et al. (2013) measured feeding behavior in 1,049 heifers from 5 to 9 mo of age and reported that the more efficient heifers (lower residual feed intake) consumed less feed, ate more slowly, spent less time eating, had longer meals, and consumed more feed during the night and less during the afternoon. Greter et al. (2013) reported that straw with either long or short particle length increased intake when heifers were limit fed an energy-dense diet and that they preferred long straw when given the opportunity. Suarez-Mena et al. (2013) observed that chewing activities were affected by forage concentration and by the addition of distillers

grains. Higher forage inclusion increased eating time and rumen digesta weight and volume, whereas feeding distillers grains increased rumination time in limit-fed heifers. Greter et al. (2015) reported that limit-fed heifers were more motivated to access a low-quality feedstuff such as straw, possibly in response to a lack of satiety or need for forage. Miller-Cushon et al. (2015) observed that the method of transitioning heifers to a novel TMR influenced sorting behavior. In their study, heifers fed a novel ration sorted against long particles and thus received a lower NDF diet.

As an alternative to limit feeding an energy-dense diet, Coblenz et al. (2015) demonstrated that low-energy forages (eastern gamagrass haylage, chopped wheat straw, or chopped corn fodder) offered to Holstein heifers for ad libitum intake as diluting agents reduced caloric density and DMI, with heifers sorting the straw diet and, more severely, the chopped corn fodder diet.

Transition to Lactation

When conducting research into the transition period, many studies included both primiparous and multiparous cows. This has increased our understanding of the similarities and differences between heifers entering their first lactation and more mature animals. Drenching with propylene glycol (Grummer et al., 1994) or feeding diets with greater nutrient density (Minor et al., 1998; Vandehaar et al., 1999) can reduce plasma NEFA concentrations and improve energy balance (Rabelo et al., 2003) when DMI declines before calving. Although first-lactation heifers have a lower risk of ketosis and other illnesses associated with the transition period than older cows (Duffield et al., 1998b, 1999), prepartum monensin supplementation decreased BHB in early lactation regardless of parity (Duffield et al., 1998a; Petersson-Wolfe et al., 2007). In a New York study, increases in NEFA and BHB pre- and postpartum had negative effects on milk production and reproductive performance except in postpartum heifers. Heifers with NEFA ≥ 0.57 mEq/L had 488 kg more 305-d mature-equivalent milk and 403 kg more milk when BHB was ≥ 9 mg/dL (Ospina et al., 2010). Heifers also seem to respond differently than cows to anionic salts. Moore et al. (2000) found that compared with +15 or 0, diets with a DCAD balance of -15 mEq/100 g of DM reduced DMI, energy balance, and BW gain and elevated liver triglyceride in heifers when fed for 24 d before calving. Hayirli et al. (2002) evaluated 16 studies from 8 universities and found that heifer DMI before calving was fairly constant from 3 to 1 wk before calving, at around 1.7 to 1.8% of BW, but decreased to 1.23% of BW in the final week. Less overall depression

in DMI may be one factor contributing to a lower risk of health problems in the periparturient period for heifers compared with cows. Heifer DMI was also found to be more sensitive to increased ether extract in the diet compared with cows.

Daniels et al. (2007) demonstrated that milking heifers for 3 wk before their expected due date resulted in less edema, improved milk production and DMI, and lowered SCC after calving. In addition, training heifers to the parlor 2 wk before calving improved milk let down and reduced distress, but heifer temperament influenced the response to milking (Sutherland and Huddart, 2012). Kutzer et al. (2015) showed that training heifers habituated them to the milking routine but did not influence milk production.

Hoof Health

A study of lameness in Dutch herds (Amory et al., 2006) found that farms that fed corn silage to heifers had increased lameness in the milking herd compared with those that did not feed corn silage. In addition, heifers diagnosed with repeated cases of digital dermatitis during the rearing period showed decreased conception rates and less milk in first lactation (Gomez et al., 2015).

Danish researchers developed an oligofructose overload model for studying laminitis (Thoefner et al., 2004). This model successfully induced acute acidosis and enabled investigation of the clinical progression of symptoms and behavior and histological examination of lesions in hoof tissue (Thoefner et al., 2005; Danscher et al., 2009, 2010; Niss et al., 2009). This group also found that lameness, lesions, and abnormal conformation identified 41 d before calving persisted throughout first lactation (Capon et al., 2008). In addition, herd of origin and sample location affected strength of the suspensory tissue supporting the pedal bone within the claw more than induced laminitis (Danscher et al., 2010).

MODELING TO IMPROVE HEIFER MANAGEMENT DECISIONS

Modeling heifer programs has been a more recent endeavor that thus far has considered age at calving, breeding, and growth in the context of making effective management decisions. Mourits and colleagues described (Mourits et al., 1997) and then developed (Mourits et al., 2000) a dynamic programming model that would help evaluate heifer management decisions. With prepubertal ADG set at 900 g/d and maximum postpubertal ADG at 1,100 g, the model was optimized at 20.5 mo AFC and BW at calving of 563 kg. Key

factors in sensitivity analysis were growth rate and reproductive performance. Penn State researchers developed a tool to collect and calculate the costs of raising a dairy heifer (Gabler et al., 2000), which averaged approximately \$1,100 (\$1.50/d) at that time; feed costs were 62% of the total cost. This was followed by a multiple-component analysis of factors affecting the cost of raising heifers, which determined that herd cull rate and AFC had the greatest effect on the total cost (Tozer and Heinrichs, 2001). Another study incorporated nutrient variation in ration formulation for heifers (Tozer, 2000), which reduced diet cost and overfeeding of CP compared with more conventional methods of linear programming or adjusting requirements or rations to include a safety margin. Another published model found economic advantages to delaying the replacement of a culled cow with a heifer when fixed costs and net returns per space in the herd were low and seasonality of cow performance was high (de Vries, 2004).

SUMMARY AND FUTURE DIRECTIONS

The objective of rearing dairy replacement heifers has been described as minimizing required inputs while returning the most profitable outputs (Hoffman and Funk, 1992). To this, modern objectives must add limiting environmental impact and protecting animal welfare. To reduce inputs, a fundamental method is reducing rearing time. Early in the century and up to the 1980s, only modest progress was made in understanding dairy replacement heifer nutrient requirements and management in relation to improving growth rates and reducing AFC. However, in the past 30 yr, there has been consistent progress toward optimizing heifer growth rates and reducing AFC. It will be interesting to see how far and how long this trend continues until it plateaus. Continued research in this area should include information related to length and number of lactations as well as heifer age in the analysis.

In general, nutrition and management changes made in rearing the dairy heifer have been tremendous in the past 100 yr. The minimal amount of published heifer research likely slowed the rate of progress in the first half of the century. However, the second half has enjoyed significant basic nutrition research and applied management studies that have propelled our knowledge of the dairy heifer forward. Increasingly, farms have become more progressive in adopting management practices based on the physiology and nutrient needs of the heifer while refining key economic strategies to be successful. There remains opportunity for research to better understand the energy requirements and feed efficiency of heifers as they continue to mature at

younger ages of life. Along with the continuing growth in farm size and custom heifer raising, the heifer operation will increasingly be managed as its own enterprise on individual farms. By integrating reproductive (sexed semen), genetic (genomic testing and strategic culling), nutrition (limit feeding or other systems) with relation to environmental impacts, and management technologies (animal handling and behavior with an emphasis on animal well-being), the heifer operation will be a critical control point for accelerating whole-farm efficiency and sustainability. Research published in JDS has clearly had and will continue to have a tremendous influence on the progress of dairy heifer programs around the world.

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APPENDIX**Table A1.** Major milestones in the study of dairy heifer nutrition and management

Date	Milestone	Reference
1920	First growth standards for dairy heifers are published.	Eckles, 1920
1926	Research shows that vitamin A is essential, B is produced by rumen bacteria, and heifers can synthesize vitamin C.	Bechdel et al., 1926; Jones et al., 1926; Thurston et al., 1926
1939	The first studies using NPN to supplement protein in growing heifer diets are conducted.	Hart et al., 1939
1951	Feeding high energy could improve nitrogen retention of low-protein diets.	Lofgreen et al., 1951
1954	Beltsville heifer growth standards are published.	Matthews and Fohrman, 1954
1967	A series of papers is published describing optimal heifer growth to develop full lactation potential with minimum expense.	Swanson et al., 1967
1969	Schultz identifies a trend for earlier age at breeding and describes changes in the rearing system that would enable producers to reduce age at first calving.	Schultz, 1969
1971	A growth prediction equation is published based on diet energy and animal BW for heifers of all breeds from 4 to 22 mo of age.	Swanson, 1971
1976	Optimal age at first calving for total lifetime production is reported to be 22.5 to 23.5 mo.	Gill and Allaire, 1976
1977	The first study of accelerated growth and early breeding is published by Gardner et al. Heifers on the early breeding treatment calve at 19.7 mo of age.	Gardner et al., 1977
1986	Quigley and colleagues develop the first predictions of DMI for heifers.	Quigley et al., 1986a,b
1987	Growth standards based on population surveys are published for all dairy breeds.	Heinrichs and Hargrove, 1987
1988	Research shows that earlier age at first calving could be accomplished without hurting production and reproduction. From this point forward, average age at first calving declines in the industry.	Gardner et al., 1988; Lin et al., 1988
1992	The equation relating BW to heart girth is updated.	Heinrichs et al., 1992
1999	Limit feeding is introduced as a strategy for improving feed efficiency of dairy heifers.	Lammers et al., 1999
1999	Equations for beef cattle are adapted to develop targeted growth equations for dairy heifers based on mature size.	Fox et al., 1999
2004	The average age at first calving is 25.5 mo for Holsteins in the United States.	Hare et al., 2006
2005	A meta-analysis shows that the optimal ADG before puberty is 799 g/d.	Zanton and Heinrichs, 2005
2009	The optimal nitrogen intake for heifers is 1.67 g/kg of metabolic BW.	Zanton and Heinrichs, 2009