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Immunology

Concentration and heritability of immunoglobulin G and natural antibody immunoglobulin M in dairy and beef colostrum along with serum total protein in their calves

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Abstract

Immunoglobulin (**Ig**) G and natural antibody (**NAb**) IgM are passively transferred to the neonatal calf through bovine colostrum. Maternal IgG provides pathogen- or vaccine-specific protection and comprises about 85% of colostral Ig. NAb-IgM is less abundant but provides broad and nonspecific reactivity, potentially contributing to protection against the dissemination of pathogens in the blood (septicemia) in a calf's first days of life. In the dairy and beef industries, failure of passive transfer (**FPT**) of colostral Ig (serum total protein [**STP**] <5.2 g/dL) is still a common concern. The objectives of this study were to: (1) compare colostral IgG concentrations and NAb-IgM titers between dairy and beef cows; (2) assess the effect of beef breed on colostral IgG; (3) compare passive transfer of colostral Ig in dairy and beef calves; and (4) estimate the heritability of colostral IgG and NAb-IgM. Colostrum was collected from Holstein dairy (n = 282) and crossbred beef (n = 168) cows at the University of Guelph dairy and beef research centers. Colostral IgG was quantified by radial immunodiffusion and NAb-IgM was quantified by an enzyme-linked immunosorbent assay. In dairy (n = 308) and beef (n = 169) calves, STP was estimated by digital refractometry. Beef cows had significantly greater colostral IgG (146.5 ± 9.5 standard error of the mean [SEM] g/L) than dairy cows (92.4 ± 5.2 g/L, P <0.01). Beef cows with a higher proportion of Angus ancestry had significantly lower colostral IgG (125.5 ± 5.8 g/L) than cows grouped as "Other" (142.5 ± 4.9 g/L, P = 0.02). Using the FPT cutoff, 13% of dairy and 16% of beef calves had FPT; still, beef calves had a significantly larger proportion with excellent passive transfer (STP ≥6.2 g/dL, P <0.01). The heritability of colostral IgG was 0.04 (±0.14) in dairy and 0.14 (±0.32) in beef. Colostral NAb-IgM titers in dairy (12.12 ± 0.22, $\log_2$ [reciprocal of titer]) and beef cows (12.03 ± 0.19) did not differ significantly (P = 0.71). The range of NAb-IgM titers was 9.18–14.60, equivalent to a 42-fold range in antibody concentration. The heritability of colostral NAb was 0.24 (±0.16) in dairy and 0.11 (±0.19) in beef cows. This study is the first to compare colostral NAb-IgM between dairy and beef cows. Based on the range in NAb-IgM titers and the heritability, selective breeding may improve colostrum quality and protection for neonatal calves in the early days of life.

Lay Summary

Understanding how breed influences immunoglobulin (**Ig**) G and natural antibody (**NAb**) IgM concentrations in colostrum can improve bovine colostrum quality and calf health. Maternal colostral IgG is abundant, persistent, and pathogen specific. Natural antibody-IgM is less abundant but mediates broad, short-lived, nonspecific pathogen protection, and potentially important against septicemia. Colostral IgG and NAb-IgM concentrations were compared between dairy and beef cows and among cross-bred beef cows. Heritabilities were calculated to assess the practicality of selective breeding. Serum total protein (**STP**) in neonatal dairy and beef calves was estimated using refractometry. Colostrum from beef cows had higher concentrations of IgG than dairy cows. Beef cows with higher Angus ancestry produced colostrum with lower IgG concentrations than other mixed breeds. Heritability of colostral IgG was low (0.04–0.14). Failure of passive transfer was similar in dairy and beef calves, but a significantly larger proportion of beef calves had excellent STP (≥6.2 g/dL). There were no differences in NAb-IgM titers between dairy and beef cows or among beef breeds. Colostral NAb-IgM varied widely among individuals (42-fold) and was moderately heritable (0.11–0.24). These results suggest that selective breeding to improve colostrum quality is feasible and practical to improve calf health.

Key words: beef, colostrum, dairy, immunoglobulin, natural antibodies, passive transfer

Abbreviations: AIC, Akaike information criterion;ELISA, enzyme-linked immunosorbent assay;FcR, fragment crystallizable receptor;FPT, failure of passive transfer;IgG, immunoglobulin G;IgM, immunoglobulin M;KLH, keyhole limpet hemocyanin;NAb, natural antibody;PBS, phosphate buffered saline;RID, radial imm unodiffusion;STP, serum total protein

Introduction

Maternal immunoglobulins (**Ig**) are not transferred across the placenta to the fetal calf and are instead supplied through the colostrum (Godden et al., 2019). In colostrum, isotype IgG comprises 85% of total Ig, while IgM and IgA are present in lower quantities (Butler, 1983; Godden et al., 2019). Previous studies have estimated that the approximate half-life of colostral IgG is 20 d and IgM is 4.8 d (Butler, 1986; Murphy et al., 2014).

Factors such as production type (dairy or beef), breed, diet, colostral volume, season, parity, management, and environment can influence colostral components (McGee et al., 2005; Conneely et al., 2013; McGee & Earley, 2019). Colostrum quality is assessed by IgG content, with good quality

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colostrum containing >50 g/L (Kruse, 1970; Fleenor & Stott, 1980; Godden et al., 2019). If a calf does not receive an adequate mass of IgG in the first hours after birth, failure of passive transfer (**FPT**) occurs, resulting in limited absorption of IgG into the calf's circulation (Gay, 1983). Calves are negatively impacted by FPT, with decreased average daily weight gain and increased morbidity and mortality rates (Wittum & Perino, 1995; Waldner & Rosengren, 2009; Windeyer et al., 2014). Tyler et al. (1996) considered a calf serum total protein (**STP**) concentration <5.2 g/dL to indicate FPT; more recently, additional categories have been added to better quantify passive transfer. In addition, Windeyer et al. (2014) have noted that STP <5.7g/dL was a predictor for respiratory illness. Previous estimates of FPT in the literature range from 4.2% to 33.0% in dairy calves (Cuttance et al., 2017; Lopez et al., 2021) and 6.0% to 19.0% in beef calves (Filteau et al., 2003; Waldner & Rosengren, 2009).

Natural antibodies (**NAb**) are germline-encoded with minimal alterations and have an apparent ability to recognize a range of pathogens without exogenous antigen stimulation (Ochsenbein & Zinkernagel, 2000; Baumgarth et al., 2005). NAb represents a bridge between the innate and adaptive arms of the immune system with broad specificity (Ochsenbein & Zinkernagel, 2000). Reportedly, NAb is mainly of the IgM isotype and is derived from uncharacterized antibody-secreting cells in cattle. Natural antibody-IgM is found in circulation with an unknown half-life and has numerous characteristics including, polyreactive qualities, activating the complement system, preventing pathogen dissemination, and binding conserved epitopes (Thornton et al., 1996; Ochsenbein & Zinkernagel, 2000). Although NAb may have low-affinity binding power, IgM has a pentameric structure that increases the antigen-binding capability, which is useful for repetitive epitopes found on bacterial surfaces (Ochsenbein & Zinkernagel, 2000). Natural antibodies have been identified in bovine colostrum and can be passively transferred to the calf (Cordero-Solorzano et al., 2021). The ability of NAb-IgM to activate complement and assist in opsonization in a nonspecific manner could directly play a role in preventing pathogen dissemination in blood (septicemia), a common issue in neonates.

Assessing the differences in colostrum composition between dairy and beef cows and among beef breeds is valuable to highlight areas of improvement in management and breeding decisions to improve colostrum quality and calf health. The objectives of this study were to (1) compare colostral IgG concentrations and NAb-IgM titers between dairy and beef cows; (2) assess the effect of beef breed on colostral IgG; (3) compare passive transfer of colostral Ig in dairy and beef calves; and (4) estimate the heritabilities of colostral IgG and NAb-IgM. We hypothesized that beef cows would produce a greater concentration of colostral IgG, NAb-IgM, and have improved passive transfer in calves compared to dairy cows.

Materials and Methods

Animals

All procedures and samples collected for this study were approved under the University of Guelph Animal Utilization Protocol number 4449, and all guidelines were followed appropriately. Animals in this study were from the University of Guelph research herds at the Ontario Dairy Research Centre and Ontario Beef Research Centre, located near Elora, Ontario. All information on the cows were either gathered from the dairy's Dairy comp 305 via Valley Agriculture Software (VAS, Tulare, CA) or records obtained were from the beef research facility.

Over 2 yr, 50 mL of colostrum was collected, from each animal, within the first 14 h after calving from primiparous and multiparous dairy (n = 282) and beef (n = 168) cows. In dairy cattle, year-round from June 2018 to January 2020, colostrum was milked out, mixed well in a bucket milker, and a 50-mL sample was collected using a ladle. After collection at the dairy farm, refractometry readings were taken using a digital Brix refractometer (Calf Hero Colostrum Supplies) to assess total colostral protein. Samples of beef cow colostrum and calf serum were collected in 2018 and 2019 during the spring calving season from March to May. The 2018 beef colostrum and calf serum samples were graciously provided by Dr. Katie Wood's laboratory from the Department of Animal Biosciences at the University of Guelph. In beef cows, the collection method differed such that teats were stripped by hand, and samples from all four quarters were collected into a strip cup and then transferred into a 50-mL conical tube. Refractometry readings were collected at a later date from beef colostral samples using the same digital Brix refractometer used at the dairy farm. A portion of dairy colostrum samples (n = 11) were collected using the same method as beef colostrum and compared to colostrum collected from the same dairy cows using a bucket milker. Samples collected more than 14 h after calving were removed from the data set. Once colostrum was collected, it was immediately frozen at −20 °C. When samples were processed, colostrum was thawed overnight at 4 °C. The following day, quality notes were taken, and the sample was centrifuged for 15 min at 5,000 × g. Samples were then defatted and centrifuged for another 15 min at 11,000 × g. If there was any remaining fat, the sample was defatted and then aliquoted and stored at −20 °C.

In this study, all dairy cows were purebred Holstein-Friesians. Beef breed data were available from the Go360 bioTrack database (Agsights, Elora, ON). The beef cows in the University of Guelph research herd are crossbreeds, assessed by the number of progenitors in each breed category. For the analysis, information on 32 progenitors (accounting for 5 generations) was used to categorize animals by breed proportions. Angus, Simmental, and Piedmontese breeds contributed to the mixed parentage of the herd. During our study, dairy cows received dry period diets that differed as either low energy with high fiber or a control diet. Over the 2-yr study period, there were eight different diet groups for beef cows that were ongoing trials. These diets differed in crude protein and supplementation of rumen methionine.

Holstein-Friesian dairy calves were born year-round from dams aged 2–10 yr of age. Both heifer (n = 156) and bull calves (n = 153) were included in this study. Dairy calves received a 2.5% iodine navel dip immediately following calving and were administered an oral bovine rotavirus-coronavirus vaccination 30 min before colostrum consumption. The calf was then fed 3 L of colostrum via bottle or esophageal tube during the first 2 h of life. If the calf was born overnight, colostrum was fed as soon as possible. Calves were fed fresh colostrum from their dam unless the specific gravity was <22%Brix, then the calf was fed high-quality frozen colostrum or colostrum replacer. Only calves that received their own dam's colostrum were included in this study. Following colostrum consumption, calves received a vitamin E/selenium

injection. Calves were offered another 3 L of colostrum or two bags of colostrum replacer 6–12 h after the first feeding.

Crossbreed beef calves were born to dams aged 2–10 yr of age. Both heifer (n = 101) and bull (n = 68) beef calves were included in this study. Beef calves received a navel dip and a vitamin E/selenium injection. In addition, calves were monitored for colostrum feeding while remaining with their dam. Calves that had difficulties suckling from their dams were assisted by staff to ensure adequate colostrum intake.

A single 10 mL tube of blood was collected with BD vacutainer blood tubes with no anticoagulant (Thermo Fischer Scientific, Waltham, MA) from the jugular vein of dairy (n = 308) and beef (n = 169) calves at 2–8 d of age. Blood was centrifuged at 1,000 × g for 15 min, and serum was collected. A digital refractometer (model KS-0050, Kernco Instruments, El Paso, TX) was used to estimate STP after collection, and then serum samples were stored at –20 °C.

Total IgG

According to the manufacturer's guidelines, total IgG concentrations of colostrum were measured using radial immunodiffusion (**RID**; Triple J Farms, Bellingham, WA). Colostrum samples were diluted 1/8, and then a single sample was added at 5 µL/well. After 24 h, the diameter of the precipitin ring that formed was measured. If the precipitin ring formed was outside of the range of the assay standards, the dilution was adjusted accordingly, and the sample was retested. A standard curve was derived from the standards 2,803, 1,472, and 180 mg/dL provided in the kit, and the sample IgG concentration was derived from the standard curve. All RID plates (Lot#728411) and standards (Lot#7286) used in this study were consistent.

Natural antibody

An indirect enzyme-linked immunosorbent assay (**ELISA**) method was used to assess colostral NAb-IgM titers. Keyhole limpet hemocyanin (**KLH**) was used as an antigen to provide a surrogate measure of NAb (de Klerk et al., 2018; Cordero-Solorzano et al., 2019; Chen et al., 2020). The antigen KLH is derived from *Megathura crenulata*, a mollusc species cattle have likely not encountered in their environment. Immulon 2HB 96 well plates (catalog #14-245-61, Thermo Fisher) were coated for 12 h at 4 °C with 50 µg/mL of KLH (catalog #H7017, Sigma-Aldrich, St. Louis, MO) in phosphate-buffered saline (PBS, pH 7.4). Plates were then washed three times using a wash buffer (PBS with 1% tween-20) and then blocked with 5% fish skin gelatin (catalog #G7765, Sigma-Aldrich) in PBS. Plates were then incubated for 1 h at room temperature, and then plates were washed three times with wash buffer. Colostral samples were diluted 1/300 and 1/600 in wash buffer containing 2.34M NaCl with 1% tween-20. About 100 µL of each sample and controls were added to wells in quadruplicate. Plates were incubated for 2 h at room temperature and then washed three times with wash buffer. A primary monoclonal mouse anti-bovine IgM antibody solution of 1/6,500 in wash buffer (BM-23, catalog #I6137, Sigma-Aldrich) was added to the plate (100 µL/well) and incubated for 1 h at room temperature. Following the primary antibody, plates were washed five times with wash buffer. Then the secondary reagent of monoclonal rat anti-mouse IgG1 antibody conjugated to alkaline phosphatase (clone X56, catalog #557272, BD Pharmingen, Franklin Lakes, NJ) was added at 1/2,000 in tris-buffered saline and incubated for 1 h at room temperature. Plates were washed five times with wash buffer, and 100 µL of *p*-nitrophenyl phosphate substrate buffer (catalog #N2770, Sigma-Aldrich) was added to induce a color change. Plates were developed in the dark, and after 30 min, plates were read using a BioTek ELISA plate reader (BioTek Winooski, VT) at 405 and 630 nm to obtain optical densities. If the coefficient of variation among quadruplicates of positive controls or samples was >15%, the value was rejected, and the sample was rerun.

Preliminary ELISA allowed for the identification of colostral samples with high NAb-IgM titers. High titer colostrum samples were then pooled to form a positive control preparation. A dilution series of the positive control was included on all plates. Colostral samples were assayed at a fixed dilution, sample optical densities were averaged, and titers were calculated relative to the standard curve after adjusting for dilution (Leinikki & Passila, 1977; Sacks et al., 1988). Titers are reported as the $\log_2$ of the reciprocal of the calculated titer. Fetal bovine serum was used as a negative control. Colostrum samples were run in parallel on PBS-coated wells (with no bound KLH) to monitor the nonspecific binding of IgM directly to the plates. The intraplate and interplate coefficients of variation were 0.46% and 1.93%, respectively.

Statistical analysis

Samples were collected from dairy and beef cows in different parities (1, 2, and ≥3), and cows were from various ages (2–10 yr of age). Cows over 10 yr of age were removed from the mixed model analyses. The season of sample collection was included as spring (March 21–June 20), summer (June 21–September 20), fall (September 21–December 20), and winter (December 21–March 20). The year of calving (2018, 2019, and 2020) was also included in models when significant. In total, there were 10 different diet groups. The calving time (a.m., p.m., and overnight) was included to account for overnight births, which were mainly unmonitored. The month that the RID or ELISA was completed was included in the model to help act as a laboratory control in addition to the positive and negative controls. Mixed models were chosen according to the Akaike information criterion (**AIC**).

Data for colostral IgG and NAb-IgM were available for 282 dairy cows and 168 beef cows. The data from this study were analyzed using the mixed model procedure of Statistical Analysis Software (**SAS**) version 9.4 (SAS Institute Inc., Raleigh, NC). Categorical variables such as calving time, the month that the RID assay was performed (January–December), parity (1, 2, and ≥3), production type (dairy or beef), and the interaction between production type and parity were included in the model to assess colostral IgG. In addition, the random effect of individual cows was included. Variables such as season, diet, age, and year were removed from the model due to a lack of significance. Parity was used instead of age according to the AIC value.

For the analysis of NAb-IgM titers, the colostral refractometry %Brix was included as a covariate. Categorical variables such as production type (dairy or beef), year of sampling, calving time, parity, and the month the NAb ELISA was completed were included. In addition, the random effect of individual cows was included. The variables season, age, and diet were excluded from the models due to a lack of significance. Parity was used instead of age according to the AIC value. The Proc Corr function was used in SAS to calculate the Pearson correlation coefficient and P-value of the association between

colostral IgG concentration and NAb-IgM titers as well as the association between volume of dairy colostrum produced and IgG concentration or NAb-IgM titer.

To evaluate differences associated with breed proportions, cows were grouped into "high Angus ancestry" if >50% of their progenitors were Angus (n = 68) or "Other" if they had ≥50% of progenitors grouped in Piedmontese, Simmental, and other (n = 100). The mixed model to assess differences in colostral IgG by beef breeds included the breed group (high Angus ancestry or Other), parity (1, 2, and ≥3), and calving time (a.m., p.m., or overnight) as categorical variables. The model also included the random effect of individual cows. Variables such as season, year, age, diet, and month of the RID assay were excluded due to a lack of significance. The least square (**LS**) means were computed, and significant differences were reported at a P-value of ≤0.05, while tendencies were reported at P-value ≤0.10. The same analysis was completed to assess colostral IgG and NAb-IgM associations with breeds such as Simmental and Piedmontese. Data were normally distributed, except for the comparison between dairy and beef colostral IgG, where data were transformed by taking the square root and then LS means were transformed back to the original units.

Distributions of estimated STP in neonatal dairy and beef calves were compared using a Wilcoxon–Mann–Whitney nonparametric test. Estimated STP was assessed using Windeyer et al. (2014) predictor values for mortality (FPT <5.2 g/dL) and respiratory illness (<5.7 g/dL). Estimated STP was also evaluated using Godden et al. (2019) guidelines (poor [<5.1 g/dL], fair [5.1–5.7 g/dL], good [5.8–6.1g/dL], and excellent [≥6.2 g/dL]). Fisher's exact test was used to assess the difference between the proportion of dairy and beef calves with FPT (STP <5.2 g/dL) or excellent transfer (STP ≥6.2 g/dL). The Proc Corr procedure in SAS was used to obtain the Pearson correlation coefficients and their P-values to quantify associations between dam colostral IgG and the calf STP, STP and calf weight, and STP and day of blood sampling.

The intra-herd heritability estimates of colostral IgG and NAb-IgM were calculated separately in dairy and beef cows using ASReml 4.1 (Gilmour et al., 2015). For beef cows, the pedigree file contained 1,345 identities over 8 generations. For dairy, a pedigree including 18,074 identities over 44 generations was provided by Lactanet (Guelph, ON). The models for dairy and beef contained the fixed effect of parity, year of sampling, age, antibody-mediated immune response category based on estimated breeding value (high, average, or low), the number of Angus progenitors, the random effect of animal, and residual error. Heritability was calculated as the ratio of additive genetic variance to total phenotypic variance (sum of additive genetic variance and residual variance).

Results

Comparison of total IgG between dairy and beef colostrum

Colostral IgG in dairy and beef cows ranged from 15.4 to 274.4 g/L (Supplementary Figure S1), with an arithmetic mean of 111.7 g/L. Descriptive statistics for IgG in dairy and beef colostrum can be found in Table 1. Total IgG was significantly greater in colostrum from beef cows (LS mean 146.5 ± 9.5 standard error of the mean [**SEM**] g/L) than dairy cows (LS mean 92.4 ± 5.2 SEM g/L, P < 0.01). Calving time as a categorical variable was significant (P < 0.01), and cows that calved overnight had colostrum samples with significantly less IgG than cows that calved in the morning or afternoon (P < 0.01). The month that the RID assay was completed was not significant (P = 0.12) but was forced into the model since it improved the AIC and acted as a control for laboratory conditions and the date of testing. Parity (P < 0.01) and the interaction between production type and parity were significant (P < 0.01). Colostral IgG increased with parity, but the increase was more prominent in dairy cows. In beef cows, there was no significant increase with parity (Supplementary Figure S2).

Table 1. Descriptive statistics of colostral IgG, NAb-IgM to KLH, and STP in dairy and beef cows and calves

Herd	Component	Mean	Median	Standard deviation
Dairy	IgG, g/L[1]	102.34	97.18	45.58
	NAb-IgM, titer[2]	11.84	11.96	0.83
	Calf STP, g/dL[3]	5.77	5.70	0.71
Beef	IgG, g/L	143.04	142.10	46.10
	NAb-IgM, titer	11.94	12.06	0.87
	Calf STP, g/dL	6.07	6.00	1.04

[1]Descriptive statistics including the arithmetic mean, median, and standard deviation of the concentration of IgG (g/L) in colostrum from Holstein-Friesian dairy (n = 282) and crossbred beef (n = 168) cows.
[2]Descriptive statistics including the arithmetic mean, median, and standard deviation of NAb-IgM to KLH in colostrum from Holstein-Friesian dairy (n = 282) and crossbred beef (n = 168) cows. Titers are expressed as the $\log_2$ of the reciprocal of the calculated titer.
[3]Descriptive statistics including the arithmetic mean, median and standard deviation of STP (g/dL) in dairy (n = 308) and beef calves (n = 169) at 2–8 d of age.

In beef cows, 98.2% of colostral samples had IgG concentrations greater than the recommended 50 g/L. In dairy cows, 90.1% of colostrum samples had greater IgG concentrations than the recommended 50 g/L. Volume data were not available on colostrum produced from beef cows, but in dairy, there was no correlation between colostral IgG and volume of colostrum produced (R = –0.02, P = 0.73, Supplementary Figure S3).

As mentioned in the Material and Methods section, dairy and beef colostrum collection methods were compared. Hand-stripped samples and samples collected using a bucket milker were analyzed using linear regression. The correlation of colostral IgG concentrations between the two collection methods was 0.98 (P < 0.01), with a range in differences (bucket-milked minus hand-milked) of samples from –2.2 to 8.0 g/L. On average, hand-stripped samples had lower concentrations of IgG by 6.4 g/L in comparison to samples collected using a bucket milker (data not shown). Thus, there was a high correlation between the IgG concentrations in samples collected by the two methods, and the magnitude of the differences was small relative to the mean concentration of IgG in colostrum.

Effect of Angus progenitors on colostral IgG

The range in colostral IgG was large in beef cows (15.8–274.4 g/L) with an arithmetic mean of 143.1 g/L. Cows grouped as high Angus ancestry had significantly lower colostral IgG (LS means 125.5 ± 5.8 SEM g/L) than cows grouped as "Other" (LS means 142.5 ± 4.9 SEM g/L, P = 0.02). No significant differences in colostral IgG concentration were

seen with Simmental and Piedmontese breed classifications, and there were no significant differences in NAb-IgM titers among breed classifications. Neither cow age nor parity was significant separately, so parity was forced into the model. Calving time as a categorical variable was significant in the model; colostral samples from cows that calved overnight had significantly lower IgG concentrations than cows that calved in the morning ($P < 0.01$) or afternoon ($P < 0.01$).

Comparison of colostral NAb-IgM titers between dairy and beef

The colostral NAb-IgM titers varied among individuals (9.18–14.60, $\log_2$ of the reciprocal of the calculated titer) and was equivalent to a 42-fold range in antibody concentrations, with an arithmetic mean of 11.88 ($\log_2$ scale). Descriptive statistics on NAb-IgM titers in colostrum from dairy and beef cows can be found in Table 1. The LS mean titers of NAb-IgM were slightly higher for colostrum from dairy cows (12.12 ± 0.22 SEM $\log_2$ scale) than for beef cows (12.03 ± 0.19 SEM $\log_2$ scale), but the difference was not significant ($P = 0.71$). Parity was not significant, but it was forced into the model (data not shown). The covariate, %Brix was significant in the model ($P < 0.01$) and was positively associated with colostral NAb-IgM. There was a trend for the categorical variable calving time ($P = 0.068$), where overnight calvings resulted in lower NAb-IgM titers in colostrum than morning or afternoon calvings. The year of sample collection was not significant. The month that the NAb ELISA was completed in the laboratory was significant in the model and was included to act as a control for laboratory conditions.

For both dairy and beef cattle, colostral NAb-IgM titers were positively and significantly correlated with colostral IgG concentrations. In dairy cows, the correlation of colostral NAb-IgM titers with colostral IgG concentration was 0.36 ($P < 0.01$). In beef cows, the correlation of colostral NAb-IgM titers with colostral IgG concentration was 0.29 ($P < 0.01$). There was no correlation between the volume of colostrum produced by dairy cows and colostral NAb-IgM titers ($R = 0.07$, $P = 0.25$, Supplementary Figure S4).

Passive transfer in dairy and beef calves

Estimates of STP in dairy calves ranged from 3.8 to 8.1 g/dL, with a median of 5.7 g/dL. In dairy calves, 13.0% experienced FPT with estimates of STP <5.2 g/dL, and 46.0% were at an increased risk for respiratory illness before 5 wk of age using the predictor value of <5.7 g/dL. In beef calves, estimates of STP ranged from 3.3 to 9.1 g/dL, with a median of 6.0 g/dL. In the beef calves, 16.4% experienced FPT with estimated STP <5.2 g/dL, and 36% were at risk for developing respiratory illness before 5 wk of age using the predictor value of <5.7 g/dL. According to Fisher's exact test, there was no significant difference between dairy and beef FPT groups (<5.2 g/dL, $P = 0.29$). According to the recent calf STP guidelines published by Godden et al. (2019), 10.7%, 44.0%, 20.7%, and 24.6% of dairy calves fell into the categories of poor, fair, good, and excellent passive transfer, respectively. In beef calves, 15.3%, 23.8%, 19.6%, and 41.3% fell into the categories of poor, fair, good, and excellent passive transfer, respectively. Using Fisher's exact test, there was a significantly larger proportion of beef calves that fell into the "excellent" passive transfer group (STP ≥ 6.2 g/L) than dairy calves ($P < 0.01$). The distribution of calf STP, as described above, differed significantly between dairy and beef calves (Wilcoxon–Mann–Whitney nonparametric distribution test, $P < 0.01$, Figure 1). There were no significant differences in the distribution of calf STP by year or sex in either beef or dairy calves using a Wilcoxon–Mann–Whitney nonparametric test.

There was a significant and positive correlation between IgG in beef cow colostrum and estimated STP in beef calves in 2018 ($R = 0.38$, $P < 0.01$, $n = 59$ cow–calf pairs) but less so in 2019 ($R = 0.10$, $P = 0.51$, $n = 43$ cow–calf pairs). In dairy calves, the significant and positive correlation of estimated STP in calves with their dam's colostrum was 0.37 ($P = 0.02$, $n = 40$ cow–calf pairs). There was a negative and significant correlation with STP and the day the serum sample was collected following calving ($R = -0.23$, $P < 0.01$); as the number of days increased before sampling, there was a decrease in STP. Based on the linear regression, with each increase in day from the second day of sampling, STP values decrease by 0.12 g/dL, meaning by day 8 of sampling, STP values may have decreased by 0.71 g/dL. There was no significant correlation between STP readings and calf birth weight (data not shown).

Heritability of colostral IgG and NAb-IgM titers in dairy and beef cows

The heritability of IgG and NAb-IgM to KLH in dairy and beef cows was calculated using ASReml. The heritability of colostral IgG and NAb-IgM in dairy cows was 0.04 (SE ± 0.14) and 0.24 (SE ± 0.16), respectively. The heritability of colostral IgG and NAb-IgM in beef cows was 0.14 (SE ± 0.32) and 0.11 (SE ± 0.19), respectively. Heritability estimates for both dairy and beef cows are imprecise due to the small sample size.

Discussion

Colostral IgG in dairy and beef cows

The current study findings are consistent with estimates of IgG concentrations in dairy (65.7–112.0 g/L; Conneely et al., 2013; Elsohaby et al., 2018) and beef colostrum (143.3–154.7 g/L) (Homerosky et al., 2017; Elsohaby et al., 2018). Guy et al. (1994) suggested that lower colostral IgG

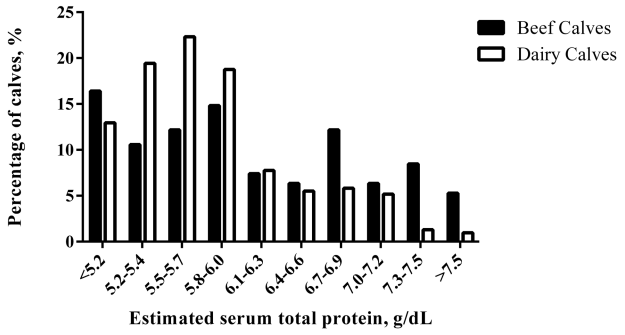

Figure 1. Estimated STP distribution in dairy (white, $n = 308$) and beef (black, $n = 169$) calves aged 2–8 d of age. STP was measured using a digital refractometer and the distribution was compared using a Wilcoxon–Mann–Whitney nonparametric test ($P < 0.001$). Refractometry values range from 3.3 to 9.1 g/dL. The median STP estimate for dairy calves was 5.7 g/dL and for beef calves, the median STP estimate was 6.0 g/dL.

concentrations in dairy may be attributable to a dilution factor caused by the larger volume produced by dairy cows. There was no correlation between colostrum volume and IgG in dairy in the current study, which suggests the difference between dairy and beef colostrum is not entirely attributable to volume.

In dairy cows in this study, colostral IgG significantly increased with increasing parity. Moore et al. (2005) and Tyler et al. (1996) have reported higher concentrations of colostral IgG in dairy cows with increasing parity, but Johnsen et al. (2019) reported no effect of parity. In beef cows, concentrations of colostral IgG did not differ significantly by parity; first-calf beef heifers produced colostrum with high concentrations of IgG, comparable to those of high parity beef cows. Genetics can also influence colostral IgG. Fleming et al. (2016) reported that dairy cows identified as high antibody-mediated immune responders produced colostrum with significantly greater colostral IgG concentrations than average or low immune responders. A similar analysis should be completed on beef cows to assess the effect of genetics on colostral IgG.

Time of colostrum collection can also influence colostral IgG. Moore et al. (2005) have reported a significant decrease in colostral IgG collected 6 and 14 h following calving compared to 2 h. In the current study, calvings that occurred overnight had significantly lower IgG in colostrum, likely caused by a delay in collection or the calf suckling before sample collection.

The effect of Angus progenitors on colostral IgG

In the current study, cows with a high Angus ancestry had significantly lower colostral IgG than cows with more diverse ancestry. These findings support other studies investigating breed effect on colostral IgG. McGee et al. (2005) reported cows of a beef × Holstein-Friesian cross produced colostrum with a greater concentration of IgG than purebred Charolais beef cows. In addition, Norman et al. (1981) reported that Hereford × Angus cows produced colostrum with greater IgG than purebred Hereford cows. However, there are conflicting results regarding the influence of breed on colostral IgG. For example, studies report no difference in colostral IgG in beef breeds (Vandeputte et al., 2014; Earley et al., 2018). Further studies with larger sample sizes are needed to investigate breed and crossbreeding effects on colostral components.

Colostral IgM natural antibodies in dairy and beef cows

To the authors' knowledge, this study is the first to compare NAb-IgM in colostrum from dairy and beef cows. Due to previous comparisons, it was hypothesized that colostral NAb-IgM titers would be greater in beef colostrum due to a dilution factor in dairy cows. In this study, there was no significant difference between colostral NAb-IgM titers in dairy and beef cows and no effect of volume; however, there was a 42-fold difference in concentrations of probable biological importance. The half-life of maternal IgM in the circulation of neonatal calves has been estimated to be 4.8 d (Butler, 1986). Maternal (colostral) NAb-IgM, that is primarily confined to the circulatory system of calves due to its large molecular size, could be crucial for defense against septicemia in the first days of life. Polyvalent NAb-IgM can bind repetitive and conserved epitopes on bacterial surfaces (Wang et al., 2016). Although NAb-IgM may have low affinity, the pentameric structure of IgM provides highly efficient complement activation (Thornton et al., 1996). Fragment crystallizable receptors (FcR) for IgM have not yet been identified in cattle, but two distinct receptors (Fc alpha/mu R [Fcα/μR] and Fc mu R [FcμR]) have been identified in both mice and humans (Shibuya et al., 2000; Wang et al., 2016). Thus, IgM can enhance phagocytosis of pathogens due to the deposition of complement proteins on the microbial surface, which leads to the uptake by phagocytes via complement receptors or receptors for the Fc region of IgM (Wang et al., 2016). Since IgM is a major circulatory Ig isotype, it can recognize initial bacterial infections and prevent dissemination throughout the body (Ochsenbein & Zinkernagel, 2000) of the neonatal calf. The wide range of colostral concentrations of NAb-IgM among cows presents a promising opportunity for selective breeding to improve colostrum quality and neonatal health.

Reports of the impact of parity on NAb-IgM are inconsistent. Ploegaert et al. (2011) and Thompson-Crispi et al. (2013) reported no difference in NAb-IgM by parity in serum or milk; however other studies have noted increases in NAb-IgM with increasing parity in serum and milk (Van Knegsel et al., 2007; de Klerk et al., 2015). In this study, parity was not significant. Interestingly, overnight calvings resulted in decreased colostral NAb-IgM titers, which is likely due to a delay in collection (Moore et al., 2005) and calves suckling. Further work is needed to understand the influence of environmental factors on NAb-IgM.

Passive transfer in dairy and beef calves

The median STP estimates for calves in this study were consistent with published data for dairy (5.7–6.2 g/dL; Todd et al., 2018; Renaud et al., 2020) and beef calves (5.9–6.6 g/dL; Todd et al. 2018; Gamsjäger et al., 2021). Using the STP cutoff <5.2 g/dL, Windeyer et al. (2014) found that 11% of dairy calves had FPT, whereas Renaud et al. (2020) found that 24% of dairy calves had FPT. The predictor STP value <5.2 g/dL suggests these calves would have an increased mortality risk in the first 5 wk of life, consistent with findings from Wittum et al. (1995). Higher calf serum IgG is associated with decreased morbidity and increased average daily gain (Waldner & Rosengren, 2009; Urie et al., 2018). Windeyer et al. (2014), using the 5.7 predictor value for respiratory illness, reported that 32% of pre-weaned dairy calves were at risk. Using the same predictor value in the current study, 46% of preweaned dairy calves and 36% of beef calves were at risk. The use of the respiratory illness predictor value (5.7 g/dL) for beef calves needs to be validated since beef calves are raised in different environments with different pathogenic pressures.

According to recent guidelines to reduce calf morbidity (Godden et al., 2019), beef calves had the largest proportion of calves in the "excellent" passive transfer category (STP ≥ 6.2 g/dL). Beef calves can suckle freely from the dam allowing unrestricted colostrum consumption and natural mothering behaviors. On the other hand, beef calves may also have issues with vigor, causing a delay in colostrum consumption, contributing to calves with FPT. Homerosky et al. (2017) and Stott et al. (1979) noted that beef calf vigor and calving ease play a crucial role in the success of passive transfer. In contrast, dairy calves often receive monitored bottle-feedings to ensure adequate volume and quickness, leading to uniform consumption.

Heritability of colostral IgG and NAb-IgM

The estimates of the heritability of IgG and NAb-IgM in dairy and beef cows were relatively low with large standard errors, attributable to this study's small sample size. The heritability of colostral IgG1 has been estimated to be 0.28 ± 0.14 SE in Charolais beef cows (Martin et al., 2021). In Irish dairy cows, Conneely et al. (2013) estimated the heritability of colostral IgG to be 0.10 ± 0.07 SE, similar to the results of our study. In our study, heritability estimates of colostral IgG were low in dairy and beef, but the higher heritability in beef cows may be associated with low colostrum volume with high IgG concentrations.

The heritability of NAb-IgM from Holstein-Friesian cows has been estimated to be 0.31 ± 0.065 in serum (de Klerk et al., 2018) and 0.41 ± 0.09 in milk (Cordero-Solorzano et al., 2019). Recently, the heritability of colostral NAb-IgM in dairy cows was estimated to be 0.23 ± 0.13 (Cordero-Solorzano et al., 2021), consistent with the current study's findings. To the authors' knowledge, the current study is the first attempt to estimate the heritability of colostral NAb-IgM in beef cows. In beef cows, the estimated heritability of colostral NAb-IgM is lower than in dairy, which may be an artifact of the sample size and possible breed effects. Confirming the findings from the research herds in commercial herds will provide more confidence in the heritability estimates and in the practicality of selecting for these traits on farm.

Conclusion

Evaluating colostral components between dairy and beef cows is difficult due to the large differences in management and environment, but the comparison is still valuable in understanding the influence of breed and production type. As previously noted in the literature, colostral IgG concentrations were higher for beef cows than dairy cows. Colostral IgG was significantly lower in beef cows with high Angus ancestry, which may warrant further investigation of the effect of crossbreeding on colostral components. This study is the first to measure and estimate the heritability of NAb-IgM in beef colostrum while producing a comparison with dairy colostrum. There was no significant difference in colostral NAb-IgM between dairy and beef, but there was a 42-fold range in concentration of colostral antibodies among individuals showing potential for selective breeding. Although the role and half-life of NAb-IgM in the first week of life requires further investigation, colostral NAb-IgM could help protect against septicemia. Determining the heritability and feasibility of selecting cows with improved colostrum quality will improve calf health.

Our study suggests similarities in the trends of passive transfer between dairy and beef calves, but the factors contributing to success may differ. Understanding these trends will provide further insight into management or genetic causes that could be modified to provide better passive immunity to calves, ultimately improving protection to the neonatal calf.

Supplementary Data

Supplementary data are available at *Journal of Animal Science* online.

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Conflict of Interest Statement

The authors declare that there are no conflicts of interest in the publication of this article.

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