Effects of spring- versus fall-calving on perinatal nutrient availability and neonatal vigor in beef cattle

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ABSTRACT
To determine the effect of calving season on perinatal nutrient availability and neonatal beef calf vigor, data were collected from 4 spring-average calving date: February 14; n = 203 total) and 4 fall- (average calving date: September 20; n = 179 total) calving experiments. Time to stand was determined as minutes from birth to standing for 5 s. After birth, calf weight and size (length, heart and abdominal girth, and cannon circumference) were recorded. Jugular blood samples and rectal temperatures were obtained at 0, 6, 12, and 24 h postnatally in 6 experiments and at 48 h postnatally in Exp. 2 to 8. Data were analyzed with fixed effects of season (single point) or season, hour, and their interaction (over time, using repeated measures). Experiment was a random effect; calf sex was included when P ≤ 0.25. Within calving season, correlations were determined between calf size, vigor, and 48-h serum total protein. Fall-born calves tended to have lighter (P = 0.09) birth weight and faster (P = 0.05) time to stand than spring-born calves. Season did not affect (P ≥ 0.18) gestation length, other calf size measures, or 48-h serum total protein. Fall-born calves had greater (P ≤ 0.003) rectal temperature at 0, 24, and 48 h postnatal. Spring-born calves had greater (P ≤ 0.009) circulating glucose at 0 h, serum non-esterified fatty acids at 0 and 6 h, and plasma triglycerides at 0, 6, 12, and 48 h. Fall-born calves had greater (P ≤ 0.03) sodium from 6 to 48 h and magnesium from 0 to 24 h of age. Phosphorus was greater (P ≤ 0.02) at 6 and 12 h of age in spring-born calves. Spring-born calves had greater (P ≤ 0.04) aspartate aminotransferase at 12 and 24 h and creatine kinase at 0 and 12 h of age. Fall-born calves had greater (P ≤ 0.03) albumin, calcium, and chloride, had lower (P < 0.03) bicarbonate and direct bilirubin, and tended to have greater (P = 0.10) anion gap (all main effects of calving season). Calf birth weight had a weak positive relationship (P ≤ 0.003) with 48-h serum total protein and time to stand in fall-born, but not spring-born, calves. Overall, fetal growth was restricted and neonatal dehydration was increased by warm conditions for fall-born calves, but vigor and metabolism were negatively affected by cold conditions in spring-born calves. These data suggest that calving season influences perinatal nutrient availability, which may impact the transition of beef calves to postnatal life.

Key words: cold stress, developmental programming, heat stress, metabolism, neonate, pregnancy

INTRODUCTION
Survival of beef calves requires appropriate fetal development and successful transition from intra- to extra-uterine life (Danijela, 2015). Both the maternal environment and outside environment into which they are born can greatly affect the perinatal nutrient availability and survival of calves (Arnott et al., 2012). Beef cows and heifers in the U.S. are commonly bred to calve in 2 general calving seasons: “spring” (often considered January to May) and “fall” (often considered late August to November). In many regions of the U.S., such as the lower Midwest, these seasons can have very different calving conditions. Calves born in spring may experience cold stress conditions following birth which suppresses neonatal vigor (Olson et al., 1980b) and increases mobilization of their energy stores to maintain body temperature, impacting their metabolic status (Vermorel et al., 1983). Conversely, calves born in fall often experience late gestational heat stress in utero, which has been shown in dairy calves to compromise fetal growth and alter neonatal metabolism and immune function (Dahl et al., 2019).

Additionally, forage quality and availability during late gestation can vary widely for spring- and fall-calving dams, along with differing energy demands and forage intakes of beef females due to ambient temperatures. Despite the wealth of knowledge on how maternal nutrition during gestation influences fetal growth and development in cattle (Caton and Hess, 2010; Funston et al., 2010; Perry et al., 2019), limited research has been conducted on how calving season differences may affect perinatal nutrient availability of calves. Therefore, our objectives were to: 1) determine the effect of calving season on perinatal nutrient availability and neonatal vigor in beef calves and 2) determine the relationships of beef calf vigor and size with passive transfer within calving season. We hypothesized that fall-born calves have decreased fetal growth but improved vigor and passive transfer compared with spring-born calves, and that postnatal cold stress would alter neonatal circulating metabolites of spring-born calves.
Gestating Animal Management

**All experiments.** Four spring-calving experiments with an average calving date of February 14 and 4 fall-calving experiments with an average calving date of September 20 were conducted at the University of Missouri Beef Research and Teaching Farm (Columbia, Missouri). Calving experiment details, weather conditions (from a weather station located on the same farm), calf sex, and dam characteristics are provided for each of the 8 experiments in Table 1. Multiparous and primiparous beef dams were utilized in 1 spring (Exp. 5) and 2 fall (Exp. 3 and 7) experiments, whereas the other 3 spring (Exp. 2, 4, and 5) and 2 fall (Exp. 6 and 8) experiments used strictly multiparous beef cows. Females were either bred only by artificial insemination (AI; Exp. 3 and 5) or AI followed by natural service (all other experiments). Sire number per experiment ranged from 1 to 4, and natural service sires had overlap between seasons. In all 8 experiments, animals were part of larger groups of females observed for peripartum data collection, and animal numbers included in this analysis are reported for each experiment in Table 1.

Pregnant females were weighed [single-day body weights (BW), 12 ± 9.4 d (standard deviation here and throughout) pre-calving] and moved to well-drained 18 × 61 m dry lot calving pens (description and diagram in Duncan and Meyer, 2019) for observation and data collection during the peripartum period. Peripartum body condition score (BCS; −9.1 ± 14.4 d (SD) relative to calving) was determined by 2–3 trained technicians (depending on experiment, 1 common technician for all experiments) using a 1 to 9 scale (1 = emaciated, 9 = obese), and the mean BCS across technicians was used.

During the peripartum period, harvested forage (described below for each experiment) was fed ad libitum in round bale feeders with cone chains placed on 9.1 × 9.1 m concrete pads in the middle of these calving pens to minimize waste and excessive mud accumulation around feeders. Cows had free access to automatic watering systems and a mineral and vitamin supplement in all experiments except Exp. 6 (Exp. 1, 2, and 4: Gold Star MFA Breeder 12 Mineral: MFA, Midcontinent Livestock Supplements, Inc., Moberly, MO; Exp. 3, 5, 7, and 8: MLS #12 MINERA-LIX, Midcontinent Livestock Supplements, Inc., Moberly, MO; Exp. 6 described in Stephenson, 2019). Sheds in calving pens were kept closed except during inclement weather in spring-calving experiments (Exp. 1, 2, 4, and 5), when a single pair was then moved under cover. Gates were hung from the front of each shed to provide a clean, shaded area for calves during fall-calving experiments (Exp. 3, 6, 7, and 8). Approximately 20% of pen area at the opposite end of waterers was bedded with fescue straw to mitigate calf cold stress during spring-calving (Exp. 1, 2, 4, and 5), 20% of pen area at the opposite end of waterers was bedded with fescue straw to mitigate calf cold stress during spring-calving (Exp. 1, 2, 4, and 5), but pens were not bedded during fall-calving (Exp. 3, 6, 7, and 8).

**Experiments 1, 2, and 4.** Management of spring-calving Sim-Angus cows in Exp. 1 and 2 have been previously described by Niederecker et al. (2018), and Exp. 4 followed a similar experimental design. Briefly, cows were assigned to either strip-graze endophyte-infected stockpiled tall fescue or receive ad libitum endophyte-infected tall fescue hay beginning on d 188 ± 14 of gestation (Exp. 1 and 2) or 75 ± 12 d pre-calving (Exp. 4). Cows receiving hay were housed in the same dry lots as those used during calving and remained on their treatment through calving. Prior to parturition (Exp. 1: −19.2 ± 14.2 d, Exp. 2: −13.8 ± 11.8 d, Exp. 4: −14.7 ± 11.8 d), cows grazing stockpiled tall fescue were moved to dry lots adjacent to pens receiving hay and were fed rye haylage that more closely matched nutrient composition of stockpiled tall fescue during calving data and sample collection.

**Experiment 3.** Fall-calving Angus-cross or purebred Hereford heifers and cows grazed tall fescue-based pasture during late gestation. Females were then confined to 6 dry lots for observation beginning at 4.1 ± 2.1 d and fed ad libitum endophyte-infected tall fescue haylage and managed as described in Larson-Peine et al. (2022).

**Experiment 5.** Spring-calving Sim-Angus heifers and cows were managed in two groups (parities 1 and 2 vs. parity > 3) beginning in mid-gestation. These groups were treated similarly and grazed tall fescue-based pasture and then fed harvested forage until 6.7 ± 3.0 d pre-calving, when females were moved to 6 dry lots for observation. Animals were allowed ad libitum access to endophyte-infected tall fescue hay and supplemented with 1.0 kg dry matter (DM) per animal per day dried distillers grains with solubles (DDGS) at approximately 1700 h daily while in dry lots.

**Experiment 6.** Fall-calving Sim-Angus-Hereford cows were individually-fed to investigate the effects of copper, zinc, and manganese source and inclusion during late gestation (Stephenson, 2019) using a Calan gate system (Calan Broadbent Feeding System; American Calan, Northwood, NH). Cows were moved at 17.3 ± 7.0 d prepartum to 4 of the dry lots, where they had ad libitum access to endophyte-infected tall fescue hay and supplemented with 1.0 kg DM per animal per day of a DDGS-based supplement fed to be 11.5% of total pen dry matter intake daily at 1800 h.

**Experiment 7.** Fall-calving Sim-Angus-Hereford heifers and cows were managed together while grazing tall fescue-based pasture during late gestation. Dams were moved to 3 dry lots 30 ± 9.9 d pre-calving where they had ad libitum access to endophyte-infected tall fescue hay. During both late gestation and calving, females were supplemented 4 to 7 d/wk with 0.91 kg DM per animal per day of a DDGS and corn mixture.

**Experiment 8.** Fall-calving Sim-Angus-Hereford cows were managed together grazing tall fescue-based pasture until 95.1 ± 14.1 d pre-calving when a subset (n = 20) of cows were moved to graze a separate tall fescue-based paddock and supplemented 4 to 5 d/wk with 1.19 kg DM per animal per day of a DDGS and corn mixture to collect late gestation uterine blood flow data (data not shown). The remaining dams continued rotationally grazing tall fescue-based pasture. Cows were moved to 4 dry lots for observation in groups based on expected calving date (11.6 ± 6.9 d pre-calving) and given ad libitum access to endophyte-infected tall fescue hay supplemented with 1.19 kg DM per animal per day of a DDGS and corn mixture at 1700 h.

**Pre-calving Blood Collection**

Jugular venous blood samples were collected from prepartum dams in all experiments prior to being moved into the dry lot calving pens. Blood samples were collected into tubes [2 Vacutainer serum collection tubes containing no additives (10 mL draw; Becton Dickinson, Franklin Lakes, NJ), 1 Monoject plasma collection tube containing 0.10 mL of 15% K3EDTA (10 mL draw, Covidien, Mansfield, MA), and
Table 1. Description of calving experiments for determination of calving season effects (mean ± SD)\(^1\)

| Variables                      | Spring                                      | Fall                                      |
|--------------------------------|---------------------------------------------|-------------------------------------------|
|                                | Exp. 1 | Exp. 2 | Exp. 4 | Exp. 5 | Exp. 3 | Exp. 6 | Exp. 7 | Exp. 8 |
| First calving date             | February 2, 2014 | January 27, 2015 | February 2, 2016 | January 28, 2017 | September 5, 2015 | September 7, 2017 | September 9, 2018 | September 1, 2019 |
| Length of calving period, d    | 46     | 83     | 44     | 15     | 11     | 36     | 55     | 55     |
| Average calving date           | February 18, 2014 | February 18, 2015 | February 17, 2016 | February 4, 2017 | September 10, 2015 | September 19, 2017 | September 28, 2018 | September 25, 2019 |
| Weather conditions\(^2\)       |        |        |        |        |        |        |        |        |
| Average daily air temperature, °C | -6.2 ± 7.4 | 1.7 ± 6.8 | 2.0 ± 6.9 | 3.8 ± 5.5 | 22.0 ± 4.1 | 21.5 ± 3.1 | 18.8 ± 5.9 | 20.9 ± 6.2 |
| Minimum daily air temperature, °C | -12.7 ± 7.0 | -4.4 ± 6.6 | -2.8 ± 5.7 | -2.3 ± 4.4 | 15.9 ± 5.3 | 15.5 ± 3.9 | 13.0 ± 5.6 | 15.5 ± 6.7 |
| Maximum daily air temperature, °C | 0.13 ± 8.7 | 7.7 ± 7.9 | 7.6 ± 8.6 | 9.9 ± 7.0 | 28.1 ± 4.1 | 28.1 ± 3.7 | 25.1 ± 6.8 | 26.7 ± 6.7 |
| Average daily precipitation, cm | 0.02 ± 0.02 | 0.07 ± 0.22 | 0.07 ± 0.23 | 0.002 ± 0.01 | 0.13 ± 0.41 | 0.24 ± 0.61 | 0.35 ± 1.64 | 0.33 ± 0.84 |
| Calf sex                        |        |        |        |        |        |        |        |        |
| Heifers, n                     | 26     | 22     | 23     | 26     | 32     | 24     | 17     | 44     |
| Bulls, n                       | 20     | 31     | 27     | 28     | 17     | 18     | 15     | 12     |
| Parity of dams                 |        |        |        |        |        |        |        |        |
| Primiparous, n                 | –      | –      | –      | 18     | 13     | –      | 18     | –      |
| Multiparous, n                 | 46     | 53     | 50     | 36     | 36     | 42     | 14     | 56     |
| Prepartum dam body weight, kg\(^3\) | 690 ± 73 | 678 ± 71 | 663 ± 78 | 624 ± 81 | 595 ± 79 | 704 ± 85 | 624 ± 98 | 666 ± 75 |
| Peripartum dam body condition score\(^4\) | 5.8 ± 0.5 | 5.2 ± 0.5 | 5.2 ± 0.6 | 5.2 ± 0.5 | 5.2 ± 0.7 | 5.5 ± 0.5 | 5.5 ± 0.5 | 5.4 ± 0.9 |
| Dam age, yr                    | 6.1 ± 2.4 | 5.6 ± 2.8 | 5.3 ± 2.5 | 4.2 ± 2.8 | 4.1 ± 2.4 | 4.3 ± 1.2 | 3.0 ± 1.1 | 5.1 ± 1.8 |
| Dam age range, yr              | 3–12   | 3–13   | 3–14   | 2–15   | 2–12   | 3–7    | 2–5    | 3–10   |

\(^1\)Description of total number of animals, excluding data from dams that had twins or still-births, from each experiment that was used in this study.

\(^2\)Data collected from a weather station located on the same farm as experiments took place, as a weighted average based on calving date of each calf born.

\(^3\)Measured at 12 ± 9.4 d [SD] pre-calving.

\(^4\)Determined at 9.1 ± 14.4 d [SD] pre-calving on scale 1–9 (1 = emaciated, 9 = obese) by 2–3 technicians and averaged.
Serum non-microcentrifuge tubes and stored at −20 °C until analysis. Serum and plasma were then aliquoted into 2-mL microcentrifuge tubes and stored at −20 °C until analysis.

Calving Monitoring and Data Collection
Trained personnel monitored cows and heifers in calving pens for physical signs of labor at least hourly from at least 0600 to 2200 h, with additional checks occurring overnight during periods of heavy calving and as blood sampling times required. Three stadium lights were located in the back of the lot to illuminate the calving pens during the night to allow for monitoring of cows and calves, and a handheld spotlight was used to visualize animals when necessary. Continuous monitoring of dams began when a female reached stage 2 of parturition (appearance of amniotic membranes or calf feet) in order to record actual time of birth (expulsion of entire calf, including all 4 legs). Calving assistance was provided if malpresentation was suspected, after a prolonged duration since first appearance of fetal membranes or feet, or if progress slowed during contractions. Calving difficulty score ranging 1–5 was assigned (1: no assistance, 2: easy pull, 3: mechanically-assisted pull, 4: abnormal presentation, and 5: cesarean-section). Beginning in Exp. 2, calves were then closely monitored to record time of first standing (defined as the calf standing on all 4 legs for ≥ 5 consecutive seconds) to quantify calf vigor at birth. The time of birth was then subtracted from the time of first standing to obtain a calf’s time to stand in minutes.

Calves were measured and processed at 8.9 ± 10.8 h of age. At this time, each calf was given visual identification (ear tags), and its umbilicus was sprayed with dilute chlorhexidine. Calf sex was recorded, and birth weight and size were measured as described by Redifer et al. (2021). Calf size measures included shoulder to rump length (length from neck–shoulder junction to the end of the tailhead, following the spine), heart girth (body circumference immediately posterior to the shoulders and front legs), abdominal girth (body circumference at the umbilicus), and rear cannon bone circumference (circumference of a rear leg metatarsus at the smallest point). As an indicator of calf shape, calf ponderal index was calculated using the equation ponderal index = calf birth weight (kg)/shoulder to rump length (m³) based on human medicine calculations for infant shape (Walther and Ramaekers, 1982). Calf heart girth:length ratio was calculated as a second indicator of shape, using both measures in cm. Gestation length was calculated for calves resulting from AI with known breeding dates. Jugular blood samples were collected from all possible calves at 48 h of age in Exp. 2 to 8 unless dam temperament, unknown time of birth, or sampling time conflicts prevented blood collection. Beginning in Exp. 3, calf jugular blood samples were obtained from a subset of calves in each experiment at 0 (before suckling but after standing), 6, 12, 24, and 48 h postnatally (0.63 ± 0.4 h; 6.2 ± 0.4 h; 12.2 ± 0.4 h; 24.2 ± 0.4 h; 48.1 ± 0.4 h, respectively). The subset of calves selected in each experiment was due to permissive dam temperament, known time of birth, and availability to collect blood samples at appropriate times.

Calf rectal temperatures were also recorded using a digital thermometer prior to blood sample collection at these 5 time points. Blood was collected into 2 to 4 tubes at each time point, depending on the experiment (same as given for maternal blood; 1 to 2 Vacutainer serum collection tube containing no additives in all experiments, at least 1 Monoject plasma collection tube containing 0.10 mL of 15% K3EDTA in all experiments, and 1 Vacutainer plasma collection tube containing 15 mg of sodium fluoride and 12 mg of potassium oxalate for glucose determination in some experiments). Calf serum and plasma were processed as described above for maternal samples.

Blood Chemistry and Metabolite Analyses
One aliquot of calf serum (0 through 48-h samples in Exp. 3 to 6) was refrigerated and transported to the University of Missouri Veterinary Medical Diagnostic Clinical Pathology Laboratory (VMDL) on the day of collection or within 48 h when collected in the evening or on weekends for a complete chemistry analysis (Food Animal Maxi Panel). Serum glucose, urea N, creatinine, total protein, globulin, albumin, sodium, calcium, chloride, phosphorus, potassium, magnesium, aspartate aminotransferase (AST), creatine kinase (CK), gamma-glutamyl transferase (GGT), bicarbonate, anion gap, total bilirubin, and direct bilirubin were determined using a Beckman Coulter AU 400e Chemistry System (Beckman Coulter Inc., Brea, CA).

Serum total protein was determined for 48-h samples, either as a part of the serum chemistry panel above or separately to be used as an indicator of passive transfer of immunity for Exp. 2 through 8. Frozen 48-h serum samples from Exp. 7, 8, and a subset of samples (n = 17; not previously analyzed by VMDL) from Exp. 3 were delivered to VMDL for determination of total protein concentration using a Beckman Coulter AU480 Chemistry Analyzer (Beckman Coulter Inc., Brea, CA). The 2 Beckman Coulter analyzers used the same methodology in determination of serum total protein. Additionally, for both instruments, internal quality control, and verification of performance within specific CV were conducted daily. Upon delivery (or thawing for frozen samples), samples were analyzed through the instrument’s completely automated process.

For neonatal calf samples from Exp. 7 and 8 and prepartum maternal samples from all experiments, serum urea N and plasma glucose were analyzed using commercially-available kits as described by Niederecker et al. (2018). Serum non-esterified fatty acids (NEFA) were determined for all neonatal calf samples over time (0 through 48 h samples, Exp. 3 to 8) and prepartum maternal samples as described previously (Niederecker et al., 2018), and plasma triglycerides were determined for all neonatal calf samples over time (0 through 48 h samples, Exp. 3 to 8) as described previously (Larson-Peine et al., 2022). For each assay, samples were analyzed in duplicate, and pooled control samples were used for all assays. Within each experiment, the intra-assay and inter-assay CV were < 10 % (majority < 5%) for all assays across all experiments. Meyer et al. (2017) previously reported that serum urea N values determined with the commercial kit and those performed by VMDL were highly correlated (r² = 0.82). Additionally, plasma glucose (commercial kit) and serum glucose (VMDL) were also highly correlated (r² = 0.94; Meyer et al., 2017). Therefore, serum urea N and glucose data obtained from the VMDL in Exp. 3, 4, 5, and 6 were used with serum...
urea N and plasma glucose analyzed by our lab for Exp. 7 and 8 for neonatal calf analyses.

**Statistical Analysis**

Data collected from the 8 calving experiments were entered into and managed in a custom-designed Microsoft Access database (Microsoft Cooperation, Redmond, WA). The select query function was then used to retrieve desired dam and calf data from multiple tables within Access and was consolidated into one Microsoft Excel datasheet.

Data were checked for outliers prior to analysis, and data from any twins (n = 3) or stillborn calves (n = 6) were excluded. This resulted in n = 203 total for spring-born calves, and n = 179 total for fall-born calves. Dam data were included only when a cow or heifer’s calf had at least one data point included in the analyses. Data from calves with a calving difficulty score > 1 (n = 19) were excluded from all calf-related analyses except calf size. If exact time of birth or first standing was unknown, time to stand data were not calculated. Data from calves that received colostrum via an esophageal tube (n = 6) within the first 48 h postnatal were excluded from analyses of metabolites and serum chemistry. In order for data to be included in neonatal analyses of rectal temperature and serum chemistry over time (Exp. 3 through 8), data from at least 4 of the 5 time points were required from an individual calf. Final sample n for each variable are given in data tables and figure descriptions.

Data were analyzed using the MIXED procedure in SAS 9.4 (SAS Institute Inc., Cary, NC) with calving season as a fixed effect and animal as the experimental unit. Experiment was included as a random effect to account for variation among experiments for all measures. For neonatal calf rectal temperature and serum chemistry over time, calving season, sampling hour, and their interaction were considered fixed effects. These were analyzed as repeated measures using the best-fit covariance structure (based on AIC, BIC, and BICc) specific for each variable (chosen from unstructured, compound symmetry, heterogeneous compound symmetry, autoregressive, and heterogeneous autoregressive). Additionally, calf sex was included as a fixed effect for all calf variables when P ≤ 0.25. In the absence of interactions (P > 0.10), main effects of calving season are reported. Means were separated using least significant difference and considered different when P ≤ 0.05 and tendencies considered when 0.05 < P ≤ 0.10. Pearson correlation coefficients were determined between calf size, vigor, and 48-h serum total protein concentration within calving season using PROC CORR in SAS 9.4.

**RESULTS**

**Dam BW, BCS, Age, and Prepartum Metabolites**

There was no effect (P ≥ 0.61) of calving season on dam prepartum BW or peripartum BCS, but fall-calving dams were younger (P = 0.05) than those dams calving in the spring (Table 2). The age difference between calving seasons in this study is due to dams used in the spring experiments having a wider age range than dams used in 2 of the fall experiments. Overall, 82% of fall calves were born to multiparous cows versus 91% of spring calves. Spring-calving dams had greater (P < 0.001) prepartum serum NEFA; however, there was no effect (P ≥ 0.14) of calving season on dam prepartum plasma glucose or serum urea N (Table 2).

| Variables                  | Calving season | P-value |
|----------------------------|----------------|---------|
|                            | Spring         | Fall    |
| Prepartum body weight, kg  | 663 ± 19       | 649 ± 20| 0.61   |
| Peripartum body condition score | 5.34 ± 0.11   | 5.37 ± 0.11| 0.85   |
| Dam age, yr                | 5.26 ± 0.41    | 4.13 ± 0.41| 0.05   |
| Plasma glucose, mg/dL      | 63.7 ± 1.9     | 63.7 ± 2.0| 0.98   |
| Serum non-esterified fatty acids, μEq/L | 712 ± 61 | 368 ± 72| <0.001 |
| Serum urea N, mg/dL        | 8.5 ± 2.9      | 14.5 ± 2.9| 0.14   |

1 Mean ± SEM presented for measures.
2 Calving date range: January 28–April 20; Average calving date: February 13.
3 Calving date range: September 1–November 3; Average calving date: September 19.
4 Measured at 12 ± 9.4 d [SD] pre-calving. Spring n = 195, Fall n = 141.
5 Determined at 9.1 ± 14.4 d [SD] pre-calving on scale 1–9 (1 = emaciated, 9 = obese). Spring n = 200, Fall n = 161.
6 Spring n = 192, Fall n = 179.
7 Jugular blood samples collected at 11.2 ± 8.0 d [SD] pre-calving. Spring n = 194, Fall n = 137.

**Calf Gestation Length, Size at Birth, Vigor, Passive Transfer, and Rectal Temperature**

There was no effect (P = 0.48) of calving season on gestation length (Table 3), but calves born in the fall tended to have lighter (P = 0.09) birth weight than calves born in the spring (Table 3). Other calf size measures, including shoulder to rump length, heart girth, abdominal girth, and cannon circumference, were not affected (P ≥ 0.18) by calving season in the current study (Table 3). There was also no effect (P ≥ 0.40) of calving season on the indicators of calf shape, either calf ponderal index, or heart girth:length ratio.

Calves born in the fall had a faster (P = 0.05) time to stand immediately after birth than calves born in the spring (Table 3). There was no effect (P = 0.91) of calving season on calf 48-h serum total protein concentration (Table 3), which is often used as a clinical indicator of passive transfer.

Partial correlation coefficients of 48-h total protein and time to stand with calf size measures are presented in Table 4. Time to stand was not correlated (P ≥ 0.27) with total protein at 48 h in fall- or spring-born calves. However, in fall-born calves, calf birth weight had a weak positive correlation (P = 0.03) with time to stand. In calves born in the fall, both calf birth weight and calf heart girth had a weak positive correlation (P ≤ 0.02) with 48-h serum total protein. Abdominal girth also tended to have a very weak positive correlation (P = 0.09) with 48-h serum total protein. Other calf size measures were not correlated (P ≥ 0.14) with time to stand or 48-h serum total protein in fall-born calves. In spring-born calves, calf size measures were not correlated (P ≥ 0.31) with 48-h serum total protein or time to stand.

The interaction of calving season × sampling hour affected (P = 0.009) neonatal calf rectal temperature (Figure 1). Fall-born calves had greater (P ≤ 0.003) rectal temperature at 0, 24, and 48 h postnatal when compared with calves born in
the spring. Rectal temperature in spring-born calves increased ($P \leq 0.005$) from 0 to 6 h and 24 to 48 h of age. In calves born in the fall, rectal temperature decreased ($P = 0.02$) from 6 to 12 h, followed by an increase ($P \leq 0.007$) from 12 to 48 h of age.

### Table 3. Effects of calving season on calf gestation length, size, vigor, and 48-h serum total protein

| Variables                          | Calving season | P-value |
|-----------------------------------|----------------|---------|
|                                   | Spring$^2$     | Fall$^3$|         |
| Gestation length$^4$, d           | 279.3 ± 1.3    | 280.6 ± 1.4 | 0.48   |
| Calf size$^5$                     |                |         |         |
| Birth weight, kg                  | 36.1 ± 0.9     | 33.9 ± 0.9 | 0.09   |
| Shoulder to rump length, cm       | 59.0 ± 1.2     | 58.2 ± 0.8 | 0.58   |
| Heart girth, cm                   | 76.3 ± 1.9     | 73.6 ± 1.3 | 0.25   |
| Abdominal girth, cm               | 75.3 ± 3.5     | 69.6 ± 2.5 | 0.18   |
| Cannon circumference, cm          | 12.7 ± 0.4     | 12.1 ± 0.3 | 0.25   |
| Ponderal index$^6$, kg/m$^3$      | 176 ± 12       | 176 ± 8   | 0.97   |
| Heart girth:Length$^7$            | 1.30 ± 0.03    | 1.27 ± 0.02 | 0.40   |
| Time to stand$^8$, min            | 28.8 ± 2.1     | 23.4 ± 1.8 | 0.05   |
| 48-h serum total protein, g/dL$^9$| 6.62 ± 0.18    | 6.65 ± 0.16 | 0.91   |

$^1$Mean ± SEM presented for measures.

$^2$Calving date range: January 28–April 20; Average calving date: February 13.

$^3$Calving date range: September 1–November 3; Average calving date: September 19.

$^4$Calculated for calves conceived by artificial insemination. Spring $n = 145$, Fall $n = 116$.

$^5$Calves were weighed and measured at 8.9 ± 10.8 h [SD] of age. Birth weight: Spring $n = 202$, Fall $n = 177$; other size measures: Spring $n = 99$, Fall $n = 170$.

$^6$Ponderal index = calf birth weight (kg)/shoulder to rump length (m)$^3$.

$^7$Ratio of heart girth (cm):shoulder to rump length (cm).

$^8$Defined as time from birth to calf standing on all 4 legs for a minimum of 5 consecutive seconds. Spring $n = 67$, Fall $n = 103$.

$^9$Spring $n = 124$, Fall $n = 125$.

### Table 4. Partial correlation coefficients ($r$) and associated $P$-values between 48-h calf serum total protein, time to stand, and calf size from calves born in the fall or spring

#### Spring$^4$ variable

|                  | Time to stand$^9$, min | Calf birth weight, kg | Shoulder to rump length, cm | Heart girth, cm | Abdominal girth, cm | Cannon circumference, cm | Ponderal index$^6$, kg/m$^3$ | Heart girth:Length$^7$ |
|------------------|------------------------|-----------------------|-----------------------------|-----------------|---------------------|--------------------------|----------------------------|--------------------------|
| 48-h total protein, g/dL | -0.02 ($P = 0.86$)      | -0.01 ($P = 0.90$)    | 0.06 ($P = 0.63$)           | 0.008 ($P = 0.95$) | 0.08 ($P = 0.50$) | 0.002 ($P = 0.99$) | 0.05 ($P = 0.68$) | -0.06 ($P = 0.62$) |
|                  | $n = 58$               | $n = 124$             | $n = 77$                    | $n = 74$        | $n = 77$            | $n = 76$                  | $n = 77$                   | $n = 74$                  |
| Time to stand, min | -0.13 ($P = 0.31$)      | 0.07 ($P = 0.67$)     | -0.04 ($P = 0.81$)          | -0.09 ($P = 0.55$) | -0.10 ($P = 0.52$) | -0.09 ($P = 0.56$) | -0.12 ($P = 0.46$) | -0.12 ($P = 0.46$) |
|                  | $n = 66$               | $n = 43$              | $n = 41$                    | $n = 43$        | $n = 43$            | $n = 43$                  | $n = 43$                   | $n = 41$                  |

#### Fall$^3$ variable

|                  | Time to stand$^9$, min | Calf birth weight, kg | Shoulder to rump length, cm | Heart girth, cm | Abdominal girth, cm | Cannon circumference, cm | Ponderal index$^6$, kg/m$^3$ | Heart girth:Length$^7$ |
|------------------|------------------------|-----------------------|-----------------------------|-----------------|---------------------|--------------------------|----------------------------|--------------------------|
| 48-h total protein, g/dL | 0.12 ($P = 0.27$)      | 0.24 ($P = 0.006$)    | 0.12 ($P = 0.18$)           | 0.21 ($P = 0.02$) | 0.15 ($P = 0.09$) | 0.12 ($P = 0.20$) | 0.003 ($P = 0.97$) | 0.04 ($P = 0.69$) |
|                  | $n = 84$               | $n = 125$             | $n = 123$                   | $n = 124$       | $n = 121$           | $n = 124$                 | $n = 123$                  | $n = 123$                  |
| Time to stand, min | 0.21 ($P = 0.03$)      | 0.07 ($P = 0.47$)     | 0.13 ($P = 0.21$)           | 0.05 ($P = 0.66$) | 0.15 ($P = 0.14$) | 0.02 ($P = 0.86$) | 0.005 ($P = 0.96$) | 0.005 ($P = 0.96$) |
|                  | $n = 102$              | $n = 97$              | $n = 98$                    | $n = 95$        | $n = 98$            | $n = 97$                  | $n = 97$                   | $n = 97$                  |

$^1$Defined as time from birth to calf standing on all 4 legs for a minimum of 5 consecutive seconds.

$^2$Ponderal index = calf birth weight (kg)/shoulder to rump length (m)$^3$.

$^3$Ratio of heart girth (cm):shoulder to rump length (cm).

$^4$Calving date range: January 28–April 20; Average calving date: February 13.

$^5$Calving date range: September 1–November 3; Average calving date: September 19.

### Neonatal Calf Metabolites and Blood Chemistry

Neonatal calf blood chemistry variables that were affected or tended to be affected by the calving season × sampling hour interaction are displayed in Figures 2 to 5. Main effect means for calving season are shown in Table 5 for those blood chemistry variables that were not affected by the calving season × sampling hour interaction.

#### Energy-related metabolites.

There was an interaction ($P < 0.001$) of calving season × sampling hour for circulating glucose (Figure 2A). Calves born in the spring had greater ($P = 0.007$) glucose at 0 h of age than fall-born calves. In calves born in the spring, circulating glucose increased ($P < 0.001$) from 6 to 24 h of age. Within fall-born calves, circulating glucose increased ($P \leq 0.02$) from 0 to 48 h postnatal.

Calving season × sampling hour affected ($P < 0.001$) serum NEFA in neonatal calves (Figure 2B). Serum NEFA concentrations were greater ($P < 0.001$) at 0 and 6 h of age in calves born in the spring than those born in the fall. In calves born in the spring, NEFA concentrations decreased ($P < 0.001$) from 6 to 24 h of age. Serum NEFA in fall-born calves increased ($P < 0.001$) from 0 to 6 h and then decreased ($P < 0.001$) from 12 to 48 h postnatal.

Plasma triglycerides were also affected ($P < 0.001$) by the interaction of calving season × sampling hour (Figure 2C). Triglyceride concentrations were greater ($P \leq 0.009$) in spring-born calves at 0, 6, 12, and 48 h of age compared with those born in the fall. Plasma triglycerides increased ($P < 0.001$) from 0 to 6 and 24 to 48 h of age in both spring- and fall-born calves. In calves born in the spring, triglycerides also decreased ($P = 0.03$) between 6 and 12 h.

#### Protein-related metabolites.

The interaction of calving season × sampling hour affected ($P = 0.02$) serum urea N (Figure 3A). Fall-born calves tended to have greater ($P < 0.10$) urea N at 48 h than calves born in the spring. Concentrations of serum urea N increased ($P \leq 0.01$) from 0 to 12 h of age in...
Calving season affects neonatal beef calves

Calving season affects neonatal beef calves during the first 48 h postnatal. Least squares means ± SEM are presented (Spring n = 52, Fall n = 79). Open circles (●) represent calves born in the spring and solid circles (○) represent calves born in the fall. There was a calving season × sampling hour interaction (P = 0.009). Calving season means within hour *differ (P ≤ 0.05). Means differ (P ≤ 0.05) for spring-born calves across hours. *Means differ (P ≤ 0.05) for fall-born calves across hours.

Electrolytes and acid-base status. There was an interaction (P = 0.01) of calving season × sampling hour for neonatal serum sodium (Figure 4A), phosphorus (Figure 4B), and magnesium (Figure 4C). Calves born in the spring had greater (P = 0.03) serum sodium concentrations at 6, 12, 24, and 48 h of age compared with spring-born calves. In calves born in the spring, sodium decreased (P < 0.001) from 0 to 24 h of age, whereas this decrease (P < 0.001) occurred only from 0 to 12 h in fall-born calves. Phosphorus concentrations were greater (P ≤ 0.02) in spring-born calves at 6 and 12 h of age. Phosphorus decreased (P ≤ 0.001) from 0 to 6 h of age in both spring- and fall-born calves, followed by an increase (P = 0.02) from 12 to 24 h for spring-born and 12 to 48 h for fall-born calves. Serum magnesium was greater (P ≤ 0.03) in calves born in the fall at 0, 6, 12, and 24 h of age. Magnesium concentrations in calves born in both the spring and fall increased (P < 0.001) from 0 to 12 h of age, followed by a subsequent decrease (P < 0.001) from 12 to 48 h postnatal in both calving seasons.

Calves born in the fall had greater serum calcium (P = 0.03) and chloride (P = 0.006) compared with spring-born calves (main effects, Table 5). Calving season did not affect (P ≥ 0.16) serum potassium in this study (Table 5). Serum bicarbonate was greater (P = 0.03) in spring-born calves than those born in the fall (main effect, Table 5). Anion gap tended to be greater (P = 0.10) in calves born in the fall (main effect, Table 5).

Metabolic enzymes and bilirubin. There was a tendency of the calving season × sampling hour interaction (P = 0.06) for AST (Figure 5A) and an interaction (P = 0.004) of calving season × sampling hour for CK (Figure 5B). Spring-born calves had greater (P = 0.03) serum AST activity at 12 and 24 h of age compared with calves born in the fall. In both spring- and fall-born calves, serum AST increased (P < 0.001) from 0 to 12 h, and then decreased (P < 0.001) from 24 to 48 h of age. Serum CK activity was greater (P ≤ 0.04) at 0 and 12 h and tended to be greater (P = 0.07) at 6 h of age for calves born in the spring. In calves born in the spring, serum CK increased (P < 0.001) from 0 to 12 h postnatal, followed by a decrease (P < 0.001) from 12 to 48 h. Serum CK increased (P < 0.001) from 0 to 6 h of age, then decreased (P < 0.001) between 24 and 48 h in fall-born calves. Calving season did not affect (P ≥ 0.14) neonatal calf GGT activity in this study (Table 5).

Calves born in the spring had greater (P = 0.007, main effect) direct bilirubin compared with calves born in the fall.
Despite this, there was no effect ($P = 0.15$) of calving season for total bilirubin.

**DISCUSSION**

To our knowledge, this is the first study comparing neonatal beef calf metabolism in spring- and fall-calving systems in the U.S. Researchers have primarily investigated impacts of calving season in *Bos taurus* beef cowherds on cow and calf performance (Bagley et al., 1987; Griffin et al., 2012a; Caldwell et al., 2013) and herd-level economics (Griffin et al., 2012b; Henry et al., 2016). Although effects of cold stress during the neonatal period on beef calves (Bull et al., 1991; Lammoglia et al., 1999; Bellows and Lammoglia, 2000) and heat stress during pregnancy on fetal growth in ruminants (Reynolds et al., 1985; Bell et al., 1987; Tao et al., 2012) have also been studied, these have not been combined to determine the effects of spring- versus fall-calving seasons on beef calf fetal growth and neonatal metabolism in an applied research setting. Overall, our data suggest that neonatal beef calves in the lower mid western or upper southern regions of the U.S. are affected by the season of their birth, where fetal growth is restricted and neonatal dehydration is increased by warm conditions for fall-born calves, but vigor and metabolism are negatively affected by cold conditions in spring-born calves. These observations are likely due to 3 reasons: 1) environmental and nutritional effects of season on beef cows and heifers during late gestation, 2) ambient temperature at birth and during the neonatal period, and 3) effects of season on colostrum and early milk production.

**Maternal Effects During Late Gestation**

Nutrient requirements of cows and heifers increase dramatically during late gestation, as fetal and uteroplacental
Calving season affects neonatal beef calves

Figure 5. Effects of calving season on serum metabolic enzymes including aspartate aminotransferase (AST; Panel A) and creatine kinase (CK; Panel B) of neonatal beef calves during the first 48 h postnatal. Least squares means ± SEM are presented (Spring n = 63, Fall n = 43). Open circles (○) represent calves born in the spring and solid circles (●) represent calves born in the fall. There was a tendency for a calving season × hour interaction (P = 0.06) for AST and a calving season × hour interaction (P = 0.004) for CK. Calving season means within hour *differ (P ≤ 0.05) or †tend to differ (P ≤ 0.10). a–eMeans differ (P ≤ 0.05) for spring-born calves across hours. a–eMeans differ (P ≤ 0.05) for fall-born calves across hours.

Calving season affects neonatal beef calves (NASEM, 2016). Differences in environmental conditions, nutrition, and management during late gestation experienced in the winter versus summer likely affect nutrient availability and intake by the pregnant female and her subsequent nutrient delivery to the uteroplacenta and fetus. Overall, data in the current study suggest that calves born in the fall had decreased fetal growth, and therefore less prenatal nutrient availability.

Previously, Caldwell et al. (2013) reported that fall-calving beef females gave birth to smaller calves than spring-calving females in endophyte-infected tall fescue-based grazing systems in Arkansas, even though fall-calving dams had greater BCs at all times measured. Additionally, Bos taurus and Bos taurus × Bos indicus beef heifers (McCarter et al., 1990) and cows (McCarter et al., 1991) had offspring with lower birth weights in the fall versus spring in Oklahoma. Conversely, Bagley et al. (1987) reported no difference in beef calf birth weights between those born in the fall- or spring-calving seasons in Louisiana, and Griffin et al. (2012a) reported no difference in birth weights between beef cows with average calving dates of late March and early August in western Nebraska. This suggests that geographic location, management, specific timing of calving, and other factors likely affect whether intrauterine growth restriction occurs in late summer or fall-born calves.

Spring- and fall-calving females in the current study had similar prepartum BW at a similar BCS; thus, it is reasonable to assume that in the same season, mated with the same sire, their fetuses would have similar genetic growth potential. Nutritional management of beef cows and heifers can vary within season, but spring-calving females in late gestation generally consume forage that grew previously and was harvested or stockpiled for use over winter, whereas fall-calving females in late gestation generally consume forage while it grows during the summer and fall growing seasons unless drought necessitates use of harvested forage. One season does not necessarily have better quality forage available, due to variation in grazing systems and nutritional management, growth patterns of forage species, and weather patterns among regions and operations. Pregnant females in the experiments represented here were managed using common practices for Missouri beef cow-calf herds and tall fescue-based forage (both grazed and harvested), except for Exp. 6 in which fall-calving cows consumed hay and supplement during late gestation rather than grazing over summer. Given that spring- and fall-calving cow prepartum BW and peripartum BCS were not different, along with similar circulating glucose and serum urea N in the current study, overall nutrition of the late pregnant dams were unlikely to be widely different. Differences in prepartum serum NEFA are likely due to spring-calving dams mobilizing more body reserves during colder conditions (Slee and Halliday, 1968), but may also indicate mobilization of energy reserves due to nutrient restriction during late gestation.

Average air temperatures for late gestation from the on-farm weather station (November to March for spring-calving and June to October for fall-calving) averaged 2 °C for spring-calving and 23.5 °C for fall-calving experiments represented here. Heat stress is known to decrease feed intake and alter animal metabolism even when feed intake is unaffected (reviewed by Baumgard and Rhoads, 2013), but cold stress also increases energy requirements for thermoregulation (NASEM, 2016). Recently, heat stress has been studied extensively in late gestation dairy cattle during the dry period (reviewed by Dado-Senn et al., 2020 and Ouellet et al., 2020). Overall, unabated maternal heat stress during late gestation reduced calf birth weights (Tao et al., 2012), even when independent of reduced maternal nutrient intake (Almoosavi et al., 2020). Heat stress can decrease blood flow to the uteroplacenta (Reynolds et al., 1985); thus, blood flow or other mechanisms may play a bigger role than decreased maternal nutrient intake in reducing nutrient delivery to fetuses gestated during summer. Some aspects of neonatal calf metabolic status further support reduced prenatal nutrient supply and restricted fetal growth in fall-born calves. Calves born in the fall had less circulating triglycerides presuckling (at 0 h) in the current study, which has previously been reported in ovine fetuses that were considered small for gestational age in nutrient restricted ewes (Steinhauser et al., 2021). Although fat mobilization in spring-born calves was likely influenced by colder calving conditions, the greater circulating NEFA peak observed compared with fall-born calves may also indicate greater adipose deposition prenatally.

Tao et al. (2012) suggested that 33% of the decrease in birth weights of Holstein calves born to heat-stressed dams could be attributed to their shorter gestation lengths, which has also been observed in other studies (reviewed in Dado-Senn et al., 2020). Anecdotally, beef cow-calf producers report shorter gestation lengths in fall-calving herds, especially when grazing endophyte-infected tall fescue. This has
not been investigated widely, but is supported by studies in Oklahoma in which beef calves born in August or September had 3 d shorter gestation length than those born in October or November (Kastner, 2006) or 4 d shorter gestation length for mid-August versus October (Wright et al., 2014). Because gestation length was unaffected by calving season in the current study, the difference in calf birth weight can be attributed to altered fetal growth rather than fetal age, and differences in calf vigor and metabolism are unlikely to have been affected by differing in cull vigor and metabolism in fetal, muscle, and organ growth that contributed to reduced total birth weight rather than disproportionate growth.

Cold conditions and cold stress during late gestation may also contribute differences in to fetal growth. One study observed changes in spring-born beef calf birth weights to have a 0.56 °C:0.454 kg BW ratio with the change in ambient air temperatures, where birth weights were heavier for calves from dams that experienced colder temperatures during late gestation (Colburn et al., 1996). The same authors later suggested that the colder conditions during late gestation increased blood flow to the uterus when peripheral blood flow decreased to maintain maternal body temperature (Colburn et al., 1997). Although this has become a popular theory anecdotally, increased blood flow to the uteroplacenta during cold conditions has not been confirmed experimentally in cattle. Shearing ewes during pregnancy generally increases fetal growth regardless of environment (reviewed in Sinclair et al., 2016), which may be a cold stress response or due to other physiological outcomes of shearing. Additionally, spring-calving dams were mobilizing more body reserves shortly prepartum, as demonstrated by their greater NEFA concentrations, which has previously been associated with increased birth weights in beef females that were not nutrient restricted (Guedon et al., 1999; Abeni et al., 2004). In summary, late gestation occurring during cold conditions may help calves to reach their genetic potential for fetal growth, although the exact mechanism is unclear and may simply be the lack of heat stress during rapid fetal growth.

Research in dairy cattle has demonstrated that both season of birth (Van Eetvelde et al., 2017) and heat stress during late gestation prenatally (Ouellet et al., 2020) can program subsequent milk yield of females as adults. Thus, it is important to consider that any programming of beef females during development in their respective prenatal and postnatal environments may affect them long-term and thereby impact their calves as well. Both spring- and fall-calving herds in this study were made up of females that were born in their respective calving season. Removing this confounding effect of dam season of birth would require altering age at calving or calving interval, but future research is warranted to better understand both mechanisms and long-term impacts of calving season on beef females.

**Ambient Temperature Effects During Calving and Neonatal Periods**

Based on average air temperature data for each experiment (Table 1), spring-born beef calves encountered more cold stress, as temperatures were below estimated lower critical temperatures for neonatal calves (Carstens, 1994). No average maximum air temperature for calving dates in the spring overlapped with an average minimum air temperature for calving dates in the fall, despite some individual days within each calving season doing so (data not shown). Cold stress likely caused greater heat loss and depressed vigor for spring-born calves when compared with fall-born calves who were born into thermo neutral or warmer conditions.

Following parturition, the neonate must generate enough heat to offset the heat loss caused by its large surface area-to-body mass ratio, evaporation of amniotic fluids, and weather conditions that are often colder than the intrauterine environment (Vermorel et al., 1983; Azzam et al., 1993; Carstens, 1994). Failure to thermo regulate leads to hypothermia and can increase incidence of neonatal mortality; this has especially been shown in spring-born beef calves that often

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**Table 5. Effects of calving season and sampling hour on neonatal calf blood chemistry during the first 48 h postnatal**

| Variable          | Calving season | P-values |
|-------------------|----------------|----------|
|                   | Spring¹       | Fall²    | Season   | Hour   | Season × hour |
| Creatinine, mg/dL | 2.49 ± 0.10   | 2.56 ± 0.12 | 0.66     | < 0.001 | 0.31         |
| Albumin, g/dL     | 2.24 ± 0.05   | 2.46 ± 0.05 | 0.003    | < 0.001 | 0.40         |
| Calcium, mg/dL    | 10.9 ± 0.1    | 11.3 ± 0.1 | 0.03     | < 0.001 | 0.20         |
| Chloride, mEq/L   | 98.0 ± 1.0    | 101.8 ± 1.0 | 0.006    | < 0.001 | 0.31         |
| Potassium, mEq/L  | 5.39 ± 0.05   | 5.29 ± 0.05 | 0.16     | < 0.001 | 0.43         |
| Bicarbonate, mEq/L| 28.6 ± 0.6    | 26.6 ± 0.6 | 0.03     | 0.002   | 0.48         |
| Anion gap, mEq/L  | 19.1 ± 0.4    | 20.1 ± 0.4 | 0.10     | < 0.001 | 0.20         |
| Gamma-glutamyl transferase, U/L | 1,088 ± 76 | 911 ± 93 | 0.14 | < 0.001 | 0.17 |
| Total bilirubin, mg/dL | 0.745 ± 0.026 | 0.685 ± 0.031 | 0.15 | < 0.001 | 0.64 |
| Direct bilirubin, mg/dL | 0.319 ± 0.009 | 0.280 ± 0.011 | 0.007 | < 0.001 | 0.89 |

¹Mean ± SEM presented for measures that do not have a significant interaction of calving season × sampling hour. Those affected by the interaction are displayed in Figures 2–5.

²Jugular blood samples collected at 0 (after standing and before suckling), 6, 12, 24, and 48 h postnatal. Calves needed to have a blood sample for at least 4 of the 5 time points to be included in the analysis. Spring n = 63, Fall n = 43.

³Calving date range: January 28–April 20; Average calving date: February 13.

⁴Calving date range: September 1–November 3; Average calving date: September 19.
experience low ambient temperatures and greater incidence of precipitation at birth (Bagley et al., 1987; Azzam et al., 1993). The difference in rectal temperature at 0 h postnatal, following standing but before suckling, indicates cold stress of spring-born calves shortly after birth. Average rectal temperatures of spring-born calves in the current study do not indicate hypothermia, which has been considered to occur at a body temperature of 37 °C (Carstens, 1994), but this may be higher than necessary given the 35.4 °C rectal temperature for summit metabolism in dairy calves (Okamoto et al., 1986). Spring-born calves’ rectal temperatures were similar to other studies in beef (Egli and Blum, 1998) and dairy calves (Hadorn et al., 1997), but may have been improved by the cold stress mitigation efforts (bedding, using open-sided sheds to provide windbreaks when necessary at birth) in spring experiments. Fall-born calves had similar rectal temperature within the first 48 h to previous reports of calves considered high vitality (Vermorel et al., 1983), suggesting that they were unlikely to be experiencing heat stress at these times. Despite this, fall-born calves early in the calving seasons often showed signs of heat stress after 48 h of age (data not shown), including high rectal temperature and open-mouth panting, which resolved after 7 to 10 d of age. More research is necessary to explore heat stress in Bos taurus calves born in high ambient temperature.

**Vigor and passive transfer.** Cold stress and lower body temperature of spring-born calves likely contributed to their increased time to stand successfully after birth. Induced cold stress in dairy calves has been reported to reduce neonatal vigor, where hypothermic calves were reluctant to stand and suckle, showing signs of muscle weakness (Olson et al., 1980b). Additionally, Dwyer and Morgan (2006) observed that lambs with lower rectal temperatures were slower to stand and suckle after birth. When neonates display the proper vigor behaviors and rapidly stand and suckle, particularly in cold stress conditions, convective heat loss to the ground may be reduced and they are able to better maintain body temperature after consuming colostrum (Dwyer and Morgan, 2006).

Lamb mortality was increased with longer times to stand and suckle (Dwyer et al., 2001), and time to stand and time to suckle have been positively correlated in beef calves (Wichman et al., 2019). Therefore, it can be inferred that because spring-born calves had longer times to stand, they would also have longer times to reach the udder and suckle, although this was not measured in the current study due to pre-suckling sampling of blood. A delay in suckling may limit the colostrum ingested during the period of absorption for successful passive transfer (Stott et al., 1979). Serum total protein is often used as an indicator of passive transfer in calves (Weaver et al., 2000). Despite the differences in the time to stand in this study, there was no difference between 48-h serum total protein concentrations of fall- and spring-born calves. In the smaller dataset of calves over time (Figure 3), differences in circulating total protein at 24 and 48 h are likely due to differences in animal numbers and experiments for which calf serum over time was analyzed. Furthermore, elevated serum total protein in fall-born calves may not be indicative of improved passive transfer, but instead indicate a slight dehydration status (Thornton et al., 1972; Russell and Roussel, 2007), as observed in summer-born lambs (Chniter et al., 2013).

Serum GGT can also be an indicator of passive transfer; the lack of difference in serum GGT in the present study further supports that calving season did not affect the ability of calves to achieve passive transfer (Perino et al., 1993). In previous dairy calf studies, cold stress or hypothermic conditions decreased concentrations of serum IgG up to 18 h after the first ingestion of colostrum (Olson et al., 1980b), and maternal heat stress during late gestation decreased dairy calf plasma total protein and serum IgG (Tao et al., 2012; Monteiro et al., 2014). Effects of late gestational heat stress on colostrum IgG have been variable, and decreased serum IgG of calves born to heat-stressed dairy cows may be more due to the ability of the small intestine to absorb IgG (reviewed by Dahl et al., 2020). Although both spring- and fall-calving conditions pose their own unique challenges, the current study demonstrates that beef calves of both calving seasons are generally likely to achieve successful passive transfer of immunity if they have adequate vigor.

In the current study, average 48-h serum total protein concentrations for the larger population sampled (Table 3) were greater than the minimum recommended value of 5.0–5.5 g/dL (often 5.2 g/dL) for passive transfer of immunity in dairy calves (Tyler et al., 1998; Weaver et al., 2000). Proportions of calves failing to meet this 5.0 g/dL threshold were 5.6% of spring-born and 3.2% of fall-born calves. A more recent study suggested serum total protein concentrations of 5.6–6.1 g/dL as a new cut-off for optimal calf health outcomes (Todd et al., 2018); 16.9% of spring-born calves and 12.8% of fall-born calves did not meet these minimums. Nevertheless, most calves of both calving seasons likely achieved successful passive transfer in the current study based on observed performance.

The lack of a relationship between time to stand and 48-h serum total protein for fall- or spring-born calves in the current study is probably due to the type of calves being included in this analysis. Calves that experienced dystocia or were fed additional colostrum were minimal and excluded from the correlation analysis, and calves that did not stand within 2 h postnatal were removed from calving pens, processed, and assisted in suckling; therefore, no time to stand was calculated. Overall, calves in the current dataset were under a high standard of management and managed more intensively if failure of passive transfer was expected; thus, removal of these calves due to management changes likely influenced the relationships of calf vigor with total protein.

In fall-born calves, which experienced thermo neutral or warmer conditions after birth, calf size was related to time to stand, where lower birth weight was associated with a faster time to stand. This may be due to lighter calves having less body mass to coordinate to achieve standing compared with heavier calves or heavier calves experiencing more calving difficulty, as suggested for dairy calves by Johanson and Berger (2003). Despite this, the weak relationship between calf size and 48-h serum total protein in fall-born calves indicates that bigger calves are able to consume more colostrum during the first 48 h than smaller calves. These relationships were not present for spring-born calves in the current study, despite previous reports of reduced vigor in calves experiencing cold stress and that smaller calves are more susceptible to cold stress (Olson et al., 1980b; Carstens, 1994).
Neonatal calf metabolism. Many metabolic differences between spring- and fall-born calves are likely due to differences in experiencing cold versus warm conditions in the early neonatal period. We have previously reported and discussed changes in neonatal calf metabolism and blood chemistry over time in fall-born beef calves from Exp. 3 (Larson-Peine et al., 2022), and many of these general patterns were observed in both spring- and fall-born calves in the current study.

In attempts to cope with cold conditions and to increase their body temperature, spring-born calves likely relied more heavily on mobilization of their energy stores, both in glycogen and white adipose, along with use of brown adipose tissue for rapid thermogenesis during the first 6 h postnatal than calves born in the fall (Vermorel et al., 1983; Hammon et al., 2012). Greater circulating glucose pre-suckling in spring-born calves suggests that spring-born calves mobilized more glycogen immediately after birth to support thermogenesis. Studies that exposed dairy (Okamoto et al., 1986) or Brahman-influenced (Godfrey et al., 1991) calves to cold stress conditions within the first 24 h postnatal reported increased circulating glucose concentrations following the cold exposure, which indicates increased glycolysis and/or gluconeogenesis during hypothermia. Additionally, calves whose birth required assistance had greater glucose at 30 min of age compared with those who were born without human assistance (Bellows and Lammoglia, 2000), suggesting stress or trauma of birth associated with larger birth weights or cold may also have played a role. In cold-stressed calves, NEFA are used as a substrate for non-shivering thermogenesis by brown adipose tissue and shivering thermogenesis by muscle (Vermorel et al., 1983; Okamoto et al., 1986; Carstens, 1994). Spring-born calves in the present study had greater serum NEFA during the first 6 h postnatal and likely relied on mobilization of their body lipid reserves for energy, including that to maintain body temperature, compared with calves born in the fall.

When muscle or organ damage occurs, concentrations of AST and CK will increase and therefore can be used as indicators of muscle or organ trauma (Russell and Roussel, 2007; Pearson et al., 2019). This suggests that calves born in the spring experienced more trauma during parturition, although it is unclear if this stress was caused by cold conditions, larger size at birth, and/or other factors. Pearson et al. (2019) observed that beef calves with greater AST and CK concentrations were less vigorous, which corroborates with the increased time to stand for spring-born calves in the current study. Greater incidence of subcutaneous hemorrhage can also occur when calves are exposed to cold stress (Olson et al., 1980a), leading to greater hemoglobin breakdown and increased total bilirubin concentrations in cold-stressed calves (Bull et al., 1991). This may have occurred in the current study’s spring-born calves, contributing to their greater direct bilirubin concentrations.

Heat stress may alter the glucose utilization hierarchy causing an increase in protein catabolism for gluconeogenic precursors (Baumgard and Rhoads, 2013) and therefore potentially lead to higher blood urea concentrations (Wang et al., 2020). Additionally, urea N in maternal and neonatal calf serum has been positively correlated at 1 h post-calving (Meyer et al., 2018), so numerically greater serum urea N in fall-calving dams may have contributed to greater concentrations in the fall-born calves. Furthermore, in incidences of dehydration, the inability to concentrate urine can lead to increased urea in the blood (Russell and Roussel, 2007); thus greater urea N of fall-born calves may have been due to heat stress in the current study.

The differences observed in serum electrolytes where concentrations of sodium, chloride, magnesium, and calcium were greater in fall-born calves also suggest that they were moderately dehydrated (Russell and Roussel, 2007). Additionally, electrolyte status can be influenced by metabolic-respiratory acidosis (Russell and Roussel, 2007), which calves born in the fall may have experienced, as evidenced by greater anion gap and lower bicarbonate. Similarly, dairy calves born in summer also had greater anion gap and lower bicarbonate concentrations during the first 24 h postnatal (Kovács et al., 2017). Calves born into warmer ambient temperature may experience metabolic alkalosis caused by heat stress-induced increases in respiratory rates that increase CO₂ expiration (West, 2003). In attempts to compensate for the induced respiratory alkalosis, increased urinary excretion of bicarbonate can lead to decreased blood pH and then metabolic acidosis, as has been noted in adults (West, 2003).

Season Effects on Colostrum and Milk
Limited research has been done to determine how season and or environmental conditions affect colostrum and milk yield and composition, especially in beef cows. Given the timing of data collection in the current study (birth to 48 h of age), colostrum and early milk are the most relevant to this period. Colostrum was collected postpartum but prior to the calf suckling in Exp. 6, 7, and 8, but was not collected pre-suckling in any spring-calving experiments; thus, it could not be included in the current dataset. Differences in postnatal nutrient availability from colostrum may have influenced calf metabolism, however, as many metabolic shifts can be attributed to colostrum intake (Blum et al., 1997; Rauprich et al., 2000). For example, differences observed in plasma triglycerides at 6, 12, and 48 h could be due to spring dams having greater colostral lipid content. Heat stress during the dry period can impact mammary gland development and subsequent milk yield (reviewed by Tao et al., 2018 and Ouellet et al., 2020), and colostrum yield was decreased by late gestational heat stress, even independent of decreased feed intake in one study (Seyed Almoosavi et al., 2021). Moreover, Nardone et al. (1997) reported that colostrum yield was not affected by heat stress during the last 3 wk of gestation and first 36 h postpartum, but that fat and lactose concentrations were decreased 12 h postpartum in heat-stressed heifers. Seasonal differences have been observed in dairy cow milk phosphorous and sodium content by d 3 and 5 postpartum, respectively, where concentrations were greater in dams calving in February than in June (Klimoš et al., 1986). These data suggest that seasonal differences in colostrum yield or its macronutrient and mineral concentrations might affect spring- and fall-born beef calves differently as well.

Development of the dam due to the season of her birth may also affect her mammary function. Van Eetvelde et al. (2017) reported that Holstein Friesian cows born in the winter (December 21 to March 20 in Northern hemisphere) had lower energy-corrected milk yields during their first lactation compared with other calving seasons, whereas daughters of dams with unabated heat stress in late gestation had decreased milk yields in other studies (reviewed by Ouellet et al., 2020). These observations suggest that season of birth has long-lasting influence on the dam’s lactation that is likely a portion of the offspring response to season.
CONCLUSION

Results from this study indicate that calving season influences perinatal nutrient availability, which may impact the transition to postnatal life for beef calves. Although fall-born calves likely experienced intrauterine growth restriction due to heat stress during late gestation, spring-born calves were less vigorous due to cold ambient calving conditions. Neonatal metabolic differences between calving seasons demonstrate that calves adapt to postnatal life differently depending on ambient conditions of calving, although it is unknown if colostrum nutrient availability also plays a role. In the present study, there was no effect of calving season on 48-h serum total protein, suggesting that both spring- and fall-born calves were predominantly able to achieve passive transfer of immunity. Overall, these data indicate that spring- and fall-born calves both experience physiological and metabolic challenges that differ widely, likely due to environmental and nutritional effects of season on beef cows and heifers during late gestation and ambient temperature at birth and during the neonatal period. Further research is necessary to determine potential effects of season on colostrum and early milk production. Additionally, these data show that calving season should be considered in the interpretation of data from pregnant beef females and their neonatal calves.

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Disclosures

Authors declare no conflict of interest.

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