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ANIMAL PRODUCTION SCIENCE

Immediate prepartum supplementation accelerates progesterone decline, boosting passive immunity transfer in tropically adapted beef cattle

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ABSTRACT

Context. Poor nutrition of late-pregnant cows is highly prevalent in the dry tropics and associated with high levels of calf mortality. **Aims.** It was hypothesised that supplementation with protein to prepartum cows would restore the normal decline in progesterone prepartum and increase the transfer of passive immunity to calves, with this being further enhanced by inclusion of yeast fermentation products. **Methods.** In total, 84 heifers and 45 cows were selected for a completely randomised block design, with the following three dietary treatments: unsupplemented, receiving *ad libitum* low-protein hay only; hay supplemented with 1 kg/day of protein; and supplementation with both protein and 14 g/day of a *Saccharomyces cerevisiae* fermentation product. Supplementation occurred for an average of 14 days before calving. Cow plasma samples in the week before parturition, and the first plasma sample after parturition, were analysed for progesterone and metabolites. Newborn calves were weighed and blood-sampled three times per week during the first 2 weeks after birth. The first two calf plasma samples were analysed for total protein, albumin, and globulin concentrations. Data were analysed using a mixed-effects model and the decline of progesterone concentration over time was modelled using a non-linear segmented model. **Key results.** Prepartum supplementation reduced cow liveweight loss, increased glucose, reduced fat mobilisation metabolites and tended to increase average daily weight gain of calves. Including yeast fermentation products in the supplement tended to increase the transfer of passive immunity to calves. Supplementation decreased plasma progesterone before parturition and including yeast fermentation products further advanced the initiation of progesterone decline. **Conclusion.** Protein supplementation of protein-deficient beef cows during late pregnancy helps restore the normal decrease in progesterone before parturition. **Implications.** This study identified a plausible hormonal mechanism explaining how poor nutrition around birth can increase calf loss, opening new possibilities for short-term diet management strategies to reduce calf mortality and improve calf health.

Keywords: *Bos indicus*, calf loss, colostrum, luteolysis, maternal nutrition, mortality, probiotic, *Saccharomyces cerevisiae*.

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Introduction

Calf mortality is an ongoing problem across the dry tropics, with most losses occurring within the first week after birth and for unexplained reasons (Bunter *et al.* 2014). With the normally high temperatures during peak calving of tropical beef systems, any delay in milk delivery during the first 3 days after calving substantially increases the risk of dehydration-mediated calf mortality (Muller 2017). Pronounced deficits in metabolisable protein and energy and other nutrients during the prepartum period could be modulating colostrum yield and milk delivery, and a high incidence of calf mortality has been associated with poor cow nutrition and elevated environmental stress (McGowan *et al.* 2014).

Although poor nutrition and low body reserves during the prepartum period have been associated with low colostrum yield and increased risk of failure of passive transfer, the mechanism for this modulation is not well understood (McGee *et al.* 2006).

One possible mechanism modulating the nutritional effect on colostrogenesis is through alterations in the prepartum serum concentrations of progesterone. A decline in circulating concentrations of progesterone is needed for lactogenesis to occur, with basal concentrations required at calving for full lactation to commence (Guy *et al.* 1994). In sheep, supplementation with protein meals around parturition has been shown to decrease circulating concentrations of progesterone and increase colostrum yield (O'Doherty and Crosby 1996). Therefore, in the current study, it was hypothesised that a lack of metabolisable protein during the periparturient period interferes with the normal decline in circulating concentrations of progesterone before parturition, resulting in reduced lactogenesis and transfer of passive immunity to calves.

Supplementation with macrominerals, such as phosphorus (P), have been shown to increase colostrum yield (Dixon *et al.* 2017) and supplementation with microminerals and vitamins, such as selenium and vitamin E, have also been reported as beneficial for transfer of passive immunity (Moeini *et al.* 2011). Considering that *Saccharomyces cerevisiae* fermentation products contain trace minerals, vitamins and rumen bacteria growth factors, its use during the periparturient period can also improve passive immunity transfer to calves (Kinal *et al.* 2007). Therefore, a second hypothesis for the current experiment was that inclusion of yeast fermentation products (YFP) in the protein supplement, and thus further supply of micronutrients, would improve lactogenesis and passive immunity transfer to calves via colostrum.

Materials and methods

The Queensland Department of Agriculture and Fisheries Animal Ethics Committee approved the animal care and use in this study (reference number SA 2018/05/638).

Animals and experimental design

The experiment was conducted at two locations in a dry tropical environment during the typical end of the dry season calving period. In June 2018 at Spyglass Beef Research Facility (Charters Towers, Queensland (Qld), Australia, 19.45°S, 145.75°E), a cohort of 109 nulliparous pregnant Droughtmaster heifers with similar expected calving date (1 October to 1 November 2018) was selected for this study. In the same month, at the James Cook University Tropical Veterinary Research Station, Fletcherview (Charters Towers, Qld, Australia, 19.53°S, 146.10°E), a cohort of 50 multiparous pregnant Brahman cows were selected on the basis of a similar expected calving date (2–21 December 2018).

Before the start of the trial, nulliparous and multiparous cows grazed open rangeland in paddocks adjacent to the yards. Once the first calf was born at the Spyglass cohort (5 October 2018), 84 nulliparous Droughtmaster cows [liveweight (LW) = 481 ± 39 kg, body condition score (BCS; 1–5 scale) = 3.2 ± 0.4] were stratified into two blocks based on LW, randomly allocated within each block into three pens (14 cows per pen), and the feeding of nutritional treatments began. At Fletcherview, the first calf in the cohort was born on 12 November 2018, and 45 multiparous Brahman cows (LW = 502 ± 37 kg, BCS = 3.0 ± 0.2) were randomly allocated into three pens (15 cows per pen) for the start of the nutritional treatments.

Cows were confined in uncovered dry lot pens (average of 103 m^2 per cow) with access to shade and *ad libitum* access to hay and water. Supplements were supplied daily at 1 kg/cow. Because the cows were grouped in pens (14 or 15 cows per pen), individual supplement intake was not known. Each cow remained in the dry lot receiving the experimental diets (Table 1) for 14 days after calving. All cows were fed low-quality Rhodes grass hay and the treatments were as follows: (1) control (CTR), in which cows received hay only; (2) protein (PRO), in which cows were supplemented with 1 kg/day of protein supplement; or (3) YFP, in which cows received the protein supplement plus 14 g/day *Saccharomyces cerevisiae* fermentation product (NaturSafe, Diamond V, Cedar Rapids, IA, USA). The PRO supplement contained bentonite at 1.4 kg/100 kg, which was replaced with the *Saccharomyces cerevisiae* fermentation product when preparing the YFP supplement.

Blood collection and analysis

Blood was collected from the coccygeal vein of cows three times per week until 2 days after calving, by using Vacutainer plasma collection tubes containing lithium heparin (Becton Dickinson, NJ, USA). Blood from the jugular vein was collected from newborn calves within 48 h of birth, by using the same type of tubes. Tubes were inverted five times and placed in ice water immediately following collection. Ice cold blood samples were centrifuged at 1500*g* for 13 min at room temperature, and plasma was transferred into 2 mL microcentrifuge tubes and stored at −20°C.

The plasma samples collected during the last week of gestation were analysed for metabolites representing protein metabolism (albumin, creatinine, total protein, urea, and globulins), energy metabolism [glucose, triglycerides, β-hydroxybutyrate (BHB), glucose, non-esterified fatty acids (NEFA)], mineral metabolism (Ca, P, Mg, Na, K, chlorine (Cl), bicarbonate) and liver metabolism [aspartate aminotransferase (AST), creatine kinase (CK), bile acids, gamma-glutamyl transferase (GGT), bilirubin, glutamate dehydrogenase (GLDH)] using an Olympus AU480 chemistry analyser (Beckman Coulter Diagnostic Systems Division, Melville, NY, USA).

Plasma progesterone concentration was determined on plasma samples collected during the last week before calving and on the first two cow plasma samples after calving, by using an Immulite 1000 (Siemens Healthcare Diagnostics Inc, Los Angeles, CA, USA) and a commercial kit (Siemens

Table 1. Chemical composition of hay, water, and protein supplement.

Item	Supplement	Rhodes grass hay	Water Spyglass	Water Fletcherview
Ingredients (% of the diet as fed)				
Soybean meal	34.6	–	–	–
Cottonseed meal	20.0	–	–	–
Sorghum grain	13.5	–	–	–
Palm kernel meal	10.0	–	–	–
Salt	6.0	–	–	–
Mono-dicalcium phosphate	4.0	–	–	–
Urea	3.5	–	–	–
Ammonium sulfate	3.0	–	–	–
Molasses	2.0	–	–	–
Limestone	2.0	–	–	–
Bentonite	1.4	–	–	–
Chemical composition (% dry matter)				
Dry matter	91.0	85.8	–	–
Crude protein	42.4	4.1	–	–
Neutral detergent fibre	17.6	74.5	–	–
Ether extract	2.5	1.4	–	–
Ash	21.0	8.9	–	–
Calcium (Ca)	1.8	0.3	0.08	0.10
Phosphorus (P)	1.5	0.3	0.00	0.00
Magnesium (Mg)	0.3	0.2	0.02	0.11
Potassium (K)	1.2	1.7	0.02	0.08
Sodium (Na)	2.6	0.02	0.13	0.30
Sulfur (S)	1.1	0.09	0.00	0.00
Iron (Fe, mg/kg)	127.6	204.4	0.00	0.00
Manganese (Mn, mg/kg)	47.7	38.6	0.00	0.00
Zinc (Zn, mg/kg)	48.7	27.9	0.00	0.00
Copper (Cu, mg/kg)	14.9	3.1	–	–
Selenium (Se, mg/kg)	0.4	–	–	–

For supplement, bentonite was replaced with yeast fermentation products (NaturSafe, Diamond V, Cedar Rapids, USA) for YFP-treated cows.

Healthcare Diagnostics Products Ltd, Glyn Rhonwy, UK). The first two calf plasma samples after birth were analysed for total protein, albumin and globulin concentration, as described above. Calf plasma samples were submitted for determination of immunoglobulin G (IgG) concentration by radial immunodiffusion (Chelack *et al.* 1993) using rabbit anti-bovine IgG (Jackson ImmunoResearch Laboratories Inc., West Grove, PA, USA) as the antiserum incorporated into the gel and bovine reference serum for standard curve (Fortis Life Sciences, Auburndale, MA, USA).

Cow and calf performance measurements

The same trained technician visually assessed cows for BCS (1–5 scale, 1 = emaciated and 5 = obese) at least once per week. Cows were weighed three times per week, on the same days as blood collection. Average daily weight change (gain or loss) of cows during the prepartum period was calculated by regressing weight over time. LW at calving was determined by the regression equation as LW on Day 0, before calving. Therefore, the reported LW at calving includes the conceptus weight. Newborn calves were weighed three times per week during the first 2 weeks after birth, by using a hanging scale (Kain Chung Scale Factory, KC-08, 100 kg) and a metal cradle. Average daily weight gain of calves during the initial 2 weeks after parturition was calculated by regressing weight over time.

Chemical analysis of feed

Hay, water and supplement on offer to each group were sampled and composited for chemical analysis at Spyglass

(2 November 2018) and Fletcherview (18 December 2018) and transported to the University of Queensland, Gatton, for analysis. Hay and supplements were dried at 60°C for 72 h in a forced-air oven and ground to pass a 2 mm sieve (Retsch ZM 200; Haan, NW, Germany). Final dry-matter content was determined after drying the samples for 24 h at 105°C and ash content was determined by the residue on ignition at 550°C for 8 h (Modutemp; Perth, WA, Australia). The crude protein content was calculated by multiplying by 6.25 the nitrogen (N) content determined by the Dumas combustion method, using a LECO CN928 analyser (LECO Corporation; St Joseph, MI, USA). Ether extract content was determined after extraction with petroleum spirit by using a SER148 Solvent Extraction Unit (VELP Scientifica S.R.L.; Usmate, MI, Italy). Neutral detergent fibre concentration was determined using heat-stable α-amylase (Van Soest *et al.* 1991) in an ANKOM A200 Fibre Analyser (ANKOM Technology Corporation, Fairport, NY, USA).

Mineral content (P, Ca, Mg, K, Na, S, Fe, Mn, Zn, Cu and Se) of the feedstuff and water samples was determined by digesting 0.3 g of sample in 6 mL nitric acid and 2 mL perchloric acid, made up to 20 mL with reverse osmosis water. The digested samples were analysed using an inductively coupled plasma–atomic emission spectrometer (Optima 7300 DV, Perkin Elmer, Wellesley, MA, USA).

Statistical analyses

Nine cows that failed to calve by 40 days after the start of the trial were removed from the analysis, as were two cows because of dystocia, one because of very large teats preventing normal suckling, and three whose calves were stillborn. Data were analysed as a completely randomised block design with subsampling (animals within block), considering each pen as the experimental unit, using the MIXED procedure of SAS. The effect of breed, parity, and location cannot be evaluated in this study, because these were confounded with blocks. The model included the fixed effects of treatment and the random effects of block, the experimental error and the sampling error, as

$$Y_{ij} = \mu + \alpha_i + B_j + B_j \times \alpha_i + e_{ij},$$

where Y_{ij} = dependent variable; μ = overall mean; α_i = fixed effect of treatment i {CTR, PRO, YFP}; B_j = random effect of block j {j = 1, 2, 3}; $B_j \times \alpha_i$ = random effect of block B_j and treatment α_i; e_{ij} = random residual variation.

Calf sex was included in the model for offspring measures (birth weight and weaning weight) but removed from the model when $P > 0.50$ (average daily weight gain, IgG, globulins). Days on supplement (dams), varying from 4 to 39 days, was also tested as a covariate in the model and removed when $P > 0.50$. The only response variable with a $P < 0.50$ for days on supplement was calf daily weight gain ($P = 0.13$). Therefore, the effect of days on supplement is not discussed in the paper.

Treatment differences were determined using orthogonal contrasts for the effect of supplementation (CTR vs PRO + YFP) and the inclusion of YFP in the supplement (PRO vs YFP). Significance was declared at $P \leq 0.05$. Data on the decline of plasma progesterone concentration over time was modelled using the NLIN procedure of SAS, fitting a non-linear segmented model (Fadel 2004) to estimate the following four parameters: plasma progesterone before parturition (P_4pre), the start (P_4st) and the rate of progesterone decline (P_4dec), and progesterone 2 days after parturition (P_4post). It was hypothesised that treatments would alter the start of plasma progesterone decline relative to calving. Data were fitted using the following model:

$$\text{Progesterone} = P_4\text{pre}, \text{ if time} \leq P_4\text{st}$$

$$\text{Progesterone} = [(P_4\text{pre} - P_4\text{post}) \times \text{EXP}[-P_4\text{dec} \times (\text{time} - P_4\text{st})]] + P_4\text{post}, \text{ if time} > P_4\text{st}.$$

The effect of treatment on model parameters was compared using the 95% confidence interval.

Results

Cow performance, decline in plasma progesterone and blood metabolites before parturition

Pregnant cows received the treatments for an average of 14 days before parturition, ranging from 1 to 40 days. As late-pregnant cows of ~500 kg LW require a diet with ~90 g crude protein/100 kg of dry matter, the unsupplemented diet was supplying 47% of the daily protein requirements, while the protein-supplemented diets were supplying 87% of the estimated requirements (NASEM 2016). There was no effect of treatments on LW or body condition at calving. However, protein supplementation ameliorated the weekly LW loss ($P = 0.01$; Table 2), with no additional effect of YFP ($P = 0.47$).

Protein supplementation reduced the concentration of progesterone in plasma in cows at Days 4, 3, and 1 before parturition ($P < 0.01$; Fig. 1), with no further effect of YFP ($P > 0.10$). There was no treatment effect ($P = 0.17$) on plasma progesterone 2 days before parturition (Fig. 1). The non-linear modelling of progesterone decline before parturition (Fig. 1, Table 2) indicated that protein supplementation advanced its initiation ($P < 0.05$) and reduced its rate of decline ($P < 0.05$). There was no significant effect of protein supplementation on concentration of plasma progesterone either 6 days before or 2 days after calving ($P > 0.05$). Including YFP in the supplement advanced the initiation of progesterone decline by a further 20 h relative to

Table 2. Effect of supplementation on growth, progesterone decrease and plasma concentration of metabolites in prepartum cows.

Item	CTR	PRO	YFP	SEM	*P*-value	
					Supp	YFP
Growth						
Body condition score at calving	3.1	3.1	3.0	0.09	0.86	0.40
Body condition score change per week	−0.02	−0.06	−0.14	0.08	0.36	0.40
Liveweight at calving (kg)	483	496	503	9.4	0.15	0.63
Liveweight change per week (kg)	−5.8	−1.1	0.86	1.9	0.01	0.47
Modelled predictions for plasma progesterone						
P_4 before calving (nmol/L)	21.1	19.2	20.6	3.5	n.s.	n.s.
Start of P_4 decline (h before calving)	24	61	81	2.7	<0.05	<0.05
Rate of P_4 decline (nmol/h)	0.12	0.02	0.02	0.01	<0.05	n.s.
P_4 after calving (nmol/L)	2.0	0.0	0.0	1.2	n.s.	n.s.
Protein metabolism						
Albumin (g/L)	35.9	34.1	34.0	0.41	<0.01	0.84
Creatinine (μmol/L)	177.0	153.1	163.1	3.3	<0.01	0.02
Total protein (g/L)	71.1	66.4	67.5	1.1	<0.01	0.46
Urea (mmol/L)	1.58	4.91	4.64	0.24	<0.01	0.40
Globulins (g/L)	35.1	32.4	33.5	0.93	0.05	0.33
Energy metabolism						
Glucose (mmol/L)	3.75	4.28	4.02	0.09	<0.01	0.03
Triglycerides (mmol/L)	0.33	0.35	0.30	0.01	0.89	0.01
NEFA (meq/L)	1.59	1.02	0.99	0.07	<0.01	0.74
BHB (mmol/L)	0.99	0.77	0.86	0.05	<0.01	0.13
Mineral metabolism						
Ca (mmol/L)	2.07	2.06	2.07	0.02	0.68	0.73
P (mmol/L)	2.13	2.46	2.34	0.06	<0.01	0.11
Mg (mmol/L)	1.04	1.00	0.98	0.02	0.06	0.40
Na (mmol/L)	144	144	145	0.40	0.66	0.07
K (mmol/L)	5.05	4.75	4.87	0.07	0.01	0.22
Cl (mmol/L)	107	107	109	0.39	0.03	<0.01
Bicarbonate (mmol/L)	20.0	18.9	18.5	0.40	0.01	0.17
Liver metabolism						
AST (U/L)	71.5	56.2	60.2	2.43	<0.01	0.21
CK (U/L)	201	181	182	46.2	0.72	0.99
Bile acids (μmol/L)	22.2	18.7	16.0	1.46	0.01	0.16
GGT (U/L)	10.0	8.5	10.9	0.65	0.70	0.01
Bilirubin (μmol/L)	5.07	3.67	3.71	0.24	<0.01	0.90
GLDH (U/L)	17.0	9.2	11.2	0.95	<0.01	0.11

In Supp column, *P*-values are for contrast for the supplementation effect (CTR vs PRO + YFP). In YFP column, *P*-values are for contrast for the YFP effect (PRO vs YFP). CTR, control with *ad libitum* hay only; PRO, hay + 1 kg/day of protein meal; YFP, PRO + yeast fermentation products; P_4, progesterone; NEFA, non-esterified fatty acids; BHB, beta hydroxy-butyrate; AST, aspartate aminotransferase; CK, creatine kinase; GGT, gamma glutamyl transpeptidase; GLDH, glutamate dehydrogenase.

parturition, ($P < 0.05$), with there being no effect on other parameters (Table 2).

There was a clear effect of protein supplementation on prepartum plasma metabolites (Table 2). Supplementation was associated with a two-fold increase in plasma urea concentration ($P < 0.01$) and reduced plasma albumin, creatinine, globulins and total protein. Including YFP in the supplement was associated with an increase in plasma creatinine concentration ($P = 0.02$), with no effect on the other metabolites related to protein metabolism. For energy

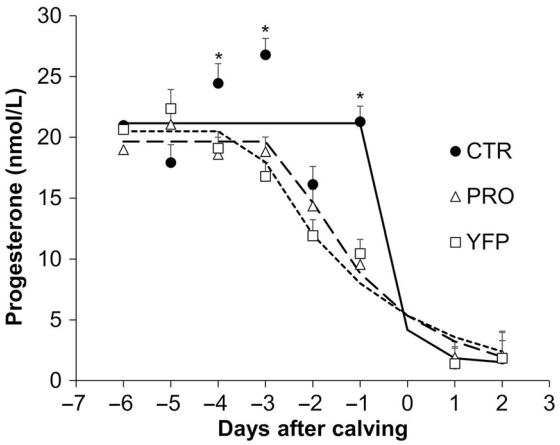

Fig. 1. Plasma concentration of progesterone in cows fed three experimental diets (CTR, control with *ad libitum* hay only; PRO, hay + 1 kg/day of protein meal; YFP, PRO + yeast fermentation products). Symbols are experimental data, and the curves are the least-squares line fitted by a non-linear segmented model (— CTR; – – PRO; ——— YFP). *CTR vs PRO + YFP ($P < 0.05$).

metabolism, supplementation increased plasma glucose ($P < 0.01$) and decreased ($P < 0.01$) NEFA and BHB concentration, with no effect on total triglycerides ($P = 0.58$). Including YFP reduced plasma glucose ($P = 0.03$) and total triglycerides ($P = 0.01$), with no effect on NEFA and BHB. Supplementation also modified prepartum plasma minerals, increasing P ($P < 0.01$) and reducing K ($P = 0.01$) and bicarbonate ($P = 0.01$), with there being no effect on Ca ($P = 0.88$), Mg ($P = 0.10$), Na ($P = 0.33$) and Cl ($P = 0.25$). Inclusion of YFP increased plasma Na ($P = 0.02$) and Cl ($P < 0.01$) compared with protein supplementation alone. For metabolites representing liver function, supplementation decreased AST ($P < 0.01$), bile acids ($P < 0.01$), bilirubin ($P < 0.01$) and GLDH compared with levels in unsupplemented cows ($P < 0.01$). Inclusion of YFP increased plasma concentration of GGT ($P = 0.01$), with there being no effect for the other liver metabolites ($P > 0.10$).

Calf performance and transfer of passive immunity

Average male and female calf birth weights were 32.8 kg and 30.7 kg respectively ($P = 0.05$), with YFP supplementation tending to increase birth weight of male but not of female calves ($P = 0.06$; Table 3). Calf birth weight was influenced by the dam LW at calving ($P < 0.01$; data not shown). However, because the treatments also influenced dam LW at calving, this factor was not used as a covariate when testing for treatments effects on calf birth weight. Prepartum supplementation tended to increase calf average daily weight gain by 13% ($P = 0.09$) during the initial 14 days of life. Protein supplementation tended ($P = 0.08$) to increase plasma IgG concentration of newborn calves, with no effect on plasma total protein ($P = 0.56$) or globulin concentrations ($P = 0.40$). However, inclusion of YFP tended to increase plasma IgG ($P = 0.10$) and increased plasma total protein ($P = 0.03$) and plasma globulin ($P = 0.05$) concentrations.

Discussion

It was initially hypothesised that a deficiency of metabolisable protein during the periparturient period would interfere with the normal decline of progesterone before parturition in beef cows, resulting in reduced transfer of passive immunity and milk production in the days immediately after parturition. The results from the present study and previous studies with sheep (O'Doherty and Crosby 1996) partially corroborate this hypothesis, as short-term supplementation hastened the progesterone decline and increased milk yield, as measured by calf growth. This outcome is consistent with a previously demonstrated increased risk of failure of passive immunity

Table 3. Effect of dam prepartum supplementation on calf growth performance and transfer of passive immunity.

Item	CTR	PRO	YFP	SEM	*P*-value	
					Supp	YFP
Calf performance						
Male calf birth weight (kg)	31.9	31.5	34.9	1.1	0.33	0.06
Female calf birth weight (kg)	31.3	31.5	29.4	1.1	0.41	0.17
0–14 days average daily weight gain (kg/day)	0.91	0.99	1.06	0.06	0.09	0.42
Transfer of passive immunity						
Plasma bovine IgG (g/L)	22.2	25.6	32.6	2.6	0.08	0.10
Plasma total protein (g/L)	65.1	62.2	71.0	2.0	0.56	0.03
Plasma globulin (g/L)	39.9	38.7	45.4	1.9	0.40	0.05

In Supp column, P-values are for contrast for the supplementation effect (CTR vs PRO + YFP). In YFP column, *P*-values are for contrast for the YFP effect (PRO vs YFP). CTR, control with *ad libitum* hay only; PRO, hay + 1 kg/day of protein meal; YFP, PRO + yeast fermentation products; IgG, immunoglobulin G.

transfer being associated with poor cow nutrition during the 2 weeks before parturition (McGee *et al.* 2006).

The findings from the present study suggest a new hypothesis for the high rates of calf mortality and morbidity associated with poor pregnant cow nutrition in dry tropics beef production systems (Fordyce *et al.* 2021), which opens the possibility for practical interventions to ameliorate the problem. As short-term improvements in nutrition can assist with the progesterone decline, the use of improved or spelled pasture and protein supplements around calving, together with group segregation, auto-drafters, and automated individual feeders, could be considered to develop cost-effective management strategies to improve milk delivery and reduce calf losses. The benefits of reducing calf losses and improving calf health should be considered in a whole-business approach as it likely extends from the immediate profit in selling more calves.

The critical factor for successful transfer of passive immunity and calf survival is abundant colostrum and milk production in the first hours after birth. In this study, calf growth during the initial 14 days after birth was used as a proxy for milk delivery. The 13% increase in calf average daily weight gain associated with dam supplementation implies enhanced milk production and delivery. Cows having a low body condition before calving has been proposed as the main risk factor modulating the effect of poor nutrition during the third trimester of pregnancy on reduced colostrum quality, increased risk of failed transfer of passive immunity, and reduced neonatal calf growth (Bohnert *et al.* 2013). In contrast, there had been a proposal that short-term periparturient supplementation may ameliorate failure of passive transfer of immunity to calves (McGee and Earley 2019); i.e. the specific risk factor was low-diet quality in the prepartum period rather than low body condition.

In the present study, the dietary treatments did not change body condition and the cows were in good body condition at parturition, suggesting that the supplementation effect on calf average daily weight gain was independent of body condition of the dam. This indicates that a better supply of dietary nutrients to the mammary gland is modulating the milk yield response. Apart from the increased supply of dietary amino acids, greater glucose concentrations in plasma of supplemented cows may also have contributed to greater milk yield (Ingvartsen and Friggens 2005). Poor maternal nutrition during late pregnancy in ewes has also been shown to modulate the somatotrophic axis in the offspring, with a lower growth rate of lambs being associated with reduced expression of muscle IGF-I and a reduced circulating concentration of IGF-I in the offspring (Hoffman *et al.* 2014).

The inclusion of YFP in protein supplements to late-pregnant cows has been demonstrated to increase colostrum immunoglobulin concentration and to improve the immunity transfer in calves (Kinal *et al.* 2007), which the present study has corroborated. The mechanism of action of YFP on enhanced colostrum quality is unknown. However, it is known that the addition of trace minerals and vitamins to deficient diets can enhance colostrum production and quality (Kincaid and Socha 2004; Kinal *et al.* 2007), and that YFP contains bioactive compounds, such as antioxidants, B vitamins, trace minerals, and nucleotides, which can serve as growth promoters for the rumen bacteria (Shurson 2018). Supplementation with post-ruminal methionine in cattle (Elolimy *et al.* 2019) and with selenium in sheep (Meyer *et al.* 2010) during late pregnancy can increase birth weight of offspring. Also, in ewes, restricted diets have been demonstrated to reduce birth weight in female lambs more than in male lambs (Neville *et al.* 2010). Therefore, it is possible that YFP supplementation is enhancing the supply of microminerals, amino acids, or growth factors to the uterus and having a positive influence on male calf birth weight, although this remains untested.

Besides flow of nutrients to the mammary gland, another important factor controlling colostrum delivery is the blood concentration of progesterone before parturition. Progesterone declines rapidly before parturition, and a delay in the decline of progesterone before parturition has been associated with reduced colostrum secretion and delayed lactation (Banchero *et al.* 2006). Elevated circulating concentrations of progesterone seem to modulate colostrogenesis by inhibition of milk synthesis through α-lactalbumin (Gross and Bruckmaier 2019), a component of the lactose synthetase complex, and through lower blood flow to the mammary gland (Mordhorst *et al.* 2017). The newborn calf requires immediate colostrum intake to maintain adequate hydration and immune competence, and any delay in milk delivery could harm its survivability.

When the progesterone decay curve was fitted to the non-linear model, it became clear that the higher prepartum progesterone in the unsupplemented animals was because of a delay in commencement of progesterone decline, and not because of a reduced progesterone clearance rate. The inclusion of YFP in the protein meal supplement further advanced the initiation of plasma progesterone decline, which could also be a factor explaining the higher IgG in the plasma of their calves. These results suggest that undernutrition is delaying luteolysis, because, in the bovine, in contrast to sheep, the *corpus luteum* and not the placenta is the major source of progesterone in the pregnant cow (Shenavai *et al.* 2012). However, the mechanism by which undernutrition would be influencing the prepartum luteolytic cascade is largely unknown.

In sheep, evidence has been provided that a cortisol-dependent, oestrogen-independent mechanism operates within the fetal membranes, leading to elevations in fetal plasma prostaglandins, while an oestrogen-dependent mechanism operates within the maternal endometrium, leading to increased maternal plasma prostaglandins (Whittle *et al.* 2000). Both mechanisms act to induce luteolysis prepartum (Whittle *et al.* 2000). In addition, prostaglandins are synthesised from arachidonic acid in a reaction controlled

by the activity of cyclooxygenases, mostly COX2, and it has been reported that undernutrition decreases COX2 and prostaglandin E2 mRNA expression in sheep (Sosa *et al.* 2009). This suggests that peripheral concentrations of progesterone in the immediate prepartum period could be influenced by fetal syntheses of cortisol, placental synthesis of oestrogens and endometrial synthesis of prostaglandins.

Oestradiol also plays an important role in luteolysis in cattle, with lower concentrations of oestradiol delaying luteolysis in non-pregnant animals (Araujo *et al.* 2009) and decreasing the interval to luteolysis during the subsequent luteal phase due to impaired inhibition of oxytocin receptors allowing increased prostaglandin release (Mann and Lamming 2000). During late pregnancy, concentrations of oestrogens peak within the last few days before parturition in cattle (Dobson and Dean 1974). Differences in nutrition in this study may have altered synthesis of cortisol and fetal–placental synthesis of oestrogens, both of which could have influenced concentrations of progesterone in the prepartum period. Changes in peripheral concentrations of oestradiol and cortisol in the days immediately prior to parturition could be investigated in future studies to determine potential effects of nutrition on prepartum concentrations of progesterone.

During the prepartum phases of colostrogenesis, immunoglobulins and other blood nutrients, such as Ca and P, are transferred into the mammary gland, which may cause a decline in cow plasma protein fractions (Brandon *et al.* 1971). The hypothesis was that short-term supplementation would enhance blood protein fractions, energy substrates and minerals, which could facilitate colostrogenesis and milk delivery. The marked increase in plasma urea concentration in supplemented cows illustrates increased absorption of soluble N from the rumen, as the supplement contained 3.5% urea and as the protein meals would be partially degraded and absorbed as ammonia through the rumen wall. Conversely, the lower plasma prepartum concentration of total protein, albumin and globulins in supplemented cows may be related to an increased colostrogenesis, although the volume and composition of the colostrum were not analysed.

Supplemented animals also had improved energy status, as demonstrated by the higher glucose and lower NEFA and BHB plasma concentrations. Total energy intake was not evaluated in this trial; however, it is common for cattle receiving poor-quality forage (crude protein below 80 g/kg of dry matter) to increase total energy intake when supplemented with protein meals (Poppi and McLennan 1995). The lower concentration of plasma creatinine in supplemented cows is also likely to be reflecting the improved energy status and lower rate of muscle degradation, as more amino acids are available from the diet. Creatinine originates from the breakdown process of creatinine phosphate in muscle and creatinine excretion increases with the onset of endogenous protein catabolism (Russell and Roussel 2007). Supplementation also improved liver function, given the respective decreases in GLDH, AST, bilirubin, and bile acids (Russell and Roussel 2007). Thus supplementation was associated with increased signalling of food availability to the body, via the bile acids (Russell and Roussel 2007), and with decreased AST level, which has been associated with higher body weight and body condition (Cavestany *et al.* 2005).

Phosphorus deficiency is a widespread problem in vast, dry tropical areas in northern Australia, reflecting the low soil concentration (Dixon *et al.* 2017). During the periparturient period, there is high demand for minerals to support late pregnancy and colostrogenesis, and mineral deficiencies have been related to feed intake and reduced milk yield in early lactation (Dixon *et al.* 2017). Therefore, it is reasonable to suspect that the enhanced mineral supply in protein-supplemented cows could be partially responsible for the beneficial effects on progesterone decline, calf growth and immunity transfer. However, although supplementation did increase plasma P concentration during the prepartum period, concentrations in unsupplemented cows were well above the critical value of 1.5 mmol/L (Anderson *et al.* 2017). This strongly suggests that prepartum plasma P was not an important factor limiting colostrum yield or milk delivery during the trial.

Besides increasing plasma P, supplementation also decreased K and bicarbonate concentration in the prepartum cows. These changes are probably associated with the higher plasma urea concentration and the increased ureagenesis in the liver. Dietary protein and urea are degraded in the rumen and absorbed as ammonium into the blood circulation. In the liver, ammonia is detoxified via ureagenesis, a process that removes bicarbonate from the blood (Atkinson and Bourke 1984). The slight increase in plasma chloride in cows supplemented with YFP could also be related to the blood acid–base balance (Tucker *et al.* 1991); however, we could not find a direct link between YFP supplementation and higher plasma chloride.

In conclusion, the results from this study propose an endocrine mechanism that may explain some of the calf mortality observed in beef cattle systems in the dry tropics rangelands; i.e. severe undernutrition in the periparturient period delays progesterone decline in the immediate prepartum period and, consequently, impairs colostrogenesis and milk delivery immediately after parturition. It can be concluded that a protein-rich supplement for an average of 14 days prepartum for beef cows consuming a protein-deficient diet improves their capacity to abolish plasma progesterone before parturition. It appears the mechanism by which nutrition is modulating progesterone concentration is through the initiation of luteolysis or reduced progesterone synthesis by the placenta, rather than progesterone clearance rate. This study implies that it would be feasible to develop specific short-term diet management strategies in the dry tropics to reduce calf mortality and improve calf health.

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Data availability. Data are available from the authors upon reasonable request.

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