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Direct and carry-over effect of grassland herbage allowance on metabolic hormones and reproduction in primiparous beef cows undergoing temporary weaning and flushing

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ABSTRACT

Grazing management significantly contributes to low beef production in cow-calf systems within the Rio de la Plata native grasslands. An herbage allowance (**HA**) of 4 kg DM/kg BW increased the productive response of primiparous cows grazing shallow soils compared to 2.5. However, the impact of HA on metabolic changes and its association with productive response were not studied. We studied two levels of native grassland HA from −150 days relative to calving (**DC**) to weaning (195 DC) in spring-calving primiparous beef cows undergoing temporary weaning (**TW**) and flushing at 86 ± 12 DC on herbage intake (**HI**), body condition score (**BCS**), BW, milk yield, calf weight, concentrations of metabolic hormones, and the probability of ovulation and pregnancy. Thirty-one heifers were assigned to HA treatments that fluctuated throughout seasons: autumn (−150 to −90 DC) at 5 and 3 kg DM/kg BW, winter (−90 to 0 DC) at 3 and 3 kg DM/kg BW, and spring-summer (0 to 195 DC) at 4 and 2 kg DM/kg BW for High and Low HA, respectively. Data were analysed using linear models and generalised linear models for continuous and categorical variables, respectively. During the autumn period, HI, insulin, IGF-I, BCS, and BW were higher in High HA than Low, despite small differences in herbage mass between HA. Throughout the winter, spring, and summer, HI, insulin, leptin, and BCS changes did not differ between HA. However, IGF-I concentrations were greater at −65 and −40 DC (84 vs 55 ± 8.6 ng/mL; $P < 0.05$) and tended to be greater after TW in High HA than Low. The probability of ovulation did not reach significance (0.94 vs 0.75 ± 0.11 for High and Low HA, respectively; $P = 0.125$), while the probability of pregnancy was greater in High HA than in Low HA (0.9 vs 0.61 ± 0.10; $P = 0.07$). Ovulation probability exhibited a positive association with IGF-I concentrations at −90 and −40 DC ($P < 0.05$), but not postpartum. Milk yield did not differ between treatments, while calf weight was heavier at weaning in High HA cows (194 vs 178 ± 3.3 kg; $P < 0.05$). High HA enhances autumn HI and BCS and generates a carry-over effect on IGF-I concentrations throughout winter and after TW ("metabolic memory"), explaining the better reproductive response. Moderate changes in cows' nutrition during autumn contribute to changes in metabolic status and reproductive outcomes in primiparous cows grazing moderate herbage production native grasslands.

Implications

The postpartum reproductive response of primiparous spring-calving cows grazing native grasslands is influenced by their nutritional status during the preceding autumn, associated with a carry-over or "memory" effect of autumn nutrition over IGF-I concentrations during winter and after temporary weaning and flushing. Changes in herbage allowance during autumn, even with moderate differences in herbage mass (approximately 1 cm herbage height), affect the nutritional and metabolic status of the cows and their reproductive response. Accurate herbage mass quantification and effective management of herbage allowance are needed to achieve high productive and reproductive outcomes in primiparous cows grazing native grasslands.

Introduction

The Rio de la Plata grasslands occupy central-eastern Argentina, Uruguay, and southern Brazil representing one of the most diverse,

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largest (853 000 km^2), and less transformed grassland areas in the world (Oyarzabal et al., 2020). Its main use is grazing for beef production where cow-calf systems are dominant (Modernel et al., 2018). Those production systems record low pregnancy (74%) rates, calf weaning weight (145 kg), and meat production per cow and area (75 kg/ha) that compromise the sustainability of livestock farmers and grassland conservation (Modernel et al., 2018; Ruggia et al., 2021; Oyarzabal et al., 2020; Paparamborda et al., 2023). Proposals for ecological intensification to enhance the productive indicators and sustainability of cow-calf systems in Rio de la Plata grasslands are based on: (1) placing the calving season in spring and calf definitive weaning and pregnancy diagnosis early in autumn, (2) allocating paddocks with more herbage height to groups of cows with higher requirements (i.e. heifers, pregnant cows, cows with sub-optimal body condition score, **BCS**), (3) functional relationships between herbage height, BCS, and pregnancy rates, (4) tactical use of temporary weaning (**TW**) and TW with flushing (**F**) at the start of the breeding season to improve the reproductive performance of cows with sub-optimal BCS (Do Carmo et al., 2016). The application of this proposal at the farm level has demonstrated that, even in its partial implementation, enhances pregnancy rates (21%) and meat production per area (22%) than the baseline (Ruggia et al., 2021).

Herbage height and mass are affected by herbage allowance (**HA**) by its effect on herbage growth and intake (Nabinger et al., 2000). This justified the study of HA levels on herbage production, utilisation, efficiency of use, and production in multiparous (Do Carmo et al., 2018) and primiparous cows (Claramunt et al., 2018). An HA of 5 kg DM/kg BW exhibited greater herbage mass (1 650 vs 910 ± 68 kg DM/ha) and height (5.5 vs 3.5 ± 0.18 cm) than 3 kg DM/kg BW, resulting in greater herbage intake, BCS, insulin, and IGF-I, and an earlier postpartum luteal activity in multíparous cows (Laporta et al., 2014; Do Carmo et al., 2018; Do Carmo et al., 2021). In shallower soils and more sensitive to summer droughts, herbage mass differences between HA treatments were lower (1 474 vs 1 212 ± 86 kg DM/ha) and resulted in lower differences in BCS (0.5 units on a 1–8 scale) limited to prepartum (Claramunt et al., 2018). Beyond the moderate differences, greater HA increased pregnancy rates by 35% than low HA (Claramunt et al., 2018), suggesting an effect of nutrition and metabolic hormones on follicular development in early stages that could explain the improvement in the reproductive response (Britt, 1991; Webb et al., 2003; Meikle et al., 2018). Previous studies in multiparous cows (Laporta et al., 2014) and primiparous cows (Soca et al., 2014a; Astessiano et al., 2014) grazing native grasslands reported higher concentrations of IGF-I during the second trimester of gestation and shorter postpartum anoestrus in cows with greater prepartum and calving BCS. The significance of BCS management during the second trimester of gestation to achieve optimal BCS at calving was previously addressed for multiparous cows (Do Carmo et al., 2016); however, the possibility of intervening through HA during the second trimester of gestation, its effect on cow nutritional and metabolic status, and its association with reproductive response in primiparous cows grazing native grassland, was not investigated.

Primiparous cows experience longer postpartum anestrus periods than multiparous cows which has been explained by the higher nutrient requirements for growth (Short et al., 1990; Quintans et al., 2009). Temporary weaning and F at the start of the breeding season in primiparous cows with sub-optimal BCS at calving (below 4.5 units) have been shown to increase early pregnancy rates by reducing postpartum anestrus and improving conception rates (Soca et al., 2013). The improvement in reproductive events was linked to the "metabolic memory" hypothesis (Blanc et al., 2006; Meikle et al., 2018) as cows with greater BCS prepartum showed greater insulin and IGF-I concentrations when TW and F were applied (Soca et al., 2014b; Meikle et al., 2018). However, we do not know if it is possible through HA, to influence insulin and IGF-I concentrations during TW and F at the start of the breeding season and affect the reproductive response.

This study aims to investigate the impact of increased HA during autumn, spring, and summer on estimated herbage intake (**HI**), BCS, BW, insulin, IGF-I, and leptin concentrations during gestation and lactation of primiparous beef cows subjected to TW and F at the start of the breeding season in grasslands over shallow soils. Furthermore, it seeks to understand the association between these factors and the probability of ovulation and pregnancy. We hypothesise that an HA of 4 kg DM/kg BW (annual average) will increase insulin, IGF-I, and leptin concentrations, particularly during gestation and TW and F than an HA of 2.5 kg DM/kg BW, and that these changes will positively associate with the probability of ovulation and pregnancy.

Material and methods

Location description and experimental design

The experiment was conducted as part of a long-term study on the effect of two levels of native grassland herbage allowance on the metabolism, behaviour, and productive and reproductive response of primiparous cows. The location of the experimental area, soils, botanical composition, animal management, and experimental design were previously described (Claramunt et al., 2018). Briefly, the experiment was conducted in a completely randomised block design with two blocks, where two HA treatments were applied in each block which covered an area of 92 ha of Campos native grassland. Blocks were a spatial replica and considered differences in soil depth proportions. The HA treatments (ratio between herbage mass and kg of BW stocked, kg DM/kg BW) (Sollenberger et al., 2005) fluctuated throughout the seasons, as follows: autumn 5 and 3; winter 3 and 3; spring and summer 4 and 2 kg DM/kg BW, for High and Low HA, respectively (4 and 2.5 kg DM/kg BW the annual mean for High and Low HA, respectively). Put-and-take method (Mott and Lucas, 1952; Aiken, 2016) was employed to adjust HA based on herbage mass, and cows BW. Cows of the same breed and physiological status, and similar BW and BCS to experimental cows were used to adjust the HA.

Animals and management

Animal procedures were approved by the Animal Experimentation Committee of Universidad de la República, Uruguay N° 021130-006374-12. Thirty-one 30 ± 1.8 months Hereford heifers were blocked by initial BW, BCS, and gestational age (Beal et al., 1992) and allocated to treatments (15 cows for High HA and 16 for Low HA) at −150 ± 12 days relative to calving [**DC**]/second trimester of gestation/autumn. Cows were maintained in the experimental paddocks until weaning (195 ± 12 DC) in a continuous grazing system (Fig. 1). The initial BW was 394 ± 4.4 kg, and BCS was 5.7 ± 0.1 (least-square means ± s.e.; 1–8 scale; Vizcarra et al., 1986). At 86 ± 12 DC, TW was applied using nose plates (Walmur Ltda, Montevideo, Uruguay) on calves for 12 days (Quintans et al., 2009; Fig. 1). A nose plate is a physical barrier, which prevents nursing but does not interfere with grazing, eating, or drinking. At 92 ± 12 DC, the cows were exposed to tested bulls for 80 days (bull/cow rate: 1/20; McGowan et al., 1995) while 6 days after (end of TW) cows were supplemented (dietary flushing; Soca et al., 2013) each morning with 2 kg (as-fed basis)/cow/day of whole-rice middling (Oryza sativa; 86.5% DM; 13.5% CP; 44% neutral detergent fibre; 13.5% ether extract) during 22 days

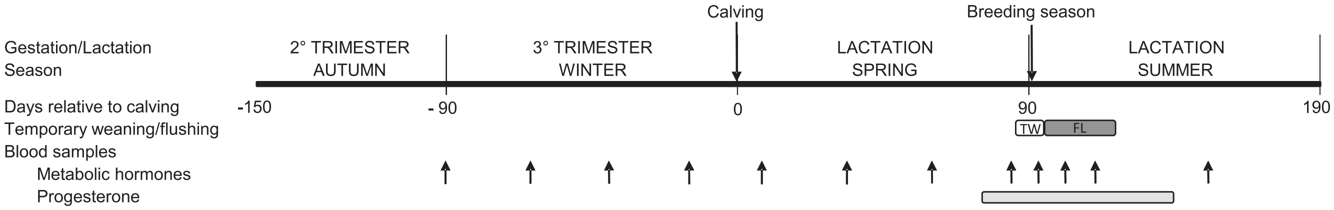

Fig. 1. Schematic representation of cows' physiological status, seasons, calving, breeding season, temporary weaning, flushing, and taking of plasma samples for determination of metabolic hormones and probability of ovulation throughout the experiment related to days relative to calving (black horizontal bar). TW=Temporary weaning; FL=flushing.

(Fig. 1). A trained observer verified that the cows ingested the supplements each day. The calves were weaned at 195 ± 12 DC. Cows were a sub-sample of an experiment where details on weather parameters, aboveground net primary production, and herbage mass have been previously reported (Claramunt et al., 2018). Briefly, monthly rainfall was below the historical average (1999–2007) from autumn up to the last spring month and above the historical average during summer (breeding season). The winter temperatures were below, and frozen days (days with temperatures < 0 °C at 5 cm aboveground) were above the historical records. Herbage mass tended to be greater whereas the stocking rate was lower in High HA than Low HA. Throughout the year, herbage mass remained stable under 1 000 kg DM/ha during autumn, winter, and spring (−150 to 90 DC/second trimester of gestation to mid-lactation), and markedly increased in summer (Table 1). Horizontal heterogeneity of herbage structure was described via the frequency of records in three mass levels (Table 1): (1) < 1 400 kg DM/ha which could associated with reductions in herbage intake rate without compensation via grazing time; (2) 1 400–2 400 kg DM/ha intake rate is optimised; (3) > 2 400 kg DM/ha, intake rate is reduced via an increase in searching effort (Da Trindade et al., 2016).

Body condition score, BW, milk yield, and, herbage intake estimation

The BCS and BW of the cows were assessed at −150, −90 DC, then monthly until the start of the TW, and the last assessment was at 170 DC. The BCS score was assessed using a 1–8 units visual scale developed for Hereford beef cows (Vizcarra et al., 1986) and was assigned by one experienced technician.

Calf BW was recorded at birth, 60, 120, and 195 DC. The BW of both cows and calves were measured early in the morning without prior fasting (Coates and Penning, 2000) Cow milk yield was individually measured at 50, 85, and 190 DC via machine milking according to Quintans et al. (2010). Individual metabolisable energy requirements were calculated seasonally using collected cow data (Coates and Penning, 2000) to estimate cows' HI using the NASEM (2016) models. Estimations include energy requirements for maintenance, gestation, lactation, BCS changes, and grazing activities and were expressed as gs DM/$\text{BW}^{0.75}$*day.

Blood sampling, hormone determination, ovulation, and pregnancy

Blood samples were collected every 25 days from −90 (end of autumn/mid-gestation) to 60 (spring/early lactation) DC (Fig. 1) and then before suckling restriction (day 0 = 86 ± 12 DC), at suckling restriction (day 10), two times during F (19 and 28 days), and 65 days after suckling restriction initiation (151 ± 12 DC; Fig. 1). To determine the probability of ovulation, blood samples for progesterone determinations were taken weekly from 2 weeks before the calf suckling restriction was applied until 2 weeks after the end of F (74 to 135 ± 12 DC; Fig. 1). Blood was collected by jugular venipuncture, stored in heparinised tubes, centrifuged at 2 000g for 15 min within 3 h of collection to obtain plasma, and plasma was stored at −20 °C until assayed. Plasma samples were assayed for insulin, IGF-I, leptin, and progesterone concentrations at the Laboratory of Animal Endocrinology and Metabolism, Veterinary Faculty, Uruguay. The concentration of insulin and IGF-I were quantified by commercial immunoradiometric assay kits (insulin: DIAsource Immuno Assays S.A, Nivelles, Belgium; IGF-I: IGF1-RIACT Cis Bio International, GIF-SUR-YVETTE CEDEX, France) previously used in dairy and beef cows (Adrien et al., 2012; Soca et al., 2014a). The plasma leptin concentrations were quantified by a liquid-phase radioimmunoassay using a commercial Multi-Species Leptin kit (RIA kit, Millipore, Cat XL-85 K) while progesterone concentrations by a direct solid-phase radioimmunoassay using MP kits (MP BIOMEDICALS, INC. Solon, OH, USA). The sensitivity of the assays, as well as the coefficients of variation (CVs) for intra and inter-assay controls, are provided in Supplementary Material S1. Ovulation was defined as the interval between calving to the day of the first plasma samples with progesterone ≥ 1 ng/mL (Adrien et al., 2012). Pregnancy diagnoses via rectal palpation were performed at 205 DC and were confirmed with the subsequent calving date.

Table 1
Characterisation of primiparous cows' pasture herbage mass and proportion of records per herbage mass class for High and Low Herbage Allowance (HA) during autumn, winter, spring, and summer.

Season	HA	Herbage mass (kgDM/ha)	Proportion of records per Herbage mass class		
			<1 400	1 400–2 400	>2 400
Autumn	High	982	86	14	0
	Low	671	94	4	0
Winter	High	612	94	6	0
	Low	463	99	1	0
Spring	High	961	88	12	0
	Low	795	95	5	0
Summer	High	2 499	9	36	55
	Low	2 090	12	51	37

Statistical analyses

All data were analysed using the SAS Systems program (SAS Institute Inc., Cary, NC, USA). Endocrine profiles, BCS, milk yield, cow and calf BW, and estimated herbage intake were analysed by repeated measures using the MIXED procedure with DC as the repeated effect. The covariance matrix for each response variable was selected based on the lowest Akaike information criterion. The effect of HA on the probability of ovulation and pregnancy was fit based on generalised linear models using the GLIMMIX procedure. Probability analysis assumed a binomial distribution and Logit was used as the link function. The models included HA as a fixed effect, block as a random effect, and in repeated measurements the HA and days interaction. The experimental unit was the cow or calf. The analysis of cow response variables included calving date as a covariate and sex as a fixed effect. The df were adjusted via the Satterthwaite method. The interaction between block and HA was tested on each response variable and was not significant. Effects were considered significant at $P \leq 0.05$ except for reproductive variables that were considered different at $P \leq 0.10$. The data were expressed as least square means ± SE and were separated using the PDIFF option. The relationships between the probability of ovulation or pregnancy with the hormone concentrations at −90, −65, −40, 10, 60, and 85 DC, and an average of TW and F samples were evaluated using the GLIMMIX procedure assumed a binomial distribution and Logit as the link function. Non-significant models ($P > 0.05$) were not presented. An example of SAS codes used in time-repeated measurement analyses and generalised linear models is included in Supplementary Material S2.

Results

Insulin, IGF-I, and leptin concentrations during −90 to 60 days relative to calving

Cows in High HA had greater insulin concentrations at −90 DC than Low HA cows ($P < 0.05$; Fig. 2a). Insulin concentrations remained stable from −90 to −15 DC, decreased at 10 DC ($P < 0.05$), and rebounded to prepartum levels at 60 DC ($P < 0.05$; Fig. 2a). The concentrations of IGF-I were higher between −90 and −40 DC in cows grazing High HA than in Low HA ($P < 0.05$; Fig. 2b) and did not differ thereafter. The IGF-I concentrations decreased in both treatments between −90 and −15 DC (last trimester of gestation/winter), remained stable during the −15 to 35 DC period, and increased at 60 DC (Fig. 2b). Leptin concentration increased from −90 to −15 DC and did not change between −15 and 60 DC (Fig. 2c; Table 2).

Cows' herbage intake, BW, and body condition score

Herbage intake was greater in High HA cows than Low HA cows during the −150 to −90 DC period (86 vs 76 ± 5.1 g. DM/BW$^{0.75*}$day; $P < 0.05$) while did not differ between treatments during −90 to 0, 0 to 90, and 90 to 190 DC (Table 2). The HI during −150 to −90 DC was lower than other periods while during 0 to 90 DC was greater (81, 88, 91, and 87 ± 4 g.DM/BW$^{0.75*}$day for −150 to −90, −90 to 0, 0 to 90, and 90 to 190 DC respectively; $P < 0.05$). Cows BCS was greater in High HA than Low HA ($P < 0.05$; Table 2). Low HA cows lost BCS from the start of the experiment, whereas in High HA cows, BCS losses started during the −90 to 0 DC period/winter (Fig. 3a). Cows attained BCS nadir at 15 DC and then BCS increased throughout lactation/spring-summer in both groups (Fig. 3a). Cow BW was affected by the HA and days interaction (Table 2) as BW was increased in High HA during the second trimester of gestation/autumn (−150 to −90 DC), whereas Low HA cows maintained BW during this period (Fig. 3b). These differences in BW change resulted in greater BW from −65 to 45 DC in High HA cows than Low HA ($P < 0.05$; Fig. 3b). From 45 DC until the end of the experiment, cows gained BW, and no differences between treatments were found (Fig. 3b).

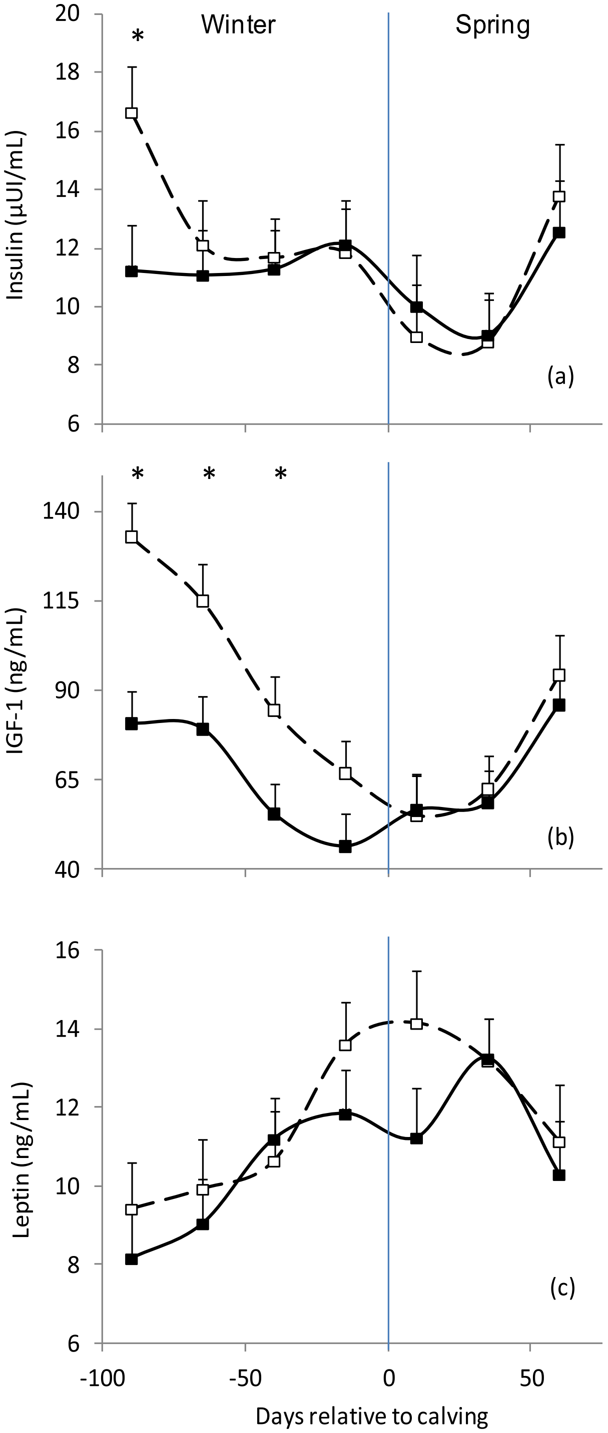

Fig. 2. Cow (a) insulin, (b) IGF-I, and (c) leptin concentrations in plasma from −90 to 60 days relative to calving for high (dashed lines and open squares) and low (solid lines and black squares) herbage allowance (4 and 2.5 kg DM/kg BW annual average, respectively). The least-square means ± SEs are presented. Vertical lines separate the winter and spring seasons. Days with an asterisk differ significantly at $P < 0.05$ between herbage allowances.

Table 2
Effects of herbage allowance (HA), days, and their interaction on estimated herbage intake, BCS, BW, calf BW, milk yield, and plasma insulin, IGF-I, and leptin concentrations in primiparous cows. Least square means, SE and the *P*-values of F-tests are presented.

	Herbage allowance			*P*-Value		
Item	High	Low	SE	HA	Days	HA×Days
Estimated herbage intake (g.DM/kgBW$^{0.75}$/d)	88.2	85.2	3.1	0.263	<0.01	0.042
Cow BCS (1–8 units)	4.58	4.22	0.13	0.049	<0.01	0.388
Cow BW (kg)	393	371	4.9	0.33	<0.01	<0.01
Metabolic hormones						
−90 to 60 days relative to calving						
Insulin (µUI/ml)	11.9	11.1	1.0	0.52	<0.01	0.141
IGF-I (ng/mL)	87.2	66.1	6.7	0.038	<0.01	0.004
Leptin (ng/mL)	11.1	10.4	0.6	0.205	<0.01	0.806
After the initiation of temporary weaning						
Insulin (µUI/ml)	13.4	13	0.8	0.759	<0.01	0.301
IGF-I (ng/mL)	123.2	102.6	8.8	0.1	<0.01	0.329
Leptin (ng/mL)	11	11.2	0.9	0.851	<0.01	0.314
Calf BW (kg)	115.1	105.2	3.4	0.047	<0.01	0.04
Milk yield (kg/d)	5.1	4.7	0.2	0.213	<0.01	0.482

Abbreviations: HA=herbage allowance; BCS=body condition score. 1–8 units scale (Vizcarra et al., 1986).

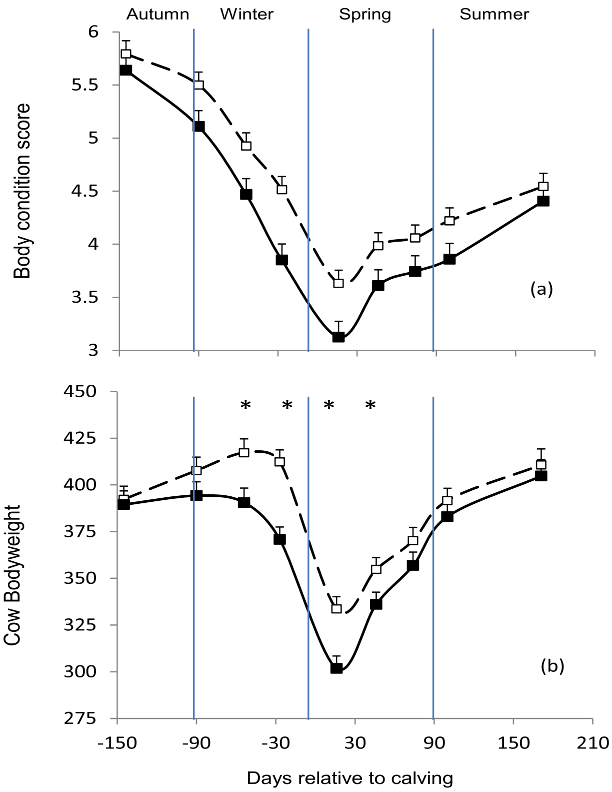

Fig. 3. Cow (a) body condition score and (b) bodyweight from −150 to 180 days relative to calving for high (dashed lines and open squares) and low (solid lines and black squares) herbage allowance (4 and 2.5 kg DM/kg BW annual average, respectively). The least-square means ± SEs are presented. Days with an asterisk differ significantly at $P < 0.05$ between herbage allowances. Autumn, winter, spring, and summer correspond to −150 to −90, −90 to 0, 0 to 90, and 90 to 180 days relative to calving periods respectively. Vertical lines separate the autumn, winter, spring and summer seasons.

Insulin, IGF-I, and leptin concentrations during temporary weaning and flushing

Insulin, IGF-I, and leptin concentrations during TW and F were affected by days (Table 2). Insulin concentration 10 days after the initiation of TW doubled the concentrations before the suckling restriction. Insulin returned to pre-TW levels at the first sample during F and then increased until 65 days (Fig. 4a). The IGF-I concentrations increased during TW, decreased at the end of F, and remained stable until 65 days (Fig. 4b). Leptin concentration was increased at suckling restriction than previous levels and remained stable until the first sample during F. Leptin concentrations were reduced at 28 days and increased again at 65 days (Fig. 4c). The IGF-I concentrations tended to be greater in High HA than in Low HA cows (Table 2; Fig. 4b).

The probability of ovulation and pregnancy

The probability of ovulation was not influenced by HA ($P = 0.125$; 0.94 vs 0.75 ± 0.11 for High and Low HA, respectively). The IGF-I concentrations at −90 ($P = 0.050$) and −40 ($P = 0.036$) DC (winter) were positively associated with the probability of ovulation (Fig. 5a and 5b). The probability of ovulation increased from 0.2 to 0.9 in the range of 30 to 120 ng/mL IGF-I concentrations at −90 days relative to calving (Fig. 5a), whereas had a marked reduction when concentrations at −40 days relative to calving were less than 55 ng/mL (Fig. 5b). The probability of pregnancy was greater in High HA than in Low HA cows (0.9 vs 0.61 ± 0.10; $P = 0.07$). Insulin concentrations at 10 days postpartum were positively associated with pregnancy ($P = 0.04$; $\text{Probability} = 1/\ (1 + \exp^{((2.278\ -\ 0.4012\ *\ \text{insulin}))})$. The probability of pregnancy increased almost linearly with the increase of the insulin concentrations at 10 days postpartum, from a probability of 0.55 with 6 µUI/mL of insulin to 0.98 with 16 µUI/mL.

Calves BW and milk yield

Calf weight did not differ at 0 (34 vs 31.5 ± 4 kg) and 60 (88.5 vs 80 ± 4 kg) days; however, calf weight tended to be greater at 120 (143 vs 133 ± 3.95 kg; $P = 0.087$) and was greater at weaning (195 DC) in High HA than Low HA groups (193.9 vs 178.5 ± 3.3 kg; $P < 0.05$; Table 2). Milk yield was affected by days (Table 2); milk yield at 50 days (6.45 ± 0.5 kg/day) did not differ from milk yield at 85 days (5.5 ± 0.3 kg/day) but decreased at 190 days (2.85 ± 0.2 kg/day; $P < 0.05$).

Discussion

To our knowledge, this is the first study to investigate the impact of changes in HA levels on insulin, IGF-I, and leptin profiles throughout the gestation and lactation periods in primiparous beef cows grazing on native grasslands subjected to TW and F. The

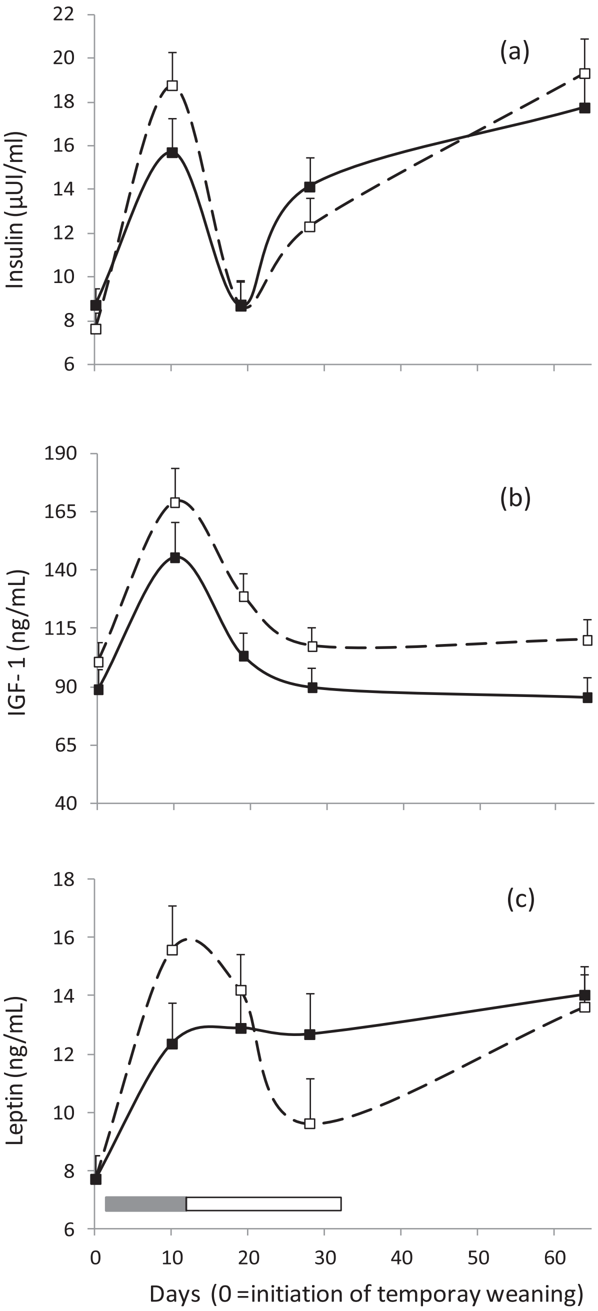

Fig. 4. Cow (a) insulin, (b) IGF-I, and (c) leptin concentrations in plasma from the initiation of temporary weaning up to 65 days after for high (dashed lines and open squares) and low (solid lines and black squares) herbage allowance (4 and 2.5 kg DM/kg BW annual average, respectively). The least-square means ± SEs are presented. Temporary weaning (grey rectangle) and flushing (open rectangle) with whole-rice bran were applied from 86 to 121 days relative to calving.

study also aims to elucidate the relationship between these metabolic hormone profiles throughout gestation and lactation and the nutritional status and reproductive response of the cows. Despite moderate differences in herbage mass and changes in cow HI and BCS limited to −150 to −90 DC/second trimester of gestation, cows in High HA exhibited greater IGF-I concentrations during the last trimester of gestation and after the start of TW which were positively associated with the probability of ovulation. The effect of HA even under conditions of moderate differences in herbage mass makes the results particularly valuable for cow-calf production systems in low-herbage production grasslands.

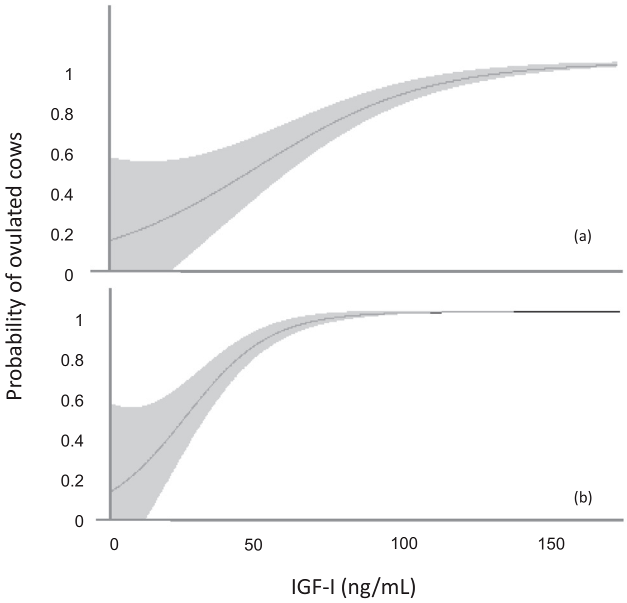

Fig. 5. Estimated means and SEs of the probability of ovulated cows, according to the IGF-I concentrations in plasma at (a) −90, and (b) −40 days relative to calving. Probability of ovulated cows $_{\text{(IGF-I -90 days)}} = 1/\ (1 + \exp^{((1.748\ -\ 0.0354\ *\ \text{IGF-I}))})$. Probability of ovulated cows $_{\text{(IGF-I -40 days)}} = 1/\ (1 + \exp^{((1.77\ -\ 0.0716\ *\ \text{IGF-I}))})$.

Cows grazing High HA had elevated concentrations of insulin and IGF-I, and greater BCS at −90 DC than Low HA, which could be attributed to greater HI. High HA paddocks exhibited greater herbage mass and a higher proportion of sites with herbage mass in the class between 1 400 and 2 400 kg DM/ha than Low HA (Table 1) which could improve energy intake through greater HI and diet digestibility (Do Carmo et al., 2021). The higher HI explains the increase in insulin levels, which subsequently could affect the concentrations of IGF-I through changes in IGF-I synthesis and/or its half-life (increase of hepatic GH receptors and alterations in IGF-I binding proteins), as reported in previous studies conducted on both beef and dairy cows (Fenwick et al., 2008; Laporta et al., 2014). The increase in IGF-I concentrations observed due to the HA change during autumn is noteworthy, considering the differences in HI between treatments and the relatively short period since the start of the experiment (60 days). Previous studies have reported similar or even greater increases in IGF-I concentrations when energy and protein intake were increased through supplementation during the second trimester of gestation in both primiparous (Perry et al., 2002; Sullivan et al., 2009) and multiparous beef cows (Lents et al., 2005). This notable rise in IGF-I concentrations due to intake may be characteristic of this stage of gestation as IGF-I concentrations tend to decrease after the second trimester, possibly as a result of increased foetal nutrient demand and a decrease in intake (Perry et al., 2002; Lents et al., 2005; Sullivan et al., 2009; Soca et al., 2014a).

The IGF-I concentrations remained greater at −65 and −40 DC and after the initiation of TW, periods where no discernible differences in herbage intake or cow energy balance were expected based on comparable HI, insulin concentrations, and BW and BCS levels. Previous studies have indicated that IGF-I concentrations during the prepartum period and after the start of TW and F depend on calving BCS which reflects prepartum energy nutrition suggesting the existence of a “metabolic memory” (Blanc et al., 2006; Soca et al., 2014a,b; Meikle et al., 2018) influencing the IGF-I dynamics. Similar results were observed in primiparous beef cows that were categorised based on their BCS at calving (≥4 vs ≤ 3.5); those with a greater BCS had elevated concentrations of

IGF-I during the last trimester of gestation (Soca et al., 2014a; Astessiano et al., 2014) and after the start of breeding season when TW and F were applied, than cows with lower BCS calving (Soca et al., 2014b). Claramunt et al. (2020) found that IGF-I concentrations after the start of TW were higher in cows with greater BCS prepartum achieved through similar levels of HA than in the current study. Despite moderate differences in herbage mass and HI, High HA exerted a direct impact during the second trimester of gestation and a sustained carry-over effect on IGF-I concentrations throughout the last trimester of gestation and advanced lactation. No differences in leptin concentrations were observed between treatments throughout the study. This lack of differences could be attributed to the moderate differences in herbage intake and BCS observed between treatments. Previous studies suggest that more substantial BCS and intake differences are necessary to elicit changes in leptin concentrations (Garcia et al., 2002; Lents et al., 2005; Chilliard et al., 2005).

Alterations in IGF-I concentrations between treatments provide insights into the mechanisms through which the HA affected the reproductive response. The effect of HA on IGF-I prepartum, coupled with the associations between IGF-I concentrations at −40 DC with the probability of ovulation, could connect IGF-I prepartum with early follicle growth and development, and the initiation of postpartum luteal activity and subsequent pregnancy probability. Roberts (2008) and Laporta et al. (2014) also reported a positive association between prepartum IGF-I levels and postpartum commencement of luteal activity in beef cows. The identification of IGF receptors in the ovary, spanning from the early stages of follicular development (Britt, 1991; Webb et al., 2003) implies a 180-day IGF-I-sensitive period before postpartum ovulation (Aerts and Bols, 2010). This critical period encompasses the last trimester of gestation, during which the higher IGF-I concentrations in High HA cows could exert a positive influence on follicles in the early stages of development and enhance the probability of early ovulation (Britt 1991; Webb et al., 2003).

The elevated concentrations of IGF-I after the initiation of TW in High HA cows also may contribute to explaining improvement in reproductive response. Postpartum IGF-I concentrations have been linked to shorter intervals from calving to first estrus in primiparous beef cows (Ciccioli et al., 2003; Soca et al., 2014b; Rubio et al., 2021), as IGF-I acts as a stimulator of steroidogenesis in cow follicles (Spicer et al., 2002; Lents et al., 2013). The IGF-I following the commencement of TW could also exert a positive influence on cow fertility. The IGF-I concentrations postpartum have been shown to exhibit a positive association with the probability of pregnancy during fixed-time embryo transfer in beef and dairy cows (Grimard et al., 2013; Gobikrushanth et al., 2018; Fontes et al., 2021) associated with enhanced progesterone production and uterine function, both of which contribute positively to early embryo development and survival (Wathes et al., 1998; Meikle et al., 2018).

Calf weight remained similar until 120 days, aligning with the absence of a treatment effect on the metabolic status of cows and milk yield. However, after the 120-day where they primarily rely on herbage intake (Wright and Russel, 1987; Ansotegui et al., 1991), High HA calves exhibited greater weight. A prior study by our group also concluded that calf weight was primarily influenced by calves' herbage intake, as the increased milk yield in High HA cows did not account for the differences in calf weight between treatments (Claramunt et al., 2020). Consistent with the current study, similar differences in cows' IGF-I concentrations were noted in a previous study, associated with a lower cow-calf distance in High HA cows than in Low HA (Claramunt et al., 2020). The higher calf weight in the High HA group was not attributable to milk production but rather appeared to be associated with a better metabolic status of the cow and a greater calf forage intake.

In summary, changes in HA from Low to High HA during the second trimester of gestation/autumn demonstrated a direct impact on cows' metabolic hormone concentrations, BCS, and BW, even under conditions of slight differences in herbage mass. Those changes yielded a positive carry-over effect on cow IGF-I concentrations during the last trimester of gestation/winter and following the initiation of TW, providing an explanatory framework for the observed greater probability of ovulation and pregnancy in High HA. The study shows a complex response that integrated several processes that were connected over time and highlights that intervening in the nutritional plane of spring-calving cows during the preceding autumn, can have medium-term effects on the metabolic status, reproduction, and efficiency in herbage use in primiparous beef cows grazing native grasslands. The results contribute to an understanding of the management needs of primiparous cows grazing moderate-production native grasslands and show that, even under conditions of low herbage mass frequent in such grasslands, changes in HA influence metabolic hormone concentrations and productive response.

Supplementary material

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Ethics approval

Animal procedures were approved by the Animal Experimentation Committee of Universidad de la República, Uruguay, number 021130-006374-12.

Data and model availability statement

None of the data were deposited in an official repository. Information can be made available from the authors upon request.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

None.

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