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Beef cow weight variations during gestation and offspring performance: a meta-analysis

Variação de peso de vacas de corte durante a gestação e o desempenho da progênie: uma meta-análise

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Highlights _

The progeny of cows that gain weight during gestation has greater growth potential. Weight loss of the pregnant cow produces a phenotype with greater adaptive capacity. The effects of fetal programming are most evident in the early months of life.

Abstract _

The objective of this meta-analysis was to evaluate the effects of weight loss or weight gain of beef cows during the second and/or third trimester of gestation on the postnatal performance of the progeny. The variation in cow weight during the gestational period was calculated to standardize the treatments, being them: severe loss (SL = cows that lost more than 10% of weight); moderate loss (ML = cows that lost from 0 to 10% of weight) and weight gain (WG = cows that gained weight). The intensity of the cow weight variation effect was calculated as the mean difference (MD) with a 95% confidence interval and heterogeneity determined using the Q test and the I2 statistic. A meta-analysis of random effects was conducted for each indicator separately with the means of the control and experimental groups. Calves from WG cows were higher for birth weight (P = 0.0094); weight adjusted to 205 days (P = 0.0127) and average daily gain during pre-weaning (P < 0.0001) in relation to calves from ML cows. The W205 of calves from SL cows was 11.6 kg lower than the progeny from ML cows. The post-weaning performance of the progeny tended (P = 0.0868) to be higher in the progeny of WG cows than ML ones. The weight gain of beef cows during gestation improves the pre- and post-weaning performance of the progeny, with more evident effects in the early months of life of the offspring.

Key words: Birth weight. Calves. Fetal programming.

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Resumo _

Objetivou-se avaliar nesta meta-análise os efeitos da perda ou ganho de peso de vacas de corte durante o 2º e/ou 3º trimestre de gestação sobre o desempenho pós-natal da progênie. A variação de peso da vaca no período gestacional foi calculada para padronização dos tratamentos, sendo: perda severa (PS = vacas que perderam mais de 10% de peso); perda moderada (PM = vacas que perderam de 0 a 10% do peso) e ganho de peso (GA = vacas que ganharam peso). A intensidade do efeito da variação de peso da vaca foi calculada como diferença média (MD) com um intervalo de confiança de 95% e a heterogeneidade determinada usando o teste Q e a estatística I2. Uma meta-análise de efeitos aleatórios foi conduzida para cada indicador separadamente com as médias do grupo controle e experimental. Bezerros de vacas GA foram superiores para peso ao nascer (P = 0.0094); peso ajustado aos 205 (P = 0.0127) e para o GMD pré-desmame (P < 0.0001) em relação aos bezerros de vacas PM. O P205 dos bezerros filhos de vacas PS foi 11,6 kg menor que a progênie de vacas PM. O desempenho pós-desmame da progênie tendeu (P = 0.0868) a ser maior na progênie de vacas GA em relação às vacas PM. O ganho de peso de vacas de corte durante a gestação melhora o desempenho pré e pós-desmame da progênie, com efeitos mais evidentes nos meses inicias de vida dos descendentes.

Palavras-chave: Bezerros. Peso ao nascer. Programação fetal.

Introduction _____

Calf production almost exclusively happens in forage systems, where the amount and quality of nutrients available to pregnant cows fluctuate during the year. This nutritional supply variation subjects pregnant cows to food restrictions during certain periods (Gutiérrez et al., 2014). One way to measure the nutritional balance of the pregnant cow is through weight variation since weight loss may indicate a restriction of nutrients to the maternal organism, compromising fetal growth. According to Rodrigues et al. (2021), inadequate nutrition of pregnant cows may be caused by climatic conditions or a decline in the quality or quantity of available forage on pasture, impacting the weight of cows during gestation.

Food scarcity is common in several regions of the world, resulting in cows under food restriction conditions during gestation, and this low nutrient intake is associated with the future development of the progeny (Du et al., 2013). Du, Wang, Fu, Yang and Zhu (2015) also indicate that calves born from cows maintained under a restricted nutrient supply during gestation present compromised meat production potential. Thus, structural and functional changes in organs and tissues resulting from nutrient supply during gestation allow for rapid adaptations of the developing fetus to uterine environmental selection pressure (Reynolds et al., 2019). Therefore, fetal formation alterations directly influence progeny productive potential.

In general, the recent literature has pointed outseveral maternal nutrition gestation effects on progeny quality and performance. In a literature review on fetal programming in beef cattle, Klein, Machado, Adams, Alves and Brondani (2021) state that the divergences in the effects of fetal programming on the quality of the progeny are consequences of the variability of the studied nutrients, gestational period and intensity of nutritional restriction, as well as of the characteristics evaluated in the progeny. These factors make nutritional recommendations for pregnant cows inconclusive. In this context, the present study aimed to evaluate the effects of cow weight variations during gestation on progeny performance after birth through a metaanalysis.

Material and Methods __

Literature search

The literature search was performed using specific search databases on the platforms: Scientific Electronic Library Online (https://scielo.br; Scielo 2020), Portal de Periódicos Capes (https://www.periodicos. capes.gov.br; Capes, 2020), ScienceDirect (https://www.sciencedirect.com; Elsevier, 2020) and Google Scholar (http://scholar. google.com; Google Scholar, 2020). The searches were based on the following keywords: "fetal programming in beef cows and the performance of steers progeny" or "fetal programming in beef cattle and the performance of the progeny." The literature searches included studies from the last ten years of publications (2009 - 2019).

This meta-analysis was performed using combined data from 12 studies (ten peerreviewed articles, one doctoral thesis and one master's dissertation), with total records of 2,275 calves during the breastfeeding and post-weaning growth phases. When possible, the same study was inserted two or more times in the meta-analysis database to explore the manuscript data fully. The studies used in this meta-analysis evaluated the effects of maternal nutrition and the consequent variation in body weight of cows during gestation on progeny performance (Table 1).

Inclusion and exclusion criteria

In total, 199 studies published between 2009 and 2019 were identified, following the pre-established search criteria. For this metaanalysis, only studies with multiparous cows were considered. The criteria established for the inclusion of studies in the database were: 1) the possibility of calculating the daily body weight variation of cows during gestation and adequacy to treatments; 2) the variation in weight of cows during gestation fits into the proposed groups; 3) provide the following progeny performance variables: weight at birth, adjusted weight at 205 days, and average daily gain pre- and post-weaning; 4) the period of nutritional evaluation occurs in the second or third trimester of gestation; and 5) report information on sample size and variability of the measurements of interest (i.e., deviation or standard error). In the case of studies that reported the standard error of mean (SEM), the standard deviation (σ) was obtained through the equation:

$$\sigma = \frac{SEM}{\sqrt{n}}$$

A large number of studies were excluded from this research for not meeting the inclusion criteria. In addition, this is justified by the wide variation between studies, especially concerning the intensity of food restriction and distance between treatments, period of food restriction, as well as the great diversity of variables evaluated, as reported by Klein et al. (2021) in a literature review on the subject.



Data selection and group formation

The growth traits of progeny from birth to rearing period were selected as response variables, including male and female calves. The birth weight (BiW) of the calves was collected in the first 24 h after calving. Weaning weight information was also collected. Due to different durations in the pre-weaning period, the weight adjusted at 205 days of age (W205) was considered for standardization of calf weaning weight between studies in this meta-analysis. The average daily weight gain (ADG) was evaluated during the pre- and post-weaning periods, with the post-weaning period being considered until the finishing phase of the animals.

The weight variation of cows during gestation was used to standardize the tested effects (treatments), according to the equation below:

$$WV = \frac{(IW - FW)}{IW} X \ 100$$

where WV represents the variation in weight of cow between the beginning of the experimental period and calving; IW represents the weight of cow at the beginning of the experiment; FW represents the weight of cow at calving. Description of the studies included in the database for conducting the meta-analysis.

C+	2007		Cow					Nur	mber of obse	ervations	: used
Siuuy	Leal		breed	X D G		dnoificine		BiW ^c	ADGpre ^D	205⊧	ADGpost ^F
Bohnert, Satlker, Nyman, Falck and Cooke	2013	NSA	AaxH	AII	Supl. X No Supl.	Gain	534 ±14	228	228	228	113
Bohnert et al.	2013	NSA	AaxH	AII	High BCS X Low BCS	Gain	534 ±14	228	228	228	113
Larson, Martin, Adams and Funston	2009	NSA	Aa x Sim	AII	Supl. X No Supl.	Gain	498 ±15	24	ı	24	I
Larson et al.	2009	NSA	Aa x Sim	Male	Supl. X No Supl.	Gain	498 ±15	24	ı	24	ı
LeMaster, Taylor, Ricks and Long	2017	NSA	Aa x Sim x H	AII	Maintenance x Restriction	Gain	620 ±19	38	ı	38	I
Ramírez et al.	2020	ARG	Aa	Male	75% TDN x No Restricted	Gain	492 ±24	17	17	17	17

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Table 1

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Maresca et al.	2018	ARG	Aa	Male	High CP x Low CP	Gain	408 ±54	34	34	34	ı
Maresca et al.	2018	ARG	Aa	Female	High CP x Low CP	Gain	408 ±54	34	34	34	,
Maresca et al.	2019	ARG	Aa	Male	High CP x Low CP	Gain	408 ±54	,	ı		24
Mulliniks, Mathis, Cox and Petersen	2013	NSA	Аа	Male	Supl. X No Supl.	Gain	575 ±9	I	I	I	ı.
Wilson, Schroeder, Ireland, Faulkner and Shike	2015	NSA	Aa x Sim	AII	Supl. X No Supl.	Gain	600 ±7	177	177	177	ī
Wilson et al.	2015	NSA	Aa x Sim	Male	Supl. X No Supl.	Gain	600 ±7	71	71	71	ı
Wilson, Faulkner and Shike	2016	NSA	Aa x Sim	Male	100% TDN x 125% TDN	Gain	684 ±7	86	86	86	I
Taylor et al.	2016	NSA	Aa x Sim	AII	Positive energy x Negative	Gain	462 ±3	139	I	139	ī
Klein	2019	BRA	Ch x Ne	AII	Supl. 100% TDN x N. Supl.	Gain	464 ±9	30	30	30	30
Klein	2019	BRA	Ch x Ne	AII	Supl. 150% TDN x N. Supl.	Gain	464 ±9	26	26	26	26
Klein	2019	BRA	Ch x Ne	Female	Supl. 100% TDN x N. Supl.	Gain	464 ±9	26	26	26	26
Klein	2019	BRA	Ch x Ne	Female	Supl. 150% TDN x N. Supl.	Gain	464 ±9	29	29	29	29
Rodrigues	2019	BRA	Ch x Ne	Male	Weight Gain x Severe Loss	Severe Loss	413 ±8	260	I	260	ı
Rodrigues	2019	BRA	Ch x Ne	Male	Weight Gain x Moderate Loss	Gain	410 ±8	240	ı	240	ī
Rodrigues	2019	BRA	Ch x Ne	Female	Weight Gain x Severe Loss	Severe Loss	410 ±8	282	I	282	I
Rodrigues	2019	BRA	Ch x Ne	Female	Weight Gain x Moderate Loss	Gain	405 ±8	282	ı	282	ı.
Total	ı	ı		ı	ı	ı		2,275	986	2,275	378
^A BCS: body condition score; ^B Initial body weight of cows ¢	CP: crude expressed	e protein; d as mear	TDN: total d ı ± standard	ligestible error (SE	nutrients.						



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^cBirth weight; ^DAverage daily gain pre-weaning: ^EWeight at 205 days of age; ^FAverage daily gain post-weaning. Aa, Aberdeen Angus; H, Hereford; Sim, Simental; Ch, Charolês; Ne, Nelore.

This standardization was necessary due to the great variability of the researches treatments included in the database. Thus, the meta-analysis consists of three groups according to weight variation classes: severe loss (SL = cows that lost more than 10% of body weight during gestation); moderate loss (ML = cows that lost from 0 to 10% of body)weight during gestation) and weight gain (WG = cows that gained body weight during gestation). In this meta-analysis, the moderate loss (ML) of weight was used as a control group. This choice was based on the fact that, in general, beef cows are kept exclusively in pastoral systems, with higher nutritional challenges during gestation, an aspect that, according to Gutiérrez et al. (2014), subjects cows to nutritional restriction and malnutrition crises. For further analysis, the data for each study, such as the number of replicates, means and standard deviations, were organized in Microsoft[®] Office Excel[®] spreadsheets.

Meta-analytical procedure

Statistical analyses were performed using the software R version 4.0.2 (R Core Team [R], 2020) through the 'meta' package, 'metacont' function (Schwarzer, 2016). Egger's linear regression asymmetry was used to examine the presence of publication bias (Egger, Smith, Schneider, & Minder, 1997), with a significant bias value when P <0.05, through the 'metabias' function. In addition, funnel plots were used to evaluate publication bias in meta-analysis through the 'funnel' function. The funnel plot graphically shows the precision of the estimated intervention effect, where smaller studies had a wider variance and larger ones had less spread of variability. In the absence of bias, the funnel plot should be approximately symmetrical.

The effect size was calculated as the mean difference (MD), which is the difference between control (ML) and experimental groups (subgroups WG and SL). The effects of variation in cow weight during gestation were expressed in forest plot graphs, constructed from the 'forest' function, using the estimated MD, that allowed evaluating the size effect and weighted contribution to each study from fixed and random effect models (Schwarzer, 2016).

The consistency of results between the experiments was quantified using the measures of heterogeneity of the Chi-square test (Q) and I² statistics (Higgins, Thompson, Deeks, & Altman, 2003), which quantifies the impact of heterogeneity on the meta-analysis, with a mathematical criterion independent of the number of studies and the metric effect of each treatment. Although the Q test helps identify heterogeneity, I² was used to measure heterogeneity (Lean, Thompson and Dunshea, 2014). The I2 statistic is given by:

$$I^{2}(\%) = \frac{Q - (k - 1)}{Q} X \, 100$$

where Q is the χ^2 heterogeneity statistic and k is the number of trials. The I² statistic describes the percentage of variation across studies due to heterogeneity. Negative values of I² are set equal to zero; consequently, I² lies between 0 and 100% (Lean et al., 2014). Its value might not be important if it falls within the range of 0-40%. However, a value of 30-60% often indicates moderate heterogeneity, 50-90% might represent substantial heterogeneity, and a value in the range of 75-100% represents considerable heterogeneity (Higgins et al., 2003).



Results and Discussion _

The funnel plots for the effect of the cow weight variation during gestation on the growth characteristics of the progeny (Figure 1) indicated no substantial asymmetry in most of the characteristics analyzed (Higgins et al., 2003). The weight variation of the cows (SL, ML and WG), the number of studies used, the mean gross difference and the size of the effect of each variable of interest, P values, heterogeneity and the Egger's test are described in Table 2. Egger's test showed that the variable calf birth weight presented a publication bias (P = 0.0074), despite the low to moderate heterogeneity (38 and 46%) for this characteristic, according to the classification by Higgins et al. (2003).



Figure 1. Funnel plot of the effect of the variation in the cow weight during gestation on progeny performance.

a) birth weight; b) weight adjusted to 205 days of age; c) average daily gain during the lactation; d) average daily gain post-weaning. Each point represents an individual randomized trial. The y-axis is the standard error of the trials and the x-axis is the effect size. The Larger studies appear toward the top of the plot and cluster around the effect size (mean) and smaller studies appear toward the bottom. When publication bias has occurred, one expects an asymmetry in the scatters of small studies, with more studies showing a positive result than those showing a negative result.

0.5046

Table 2

ADG lactation

weaning (kg/d)

(kg/d) ADG post-

ltem ^A	Subgroup	Number of studies	MD	95% confidence intervals	P-value ^B	Q	P-value ^c	² (%)	P-value ^D
	Gain	17	1.17	0.34, 2.00	0.0094	7	0.0637	38	0.0074
BiW (kg)	Severe loss	2	0.14	-1.62, 1.89	-	4	0.1848	46	-
	Gain	17	6.19	2.88, 9.49	0.0127	23.35	0.1052	31	0.1284
W205 (kg)	Severe	2	-11.06	-19.22, -2.90	_	0.06	0.8104	0	-

Effect size and heterogeneity for weight variation in beef cows during gestation on progeny performance.

^ABiW: Birth weight; W205: Weight at 205 days of age; ADG: Average daily gain.

12

8

0.05

0.05

^B*P*-value for MD; ^c*P*-value for Q statistics; ^D*P*-value for Egger's test - Number of studies (k < 10) too small to test for small study effects (Egger et al., 1997).

0.03, 0.08

-0.01, 0.11

< 0.0001 11.59

0.0868

17.77

I², Statistic of the estimated heterogeneity.

loss

Gain

Gain

It was identified through the metaanalysis the birth weight of the progeny (P = 0.0094). Calves from WG cows were higher than those from ML cows, being 1.17 kg heavier at birth (Figure 2). However, when there was weight loss, the birth weight of the calves was similar between SL and ML. The body weight loss in cows during late gestation is mainly related to nutritional imbalance on pasture-based systems. In addition, Rodrigues et al. (2021) comment on the weight variations. Tsuneda et al. (2017) indicate that nutrition is one of the main factors that alter the uterine environment during gestation, which can modify calf metabolism and physiology after birth. Du et al. (2010) state that the higher birth weight of calves born from cows with better nutritional status is a consequence of hyperplasia and muscle hypertrophy during gestation.

0.4021

0.0131

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		Expe	erimental			Control					
Study	Total	Mean	SD	Total	Mean	SD	Me	ean Difference	MD	95%-CI	Weight
subaroup = gain											
Bohnert et al. (2013) sup	116	40 80	23 0485	112	39 30	22 6476			<u> </u>	[-4 43 [·] 7 43]	1 4%
Bohnert et al. (2013) ecc	108	38.80	22.2395	120	41.40	23.4425 -			-2.60	[-8.53: 3.33]	1.4%
Larson et al. (2009)	12	36.90	1.7000	12	36.10	1.7000		<u>+</u>	0.80	[-0.56; 2.16]	10.5%
Larson et al. (2009) m	12	38.50	3.8105	12	36.95	3.8105			1.55	[-1.50; 4.60]	4.3%
LeMaster et al. (2017)	19	37.20	5.2307	19	33.40	5.6666			3.80	[0.33; 7.27]	3.6%
Maresca et al. (2018) m	17	29.30	4.5354	17	27.80	4.5354			1.50	[-1.55; 4.55]	4.3%
Maresca et al. (2018) f	17	27.90	4.5354	17	25.40	4.5354			- 2.50	[-0.55; 5.55]	4.3%
Wilson et al. (2015)	91	34.00	19.0788	86	33.00	18.5472		+		[-4.54; 6.54]	1.6%
Wilson et al. (2015) m	37	36.00	6.0828	34	36.00	5.8310			0.00	[-2.77; 2.77]	5.0%
Wilson et al. (2016) m	41	44.00	6.4031	45	41.00	6.7082			- 3.00	[0.23; 5.77]	5.0%
Taylor et al. (2016)	72	38.00	3.9881	67	38.00	3.8471			0.00	[-1.30; 1.30]	10.8%
Klein (2019) m SP100	16	39.28	4.8000	14	34.58	4.8642			4.70	[1.23; 8.17]	3.6%
Klein (2019) m SP150	12	39.13	4.8497	14	34.58	4.8642			4.55	[0.81; 8.29]	3.2%
Klein (2019) f SP100	12	35.45	4.5033	14	32.79	4.4900			- 2.66	[-0.81; 6.13]	3.6%
Klein (2019) f SP150	15	34.01	4.6476	14	32.79	4.4900			1.22	[-2.11; 4.55]	3.8%
Rodrigues (2019) m	49	31.50	7.6300	191	32.40	10.5034	-		-0.90	[-3.50; 1.70]	5.4%
Rodrigues (2019) f	73	31.00	4.7846	209	31.50	4.1925			-0.50	[-1.74; 0.74]	11.2%
Random effects model	719			997					1.17	[0.34; 2.00]	82.9%
Heterogeneity: $I^2 = 38\%$, τ^2	= 0.97	′10, p =	0.06								
	_										
Subgroup = severe loss	5 60	22.00	0 2066	101	22.40	10 5024			1.40	1 4 06: 2 061	E 00/
Rodrigues (2019) III	72	33.00	0.0000	200	32.40	10.0004			1.40	[-1.00, 3.00]	0.0%
Roungues (2019)1	1/3	51.00	4.0992	209	51.50	4.1920			-0.50	[-1.72, 0.72]	17.1%
Random enects model	14Z	20	0.10	400					0.14	[-1.02, 1.09]	17.170
neuerogeneity. $I = 46\%$, τ	- 0.82	29, p =	U. Iŏ								
Random effects model	861			1397				-	0.98	[0.24; 1.72]	100.0%
Heterogeneity: $I^2 = 39\%$, τ^2	² = 0.88	858, p =	0.04						1		
Residual heterogeneity: I ²	= 38%,	p = 0.0	5				-5	0	5		

Figure 2. Forest plot for birth weight (BiW) of the progeny from cows with different weight variations during gestation. The solid line of the x-axis is the no-effect line, and dotted lines represent the estimated difference of random model; therefore, the points to the left of the line represent a reduction in the trait, while the points to the right of the line indicate an increase. Each square represents the relative weight of the study of the overall estimate of effect size, with the larger squares representing a larger weight. The upper and lower bound of the squared line represents the upper and lower confidence intervals of 95% for the size of the effect. The diamond at the bottom represents the 95% confidence interval for the global estimate.

The W205 of the progeny was influenced (P = 0.0127) by the different weight variations of the cow during gestation (Figure 3). In the last two-thirds of gestation, calves from cows that gained weight had 6.19 kg more at 205 days of age than the control group. However, calves from cows with severe weight loss in this gestational period (> 10%) were 11.06 kg lighter than those born from cows with moderate loss. However, we must

emphasize the low weight of the severe loss subgroup in the meta-analysis (two studies, 11.5%) since a small number of studies met the inclusion criteria in the database (Figure 3). The effect of fetal programming on progeny growth potential was observed in this metaanalysis when the W205 was analyzed, as it decreased with increasing cow weight loss during gestation (Figure 3).



		Expe	erimental			Control				
Study	Total	Mean	SD	Total	Mean	SD	Mean Differe	ence MD	95%-CI	Weight
subgroup = gain										
Bohnert et al. (2013) sup	116	260.15	24.7718	112	252.50	24.3409		- 7.65	[1.27; 14.03]	9.1%
Bohnert et al. (2013) ecc	108	254.05	23.9023	120	258.70	25.1952	-+++	-4.65	[-11.03; 1.73]	9.1%
Larson et al. (2009)	12	223.50	13.8500	12	219.00	13.8500		- 4.50	[-6.58; 15.58]	6.0%
Larson et al. (2009) m	12	223.50	20.7000	12	218.00	20.7000			[-11.06; 22.06]	3.7%
LeMaster et al. (2017)	19	234.07	39.2301	19	225.21	34.8712		8.86	[-14.74; 32.46]	2.1%
Maresca et al. (2018) m	17	218.00	32.9848	17	219.00	32.9848		-1.00	[-23.17; 21.17]	2.4%
Maresca et al. (2018) f	17	213.00	32.9848	17	202.00	32.9848		─── 11.00	[-11.17; 33.17]	2.4%
Wilson et al. (2015)	91	222.00	19.0788	86	219.55	18.5472		2.45	[-3.09; 7.99]	9.7%
Wilson et al. (2015) m	37	232.80	18.2483	34	224.60	17.4929		- 8.20	[-0.12; 16.52]	7.7%
Wilson et al. (2016) m	41	242 .85	32.0156	45	235.75	33.5410		- 7.10	[-6.76; 20.96]	4.7%
Taylor et al. (2016)	72	249.00	21.7223	67	244.00	20.9545		- 5.00	[-2.10; 12.10]	8.6%
Klein (2019) m SP100	16	220.76	28.8000	14	199.75	28.8108		21.01	[0.35; 41.67]	2.6%
Klein (2019) m SP150	12	215.93	28.7520	14	199.75	28.8108	-+	16.18	[-6.01; 38.37]	2.4%
Klein (2019) f SP100	12	211.58	24.9415	14	187.76	23.9466		23.82	[4.94; 42.70]	3.0%
Klein (2019) f SP150	15	210.95	23.2379	14	187.76	23.9466		23.19	[6.00; 40.38]	3.5%
Rodrigues (2019) m	49	135.00	35.4200	191	129.00	51.8260		- 6.00	[-6.34; 18.34]	5.3%
Rodrigues (2019) f	73	144.00	35.7994	209	136.00	47.5630	+	- 8.00	[-2.44; 18.44]	6.4%
Random effects model	719			997			†	6.19	[2.88; 9.49]	88.5%
Heterogeneity: $I^2 = 31\%$, τ^4	2 = 13.0)832, p =	0.10							
subaroup = severe los	9									
Rodrigues (2019) m	<u>69</u>	119.00	39 7887	191	129.00	51 8260		-10.00	[-21 92 1 92]	5.5%
Rodrigues (2019) f	73	124 00	39 9005	209	136.00	47 5630		-12.00	[-23 20 -0 80]	5.9%
Random effects model	142	121.00	00.0000	400	100.00		\sim	-11.06	[-19.22: -2.90]	11.5%
Heterogeneity: $I^2 = 0\%$, τ^2	= 0, p =	= 0.81								
Random effects model	861			1397				4.83	[1.03; 8.63]	100.0%
Heterogeneity: $I^2 = 52\%$, τ^2	2 = 30.8	3265, p <	0.01					I I		
Residual heterogeneity: 1 ²	= 27%,	p = 0.14	ł				-40 -20 0	20 40		

Figure 3. Forest plot for weight adjusted to 205 days of age (W205) of the progeny from cows with different weight variations during gestation. The solid line of the x-axis is the no-effect line, and dotted lines represent the estimated difference of random model; therefore, the points to the left of the line represent a reduction in the trait, while the points to the right of the line indicate an increase. Each square represents the relative weight of the study of the overall estimate of effect size, with the larger squares representing a larger weight. The upper and lower bound of the squared line represents the upper and lower confidence intervals of 95% for the size of the effect. The diamond at the bottom represents the 95% confidence interval for the global estimate.

Skeletal muscle tissue formation is susceptible to intrauterine nutritional insults. This process exhibits low nutritional priority in the fetal organism (Funston, Martin, Adams, & Larson, 2010) once maternal dietary restrictions can reduce progeny muscle mass and body weight. This theory is presented by Du et al. (2010), who claim that nutritional restriction during the second and third trimester of gestation reduces muscle mass and body weight of the offspring at

birth. The authors complement that this result is a consequence of reduced myogenesis. Structural and functional organ changes caused by nutrient supplies during gestation, according to Reynolds et al. (2019), allow rapid developing fetus adaptation to uterine environmental selection pressure.

The average daily weight gain of calves during the breastfeeding phase was higher (P < 0.0001) for calves from cows that gained



weight in relation to cows in the control group (Figure 4). However, there was a difference only in three studies, resulting in a slight numerical difference (50 g day⁻¹). The effects of fetal programming are difficult to measure during the lactation period since cow milk production can also influence calf performance. Few studies have measured the production of beef cattle milk. Wilson et al. (2016) did not observe any nutritional cow level effects during the final third of gestation (100 vs. 125% of energy requirements) on milk production during the lactation period. Similarly, Marques, Cooke, Rodrigues, Moriel and Bohnert (2016) tested the effects of high and low cow body scores during gestation (5.85 vs. 4.75 points) and did not observe changes in milk productivity during the lactation period. Thus, we suggest that the higher progeny ADG from cows that gained weight during gestation compared to those that presented moderate loss is the result of the better fetal calf formation (Figure 4).

		Experi	mental		0	Control							
Study	Total	Mean	SD	Total	Mean	SD		Mean [Difference		MD	95%-CI	Weight
subaroup = gain													
Bohnert et al. (2013) sup	116	1.07	0.6139	112	1.04	0.6032			-		0.03	[-0.13; 0.19]	2.3%
Bohnert et al. (2013) ecc	108	1.05	0.5924	120	1.06	0.6244	_				-0.01	[-0.17; 0.15]	2.3%
Ramirez et al. (2020) m	8	0.95	0.1697	9	0.87	0.1800					0.08	[-0.09; 0.24]	2.1%
Maresca et al. (2018) m	17	0.92	0.1237	17	0.93	0.1237					-0.01	[-0.09; 0.07]	8.0%
Maresca et al. (2018) f	17	0.90	0.1237	17	0.86	0.1237		_			0.04	[-0.04; 0.12]	8.0%
Wilson et al. (2015)	91	0.92	0.1908	86	0.91	0.1855		-	- - -		0.01	[-0.05; 0.07]	17.0%
Wilson et al. (2015) m	37	0.96	0.1825	34	0.92	0.1749		_	-		0.04	[-0.04; 0.12]	8.0%
Wilson et al. (2016) m	41	0.97	0.1921	45	0.95	0.2012			-		0.02	[-0.06; 0.10]	8.0%
Klein (2019) m SP100	16	0.88	0.1200	14	0.80	0.1122				_	0.08	[0.00; 0.16]	8.0%
Klein (2019) m SP150	12	0.86	0.1039	14	0.80	0.1122			-	-	0.06	[-0.02; 0.14]	8.0%
Klein (2019) f SP100	12	0.86	0.1039	14	0.76	0.0748			-		0.10	[0.03; 0.17]	10.9%
Klein (2019) f SP150	15	0.86	0.0775	14	0.76	0.0748				_	0.10	[0.05; 0.16]	17.0%
Random effects model	490			496							0.05	[0.03; 0.08]	100.0%
Heterogeneity: $I^2 = 5\%$, $\tau^2 =$	= < 0.0	001, <i>p</i> =	0.40										
Random effects model	490			496							0.05	[0.03; 0.08]	100.0%
Heterogeneity: $I^2 = 5\%$, τ^2	< 0.000	(1, p = 0)	.40				I	I		I			
Residual heterogeneity: 12:	= 5%, <i>µ</i>	0 = 0.40					-0.2	-0.1	0 0.1	0.2			

Figure 4. Forest plot for ADG during the lactation (ADGpre) of the progeny from cows with different weight variations during gestation. The solid line of the x-axis is the no-effect line, and dotted lines represent the estimated difference of random model; therefore, the points to the left of the line represent a reduction in the trait, while the points to the right of the line indicate an increase. Each square represents the relative weight of the study of the overall estimate of effect size, with the larger squares representing a larger weight. The upper and lower bound of the squared line represents the upper and lower confidence intervals of 95% for the size of the effect. The diamond at the bottom represents the 95% confidence interval for the global estimate.

When the ADG in the post-weaning phase was evaluated, in which the maternal effect reduces the influence on the progeny growth, there was no research with cows in the severe loss subgroup (SL) of weight during gestation. However, there was a tendency (P = 0.0868) for better performance of the calves of cows that gained weight (50 g day⁻¹) concerning those who lost up to 10% of weight during the gestation period (Figure 5). Thus, through this

meta-analysis, it was found that the effects of fetal programming are more evident in the first months of the progeny life.

The lesser influence of the variation in cow weight during gestation on the postweaning performance of calves can be explained by the greater adaptive capacity of the progeny formed in nutrient-restricted intrauterine environments. According to Brameld, Greenwood and Bell (2010), if there is enough time during postnatal life, the animal can overcome or compensate for most of the initial differences caused by fetal programming, resulting in only minor (if any) residual effects on body composition of the calf in later growth stages. Ramírez et al. (2020) add that severe nutrient restriction during gestation can also compensate for individual growth after birth, when the calf is exposed to more challenging environments during adult life.



Figure 5. Forest plot for ADG post-weaning (ADGpost) of the progeny from cows with different weight variations during gestation. The solid line of the x-axis is the no-effect line, and dotted lines represent the estimated difference of random model; therefore, the points to the left of the line represent a reduction in the trait, while the points to the right of the line indicate an increase. Each square represents the relative weight of the study of the overall estimate of effect size, with the larger squares representing a larger weight. The upper and lower bound of the squared line represents the upper and lower confidence intervals of 95% for the size of the effect. The diamond at the bottom represents the 95% confidence interval for the global estimate.

In addition to compensatory gains, Webb et al. (2019) state that food restrictions during gestation can induce epigenetic changes, resulting in an "economic" phenotype. In this case, according to Greenwood, Thompsom and Ford (2010), the animal exhibits greater metabolic adaptation capacity to less favorable environments during postnatal life, which may result in greater weight gains than animals with better fetal formation. This greater adaptation capacity may result from alterations in liver and pancreas homeostatic mechanisms, which influence the ability of the progeny to metabolize nutrients (Keomanivong et al., 2016; McCarty, Washburn, Taylor, & Long, 2020). In this sense, it was found that the performance of the progeny is strongly influenced by the variation in cow weight during the second or third trimester of gestation. Furthermore, the response of the offspring seems to be altered according to the intensity of the postpartum rearing system. Thus, further research is needed to assess how fetal programming responses will be on offspring submitted to different beef cattle production systems during adult life.

Conclusions _

The weight gain of beef cows during gestation improves the pre- and post-weaning performance of the progeny. However, the effects of the variation in maternal weight during gestation on the growth of the progeny are more evident in the early months of its life.

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