Direct and indirect nutritional factors that determine reproductive performance of heifer and primiparous cows

Nutritional factors determining performance of heifers and cows

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22 Abstract

23 Pregnancy rate is a major determinant of population dynamics of wild ungulates
 24 and of productivity of livestock systems. Allocation of feeding resources, including
 25 stocking rates, prior to and during the breeding season is a crucial determinant of this vital
 26 rate. Thus, quantification of effects and interaction among multiple factors that affect
 27 pregnancy rate is essential for management and conservation of pasture-based systems.
 28 Pregnancy rate of 2982 heifers and primiparous cows was studied as a function of animal
 29 category, average daily gain during the breeding season, stocking rate, pasture type and
 30 body weight at the beginning of the breeding season. Data were obtained from 43
 31 experiments conducted in commercial ranches and research stations in the Pampas region
 32 between 1976 and 2015. Stocking rate ranged from 200 to 464 kg live weight/ha, which
 33 brackets values for most of the grazinglands in similar regions. Age at breeding was 14-
 34 36 months (24.6 ± 7.5 months); initial breeding weights were 129-506 kg and 194-570
 35 kg for heifers and primiparous cows. Pregnancy rate was modeled with an apriori set of
 36 explanatory variables where proximate variables (breed, body weight at start of breeding,
 37 weight gain during breeding and category) were included first and subsequently modeled
 38 as functions of other variables (pasture type, supplementation and stocking rate). This
 39 modeling approach allowed detection of direct and indirect effects (through nutrition and
 40 body weight) of factors that affect pregnancy rate. Taurine (*Bos taurus* breeds, N = 1058)
 41 had higher pregnancy rate than *B. Taurus* x *B. indicus* crossbreed (N = 1924) females.
 42 Pregnancy rate of heifers and primiparous cows grazing in natural grasslands decreased
 43 with increasing stocking rate, but no effect of stocking rate was detected in cultivated and
 44 improved pastures. Pregnancy rate increased with increasing average daily gain during
 45 the breeding season. Use of cultivated or improved natural pastures promotes higher

46 pregnancy rate, as well as allows higher in stocking rate at the regional level. Body weight
47 at the start of the breeding season is the primary determinant of pregnancy rates in heifer
48 and primiparous cows.

49

50 **Introduction**

51 Although fundamental cattle physiology and its relation to nutrition are well
52 known, there is not sufficient quantitative information about how management affects
53 nutrition and reproduction, especially under natural grasslands conditions. In particular,
54 few studies have been done to evaluate the relative effects of stocking rate and other
55 nutritional management factors on pregnancy rates at a regional level (Gottschall &
56 Lobato 1996; Simeone & Lobato 1996; Quadros & Lobato 1996; Fagundes, Lobato &
57 Schenkel 2003; Pötter *et al.* 2010; Sartori & Guardieiro 2010). The lack of single studies
58 with regional scope is understandable because such studies with livestock are logistically
59 complex and extremely expensive.

60 An alternative to specific comprehensive studies is to analyze data pooled from
61 multiple studies (Duffield, Merrill & Bagg 2012; Lean, Thompson & Dunshea 2014) that
62 address the same research question using equivalent response and explanatory variables,
63 that is, a meta-analysis (Schwarzer, Carpenter & Rücker 2015). Meta-analysis requires
64 care in the process of systematizing results from multiple studies but it has the advantage
65 of increasing precision, decreasing costs and research time, and increasing the degrees of
66 freedom in the analysis (Fisher 1999; Lovatto, Lehen, Andretta, Carvalho & Hauschild
67 2007).

68 Livestock production in the Pampas region of Southern Brazil is characterized by
69 a low pregnancy rate that has remained stagnant over many years, despite multiple

changes in economic and technological factors that affect productivity (IBGE 2020). Low pregnancy rates prevent full development of the livestock sector in many regions of the world, and it may be associated with poor pasture management, overstocking and lack of differential nutritional management for animal categories with different requirements. Stocking rate is considered the most important decision in grazing management because it affects the forage base, herbage allowance, intake and animal performance (Sollenberger, Agouridis, Vanzant, Franzluebbbers & Owens 2012). Nutritional limitation during periods of high requirement can compromise development and delay puberty of heifers, as well as inhibit ovulation of cows (Rocha & Lobato 2002).

Time at which puberty occurs relative to the start of breeding season is what determines pregnancy rate in the first breeding season of heifers (Sparke & Lamond 1968), which influences a cow's ability to get pregnant in subsequent years and remain in the herd, determining her lifetime productivity. Puberty of heifers is influenced by management of the annual production cycle, as well as the physiology (production and release of hormones) and its genetic (breed and size of mature age) (Day 2015). In addition to the use of pastures, body weight at the beginning of the breeding season is associated with animal nutrition and it is an important factor influencing the reproductive performance of heifers and beef cows (Richards, Spitzer & Warner 1986; Osoro & Wring 1992; Roso *et al.* 2009).

Natural grasslands and cultivated pastures constitute the forage basis for beef cow herds in many regions of the world, including the US (USDA-ERS 2020). The grasslands that support cow-calf operation in the Pampas are characterized by spring-summer growth, with quality and availability reduced in autumn and winter. Cultivated and improved pastures are utilized to satisfy the nutritional requirements of cattle, especially

94 during the cooler months when natural pasture growth is limited. Combined with
95 cultivated and improved pastures, supplements may be used to increase average daily gain
96 of grazing animals and to promote greater reproductive development (Frizzo *et al.* 2003).

97 The aim of the present study was to integrate information from multiple studies of
98 factors that affect pregnancy rates under production conditions in the Pampas to carefully
99 quantify response curves relating pregnancy rate to the most important predictors. First,
100 we take an approach where pregnancy rate is analyzed as a function of known proximate
101 factors such as body weight, category and changes in body weight per day during the
102 breeding season. Second, we add the effects of stocking rate, supplementation and pasture
103 type on proximate factors and directly on pregnancy rate to account for effects not
104 mediated by the proximate factors evaluated. Because of the long term, large geographic
105 region and large number of cows involved in this synthesis, results should be useful not
106 only for ranch-level management but also for regional agricultural policy.

107

108 **Materials and Methods**

109

110 **Study Sample**

111 Data used in this paper were obtained from published literature. Experiments were
112 conducted at the Agronomic Experimental Station of Federal University of Rio Grande
113 do Sul and in private ranches in Rio Grande do Sul, Southern Brazil, to investigate the
114 effects of several factors on pregnancy rate of heifers and primiparous cows (Table 1)
115 between 1976 and 2015. Data include records from 29 doctoral dissertations or master's
116 theses for a total of 43 experiments (some studies had more than one experiment).

117 Experiments were selected because the original raw data were available for all of them.
118 According to Köppen (Wrege, Steinmetz, Reisser Junior & Almeida 2011), climate in all
119 sites represented in the data is subtropical humid.
120

Table 1 - Relation of studies of database with n (number of animals), location, coordinated geographic, precipitation and type of pasture in southern Brazil

Author	n	Local	Coordinated geographic	Precipitation (mm/year)	Type of pasture*
Albospino, 1990	23	Eldorado do Sul	30°52'/51°39'	1332	Italian ryegrass (<i>Lolium multiflorum</i> Lam.) Arrowleaf clover (<i>Trifolium vesiculosum</i>)
Azambuja, 2003	216	Arambaré	31°11'/51°74'	-	Natural pasture
Beretta, 1994	113	Eldorado do Sul	30°52'/51°39'	1398	Annual ryegrass (<i>Lolium multiflorum</i> Lam.) Arrowleaf clover (<i>Trifolium vesiculosum</i>)
Cachapuz, 1976	57	Dom Pedrito	30°99'/54°70'	1376	Natural pasture Common vetch (<i>Vicia sativa</i>)
Deresz, 1976	110	Pelotas	30°58'/50°40'	1285	Natural pasture Annual ryegrass (<i>Lolium multiflorum</i> Lam.) Arrowleaf clover (<i>Trifolium vesiculosum</i>)
Fagundes, 2001	87	Itaqui	29°24'/56°47'	1500	Natural pasture
Freitas, 2005	350	São Gabriel	30°33'/54°32'	1193	Annual ryegrass (<i>Lolium multiflorum</i> Lam.) White clover (<i>Trifolium repens</i>) Bird's-foot trefoil (<i>Lotus corniculatus</i>)
Gottschall, 1994	114	São Gabriel	30°33'/54°32'	1512	Natural pasture
Lopes, 2004	39	Eldorado do Sul	30°52'/51°39'	1446	Black oats (<i>Avena strigosa</i>) Annual ryegrass (<i>Lolium multiflorum</i> Lam.) Arrowleaf clover (<i>Trifolium vesiculosum</i>) Pearl millet (<i>Pennisetum americanum</i>)

*Natural pasture with prevalence of Bahiagrass (*Paspalum notatum*), Dallisgrass (*Paspalum dilatatum*), *Axonopus affinis*, *Andropogon lateralis*, *Trifolium polymorphum*

Table 1 ... Continued

Author	n	Local	Coordinated geographic	Precipitation (mm/year)	Type of pasture*
Magalhães, 1992	210	Rosário do Sul	30°25'/54°92'	1550	Annual ryegrass (<i>Lolium multiflorum</i> Lam.)
Marques, 2001	231	Eldorado do Sul	30°52'/51°39'	1440	Black oats (<i>Avena strigosa</i>) Annual ryegrass (<i>Lolium multiflorum</i> Lam.) Arrowleaf clover (<i>Trifolium vesiculosum</i>)
Menegaz, 2006	323	Uruguaiana	29°76'/57°09'	1500	Natural pasture Annual ryegrass (<i>Lolium multiflorum</i> Lam.) White clover (<i>Trifolium repens</i>) Bird's-foot trefoil (<i>Lotus corniculatus</i>)
Moraes, 1991	60	Dom Pedrito	30°99'/54°70'	1300	Annual ryegrass (<i>Lolium multiflorum</i> Lam.) White clover (<i>Trifolium repens</i>) Sorghum (<i>Sorghum bicolor</i>) Bird's-foot trefoil (<i>Lotus corniculatus</i>)
Müller, 1998	50	Eldorado do Sul	30°52'/51°39'	1440	Annual ryegrass (<i>Lolium multiflorum</i> Lam.) Arrowleaf clover (<i>Trifolium vesiculosum</i>)
Nardon, 1985	65	Eldorado do Sul	30°52'/51°39'	1398	Annual ryegrass (<i>Lolium multiflorum</i> Lam.) Arrowleaf clover (<i>Trifolium vesiculosum</i>)
Pereira Neto, 1996	62	Eldorado do Sul	30°52'/51°39'	1332	Annual ryegrass (<i>Lolium multiflorum</i> Lam.) Arrowleaf clover (<i>Trifolium vesiculosum</i>)
Pilau, 2007	234	Tupanciretã	29°03'/53°48'	-	Black oats (<i>Avena strigosa</i>) Annual ryegrass (<i>Lolium multiflorum</i> Lam.)
Polli, 1986	71	Eldorado do Sul	30°52'/51°39'	1398	Natural pasture Annual ryegrass (<i>Lolium multiflorum</i> Lam.) Arrowleaf clover (<i>Trifolium vesiculosum</i>)

126 *Natural pasture with prevalence of Bahiagrass (*Paspalum notatum*), Dallisgrass (*Paspalum dilatatum*), *Axonopus affinis*, *Andropogon lateralis*, *Trifolium*
 127 *polymorphum*

Table 1... Continued

Author	n	Local	Coordinated geographic	Precipitation (mm/year)	Type of pasture*
Pötter, 2002	92	Quaraí	30°26'/56°01'	1356	Natural pasture Annual ryegrass (<i>Lolium multiflorum</i> Lam.) Bird's-foot trefoil (<i>Lotus corniculatus</i>)
Quadros, 1991	69	Dom Pedrito	30°99'/54°70'	1540	Natural pasture
Ribeiro, 1986	70	Cachoeira do Sul	30°03'/52°89'	1621	Natural pasture
Rocha, 1997	394	Dom Pedrito	30°44'/54°47'	1450	Annual ryegrass (<i>Lolium multiflorum</i> Lam.) White clover (<i>Trifolium repens</i>) Red clover (<i>Trifolium pratensis</i>) Bird's-foot trefoil (<i>Lotus corniculatus</i>)
Rosa, 2010	241	Dom Pedrito	30°44'/54°47'	1300	Natural pasture Annual ryegrass (<i>Lolium multiflorum</i> Lam.) White clover (<i>Trifolium repens</i>) Bird's-foot trefoil (<i>Lotus corniculatus</i>)
Silva, 2010	142	Bagé	31°22'/54°39'	1300	Annual ryegrass (<i>Lolium multiflorum</i> Lam.)
Simeone, 1995	119	Bagé	31°22'/54°39'	1350	Natural pasture
Souza, 2005	64	Dom Pedrito	30°99'/54°70'	1376	Annual ryegrass (<i>Lolium multiflorum</i> Lam.) White clover (<i>Trifolium repens</i> L.)
Souza, 2015	49	Júlio de Castilhos	29°23'/53°68'	-	Black oats (<i>Avena strigosa</i> Schreb.) Palisade grass (<i>Urochloa brizantha</i>)
Tanure, 2008	194	Quaraí	30°26'/56°01'	1356	Natural pasture
Zanotta Jr, 1984	84	Pelotas	30°58'/50°40'	1285	Natural pasture Annual ryegrass (<i>Lolium multiflorum</i> Lam.) White clover (<i>Trifolium repens</i>)

128 *Natural pasture with prevalence of Bahiagrass (*Paspalum notatum*), Dallisgrass (*Paspalum dilatatum*), *Axonopus affinis*, *Andropogon lateralis*, *Trifolium*
129 *polymorphum*

130 **Data**

131 The initial database created contained the following variables for each of 3933
132 animals: age at the beginning of the breeding season was 14 to 36 months (average was
133 24.6 ± 7.5 months); animal categories were heifers ($n = 2257$) and primiparous cows (n
134 $= 1676$); average animal weight was 315.4 ± 55.9 kg at the beginning and 337.3 ± 53.4
135 kg at the end of the breeding season; body condition score in a 0-5 scale was 3.2 ± 0.6 at
136 the beginning and 3.4 ± 0.6 at the end of the breeding season; breeds were Angus ($n =$
137 306), Braford ($n = 499$), Brangus ($n = 323$), Crossbred ($n = 1928$), Devon ($n = 110$) and
138 Hereford ($n = 767$); stocking rate ranged from 200 to 464 kg of body weight per hectare
139 (kg BW/ha) and averaged 337.32 ± 54.68 kg BW/ha; pasture types were cultivated
140 ($n=2050$), improved ($n=324$) or natural grassland ($n=1559$); feed supplementation before
141 the breeding season was recorded as a binary variable (supplemented vs. not
142 supplemented).

143 Breeds were recoded as crossbred (final $N = 1924$) vs. *B. Taurus* (final $N = 1058$).
144 One experiment with an extreme stocking rate of 800.0 kg of body weight per hectare
145 was excluded from the analysis. The remaining data had stocking rates ranging from 200
146 to 463.5 (average was 336.85 ± 54.92) kg BW/ha, which are more typical for the region.
147 Columns with large number of missing values and rows without complete multivariate
148 records were excluded, resulting in a final data set of 2982 records (animals) for which
149 all variables depicted in Fig 1 were available.

150

151 **Fig. 1.** Schematic structure of the hypothesized determinants of pregnancy rate (PR).

152

153 **Statistical Analyses**

154 Statistical analyses were conducted using R (R Development Core Team 2015).
 155 We used generalized linear mixed models (GLMM) based on the logit link function, as
 156 they are generally recommended for binary data (Agresti 2002; Sauvant, Schmidely,
 157 Daudin & St-Pierre 2008). Data for each heifer and primiparous cow were available,
 158 allowing an analysis analogous to an incomplete block design, with a random intercept
 159 for each experiment (Senn, Gavini, Magrez & Scheen 2011).

160 The main response variable was pregnancy rate as evaluated by the relation
 161 between the number of pregnant heifers or primiparous cows and the total number of
 162 heifers or primiparous cows in each experiment. Explanatory factors considered were
 163 category, weight at the beginning of the breeding season, weight change during the
 164 breeding season, breed, stocking rate, and type of pasture before and after the breeding
 165 season. All quantitative variables were standardized to facilitate the convergence of the
 166 computations to estimate parameters. A structure of causal effects was established a priori
 167 (Fig 1) and then simplified by removing nonsignificant components.

168 First, pregnancy rate (PR) was analyzed using *glmer* with a binomial distribution
 169 and a logit link, as a function of known proximate factors such as body weight and
 170 category. Breed was included to account for inherent differences in breeds that could
 171 modulate the effects of body weight, for example, due to differences in mature body or
 172 frame size. Model selection proceeded by simplification of a full model until it had only
 173 those effects that were significant or part of significant interactions. Significance of terms
 174 was assessed by type II Wald tests using the *Anova()* function of the *car* package (Fox &
 175 Weisberg 2011). The initial full model, expressed as an R formula for the generalized
 176 linear mixed-effects model (*glmer*) function of the *lme4* package (Bates, Maechler,
 177 Bolker & Walker 2014) was

$$\begin{aligned} \text{PR} &\sim \text{breed} * \text{start.bw} + \text{categ} * \text{s.dwt} + \text{s.dwt} * \text{breed} + \\ &\text{s.dwt} * \text{start.bw} + I(\text{start.bw}^2) + I(\text{s.dwt}^2) + (1 | \text{experiment}) \end{aligned}$$

where *categ* is animal category, *start.bw* is weight at the beginning of the breeding season, *s.dwt* is daily weight gain, $I(\text{start.bw}^2)$ is squared weight at the beginning of the breeding season, $I(\text{s.dwt}^2)$ is daily weight gain squared and *experiment* is a categorical variable or factor with a different value for each experiment. Each experiment was allowed a random effect to account for the potential intraclass correlation caused by common condition for all animals in each experiment. The “*” operator indicates that both main effects and their interaction are included in the model. This final model was tested against the full model by a likelihood-ratio test using the `anova()` function to make sure they were not significantly different.

Second, stocking rate was added as the last term to the resulting model to determine if stocking rate had significant effects beyond those effected via proximate factors. Significance of stocking rate effects was assessed with the same Wald test as before. Third, body weight at the beginning of the breeding season was modeled with the following full model:

$$\begin{aligned} \text{start.bwt} &\sim \text{categ} + \text{breed} + \text{pasture.pre} * \text{s.sr} + \\ &\text{pasture.pre} * I(\text{s.sr}^2) + \text{sup.pre} + (1 | \text{experiment}) \end{aligned}$$

where *pasture.pre* is a factor indicating whether animals grazed natural grassland, cultivated pastures or improved grassland prior to the breeding period; *s.sr* is stocking rate, and $I(\text{s.sr}^2)$ is the quadratic effect of stocking rate. Other terms were defined above. Finally, change in body weight during the breeding period (*s.dwt*) was analyzed starting with the following full model:

201 $s.dwt \sim \text{categ} + \text{breed} + \text{pasture.breed} + s.sr + \text{sup.breed} +$

202 $I(s.sr^2) + \text{pasture.breed}:s.sr + \text{categ}:s.sr + \text{breed}:s.sr + (1 |$

203 $\text{experiment})$

204 where pasture.breed is the type of pasture grazed during the breeding period and sup.pre

205 is a binary variable indicating whether animals received supplementation during the

206 breeding period. Models for start.bwt and s.dwt were simplified and final models were

207 tested following the same procedures as before. For all models, assumptions were

208 assessed by inspection of residual plots.

209

210 **Results**

211

212 **Effects of proximate causal factors on pregnancy rate**

213 The final model for selected pregnancy rate was:

214 $PR \sim \text{categ} + \text{start.bw} * \text{breed} + s.dwt + I(\text{start}^2) + (1 | \text{experiment}).$

215 The most important factor affecting pregnancy rate was body weight at the

216 beginning of the breeding season (Table 2), which accounted for 68 % of the model sum

217 of squares. Mc Fadden's pseudo R^2 (Domencich & McFadden 1974) for fixed effects of

218 the complete final model was 9.53%, whereas a model with only the linear and quadratic

219 effects of initial body weight had a pseudo R^2 equal to 8.8%.

220

221 **Table 2 – Analysis of variance of the model for pregnancy rate with proximate factors.**

Effect	Wald's Chi-sq (type II)	df	p-value
start.bw ¹	234.9	1	<0.0001
I(start.bw ²) ²	48.2	1	<0.0001
s.dwt ³	11.1	1	0.0009

categ ⁴	10.7	1	0.0011
start.bw:breed ⁵	6.2	1	0.0141
breed ⁶	2.7	1	0.0995

¹Weight at the beginning of the breeding period (standardized using mean = 318 kg, s = 69 kg).

²Quadratic effect of weight at the beginning of the breeding season.

³Average daily gain during the breeding season (standardized using mean = 0.264 kg/day, s = 0.314 kg/day).

⁴Animal category (heifer or primiparous cow).

⁵Interaction between weight at the beginning of the breeding season and breed.

⁶ Breed type (crossbred or taurine).

230

Pregnancy rate increased steeply with increasing body weight at the beginning of the breeding season for crossbred and taurine females, but for taurine females it increased faster and reached a higher maximum than for crossbred females. Taurine females starting the breeding season with an average weight of 440.0 kg or more and had an expected pregnancy rate of 99.0 %, whereas crossbred females that started the breeding season with similar weight had an expected pregnancy rate of 91.0 % (Fig 2).

237

Fig. 2. Interaction between body weight at the beginning of the breeding season and Breed to pregnancy rate of heifers and primiparous cows (Sint: crossbred, Taur: taurine females). Shaded strips represent 95 % confidence intervals for the expected value. Body mass average and standard deviation were 318 and 69 kg.

242

Pregnancy rate increased with increasing average daily gain during the breeding period. Averaging over other predictors, the model estimated that pregnancy rate increases from 59 % when animals lose 340 g per day to 79 % when they gain 890 g per day during the breeding season. When daily gain was at its average (0.264 ± 0.006 kg/day), pregnancy rate increased 1.7 % per 100 g of daily gain during the breeding

247

248 period. When all covariates are at their average values for both categories, pregnancy rate
249 was 25 percentage points higher for heifers than for primiparous cows (80 vs. 55 %).

250

251 **Effects of stocking rate not mediated by proximate factors**

252 The addition of stocking rate as an explanatory factor resulted in the following
253 model:

254 $\text{preg} \sim \text{start.bw} + \text{s.dwt} + \text{I}(\text{start.bw}^2) + \text{breed} + \text{categ} + \text{s.sr} +$
255 $\text{start.bw} : \text{breed} + \text{s.sr} : \text{start.bw} + (1 | \text{experiment}).$

256 The contribution of stocking rate to explain variation in pregnancy rate was
257 evaluated by entering stocking rate and its interactions last into the model and using a
258 type II Wald test. Stocking rate and its interaction with body weight at the start of the
259 breeding season contributed 4.7 % of the total sum of squares of the model and had direct
260 effects on pregnancy rate that were significant even after controlling for the potential
261 indirect effects through proximate variables such as body weight and weight change
262 during breeding (Table 3). Stocking rate exhibited a significant interaction with weight at
263 the start of the breeding season by which the effect of stocking rate was small for body
264 weight below the 318 kg average and negative for heavier animals (Fig 3).

265

266 **Fig. 3.** Interaction between body weight at the beginning of the breeding season and
267 stocking rate on pregnancy rate of heifers and primiparous cows. Shaded areas are 95%
268 confidence intervals. Tickmarks above the horizontal axis represent observations.

269

270 Table 3 - Analysis of variance of the pregnancy rate model with proximate factors and
271 stocking rate

Variables	Wald's Chi-sq (type II)	df	p-value
-----------	-------------------------	----	---------

start.bw	227.4	1	<0.0001
I(start.bw^2)	44.1	1	<0.0001
s.dwt	9.5	1	0.0021
categ	7.7	1	0.0054
start.bw:breed	7.1	1	0.0076
s.sr ¹	6.1	1	0.0135
start.bw:s.sr ²	6.0	1	0.0144
breed	2.9	1	0.0883

¹Stocking rate (standardized using mean = 328 kg/ha and s = 58.9 kg/ha).

²Interaction between weight at the start of the breeding season and stocking rate.

Although stocking rate did have effects on pregnancy rate beyond those through proximate causal variables, the effects of other variables did not change much by the incorporation of stocking rate. The most important factor affecting pregnancy rate when stocking rate was added in the model continued to be body weight at the beginning of the breeding season, accounting for 84.4 % of the sum of squares explained by the generalized mixed model (Table 3). The second largest contribution to the sum of squares of the model was due to average daily gain during the breeding season, which accounted for 4.3 % of the explained variation (Table 3). The response to daily gain was similar to that in the model without stocking rate; pregnancy rate increased 1.5 % per 100 g of daily gain when daily gain was near its average. The third largest contribution to the model's sum of squares was due to animal category, accounting for 3.0 % of the explained variation. Pregnancy rate was greater in heifers than in primiparous cows (81 vs. 56 %, $p = 0.0054$).

Body weight at the beginning of the breeding season

Because supplementation did not have detectable effects on body weight at the start of the breeding season, the final model was

292 $\text{start.breed.wt} \sim \text{categ} + \text{breed} + \text{pasture.pre} + \text{s.sr} + \text{I}(\text{s.sr}^2) +$
 293 $\text{pasture.pre:s.sr} + \text{pasture.pre:I}(\text{s.sr}^2) + (1 \mid \text{experiment}),$

294 where *start.breed.wt* is body weight in kg at the start of the breeding season and
 295 *pasture.pre* is the type of pasture grazed prior to the breeding season. Thirty nine percent
 296 of the variation in initial body weight was explained by the fixed effects of the model,
 297 and an additional 41 % was explained by variation among experiments (random effects
 298 variation due to differences between experiments in variables not measured). Pasture type
 299 accounted for 60 % of the sum of squares explained by fixed effects, whereas an
 300 additional 27.9 % was explained by stocking rate and its interaction with pasture type.
 301 Body weight declined quadratically with increasing stocking rate in natural pastures, but
 302 it was not affected by the range of stocking rates studied in cultivated or improved
 303 pastures (Fig 4). At the average stocking rate of 328 kg/ha, initial body weight of animals
 304 grazing cultivated and improved pastures was 15 kg greater than that of animals grazing
 305 natural pastures, and this difference increased to 44 kg when stocking rate increased to
 306 388 kg/ha.

307

308 **Fig. 4.** Effects of stocking rate and type of pasture on body weight at the beginning of the
 309 breeding season of heifers and primiparous cows. Effects of stocking rate were not
 310 significant for cultivated (PCult) and improved (PNMelh) pastures, but there was a
 311 significant quadratic effect in native grasslands (PNat).

312

313 Breed type and category had effects on initial weight that were independent of
 314 stocking rate. Ninety five percent confidence intervals for weight at the start of the
 315 breeding season were 303 to 338 and 295 to 330 kg for crossbred and taurine types.

Confidence intervals for heifers and primiparous cows were 263 to 313 and 332 to 380 kg.

This reflects the fact that multiple factors determine pregnancy rate, many of which are not closely related to body weight, animal category or breed. Other factors explored in some experiments, such as weaning method and use of artificial insemination, were considered and did not have detectable effects in preliminary models for pregnancy rate. However, the different weaning methods and use of artificial insemination were not represented across a good range of values in the other factors.

Change in body weight during the breeding season

The final model for average daily gain during the breeding season was $s.dwt \sim \text{pasture.breed} + s.sr + I(s.sr^2) + (1 | \text{experiment})$, where *pasture.breed* is the type of pasture grazed during the breeding season.

Stocking rate and type of pasture grazed accounted for equal parts of the total variation explained by the fixed effects of the model. Average daily gain during the breeding season decreased quadratically with increasing stocking rate (Fig 5).

Fig. 5. Average daily gain during the breeding season and stocking rate of heifers and primiparous cows. Shaded strip shows the 95 % confidence band.

Discussion

This study is unique because it integrated data from thousands of individual animals from multiple sites and experiments and because it established quantitative relationships between reproductive performance and stocking rate. Although stocking

rate is recognized as one of the most important factors determining productivity of grazing systems (Hunt, McIvor, Grice & Bray 2014), studies relating grazing animal performance to stocking rate are rare. A Web of Science search performed on 04 Jan 2020 with the terms “beef cattle” AND “pregnancy rate” AND “stocking rate” yielded nine articles, only one of which (Renquist, Oltjen, Sainz, Connor & Calvert 2005) presented original data on the effects of stocking rate on pregnancy rates. Most of the studies where stocking rate is considered as one of the explanatory variables for animal performance include few levels of stocking rate that explore a very limited range. We surmise that as a consequence of the limited range explored and the inherent high variability of herd-level studies, many studies failed to detect effects of stocking rate. The present study included 16 levels of stocking rate ranging from 0.5 to 1.2 head/ha or 200 to 464 kg/ha, which allowed quantification of response curves.

352

353 **Effects of proximate causal factors on pregnancy rate**

354 The effects of body weight at the beginning of the breeding season, animal
355 category and changes in body weight during the breeding season were quantified and
356 yielded response curves with low variance. For example, the pseudo coefficient of
357 variation (CI half width/(2 expected value) of pregnancy rate for taurine cows at average
358 weight at the beginning of the breeding season was 6.5%. The most important causal
359 factor influencing pregnancy rate was body weight at the beginning of the breeding
360 season, which interacted with breed to determine that at high initial weights, taurine
361 females had higher pregnancy rate than crossbred females (Fig 2). Pregnancy rate is
362 influenced by nutrition, because it directly affects the reproductive physiology in beef
363 cows [6], mainly in periods of higher requirements like pre and postpartum. If nutrition

is inadequate, body reserves become depleted and body condition declines (Diskin & Kenny 2016), resulting in low ovulation rate. Females with adequate metabolic status and high body weight have high levels of glucose, insulin and growth factor I (IGF-I) (Yelich *et al.* 1995; Santos & Amstalden 1998), potentiating the effect of gonadotrophins (LH and FSH) (Spicer & Echternkamp 1995) and promoting ovulation (Sirois & Fortune 1988). Pre and postpartum periods coincide with low availability of nutrients in natural grasslands, which are characterized by variation in composition, structure and seasonality of production and quality (Mezzalana *et al.* 2014; Neves *et al.* 2009).

Animals with smaller frame reach physiological maturity earlier, at a lower weight and with greater fat content than larger animals (Owens, Dubeski & Hanson 1993). When growth rate decreases and the process of fat deposition begins, larger animals are still in the growth phase (Mckiernan 2005). In addition, the higher pregnancy rate observed in the taurine females can be explained by the greater selection for precocity carried out in the herds from which these females proceed (Diskin & Kenny 2016). When heifers reach puberty and mate earlier the biological efficiency of the herd is improved for as long as the early mating does not compromise full development. These characteristics become more important as production systems become more intensive and competitive. Reducing the age at first conception alters the structure of the herd and shortens the interval between generations, thus decreasing the participation of unproductive animals in the composition of the herd (Pötter, Lobato & Mielitz Neto 1998; Beretta, Lobato & Mielitz Neto 2001).

Weight gain during the breeding season is clearly important for cows to become pregnant. Greater weight gain in this period indicates that forage is less limiting, and that sufficient quantity and quality of food intake is obtained to support ovarian activity (Vieira, Lobato, Torres Junior, Cezar & Correa 2005). According to Carter & Cox (1973),

there is greater biological efficacy in females that have their first calf at about two, rather than three or more years of age. Adequate weights at the beginning of the breeding season are decisive for a high conception rate (Wiltbank, Rowden, Ingalls, Gegeoey & Koch 1962).

The lower pregnancy rate of primiparous cows than heifers may be related to the stress of calving and the combined effects of growth and first lactation requirements of primiparous cows. Low reproductive success has been documented for primiparous animals when they are subjected to periods of pre or postpartum feeding restriction (Spitzer, Morrison & Wettemann 1995). The negative direct effect of primiparous condition on pregnancy rate appeared with the inclusion of initial body weight, but primiparous condition had an indirect positive effect on pregnancy rate relative to heifers through the fact that they were heavier than heifers at the beginning of the mating period (Fig 6).

Fig. 6. Schematic representation of modeling results showing effects of animal factors (category and breed type), foraging environment (pasture type, stocking rate and supplementation) on body weight and reproductive performance of beef cattle. In the broader lines are observed direct effects on the pregnancy rate. In the thinner lines are observed indirect effects of body weight prior to breeding and in fine and dotted lines, indirect effects of the change in body weight during breeding.

Stocking rate interacted with body weight at the beginning of the breeding season, whereby higher stocking rates were associated with lower pregnancy rate only in the high range of body weight (Fig 3). Lower stocking rates allow greater development of the

412 animal, due to the higher forage accumulation, making it possible for females to have
413 more food available (Euclides & Euclides Filho 1998). Stocking rate is a primary
414 management variable in grazing systems because it modulates the interactions between
415 animals and pasture (Bransby & Maclaurin 2000; Carvalho & Batello 2009). As stocking
416 rate increases, herbage allowance decreases and can reach levels where intake per animal
417 is too low for production, but intake per unit area surpasses the ability of pastures to
418 produce and recover. Individual animal performance decreases as stocking rate increases,
419 because the daily intake is constrained by limiting sward structure at low herbage
420 allowance (Da Trindade *et al.* 2014), but production per unit area increases and then
421 decreases with increasing stocking rate (Mezzalana *et al.* 2012; Neves *et al.* 2009;
422 Petersen, Lucas & Mott 1965). High stocking rates pre and post partum make it difficult
423 for cows to recover good body condition after calving, compromising the reproductive
424 performance of the cow and the productivity in subsequent seasons and reproductive
425 years (Osoro 1989). Therefore, stocking decisions must be informed by curves that relate
426 individual performance to stocking rate like the ones provided in the present study. These
427 curves are particularly important for the integration of biological and economic functions
428 to determine optimal stocking rates.

429 As expected, heifers achieve greater pregnancy rates when maintained in good
430 nutritional conditions. Inadequate management practices, such as excessive stocking rate
431 and lack of custom management for certain animal categories have led to generally low
432 indices of productivity in the region. However, there are possibilities for reducing the age
433 of slaughter and the age at first breeding, which may allow the improvement of productive
434 and reproductive indices (Pötter, Lobato & Mielitz Neto 2000; Beretta, Lobato & Mielitz
435 Neto 2002). Because natural pastures of the region are dominated by warm season grasses

with low productivity and quality in the cold season, grazing of cultivated cool-season pastures significantly increases indicators of reproductive performance, beef yield and economic results (Lupatini & Neumann 2002).

In agreement with (Rovira 1974), we observed that when heifers and primiparous cows are maintained in optimal conditions of grazing and nutrition, that is, maintained in high quality pastures, with sufficient body weight and intermediate stocking rates, they achieve near maximal reproductive success. Sufficient nutrition allows early breeding, which increases the overall efficiency of production for the herd.

Effects of stocking rate not mediated by proximate factors

Our results show that stocking rate has an effect on pregnancy rate that is not explained by any of the other variables considered. Even after controlling for effects of starting body weight and weight change during the breeding season, when body weight at the beginning of the breeding season is greater than average, pregnancy rate declines with increasing stocking rate. This effect of stocking rate appears to be restricted to the range of starting body weight where pregnancy rate no longer responds to body weight. This further suggests that stocking rate had an effect that was not mediated by the observed effects of stocking rate on body weight at the start of the breeding period and weight change during breeding (Fig 6).

Effects of stocking rate on pregnancy rate that are not related to nutritional condition, as reflected in body weight and daily gain, might be related to animal health and associated management variables. Higher stocking rates may result in greater load of external and internal parasites (Gasser 2013). Tick infestation is common in this region, and ticks frequently carry *Babesia* (Bilhasi *et al.* 2014). When grazing at higher stocking

460 rates, animals are forced to graze closer to the soil and increase the rate of ingestion of
461 parasite helminth larvae.

462

463 **Body weight at the start of breeding season and changes in** 464 **body weight during the breeding season**

465 Our results agree with the conventional wisdom that stocking rate is one of the
466 most important factors in grazing management. Stocking rate interacting with type of
467 pasture before mating was the most important factor influencing body weight at the
468 beginning of the breeding season (Fig 4) and it was the most important factor affecting
469 the changes in body weight during the breeding season (Fig 5). The lowest weights at the
470 beginning of the breeding season observed in this study are close to the minimum weight
471 recommended for the first breeding season (50 - 57 % of adult weight) to avoid
472 impairment of life-long reproductive performance (Funston & Deutscher 2004; Roberts,
473 Geary, Grings, Waterman & MacNeil 2009). Body weight of heifers and cows grazing
474 cultivated or improved pastures was high and did not respond to stocking rate, presumably
475 because the level of feeding and pasture production was sufficient to provide enough
476 nutrition at all stocking rates studies. On the other hand, we observed a typical response
477 of declining in body weight and average daily gain during the breeding season for animals
478 grazing native pastures where forage amount and quality are lower than in cultivated and
479 improved pastures. Lower stocking rates allow animals to select better-quality diets,
480 while higher stocking rates reduce vegetation abundance, constraining daily intake (Da
481 Trindade et al., 2016).

482

483 **Conclusions**

484 This synthesis of a large number of experiments conducted over decades in the
485 Pampas region confirms the importance of body weight at the start of the breeding season
486 to achieve high pregnancy rates in cattle. Body weight at the beginning of the breeding
487 season is an easily measurable variable and can be used herd reproductive management.
488 Stocking rate had a negative effect on pregnancy rate both through its negative effects on
489 initial body weight and weight change during the breeding season, and its direct negative
490 effects on pregnancy rates when body weight was not limiting. Heifers tended to have
491 lower body weight than primiparous cows, but after correction for body weight, they had
492 greater pregnancy rates than primiparous cows, most likely due to the fact that
493 primiparous cows were simultaneously lactating and growing. Response curves derived
494 from out study can be used to optimize stocking rates under various economic conditions
495 and to guide policies to improve the efficiency of reproductive livestock herds under free-
496 grazing conditions.

497

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Figure 1. Schematic structure of the hypothesized determinants of pregnancy rate (PR).

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Figure 2. Interaction between body weight at the beginning of the breeding season and Breed to pregnancy rate of heifers and primiparous cows (Sint: crossbred, Taur: taurine females). Shaded strips represent 95% confidence intervals for the expected value. Body mass average and standard deviation were 318 and 69 kg.

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Figure 3 – Interaction between body weight at the beginning of the breeding season and stocking rate on pregnancy rate of heifers and primiparous cows. Shaded areas are 95% confidence intervals. Tickmarks above the horizontal axis represent observations.

Figure 4 – Effects of stocking rate and type of pasture on body weight at the beginning of the breeding season of heifers and primiparous cows. Effects of stocking rate were not significant for cultivated (PCult) and improved (PNMelh) pastures, but there was a significant quadratic effect in native grasslands (PNat).

Figure 4

Figure 5 – Average daily gain during the breeding season and stocking rate of heifers and primiparous cows.

Shaded strip shows the 95% confidence band.

Figure 6. Schematic representation of modeling results showing effects of animal factors (category and breed type), foraging environment (pasture type, stocking rate and supplementation) on body weight and reproductive performance of beef cattle. In the broader lines are observed direct effects on the pregnancy rate. In the thinner lines are observed indirect effects of body weight prior to breeding and in fine and dotted lines, indirect effects of the change in body weight during breeding.