Abstract. The long-term reproductive performance of beef breeding herds grazing sown pastures in the neotropical savanna environment of Eastern Colombia (Llanos) and the lifelong reproductive consequences of raising replacement heifers subject to different growth regimes are not well documented. The aim of the study was to assess the effects of live weight (LW), age, and their interaction on conception probabilities of Bos indicus replacement females by analyzing two seven- and eight-years lasting experiments that used commercial Brahman heifers subjected initially to different growth rates on Urochloa humidicola pastures. The experiments included two periods, namely the growth period from weaning until 270 kg of LW during which heifers were subjected to three stocking rates (1.28; 1.71; 2.24 head/ha respectively) to attain different gain rates, and the subsequent reproduction phase subject to common grazing for all growth treatments. The conception data fitted well logistic regressions in which LW and age were the predictor variables during the first two conceptions, but the relationship disappeared in subsequent conceptions. Prediction equations compared well with extensive data from northern Australia that showed similar trends. The LW of adult cows only increased consistently during pregnancy but following weaning their LWs returned to the initial low LWs attained at conception. Weaned calves as percentages of those born were 88% for the two treatments with higher LW gains during the growth period and 81% for animals with lower weight gain. Calving intervals were 19-20 months across treatments. Liveweight and its interaction with age had a close, logistical relationship to the occurrence of the first two conceptions but not thereafter.

Keywords: animal performance, reproduction, savanna, tropical pastures

Modelación del desempeño reproductivo de ganado de carne tropical considerando datos experimentales de pastoreo de largo plazo en Urochloa humidicola en los Llanos de Colombia

Resumen. El desempeño reproductivo de largo plazo de hatos de carne pastoreando gramíneas sembradas en el ambiente de las sabanas neotropicales del oriente de Colombia no ha sido bien documentado mientras el impacto de ganancias de peso en novillas de reemplazo en su desempeño posterior es también de interés. Dos experimentos de siete y ocho años respectivamente utilizando novillas comerciales Brahman (Bos indicus) sometidas a diferentes tasas de crecimiento (con cargas de 1.28; 1.71; 2.24 animales/ha) pastoreando Urochloa humidicola hasta alcanzar 270 kg de peso fueron reanalizados para determinar el impacto del peso, edad y su interacción sobre la probabilidad de concepción durante la fase adulta bajo pastoreo común. Los datos se ajustaron bien a regresiones logísticas durante las primeras dos concepciones, pero no posteriormente, Las ecuaciones de predicción mostraron tendencias comparables con abundantes observaciones del norte de Australia. El peso de vacas adultas sólo aumentó debido a la gestación, pero al destete regresó al peso inicial de concepción. En promedio, a lo largo de los experimentos, los porcentajes de destete en relación a los terneros nacidos vivos fueron de 88% para las novillas que experimentaron las mayores ganancias de peso, y 81% para las de menor ganancia. Los intervalos entre partos fueron de 19-20 meses sin diferencias entre tratamientos. El peso vivo y su interacción con la edad tuvieron una relación logística estrecha con la ocurrencia de las dos primeras concepciones, lo que no se repitió en concepciones posteriores.

Palabras clave: desempeño animal, pasturas tropicales, reproducción, sabana
Modelagem do desempenho reprodutivo de bovinos de corte tropicais considerando dados pastoreio experimental de longa duração em Urochloa humidicola nos Llanos da Colômbia

Resumo. A longo prazo o desempenho reprodutivo de bovinos de corte mantidos em pastejo direto em gramíneas cultivadas em região de savana neotropical do leste da Colômbia foi pouco documentado, bem como o impacto no ganho de peso de novilhas de reposição e seu desempenho reprodutivo posterior. Dois experimentos de sete e oito anos com novilhas Brahman comerciais (Bos indicus) foram submetidas (Urochloa humidicola) a diferentes taxas de crescimento (mediante lotação de 1.28; 1.71; 2.24 animais/ha) até atingir 270 kg de peso vivo. As novilhas foram reanalisadas para determinar peso, idade e interação na probabilidade de concepção durante a fase adulta mantida em sistema extensivo (pastejo direto). Os dados de concepção se ajustaram bem a regressões logísticas durante as duas primeiras concepções. As equações de previsão mostraram tendências comparáveis às que foram encontradas em observações registradas no norte da Austrália. O peso das vacas adultas aumentou de forma sistemática com a gestação, mas ao desmame voltou ao peso inicial da concepção. Em média ao longo dos experimentos, as porcentagens de desmame em relação aos bezerros nascidos vivos foram de 88% para as novilhas que tiveram os maiores ganhos de peso e 81% para aquelas com os menores ganhos. Os intervalos entre partos foram de 19-20 meses no conjunto dos tratamentos. O peso vivo e a idade tiveram estreita relação logística com a ocorrência das duas primeiras concepções, o que não se repetiu nas concepções posteriores.

Palavras-chave: desempenho animal, pastagens tropicais, reprodução, savana

Introduction

The extensive Neotropical savannas (Llanos) of Colombia’s Orinoco River basin have long been expected to contribute to food production, mainly grain, vegetable oils, and beef production (Rodríguez Borray and Cubillos, 2019). Nevertheless, during the last decade and contrary to initial expectations, many efforts to expand crop and plantation production had limited success due to policies, input/output prices, and soil constraints. Thus, most producers in the well-drained, relatively flat, and tillable Llanos, located south of the Meta River, have partially returned to traditional beef breeding systems subject to a modest degree of intensification (Rodríguez-Borray and Cubillos, 2019). Surprisingly, despite the commercial release of new productive and nutritive grass cultivars, breeding herds continue grazing older Urochloa humidicola [Urb; cultivars Tully (CIAT 679) and Llanero (CIAT 6133; syn B. decumbens)], and U. decumbens (Udz; syn. Brachiaria decumbens) germplasm, combined with variable areas of native savanna depending upon location, topography, and the proportion of tillable soils in the farm (Romero et al., 2018; Rodríguez-Borray et al., 2019; Enciso et al., 2022). In this context, although the growth of replacement heifers and cows’ reproductive performance (RP) in native savannas has been documented for decades (Levine et al., 1980; Stonaker et al., 1984; Rivera, 1988; Vera and Seré, 1985; Pérez et al., 2017), the long-term RP of Brahman (Bos indicus) or Brahman crossbred replacement heifers and cows grazing sown grasses are still poorly quantified.

A symposium (SSAESD, 2005) reviewed in detail the physiological mechanisms underlying reproduction in adapted B. indicus breeds and crosses in the southern USA, and it included a comprehensive literature review by Randel (2005), who concluded that there are subtle differences with the RP of B. taurus that deserve special attention. Moreover, Ferrell et al. (2005) did not find differences in feed efficiency between B. indicus and taurus cattle in feedlot conditions, but Forbes (2005) noted differences in the size of the digestive tract and passage rates, and grazing behavior was affected by perceived heat stress. Overall, year-round grazing of tropical cattle is heavily influenced by environmental conditions, since pasture growth and quality vary greatly between seasons and years (Durmic et al., 2017) and also in response to continually changing grazing pressure as live weights (LWs) vary with time (Stuth et al., 1996; Ramírez-Restrepo and Vera, 2019; Ramírez-Restrepo et al., 2020). In the extensive grazing conditions of northern Australia, the above factors led to 22% losses of suckling calves (Schatz, 2011), a wide range (53% to 76%) of weaning rates (Fordyce et al., 2013), and low (25%) re-conception rates in 3-year-old lactating animals (Schatz, 2011). In the Llanos, Florez (2015) reported calving intervals of un-supplemented B. indicus females between the 2nd and 5th calving range of 326 and 596 open days at Carimagua Research Centre (CRC). Under these conditions and lacking improved feed strategies, the introduction of costly reproductive technologies is futile, as shown by Jimenez-Rodríguez and Manrique Perdomo (2018) in on-farm tests in the Colombian Vichada Department. More recently, Pérez et al. (2019) showed improved cows’ performance and reduced mortality at CRC when silage of annual crops was fed to animals browsing and grazing silvopastoral systems, at the cost of assumed larger GHG emissions. Nevertheless, Pérez et al. (2019) expressed reservations about the long-term sustainability of the system.
The main hypothesis of this study was that the LWs and/or age of Brahman heifers, determined by their earlier growth rates, may serve as useful empirical predictors of their conception probabilities and can therefore be represented in a dynamic simulation model. Furthermore, the initial growth rates have consequences in their later male reproductive life.

Database

The dataset gathered includes two grazing experiments conducted between 1985 and 1997 at CRC (4°36′44.6″N, 74°08′42.2″W) on the Neotropical savannas of the Colombian Meta Department. The empirical strategy led to new data analyses and interpretation to extend the boundaries of Vera (1991) and Vera et al. (1993). The tactical use of existing long-term data following newer analytical approaches is a relevant procedure to overcome the high cost of large grazing experiments (Tedeschi, 2019; Nizar et al., 2021). This is particularly applicable when the studied production system remains current (Rodríguez-Borray and Cubillos, 2019; Enciso et al., 2022). Climatic conditions at CRC over the selected experimental period were reported previously by Vera and Ramírez-Restrepo (2017).

Experiment 1

The trial lasted for 8 years and extended from the time heifers weaned on savanna were introduced to the trial on U. until soon after the 4th calving when it was discontinued due to administrative reasons, together with the second experiment. This first experiment involved raising 50 heifers [165 ± 2 kg (least square mean ± s.e.m) and 410 ± 17 days of initial age] until reaching a target mating LW (270 kg) subjected to low (L, 1.28; n= 16), medium (M, 1.71; n= 17), and high (H, 2.24; n= 17) stocking rates (SRs, head/ha) to provide a comprehensible range of growth rates.

A second low SR (L-2) with 15 heifers [174 ± 1.5 kg; 531 ± 4 days] was implemented one year later and lasted for 7 years to provide a temporal replicate of the SR with the highest expected daily LW gain (DLWG). The SRs were chosen based on the results of a series of three earlier experiments using yearling steers on U. (Tergas et al., 1982). Upon reaching the target LW, all heifers were transferred to another U. pasture under common grazing and stocked at 1.28 head/ha. Animals were mated (April-November; wet season) with purebred Brahman bulls regularly rotated at 3:42 female ratios while calves were weaned at a target age of 270 days.

Experiment 2

The second experiment lasted for 5.9 years, starting two years after the first one. During the growth phase on U., it replicated the SRs of Experiment 1. Following attainment of the 270 kg target, heifers were randomly split to a single U. pasture, or to a well-maintained U. pasture stocked at 1.2 head/ha and mated as above. Thus, the experimental structure followed a classical compensatory growth design (Wilson and Osbourn, 1960), where compensatory periods were identified as high (h) for the U. and low (l) for the U. pasture treatments, respectively.

Animal and pasture management

In all cases, pastures were at least 3-years-old when the experiments began, thereby avoiding the flush of growth common to newly sown forages. During the establishment phase, 20 P, 20 K, 48 Ca, 14 Mg, and 10 S kg/ha were applied, while a third of that dosage was used every 3 years for maintenance. The pastures were subjected to continuous grazing and occasional sampling complemented with a visual appraisal by experienced technicians and researchers verified that forage on offer stayed within the range of 1-3 t DM/ha during the rainy season, depending upon the SR implemented during the growth period. The conditions of U. pastures in the present experiments have been thoroughly documented (Cajas et al., 1985; Velásquez Valbuena, 1991; Ramírez-Restrepo and Vera, 2019). The chemical composition of the forage on offer conformed to the well documented low nutritive value of U. (Lascano, Hoyos, and Velásquez, 1982; Pérez and Lascano, 1992) and the higher quality of U. (Lascano and Euclides, 1996) at CRC. Their nutritive value varied little across the SRs used in the experiments, regardless of forage availability (Cajas et al., 1985). However, essential nutrients decreased markedly during the dry season, leading to modest weight losses during that season (Ramírez-Restrepo and Vera, 2019). Additionally, paddocks of U. were found to be remarkably similar across several hundred hectares monitored and sampled on numerous farms over 17 years (Vera-Infanzón and Hoyos, 1999). In parallel, soils under the experimental pastures at CRC have been characterized in depth by Rao (2021).

During the initial growth period, animals were weighed every 14 days and were carefully observed daily for signs of estrus only in Experiment 1 (Cajas et al., 1985). Beginning with the initial mating season, pregnancy was diagnosed by rectal palpation, and parasite diagnosis and LWs records were performed approximately every 3 months. Calves’ birth dates,
LWs, and sequential numerical identification were recorded within 24 h of calving, thus allowing subsequent calculation of ages at the different reproductive events. Dates of conception and age were calculated by subtracting 285 days from the recorded calving date. Liveweight at conception (CONCEP) was that of the nearest conception date, and LW at calving was also the nearest LW before calving (PRECALV).

Cattle had free access to fresh water and a complete mineral commercial product (80 g P plus macro and micro minerals/kg of commercial product). Welfare regulations across all animal manipulations in the field were ensured by registered Colombian Doctor of Veterinary Medicine.

**Statistical analysis**

Numerous graphical analyses for the two experiments were carried out initially in EXCEL® to identify recording errors if any, possible outliers, ranges of values, and trends over time. Subsequently, the distribution properties of all animal parameters were examined using SAS® Univariate procedure.

The analyses of growth rates, LWs at or near reproductive events, and the corresponding ages were conducted using the Statistical Analysis System (SAS® 2016; version 3.5) GLIMMIX procedure with treatment as fixed and animals as random effects. When required, repeated measures of LW and ages were specified in the model as in Gbur et al. (2012), further discussed by Bello and Rent (2018) and Reuter and Moffet (2016).

The occurrence of conceptions was fitted to a logistic model using SAS® LOGISTIC procedure. The logistic regression was fitted to the data with the response regarding conception assumed to be binary (0,1), following the Bernoulli distribution. Given its exponential nature, the coefficients of the regressions could be interpreted as odds ratios. Independent variables included treatment (TRT), CONCEP number, age in days (Age), and LW (kg) and the respective interactions using a forward stepwise method. The suitability of the final model was judged from the Akaike information and Schwarz criteria, while the model and the independent variables were also evaluated with the Ward Chi-square. Lack of fit was estimated with the Hosmer-Lemeshow test, where non-significant values were interpreted as no evidence of lack of fit.

As is common in this type of research, full contemporary field replication of TRTs was not available due to the magnitude of the pasture areas and the number of animals required, with implications discussed at length by Bello and Rent (2018), but treatment 1-2 constituted a temporal replicate of L, and Experiment 2 a full temporal replicate of the growth phase of Experiment 1.

**Simple simulation model**

To illustrate the use of the prediction equations of CONCEPT rates, an exemplary, very simple model was developed in VENSIM PLE® using LWs, growth rates, mortality, and other parameters recorded in Experiment 1 to illustrate one possible approach to the prediction of the first two conceptions (Supplementary figure).

**Results**

**Growth period**

Detailed analyses of the growth period for Experiments 1 and 2 were previously reported by Vera (1991) and Vera et al. (2002), respectively. Briefly, in Experiment 1, the H SR was discontinued due to stagnant LW that made it impossible to attain the target LW (270 kg), and the animals were transferred to the common U/p paddock simultaneously with animals from the M SR treatment. During the growth phase, DLWG were 0.259, 0.232, 0.215, and 0.097 kg/head, for L, L2, M, and H SRs, respectively (Vera, 1991). Daily LWGs during the growth phase of Experiment 2 were 0.197, 0.192, and 0.096 kg/day, for the L, M, and H SRs, respectively (Vera et al., 2002).

**Breeding phase**

**Experiment 1**

Descriptive statistics for RP are shown in Table 1, while Table 2 lists LWs at biologically and practically significant ages frequently used to benchmark beef production systems. Least square means (LSMEANS) of LW and age for the first two conceptions are listed in Table 3. Data show that conception number had a significant effect on age and LW (p = 0.0001 and 0.002 respectively), whereas the interaction between TRT x CONCEP was non-significant. However, a slightly different picture emerged from the more correct (given the distribution properties of the two parameters) logistic analysis that followed. In effect, the distribution of LW at the 1st conception was well fitted by the normal distribution (mean = 296.2, s = 33.89), whereas that of age was lognormal (= normal distribution of the logs) skewed to the right with a long tail, and with parameters Theta, (threshold) = 0, n = 93; sigma (form) = 0.26, and Zeta (scale) = 7.16. Similar distributions applied to the 2nd conception, but trends disappeared in the subsequent parities.
Table 1. Summary of reproductive performance in Experiment 1, in relation to initial stocking rates during the growth period on U. (Low = 1.28; Medium = 1.71, High = 2.24 head/ha), followed by grazing a common paddock of U. at 1.71 head/ha during the breeding phase. Low-2 is a replicate of Low implemented one year later. Data are least squares means ± s.e.m. The numbers of available records for calving intervals are in parentheses.

<table>
<thead>
<tr>
<th>Stocking rate</th>
<th>Low</th>
<th>Low-2</th>
<th>Medium</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of animals</td>
<td>17</td>
<td>15</td>
<td>17</td>
<td>16</td>
</tr>
<tr>
<td><strong>Growth phase</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Initial liveweight (LW), kg</td>
<td>173 ± 4.4</td>
<td>174 ± 4.1</td>
<td>171 ± 4.0</td>
<td>170 ± 5.3</td>
</tr>
<tr>
<td>Initial age; days</td>
<td>442 ± 4.7</td>
<td>531 ± 4.1</td>
<td>447 ± 3.5</td>
<td>435 ± 4.2</td>
</tr>
<tr>
<td>LW at 1st detected heat, kg</td>
<td>241 ± 6.3</td>
<td>n.d.</td>
<td>231 ± 6.3</td>
<td>214 ± 6.5</td>
</tr>
<tr>
<td>Age at 1st detected heat, days</td>
<td>856 ± 31.5</td>
<td>n.d.</td>
<td>829 ± 31.5</td>
<td>846 ± 32.7</td>
</tr>
<tr>
<td>Age at 270 kg, months</td>
<td>26.8</td>
<td>30.1</td>
<td>29.2</td>
<td>38.4</td>
</tr>
<tr>
<td><strong>Breeding phase under common grazing</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age at 1st calving, months</td>
<td>44.9 ± 1.9</td>
<td>46.0 ± 1.1</td>
<td>44.8 ± 1.6</td>
<td>49.1 ± 1.5</td>
</tr>
<tr>
<td>Age at 2nd calving, months</td>
<td>64.3 ± 2.1</td>
<td>66.0 ± 1.8</td>
<td>63.6 ± 1.4</td>
<td>69.4 ± 1.7</td>
</tr>
<tr>
<td>Age at 3rd calving, months</td>
<td>77.7 ± 3.2</td>
<td>76.7 ± 2.0</td>
<td>80.6 ± 3.5</td>
<td>85.6 ± 2.4</td>
</tr>
<tr>
<td>1st calving interval, months</td>
<td>19.5 ± 2.6 (16)</td>
<td>20.2 ± 5.2 (13)</td>
<td>18.8 ± 2.7 (17)</td>
<td>19.5 ± 4.9 (14)</td>
</tr>
<tr>
<td>2nd calving interval, months</td>
<td>19.6 ± 3.4 (10)</td>
<td>20.1 ± 6.6 (4) †</td>
<td>19.7 ± 2.9 (13)</td>
<td>20.3 ± 2.5 (7)</td>
</tr>
</tbody>
</table>

† Experiment discontinued, n.d.: not determined. † Stocking rate discontinued due to inability to reach the target breeding liveweight.

Table 2. Summary of least squares means (live weight, kg) ± s.e.m. in Experiment 1 at key ages in relation to stocking rate (Low = 1.28; Medium = 1.71, High = 2.24 head/ha) during the growth period of heifers (weaning to target live weight of 270 kg).†

<table>
<thead>
<tr>
<th>Stocking rates</th>
<th>Animal age (months)</th>
<th>Low</th>
<th>Medium</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>18</td>
<td>186 ± 5.7</td>
<td>186 ± 5.7</td>
<td>186 ± 527</td>
</tr>
<tr>
<td></td>
<td>24</td>
<td>226 ± 6.9</td>
<td>204 ± 4.8</td>
<td>186 ± 4.8</td>
</tr>
<tr>
<td></td>
<td>36</td>
<td>271 ± 9.7</td>
<td>275 ± 4.7</td>
<td>252 ± 4.7 †</td>
</tr>
</tbody>
</table>

† Stocking rate discontinued due to inability to reach the target breeding liveweight.
† As expected, differences between ages differ from each other (p < 0.001) for all stocking rates.

Table 3. Age (days) and liveweight (kg) at the first two conceptions in Experiment 1 in relation to stocking rate during the growth phase (Low = 1.28; Low-2 = 1.28; Medium = 1.71, High = 2.24 head/ha). Liveweights are those recorded closest to calculated conception dates.

<table>
<thead>
<tr>
<th>Stocking rate</th>
<th>1st conception</th>
<th>2nd conception</th>
<th>1st conception</th>
<th>2nd conception</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>1051 ± 31.4 a</td>
<td>1845 ± 66.9 a</td>
<td>287 ± 6.1 a</td>
<td>310 ± 9.9 a</td>
</tr>
<tr>
<td>Medium</td>
<td>1057 ± 27.0 a</td>
<td>1716 ± 43.0 a</td>
<td>285 ± 6.9 a</td>
<td>298 ± 7.9 a</td>
</tr>
<tr>
<td>High</td>
<td>1250 ± 51.1 b</td>
<td>1839 ± 54.3 a</td>
<td>278 ± 11.8 a</td>
<td>325 ± 12.5 b</td>
</tr>
<tr>
<td>Low-2</td>
<td>1072 ± 24.3 a</td>
<td>1793 ± 70.7 a</td>
<td>298 ± 4.3 a</td>
<td>311 ± 11.7 a</td>
</tr>
</tbody>
</table>

† Age and liveweight means followed by different subscripts within each conception differ at p < 0.01. Differences in liveweight between conceptions within stocking rates differed at p < 0.05.

Conception probabilities
As indicated earlier, the occurrence of conceptions was fitted to logistic models, and the variables selected by the stepwise method included LW, Age, CONC, and the interaction between LW and Age. Separate analyses were carried out for each conception. The fit of the model was high during the 1st conception, somewhat less for the 2nd conception, and not significant thereafter.
Table 4. Given that precise age is seldom available for commercial cattle in extensive systems, the simpler model using LW only as a predictor variable is also included in the results (Figure 1) since it may be more easily applicable to the majority of practical applications. Nevertheless, the full logistic regressions equations were used to show the large interaction of LW and Age for two predetermined and illustrative conception probabilities (0.50 and 0.75, respectively) in the first two parities (Figure 2).

<table>
<thead>
<tr>
<th>Reproductive event</th>
<th>n</th>
<th>Intercept</th>
<th>Coefficient</th>
<th>$\chi^2$</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>LW as a predictor variable</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st conception, Experiment 1</td>
<td>93</td>
<td>-6.672541</td>
<td>0.0208803</td>
<td>6.04</td>
<td>&lt; 0.014</td>
</tr>
<tr>
<td>1st conception, Experiment 2</td>
<td>64</td>
<td>-8.491598</td>
<td>0.00269403</td>
<td>7.85</td>
<td>&lt; 0.0051</td>
</tr>
<tr>
<td>2nd conception, Experiment 1</td>
<td>72</td>
<td>-5.22217</td>
<td>0.011661</td>
<td>5.14</td>
<td>&lt; 0.023</td>
</tr>
<tr>
<td>(LW*age/1000) as predictor variable</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st conception, Experiment 1</td>
<td>93</td>
<td>-7.21049</td>
<td>0.0229</td>
<td>17.66</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>2nd conception, Experiment 1</td>
<td>72</td>
<td>-3.13323</td>
<td>0.0055</td>
<td>5.10</td>
<td>&lt; 0.024</td>
</tr>
</tbody>
</table>

n: number of observations.

With two exceptions, re-conceptions during the 1st lactation did not occur, but most animals re-conceived within 60 days or less after weaning.

The amount of data regarding conceptions was much less in Experiment 2, and the most reliable data based on the numbers of observations available refer only to the 1st conception. Fitting of the logistic model as above, using LW as the main effect, resulted in marginally different parameters (Table 4), but the location and shape of the curve largely overlap that of Experiment 1 (Figure 1).

**Figure 1.** Logistic regression of the probability of conception on liveweight. See details in Table 4. Experiment 1: solid line; Experiment 2: dotted line.

Logistic regressions regarding probabilities of conception in relation to LW can be used to develop a simple exemplary simulation model to simulate the dynamics of conceptions over a period of 12 months, based on the monthly evolution of LWGs shown as a horizontal table in the supplementary material. The latter includes the model equations, parameters, and outputs using actual and independent field data as input parameters.

**Figure 2.** Isolines depicting the interaction between age and liveweight for two exemplary probabilities (0.50 and 0.75 respectively) of conception on two consecutive parities. Lines are derived by solving equations shown in Table 4.

**Evolution of live weights in relation to parity**

Table 5 shows cows' LWs nearest conception, calving, and at weaning (adjusted to 240 days) for all of the reproductive cycles across all treatments in Experiment 1. Five-year average values for a large, contemporaneous and contiguous experiment with mature cows grazing conservatively managed native savannas reported average LWs of 332, 344, and 299-316 kg for CONCEP, PRECALV, and weaning, respectively (Rivera, 1988). Despite significant differences between parities, the only discernible trend is that of LW at conception that increased slightly with parity, and a non-significant effect of earlier treatments on LWs, but of course, differences in age persisted throughout the experiment (p < 0.01).

Over the total length of the breeding phase of Experiment 1 for the higher yielding treatments (6.68, 6.53, and 6.00 years...
for L, M, and L-2 respectively) there were 151 calving events (sum of the 3 treatments) that led to 133 weaned calves (88.1%), versus 43 weaned calves out of 55 calvings (81.1%) for the H treatment. These values imply calf losses of 12-19% between birth and weaning.

Table 5. Liveweights (kg, least squares means ± s.e.m.) near conception (CONCEP), calving (PRECALV), and at weaning (WEANING) in relation to reproductive cycle. The effect of initial treatment became non-significant after the second calving.

<table>
<thead>
<tr>
<th>Reproductive cycle</th>
<th>CONCEP</th>
<th>PRECALV</th>
<th>WEANING</th>
</tr>
</thead>
<tbody>
<tr>
<td>First</td>
<td>291 ± 5.4</td>
<td>347 ± 5.6</td>
<td>271 ± 4.9</td>
</tr>
<tr>
<td>Second</td>
<td>302 ± 5.3</td>
<td>381 ± 5.7</td>
<td>302 ± 4.8</td>
</tr>
<tr>
<td>Third</td>
<td>319 ± 5.6</td>
<td>380 ± 6.0</td>
<td>311 ± 5.1</td>
</tr>
<tr>
<td>Fourth</td>
<td>327 ± 6.9</td>
<td>357 ± 7.0</td>
<td>325 ± 7.5</td>
</tr>
<tr>
<td>Fifth</td>
<td>328 ± 15.0</td>
<td>379 ± 18.3</td>
<td>n.d.</td>
</tr>
<tr>
<td>p-value</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

n.d.: not determined.

**Discussion**

D’Occhio et al. (2018) recently reviewed the influence of nutrition operating via LW and body condition on heifers’ fertility and in postpartum cows. They noted that heifers’ weaning weight and their subsequent weight gains determine Age and LW at puberty, as well as lifetime RP. The present results coincide with that assertion, and apply to commercial Brahman heifers under the extensive management conditions of the Colombian Llanos when grazing low quality Ud pastures up until the fifth parity. Average calf weaning LWs, number of conceptions observed, and the yearly output of LW per cow were reported by Vera et al. (1993) and showed a distinctive difference between L and M relative to H in both experiments (Vera et al. 2002).

The present findings allowed the development of predictive logistic equations using LW and age as effector variables, for the first two conceptions, both of which were determined by earlier LWGs. It was further shown that the interaction of LW with Age influences conception probabilities, but that LW alone may be sufficiently accurate under commercial conditions that most frequently lack precise age information and also body condition scores. Similarly, mean Ages and their respective experimental errors allow predictions of subsequent conceptions in the third to fifth parities that complete lifetime performance under extensive tropical ranching conditions (Kleinheisterkamp and Habich 1985). In an earlier analysis, Vera (1991) analyzed the cumulative proportion of the first conception in Experiment 1 in relation to LW nearest that conception, whereas the more comprehensive and correct present analyses fitted logistic models to conceptions in relation to LW, Age, and their interaction from the first to fourth parities. This was accomplished using a Bernoulli distribution (using values of 0 and 1 for the absence and presence of conception respectively), with the result that starting on the third parity LW became non-significant, and Age at conception became nearly constant without a significant influence of the third and later parities. Thus, the present results provide a valid and fairly accurate long-term representation of conceptions throughout the females’ lifetime that could be used in developing a comprehensive, empirical simulation model of RP in Brahman herds experiencing low lifetime LWGs in tropical extensive systems.

Numerous initiatives have modelled reproductive events as reviewed by Blanc et al. (2001) at various organismic levels, ranging from endocrinology-driven conceptions to highly empirical approaches as in the present case. Nevertheless, Blanc et al. (2001) also noted that the prediction of reproduction under a wide range of environmental conditions continues to be a major challenge, and it can be inferred that models that apply to more constrained, and less data-rich, environments are useful, a situation that applies in the current case. The exemplary simulation model applicable to the first two parities and listed in the supplementary material fits the above conditions when LW is the only variable available, and it is driven by monthly LWGs that are available for a wide range of grazing situations in the Llanos (e.g., Depablos et al., 2009; Pérez et al., 2017; Rodríguez Borray and Cubillos, 2019).

Attainment of puberty in cattle is generally related to the body LW observed at maturity. Fordyce et al. (2013) provided a detailed review of findings in extensive systems of northern Australia and stated that puberty in B. indicus reached about 70% of mature LW, as opposed to 60% in B. taurus. In the present case, LWs of 230-240 kg associated with the first detected heat in the L and M SRs would be equivalent to 344 kg mature size, well within the range of 325-350 kg estimated by Vera (1991) and Vera et al. (2002) for animals that were bred while on Ud. Nevertheless, the cows that were bred on Ud in Experiment 2 reached asymptotic LWs of 380-390 kg
(Vera et al., 2002), implying conception at a proportion closer to 60–65% of mature size. It should be noted that the previous mature sizes are those allowed for by the nutritional regime used and cannot be taken as the potential LW determined by the genotype.

As shown in the present experiments, as well as in Pérez et al. (2019) for the Llanos of Colombia, Mora-Luna et al. (2014) in Venezuela, and Australian data (Schatz et al., 2011), RP on extensive, low external input systems based on low quality and un-supplemented pastures is modest but it is postulated that it is proportional to the low management demands of these types of pastures and systems. Under these conditions, on-farm data (Jiménez-Rodríguez and Manrique Perdomo, 2018) clearly demonstrates the futility of trying to incorporate sophisticated and expensive breeding technologies into systems that rely on low-quality forage resources. On the contrary, RP on higher-quality Ud (Vera et al., 2002) shows the marked difference made by better forage resources, and it is hypothesized that the latter case may offer somewhat better opportunities for the introduction of more demanding breeding technologies. In fact, under the extensive conditions of northern Australia, the on-farm study of Bortolussi et al. (2005) found that “the results suggest that producers associated increasing turn-off weight or decreasing turn-off age more with pasture improvement than with bulls of higher genetic merit for growth”. Advances in RP need therefore to be paralleled by improved animal management, keeping records of production, and closer scrutiny of the breeding herd.

Ezenwa et al. (2006) studied the RP of Brahman x British beef cows during 6 months of the warm season at Ona, Florida, USA, grazing either Ud or Pastinachus notatum pastures during 4 consecutive years, but with different cows every year. The cows were well fed as attested by cows weaning LW of 517 kg on Ud, and calf weaning LW of 250 kg (DLWG = 0.660 kg). During the 90 days following weaning, cows LWs increased very significantly, and exceeded the LW of those on P. notatum suggesting that Ud may provide enhanced LWG when grown on fertile soils. Ezenwa et al. (2006) suggested that cattlemen in the region, as in the Llanos (Vera and Ramírez-Restrepo, 2017; Vera and Hoyos, 2019) prefer to use these low input grasses for breeding cows, rather than better quality but more expensive alternative species. As the authors indicate, differences with observations in South America may be due to soil and fertility differences. Nevertheless, in a transitional savanna in Venezuela based on more fertile soils than in the present case, Depablos et al. (2009) provided three levels of supplementation to 166 beef heifers (636.0 ± 2.46 days of age and 219.6 ± 15.68 kg LW) grazing paddocks with a mixture of Urochloa spp. and Cynodon dactylon. Even the un-supplemented animals had much higher DLWG during the dry season (0.483 kg) and RP than in the present experiments, reaching 82% pregnancy. Thus, LWGs, LWs, and pregnancy success need to be referred to the specific nutritional strategy used in growing and breeding female cattle.

The present paper is predicated on the hypothesis that the probability of conception during the first two reproductive cycles by females (3-5-years-old) can be predicted with reasonable accuracy from an easy-to-measure parameter such as LW. Similarly, age, if available, interacts with LW as shown in Figure 2 and Tables 1 and 4 early in reproductive life, whereas later reproduction performance during the 3rd to 5th parities is associated with fairly constant LWs (Table 5 and Vera et al., 1993) if the nutritional strategy persists. The current results are supported by data from very different, but still extensive, cattle systems of northern Australia (Schatz et al., 2011; Schatz and Hearnden, 2017) that were derived from several thousands of records pertaining to breeding heifers and cows in different physiological conditions that were also included for comparison in Figure 3. It should be noted that the “maiden” heifers of Schatz et al. (2017) were at least one year older than their yearling heifers and showed much larger pregnancy rates at similar LW, thus adding support to the effect of the LW by Age interaction reported in the current results. The coincidence between our estimates and that of Schatz et al. (2017) with their yearling heifers is remarkable (Figure 3).

As shown in Table 1, long calving intervals characterize these extensive systems, a result that coincides among others, with Burns et al. (2010), Sierra-Montoya et al. (2013), and Pérez et al. (2019). Sierra-Montoya et al. (2013) reported on-farm data showing that cows fed on enriched rice residues, not dissimilar in quality to Ud, had a mean Age at 1st calving of 41.
months and subsequent calving intervals of 17.5 months. It should be noted that calving intervals of 18-20 months may inevitably lead to years of high RP alternating with years of very low outputs, as reported by Kleinheisterkamp and Habich (1985).

Our results show that loss of suckling calves, particularly during the first pregnancy, can be considerable. Scharz (2011) found that although pregnancy rates in 2-year-old maiden heifers were generally adequate (> 75%), calf loss rates averaged 22% in first-calf heifers, and re-conception rates were also low (< 25%).

Lastly, the remarkable behavior of LW during late pregnancies reported in Table 5 should be noted, in that cows' LWs only consistently increased due to pregnancy, but returned to the initial CONCEP LW following weaning. This observation coincides with the observations made by Vera-Infanzón and Ramírez-Restrepo (2020) in that the only meaningful weight increase in these extensive systems is the weaning LW of their calves since cows contribute very little to systems’ outputs other than when culled from the herd. Although not documented in the Colombian case (except by occasional observations by the authors), cows older than 8 years of age may show an accelerated rate of tooth erosion (Jones and Sadler, 2012), exposing them to severe undernutrition and even death (Fordyce et al., 1990). Given that culled cows constitute a large fraction of slaughter animals in breeding systems (Florez, 2010; Ramírez-Restrepo et al., 2020), earlier culling would therefore seem advisable.

The implications of RP in extensive systems on GHG emissions remain to be analyzed, but Garnsworthy (2004) suggested that changes in RP associated with changes in the proportion of different animal categories in the breeding herd may have an important influence on environmental efficiency, a carbon footprint dimension proved on well-managed B. decumbens pastures (Ramírez-Restrepo et al., 2020).

Conclusions

The long-term data analyzed show the close relationship of conceptions in extensive Brahman cattle systems with LW and age in the initial two reproductive cycles, whereas more advanced conceptions relied largely on the age of the females. The quantitative relationships between probability of conception and both LW and Age were established, and it is suggested that they can be an adjunct in decision-making regarding mating and its success in accomplishing pregnancy.

Thus, using the proposed equations can help establish thresholds for achieving desired levels of conception, as exemplified in the supplementary material. The production systems investigated rely on low-quality extensive pastures subject to minimal external and human-management inputs and support low to medium rates of RP at the cost of maintaining heifers and cows with low LWs. Beef outputs of these systems are therefore largely due to the production of weaners, complemented eventually with the sale of culled cows.

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Literature cited


Beef cattle reproduction on *Urochloa humidicola*


SAAESD. 2005. A compilation of research results involving tropically adapted beef cattle breeds. Southern Association of Agriculture Experiment Station Directors (SAAESD), Batton Rouge: Southern Cooperative Series Bulletin 405, 227 pp. https://www.lsuagcenter.com/~media/system/2/c/4/2/2c42768016a444c47e6187e6e3b5b296/researchresultsstrophicallyadaptedbeefcattlebreedsLpdpf


