Translational Animal Science, 2022, **6**, 1–10
https://doi.org/10.1093/tas/txac035
Advance access publication 30 March 2022
Forage Based Livestock Systems

Environmental variation effects fertility in tropical beef cattle

James P. Copley,[†,1] **Bailey N. Engle,**[†] **Elizabeth M. Ross,**[†] **Shannon Speight,**[†,‡] **Geoffry Fordyce,**[†] **Benjamin J. Wood,**[‖] **Kai P. Voss-Fels,**[†,$] **and Benjamin J. Hayes**[†]

[†]Centre for Animal Science, Queensland Alliance for Agriculture and Food Innovation, St Lucia, QLD 4072, Australia
[‡]Black Box Co, Mareeba, QLD 4880, Australia
[‖]School of Veterinary Science, University of Queensland, Gatton, QLD 4343, Australia
[$]Institute for Grapevine Breeding, Hochschule Geisenheim University, Geisenheim 65366, Germany

[1]Corresponding author: james.copley@uq.edu.au

ABSTRACT

The northern Australia beef cattle industry operates in harsh environmental conditions which consistently suppress female fertility. To better understand the environmental effect on cattle raised extensively in northern Australia, new environmental descriptors were defined for 54 commercial herds located across the region. Three fertility traits, based on the presence of a *corpus luteum* at 600 d of age, indicating puberty, (CL Presence, $n = 25{,}176$), heifer pregnancy ($n = 20{,}989$) and first lactation pregnancy ($n = 10{,}072$) were recorded. Temperature, humidity, and rainfall were obtained from publicly available data based on herd location. Being pubertal at 600 d (i.e. CL Presence) increased the likelihood of success at heifer pregnancy and first lactation pregnancy ($P < 0.05$), underscoring the importance of early puberty in reproductive success. A temperature humidity index (THI) of 65–70 had a significant ($P < 0.05$) negative effect on first lactation pregnancy rate, heifer pregnancy and puberty at 600 d of age. Area under the curve of daily THI was significant ($P < 0.05$) and reduced the likelihood of pregnancy at first lactation and puberty at 600 days. Deviation from long-term average rainfall was not significant ($P < 0.05$) for any trait. Average daily weight gain had a significant and positive relationship ($P < 0.05$) for heifer and first lactation pregnancy. The results indicate that chronic or cumulative heat load is more determinantal to reproductive performance than acute heat stress. The reason for the lack of a clear relationship between acute heat stress and reproductive performance is unclear but may be partially explained by peak THI and peak nutrition coinciding at the same time. Sufficient evidence was found to justify the use of average daily weight gain and chronic heat load as descriptors to define an environmental gradient.

Key words: cattle, puberty, environment, heat stress, pregnancy

INTRODUCTION

The northern Australia beef industry encompasses Queensland, the Northern Territory, and the northern half of Western Australia. This region contains 60% of Australia's national cattle herd with the majority *Bos indicus* derived breeds (Australian Bureau of Statistics (ABS) 2020). The use of cattle with *Bos indicus* content is necessary given the diverse and challenging environmental conditions of the region (Fordyce et al., 1990; O'Rourke et al., 1991; Burrow, 2012; McLean et al., 2014). Generally, in the northern Australia pastoral industry the environmental "harshness" increases as you move north. This is due to a combination of extreme temperatures, increased external parasite burden, low fertility soils and highly pronounced wet and dry seasons (Henderson et al., 1978; McLean et al., 1983). These environments require tropically adapted cattle.

Environment represents more than location or a contemporary group, it is the sum of the temperature, rainfall, pasture availability and other factors to which animals are exposed. "Environment" will; however, shift radically on an annual basis. Animals must be able to reproduce despite environmental variation. Fertility traits, such as puberty, conception, and re-conception (i.e. second conception) are important drivers of profitability in a beef enterprise (McLean et al., 2014; Harburg et al., 2020). Overall herd productivity is enhanced by large numbers of maiden heifers attaining puberty, conceiving, and subsequently calving early in the breeding season (Day and Nogueira, 2013). Such females have maximum opportunity for lifetime reproductive success (Fortes et al., 2012; Johnston et al., 2014). These same traits have been shown to be greatly affected by environmental variation (McGowan et al., 2014).

A range of approaches have been used to define the environment in northern Australia. McGowan et al. (2014) partitioned environment into several different regions based upon multiple inputs including land-type, weaning, and yearling weight. Harburg et al. (2020) adopted the regions based upon the Australian Bureau of Agricultural and Resource Economics and Sciences survey regions. In both these approaches, animals were effectively "binned" into environmental groups. Alternatively, it is possible to describe the environment as a linear covariate (Falconer, 1990; Mulder, 2016; Freitas et al., 2019). Mota et al. (2020) examined the impact of the environment on fertility traits in Brazilian beef cattle and used yearling weight to define environment. By using this approach, production and fertility traits can be modeled along an environmental gradient (Mota et al., 2020).

Received November 8, 2021 Accepted March 25, 2022.

We hypothesized that environmental factors will impact the rate of successful heifer fertility outcomes, namely attainment of puberty by an average 600 d of age, first conception, and first lactation re-conception. The aim of this paper was to define environmental descriptors with a significant effect on fertility traits. The environmental descriptors examined in this study were designed to account for environmental variation as a continuous variable based upon available weather information (rainfall and temperature humidity index) and animal weight gain performance. This information is readily available to producers and was used to maintain applicability of the results to industry.

MATERIALS AND METHODS

The data were collected with approval from the University of Queensland Production and Companion Animal Ethics Committee as Approval SAFS/253/20/Northern Genomics.

Animals and Commercial Collaborators

The project utilized data from 54 commercial producers from environmentally diverse locations across northern Australia. These data were collected as part of the Northern Genomics project (Hayes et al., 2022). Animals were born between 2016 and 2018 with primary data collection taking place between 2018 and 2021. Some historical data from 2012 to 2014 Brahman cohorts were also included. The project contained a cross-section of breeds typically found in northern Australia including Brahman, Angus, Belmont Red, Charolais, Droughtmaster, Shorthorn, Limousin, Santa Gertrudis, Boran and Wagyu (Hayes et al., 2019).

The aim of the project was to encompass the full range of breeds, country types and management systems representative of northern Australia. Management practices and enterprise type varied from smaller, intensively managed seedstock herds to large, purely commercial businesses. Most collaborators ran heifers in large contemporary groups of at least 200–300 animals. A majority of heifers were first joined at 2 yr of age, although both intentional and unintentional mating of yearling heifers occurred. Producers who practiced controlled mating typically exposed females to bulls for 3–4 mo commencing from November to January, depending on region. Animals in the project were individually identified using unique electronic identification device ear tags, required in Australia as part of the National Livestock Identification System (NLIS). Birth dates were not available for most animals due the extensive production environment, so approximate age was estimated based upon birth year.

Fertility Traits

CL presence Heifer reproductive maturity was measured in each year group when it was likely that approximately 50% were sexually mature, using a one-time ovarian ultrasound examination to detect the presence of a *corpus luteum* (CL) (n = 23,015). The original CL Score ranking from Corbet et al. (2018) was reduced to a binary trait, CL Presence (0 = "nonpubertal", 1 = "pubertal"). A rectal ultrasound examination of the reproductive tract was completed by a trained veterinarian using a 10 MHz 60 mm linear array probe (HS-2200V or HS-1600V, Honda Electronics Co Ltd.). Heifers with a CL, either functional or regressing, or were pregnant, were classified as pubertal (1), and those without these hallmarks were classified as nonpubertal (0). See Corbet et al. (2018) for a full description of the procedure. The trait was assumed to be measured at approximately 600 d of age based on the cohort. With the nature of the extensive management system and lack of precise animal age, this may have ranged from 1 to 2.5 year of age.

Pregnancy

First pregnancy diagnosis (PD1) was measured as fetal age in months (n = 20,989) at approximately 2.5 yr of age, following the heifer's first breeding season. Second pregnancy diagnosis (PD2; n = 10,072) was measured at approximately 3.5 yr of age. Some yearling mating did occur within the project cohorts, in which case, first and second pregnancy diagnosis was conducted earlier than ~2.5 and ~3.5 yr, respectively. Trained project collaborators or veterinarians conducted pregnancy testing via manual palpation or ultrasound examination approximately 2–4 mo after bull exposure, with the timing of recording optimized to coincide with the producer's management schedule. The pregnancy traits (PD1, PD2) were recorded as fetal age or "months pregnant" (with 0 = nonpregnant). This meant that animals with more advanced pregnancies at the time of ultrasound or palpation may have been assessed later in relation to their breeding season. Modeling pregnancy as a binary trait was therefore preferable, as all animals receive equal weighting for successful pregnancy. PD1 and PD2 were modeled as binary traits (0 = "nonpregnant", 1 = "pregnant") using a logistic regression.

Pregnancy within 4 mo of Calving

The ability of a first lactation cow to conceive is critical to herd profitability. Pregnancy within 4 mo of calving (P4M) was calculated from the fetal age at consecutive pregnancy diagnoses (PD1, PD2) using the approach outlined by McGowan et al. (2014). A gestation length of 290 d was used to predict calving date from PD1. A predicted conception date was derived from PD2, the difference between these two dates being used to determine whether P4M was achieved, resulting in a binary trait (1 = conceived within four months of calving, 0 = did not re-conceive within four months of calving).

Covariates At the time of ultrasound examination and fertility trait recording for CL Presence, PD1 and PD2, additional covariates and factors were also recorded:

Weight (Wt): Animal's liveweight at the time of trait recording, recorded automatically using a variety of equipment such as walkover crush scales.

Hip Height: Distance from the ground to the peak of the sacrum. Typically, a standard tape-measure was taped to the roof of the crush and measured the vertical distance from the roof to the sacrum. This measurement was subtracted from the total height of the roof to the ground to calculate the true measurement.

Body Condition Score (BCS): Defined on a 1–5 scale, 1 being poor condition and 5 being over conditioned.

Bos indicus content (BI%): A measure of *B. indicus* content expressed as a percentage. All animals were genotyped using a 35K or 50K tropBeef SNP array by Neogen, Australasia (Hayes, 2022). *Bos indicus* percentage was calculated by comparing each animal to a large purebred

B. indicus dataset (Hayes et al., 2019). Using a GBLUP model, phenotypes were assigned as 1 for *B. indicus* and 0 if not and the effect of each SNP was back-solved (Yang et al., 2011). Prediction equations for *B. indicus* purebred then directly estimated BI% (Hayes et al., 2019).

Heterozygosity (Het): Heterozygosity accounted for the effect of heterosis and was measured by the proportion of markers that were heterozygous for each animal (Hayes et al., 2019). Heterozygosity ranges from 0.25 (purebred) to 0.5 (F1 cross), this measure has been re-scaled on a 0–1 scale, where 0 = purebred and 1 = F1 cross (Hayes, 2022).

Factors

Contemporary Group (CG): Defined by collaborating herd and animal birth year.

Collaborator: Defined by herd alone, distinct from CG as some project collaborators entered up to three separate cohorts into the project.

Year: Defined as year of CL Presence recording.

Month: Month of CL Presence recording.

Environmental Descriptors

Weather data for each property was obtained using the NASAPOWER package (Sparks, 2018) in R v3.5.3. NASAPOWER data are a publicly available global climatology database with a 0.5° by 0.5° arc of longitude and latitude (Sparks, 2018). Based upon the coordinates provided for each collaborator, daily interpolated observations of rainfall, temperature and relative humidity data were downloaded for the 20 yr preceding the time of trait recording. The interpolated data were preferrable as direct observations from weather stations were not available within 300 km for multiple different collaborators.

Temperature humidity index The temperature (**T**) and relative humidity (**RH**) was used to calculate a daily temperature humidity index (THI) as per Wijffels et al. (2013).

$$THI = 0.8 * T + ((RH * 0.01) * (T - 14.4)) + 46.4$$

To assess the impact of the severity of the environment to which the heifers were exposed, the number of days where THI was equal to or exceeded different thresholds in the 120 d prior to CL Presence recording and 120 d surrounding (60 d prior and 60 d post) conception date for heifers and first-lactation cows (PD1 and PD2) were obtained. The 60 d prior and post conception approximately aligns with three complete estrus cycles (Senger, 1997). Conception date was calculated from estimated fetal age and pregnancy diagnosis date.

A THI value of 79 is the threshold of acute heat stress, where the risk of detrimental effects on animal health and production increase (Moran, 2005; McGowan et al., 2014). Incremental thresholds of 65, 70, 75 and 79 were used, with THI thresholds of 65–75 being considered chronic heat load. Chronic heat load was also modeled by calculating the area under the curve (AUC) of daily THI in 120 d surrounding (60 d prior and 60 d post) conception date for PD1 and PD2 and prior to recording date for CL Presence.

The use of this threshold however, did produce a potential sampling problem as a number of contemporary groups were not exposed to any days over the threshold of 79 within the 120 d time period. The use of alternate (chronic heat load) thresholds aimed to address for this problem.

Rainfall Rainfall descriptors were based on the daily precipitation records. Rainfall was intended to serve as a proxy for nutritional availability as rainfall received is the key determinant of nutrition in extensive grazing systems. Two separate descriptors were calculated based on the same key dates in the breeding cycle: conception date (PD1, PD2) and trait recording date (CL Presence). Total rainfall (mm) in 120 d and the standard deviation of rainfall in the 120 d were compared to the 20 yr average of the same period and location.

Average Daily Weight Gain

Average daily weight gain (ADWG) was calculated as the average daily gain from CL Presence to PD1 and from PD1 to PD2 (kg/day). ADWG measures the nutritional availability based on animal outcome. In the context of this study, ADWG was used to approximate environment. This is similar to Mota et al. (2020) who used yearling body weight to define environmental levels to analyze genotype by environment interaction for fertility traits in Brazilian Nellore cattle. The effect of ADWG on CL Presence was not modeled as no weight recording information prior to CL Presence measurement was available.

Statistical analysis Contemporary groups containing fewer than 50 records were excluded from the analysis. Second pregnancy (PD2) records were filtered based on the number of days a cow was open, or the estimated number of days between predicted calving date at PD1 (assuming a 290 d gestation length) and the predicted conception date for PD2. The time between PD1 and PD2 varied greatly within, in some cases was in excess of 600 days. Outliers of this magnitude indicated that animals were not pregnancy tested within their respective groups. In extensive herds, it is not uncommon for animals to be absent or inadvertently left behind during mustering. This was apparently the case within the dataset and such outliers were removed to ensure that PD2 was restricted to animals breeding within consecutive years. In absence of available lactation or weaning records, this also had the effect of narrowing the dataset to primarily include cows that would have been lactating at conception, although this could not be confirmed. This data filtering criteria was also used to assign P4M. The environmental descriptors were individually fit as fixed effects. Animal level fixed effects (factors and covariates) were modeled alongside environment to isolate the effect of each environmental descriptor on fertility. Using a bottom-up approach for model fitting, models only included a combination of significant fixed effects (Supplementary Table S1). In the case of PD1, BI% was kept in the model to maintain consistency with every other analysis. For pregnancy diagnosis (PD1 and PD2), the equation of each generalized linear model was:

$$Pregnancy\ status \sim HH + BCS + Wt + CG + BI\,\% + Het + ED$$

Statistical analysis was conducted using the glm.db package in R (Ripley et al., 2013). Additional analysis to examine the effect of puberty status at CL Presence on subsequent pregnancy was similarly modelled, replacing environmental descriptor for CL Presence, and completed using a least squares mean test via the emmeans package in R (Russell et al., 2018).

The relationship between CL Presence and all environmental measures was also modeled using logistic regression using the glm.db package in R (Ripley et al., 2013). The environmental descriptors for CL Presence were calculated as the same for all the animals within a herd year group. Months in which fewer than five cohorts were scanned were excluded from the analysis. For CL Presence, the equation of the generalized linear model was:

$$CL\ Score \sim HH + BCS + Wt + month + year + collaborating\ herd + BI\ \% + Het + ED$$

RESULTS

Table 1 shows descriptive statistics for CL Presence, PD1, PD2 and P4M. The presence of a CL was detected in close to 50% of heifers, corresponding to the objectives in the study design. Pubertal heifers were, on average, heavier at CL Presence recording. The pregnancy results achieved at PD1 were slightly higher than those achieved at PD2. Yearling pregnancy at the time of CL Presence recording, contained within the "pubertal results", was observed in 15.63% of heifers. The P4M results of yearling mated heifers were lower than the those achieved by heifers rebreeding at PD2.

Heifers that were pubertal at CL Presence had increased log odds of pregnancy success at both PD1 (0.56) and PD2 (0.75) compared to non-pubertal heifers ($P < 0.05$). There was substantial evidence that heifers that achieved puberty by approximately 600 d of age had improved performance for subsequent pregnancies.

Effect of Rainfall on Reproductive Traits

Neither the magnitude nor the variability of rainfall in the 120 d preceding CL Presence recording was found to have a significant effect ($P > 0.05$) on the attainment of puberty (Table 1). There was no evidence that above average rainfall in the period prior to conception/trait recording lead to a higher proportion of pubertal heifers.

Total rainfall and rainfall deviation from a 20 yr average both had no effect ($P > 0.05$) on first or second pregnancy outcome. There was no evidence that above average rainfall in the period prior to conception lead to a higher pregnancy rate at either PD1 or PD2. Rainfall was significantly ($P < 0.05$) correlated to liveweight; however, fitting rainfall independently of liveweight in the model accounted for this potentially confounding effect.

Effect of ADWG on Reproductive Traits

We found that that effect of ADWG on PD1 was significant ($P < 0.05$), with each additional kilogram of daily weight gain increasing the log odds of successful first pregnancy (Table 1). Increased ADWG from PD1 to PD2 assessment had a significant, positive effect on first lactation conception rate. There is an evidence that increased ADWG from CL Presence recording to PD1, and again from PD1 to PD2 recording, is associated with an increase in the proportion of successful pregnancies.

Effect of THI on Puberty

The effect of THI on the CL Presence was varied. Each day over the individual THI thresholds 65 and 70 had a significant ($P < 0.05$) and negative relationship to CL Presence. The cumulative daily THI for 120 d prior to trait recording was significant ($P < 0.05$) and had a negative effect on CL Presence (Table 1). However, the effect of days over 75 and 79 on CL Presence was positive. There was limited evidence that increased heat load, especially chronic heat load, in the period prior to ovarian ultrasound for CL Presence reduced the proportion of pubertal females.

Effect of THI on Pregnancy

The effect of daily THI on PD1 followed a similar pattern to CL Presence. The number of days an animal was exposed to THI thresholds of 65 and 70 in the 120 d surrounding conception date each had a significant impact ($P < 0.05$) and reduced the likelihood of pregnancy for each additional day

Table 1. Effect of environmental descriptors on fertility outcome

	CL Presence[1]		PD1[1]		PD2[1]	
N	25,176		20,989		10,072	
Proportion pubertal or pregnant	0.44		0.71		0.64	
P4M[1] rate			0.27		0.38	
Environmental Descriptor	**Estimate**	**P-value**	**Estimate**	**P-value**	**Estimate**	**P-value**
Temperature humidity index						
Number of d ≥ 79	0.12	<0.01	0.04	<0.01	−1.01	0.11
Number of d ≥ 75	0.02	0.06	0.01	0.24	−0.06	<0.01
Number of d ≥ 70	−0.05	<0.01	−0.01	<0.01	−0.05	0.01
Number of d ≥ 65	−0.06	<0.01	−0.06	<0.01	−0.15	<0.01
Area under curve in previous 120 d	0.00	<0.01	0.00	0.75	−0.01	<0.01
Deviation from average rainfall	0.00	0.21	−0.09	0.94	0.38	0.75
Total rainfall	−0.10	0.21	0.00	0.94	0.00	0.75
Average daily weight gain in previous year			0.01	<0.01	2.12	<0.01

[1] CL Presence = ovarian scanning at 600 d, PD1 = Pregnancy detection 1, PD2 = Pregnancy detection 2, P4M = conception rate within 4 mo of calving.

above the threshold (Table 1). In contrast, days above 79 had a positive effect ($P < 0.05$), while days over 75 had no effect. The AUC of daily THI for the 120 d surrounding conception date (60 d prior and 60 d post) was not associated with pregnancy outcome at first pregnancy ($P > 0.05$). The results showed that increased chronic heat load in the period surrounding conception will reduce the proportion of females that are pregnant at PD1.

The number of days an animal was exposed to THI thresholds of 65, 70, and 75 in the 120 d surrounding conception date each had a significant impact ($P < 0.05$) and reduced the likelihood of pregnancy success for every additional day above the threshold. The AUC of daily THI for the 120 d surrounding conception date (60 d prior and 60 d post) was also negatively ($P < 0.05$) associated with a positive pregnancy diagnosis at PD2. These results showed that increased heat load in the period surrounding re-conception will reduce the proportion of successful pregnancies at PD2.

Discussion

Our results have demonstrated that environmental factors impact heifer fertility traits; puberty attainment by approximately 600 d of age, first conception, and first lactation re-conception. We found that ADWG and chronic heat load descriptors had a significant relationship with reproductive outcomes and effectively model the influence of environment. By utilizing environmental information readily available to producers, the interaction between environment and reproduction may more effectively be accounted for in future efforts to improve female fertility in tropical beef herds.

Relationship Between Puberty and Pregnancy

The use of an ultrasound to examine the reproductive tract and ovaries can detect the presence of a CL (Pierson and Ginther, 1988; Johnston et al., 2009, 2014; Corbet et al., 2018). The use of a single ultrasound examination at approximately 600 d was proposed by Corbet et al. (2018) as an alternative to the intensive process of regularly conducted scanning to determine age at puberty. Its use was expanded upon by Engle et al. (2018) who estimated the genomic correlation between age at puberty and reproductive maturity score was −0.83, indicating that a single scan is an accurate measure of puberty.

Our results confirmed the beneficial relationship between these puberty measures and later reproductive success in Northern Australian beef (Johnston et al., 2014; Corbet et al., 2018). Heifers that are pubertal at the commencement of joining conceive earlier, calve earlier, and are more readily able to re-conceive during the subsequent breeding season (Day and Nogueira, 2013; Johnston et al., 2014; Corbet et al., 2018). This increases the management options available for producers, it allows for earlier weaning if required due to seasonal conditions. This study has reinforced the importance of puberty as a fertility trait as it can be measured early in life and has a positive relationship to subsequent pregnancy. These results also highlight the importance of heifer management to ensure puberty is reached prior to joining and that deliberate selection for reduced age and weight at puberty is undertaken.

Fertility variation Approximately 44% of the heifers in this study were pubertal as they had either a CL at time of CL Presence measurement or were pregnant. Heifers reaching puberty by ~600 d is typical of northern Australian production systems. Burns et al. (1992) found the average age of pubertal to be 580–650 d, which was corroborated by Johnston et al. (2009) who found 24 mo to be typical. Our results for CL Presence were comparable to past studies investigating puberty in females including results from Johnston et al., (2009) (age at first CL) and Corbet et al., (2018) (CL Presence). These findings, amongst others, demonstrate the difficulties associated with reaching puberty in tropical and subtropical Australia. In temperate environments, by 2 yr of age, heifers are expected to have already calved. The differing expectations in temperate zones is partially attributable to the widespread use of taurine breeds, breeds with earlier sexual precocity compared to the indicine breeds favored in the tropical environments of this study (Martin et al., 1992; Rodrigues et al., 2002). However, insufficient body weight, due to marginal nutrition and harsh environmental conditions, is often the primary constraint on puberty in tropical herds. Kinder et al. (1994) found that achieving 2/3 of a mature weight is critical to puberty attainment, regardless of age impractical to achieve before 2 yr of age in many northern Australia production systems (Johnston et al., 2009, Fordyce and Chandra, 2016). Scanning project heifers earlier than ~600 d would have resulted in a dataset that was heavily skewed toward “nonpubertal” due to these environmental constraints. The complex relationship between body weight, environmental conditions, and fertility outcome is beyond the scope of this study. However, liveweight, body condition score, and hip height were included in our models to account for the well-established relationship between animal weight, body condition and reproductive outcome (McCosker et al., 2021).

The observed pregnancy rates were also reflective of past research. The success rate for PD1 was fractionally less than the result reported by McGowan et al. (2014) (80%) and Schatz and Hearnden (2008) (>75%), who found marginally higher median pregnancy rates amongst cows in Queensland and the Northern Territory, respectively. Pregnancy diagnosis results at PD2 reflect rebreed rates from first-lactation cows. McGowan et al. (2014) found a higher annual pregnancy rate in first lactation cows ranging from 48% to 86% (Q1–Q3) across several regions, a median level of 77%. In contrast, Johnston et al. (2014) and Schatz and Hearnden (2008) found drastically lower rebreed rates (25%–27%), as did Sullivan et al. (1997) (18.6%), O’Rourke et al. (1995) (15%), and Holroyd et al. (1990) (38%–44%).

The re-conception rates from our study were generally higher than previous findings, except for McGowan et al. (2014), which is the most comparable study to the present work in terms of location and commercial herd structure. The seasonal conditions during the years of data collection impacted our results. Dry conditions were experienced during the project although severe weather events, including widespread flooding, directly impacted some collaborators. Our re-conception results, despite being higher than some previous studies, still illustrate that pregnancy rates in tropical Australia are not reaching the level required for sustainable self-replacing breeding herds, this is without taking pregnancy loss and calf mortality into account. This indicates that a significant proportion of breeding females in northern Australia are periodically unproductive.

Re-conception rate itself presents only part of the fertility picture; to successfully calve in consecutive years, cows must re-conceive within four months of calving, a scenario that P4M is designed to measure. We found the P4M rate at second pregnancy diagnosis, among those heifers that first calved at ~3 yr, were comparable to previous results from McGowan et al. (2014). Our results indicate that less than a third of first-lactation heifers are re-breeding in a timeframe that will allow for calving in consecutive years, increasing the numbers of unproductive (nonlacating and nonpregnant) females in the herd. For those heifers which were pregnant at CL Presence the rate of P4M was low. Animals that were pregnant at CL Presence, and were subsequently lactating at 2 yr, were comparatively less likely to be pregnant at PD1 recording compared to both nonpregnant pubertal and nonpubertal heifers. This indicates that heifers successfully producing a calf by 2 yr are at a disadvantage in extensive tropical production systems.

Fewer than half heifers in this study were pubertal at time of ovarian scanning, approximately 600 days of age, hence there is considerable scope for improvement. Heifers that were pubertal at 600 days of age were more likely to be pregnant at PD1 and PD2, thus targeted selection for earlier puberty would be beneficial to overall herd productivity. Currently, not enough heifers are pubertal prior to joining. However, the goal of selecting for reduced age and weight at puberty should be balanced with actual production constraints. In this extensive, tropical, pastoral system, calving heifers at 2 yr of age places excessive nutritional demands on growing animals, reducing their ability to produce calves in consecutive years, although the effect on the total number of calves in their lifetime is less pronounced (Burns et al., 2010; Schatz and Partridge, 2012). Selection and management must align to reduce age at puberty and ensure that heifers are sufficiently grown prior to first pregnancy, so as not to impede re-conception.

Effect of rainfall on reproduction Rainfall itself has a marginal direct effect on cattle except for extreme weather events, rather, the impact of rainfall is primarily felt through the availability and quality of feed. Rainfall received is used to calculate annual feed budgets and is the basis for tracking stock days/ha, such information is fundamental to effective grazing management and has long been utilized for tools such as grazing charts. Quantifying the exact relationship between heifer pregnancy and mm of rainfall would be extremely valuable to producers and was the key objective in defining this environmental descriptor.

The timing of rainfall relative to trait recording was used to indicate the quality of pasture at periods in the breeding cycle. In a severe and extended dry periods, the quality of feed will decline but so will the available feed, measured in kg/ha (Bowen et al., 2018). The required dry matter intake is typically expressed at a percentage of bodyweight. Cattle generally require a dry matter intake equivalent to 2.5% of liveweight, a figure that increases during lactation (MLA, 2015). Our simple contention was that rainfall has an influence on dry matter intake because it is a determining factor of feed digestibility, that more digestible a certain feedstuff is, the more cattle can consume. Young, growing pasture can be approximately 20% dry matter, compared to dry, mature pasture which can be 80%–85% dry matter (Fulkerson and Slack, 1993; Poppi et al., 2018). Increasing the nutritional availability of pasture during heifer development, before the breeding season, and during early pregnancy can improve fertility outcomes (Poppi et al., 2018).

We did not find any statistically significant relationship between fertility and rainfall, indicating that while rainfall is a key determinant of available nutrition in extensive tropical pastoral systems, the use of total rainfall and deviation from long-term average does not capture the effect of nutritional availability on fertility outcomes. The shortcomings in this modeling may have been due to a lack of precision in defining rainfall, it is based on spacial interpolation of rainfall rather than direct observations (Sparks, 2018). A potential confounding effect was the significant correlation between rainfall and liveweight; however, this was accounted for by independently fitting liveweight and rainfall to the model. This ensured that the reproductive response to rainfall was independent of weight. It should also be noted that our model does not account for supplementary feeding of protein meal or nonprotein nitrogen (urea) which is extremely common throughout tropical Australia (MLA, 2015; Bowen et al., 2018).

To overcome the shortcomings in nutritional modeling, rainfall records could be augmented with pasture growth information that is available through the Queensland government (Queensland Government, 2021). This will directly measure the level of nutrition (measured as dry matter) that is available to animals, rather than inferring this available nutrition. Additionally, Northern Genomics project collaborators have also conducted faecal sampling which raises the possibility of direct observations of animal diet in the future. However, the exact interaction between rainfall, feed availability, and fertility is complex and difficult to quantify over a diverse range of land-types and doing so is beyond the scope of this current inquiry. We found that the use of rainfall alone over-simplifies the complex issue of nutritional availability, and that additional information is required to successfully estimate nutrition using rainfall.

Effect of average daily weight gain on pregnancy Average daily weight gain is an alternative measure of nutritional availability; rather than attempting to estimate nutrition from an external factor (like rainfall), it is quantified on an outcome basis. Those animals with higher ADWG had access to better nutrition through improved pasture quality, supplementation, or other factors. A heifer's underlying genetic potential has an impact on ADWG. However, to segregate the genetic and environmental components of ADWG, measures of heifer size were included in these models, specifically Wt, BCS, and HH. Our results confirmed the link between increased ADWG, as a measure of environment, and better reproductive performance (Burrow, 2001; Boligon and Albuquerque, 2011; Mota et al., 2020).

The link between increased ADWG and improved reproductive performance has its basis in the physiological impacts of nutrition on the reproductive cycle. Nutrition acts in several ways to promote and maintain reproductive cyclicity, including to stimulate the secretion of pre-pubertal luteinizing hormone (Schillo et al., 1992; Pryce et al., 2001; Nogueira, 2004; Scaramuzzi et al., 2006; Archbold et al., 2012; D'Occhio et al., 2019). The secretion of gonadotropin-releasing hormone by the pituitary gland, is governed by the positive feedback from metabolic hormones whose secretion will be promoted by improved nutrition (D'Occhio et al., 2019). This nutritional aspect is especially influential for rebreeding success following a heifer's first pregnancy, insufficient nutrition can lengthen post-partum anoestrus interval and exacerbate lactation anestrus (Entwhistle, 1983; Scaramuzzi et al., 2006; Schatz and Hearnden, 2008; Burns et al., 2010). Lactation anestrus is prominent in the *B. indicus* breeds utilized in this study; a self-preservation mechanism, it can also reduce broader reproductive performance (Rodríguez and Segura, 1995; Petersson et al., 2007).

The relationship between lactation anestrus and postpartum anestrus interval accounts for the strong correlation observed between ADWG and PD2. Animals that were gaining weight between PD1 and PD2 had access to sufficient nutrition to avoid extended lactation anestrus. This again underlines the importance of female management in tropical pastoral systems; effectively managing cow body weight, particularly post-calving, is essential for reproductive success. By extension, these results, along with the negative relationship between hip height and reproduction, demonstrate the risks of breeding large-framed females in tropical pastoral systems. Larger animals have higher feed maintenance requirements and it is beneficial to conduct breeding programs to produce moderate-framed, and thus more efficient, females for nutritionally limited environments.

THI effects on puberty

The impacts of heat stress on fertility traits in beef cattle managed under extensive environments, such as those in tropical Australia, are not well understood. A wealth of information exists for this issue in dairy cattle and for non-reproductive feedlot cattle, but analysis of commercial female herds in extensive environments has been less common (Gilad et al., 1993; Beatty et al., 2006; Brown-Brandl et al., 2006; Ferguson et al., 2006). In this study, a THI of 79 was used, as this figure was widely accepted as the threshold to severe heat stress in cattle (Moran, 2005; McGowan et al., 2014).

Although we uncovered evidence of a negative relationship between chronic heat load and puberty (AUC and number of days over THI 65 and 70), surprisingly, a non-negative relationship ($P < 0.05$) between acute heat stress and puberty was found. In this study, puberty was defined via detection of the CL, its presence indicated that the heifer was currently within the estrus cycle or had completed this cycle at least once (Senger, 1997). The hormones produced by the structures of the reproductive tract during estrus are subject to interference under high heat stress conditions. Heat stress suppresses the secretion follicle stimulating hormone from the pituitary gland, slowing the reproductive cycle (Torres-Júnior et al., 2008; Krishnan et al., 2017). The onset of puberty itself has been shown to be delayed due to heat stress meaning that heat stress will negatively impact the reproductive cyclicity of pubertal and nonpubertal animals (Vincent, 1972; Krishnan et al., 2017). Given this, the surprising lack of significant relationship between acute heat stress and puberty may be due to the modeling of THI. The THI descriptors were the same for all animals within a contemporary group, meaning the effect of THI was partially nested. Additionally, the summer months in which animals would have been exposed to acute heat stress coincides with the wet season in tropical production systems and thus peak nutritional availability. It is possible that the opposing effects of increased pasture quality and the increased likelihood of acute heat stress are confounding the interpretation of these results. Our results suggests that cumulative, sustained heat load is detrimental to puberty attainment. We speculate that the high level of sustained heat load in the tropics could mean that acute heat stress events do not have the same impact as they would in temperate climates with temperate breeds.

THI effects on first and second pregnancy

Our results for first pregnancy indicated that significant and negative relationships were only found for sustained heat load. This was similar to the effect of THI on puberty. We also found acute heat stress (days over 79) was not significant for second pregnancy outcome, although chronic heat load was significant and the relationship was universally negative, regardless of significance. The lack of a definitive relationship between acute heat stress and pregnancy does not agree with the physiological impacts found in literature. This result, similarly found in the puberty results, may be partially explained by a large number of contemporary groups within the analysis having 0 d above the 79 threshold in the defined time period. This potential sampling problem was compensated for by modeling a number of different thresholds.

Heat stress has well-recognized effects on the survival of fertilized embryos as well as direct impacts on the estrus cycle. The effect of heat stress on the estrus cycle without fertilization of the oocyte was examined by Gilad et al. (1993) in Holstein cows. Seasonal (chronic) and acute heat stress during estrus were both found to reduce the secretion of follicular stimulating hormone and luteinizing hormone, thus slow the estrus cycle, potentially delaying pregnancy (Gilad et al., 1993). Numerous, small-scale trials involving dairy cattle have described similar suppression of embryonic survival, interference with the estrus cycle and reduced fertility rates (Roth et al., 2000; Jordan, 2003; West, 2003; Nguyen et al., 2016).

Torres-Júnior et al. (2008) conducted trials on tropically adapted Gir in Brazil, a breed and environment closer to our study, and determined that exposure to heat stress had a delayed effect on oocyte viability and suppressed the recruitment of a dominant follicle during the follicular phase. Krishnan et al. (2017) concluded that *B. indicus* animals displayed better oocyte resilience under heat stress conditions compared to *B. taurus*, this suggests that the lack of a significant relationship between acute heat stress and pregnancy may be partially due to the widespread use of *B. indicus* cattle within the study. This effect was previously noted by Turner (1982) who found that *B. taurus* females, particularly those lactating, had diminished fertility outcomes when displaying elevated rectal temperatures. Conversely, the fertility of *B. indicus* females was less affected and no significant difference in fertility outcome was observed between "wet" and "dry" cows (Turner, 1982). This affect was observed within our results as the magnitude and direction of the relationship between heat stress/load was not significantly different between PD1 (nonlactating) and PD2 (lactating) cows.

The lack of a significant relationship between heat stress and fertility outcome in this study was partially echoed by results from McGowan et al. (2014) who found that in the most marginal environments, exposure to greater than or less than 2 weeks of days over 79 made no difference to calf survival. Whilst a different reproductive trait, the result from McGowan et al. (2014), in conjunction with our results suggests that acute heat stress events may be less impactful than expected on breeding females in Northern Australia. In addition to the potential acclimatization of animals to their environment, we speculate that the influence of a distinctive wet season, peak nutrition, and peak THI occurring at the same time is partially confounding the analysis, although this is difficult to determine. Chronic heat load appears to be a more suitable environmental gradient, with greater exposure to cummulative heat load significantly affecting pregnancy.

CONCLUSION

Heifers that were pubertal at approximately 600 d of age had improved chances of being pregnant at both first and second pregnancy examinations. This shows the value of selecting for heifers that are early maturing. Heifers that are pubertal at the start of the joining period increase their chances to become pregnant early in the joining period which in turn increases the time available after parturition to re-conceive. Acute heat stress was found to have no significant impact upon reproductive performance, either expression of puberty or successful pregnancy. However, descriptors based on THI used to measure chronic heat load were found to have negative, significant relationships to heifer puberty, first pregnancy and second pregnancy rates. The use of environmental descriptors based upon rainfall produced unsignificant results, suggesting that the use of rainfall, as a surrogate for nutrition, requires additional refinement, outside of the scope of this study. Increased ADWG, modeled as an outcome of nutritional environment, was linked to improved pregnancy rates at PD1 and PD2. The descriptors based upon ADWG and chronic heat load satisfied the primary objective of the study, to define an environmental gradient based on these descriptors. Defining the relationships between these descriptors and reproductive outcomes forms the basis for future work modeling genotype by environment interactions in northern Australia.

Supplementary Data

Supplementary data are available at *Translational Animal Science* online.

Acknowledgments

Meat and Livestock Australia (MLA) provided funding for the Northern Genomics Project, P.PSH.P0833, the source of all phenotypic data for this project. The authors would like to acknowledge the collaborating producers from the Northern Genomics project for agreeing to participate and continuing to provide data. They would also like to acknowledge the Hayes Group within the Queensland Alliance for Agriculture and Food Innovation—Centre for Animal Science for their support and guidance.

Conflict of interest statement

None declared.

LITERATURE CITED

Archbold, H., L. Shalloo, E. Kennedy, K. Pierce, and F. Buckley. 2012. Influence of age, body weight and body condition score before mating start date on the pubertal rate of maiden Holstein–Friesian heifers and implications for subsequent cow performance and profitability. *Anim.* 6:1143–1151. doi:10.1017/S1751731111002692.

Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES). 2020. *Farm survey data for the beef, slaughter lambs and sheep industries.* https://www.agriculture.gov.au/abares/research-topics/surveys/farm-survey-data [accessed September 28 2021].

Beatty, D., A. Barnes, E. Taylor, D. Pethick, M. McCarthy, and S. Maloney. 2006. Physiological responses of *Bos taurus* and *Bos indicus* cattle to prolonged, continuous heat and humidity. *J. Anim. Sci.* 84:972–985. doi: 10.2527/2006.844972x.

Boligon, A. A., and L. G. Albuquerque. 2011. Genetic parameters and relationships of heifer pregnancy and age at first calving with weight gain, yearling and mature weight in Nelore cattle. *Livest. Sci.* 141:12–16. doi:10.1016/j.livsci.2011.04.009.

Bowen, M., F. Chudleigh, S. Buck, and K. Hopkins. 2018. Productivity and profitability of forage options for beef production in the subtropics of northern Australia. *Anim. Prod. Sci.* 58:332–342. doi:10.1071/AN16180.

Brown-Brandl, T. M., R. A. Eigenberg, and J. A. Nienaber. 2006. Heat stress risk factors of feedlot heifers. *Livest. Sci.* 105:57–68. doi:10.1016/j.livsci.2006.04.025.

Burns, B. M., G. Fordyce, and R. G. Holroyd. 2010. A review of factors that impact on the capacity of beef cattle females to conceive, maintain a pregnancy and wean a calf-Implications for reproductive efficiency in northern Australia. *Anim. Reprod. Sci.* 122:1–22. doi:10.1016/j.anireprosci.2010.04.010.

Burns, B., T. Tierney, T. Rudder, C. Esdale, C. Howitt, and P. O'Rourke. 1992. Productivity of Hereford, highgrade Simmental and Belmont Red beef herds in central Queensland. 1. Pregnancy, calving and weaning rates. *Aust. J. Exp. Agric.* 32:551–557. doi: 10.1071/EA9920551

Burrow, H. M. 2001. Variances and covariances between productive and adaptive traits and temperament in a composite breed of tropical beef cattle. *Livest. Prod. Sci.* 70:213–233. doi:10.1016/S0301-6226(01)00178-6.

Burrow, H. M. 2012. Importance of adaptation and genotype × environment interactions in tropical beef breeding systems. *Animal.* 6:729–740. doi:10.1017/S175173111200002X.

Corbet, N., J. Allen, A. Laing, G. Fordyce, M. McGowan, and B. M. Burns. 2018. Using ultrasound to derive new reproductive traits in tropical beef breeds: implications for genetic evaluation. *Anim. Prod. Sci.* 58:1735–1742. doi:10.1071/AN16616.

Day, M. L., and G. P. Nogueira. 2013. Management of age at puberty in beef heifers to optimize efficiency of beef production. *Anim Front.* 3:6–11. doi:10.2527/af.2013-0027.

D'Occhio, M. J., P. S. Baruselli, and G. Campanile. 2019. Influence of nutrition, body condition, and metabolic status on reproduction in female beef cattle: A review. *Theriogenology.* 125:277–284. doi:10.1016/j.theriogenology.2018.11.010.

Engle, B. N., N. J. Corbet, J. M. Allen, A. R. Laing, G. Fordyce, M. R. McGowan, B. M. Burns, R. E. Lyons, and B. J. Hayes. 2018. Multivariate genomic predictions for age at puberty in tropically adapted beef heifers. *J. Anim. Sci.* 97:90–100. doi:10.1093/jas/sky428.

Entwhistle, K. W. 1983. Factors influencing reproduction in beef cattle in Australia. *Aust. Meat Res. Committ. Rev.* 43:30.

Falconer, D. S. 1990. Selection in different environments: effects on environmental sensitivity (reaction norm) and on mean performance. *Genet. Res.* 56:57–70. doi:10.1017/S0016672300028883.

Ferguson, D., D. Johnston, H. Burrow, and A. Reverter. 2006. Relationships between temperament, feedlot performance and beef quality. In: *Australian Beef–the Leader! The impact of science on the beef industry,* Beef CRC, Armidale, NSW, Australia. p. 161–165.

Fordyce, G., and K. Chandra. 2016. Growth of Brahman cross heifers to 2 years of age in the dry tropics. *Anim. Prod. Sci.* 59:148–159. doi:10.1071/AN20342.

Fordyce, G., R.Tyler, and V. J. Anderson. 1990. Effect of reproductive status, body condition and age of *Bos indicus* cross cows early in a drought on survival and subsequent reproductive performance. *Anim. Prod. Sci.* 30:315–322. doi:10.1071/EA9900315.

Fortes, M. R. S., S. A. Lehnert, S. Bolormaa, C. Reich, G. Fordyce, N. J. Corbet, V. Whan, R. J. Hawken, and A. Reverter. 2012. Finding genes for economically important traits: Brahman cattle puberty. *Anim. Prod. Sci.* 52:143–150. doi:10.1071/AN11165.

Freitas, G. R., N. A. Hurtado-Lugo, D. J. de Abreu dos Santos, R. R. Aspilcueta Borquis, N. T. Pegolo, H. Tonhati, and F. R. de Araújo Neto. 2019. Genotype–environment interaction for age at first calving in buffaloes, using the reaction norm model. *J. Repro. Domes. Anim.* 54:727–732. doi: 10.1111/rda.13414

Fulkerson, W., and K. Slack. 1993. Estimating mass of temperate and tropical pastures in the subtropics. *Aust. J. Exper. Agri.* 33:865–869. doi:10.1071/EA9930865

Gilad, E., R. Meidan, A. Berman, Y. Graber, and D. J. R. Wolfenson. 1993. Effect of heat stress on tonic and GnRH-induced gonadotrophin secretion in relation to concentration of oestradiol in plasma of cyclic cows. *J. Repro. Fert.* 99:315–321. doi:10.1530/jrf.0.0990315.

Harburg, S., I. McLean, and B. J. Hayes. 2020. *Economic consequences of selection for cow fertility in northern Australian beef herds*. Bush Agribusiness, Queensland Alliance for Agriculture and Food Innovation. https://www.bushagri.com.au/wp-content/uploads/2020/09/QAAFI-Final-Report-v-2020.pdf [accessed September 28 2021].

Hayes, B. 2022. Accelerating genetic gain for productivity and profitability in Northern beef cattle with genomic technologies. Final Report, Project P.PSH.0833, Meat and Livestock Australia, Sydney.

Hayes, B., G. Fordyce, and S. Landmark. 2019. Genomic predictions for fertility traits in tropical beef cattle from a multi-breed, crossbred and composite reference population. In: Proceedings of the 23rd Conference of the Association for the Advancement of Animal Breeding and Genetics (AAABG). Armidale, New South Wales, Australia, 27th October-1st November 2019. p 282–285.

Henderson, A. W. K., and J. D. Kelly. 1978. Helminth parasites of beef cattle in the East Kimberley and Victoria River Districts of Northern Australia. *Trop. Anim. Health Prod.* 10: 63–73. doi:10.1007/BF02235308

Holroyd, R., T. James, V. Doogan, G. Fordyce, R. Tyler, and P. O'Rourke. 1990. The performance of Brahman-Shorthorn and Sahiwal-Shorthorn beef cattle in the dry tropics of northern Queensland. 2. Reproductive rates and liveweights of F_2et seq. females. *Aust. J. Exper. Agri.* 30:727–733. doi:10.1071/EA9900727

Johnston, D., S. Barwick, N. Corbet, G. Fordyce, R. Holroyd, P. J. Williams, and H. M. Burrow. 2009. Genetics of heifer puberty in two tropical beef genotypes in northern Australia and associations with heifer-and steer-production traits. *Anim. Prod. Sci.* 49:399–412. doi:10.1071/EA08276.

Johnston, D., S. Barwick, G. Fordyce, R. Holroyd, P. Williams, N. Corbet, and T. Grant. 2014. Genetics of early and lifetime annual reproductive performance in cows of two tropical beef genotypes in northern Australia. *Anim. Prod. Sci.* 54:1–15. doi:10.1071/AN13043.

Jordan, E. R. 2003. Effects of heat stress on reproduction. *J. Dairy. Sci.* 86:104–114. doi:10.3168/jds.S0022-0302(03)74043-0.

Kinder, J. E., E. G. Bergfield, M. E. Wehrman, K. E. Peters, and F. N. Kojima. 1994. Endocrine basis for puberty in heifers and ewes. *J. Repro. Fert.* 49:393–407. Pubmed ID: 7623330.

Krishnan, G., M. Bagath, P. Pragna, M. K. Vidya, J. Aleena, P. R. Archana, V. Sejian, and R. J. T. Bhatta. 2017. Mitigation of the heat stress impact in livestock reproduction. *Theriogenology*. 8:8–9. doi:10.5772/INTECHOPEN.69091.

Martin. L. C., J. S. Brinks, R. M. Bourdon and L. V. Cundiff. 1992. Genetic effects on beef heifer puberty and subsequent reproduction. *J. Anim. Sci.* 70:4006–4017. doi:10.2527/1992.70124006x

McCosker, K. D., N. R. Perkins, G. Fordyce, P. K. O'Rourke, and M. R. McGowan. 2021. Reproductive performance of northern Australia beef herds. 4. Factors influencing the likelihood of lactating cows becoming pregnant within four months of calving. *Anim. Prod. Sci.* 61. doi:10.1071/AN17502.

McGowan, M., K. McCosker, G. Fordyce, D. Smith, P. O'Rourke, N. Perkins, T. Barnes, L. Marquet, J. Morton, and T. Newsome. 2014. North Australian beef fertility project: Cash Cow. Final Report, Project B. NBP. 0382, Meat and Livestock Australia, Sydney.

McLean, I., P. Holmes, and D. Counsell. 2014. *The Northern beef report: 2013 Northern beef situation analysis*. Project B.COM.0348. North Sydney, Australia: Meat & Livestock Australia Limited.

McLean, R., R. McCown, D. Little, W. Winter, and R. A. Dance; Cambridge. 1983. An analysis of cattle live-weight changes on tropical grass pasture during the dry and early wet seasons in northern Australia. *J. Agric. Sci.* 101:17–24. doi:10.1017/S0021859600036315.

MLA. 2015. *Beef cattle nutrition: an introduction to the essentials*. Sydney, Australia: Meat & Livestock Australia.

Moran, J. 2005. *Tropical dairy farming: feeding management for small holder dairy farmers in the humid tropics*. Collingwood, Vic: Csiro publishing.

Mota, L., G. Fernandes, Jr, A. Herrera, D. Scalez, R. Espigolan, A. Magalhães, R. Carvalheiro, F. Baldi, and L. J. A. G. Albuquerque. 2020. Genomic reaction norm models exploiting genotype× environment interaction on sexual precocity indicator traits in Nellore cattle. *Anim. Genet.* 51:210–223. doi:10.1111/age.12902.

Mulder, H. A. 2016. Genomic selection improves response to selection in resilience by exploiting genotype by environment interactions. *Front. Genet.* 7:178. doi:10.3389/fgene.2016.00178.

Nguyen, T. T., P. J. Bowman, M. Haile-Mariam, J. E. Pryce, and B. J. Hayes. 2016. Genomic selection for tolerance to heat stress in Australian dairy cattle. *J. Dairy. Sci.* 99:2849–2862. doi:10.3168/jds.2015-9685

Nogueira, G. P. 2004. Puberty in South American Bos indicus (Zebu) cattle. *Anim. Repro. Sci.* 82–83:361–372. doi:10.1016/j.anireprosci.2004.04.007.

O'Rourke, P., V. Doogan, D. Robertson, and D. Cooke. 1991. Prediction of conception rate in extensive beef herds in north-western Australia. 2. Continuous mating and minimal management. *Aust. J. Exper. Agr.* 31:9–14. doi:10.1071/EA9910009.

O'Rourke, P., G. Fordyce, R. Holroyd, and I. Loxton. 1995. Mortality, wastage, and lifetime productivity of *Bos indicus* cows under extensive grazing in northern Australia. 1. Seasonal mating in the speargrass region. *Aus. J. Exper. Agric.* 35:285–295. doi:10.1071/EA9950285.

Petersson, K. J., B. Berglund, E. Strandberg, H. Gustafsson, A. P. Flint, J. A. Woolliams, and M. D. Royal. 2007. Genetic analysis of postpartum measures of luteal activity in dairy cows. *J. Dairy. Sci.* 90:427–434. doi:10.3168/jds.S0022-0302(07)72644-9

Pierson, R. A., and O. J. Ginther. 1988. Ultrasonic imaging of the ovaries and uterus in cattle. *Theriogenology* 29:21–37. doi:10.1016/0093-691X(88)90029-5.

Poppi, Dennis, P., Simon P. Quigley, Tiago Alves Corrêa Carvalho da Silva, and Stuart R. McLennan. 2018. Challenges of beef cattle production from tropical pastures. *R. Bras. Zootec.* 47: 12–21. doi: 10.1590/rbz4720160419

Pryce, J. E., M. P. Coffey, and G. Simm. 2001. The relationship between body condition score and reproductive performance. *J. Dairy. Sci.* 84:1508–1515. doi: 10.3168/jds.S0022-0302(01)70184-1

Queensland Government. FORAGE Reports, https://www.longpaddock.qld.gov.au/, viewed 28/09/2021.

Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, D. Firth, and M. B. Ripley. 2013. Package 'mass'. *Cran. Reposit.* 538:113–120.

Rodrigues, H. D., J. E. Kinder, and L. A. Fitzpatrick. 2002. Estradiol regulation of luteinizing hormone secretion in heifers of two breed types that reach puberty at different ages. *Bio. Repro.* 66:603–609. doi:10.1095/biolreprod66.3.603.

Rodríguez, R. O. L., and C. V. M. Segura. 1995. Effect of once-daily suckling on postpartum reproduction in zebu-cross cows in the tropics. *Anim. Repro. Sci.* 40:1–5. doi:10.1016/0378-4320(95)01417-X.

Roth, Z., R. Meidan, R. Braw-Tal, and D. Wolfenson. 2000. Immediate and delayed effects of heat stress on follicular development and its association with plasma FSH and inhibin concentration in cows. *J. Repro. Fert*. 120:83–90. doi:10.1530/rep.0.1210745.

Russell, L., S. Henrik, L. Jonathon, B. Paul, and H. Maxime. 2018. Estimated marginal means, aka least-squares means. *Amer. Statis*. 34:216–221. doi:10.1080/00031305.1980.10483031.

Scaramuzzi, R. J., B. K. Campbell, J. A. Downing, N. R. Kendall, M. Khalid, M. Muñoz-Gutiérrez, and A. Somchit. 2006. A review of the effects of supplementary nutrition in the ewe on the concentrations of reproductive and metabolic hormones and the mechanisms that regulate folliculogenesis and ovulation rate. *Reprod. Nutr. Dev*. 46:339–354. doi:10.1051/rnd:2006016.

Schatz, T. J., and M. N. Hearnden. 2008. Heifer fertility on commercial cattle properties in the Northern Territory. *Aus. J. Exper. Agr*. 48:940–944. doi:10.1071/EA08057.

Schatz, T., and I. J. Partridge. 2012. *Heifer management in northern beef herds*. North Sydney: Meat and Livestock Australia.

Schillo, K. K., J. B. Hall, and S. M. Hileman. 1992. Effects of nutrition and season on the onset of puberty in the beef heifer. *J. Anim. Sci*. 70:3994–4005. doi:10.2527/1992.70123994x

Senger, P. L. 1997. *Pathways to pregnancy and parturition*. Redmond: Current Conceptions, Inc.,.

Sparks, A. H. 2018. nasapower: a NASA POWER global meteorology, surface solar energy and climatology data client for R. *J. Open. Source. Software*. 3:30. doi:10.21105/joss.01035

Sullivan, R. M., P. K. O'Rourke, and J. A. Neale. 1997. A comparison of once- and twice-yearly weaning of an extensive herd in northern Australia. *Aus. J. Exper. Agric*. 37:287–293. doi:10.1071/EA95098.

Torres-Júnior, J. R. S., M. F. A. Pires, W. F. de Sá, A. M. Ferreira, J. H. M. Viana, L. S. A. Camargo, A. A. Ramos, I. M. Folhadella, J. Polisseni, C. de Freitas, et al. 2008. Effect of maternal heat-stress on follicular growth and oocyte competence in *Bos indicus* cattle. *Theriogenology*. 69:155–166. doi:10.1016/j.theriogenology.2007.06.023.

Turner, H. 1982. Genetic variation of rectal temperature in cows and its relationship to fertility. *Anim. Sci*. 35:401–412. doi:10.1017/S0003356100001094.

Vincent, C. K. 1972. Effects of season and high environmental temperature on fertility in cattle. *J. Am. Veter. Med. Ass*. 161:1333–1338. PubMed ID: 4565065.

West, J. W. 2003. Effects of heat-stress on production in dairy cattle. *J. Dairy. Sci*. 86:2131–2144. doi:10.3168/jds.S0022-0302(03)73803-X

Wijffels, G., J. Gaughan, D. Revell, and P. Allingham. 2013. *Heat Stress Nutrition: A comprehensive review and R&D progra*. Sydney: Meat and Livestock Australia Limited.

Yang, J., S. H. Lee, M. E. Goddard, and P. M. Visscher. 2011. GCTA: A tool for genome-wide complex trait analysis. *Am. J. Hum. Gen*. 88:76–82. doi:10.1016/j.ajhg.2010.11.011