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Defining the primary business measure of liveweight production for beef cows in northern Australia

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Abstract

Context. Annual liveweight production of a cow is the sum of the weight of its calf at weaning and its own annual liveweight change. Along with value per kg, annual liveweight production constitutes the business income contributed by the animal; however, it is not well described for north Australian beef herds.

Aims. This study aimed to quantify cow liveweight production and to measure impacts of reproduction and other risk factors.

Methods. Liveweight production data from 2122 Brahman and tropically adapted composite cows aged 2.5–8.5 years and grazing the four primary country types in northern Australia were analysed as a function of current and previous mating outcomes, mating age, breed, hip height, and body condition or liveweight.

Key results. Cow liveweight production was highly variable (coefficient of variation 40%) among and within years. Liveweight production of cows averaged 154 kg/year from their first mating, 168 kg/year from their second, and 190 kg/year from subsequent matings; however, production efficiency remained constant, with a liveweight production ratio of 0.31–0.32 kg produced annually per kg of grazing animal. Within environment, average weaner production (kg/cow) approximated the estimated average annual weight gain of yearling cattle. Weight of calves weaned contributed ~87% of annual liveweight production. Liveweight production averaged 103–143 kg higher for cows that weaned a calf than those that lost a calf, with the effect greater in older cows ($P < 0.001$). Liveweight production averaged 39–43 kg higher for non-pregnant cows than those that lost a calf ($P < 0.001$). These effects were attenuated by ~20% over a lifetime. Cows weaning a calf from a previous mating had liveweight production 57–85 kg higher ($P < 0.001$) than those not weaning a calf, having begun the year in poorer condition because of lactation. Calf weaning weight was 25 kg higher in mature cows than in first- and second-lactation cows. Liveweight production advantages of tropical composites over Brahmans appeared primarily associated with consistently higher calf weaning weights, and higher cow growth during their first reproductive year.

Conclusions. This research successfully demonstrated the concept of liveweight production in breeding beef cows, showing it to be primarily governed by available nutrition and mating outcome.

Implications. These findings provide a previously unavailable reference point for beef-systems management in northern Australia; for example, liveweight production could be used to determine the potential achievable increases in cow performance for a specific nutritional environment.

Keywords: body condition score, Brahman cross, calf loss, non-pregnancy, production, reproduction, tropical cattle, tropical pasture.

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Introduction

Liveweight production of a cow is the sum of the weight of its calf at weaning and its own liveweight change (Walmsley *et al*. 2018). Liveweight production is a measure over an annual period, with the interface between years occurring after the last annual weaning and before the main calving period, and typically concurs with opening–closing on livestock schedules, although not necessarily those maintained for taxation purposes. Cows that survive to slaughter after entry to the breeding herd as heifers will usually gain weight similar to typical calf weaning weight; for example, a heifer is first mated at 300 kg and slaughtered at a mature weight of 500 kg after weaning 200-kg calves. Cows that die are a major loss of liveweight production, usually equivalent to three times the weight of a typical weaner.

Liveweight production is a primary index of beef breeding herds because it is the major driver of business income; liveweight is the commodity sold. Considered against feed intake, liveweight production is also indicative of production efficiency (Walmsley *et al*. 2018). Feed intake by cattle grazing heterogeneous pastures over large areas is almost impossible to measure with available technology. However, when average liveweight of an animal over a year is used as a broad indicator of feed intake, then the ratio of liveweight production to average grazing liveweight, called a liveweight production ratio, is a practical, indirect measure of production efficiency at a herd or individual animal level. For example, if a group of cattle with an average total weight of 100 t graze an area over 1 year and net liveweight harvested from the group is 30 t, the liveweight production ratio is 0.3.

Beef systems in northern Australia, most of which is a dry tropical environment, are predominately extensively managed with *Bos indicus*, *Bos taurus* and composite cattle as described by McGowan *et al*. (2014). Median number of breeding female cattle per herd is 1200, ranging from <100 to almost 50 000. Median paddock size is <1000 ha and can be >50 000 ha. In at least one-third of businesses, bull access to female cattle is not controlled. Despite the importance of production measures for cow herds, published data have been very limited until recently on liveweight production of beef cows in northern Australia, and it is very rare for a north Australian beef producer to have an understanding of liveweight production of breeding herds per cow, land unit or business. When production is considered, usually measures of performance such as weaning rate are presented instead, for example, in an overview of the northe Australian beef industry (McLean *et al*. 2014). Well-managed continuously mated Brahman-cross cows in the lowly productive, Northern forest region in which yearlings gain an average of 100–105 kg/year (McLennan 2014; Fordyce and Chandra 2017) produced 132–214 kg annually at 16–51 kg/ha, depending on stocking rate and year (Smith *et al*. 2001). McGowan *et al*. (2014) reported very large variation in annual liveweight production per cow in north Australian commercial beef herds (Fig. 1), with large effects of country type and year. Their univariate regression analyses using group-level data indicated that no single herd-performance measure accurately predicts production per cow. The prevailing production variation was highlighted in a report on global beef systems (Behrendt and Weeks 2017), which cited the low production of north Australian cow herds and its potential for improvement. The primary limitations to production were considered to be associated with nutrition and genetics.

A full breeding cycle extends from when mating commences in one year to weaning in the next, which may be ≥18 months. The overlap of breeding cycles between years makes performance measurement quite problematic and fosters multiple definitions for some measures. This is further complicated in northern Australia where continuous mating and multiple weaning times are practised. In practice, breeding herds are often reformed after mating (if controlled) and multiple weaning times, and before the major calving period each year, typically around the time of annual pregnancy diagnoses if these are conducted. Therefore, it is much easier to consider performance and production from last weaning or pregnancy diagnoses in one year to the same time in the following year. The primary performance measures are cow survival, growth and becoming pregnant, and the survival and growth to weaning of the calf. This approach renders the often-quoted classical measure of weaning rate almost irrelevant. The ability to calculate weaning rates in most north Australian commercial beef businesses is usually impossible unless pregnancy rates and loss of pregnancies before weaning are known; the authors' experience is that in northern Australia, only a very small proportion collect this information.

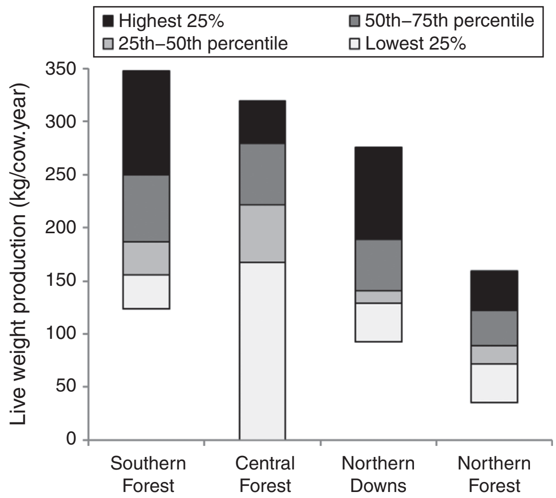

Fig. 1. Distribution of annual liveweight production per cow across the major country types of northern Australia (McGowan *et al*. 2014).

Two components of herd liveweight production are weaner production, which is reported as weight of weaned calves/ number of cows mated (Arthur *et al*. 2005), and annual cow liveweight change (Walmsley *et al*. 2018). Weaner production as reported by Arthur *et al*. (2005) cannot be calculated without weaning rate, which, as previously explained, is rarely known in northern Australia. The usual measure available is lactation rate, which is the number of calves weaned/number of cows retained for breeding after the weaning the previous year; calves weaned can be measured by number of lactating cows. Therefore, for the situation in northern Australia, herd weaner production is the product of average weaner weight and lactation rate.

Achievable levels of liveweight production for northern Australian beef cows in specific situations are poorly understood because of the paucity of data and limited understanding of associated risk factors. The data of McGowan *et al*. (2014) provided a guide, suggesting that the 75th percentile for herds within a country type (Fig. 1) was achievable; but more importantly, they demonstrated equivalence on average between weaner production and annual weight gain of yearling steers within the same situation, thus providing evidence that productivity is limited by available feed and management within a specific situation. It follows that strategies aiming to increase one performance trait in the absence of enhanced nutrition may diminish other performance; for example, if average weight of weaners is increased, lactation rate may be reduced, most likely through poorer body condition of cows, with overall weaner production (i.e. weight of weaned calves / cows retained after mating the previous year) potentially remaining similar or in some cases being lower.

In order to define the opportunity to improve liveweight production from breeding cattle in northern Australia, an understanding is needed of what regulates it, as well as the variation that exists at an individual animal and management-group level. Of particular importance is the impact of reproductive performance on production because weaner weight is expected to be the primary contributor to liveweight production. An existing dataset derived from detailed monitoring of >2000 tropically adapted cows between birth and 8.5 years of age provided an ideal platform for investigation.

Method

The methods used to generate the data have previously been described in detail (Barwick *et al*. 2009; Johnston *et al*. 2014) and are presented briefly here.

Ethics approval

Conduct of the research generating the data was approved for 1999–2006 and 2006–10 by the JM Rendel Laboratory Animal Experimental Ethics Committee (CSIRO, Rockhampton, Qld) as approvals TBC107 and RH225-06, respectively.

Animals, their management and the environment

Female Brahman and tropical composite cattle (n = 2181) in four year-groups were allocated and transported as required from eight sites as newly weaned calves to four sites (excludes Brigalow) across Queensland (Tables 1 and 2), within each of the four primary country types used for breeding cattle in northern Australia as described by McGowan *et al*. (2014). The tropical composite cattle averaged 28% Brahman (*Bos indicus*), 21% British *Bos taurus*, 5% European *Bos taurus* and 46% tropically adapted African *Bos taurus*; however, there was substantial variation in composition.

Cattle growth in this region is usually high in the hot, moist period (commencing with the start of the storm season, usually between September and January and on average in December), reducing to maintenance in the cooler dry period (June–August), and progressing to weight loss in the hot, dry period. However, at sites with fertile soils and low relative humidity (therefore reducing the rate of microbial-assisted breakdown of senesced pasture), such as at Toorak, pastures retain their nutritive value for much longer and high cattle growth may continue for much of the year, even after extended periods without rainfall.

The animals were managed within age groups to 2.5 years of age, from which time they were managed within one or two genotype groups within site. Drought conditions caused one Toorak tropical-composite management group to be transferred to a fifth site for 18 months; it was replaced by a Brian Pastures tropical-composite management group for 1 year for the same reason (Table 2). Annual multiple-sire mating with three or four fertile bulls of the same genotype per 100 females was for 12 weeks and first calving for each group

Table 1. Sites where the cattle were located between weaning and 8.5 years of age

RH, Average relative humidity at 09:00. Brigalow is the common name for the predominant tree species *Acacia harpophylla*

	Av. temp. (°C) Max.	Av. temp. (°C) Min.	Median rainfall (mm)	RH (%)	Soils	Vegetation
			Swan's Lagoon: 20.0°S, 147.3°E; Northern Forest			
Dec.–Apr.	32	21	498	72	Low-fertility duplex soils that are mostly P-deficient	Open eucalypt savannah woodland with a native pasture predominated by black spear, Indian couch, and golden beard grasses
May–Aug.	27	12	55	70		
Sept.–Nov.	32	17	45	60		
			Toorak 21.0°S, 141.8°E; Northern Downs			
Dec.–Apr.	36	21	256	59	Fertile brown and grey cracking clays	Mitchell and Flinders grass on treeless downs
May–Aug.	28	10	3	52		
Sept.–Nov.	36	17	21	41		
			Belmont: 23.4°S, 150.5°E; Central Forest			
Dec.–Apr.	31	21	360	70	A mix of fertile clays, sandy loams, podsols, and alluvial flats	Black spear and blue grasses predominate with sown stylos and other grasses and legumes
May–Aug.	24	11	88	71		
Sept.–Nov.	29	17	115	63		
			Brian Pastures: 25.7°S, 151.8°E; Southern Forest			
Dec.–Apr.	31	19	351	66	A mix of hills and alluvial flats	Mostly cleared forest predominated by black spear and wire grasses on hills, and blue grasses oversown with buffel, Rhodes and green panic grasses on flats
May–Aug.	23	9	96	69		
Sept.–Nov.	29	15	156	59		
			Brigalow: 24.8°S, 149.8°E; Central Forest			
Dec.–Apr.	32	19	300	65	A mix of clays, loams and alluvial duplex soils of moderate fertility	Cleared brigalow with native blue grasses and sown buffel, Rhodes and green panic grasses
May–Aug.	23	8	101	66		
Sept.–Nov.	30	14	144	59		

Table 2. Numbers of cattle used at each location

Site	Birth year	Brahman	Tropical composite	
Belmont	1999–00	73		
	2000–01	111	113	
	2001–02	119	140	
	2002–03	124	48	
Brian Pastures	2000–01		146	65% to Brigalow: 07 Apr.–08 May
	2001–02		272	58% to Brigalow: 07 Apr.–08 May
	2002–03		79	
Swan's Lagoon	2000–01	188		
	2001–02	219		
	2002–03	42		
Toorak	2000–01	65	160	43% to Brigalow: 05 Sept.–07 Mar.
	2001–02	98	184	50% to Brigalow: 05 Sept.–07 Mar.

was at ~3 years of age; an exception was at Belmont where sires of the opposite genotype were used in matings in 2005–06 onwards. Calves were weaned on average 8 weeks after the end of mating each year. Breeding females were retained to 8.5 years of age unless they died, failed to wean a calf in two consecutive years, or developed significant physical or behavioural problems.

Measurements

After relocation at weaning to each site, the cattle were mustered thereafter each 4–8 weeks for ultrasound examination of the reproductive tract, weighing and body condition scoring (1–5 scale; Gaden 2005). Every 6 months, height at the peak of the sacrum of each animal was measured. Early-stage pregnancies were aged using linear-array real-time ultrasound with 5–10 MHz rectal probes. Maintenance of pregnancy was checked at each muster before the start of calving. Calves were weighed and tagged at birth when dams were identified and then weighed at weaning at an average of 6 months. Dates of all cow and calf mortalities were recorded.

Data management

Cow liveweight at the previous weaning muster was transformed to a categorical variable by quartiling observations; that is, all observations within each of the 12 breed × age cohorts were split into four approximately equal categories. Exploratory analyses of hip height showed a moderate amount of variability in the measure over time that was not due to cow growth. Therefore, rather than a single measure recorded at the previous weaning, median hip height was quartiled as for liveweight, using data from the previous breeding year. Body condition score at the previous weaning was transformed to a five-category variable: $\leq$2, 2.3 or 2.6, 3, 3.3 or 3.6, and $\geq$4. For the first mating, only five heifers had a body condition score $\leq$2, and so the lower two categories were combined at $\leq$2.6

Only data for mated cows with a complete dataset for production indices (liveweight production, cow liveweight change, weaner weight) were included: 11 181 mating outcomes from 2122 cows. All production indices were recorded as missing when the mating outcome was cow loss. The outcome of each cow's current and previous mating from the first to sixth was defined as being non-pregnant, weaned a calf, or lost a calf. The latter refers to losses during pregnancy and lactation, a majority of which occurs in the first 2 weeks after calving (Bunter *et al*. 2013). Previous mating outcome was not applicable to the first mating. Weaner weight was set to 0 when the mating outcome was 'no fetus' or 'cow loss'. Combined weights of twins (0.1% of mating outcomes) were used for weaner weight. In the rare case where one cow lost a calf and raised another, the mating outcomes for cows rearing and not rearing the calf (DNA parentage verification) were set to 'wean' and 'calf loss', respectively.

Liveweight production was calculated for each cow by using annual date of weaning for the cohort as the start and end points; this was approximately April–May in each year. Liveweight production is the sum of weaner weight and the change in cow liveweight over the year, with each of these being used as a dependent variable.

For calculation of liveweight production ratios, average liveweight of a group of cows over a year (the denominator) was determined by using the only consistent data available, which were start and end weights of cows and calves, and calves' birth dates and weights, as:

$$(\mathrm{We} + \mathrm{Ws})/2 + \mathrm{LR} \times (\mathrm{Cbw} \times \mathrm{Aw}/12 + \mathrm{Wp}),$$

where We is average liveweight of cows at end of year (kg), Ws is average liveweight of cows at start of year (kg), LR is lactation rate (ratio), Cbw is average weight of calves between birth and weaning (kg), Aw is average age of calves at weaning (months), and Wp is average extra liveweight of cows due to pregnancy (kg) (O'Rourke *et al*. 1991).

Data analyses

Production data were imported into Stata Release 14 (StataCorp, College Station, TX, USA) for all analyses. The unit of analysis was an annual breeding period (i.e. mating outcome), with each cow contributing up to 6 years of data. Annual liveweight production, annual cow weight change and annual weaner weight all followed an approximately normal distribution. Because most cow growth occurs up to the end of the second weaning and the animals transition from being

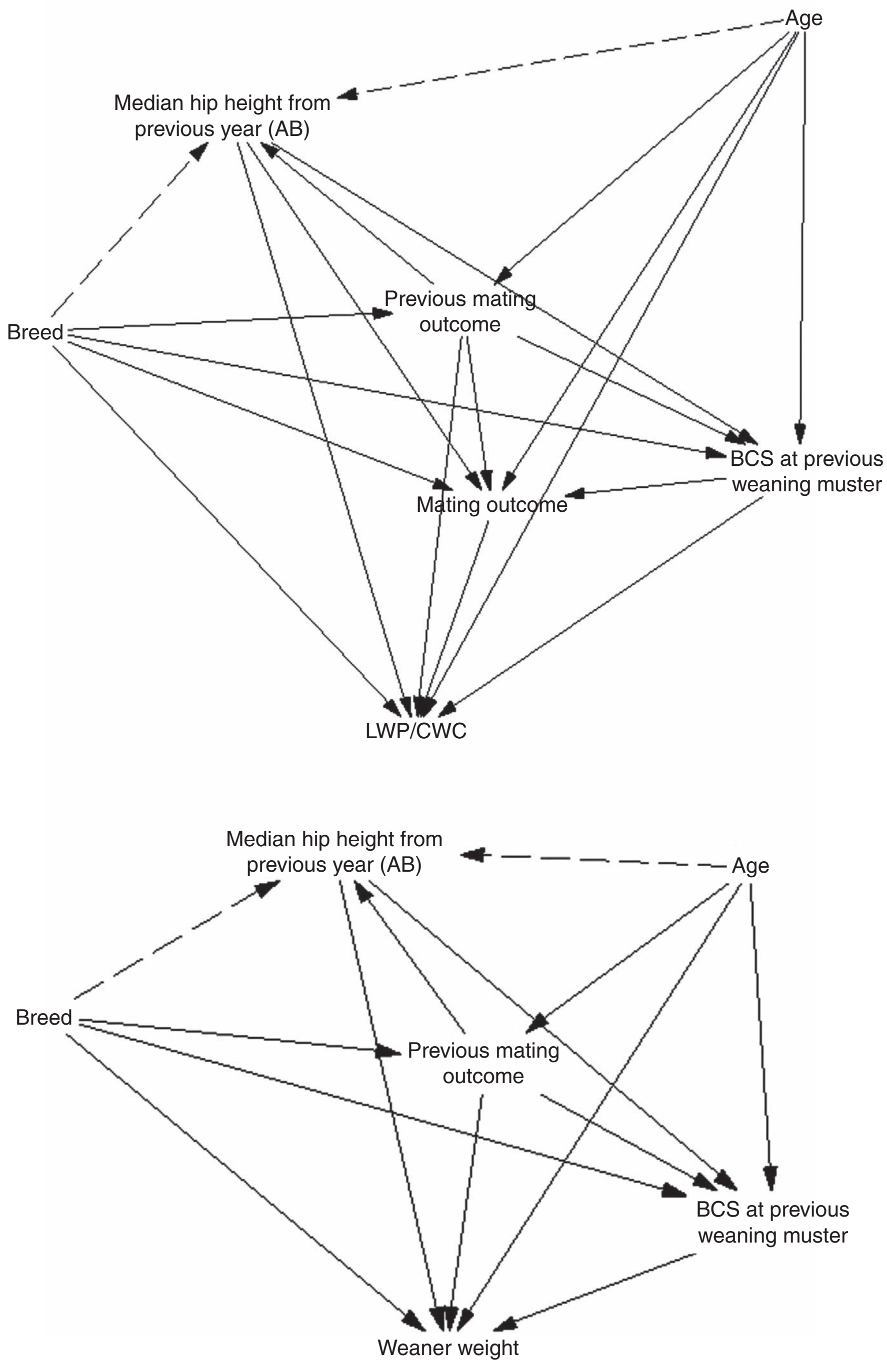

Fig. 2. Causal diagrams interlinking the measured exposure variables with each other, as appropriate, and with liveweight production (LWP), cow weight change (CWC) and weaner weight. Cow liveweight replaced body condition score (BCS) in alternate causal diagrams. Age and breed adjustment (AB) occurred if data were quartiled by age and breed. Solid lines indicate proposed causal relationships used to inform variable selection for model building. Dotted lines indicate proposed causal relationships that were not considered in variable selection for model building because the 'effect variable' has already been adjusted for the proposed 'cause'.

unmated heifers to cows from the start of the first breeding year to the start of the second, it was decided *a priori* to conduct separate analyses for outcomes from the first, second and third–sixth matings. Putative risk factors of interest for one or more of the analyses were breed, mating outcome, previous mating outcome, mating age, plus cow liveweight, body condition score and hip height at commencement of the production year. Distributions were visualised using box plots.

A causal-diagram-informed approach was used for the analyses because this method provides a conceptual framework within which the relative contributions and nature (direct and/or indirect) of various putative causes of each outcome of interest can be assessed (Dohoo *et al*. 2009). A causal diagram was constructed for each outcome of interest, linking putative risk factors with each other and the outcome (Fig. 2). Each causal diagram was reproduced within the DAGitty web interface (Textor *et al*. 2011). These diagrams informed the modelling process to estimate total and direct effects for each risk factor of interest; total and direct effects are identical when there is no intervening variable. The total effect represents the expected effect if that variable were changed, assuming the relationship is truly causal. A comparison between direct and total effects, where the latter includes indirect effects, may facilitate a better understanding of the proposed causal mechanism for the variable of interest. Direct and indirect pathways may operate in the same or different directions. Indirect effects were not estimated, but can be inferred from the difference between the total and direct effect estimates. This approach is preferred to the use of a single multivariable model because the adjusted effects from such a model for each putative risk factor of interest may be direct, partial or total and therefore cannot be readily interpreted (Westreich and Greenland 2013).

Generalised estimating equation models, using site × year as the clustering variable with robust standard errors and an exchangeable working correlation matrix, were used for the main analyses. This accounted for non-independence of observations from any given site × year combination. Risk factors were included in minimal sufficient models for each analysis, and this included any risk factor in assessments of two-way interactions. The latter were assessed by using both statistical significance and visual assessment. As recommended by Dohoo *et al*. (2009), we compiled a list of biologically plausible interactions. The only interaction proposed *a priori* was between mating outcome and previous mating outcome.

Variance components were assessed by fitting null and full (all relevant explanatory variables for that dataset) random-effects models with site and year fitted as nested random effects. Ideally these models would also have included cow as a random effect but it was not possible to fit this cross-classified model (both year and cow were nested within site, but cows had multiple observations across years). Preliminary modelling with site and animal fitted as nested random effects indicated higher variance associated with the random effect of year than with a random effect at animal level. These findings supported the use of site and year as random effects. The percentage of variance explained was calculated as reduction in total variance between the null and the full model relative to the total variance in the null model.

Results

Large variation existed in production measures with weaner weight contributing ~87% of production between 2.5 and 8.5 years of age (Table 3, Fig. 3). A moderate proportion of variance was explained by models for liveweight production and cow liveweight change, but only a small amount by weaner-weight models. Much of the unexplained variance was at the year level (Table 4). Significance is presented for total direct effects of putative risk factors on weaner weight (Table 5), cow liveweight change (Table 6) and liveweight production (Table 7).

Average lactation rates and weaner production calculated from Table 3 data are within or close to previously reported ranges (Table 8).

Liveweight production averaged 103–144 kg higher for cows that weaned a calf than those that lost a calf, with the effect greater in older cattle; there were no postulated intervening variables, so the total and direct effect estimates are the same (Table 7). Cow weight change averaged 67–83 kg lower for cows that weaned a calf (average weaner weight 205 kg) than cows that lost a calf. Cow weight change averaged 96–120 kg higher in non-pregnant cows than those that weaned a calf (Table 6). Over all age groups, liveweight production averaged 35–45 kg higher for non-pregnant cows than cows that lost a calf (Table 7). Most of this difference was a function of cow weight change, which averaged 26–37 kg greater for cows that were non-pregnant than cows that lost a calf (Table 6).

Table 3. Descriptive statistics for outcome variables by mating and age

	Liveweight production (kg/year)				Cow liveweight change (kg/year)				Weaner weight (kg)			
	No.	Mean ± s.d.	Median	Range	No.	Mean ± s.d.	Median	Range	No.	Mean ± s.d.	Median	Range
Overall	11 179	175.1 ± 71.2	177	–150, 429	11 181	21.9 ± 68.7	16	–226, 240	8337	205.4 ± 37.2	204	89, 425
Mating												
1	2117	151.7 ± 60.0	154	–84, 309	2118	16.2 ± 60.1	6	–152, 207	1502	190.9 ± 33.4	190	96, 320
2	2010	165.6 ± 62.3	168	–50, 339	2011	51.0 ± 75.8	40	–158, 240	1224	188.1 ± 30.3	188	107, 305
3	1920	182.4 ± 69.9	185	–107, 418	1920	23.0 ± 71.3	18	–167, 232	1516	201.9 ± 32.8	202	95, 325
4	1816	196.0 ± 71.6	204	–94, 429	1816	26.6 ± 65.1	24	–186, 236	1451	212.0 ± 36.5	211	108, 407
5	1701	183.1 ± 77.4	190	–150, 363	1701	7.0 ± 63.6	6	–185, 228	1356	220.9 ± 38.1	221	107, 357
6	1615	177.3 ± 78.5	179	–74, 409	1615	2.3 ± 63.2	0	–226, 208	1288	219.4 ± 37.9	219	89, 425
Site												
Brian Pastures	2678	187.4 ± 70.5	193	–150, 377	2679	15.9 ± 74.8	11	–226, 238	2138	214.8 ± 39.2	216	100, 425
Belmont	3668	185.0 ± 67.2	189	–74, 380	3669	21.0 ± 58.2	17	–172, 225	2915	206.3 ± 34.8	205	95, 358
Swan's Lagoon	2316	146.3 ± 56.8	146	–107, 344	2316	25.1 ± 84.1	12	–181, 240	1486	188.9 ± 28.7	190	96, 287
Toorak	2517	174.3 ± 81.2	182	–67, 429	2517	26.7 ± 59.0	18	–226, 236	1798	206.6 ± 40.0	203	89, 407

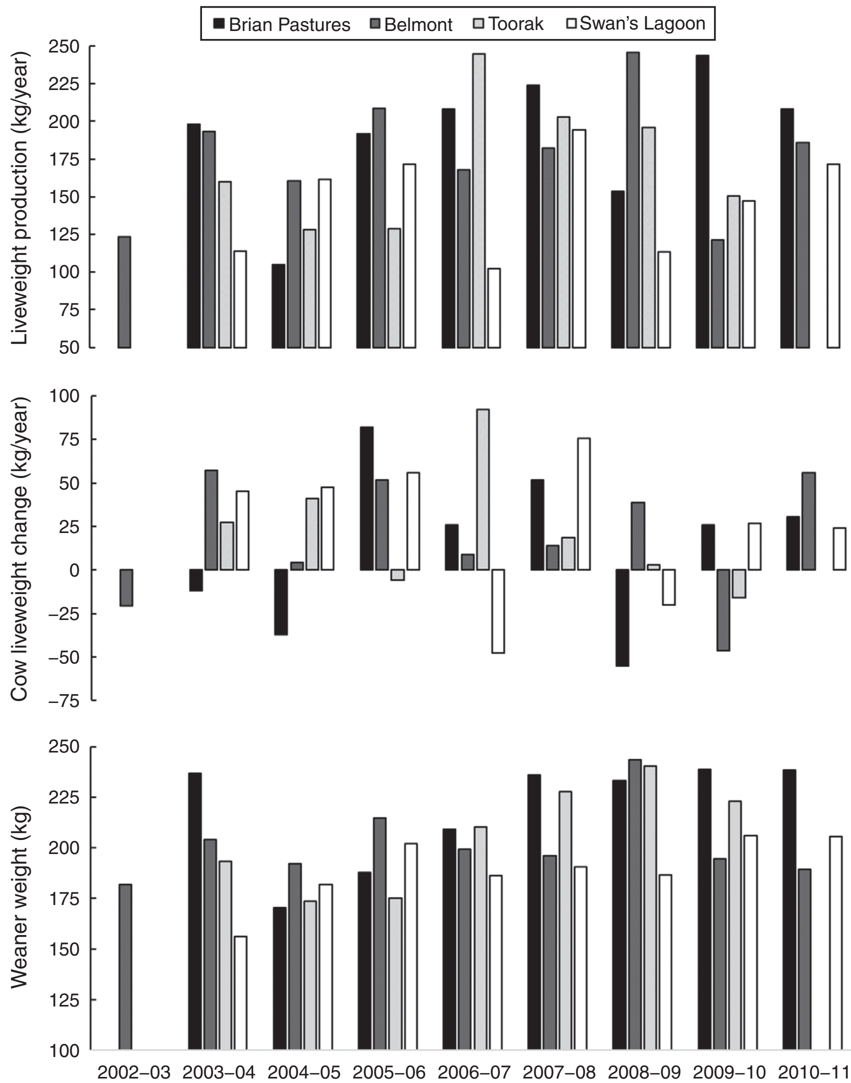

Fig. 3. Raw means for liveweight production, cow liveweight change and annual weaner weight, at each site and year.

Table 4. Variance components of null and full models for liveweight production, cow weight change and weaner weight for first (M1), second (M2) and third–sixth (M3–M6) matings

Model	Liveweight production			Cow weight change			Weaner weight		
	M1	M2	M3–M6	M1	M2	M3–M6	M1	M2	M3–M6
Null									
Site	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	4.3
Year	30.9	26.5	28.2	22.0	27.9	36.1	39.2	15.3	25.1
Residual	69.1	73.5	69.7	78.0	72.1	63.9	60.8	84.7	70.6
Full									
Site	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.0
Year	54.0	61.9	54.9	40.6	60.3	57.2	35.1	17.3	26.2
Residual	46.0	38.1	45.1	59.4	39.7	42.8	64.9	79.8	73.8
% Explained	47.6	42.2	53.2	66.9	72.0	63.0	23.3	9.4	11.4

Table 5. Estimates of total and direct effects of putative risk factors on weaner weight (WW)

Values for estimates (kg) are given as the difference (Diff.) relative to the referent level for each factor; 95% confidence intervals are in parentheses. *P*-values in bold are multiple Wald *P*-values; non-bolded *P*-values are individual Wald *P*-values. PMO, Previous mating outcome; HH, hip height; BCS, body condition score; Empty, failed to conceive; Ref, referent level; TC, tropical composite (average of 28% Brahman)

		Total effects				Direct effects			
		Diff. in WW (kg)	*P*	Covariates	No.	Diff. in WW (kg)	*P*	Covariates	No.
First mating									
Breed			**<0.001**		1502		**<0.001**		1502
	Brahman	Ref				Ref			
	TC	16.3 (10.4, 22.3)	<0.001			16.3 (10.4, 22.3)	<0.001		
Cow weight			**<0.001**	HH	1502		**<0.001**	HH	1502
	1st quartile	–8.2 (–13.4, 3.0)	0.002			–8.2 (–13.4, 3.0)	0.002		
	2nd quartile	Ref				Ref			
	3rd quartile	8.0 (3.3, 12.7)	0.001			8.0 (3.3, 12.7)	0.001		
	4th quartile	19.5 (13.6, 25.5)	<0.001			19.5 (13.6, 25.5)	<0.001		
Cow BCS			**<0.001**	HH, breed	1502		**<0.001**	HH, breed	1502
	≤2.7	–7.0 (–11.8, 2.1)	0.005			–7.0 (–11.8, 2.1)	0.005		
	3	Ref				Ref			
	3.3 or 3.7	3.7 (0.2, 7.1)	0.039			3.7 (0.2, 7.1)	0.039		
	≥4	10.3 (6.8, 13.8)	<0.001			10.3 (6.8, 13.8)	<0.001		
Cow HH			**<0.001**		1502		**0.007**	Breed, weight	1502
	1st quartile	–8.5 (–12.1, 4.8)	<0.001			–1.2 (–4.1, 1.6)	0.393		
	2nd quartile	Ref				Ref			
	3rd quartile	6.1 (2.6, 9.7)	0.001			1.4 (–2.2, 5.1)	0.446		
	4th quartile	7.2 (3.3, 11.1)	<0.001			–3.7 (–8.2, 0.7)	0.097		
Second mating									
Breed			**0.004**		1224		**0.001**	PMO, HH, BCS	1223
	Brahman	Ref				Ref			
	TC	12.7 (4.1, 21.4)	0.004			16.0 (6.9, 25.1)	0.001		
PMO			**<0.001**	Breed	1224		**<0.001**	Breed, BCS, HH	1223
	Empty	–1.3 (–7.5, 4.9)	0.687			–2.8 (–8.7, 3.0)	0.342		
	Calf loss	Ref				Ref			
	Wean	–18.7 (–24.0, 13.4)	<0.001			–13.6 (–19.0, 8.1)	<0.001		
Cow BCS			**0.161**	PMO, HH, breed	1223		**0.161**	PMO, HH, breed	1223
	≤2	–0.4 (–10.4, 9.7)	0.941			–0.4 (–10.4, 9.7)	0.941		
	2.3 or 2.7	1.5 (–2.8, 5.8)	0.497			1.5 (–2.8, 5.8)	0.497		
	3	Ref				Ref			
	3.3 or 3.7	2.4 (–4.2, 8.9)	0.482			2.4 (–4.2, 8.9)	0.482		
	≥4	7.4 (–0.6, 15.4)	0.071			7.4 (–0.6, 15.4)	0.071		
Cow HH			**<0.001**	PMO	1223		**<0.001**	Breed, PMO, BCS	1223
	1st quartile	–8.7 (–11.5, 5.9)	<0.001			–8.0 (–11.3, 4.8)	<0.001		
	2nd quartile	Ref				Ref			
	3rd quartile	1.1 (–2.8, 5.1)	0.579			1.8 (–2.8, 6.4)	0.447		
	4th quartile	6.6 (2.3, 10.9)	0.003			7.2 (2.5, 11.9)	0.003		
Third–sixth mating									
Breed			**<0.001**		5611		**<0.001**	Age, PMO, HH, BCS	5606
	Brahman	Ref				Ref			
	TC	13.3 (8.8, 17.8)	<0.001			14.6 (9.9, 19.3)	<0.001		
PMO			**<0.001**	Breed, age	5611		**<0.001**	Breed, BCS, age, HH	5606
	Empty	6.7 (2.0, 11.4)	0.005			7.3 (2.9, 11.7)	0.001		
	Calf loss	Ref				Ref			
	Wean	–8.9 (–12.7, 5.1)	<0.001			–12.0 (–16.2, 7.9)	<0.001		
Cow BCS			**0.051**	PMO, HH, age, breed	5606		**0.051**	PMO, HH, age, breed	5606
	≤2	–1.7 (–5.9, 2.5)	0.428			–1.7 (–5.9, 2.5)	0.428		
	2.3 or 2.7	0.6 (–2.5, 3.7)	0.718			0.6 (–2.5, 3.7)	0.718		
	3	Ref				Ref			
	3.3 or 3.7	–2.6 (–5.9, 0.6)	0.113			–2.6 (–5.9, 0.6)	0.113		
	≥4	–6.8 (–11.9, 1.6)	0.01			–6.8 (–11.9, 1.6)	0.01		
Cow HH			**<0.001**	PMO	5610		**0.017**	Breed, PMO, age, BCS	5606
	1st quartile	–3.8 (–6.0, 1.6)	0.001			–3.9 (–6.2, 1.6)	0.001		
	2nd quartile	Ref				Ref			
	3rd quartile	4.5 (1.8, 7.2)	0.001			4.2 (1.4, 7.0)	0.003		
	4th quartile	4.9 (1.7, 8.0)	0.002			4.3 (1.2, 7.3)	0.006		
Mating			**0.194**		5611		**0.013**	Breed, MO, PMO, HH, BCS	5606
	Third	Ref				Ref			
	Fourth	0.2 (–4.9, 5.2)	0.945			3.9 (–1.5, 9.2)	0.158		
	Fifth	1.9 (–2.5, 6.3)	0.394			6.3 (0.5, 12.2)	0.033		
	Sixth	–0.1 (–4.5, 4.3)	0.955			4.6 (–1.2, 10.4)	0.123		

Table 6. Estimates of total and direct effects of putative risk factors on cow weight change (CWC)

Values for estimates (kg/year) are given as the difference (Diff.) relative to the referent level for each factor; 95% confidence intervals are in parentheses. *P*-values in bold are multiple Wald *P*-values; non-bolded *P*-values are individual Wald *P*-values. PMO, Previous mating outcome; MO, mating outcome; HH, hip height; BCS, body condition score; Empty, failed to conceive; Ref, referent level; TC, tropical composite (average of 28% Brahman)

		Total effects				Direct effects			
		Diff. in CWC (kg/year)		Covariates	No.	Diff. in CWC (kg/year)	*P*	Covariates	No.
					First mating				
Breed			**0.584**		2118		**0.003**	HH, MO, weight	2118
	Brahman	Ref				Ref			
	TC	4.8 (–12.4, 22.0)	0.584			18.9 (6.3, 31.5)	0.003		
MO			**<0.001**	Breed, HH, weight	2118				
	Empty	37.3 (29.1, 45.4)	<0.001						
	Calf loss	Ref							
	Wean	–82.7 (–94.5, 70.9)	<0.001						
Cow weight			**<0.001**	HH	2118		**<0.001**	Breed, MO, HH	2118
	1st quartile	22.7 (1.1, 44.3)	0.04			4.9 (0.5, 9.3)	0.029		
	2nd quartile	Ref				Ref			
	3rd quartile	–16.8 (–23.2, 10.4)	<0.001			–3.9 (–7.0, 0.8)	0.014		
	4th quartile	–31.7 (–40.5, 22.9)	<0.001			–11.8 (–17.0, 6.6)	<0.001		
Cow BCS			**0.002**	HH, breed	2118		**0.011**	Breed, MO, HH	2118
	≤2.7	7.6 (2.8, 12.4)	0.002			2.7 (–1.4, 6.8)	0.2		
	3	Ref				Ref			
	3.3 or 3.7	–21.5 (–40.3, 2.8)	0.024			–4.4 (–10.5, 1.7)	0.159		
	≥4	–34.9 (–55.6, 14.2)	0.001			–9.3 (–16.2, 2.3)	0.009		
Cow HH			**0.293**		2118		**<0.001**	Breed, MO, weight	2117
	1st quartile	1.3 (–4.5, 7.1)	0.67			–2.7 (–6.8, 1.4)	0.192		
	2nd quartile	Ref				Ref			
	3rd quartile	–2.8 (–12.1, 6.5)	0.551			1.5 (–1.6, 4.6)	0.347		
	4th quartile	0.1 (–8.7, 8.9)	0.986			8.9 (5.0, 12.7)	<0.001		
					Second mating				
Breed			**0.5375**		2011		**0.033**	MO, PMO, HH, BCS	2010
	Brahman	Ref				Ref			
	TC	–6.1 (–25.5, 13.3)	0.537			7.7 (0.6, 14.8)	0.033		
MO			**<0.001**	Breed, BCS, PMO, HH	2010				
	Empty	35.7 (27.8, 43.5)	<0.001						
	Calf loss	Ref							
	Wean	–67.1 (–79.1, 55.1)	<0.001						
PMO			**<0.001**	Breed	2011		**<0.001**	Breed, MO, BCS, HH	2010
	Empty	–27.1 (–39.8, 14.3)	<0.001			–6.2 (–11.9, 0.5)	0.034		
	Calf loss	Ref				Ref			
	Wean	85.7 (63.3, 108.2)	<0.001			35.7 (31.5, 39.8)	<0.001		
Cow BCS			**<0.001**	PMO, HH, breed	2009		**<0.001**	Breed, MO, PMO, HH	2010
	≤2	50.9 (38.8, 63.0)	<0.001			18.1 (15.0, 21.3)	<0.001		
	2.3 or 2.7	19.9 (15.6, 24.2)	<0.001			6.5 (1.0, 11.9)	0.021		
	3	Ref				Ref			
	3.3 or 3.7	–5.5 (–12.1, 1.1)	0.101			–5.2 (–8.6, 1.8)	0.003		
	≥4	–35.2 (–49.9, 20.5)	<0.001			–22.9 (–28.1, 17.6)	<0.001		
Cow HH			**0.001**	PMO	2010		**0.211**	Breed, MO, PMO, BCS	2010
	1st quartile	–3.8 (–10.2, 2.5)	0.237			–1.7 (–5.0, 1.6)	0.315		
	2nd quartile	Ref				Ref			
	3rd quartile	0.4 (–8.0, 8.8)	0.926			1.1 (–3.9, 6.1)	0.675		
	4th quartile	5.4 (–3.9, 14.7)	0.257			3.4 (–3.4, 10.3)	0.327		
					Third–sixth mating				
Breed			**0.908**		7052		**0.906**	Age, MO, PMO, HH, BCS	7046
	Brahman	Ref				Ref			
	TC	–0.6 (–11.1, 9.9)	0.908			–0.4 (–6.7, 5.9)	0.901		
MO			**<0.001**	Breed, PMO, BCS, age, HH	7046				
	Empty	26.4 (21.3, 31.5)	<0.001						
	Calf loss	Ref							
	Wean	–69.9 (–75.6, 64.2)	<0.001						
PMO			**<0.001**	Breed, age	7052		**<0.001**	Breed, MO, BCS, age, HH	7046
	Empty	–24.0 (–30.5, 17.5)	<0.001			–15.0 (–19.2, 10.9)	<0.001		
	Calf loss	Ref				Ref			
	Wean	57.7 (48.4, 66.9)	<0.001			37.8 (32.8, 42.8)	<0.001		

(*continued next page*)

Table 6. (*continued*)

	Total effects				Direct effects			
	Diff. in CWC (kg/year)		Covariates	No.	Diff. in CWC (kg/year)	*P*	Covariates	No.
Cow BCS		**<0.001**	PMO, HH, age, breed	7046		**<0.001**	Breed, MO, PMO, age, HH	7046
≤2	37.7 (26.4, 48.9)	<0.001			13.9 (8.8, 19.1)	<0.001		
2.3	9.8 (5.3, 14.2)	<0.001			3.8 (0.3, 7.3)	0.031		
2.7	9.8 (5.3, 14.2)	<0.001			3.8 (0.3, 7.3)	0.031		
3	Ref				Ref			
3.3	–5.4 (–8.8, 2.0)	0.002			–3.5 (–5.8, 1.2)	0.003		
3.7	–5.4 (–8.8, 2.0)	0.002			–3.5 (–5.8, 1.2)	0.003		
≥4	–14.8 (–22.5, 7.1)	<0.001			–11.2 (–16.4, 6.0)	<0.001		
Cow HH		**0.003**	PMO	7050		**0.109**	Breed, MO, PMO, age, BCS	7046
1st quartile	–3.0 (–7.3, 1.3)	0.165			–1.2 (–3.5, 1.1)	0.307		
2nd quartile	Ref				Ref			
3rd quartile	3.0 (–0.1, 6.1)	0.055			0.7 (–1.2, 2.6)	0.481		
4th quartile	3.7 (–0.5, 8.0)	0.084			0.1 (–2.4, 2.5)	0.96		
Mating		**0.003**		7052		**<0.001**	Breed, MO, PMO, HH, BCS	7046
Third	Ref				Ref			
Fourth	0.2 (–4.7, 5.0)	0.941			–7.5 (–11.3, 3.8)	<0.001		
Fifth	–4.3 (–10.6, 2.1)	0.191			–13.0 (–16.6, 9.4)	<0.001		
Sixth	–7.9 (–14.3, 1.5)	0.015			–13.8 (–17.9, 9.7)	<0.001		

Analysis of direct effects from the previous mating found that liveweight production was 10 kg higher in cows that lost a calf than those that failed to conceive, although there was no difference in analysis of total effects (Table 7). However, cows previously weaning a calf averaged 17 and 33 kg higher liveweight production than those previously losing a calf in their second and subsequent matings, respectively; the direct effect was 24–26 kg (Table 7). The direct and indirect effects, mediated by current mating outcome, are acting in opposite directions. Weight change averaged 58–86 kg greater for cows that weaned a calf than cows that lost a calf after the previous mating, with the lower level of effect at the second mating; the direct effects were attenuated at 36–38 kg compared with the total effects, indicating that the effects are partially mediated through the current mating outcome, the postulated intervening variable (Table 6). Weaner liveweight was 9–19 kg higher in cows that did not wean a calf from their previous mating than in those that did (Table 5). Cow liveweight change was 82–103 kg higher in cows previously weaning a calf than in previously non-pregnant cows; the direct effect was 42–53 kg (Table 6). Weight change averaged 24–27 kg lower for cows that were previously non-pregnant than cows that previously lost a calf; the direct effect was 6–15 kg (Table 6).

Liveweight production of cows from their first, second and subsequent matings averaged 152, 166 and 185 kg/year, respectively (Table 3), with no total age effect apparent beyond the second mating; however, direct-effect analyses found that liveweight production and cow liveweight change reduced after 3 years of age by 5–11 kg/year and 8–14 kg/year, respectively (Tables 6 and 7, Fig. 3). Weaner weight was ~25 kg higher from the third–sixth matings than from the first two matings (Table 3); direct effects of previous mating outcome were similar for second and third–sixth matings, indicating that the magnitude of the indirect effect, mediated through previous mating outcome was minimal.

The average liveweight of the cow-calf units during the periods that cows were aged 2.5–3.5, 3.5–4.5, and 4.5–8.5 years was calculated as 491, 515 and 595 kg, respectively. Liveweight production (above) divided by these weights (i.e. liveweight production ratio) was consistent and averaged 0.32 ± 0.12 kg/kg cattle.

Tropical composites had 25–42 kg higher annual liveweight production than Brahmans, with the effect being greater for the first two matings; the difference was attenuated to 11–34 kg in direct-effect analyses (Table 7). This effect appears due partially to a combination of higher lactation rates (Table 8) and site. Tropical composites were not kept at Swan's Lagoon, which had the lowest overall liveweight production (146 kg/year vs 182–192 kg/year for other sites) and lactation rates, and Brahmans were not kept at Brian Pastures, which had the highest liveweight production. In all matings, weaners averaged 13–16 kg heavier in tropical composites than in Brahmans in both total- and direct-effect analyses (Table 5). There was no breed effect on cow liveweight change, except in the first and second matings, where direct-effect analysis revealed an advantage of 7 and 19 kg, respectively, to tropical composites over Brahmans (Table 6).

The tallest quartile of cows had 5–10 kg higher liveweight production than the shortest quartile, with most of this effect through weaning heavier calves; there was little difference between direct and total effects of hip height (Tables 5–7). The average cow liveweight difference between each hip height quartile within breed and age was 24 kg.

Hip height and breed were consistently significant as covariates across all analyses (Tables 5–7).

Compared with pregnant cows in prime body condition (score 4), those in backward body condition (score 2) after their first and second matings subsequently weaned calves that were 8–17 kg lighter; this effect was not significant in mature cows (Table 5). Subsequent annual liveweight change of prime-condition pregnant cows was 43–86 kg lower than in

Table 7. Estimates of total and direct effects of putative risk factors on liveweight production (LWP)
Values for estimates (kg/year) are given as the difference (Diff.) relative to the referent level for each factor; 95% confidence intervals are in parentheses. *P*-values in bold are multiple Wald *P*-values; non-bolded *P*-values are individual Wald *P*-values. PMO, Previous mating outcome; MO, mating outcome; HH, hip height; BCS, body condition score; Empty, failed to conceive; Ref, referent level; TC, tropical composite (average of 28% Brahman)

	Total effects				Direct effects			
	Diff. in LWP (kg/year)	*P*	Covariates	No.	Diff. in LWP (kg/year)	*P*	Covariates	No.
First mating								
Breed		**<0.001**		2117		**<0.001**	HH, MO, weight	2117
Brahman	Ref				Ref			
TC	41.6 (29.6, 53.6)	<0.001			34.0 (21.3, 46.8)	<0.001		
MO		**<0.001**	Breed, HH, weight	2117				
Empty	44.6 (31.9, 57.2)	<0.001						
Calf loss	Ref							
Wean	103.0 (89.0, 117.0)	<0.001						
Cow weight		**<0.001**	HH	2117		**<0.001**	Breed, MO, HH	2117
1st quartile	–3.3 (–13.5, 7.0)	0.533			–1.4 (–5.8, 3.0)	0.534		
2nd quartile	Ref				Ref			
3rd quartile	11.9 (6.9, 16.8)	<0.001			3.2 (–0.4, 6.7)	0.079		
4th quartile	19.2 (8.7, 29.6)	<0.001			7.2 (0.3, 14.1)	0.04		
Cow BCS		**0.014**	HH, breed	2117		**0.953**	Breed, MO, HH	2117
≤2.7	–4.4 (–11.4, 2.4)	0.204			–0.2 (–8.2, 7.8)	0.957		
3	Ref				Ref			
3.3 or 3.7	5.4 (–1.3, 12.2)	0.116			–2.3 (–10.7, 6.2)	0.598		
≥4	7.4 (2.0, 12.8)	0.008			–2.2 (–11.4, 6.9)	0.632		
Cow HH		**0.008**		2117		**0.001**	Breed, MO, weight	2117
1st quartile	–4.5 (–10, 1.0)	0.106			–4.6 (–7.9, –1.4)	0.005		
2nd quartile	Ref				Ref			
3rd quartile	0.5 (–3.9, 4.9)	0.819			1.6 (–1.9, 5.2)	0.365		
4th quartile	9.3 (3.1, 15.5)	0.003			4.7 (0.2, 9.2)	0.04		
Second mating								
Breed		**<0.001**		2010		**<0.001**	MO, PMO, HH, BCS	2009
Brahman	Ref				Ref			
TC	37.2 (27.1, 47.3)	<0.001			19.0 (8.5, 29.5)	<0.001		
MO		**<0.001**	Breed, BCS, PMO, HH	2009				
Empty	37.5 (30.1, 44.9)	<0.001						
Calf loss	Ref							
Wean	118.4 (106.4, 130.5)	<0.001						
PMO		**<0.001**	Breed	2010		**<0.001**	Breed, MO, BCS, HH	2009
Empty	–5.2 (–14.4, 4.1)	0.272			–9.5 (–18.3, –0.7)	0.035		
Calf loss	Ref				Ref			
Wean	17.4 (6.4, 28.5)	0.002			24.2 (19.8, 28.7)	<0.001		
Cow BCS		**0.797**	PMO, HH, breed	2009		**<0.001**	Breed, MO, PMO, HH	2009
≤2	–7.0 (–23.6, 9.6)	0.409			19.0 (11.3, 26.6)	<0.001		
2.3 or 2.7	–4.1 (–19.4, 11.2)	0.599			7.9 (1.7, 14.1)	0.012		
3	Ref				Ref			
3.3 or 3.7	–5.4 (–16.6, 5.9)	0.35			–2.5 (–8.6, 3.6)	0.419		
≥4	–6.3 (–25.4, 12.7)	0.515			–16.4 (–26.4, –6.3)	0.001		
Cow HH		**<0.001**	PMO	2009		**0.001**	Breed, MO, PMO, BCS	2009
1st quartile	–5.8 (–9.8, –1.8)	0.005			–7.0 (–10.5, –3.5)	<0.001		
2nd quartile	Ref				Ref			
3rd quartile	4.8 (–1.6, 11.2)	0.139			1.6 (–3.3, 6.4)	0.528		
4th quartile	9.5 (2.2, 16.8)	0.011			7.5 (2.1, 13.0)	0.007		
Third–sixth mating								
Breed		**<0.001**		7052			Age, MO, PMO, HH, BCS	7046
Brahman	Ref				Ref			
TC	25.4 (17.1, 33.7)	<0.001			11.6 (3.4, 19.8)	<0.001		
MO		**<0.001**	Breed, PMO, BCS, age, HH	7046				
Empty	35.1 (28.9, 41.2)	<0.001						
Calf loss	Ref							
Wean	144.2 (132.5, 155.9)	<0.001						
PMO		**<0.001**	Breed, age	7052		**<0.001**	Breed, MO, BCS, age, HH	7046
Empty	1.5 (–5.5, 8.5)	0.675			–9.8 (–15.3, –4.3)	<0.001		
Calf loss	Ref				Ref			
Wean	33.1 (25.5, 40.6)	<0.001			26.4 (20.3, 32.5)	<0.001		
Cow BCS		**0.797**	PMO, HH, age, breed	7046		**<0.001**	Breed, MO, PMO, age, HH	7046
≤2	–13.7 (–22.8, 4.6)	0.003			13.5 (8.7, 18.2)	<0.001		
2.3 or 2.7	–3.6 (–10.5, 3.4)	0.314			4.0 (0.4, 7.6)	0.029		
3	Ref				Ref			
3.3 or 3.7	–4.7 (–9.5, 0.0)	0.052			–6.1 (–8.5, –3.7)	<0.001		
≥4	–17.6 (–26.3, –8.8)	<0.001			–18.6 (–25.2, –12.1)	<0.001		

(*continued next page*)

Table 7. (*continued*)

	Total effects				Direct effects			
	Diff. in LWP (kg/year)	*P*	Covariates	No.	Diff. in LWP (kg/year)	*P*	Covariates	No.
Cow HH		**<0.001**	PMO	7050		**0.001**	Breed, MO, PMO, age, BCS	7046
1st quartile	–3.9 (–8.7, 0.9)	0.112			–4.1 (–7.1, –1.0)	0.009		
2nd quartile	Ref				Ref			
3rd quartile	2.0 (–1.9, 5.8)	0.311			4.0 (1.1, 7.0)	0.007		
4th quartile	–0.4 (–4.5, 3.6)	0.831			3.5 (–0.2, 7.1)	0.06		
Mating				7052		**<0.001**	Breed, MO, PMO, HH, BCS	7046
Third	Ref				Ref			
Fourth	3.2 (–4.0, 10.4)	0.389			–5.3 (–8.4, 2.1)	0.001		
Fifth	–0.4 (–7.4, 6.6)	0.918			–8.9 (–12.9, –4.9)	<0.001		
Sixth	–1.1 (–9.0, 6.8)	0.788			–11.0 (–14.9, 7.0)	<0.001		

Table 8. Calculated average herd lactation rates and average annual weaner production at each site compared with reported ranges for respective country types

McG, Data from McGowan *et al.* (2014); Ba, derived from Bortolussi *et al.* (2005*a*); Bb, annual yearling growth derived from Bortolussi *et al.* (2005*b*)

Site	No.	Lactation rate (%)			Weaner production (kg/cow)		
		Mean	McG	Ba	Mean	McG	Bb
Brian Pastures, Southern Forest	2678	80	62–88	77	171	164–240	129–193
Belmont, Central Forest	3668	79	69–87	78	164	161–220	139–198
Swan's Lagoon, Northern Forest	2316	64	44–62	64	121	74–112	100–131
Toorak, Northern Downs	2517	71	57–78	73	148	135–183	116–171

backward-condition cows, with this effect halved by correction for mating outcome in direct-effect analyses (Table 6). This large total effect was not evident in overall liveweight production, where the effects of body condition on weaner weight and cow weight change largely cancelled each other out, except in first-lactation cows (12 kg, Table 7). However, the indirect effect of body condition on cows, reflecting mating outcome, in their second and later breeding years was fully expressed in liveweight production; this did not occur in first-lactation cows (Tables 5–7).

Cow liveweight effects were considered only for cows in their first pregnancy. The heaviest quartile of cows weaned calves that were 28 kg heavier than cows in the lightest quartile (Table 5). Direct effects mediated by mating outcome showed that cow liveweight change was 16 kg lower and liveweight production was intermediate at 9 kg higher.

Using these data to calculate productivity over multiple years, average lifetime weaner weight varied little (1–2 kg) across all possible mating-outcome sequences. However, raw means for annual cow liveweight gain were reduced by 10 and 16 kg per extra calf reared compared with cows that lost a calf and non-pregnant cows, respectively, across the full range of possible mating-outcome sequences; the respective advantages in annual liveweight production of cows were an average of 82 and 36 kg per extra calf reared.

Discussion

This paper is the first to describe in detail the substantial impact of failure to conceive and of calf loss on liveweight production of breeding cows in north Australian beef herds. The importance of these results is that the sum of liveweight production for all cows in a paddock over a year is equivalent to the net liveweight harvested from the paddock when stocking rate is constant, and represents cattle growth as a function of available pastures and weaning management in particular. This liveweight either is sold directly or displaces equivalent liveweight in a business that is sold; therefore, cow-paddock liveweight production is a direct measure of business sales. Expanding on this, if an animal dies, its starting liveweight is production lost for that year for the management group. When an animal is sold, as for most of the reduction in numbers between 2.5 and 8.5 years of age in this study, then the liveweight at the point of sale is what it has accumulated during its life time in the herd and is much more than its production in that year.

The fact that average lactation rates and weaner production were within, or close to, previously reported ranges indicates that the data reported here are representative of the respective country types. These data clearly show that weaner production, which along with cow weight change constitutes liveweight production by cow herds, is very similar to that of annual yearling gain in the same country types. This concurs with McGowan *et al.* (2014), who previously suggested that liveweight production in a year by a cow–calf unit is dictated by the quality and quantity of pasture and any supplements consumed. This is corroborated by consistency of rankings for all measures across country types. This supports the hypothesis that yearling growth, a function of available diet, is a direct indicator of weaner production by breeding herds in the same situation. Therefore, expected or measured growth of small numbers (e.g. five or six) of cohabiting, non-breeding yearling cattle may provide a direct measure of production potential of cow herds from a specific pasture in that year.

Weaning achieves the highest liveweight production of all mating outcomes. The production advantage over cows not weaning a calf because they have either failed to conceive or failed to rear a calf after becoming pregnant, is on average much less than weaner weight because cows failing to rear calves have much higher weight gain themselves than lactating cows. Cows almost invariably experience significant liveweight loss in rearing a calf to weaning. This averages a little more than one body condition score unit (5-point scale) in mature cows, and almost two body condition score units in first-lactation cows. Fordyce *et al*. (2013) showed that liveweights differ by 13% per condition score unit from moderate on a 5-point scale. The higher loss in immature cows is presumably associated with energy demands of both growth and lactation, whereas mature cows do not have demands associated with skeletal growth. From the data of Fordyce *et al*. (2013), it can be calculated that just to remain in the same body condition, a typical cow must gain ~50 and ~35 kg during the ages of 2.5–3.5 and 3.5–4.5 years, respectively. Skeletal growth appears complete at 4.5 years on average (Fordyce *et al*. 2013). The lower body condition of previously lactating cows provides the opportunity to gain more weight in the following year, an indirect effect that we have demonstrated.

Our results confirm the large cost of losing a calf when the production effect is valued per kg. The loss has a lifetime impact on production despite much smaller positive effects on cow liveweight gain of failing to rear a calf. The cost in liveweight production is larger than for a cow that fails to conceive, both in the year of loss and over a lifetime. This is because most calf loss occurs soon after birth (Bunter *et al*. 2013), and the energy stored up to the point of fetal or calf death is lost and not recoverable. By contrast, a cow that fails to conceive, most often because of low body condition, has the opportunity to store large amounts of energy over the year with little risk of it being lost. This outcome indicates that culling of cows with high risk of losing a calf is warranted. However, culling of a cow that has already lost a calf by accident or mismanagement may not be efficient for a business if she has re-conceived at an optimum mating time.

Liveweight loss due to calf rearing is cumulative and in most cases leads to failure to conceive in a year when body condition during suckling is low, allowing subsequent recovery to advanced body condition. Our data show that an average non-reconceiving mature cow after weaning a calf recovers 100–130 kg in the following year; liveweight recovery was, on average, higher in non-pregnant cows after their first lactation at 145 kg. However, reflecting the huge individual variation in annual liveweight production, there are cows that wean a calf every year. The liveweight of their calves is similar to that of those weaned from lower performing cows. These highly fertile cows are able to achieve limited liveweight change over a year and are therefore highly productive; that is, they do not follow the pattern of the average cows, which lose between one and two body condition score units in the year they rear a calf. The mechanism for their advantage is unclear but the possibilities could include grazing behaviour of the cow and calf and lactation yields, and enhanced ability to recycle nutrients, in addition to ability to conceive consistently during lactation, a trait that has been shown to have high and moderate heritability in Brahman and crossbred cattle, respectively (Johnston *et al*. 2014).

The effect of increasing cow age on reducing annual average liveweight change is coupled with the average weight of calves weaned from mature cows being 25 kg higher than of calves weaned from cows at 3.5 and 4.5 years of age. Lubritz *et al*. (1989) reported the same cow-age effect on weaner weight and related it directly to higher lactation yields in older cows resulting in higher growth of suckling calves. Lower lactation yields are expected in immature cows because they partition significant energy into maintenance of body condition, which competes with the high energy requirements of milk production. Although available nutrition and energy requirements for various body functions are expected to affect lactation yields, we have shown that variable partitioning of energy to lactation is less likely than to their own tissue reserves, as reflected in relatively low variation in weaner weight compared with very high variation in annual cow liveweight gain. We found that the calves of young cows that had been in backward body condition in mid-pregnancy were 7–17 kg lighter at weaning. This suggests that low body-tissue reserves can reduce subsequent lactation yields, as previously reported by McBryde *et al*. (2013), thereby reducing calf growth by 0.05–0.10 kg/day.

We have shown that annual liveweight production of a breeding unit increases to 5.5 years of age, and thereafter is lower. Up to this age, cows have average annual liveweight gain associated with skeletal development, and increasing weight of calf weaned. Beyond this age, weight of weaned calf does not increase, and cow capacity to grow has been lost. Productivity of cows might be expected to increase in growing younger cows by virtue of their higher mass and higher feed-intake capacity; that is, efficiency of liveweight production from feed consumed remains constant, as our data suggest. Productive potential of cows and efficiency of production dramatically reduce at an age when risk of mortality increases. Annual mortality risk of cows has been reported to increase substantially at ages beyond 8 years (Fordyce *et al*. 1990) and 10 years (Henderson *et al*. 2013); however, it remains unclear why this was not corroborated in a more recent large study (McGowan *et al*. 2014). The usual practice in northern Australia to cull cows beyond 10 years of age ensures that the breeding herd holds animals that are within their band of maximum production and efficiency.

We report no overall effects of cow hip height, an indicator of frame score, on annual liveweight change. However, as expected, larger cows weaned heavier calves. There was no evidence of cow size affecting production efficiency in this population of mostly moderate mature-size cattle.

The breed effect shown is confounded by site. However, the data suggest that, at least outside the low-growth northern forest country type, tropical composite cows wean calves that are ~15 kg heavier than calves of Brahman cows. This produces most of their advantage in liveweight production except in the first breeding year when the tropical composite cows themselves have an annual liveweight gain advantage of a similar magnitude. If the cost of this extra gain does not exceed its value, then the advantage of tropical composites is a combination of higher weaner weights and higher average cow liveweight at culling.

Conclusions

This study has successfully demonstrated the concept of liveweight production of breeding beef cows, a primary business measure, and how it is related to key performance measures and basic cow traits. Productivity of grazing beef cows is limited by available nutrition as indicated by the similarity between average annual yearling growth and weaner production of cows in the same environment. Liveweight production is highest in those weaning calves. Cows failing to conceive have higher short- and long-term liveweight production than those losing a conceptus or calf before weaning. Lactating cows have lower body condition, thus subsequent higher weight gain despite weaning lighter calves than previously non-lactating cows. Older and larger cows have higher production, but there is no apparent difference in production efficiency.

Conflicts of interest

The authors declare no conflicts of interest.

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