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Growth of Brahman cross heifers to 2 years of age in the dry tropics

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Abstract. Growth of 1368 Brahman cross heifers from 6 year cohorts was monitored over the 2 years post-weaning in Australia's northern forest, a low-animal-growth dry tropical environment. Heifers weighing 47–266 kg at weaning were managed in groups weighing <100 kg, 100–149 kg, 150–199 kg, and >199 kg during the post-weaning dry season. Weaner heifers were allocated to receive 300 g/day of a protein meal during the dry season or to basic nutritional management to sustain health. Heifers in three cohorts were allocated to first mating at 1 or 2 years of age, in four cohorts to vaccination against androstenedione, and in a small proportion of two cohorts to ovariectomy post-weaning. Growth was highly variable between seasons and years; average cohort liveweight by the start of 2-year-old mating was 256–319 kg. Heifer groups not receiving protein supplementation gained –16 to 21 kg (2 kg average) during 6-month dry seasons, and 49–131 kg (101 kg average) during wet seasons to reach an average of two-thirds of mature liveweight (445 kg) and 95% of mature hip height (1350 mm) by the start of mating at 2 years. Average body condition score (1–5) fluctuated by 1–2 units between seasons. Hip height gain continued, irrespective of season, commencing at ~0.60 mm/day at 6 months of age, and decelerating by ~0.00075 mm/day through to 2.5 years of age. Standard errors of predicted means across analyses were ~0.015 for average daily weight gains, 0.4 mm for average monthly height gain and 0.06 score units for average seasonal body condition score change. Post-weaning dry-season supplementation increased gains in liveweight, height and body condition score by an average of 0.1 kg/day, 0.1 mm/day and 0.5 units, respectively, during the supplementation period. Periods of poor nutrition or high nutritional demand secondary to reproduction suppressed daily gains in liveweight and hip height, at which times body condition score was also reduced. Subsequent to this, partial to full compensation occurred for all measures. Ovariectomy had negative effects on growth. Androstenedione vaccination had no effect on growth. The main conclusion is that heifer growth in Australia's dry tropical northern forest region is highly variable between seasons and years, thus limiting significant proportions of some cohorts from reaching target weights for mating at 2 years of age, even after compensatory growth.

Additional keywords: body condition, cattle, compensatory growth, height, tropical, weight.

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Background

The overall expression of growth is liveweight gain, which is a function of growth of the musculoskeletal system, along with growth of all other body systems. There are limited reports on the growth of beef heifers in the dry tropics of northern Queensland (Holroyd *et al*. 1990; Fordyce *et al*. 1993*b*; Barwick *et al*. 2009). There are even fewer reports of skeletal measures and growth for tropically adapted cattle in northern Australia (Barwick *et al*. 2009; Wolcott *et al*. 2014) than there are of liveweight gain, and no specific reported studies on non-genetic interventions to manage heifer growth.

In survey data reported for north of the Tropic of Capricorn in Australia, Bortolussi *et al*. (2005) reported median annual steer growth at 90–136 kg for 71% of 392 beef businesses. Much of this region is classed as northern forest by McGowan *et al*. (2014) who reported median potential steer growth of 100 kg/year for 16 properties with an interquartile range of 90–130 kg/year. The primary reasons for low growth are low-fertility soils that are commonly phosphorus-deficient (McCosker and Winks 1994), and low, highly variable rainfall.

McGowan *et al*. (2014) reported that 63% of 32 study herds in the northern forest were continuously mated, a function of insufficient infrastructure to control bulls in very large paddocks. This results in calves being born year-round, and because it is also a low-growth environment weaning occurs 2–3 times per year. Therefore, calves at weaning have a large variation in age and weight. Weaning of calves as light as 100 kg, and at times lighter, is not uncommon. McGowan *et al*. (2014) reported a median weaner weight of 163 kg with an interquartile range for average weaner weight of 152–174 kg in the northern forest region. If calves are weaned at <150 kg on to nutrient-deficient pastures, they require protein and energy supplementation, and if <100 kg require a high-protein ration, to sustain health and growth, thus increasing chances of survival until wet season rains

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(Fordyce and Holroyd 2003). Though recommended, such nutritional management is not always provided, and this may be partially because the specific benefits to growth, subsequent fertility, and business profitability of low-level nutritional support for weaner heifers of all ages has not previously been reported.

There are many anecdotal reports of poor heifer growth in tropical Australia associated with low pregnancy rates. Growth influences time of puberty in heifers, thus pregnancy rates when mated as maidens at either 1, 2 or 3 years of age – all three occur in tropical Queensland. Johnston *et al*. (2009) reported that liveweight at first evidence of puberty was 330–334 $\pm$ 45 kg for north Australian cattle. If heifer growth is 8% lower in females than males (Fordyce *et al*. 1993*a*), in average years not more than 70% of heifers are likely to be able to conceive by 2.5 years of age based on the data above. This is consistent with the report by McGowan *et al*. (2014) who found a median of 67% of heifers pregnant with an interquartile range of 40–81% for this region.

Puberty is the culmination of maturation of the hormonal systems that support ovarian follicular development through to ovulation and subsequent pregnancy if it occurs. During maturation, there is sustained negative feedback from oestradiol-17β on the hypothalamus until late in the process when this feedback switches to positive which supports the final stages of maturation (Kinder *et al*. 1995). Oestrogens are also known to affect growth (Lui and Baron 2011). It was hypothesised that vaccination against a closely related hormone, androstenedione, may reduce the impact of oestradiol-17β during pre-pubertal development and advance puberty and growth (D'Occhio *et al*. 1988).

Poor bull control in the region results in unwanted pregnancies in heifers. Ovariectomy (spaying) is a common practice to prevent pregnancies in those selected for slaughter rather than breeding. Apart from recovery from surgery, this practice removes ovarian hormone supply as stated above. The longer-term effect of these changes on heifer growth in northern Australia had not been reported before this research.

This study aimed to document the growth of Brahman cross heifers post-weaning to 2.5 years of age in the northern forest of Queensland, and to determine the impact of nutritional and hormonal interventions on liveweight, body condition and skeletal growth.

Method

All experiments were approved by the Swan's Lagoon Animal Experimentation and Ethics Committee under the guidelines of 'The Australian Code for the care and Use of Animals for Scientific Purposes' (National Health and Medical Research Council: https://www.nhmrc.gov.au/guidelines-publications/ea28, accessed 27 October 2017).

The research was conducted over eight consecutive years from 1987 to 1995 with six heifer cohorts weaned in 1987 and 1989 to 1993.

Site

The studies were conducted at Swan's Lagoon Research Station (20.0°S, 147.3°E) in the sub-coastal dry tropics. This is within the area recently described by McGowan *et al*. (2014) as northern forest, which encompasses low-animal-growth tropical forested country across northern Australia. General climatic conditions from data collected on the station are summarised in Table 1. The station has predominately low-fertility duplex soils that have low available phosphorus levels averaging 6 mg/kg (Smith *et al*. 2001). The vegetation is an open eucalypt savannah woodland with a pasture predominated by three main grass species: *Heteropogon contortus*, *Bothriochloa petusa*, and *Chrysopogon fallax*. The vegetation supports cattle growth predominantly in the hot moist period, the wet season, commencing with the start of the storm season. Growth typically reduces to maintenance in the cool dry period (early dry season) and progresses to weight loss in the hot dry period (late dry season).

Animals and animal management

The cattle used in this study were mostly red tropically adapted crossbreds that were ~50% *Bos indicus* and 50% *Bos taurus*. The primary source breeds were Brahman and Beef Shorthorn, with small proportions of Angus, Hereford, Sahiwal and other unidentified breeds. Average mature cow liveweight at 445 kg and hip height at 1350 mm when aged 5 years or more, in moderate body condition, and non-pregnant (Smith *et al*. 2001) were similar to averages of 460 kg and 1370 mm, respectively, reported for 50% *Bos indicus* cows across north Queensland (McGowan *et al*. 2014).

A closed herd was maintained from 1985 with replacement breeding animals selected for high growth, good temperament, high calf output, tropical adaptation (to heat, poor nutrition, ectoparasites, and endemic infectious diseases transmitted by tropical ectoparasites), sound udders and teats and attractive conformation. The herd was continuously mated and calves were weaned twice yearly (in early May and late August). Weaners therefore ranged in age from 2 to 11 months, and were separated at weaning into groups based on their liveweight (<100 kg, 100–150 kg, >150 kg).

Six heifer year-of-weaning cohorts were enrolled in this study, with most being selected from the first annual weaning in May. The heifers were randomly selected from within the

Table 1. Swan's Lagoon climate from on-site records, 1966–2007

	Average temperature (°C) Maximum	Minimum	Median rainfall (mm)	Average relative humidity (%) at 9am
Dec.–Apr. (Wet season–Hot moist)	32	21	498	72
May–Aug. (Early-dry season–Cool dry)	27	12	55	70
Sept. –Nov. (Late dry season–Hot dry)	32	17	45	60

entire cohort available. Table 2 details the distribution of heifer weaner weights in each cohort. In 1989 when extremely wet conditions prevented treatment allocation, heifers weaned at different times within the same liveweight category were differentiated by an extra digit in their group description.

All heifers were vaccinated against botulism. At all times, heifers had ready access to plentiful pasture and clean water in troughs. If required for survival, heifers were supplemented in addition to their treatment. On average, this was needed for a few weeks every 3–5 years (Fig. 1). Heifers were grazed at approximately one adult equivalent (equivalent to a 454 kg steer) per 4 ha.

Treatments and management

At weaning, heifers were allocated to a range of treatments by stratified randomisation on their weaning weight. The different treatments included nutritional supplementation, hormonal treatments (androstenedione vaccine and ovariectomy at weaning or 7.5 months of age), and mating age. Table 3 details the allocation of animals in each weaner weight category to the different treatments. Except for the 1989 and 1992 cohorts, each weaning weight × treatment group was replicated 2–3 times (Table 3). At the end of the dry season post-weaning, when average heifer age was approximately 1 year, each allocated cell of heifers was equally and randomly distributed

Table 2. Number of heifers recruited to the study in each weaner size group in each cohort

Weaner size[A]	Weaner size abbreviation	Cohort 1987	1989	1990	1991	1992	1993
Very small (<100 kg)	WV	–	47	–	–	–	–
Small: 100–149 kg	WS	37	63	70	78	76	76
Average: 150–200 kg	WA	201	119	169			72
Average–small: 150–170 kg	W1	–	–	–	75	72	–
Average–big: 170–199 kg	W2	–	–	–	77	72	–
Big: >200 kg	WB	–	–	–	–	–	68

[A]Variations – 1987: WA >149 kg; 1991: WS <149 kg, W2 >172 kg; 1992: WS <142 kg, W2 >167 kg; 1993: WS <144 kg and WB >186 kg.

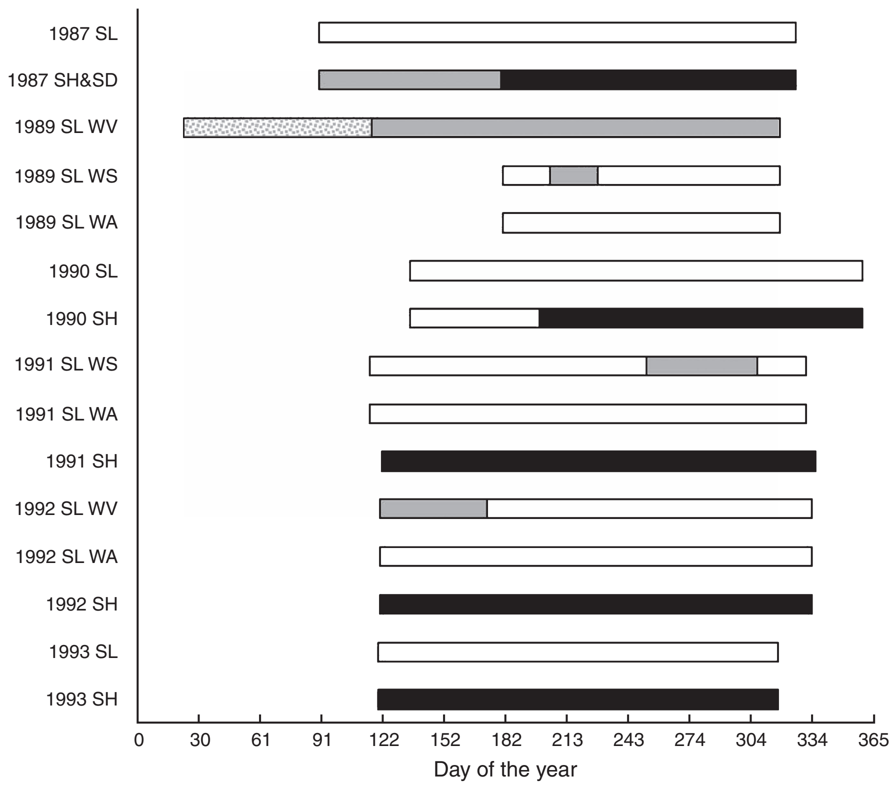

Fig. 1. Supplementation of heifers between weaning and the end of the dry season each year: blank = no supplement; grey = *ad lib.* molasses with 10% cotton seed meal and 5% urea; stippled = 1 kg/day.heifer of 16% protein pellets; black = 2.1 kg/week.heifer of cottonseed meal; digits = year cohort; SL = basic supplementation to sustain health; SH = protein meal supplementation; WV = weaned at <100 kg; WS = Weaned 100–149 kg; WA = Weaned 150–200 kg.

Table 3. Number of heifers allocated to treatments at weaning

Allocation and treatment abbreviation		Cohort 1987	1989	1990	1991	1992	1993
Total heifers		238	229	239	230	220	216
Replicates of treatment × weaner size		2	0	2	3	1	2
Heifers per treatment							
Dry season supplement							
Basic supplementation only	SL	88		119	60	55	108
2100 g/week (as two feeds) of cottonseed meal in the post-weaning dry season	SH	88[A]		120	170	165	108
As above plus 3500 g/week during October in their second dry season	SD	62[A]		–	–	–	–
Androstenedione vaccine							
No vaccine	V0	–	–	139	–	–	142
Injections 0, 1, 3 and 5 months post-weaning	VA	–	–	100	60[D]	55[D]	74[B]
Maiden mating age (mate)			–	–	–	–	–
Mate to calve at 2 years of age	M1	–	–	–	50[D]	55[D]	108
Mate to calve at 3 years of age	M2	–	–	–	–	–	108
Ovariectomy (spay)							
Remained entire	O0	–	–	214	–	–	204
Spayed at weaning or at 7.5 months of age	OS	–	–	25	–	–	12[C]

[A]Post-weaning supplement amounts were 2450 g/week for 2 months and then 3150 g/week for 3 months.
[B]WB heifers were not allocated to Androstenedione vaccination treatments.
[C]Three heifers in each weaner size × dry season supplement combination (no WB) were allocated to OS.
[D]Only SH heifers.

to graze two paddocks till the start of mating at ~26 months of age. Heifers were then allocated within their original weaner liveweight and treatment replicate and yearling paddock to one of three paddocks where they joined mixed-age herds of ~300 cows mated at 3 bulls per 100 females.

Nutritional treatments

The impact of providing 300 g/day of a protein meal, a low-level energy and protein supplement, in the post-weaning dry season was investigated over 5 years. The impact of repeating this supplementation in the second dry season was trialled in the 1987 cohort. Based on visual appraisal of animal health and available pasture, basic supplementation was only provided where it was needed to sustain health. It was not offered when it was obviated by availability of pasture that provided above-maintenance diets, i.e., during the dry seasons of 1990, 1991 and 1993. If required, weaners <100 kg were fed *ad lib*. calf pellets (16% crude protein) and heavier weaner groups were offered *ad lib*. fortified molasses (3% urea and 10% cottonseed meal), distributed twice weekly as 4-and 3-day rations. Fig. 1 details the type and duration of nutritional supplements offered in the post-weaning dry season to each weaner size and treatment group in each cohort.

Hormonal treatments

Preparation of a vaccine against androstenedione is described by D'Occhio *et al*. (1988). Heifers allocated to vaccination (1990–1993; Table 3) were injected subcutaneously 0, 1, 3 and 5 months post-weaning.

Ovariectomy (1990, 1993; Table 3) was conducted at weaning or at 7.5 months of age by flank laparotomy, which was standard regional practice at that time. Time of ovariectomy was selected for secondary studies of ovarian development. After local analgesia was applied to standing heifers and the surgical site disinfected, the skin was incised anterior to the left tubal coxa in an anterio-ventral direction. The peritoneum was incised after blunt dissection through abdominal muscles. Each ovary was located manually, cut from its attachments using shielded scalpels guided immediately adjacent to the ovary, and removed from the abdomen, after which absorbable sutures were inserted to close the skin.

Mating age treatments

Most heifers in the study were first mated at 2 years of age, except those allocated to yearling mating in the 1991–1993 cohorts (Table 3). Heifers mated as yearlings remained segregated as a group from 12 months of age until weaning of their calves the following year when they were again reunited with heifers first-mated at 2 years of age. Each yearling-mated cohort was mated to two fertile 2-year-old bulls of the same breed for 12 weeks from mid-January when they were ~15 months of age. Mating was continuous from 2 years of age.

Measurements

Heifers were mustered at least every 2 months. The standard protocol was to muster and weigh heifers before they would normally come to water in the morning. At each weighing, body condition score was assessed on a 9-point scale (CS9; Holroyd 1978). To achieve conformity with more-recent standards, the scores were transformed to a 5-point scale (CS5; Gaden 2005) using the equation $CS5 = 3 + (CS9 - 6) \times 2/3$. Height was measured at the peak of the sacrum (hip height) at seasonal interfaces. Average daily gains and changes in liveweight, body condition score and height were calculated for the seasonal periods described in Table 1.

Statistical analyses

The data for each cohort were analysed separately due to different experimental designs in each year. Analyses were performed using REML (residual maximum likelihood; Payne *et al*. 2008) methods for all growth variables on each day and season for which data were recorded (Table 4). Repeated-measures analyses were performed on weight, body condition score and height in the post-weaning dry season and from approximately 1 year of age until the time of mating at 2 years of age. In repeated-measures analyses where a sufficient number of well-spaced records were taken over the periods, analyses were performed both with and without the inclusion of splines. A step-down method of removing non-significant interactions was used for all models.

Results

Growth of heifers was highly variable and strongly associated with rainfall patterns. Rainfall measured during the study period is shown in Fig. 2. On average, heifers lost 1–2 body condition score units and gained little liveweight during dry seasons (12 kg from 6 to 12 months; –1 kg from 17–24 months), and recovered body condition with an average gain of 103 kg during wet seasons (Tables 4, 5; Fig. 3). They reached an average of two-thirds of mature liveweight at ~26 months of age. In contrast, hip height gain was steady and gradually decreasing through to ~29 months of age, even during periods of liveweight and body condition loss (Tables 4–6; Fig. 3); average hip height gains in respective 6-month periods after weaning were 97 mm, 75 mm, 42 mm and 21 mm. At ~26 months of age, heifers averaged 95% of mature hip height, having gained in the 21 months from weaning, an average of 74% of the 30 cm average gain expected in the 4 years after weaning (the average difference in hip heights between weaning and maturity). Standard errors of the predicted means across analyses were typically at or close to 0.015 for average daily weight gains, 0.4 mm for average monthly height gain and 0.06 score units for average seasonal body condition score change.

Table 4. Factors included in analytical models for each cohort

Factors and how they were included in analytical models		Cohort 1987	1989	1990	1991	1992	1993
		Single time and seasonal change analyses					
Fixed	Weaner size	x	x[A]	x	x	x	x
	Weaning weight covariate	x	x	x	x	x	x
	Breed	x	–	–	–	–	–
	Dry season supplement	x	x	x	x	x	x
	Androstenedione vaccination	–	–	–	x	x	x
	Ovariectomy	–	–	x	–	–	x
	Maiden mating age	–	–		x	x	x
	Paddock: 1–2 years of age (within Mating age)			x	x	x	x
	Replicate	x	–	x	x	–	x
Random	Post-weaning dry season paddock	x	–	x	x	–	x
		Repeated-measures analyses – additional factors					
Fixed	Day and its significant interactions	x	x	x	x	x	x
Random	Heifer	x	x	x	x	x	x
	Heifer.Day interaction	x	x	x	x	x	x

[A]Combination of weaner size and weaning age.

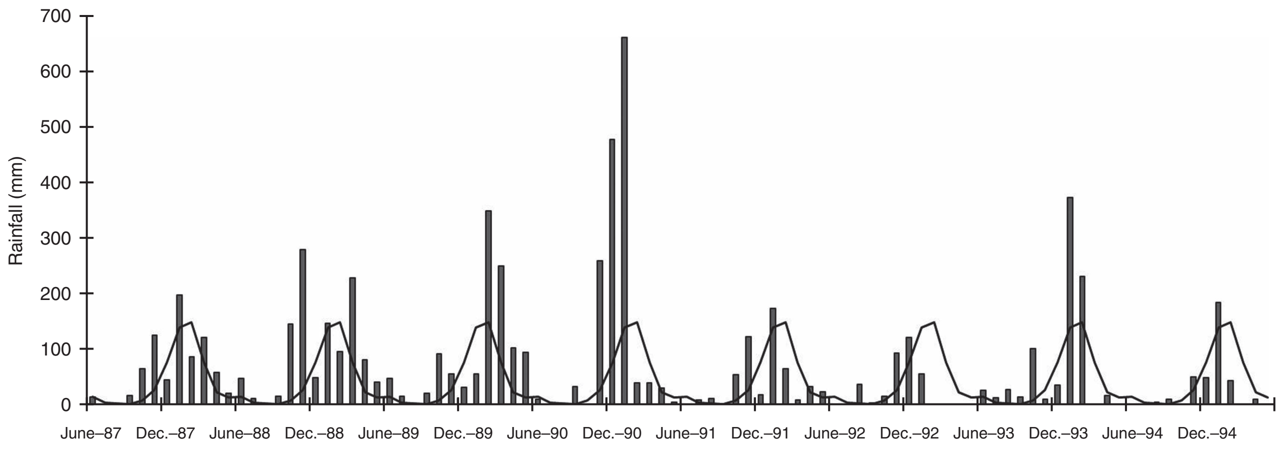

Fig. 2. Monthly rainfall during the study period: bars = recorded rainfall; line = median rainfall.

Table 5. Weaner size and dry season supplement effects on heifer weights and heights up to 2 years of age (see Tables 2 and 3 for treatment abbreviations)
Means with different letters within cohort × parameter time/period differ significantly ($P < 0.05$)

		Weights (kg)						Hip heights (mm)				
Time/Season:		Weaning	Wet start	Mate 1 year	April–May	Wet start	Mate 2 year	Weaning	Wet start	April–May	Wet start	Mate 2 year
Average heifer age (m):		5	12	14	17	24	26	5	12	17	24	26
						Post-weaning dry season supplement						
1987	SL	165	146a	235a	281a	279a	319a	1067a	1116a	1223	1264	–
	SH	163	173b	249b	297b	290b	330b	1059b	1136b	1238	1272	–
	SD	–	–	–	301b	302c	340c	–	–	–	1280	–
1989	SL	132a	159a	215a	275a	255a	258a	–	–	–	–	–
	SH	117b	152b	204b	260b	244b	248b	–	–	–	–	–
1990	SL	153	161a	176a	210a	196a	256a	–	1117a	1177a	1221	–
	SH	153	186b	197b	232b	213b	273b	–	1134b	1191b	1227	–
1991	SL	160	153a	205a	267a	266a	326a	1065	1129	1219	1278	–
	SH	159	166b	219b	278b	274b	334b	1062	1139	1225	1276	–
1992	SL	154	165a	198a	249a	252a	286a	1048	1152a	1210a	1261	–
	SH	154	184b	223b	278b	268b	302b	1044	1171b	1224b	1265	–
1993	SL	169	163a	193a	279a	301	269	1077	1154a	1238	1285	1278
	SH	169	182b	208b	292b	307	272	1074	1172b	1245	1283	1279
						Weaner size group						
1987	WS	149a	146a	226a	271a	272a	314a	1044	1105	1215	1259	–
	WA	178b	174b	257b	315b	302b	342b	1082	1146	1246	1279	–
1989[A]	WV1	86a	161c	217c	279d	260bc	264b	–	–	–	–	–
	WV2	87ab	144b	199b	258b	238a	242a	–	–	–	–	–
	WV3	100b	132a	181a	241a	227a	232a	–	–	–	–	–
	WS1	129c	157c	211c	271c	252b	257b	–	–	–	–	–
	WS2	137d	146b	197b	253ab	238a	241a	–	–	–	–	–
	WA1	158e	175d	233e	293e	271d	275c	–	–	–	–	–
	WA2	174f	174d	229d	278d	261c	261b	–				
1990	WS	132a	154a	169a	204a	192a	249a	–	1092a	1158a	1204a	–
	WA	173b	193b	204b	237b	241b	279b	–	1158b	1211b	1251b	–
1991	WS	134a	151a	203a	261a	259a	320a	1017a	1110a	1205a	1260a	–
	W1	161b	161b	212b	274b	272b	331b	1068b	1135b	1221b	1275b	–
	W2	184c	180c	237c	295c	290c	348c	1105c	1168c	1247c	1294c	–
1992	WS	128a	157a	189a	241a	243a	275a	997a	1131a	1190a	1240a	–
	W1	154b	183b	220b	270b	264b	299b	1051b	1170b	1228b	1268b	–
	W2	181c	184b	223b	279c	273c	308c	1088c	1197c	12 345c	1285c	–
1993	WS	128a	147a	175a	255a	274a	252a	1015a	1116a	1211a	1261a	1257a
	WA	163b	167b	196b	280b	298b	269b	1066b	1154b	1232b	1275a	1268b
	WB	217c	204c	231a	322c	340c	290c	1145c	1220c	1280c	1317b	1311c

[A]Heifers weaned at different times within the liveweight category at weaning were differentiated by an extra digit in their group description.

Change in body condition was almost invariably negatively correlated between seasons, i.e., heifers within treatment groups losing more condition during dry seasons, gained more in preceding or ensuing wet seasons; $r = 0.0$ to -0.9 for 82 of 83 calculations within year × weaner size × weaning supplementation groups. No consistent relationship existed between liveweight gains in the post-weaning dry season and the subsequent wet season. However, within treatment groups, 81% of correlations between heifer liveweight change in their second dry season (at 18–24 months of age) and liveweight gain in either the preceding or subsequent wet seasons were negative. Similarly, there was also a low trend for height gain during wet seasons to be negatively associated with gain during adjacent dry seasons; 72% of correlations were negative.

Growth of unsupplemented heifers was highly variable between years. Average cohort liveweight at ~26 months of age varied from 256 to 319 kg (Table 5). The range in average hip heights at the same age was 5 cm. The 1991 cohort had the lowest gains of all cohorts in liveweight, body condition score and hip height during the post-weaning dry season, a function of seasonal conditions (Figs 2, 3). From the end of the post-weaning dry season, the 1987 and 1990 cohorts, respectively, had the highest and lowest liveweight and height gains, and generally had the highest and lowest body condition scores. Wet season growth was lowest in the 1990 cohort at 50 kg and 5 cm (wet season finished early), and highest in the 1987 cohort at 134 kg and 11 cm (long wet season). Similarly, there was a large range in dry season growth, being lowest in the 1993 cohort at

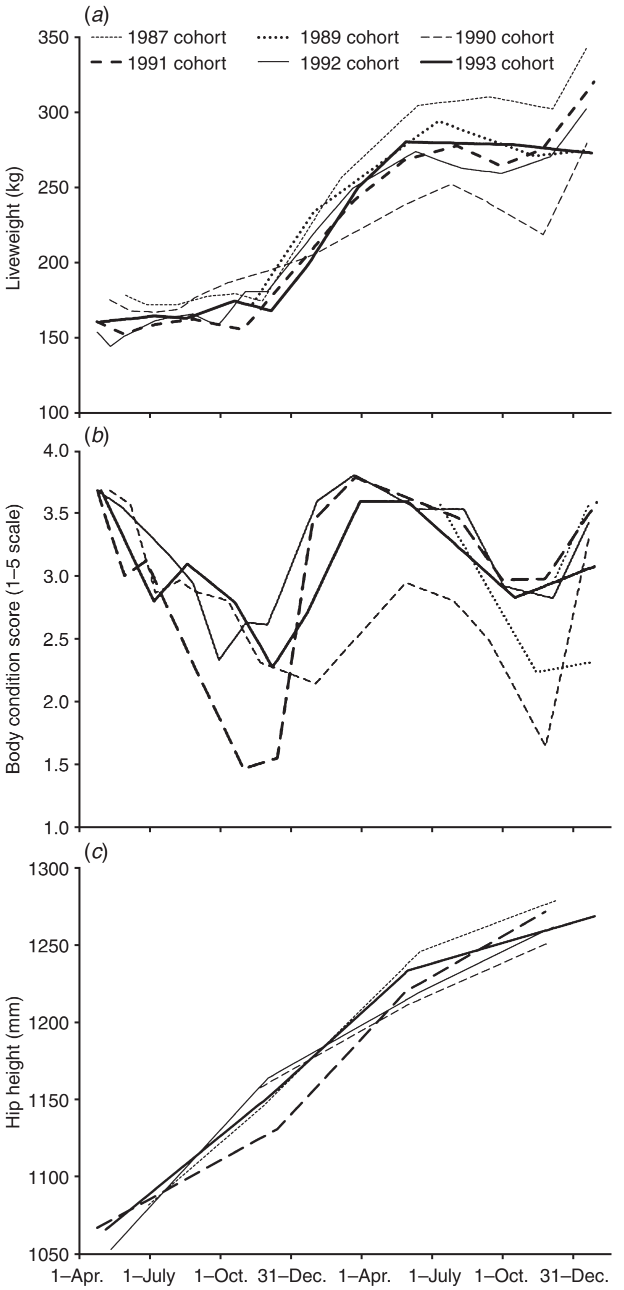

Fig. 3. Average (*a*) liveweights, (*b*) body condition scores and (*c*) hip heights over the study period for each heifer cohort (raw data).

17–24 months of age (–21 kg and +5 cm) and highest in the 1990 cohort at the same age (+14 kg and +4 cm).

Low-level post-weaning dry season supplementation (300 g/day of cottonseed meal) increased gains in liveweight, height and body condition score by an average of 0.1 kg/day, 0.1 mm/day and 0.5 units, respectively, during the supplementation period (Tables 5–7). From this time to ~29 months of age at the end of first mating for most heifers, the difference in average liveweight of 21 kg (13–27 kg) between supplemented and unsupplemented heifers reduced steadily by between 2 and 14 kg (average of 7 kg or 35%) per year (Tables 5, 6). Likewise, the 13–28 mm (average 21 mm) height advantage conferred by post-weaning dry season supplementation was subsequently steadily eroded by 3–5 mm (average 4 mm or 20%) per 100 days (Tables 5, 6). In the second dry season after weaning, heifers that had been given low-level post-weaning dry season supplementation continued to have lower rates of height gain in all cohorts in comparison to non-supplemented heifers; a non-significant trend continued into the following wet season where it was measured in two cohorts (Table 6). Condition score differences due to supplementation were eliminated during the wet season after supplementation as weaners.

In this study where heifers weighing <150 kg were offered low-energy supplements, the average difference between weaner size groups was reduced from ~40 kg to 25 kg in the post-weaning dry season (Table 5). Much of this difference was maintained through to first mating at 2 years of age. Heavier heifers as weaners gained less height in each six-month period through to 2 years of age (Table 6). Therefore, in contrast to liveweight, hip height difference between heifer groups allocated on liveweight at weaning gradually reduced between weaning and 2-year-old mating from ~6 to 3 cm (Table 5). Body condition score was higher in bigger weaners in the middle of the post-weaning dry season (Table 7), but thereafter, weaner liveweight had no effect on scores.

One month after weaning of the 1990 heifer cohort, ovariectomy had reduced liveweight by 5 kg ($P < 0.05$). This effect disappeared within a further month and there were no other recorded effects of ovariectomy in that cohort. In contrast, ovariectomised 1993 weaners were 5–10 kg lighter than entire heifers from mid-August after weaning to 2 years of age ($P < 0.05$). This was associated with a 17-mm hip height difference in the August after weaning, with no significant subsequent compensation. Body condition score was unaffected by ovariectomy.

Heifers pregnant initially at one year of age were 12–38 kg lighter, 11–14 mm shorter and up to 0.5 body condition score units lower than non-pregnant heifers at 26 months of age (Table 8).

Androstenedione vaccination had no effect on any growth parameter in any cohort.

Discussion

This research demonstrated the highly variable liveweight gain of juvenile female beef cattle between seasons in the northern forest country type of northern Australia, a function of the variation in rainfall between years, and the concentration of at least 75% of rainfall on average within 4 summer months, typically December–March. Average growth of non-supplemented heifers in the year after weaning was ~105 kg. This is consistent with the report of McLennan *et al.* (1988) that long-term average annual yearling steer growth is 100 kg at the same site with similar variation in annual and seasonal growth. Because of low and variable growth in this environment, many heifers are unable to reach weights sufficient to achieve high pregnancy rates in low-rainfall years. As the coefficient of variation for weight at puberty is 14% (Johnston *et al.* 2009) and assuming 95% of pubertal animals conceive, then to have 90% of heifers pregnant during maiden mating, they need to reach a liveweight at which the ratio with mature liveweight is at least 10% units

Table 6. Weaner size and dry season supplement effects on heifer average daily weights gains and monthly hip height gains up to 2 years of age (see Tables 2 and 3 for treatment abbreviations)

Means with different letters within cohort × parameter time/period differ significantly ($P < 0.05$)

		Growth rates (kg/day)						Hip height gain (mm/month)			
Time/Season: Average heifer age (m):		Early dry 5–9	Late dry 9–12	Wet 12–17	Early dry 17–21	Late dry 21–24	Wet 24–29	Dry 5–12	Wet 12–17	Dry 17–24	Wet 24–29
		Post-weaning dry season supplement									
1987	SL	–0.06a	–0.07a	0.65a	0.07	–0.06	0.59a	10.0a	15.4	7.5a	–
	SH	0.08b	0.13b	0.61b	0.08	–0.12	0.59a	15.7b	14.7	5.8b	–
	SD	–	–	–	–	–0.09	0.55b	–	–	8.0a	–
1989	SL	–	0.19a	0.48a	–0.16		0.53	–	–	–	–
	SH	–	0.14b	0.45b	–0.13		0.51	–	–	–	–
1990	SL	–0.04a	0.13a	0.26	0.01a	–0.24	0.91	–	9.3	7.3a	–
	SH	0.10b	0.24b	0.24	–0.01b	–0.26	0.90	–	8.9	6.1b	–
1991	SL	–0.02a	0.01	0.67	0.18	–0.02	0.60	8.4a	16.3	8.9a	–
	SH	0.07b	0.00	0.68	0.16	–0.03	0.60	10.1b	15.4	7.5b	–
1992	SL	0.09a	0.00a	0.45a	–0.08a	0.07a	0.78	14.3a	8.8a	8.1a	7.6
	SH	0.19b	0.07b	0.49b	–0.18b	0.01b	0.75	17.9b	8.4b	7.0b	6.1
1993	SL	–0.03a	–0.02	0.66	0.25	0.04	0.53	11.0a	14.5	6.8a	4.8
	SH	0.06b	0.06	0.63	0.26	0.01	0.49	14.0b	12.6	5.9b	2.8
		Weaner size group									
1987	WS	0.01	0.03	0.62a	0.09	–0.07	0.59	12.5	15.7	7.9	–
	WA	0.01	0.02	0.65b	0.06	–0.10	0.58	13.1	14.4	6.1	–
1989[A]	WV1	–	0.31a	0.49a	–0.16		0.52	–	–	–	–
	WV2	–	0.25ab	0.47ab	–0.16		0.53	–	–	–	–
	WV3	–	0.23abc	0.47abc	–0.12		0.51	–	–	–	–
	WS1	–	0.21b	0.47ab	–0.15		0.54	–	–	–	–
	WS2	–	0.09d	0.44bc	–0.12		0.54	–	–	–	–
	WA1	–	0.13cd	0.49a	–0.17		0.51	–	–	–	–
	WA2	–	–0.05e	0.43c	–0.14		0.48	–	–	–	–
1990	WS	0.04	0.19	0.26	0.01	–0.21a	0.89	–	10.1a	7.1a	–
	WA	0.01	0.18	0.23	0.01	–0.28b	0.91	–	8.2b	6.2b	–
1991	WS	0.08a	0.07a	0.65a	0.16	0.01	0.60	11.7a	17.3a	8.5a	–
	W1	0.02b	–0.03b	0.68ab	0.16	–0.02	0.60	8.4b	15.6b	8.7a	–
	W2	–0.02c	–0.02b	0.69b	0.19	–0.06	0.60	7.7b	14.6b	7.4b	–
1992	WS	0.18a	0.07a	0.44a	–0.10	0.07a	0.76	17.9a	9.4a	8.7a	6.6
	W1	0.12b	0.15b	0.46a	–0.15	0.03b	0.74	15.8b	9.0a	7.0b	7.1
	W2	0.12b	–0.12c	0.50b	–0.15	0.02b	0.81	14.5c	7.4b	6.9b	6.7
1993	WS	0.07a	0.10a	0.62	0.24	0.05	0.50	14.3a	16.5a	7.6a	3.8
	WA	0.00b	0.04a	0.64	0.26	0.02	0.51	12.5b	13.6b	6.5b	1.6
	WB	–0.03b	–0.09b	0.68	0.26	0.01	0.51	10.6c	10.6c	5.1c	6.0

[A]Heifers weaned at different times within the liveweight category at weaning were differentiated by an extra digit in their group description.

higher than that at puberty; for example, if puberty is at 63% of mature weight, heifers need to reach ~73% of mature liveweight during mating, which is 325 kg for cows with a 445-kg mature liveweight. Within cohort, up to 67% (average of 25%) of heifers weaned at 100–149 kg and up to 25% (average of 9%) of those weaned at 150+ kg within year group did not reach this target weight by 29 months of age, coinciding with the end of mating as a 2 year old.

Low-level supplementation in the post-weaning dry season that increased daily liveweight gain by an average of 0.1 kg/day preserved an average of approximately one-half of a body condition score over a 7-month period. This may be a critical reserve in years with extended dry seasons, thus reducing the risk of mortality. Supplementation did not significantly increase the percentage of any size weaners reaching the above-mentioned target liveweight of 325 kg at 29 months of age. The liveweight advantage due to low-level supplementation averaged 21 kg at the end of the post-weaning dry season; compensatory growth in unsupplemented heifers resulted in this difference averaging 14 kg and reducing at the end of the second dry season post-weaning at 24 months of age. In small weaner heifers (100–149 kg), the 15-kg extra weight preserved through fortified molasses supplementation they received would also contribute to reducing the risk of mortality.

A third of the liveweight advantage due to low-level supplementation in the post-weaning dry season was lost in the following year, a well-recognised phenomenon known as compensatory gain (Winks *et al*. 1979). Ryan *et al*. (1990*a*, 1990*b*) explained this where growth of animals that have been on a low plane of nutrition and then restored to a high-quality diet, have reduced maintenance requirements initially, followed by higher feed intakes in comparison to animals continually fed

Table 7. Weaner size and dry season supplement effects on heifer average body condition scores and seasonal changes in the post-weaning year (see Tables 2 and 3 for treatment abbreviations)
Means with different letters within cohort × parameter time/period differ significantly ($P < 0.05$)

Time/Season:		Condition			Condition change		
		Weaning	Wet start	Mate 1 year	Early dry	Late dry	Wet
Average heifer age:		9	12	14	5–9	9–12	12–17
Post-weaning dry season supplement							
1990	SL	2.5a	2.1a	2.2a	–0.9a	–0.5a	0.8a
	SH	2.9b	2.6b	2.3b	–0.5b	–0.2b	0.4b
1991	SL	2.4	1.8a	3.5	–0.7	–0.6	2.1a
	SH	2.8	2.5b	3.5	–0.3	–0.4	1.5b
1992	SL	2.9a	2.3a	3.5	–0.6a	–0.7a	1.2a
	SH	3.1b	2.7b	3.6	–0.4b	–0.5b	0.9b
1993	SL	2.8a	2.1a	2.6	0.2a	–0.7a	1.4a
	SH	3.1b	2.4b	2.7	0.3b	–0.8b	1.2b
Weaner size group							
1990	WS	2.5a	2.2a	2.2	–0.8	–0.3	0.7a
	WA	2.9b	2.5b	2.3	–0.6	–0.4	0.5b
1991	WS	2.5	2.2	3.5	–0.5	–0.3	1.7
	W1	2.6	2.0	3.4	–0.5	–0.6	1.9
	W2	2.7	2.1	3.5	–0.6	–0.6	1.8
1992	WS	2.9a	2.5b	3.5a	–0.4	–0.4a	1.0a
	W1	2.9a	2.6a	3.6b	–0.6	–0.3a	0.9a
	W2	3.3b	2.3b	3.5ab	–0.4	–0.9b	1.2b
1993	WS	2.8a	2.2	2.6	0.3a	–0.5a	1.2
	WA	3.1b	2.3	2.7	0.3a	–0.8b	1.3
	WB	3.2b	2.3	2.6	0.1b	–0.9b	1.3

Table 8. Maiden mating age effects on heifer growth between 17 months and the start of maiden mating at 2 years of age
Means with different letters within cohort × parameter time/period differ significantly ($P < 0.05$)

Time	Age (months)	1991 cohort			1992 cohort		
		Mate 1 year – Pregnant	Mate 1 year – Not Pregnant	Mate 2 year	Mate 1 year – Pregnant	Mate 1 year – Not Pregnant	Mate 2 year
Weight (kg)							
April/May	17	279	276	272	256a	256a	270b
Aug./Sept.	21	281a	279a	293b	248a	250a	261b
Wet start	24	275a	291b	281a	240a	243a	278b
Mate 2 year	26	294a	332b	331b	273a	285b	307c
Growth rate (kg/day)							
Early dry	17–21	0.03a	0.05a	0.29b	–0.13	0.10	–0.16
Late dry	21–24	–0.05a	0.11b	–0.10a	–0.08a	–0.06a	0.15b
Wet	24–29	0.25a	0.64b	0.70c	0.44a	0.95c	0.79b
Hip height (mm)							
April/May	17	1226	1226	1222	1198a	1217b	1218b
Wet start	24	1265	1268	1278	1238a	1260b	1263b
Hip height change (mm/day)							
Dry	17–24	0.214a	0.228a	0.31b	0.23	0.24	0.26
Wet	24–29				0.08a	0.28b	0.25b
Body condition score (1–5)							
April/May	17				3.4a	3.2b	3.6c
Aug./Sept.	21	3.3a	3.2a	3.7b	3.5a	3.3b	3.6a
Wet start	24	2.8	3.1	2.9	2.4a	2.3a	2.9c
Mate 2 year	26	2.8a	3.8b	3.8b	2.8a	3.4b	3.6c
Body condition score change (1–5)							
Early dry	17–21	–0.6a	–0.5a	–0.2b	0.0	0.0	0.0
Late dry	21–24	–0.4a	0.0b	–0.7c	–1.1a	–1.0a	–0.6b
Wet	24–29	0.0a	0.3b	0.5c	0.0a	1.4b	0.9c

a high-quality diet. Ryan *et al*. (1990*a*, 1990*b*) demonstrated full compensation in liveweight over an 11-month period. Our studies have shown compensation can occur over more than 1 year. In a study with steers that were supplemented in consecutive dry seasons in comparison to non-supplemented steers, McLennan (2014) also reported compensation in liveweight occurring over more than 1 year.

Compensatory growth as indicated by negative correlations of liveweight and body condition score changes between consecutive wet and dry seasons also occurred; i.e. heifers able to gain more liveweight and body condition during wet seasons, lost it at greater rates during dry seasons. A possible reason for this could be differential adaptation to stressors between dry and wet seasons; i.e., growth advantage in one season due to better adaptation to prevailing stressors may be lost in a subsequent season when different stressors exist. Wet season stressors include buffalo fly (*Haemotobia iritans exigua*), cattle tick (*Ripicephalus microplus*), high temperatures and humidity, viruses transmitted by vectors more likely to be present during moist conditions, and irregular instances of extreme weather. In contrast, the major stressors in the dry season are sub-maintenance nutrition throughout, high ambient temperatures late in the dry season, and ongoing low-level ectoparasitism. Another possible component of the seasonal effect is photoperiod as Rius *et al*. (2005) showed that long daylength alone can increase average daily gain and hip height gain in dairy calves over a 7-month period by 10% and 15%, when Control calves gained ~1 kg/day and 1.20 mm/day, respectively. Our studies were unable to verify such an effect.

At 6 months of age, heifers at weaning were on average gaining height at ~0.60 mm/day, with the rate of height gain decelerating by ~0.00075 mm/day thereafter; this result is not to be extrapolated beyond 2.5 years of age. This deceleration explains the inverse relationship between 6-monthly height gains and liveweight at weaning as taller heifers would on average be older at weaning. Deceleration of height gain is expected when annual weight gain remains relatively constant as these are single- and multi-dimensional measures, respectively.

A feature of this research was that skeletal growth, a function of bone elongation, continues while losing soft body tissue, also reported by Fordyce *et al*. (2013). This occurred during both the first and second dry seasons after weaning when reductions of up to two body condition score units were seen. Though bone growth continued during nutritional deprivation, it was retarded. Low-level dry season supplementation had smaller effects on height gain than occurred due to year effects within season. Heifers pregnant as yearlings had retarded bone growth through to 2.5 years of age in comparison to those non-pregnant as yearlings as a result of the nutritional demands of gestation and lactation. The overall impact of generally low nutrition in the study reported here was reflected in average height of the heifers at 24 months of age at the end of a dry season being 52 mm lower than the tropical composites used in the study of Fordyce *et al*. (2013), which had a mature height only 25 mm higher and which had received a higher plane of nutrition from weaning.

Other reports have also found significant differences in skeletal development of young cattle experiencing different nutrition (Matthews *et al*. 2008; McLennan 2014). Davis Rincker *et al*. (2008) showed that increasing growth rate from ~0.6 kg/day to ~1.1 kg/day in dairy heifers aged 2 months of age increased height gain by 40 mm over 12 weeks when low-growth heifers gained 100 mm in height. Gabler and Heinrichs (2003) presented evidence from studies with 4–9-month-old dairy calves that increasing dietary protein level, but keeping diet energy levels constant, increased skeletal growth without increasing overall bodyweight gain, thus indicating the importance of dietary protein in skeletal growth management. Silva *et al*. (2016) showed that restricting dietary energy reduced hip height gain in young steers from 1.05 mm to just 0.42 mm/day during a 103-day feeding period with protein restriction reducing gain even further to 0.30 mm/day.

For the first time for beef cattle in northern Australia, our research showed that compensatory skeletal development occurs following dry seasons in juvenile female cattle, and this compensation can continue for at least 12 months. Silva *et al*. (2014) had reported a non-significant trend for compensatory growth of the skeleton in a penned steer study over a short period of just 94 days. The review of Boersma and Wit (1997) from several species concluded that under-nutrition can slow overall body growth, including epiphyseal plate growth, but once growth restrictions are removed, the rate of skeletal growth can increase to return the animal to a growth plane expected without growth restriction. Bone elongation is a result of cell proliferation, hypertrophy and vascular invasion in epiphyseal growth plates. Fordyce *et al*. (2013) indicated that epiphyseal growth plate closure occurs at an average of 4.5 years of age in north Australian female beef cattle. Limited available studies from several mammalian species, including humans, suggest that ultimate bone growth may be determined by defined limited lifetime cell proliferation within growth plates (Lui and Baron 2011). Though elevated oestrogen levels around puberty are associated with higher rates of epiphyseal plate growth (Boersma and Wit 1997; Kuczmarski *et al*. 2002; cited by Lui and Baron 2011), slowing of epiphyseal plate growth is promoted by, though not dependent on, oestrogen (Lui and Baron 2011). Despite these known effects of oestrogen, vaccination against the closely related androstenedione had no impact on height gain in our studies.

The review of Boersma and Wit (1997) described accelerated or compensatory elongated bone growth following retardation as canalisation. Cell programming at the growth plate level may be responsible for recovery of bone elongation to predetermined age-related stages (Lui and Baron 2011). Gafni *et al*. (2001) previously described the possible mechanism for this using a study with rabbits where growth retardation appeared to cause growth plate senescence. Once nutritional restrictions are removed, the growth plate is more 'physiologically immature' and therefore there are higher rates of bone elongation than in animals that have not experienced the same level of growth restriction. Evidence of canalisation in the heifers in this study is provided by them being 100 mm shorter at 12 months of age than tropical composites reared under better nutritional conditions that are only slightly taller at maturity (Fordyce *et al*. 2013) with this difference being halved by 24 months age, and was expected to be 25 mm by 4.5 years of age. Whatever mechanisms are operating, female cattle may only be able to achieve growth plate compensatory growth till ~4.5 years of age as anecdotal evidence is that in very low growth regions, cows fail to reach mature size if they do not attain it at 4.5 years of age as a result of extended growth retardation; this is called stunting. This hypothesis remains to be proven.

Several studies have shown substantial reductions in daily liveweight gain following ovariectomy of heifers; these include retardation by 0.13 kg/day in the 2 months following surgery (Fordyce *et al*. 2001), 0.4 kg/day between 11 days before and 21 days after surgery (Petherick *et al*. 2011), and 0.11 kg/day in the 42 days following surgery (McCosker *et al*. 2010). Fordyce *et al*. (2001) also showed no subsequent compensatory growth. These outcomes are consistent with our findings of short-term growth retardation without subsequent compensatory growth. The reason for no growth compensation is unknown. Ovariectomy being an acute rather than chronic intervention may be associated with the reason. Also, the removal of ovaries that are a significant source of oestrogen, which promotes growth of epiphyseal plates as discussed above, may be a contributing cause.

The main conclusion from this research is that heifer growth in the dry tropical northern forest region of northern Australia is highly variable between seasons and years, thus limiting significant proportions of some cohorts from reaching target weights for mating at 2 years of age. Gains in hip height continually decelerated from weaning and were less affected by under-nutrition than either liveweight or body condition. Periods of poor nutrition, including that secondary to nutritional demand for reproduction were associated with suppressed daily gains in liveweight, hip height and reduction in body condition score. Subsequent to periods of poor nutrition, partial to full compensation occurred for all measures, with rate of recovery being highest for body condition. Though low-level supplementation in the post weaning dry season preserved half a condition score, liveweight advantages conferred by 2 years of age were very small. Ovariectomy had negative effects on growth, but vaccination had no measurable impacts.

Conflict of interest

The authors declare no conflicts of interest.

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