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Measures of Bone Morphology in the Medial and Lateral Condyles of the Metacarpus in Beef Cross Dairy Cattle at 8–12 and 24 Months of Age

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Abstract: Bone morphology in the mid-diaphysis of the metacarpus in cattle and the effect of puberty and age has been well described. However, there is limited information on how age and not attaining puberty affects bone morphology in the epiphysis of the metacarpus. The metacarpus is comprised of the third and fourth metacarpal bones fused together to create a medial and lateral epiphysis. When a cow is in stance phase there is greater pressure on the medial claw; however, the effect of this difference in loading on bone has not been described. Therefore, the aim of this experiment was to describe bone morphology in the medial and lateral epiphysis of the metacarpus at the age of puberty in steers. The metacarpus was collected from beef cross dairy steers at approximately one and two years of age. The distal epiphysis of the metacarpus was scanned using peripheral quantitative computed tomography (pQCT). Measures were corrected for body weight and demonstrated a lack of bone growth cessation at one year of age. The lack of difference in bone morphology in the medial and lateral condyles of the distal metacarpus reflects the even loading distribution observed in the forelimb of cattle.

Keywords: epiphysis; metacarpus; puberty; bone strength; pQCT

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1. Introduction

Bone responds to mechanical loading by changes in mass and architecture to maintain strain within physiological limits [1]. For example, increases in body weight result in an increase in strain on bone, requiring greater bone strength [1]. The relationship between bone and body weight has been described in the metaphysis of both the humerus and metacarpus in cattle [2,3] and in the metacarpus of foals [4]. The response to increases in body weight or loading are dependent on the location of the bone and the stage of maturation of the animal. To increase resistance to bending, bone must increase either bone mineral content or its cross-sectional area. The most efficient way to strengthen bone is by increasing bone area via appositional growth. Appositional growth occurs when bone is taken from the endosteal surface and placed on the periosteal surface to increase bone cross sectional area [5,6]. However, after bone maturity, a greater bone strength is achieved by increasing bone mineral content.

The strength and shape of a bone is also determined by its location and function. In cattle, distal bones such as the metacarpus are under compressional forces as a result of standing and locomotion, requiring a lower resistance to bending than bones in the proximal limb [7]. Bones in the distal limb have limited longitudinal growth potential compared with bones in the proximal limb, so they mature earlier [8]. For example, the metacarpus in a calf is 90% of its mature length at birth [9]. Proximal limbs such as the humerus undergo significant torsional loading by surrounding muscles requiring a greater resistance to bending [7,10,11]. Therefore, the humerus is required to continue growing in response to increases in body weight resulting in a later bone maturity (3.5–4 years of age for cattle) [12].

An important driver of bone maturity in cattle is the hormonal cue from puberty acquisition. In cattle, puberty is defined as the onset of regular oestrus cycles in a heifer and the production of viable sperm in bulls [13,14]. As a cow reaches a pubertal weight of approximately 48–51% of its mature weight [15], increases in oestrogen from the ovaries in heifers and the testes in bulls results in the elongation of long bones (growth spurt) [16]. In the later stages of puberty acquisition, longitudinal bone growth slows promoting physeal closure and increases in endosteal and trabecular bone production [17,18]. However, a lack of oestrogen in males because of castration (steers) prevents puberty acquisition and the hormonal cue for physeal closure. As a result, bone maturity will be delayed resulting in a longer bone [19,20]. At 9 months of age, bulls will be heavier than steers of the same age due to the promotion of muscling via testosterone. Conversely, at 12 months of age, steers are significantly taller than bulls due to the absence of testosterone and puberty. The lack of difference in body weight before 9 months but difference in height at 12 months demonstrates how the time of puberty plays a crucial role in the divergence of body composition in steers and bulls [21].

In cattle, the metacarpus is composed of the third (MC3) and fourth (MC4) metacarpal bones fused together providing two separate epiphyses for the third (medial side) and fourth (lateral side) condyle. The asymmetry of the two bones has been well described with the MC4 being longer than the MC3 [22]. In addition, the medial hoof is larger than the lateral indicating an asymmetrical loading pattern [23]. When the cow is standing square, the medial claw is subjected to more pressure than the lateral claw with the maximum pressure located in the heel of the hoof in both the medial and lateral claw [24]. Based on pressure plates, locomotion in the forelimb can be divided into five phases; heel strike, maximum braking, midstance, maximum propulsion and push off [25]. However, the distribution of pressure is altered during locomotion. When analyzing pressure distribution and vertical forces on the claws in cows walking on a flat surface, there was minimal differences between medial and lateral claws in the forelimb [25]. Although the loading of the bovine claw has been well described, little research has looked in to how the differences in claw size and loading pattern in the bovine forelimb affects bone morphology and changes with age in the metacarpus. While bone morphology in the metacarpus of cattle has been well described in the mid-diaphyseal site, limited research has examined growth in the epiphysis and the effect of castration on bone. Therefore, the aim of this experiment was to describe bone morphology in the medial and lateral epiphysis of the metacarpus at the pubertal age in steers (approximately one year).

2. Materials and Methods

The experiment included a cohort of 81 Hereford-sired weaner steers from predominantly Friesian-Jersey crossbred dams that were purchased from a single commercial calf rearer at approximately 100 kg (3 months of age). The calves were reared using a commercial calf rearing system that involved weaning calves at 70 kg and feeding high protein meal until approximately 100 kg body weight [26]. The predominant forage on offer was perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*). To achieve target growth rates during periods of low pasture growth, forage crops (plantain and chicory) were used to supplement the base pasture diet.

Calves were managed as a single mob and randomly assigned to a slaughter group (8, 10, 12 or 24 months) at 8 months of age with each treatment group balanced for body weight at 8 months of age [27]. Animals continued to be grazed in a single mob. Upon reaching their slaughter age, cattle were slaughtered at a commercial abattoir. Prior to slaughter, measures of body weight were obtained.

All procedures related to the management and use of these animals were approved by Massey University Animal Ethics Committee (MUAEC 17/73).

2.1. Sample Collection

Unfasted body weight and height was recorded on the farm the day before slaughter with the exclusion of height at 24 months of age. Cattle in the 24 months of age slaughter group were measured for height at 20 months of age due to resource constraints.

Cattle underwent commercial slaughter and standard dressing procedures. The left metacarpus was collected at the time of slaughter, double wrapped in cling plastic and stored at −20 °C until scanning. Metacarpus length was measured using the lateral aspect of the lateral condyle of the MC4 and the proximal aspect of the lateral MC4.

2.2. pQCT Scanning

The pQCT scanning was carried out using an adapted protocol by Gibson, Dittmer, Hickson, Back and Rogers [2]. Briefly, pQCT scanning was carried out using an XCT 2000 peripheral computed tomography machine (Stratec Medical, Pforzheim, Germany). For each bone, a 2 mm slice with a voxel size of 0.3 mm was obtained at 3 mm, 5 mm and 7 mm starting at the lateral aspect of the lateral condyle of the MC4 and moving proximally up the bone (Figure 1). Scan sites were selected based on the pattern of sclerosis observed in the palmer aspect of the distal epiphysis of the metacarpus in response to the loading provided by the sesamoid bones Firth, et al. [28].

Figure 1. Longitudinal section of metacarpus with 3,5,7 mm scan locations detailed.

Data was extracted for the medial and lateral condyle at each scan. Data derived from the scan included measures of total bone area, total bone density, total bone content, trabecular bone density, cortical bone area and cortical bone density. Cortical bone area percentage was calculated as cortical bone area divided by total bone area.

2.3. Statistical Analysis

Statistical analysis was conducted using the Statistical Analysis System software version 9.4 (SAS institute Inc., Carey, NC, USA).

Animals were grouped by age as either 8–12 months of age or 24 months. All analyses were conducted using general linear models. To compare bone morphology between age groups, the model included the covariate body weight and the fixed effect of age group (8–12 or 24 months) run separately for the medial and lateral condyle and at each scan site. To compare bone morphology in the medial and lateral condyle, the model included the covariate of body weight and the fixed effect of condyle. The model was run separately for age group and scan site. To compare bone morphology at each scan site, a model was run using body weight as a covariate and the fixed effect of scan site. The model was run for each age group and condyle.

3. Results

There was a positive linear relationship between height and body weight from 8–12 months of age. At 20 months of age, there was minimal increases in height with body weight gain (Figure 2 and Table 1). At 24 months old, steers had a significantly greater body weight, height and metacarpus length than 8–12-month-old steers (Table 1).

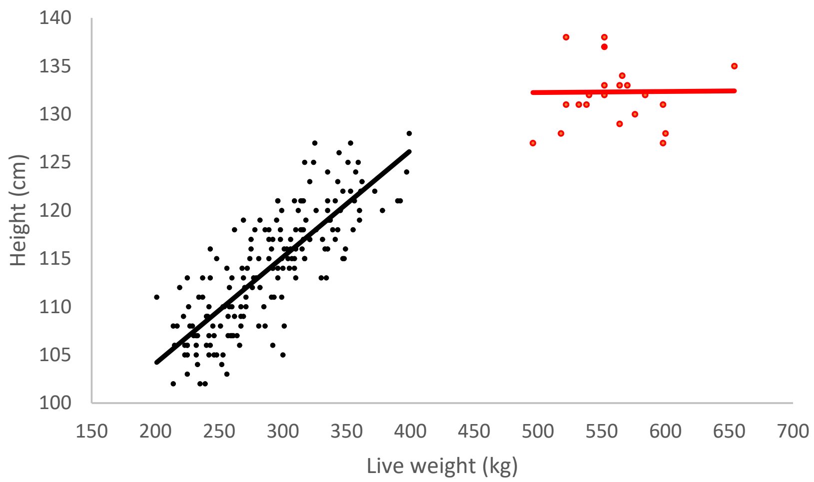

Figure 2. Plot of height vs body weight for beef cross dairy bred steers from 8–12 months (black) and 20/24 months of age (red) with trendline derived from Table 2.

Table 1. Means and standard error for body weight, height and metacarpus length for 8–12-month-old and 24 months beef cross dairy steers.

Age (Months)	8–12	20 (24 Month Age Group)	24	*p*-Value
n	59	22	22	
Weight (kg)	302.1 ± 5.7		580.1 ± 9.2	<0.001
Height (cm)	114.1 ± 0.4	132.3 ± 1.3		<0.001
Metacarpus length (mm)	204.7 ± 0.8		221.6 ± 1.4	<0.001

The models had a poor-to-moderate fit for trabecular density and trabecular area. In contrast, the models had a good fit for the measures of subcortical/cortical bone.

At the 3 mm scan, there was a positive association of body weight with bone area and content. The coefficients for body weight with bone area and content at 24 months old being ~20% greater than those observed in the yearling cohort (Table 2). There was an apparent negative relationship with total density and increasing body weight in the 24-month-old steers. This apparent negative relationship of body weight with measures of density in the 24-month-old age groups was also observed for trabecular and cortical-subcortical density.

At the 5 mm scan, there was a similar pattern of relationships as observed with the 3 mm scan. Measures of bone area and total content increased with increasing weight. The relationship (coefficient) for size at 24 months was nearly twice that of the yearling cohort. However, for total bone content, the yearling group had a coefficient similar to the relative increase in size such that a 1 kg increase in body weight resulted in almost a 1 mg/mm increase in bone content, whereas in the 24-month-old cohort increases in total bone content per 1 kg of body weight was approximately half that observed for total area. These differences in coefficients in part explain the apparent negative association of body weight with total density in the 24-month-old cohort. The same apparent negative association of body weight with total density was observed in the subcortical—cortical bone density values for the 24-month-old steers

The results from the 7 mm scan reflected the same pattern as observed in the 3 mm and 5 mm scans despite this site being more proximal from the articular surface of the epiphysis (Table 2). Body weight positively influenced total bone area in both the medial and lateral condyles and total bone content, cortical bone density and cortical bone content in the lateral condyle.

At the 3 mm scan, measures of total bone content and trabecular bone density were not significantly different between the medial and lateral condyles at 8–12 months of age (Table 3). Total and trabecular bone area were greater in the lateral condyle in steers aged 8–12 months. Cortical bone area, content and density was greater in the medial condyle than the lateral at 8–12 months of age. At the 5 mm scan there was no difference in bone measures between the medial and lateral condyle at both 8–12 and 24 months apart from trabecular density at 24 months of age. At the 7 mm scan there was no difference in bone measures between the medial and lateral condyle at both 8–12 and 24 months. The significant association of body weight with cortical bone measures was lost with age.

Table 2. Intercept and coefficient of pQCT bone parameters at the sites 3, 5 and 7 mm from the distal aspect of the articulating surface of the metacarpus. Values are adjusted for body weight of steers at 8–12 months and 24 months old with the interaction of body weight and group.

Measure		**Intercept**		**Coefficient**		***p*-Value**			
		8–12 m	**24 m**	**8–12 m**	**24 m**	**Age**	**Body Weight**	**Age × Body Weight interaction**	**R^2**
Height (cm)		82.0	131.7	0.1	0.001	<0.001	<0.001	<0.001	0.81
Bone length (mm)		183.5	137.9	0.07	0.10	0.010	<0.001	0.025	0.74
3-mm									
Total bone area (mm^2)	Medial	582.5	139.9	0.7	1.5	0.044	<0.001	0.067	0.70
	Lateral	651.5	305.8	0.6	1.2	0.101	<0.001	0.117	0.69
Total bone density (mg/cm^3)	Medial	436.6	938.6	0.4	−0.4	<0.001	0.962	<0.001	0.69
	Lateral	417.6	826.2	0.4	−0.2	0.002	0.319	0.009	0.76
Total bone content (mg/mm)	Medial	223.7	334.8	0.8	0.6	0.328	<0.001	0.417	0.91
	Lateral	247.8	331.4	0.7	0.7	0.447	<0.001	0.871	0.93
Trabecular bone area (mm^2)	Medial	717.6	−383.7	−0.3	1.5	0.001	0.067	0.004	0.33
	Lateral	785.6	−131.4	−0.3	1.0	0.009	0.304	0.039	0.51
Trabecular bone density (mg/cm^3)	Medial	488.1	640.6	0.1	−0.2	0.029	0.780	0.017	0.12
	Lateral	468.1	658.0	0.2	−0.2	0.016	0.914	0.020	0.41
Cortical/subcortical bone area (mm^2)	Medial	−135.1	523.1	1.1	−0.02	<0.001	0.005	0.004	0.88
	Lateral	−134.0	437.2	1.0	0.2	0.007	0.003	0.060	0.91
Cortical/subcortical bone density (mg/cm^3)	Medial	501.2	941.9	0.6	−0.2	0.003	0.132	0.004	0.70
	Lateral	458.9	834.0	0.7	−0.02	0.034	0.048	0.038	0.69
Cortical/subcortical bone content (mg/mm)	Medial	−130.5	496.3	0.9	−0.1	<0.001	0.021	0.002	0.88
	Lateral	−127.2	363.3	0.8	0.2	0.008	0.006	0.081	0.91
Percentage of cortical/subcortical bone area	Medial	−0.1	1.0	0.001	−0.0008	<0.001	0.532	<0.001	0.75
	Lateral	−0.1	0.8	0.001	−0.0005	<0.001	0.266	0.004	0.82
5 mm									
Total bone area (mm^2)	Medial	652.1	483.4	0.8	1.6	0.041	<0.001	0.078	0.66
	Lateral	699.1	444.7	0.7	1.1	0.219	<0.001	0.292	0.65
Total bone density (mg/cm^3)	Medial	393.4	892.3	0.5	−0.4	<0.001	0.573	<0.001	0.74
	Lateral	374.8	808.9	0.5	−0.2	0.002	0.211	0.004	0.78
Total bone content (mg/mm)	Medial	222.2	−107.0	0.9	0.7	0.365	<0.001	0.424	0.92
	Lateral	231.6	427.0	0.8	0.5	0.075	<0.001	0.163	0.93
Trabecular bone area (mm^2)	Medial	808.2	−256.1	−0.3	1.4	0.003	0.108	0.015	0.43
	Lateral	839.7	−49.7	−0.3	1.0	0.011	0.307	0.049	0.52
Trabecular bone density (mg/cm^3)	Medial	444.0	638.9	0.2	−0.2	0.010	0.742	0.005	0.28
	Lateral	422.4	633.0	0.3	−0.1	0.016	0.436	0.012	0.46
Cortical/subcortical bone area (mm2)	Medial	−156.2	424.7	1.1	0.2	0.004	<0.001	0.021	0.90
	Lateral	−143.6	494.4	1.0	0.1	0.003	0.008	0.025	0.90
Cortical/subcortical bone density (mg/cm^3)	Medial	452.6	934.8	0.7	−0.2	0.005	0.099	0.004	0.69
	Lateral	424.5	832.1	0.8	−0.02	0.025	0.030	0.021	0.69
Cortical/subcortical bone content (mg/mm)	Medial	−144.3	415.3	0.9	0.1	0.002	0.007	0.016	0.90
	Lateral	−133.7	414.5	0.8	0.1	0.003	0.018	0.037	0.90
Percentage of cortical/subcortical bone area	Medial	−0.1	0.9	0.001	−0.001	<0.001	0.327	<0.001	0.81
	Lateral	−0.1	0.8	0.001	−0.0005	<0.001	0.266	0.003	0.83
7 mm									
Total bone area (mm^2)	Medial	686.1	163.1	0.8	1.7	0.044	<0.001	0.097	0.61
	Lateral	721.4	483.3	0.7	1.0	0.238	<0.001	0.377	0.61
Total bone density (mg/cm^3)	Medial	462.4	916.8	0.2	−0.5	0.041	0.560	0.082	0.35
	Lateral	358.4	459.7	0.6	0.3	0.647	0.051	0.476	0.31
Total bone content (mg/mm)	Medial	368.0	727.6	0.5	−0.1	0.299	0.523	0.382	0.37
	Lateral	283.3	101.4	0.7	0.9	0.561	0.007	0.734	0.36
Trabecular bone area (mm^2)	Medial	815.5	−177.5	−0.1	1.3	0.008	0.077	0.039	0.41
	Lateral	820.1	−91.8	−0.1	1.1	0.005	0.087	0.035	0.52

Table 2. *Cont.*

Measure		Intercept		Coefficient		*p*-Value			
		8–12 m	24 m	8–12 m	24 m	Age	Body Weight	Age × Body Weight interaction	R^2
Trabecular bone density (mg/cm³)	Medial	408.3	674.9	0.2	−0.3	0.011	0.672	0.009	0.22
	Lateral	380.6	527.8	0.4	−0.02	0.182	0.109	0.077	0.26
Cortical/subcortical bone area (mm²)	Medial	77.5	581.0	0.4	−0.2	0.304	0.864	0.511	0.40
	Lateral	−62.1	−112.9	0.8	0.9	0.912	0.057	0.960	0.34
Cortical/subcortical bone density (mg/cm³)	Medial	567.4	947.2	0.4	−0.3	0.126	0.855	0.173	0.34
	Lateral	488.8	540.8	0.6	0.4	0.830	0.029	0.564	0.26
Cortical/subcortical bone content (mg/mm)	Medial	57.8	556.1	0.3	−0.3	0.248	0.941	0.459	0.40
	Lateral	−70.7	−173.6	0.7	0.8	0.796	0.049	0.839	0.33
Percentage of cortical/subcortical bone area	Medial	0.1	0.8	0.0003	−0.0007	0.188	0.625	0.321	0.25
	Lateral	−0.04	0.1	0.0008	0.0004	0.705	0.179	0.648	0.26

Table 3. Least squares means and standard error of pQCT bone parameters in the medial and lateral condyles at the sites 3, 5 and 7 mm from the distal aspect of the articulating surface of the metacarpus in steers 8–12 months and 24 months of age.

	8–12 Months				24 Months			
	LSMean		*p*-Value		LSMean		*p*-Value	
	Lateral	Medial	Body Weight	Condyle	Lateral	Medial	Body Weight	Condyle
3 mm								
Total bone area (mm²)	838.4 ± 7.5	799.5 ± 7.5	<0.001	<0.001	1025.6 ± 16.8	994.4 ± 16.8	<0.001	0.196
Total bone density (mg/cm³)	552.9 ± 5.2	570.6 ± 5.2	<0.001	0.017	708.6 ± 7.5	687.8 ± 7.5	0.026	0.059
Total bone content (mg/mm)	462.8 ± 3.9	456.5 ± 3.9	<0.001	0.266	724.8 ± 8.7	681.3 ± 8.7	0.001	<0.001
Trabecular bone area (mm²)	681.3 ± 13.1	612.6 ± 13.1	0.103	<0.001	457.6 ± 21.6	481.1 ± 21.6	0.003	0.447
Trabecular bone density (mg/cm³)	523.1 ± 3.0	530.1 ± 3.0	0.001	0.103	561.7 ± 3.9	539.1 ± 3.9	0.022	<0.001
Cortical/subcortical bone area (mm²)	157.1 ± 7.9	186.9 ± 7.9	<0.001	0.009	568.0 ± 12.3	513.3 ± 12.3	0.645	0.003
Cortical/subcortical bone density (mg/cm³)	662.3 ± 7.1	688.9 ± 7.1	<0.001	0.009	824.0 ± 5.1	823.9 ± 5.1	0.243	0.984
Cortical/subcortical bone content (mg/mm)	108.3 ± 6.6	132.5 ± 6.6	<0.001	0.011	468.9 ± 11.9	423.4 ± 11.9	0.898	0.010
Percentage of cortical/subcortical bone area	0.2 ± 0.01	0.2 ± 0.01	<0.001	0.003	0.6 ± 0.02	0.5 ± 0.02	0.029	0.109
5 mm								
Total bone area (mm²)	892.9 ± 7.7	888.8 ± 7.7	<0.001	0.703	1057.7 ± 17.2	1075.3 ± 17.2	<0.001	0.474
Total bone density (mg/cm³)	531.9 ± 5.2	545.2 ± 5.2	<0.001	0.072	688.5 ± 8.0	680.6 ± 8.0	0.058	0.487
Total bone content (mg/mm)	474.2 ± 4.0	484.0 ± 4.0	<0.001	0.083	726.6 ± 9.0	729.0 ± 9.0	<0.001	0.852
Trabecular bone area (mm²)	745.1 ± 13.1	722.2 ± 13.1	0.159	0.220	516.2 ± 24.2	533.5 ± 24.2	0.012	0.617
Trabecular bone density (mg/cm³)	503.7 ± 3.3	512.3 ± 3.3	<0.001	0.069	549.5 ± 4.1	534.4 ± 4.1	0.037	0.013
Cortical/subcortical bone area (mm²)	147.9 ± 7.4	166.6 ± 7.4	<0.001	0.075	541.5 ± 14.8	541.8 ± 14.8	0.603	0.989
Cortical/subcortical bone density (mg/cm³)	655.3 ± 7.6	669.9 ± 7.6	<0.001	0.176	817.6 ± 5.7	820.2 ± 5.7	0.289	0.751
Cortical/subcortical bone content (mg/mm)	100.9 ± 6.2	115.7 ± 6.2	<0.001	0.093	443.8 ± 14.3	445.2 ± 14.3	0.846	0.946
Percentage of cortical/subcortical bone area	0.2 ± 0.01	0.2 ± 0.01	<0.001	0.103	0.5 ± 0.02	0.5 ± 0.02	0.093	0.774
7 mm								
Total bone area (mm²)	928.7 ± 8.2	941.5 ± 8.2	<0.001	0.272	1075.6 ± 18.0	1122.9 ± 18.0	<0.001	0.071
Total bone density (mg/cm³)	527.6 ± 8.0	535.5 ± 8.0	0.002	0.490	612.5 ± 16.9	636.7 ± 16.9	0.724	0.318
Total bone content (mg/mm)	500.6 ± 11.5	516.7 ± 11.5	0.001	0.327	634.5 ± 26.3	683.2 ± 26.3	0.386	0.199
Trabecular bone area (mm²)	783.0 ± 12.4	783.4 ± 12.4	0.566	0.984	573.3 ± 25.4	594.8 ± 25.4	0.011	0.553
Trabecular bone density (mg/cm³)	486.6 ± 3.9	494.1 ± 3.9	<0.001	0.174	517.6 ± 7.0	519.0 ± 7.0	0.268	0.889
Cortical/subcortical bone area (mm²)	182.5 ± 16.7	192.6 ± 16.7	0.028	0.671	382.0 ± 37.4	451.4 ± 37.4	0.647	0.197
Cortical/subcortical bone density (mg/cm³)	681.1 ± 9.4	676.0 ± 9.4	0.001	0.700	757.5 ± 16.4	787.7 ± 16.4	0.870	0.199
Cortical/subcortical bone content (mg/mm)	131.7 ± 14.5	139.1 ± 14.5	0.047	0.722	303.1 ± 33.0	365.0 ± 33.0	0.684	0.191
Percentage of cortical/subcortical bone area	0.2 ± 0.02	0.2 ± 0.02	0.088	0.612	0.4 ± 0.04	0.4 ± 0.04	0.781	0.316

At 8–12 months of age, total bone area and trabecular bone area were greater as scan distance increased. Total bone density and trabecular bone density decreased with increases in scan distance at both 8–12 months of age and 24 months of age (Table 4).

Table 4. Least squares means and standard error for pQCT bone parameters of the medial and lateral condyles at sites 3, 5 and 7 mm proximal of the distal aspect of the of the articulating surface of the metacarpus of steers at 8–12 and 24 months of age.

	8–12 Months					**24 Months**				
	LSMean			***p*-Value**		**LSMean**			***p*-Value**	
	3 mm	**5 mm**	**7 mm**	**Body Weight**	**Scan**	**3 mm**	**5 mm**	**7 mm**	**Body Weight**	**Scan**
Medial										
Total bone area (mm^2)	799.5 ± 8.4 ^{a}	888.8 ± 8.4 ^{b}	941.5 ± 8.4 ^{c}	<0.001	<0.001	994.4 ± 18.2 ^{a}	1075.3 ± 18.2 ^{b}	1122.9 ± 18.2 ^{b}	<0.001	<0.001
Total bone density (mg/cm^3)	570.6 ± 6.3 ^{b}	545.2 ± 6.3 ^{a}	535.5 ± 6.3 ^{a}	<0.001	<0.001	687.8 ± 10.8 ^{b}	680.6 ± 10.8 ^{b}	636.7 ± 10.8 ^{a}	0.010	0.003
Total bone content (mg/mm)	456.5 ± 7.8 ^{a}	484.0 ± 7.8 ^{b}	516.7 ± 7.8 ^{c}	<0.001	<0.001	681.3 ± 17.4	729.0 ± 17.4	683.2 ± 17.4	0.126	0.099
Trabecular bone area (mm^2)	612.6 ± 13.3 ^{a}	722.2 ± 13.3 ^{b}	783.4 ± 13.3 ^{c}	0.161	<0.001	481.1 ± 23.2 ^{a}	533.5 ± 23.2 ^{ab}	594.8 ± 23.2 ^{b}	<0.001	0.004
Trabecular bone density (mg/cm3)	530.1 ± 3.2 ^{c}	513.3 ± 3.2 ^{b}	494.1 ± 3.2 ^{a}	<0.001	<0.001	539.1 ± 4.3 ^{b}	534.4 ± 4.3 ^{b}	519.0 ± 4.3 ^{a}	0.002	0.005
Cortical/subcortical bone area (mm^2)	186.9 ± 12.3	166.6 ± 12.3	192.6 ± 12.3	<0.001	0.293	513.3 ± 22.4 ^{ab}	541.8 ± 22.4 ^{b}	451.4 ± 22.4 ^{a}	0.970	0.018
Cortical/subcortical bone density (mg/cm^3)	688.9 ± 8.0	669.9 ± 8.0	676.0 ± 8.0	<0.001	0.236	823.9 ± 9.4 ^{b}	820.2 ± 9.4 ^{b}	787.7 ± 9.4 ^{a}	0.111	0.015
Cortical/subcortical bone content (mg/mm)	132.5 ± 10.6	115.7 ± 10.6	139.1 ± 10.6	<0.001	0.280	423.4 ± 20.5 ^{b}	445.2 ± 20.5 ^{b}	365.0 ± 20.5 ^{a}	0.661	0.021
Percentage of cortical/subcortical bone area	0.24 ± 0.01	0.19 ± 0.01	0.21 ± 0.01	<0.001	0.088	0.52 ± 0.02 ^{b}	0.51 ± 0.02 ^{b}	0.41 ± 0.02 ^{a}	0.036	<0.001
Lateral										
Total bone area (mm^2)	838.4 ± 7.2 ^{a}	892.9 ± 7.2 ^{b}	928.7 ± 7.2 ^{c}	<0.001	<0.001	1025.6 ± 16.0	1057.7 ± 16.0	1075.6 ± 16.0	<0.001	0.090
Total bone density (mg/cm^3)	552.9 ± 6.1 ^{b}	531.9 ± 6.1 ^{a}	527.6 ± 6.1 ^{a}	<0.001	0.009	708.6 ± 12.2 ^{b}	688.5 ± 12.2 ^{b}	612.5 ± 12.2 ^{a}	0.789	<0.001
Total bone content (mg/mm)	462.8 ± 7.0 ^{a}	474.2 ± 7.0 ^{a}	500.6 ± 7.0 ^{b}	<0.001	<0.001	724.8 ± 16.0 ^{b}	726.6 ± 16.0 ^{b}	634.5 ± 16.0 ^{a}	0.005	<0.001
Trabecular bone area ($mm^{2)}$	681.3 ± 12.4 ^{a}	745.1 ± 12.4 ^{b}	783.0 ± 12.4 ^{c}	0.111	<0.001	457.6 ± 24.1 ^{a}	516.2 ± 24.1 ^{ab}	573.3 ± 24.1 ^{b}	0.005	0.005
Trabecular bone density (mg/cm^3)	523.1 ± 3.6 ^{c}	503.7 ± 3.6 ^{b}	486.6 ± 3.6 ^{a}	<0.001	<0.001	561.7 ± 5.9 ^{b}	549.5 ± 5.9 ^{b}	517.6 ± 5.9 ^{a}	0.218	<0.001
Cortical/subcortical bone area (mm^2)	157.1 ± 10.7	147.9 ± 10.7	182.5 ± 10.7	<0.001	0.061	568.0 ± 25.8 ^{b}	541.5 ± 25.8 ^{b}	382.0 ± 25.8 ^{a}	0.318	<0.001
Cortical/subcortical bone density (mg/cm^3)	662.3 ± 8.2	655.3 ± 8.2	681.1 ± 8.2	<0.001	0.071	824.0 ± 11.2 ^{b}	817.6 ± 11.2 ^{b}	757.5 ± 11.2 ^{a}	0.510	<0.001
Cortical/subcortical bone content (mg/mm)	108.3 ± 9.1 ^{ab}	100.9 ± 9.1 ^{a}	131.7 ± 9.1 ^{b}	<0.001	0.048	468.9 ± 22.8 ^{b}	443.8 ± 228 ^{b}	303.1 ± 22.8 ^{a}	0.306	<0.001
Percentage of cortical/subcortical bone area	0.19 ± 0.01	0.17 ± 0.01	0.19 ± 0.01	<0.001	0.228	0.56 ± 0.03 ^{b}	0.52 ± 0.03 ^{b}	0.35 ± 0.03 ^{a}	0.626	<0.001

$^{a, b, c}$ Means with different superscript within row at each age are significantly different ($p < 0.05$).

4. Discussion

Differences in bone composition compared to what was previously reported in the mid-diaphysis are the result of differences in the structure and function of the regions of bone. The diaphysis is a hollow tubular shape made of cortical bone designed to resist bending, whereas the epiphysis is wider and filled with trabecular bone that provides long bones with the ability to compress [5]. In addition, articular cartilage on the bone surfaces in the joint disperses strain from weight bearing along the joint surface [29]. The positive relationship of bone cross sectional area and age in both the medial and lateral condyles of the metacarpus reflects the growth-related response to increases in mechanical loading from body weight gain. Increases in cross sectional area strengthens bone with minimal changes in bone mineral content. Increases in body weight up to 24 months of age were associated with a greater total bone area and a decrease in total bone density. This increase in cross sectional area is a similar growth response to that observed in the e mid-diaphysis of the metacarpus [3,30]. However, as the metacarpus reaches maturity, additional bone strength will be the result of increases in bone content.

The lack of increases in trabecular and cortical bone density in the epiphysis agrees with previous research where normal cattle locomotion provided insufficient strain to induce an increase in bone density even when managed on hill country [31]. Cattle are not cursorial animals, they do not run at a speed that induces sufficient microstrain to induce large changes in bone morphology [32]. Therefore, any increases in bone strength are in response to a greater body weight and bone maturity. In cursorial animals such as horses, compressive forces placed on the distal aspect of the metacarpus are created from the action of the sesamoids and the proximal phalanx during the stance phase [33]. When the workload is increased (i.e., galloping exercise), forces placed on the distal metacarpus induce a localized increase in bone density [28].

There was no effect of body weight and age on the 7 mm scans on bone measures reflecting the location of the scan. Measures at 3 mm and 5 mm are closer to the distal aspect of the metacarpus where forces of the proximal phalanx and sesamoid bones are greater. However, at 7 mm there is limited effect from the compressive forces of the proximal phalanx and sesamoid bones, and limited bending strain from locomotion, resulting in the lower requirement to respond to increases in body weight.

With only differences in bone area at the 3 mm scan between the medial and lateral condyles, it is possible the effect is due to the bone orientation in the pQCT scanner. If it were a true effect of the bone size, it would be expected that the difference between condyles would also be present at 5 and 7 mm scans. However, given the low compressional forces expected to be placed on the metacarpus during locomotion in cattle, the force appears to be inadequate to induce differences in bone morphology of the medial and lateral condyle. Therefore, differences in these structures may have only been observed in the 3 mm scan because there were inadequate compressive forces to initiate a response at the more proximal sites. In addition, the similarity in medial and lateral loading of the claw in the forelimb during locomotion prevents differences in the medial and lateral condyles [25]. However, in the hindlimb loading is asymmetrical with a greater loading on the lateral claw [25]. It would therefore be expected that the differences in loading could affect bone morphology between the medial and lateral condyles of the metatarsus. The result of uneven loading in the forelimb on bone morphology has been described in horses, where the smaller lateral metacarpal condyle had a greater density than the medial condyle [33].

The effect of increasing body weight on height decreased over time indicating the cessation of longitudinal bone growth in the forelimb. Typically, 90% of height is achieved in the first year of life in cattle, so longitudinal bone growth would be expected to be limited after a year [34]. In addition, at a year-old cattle have only reached 35–45% of their mature weight, so increases in body weight are primarily driven by a greater capacity as such proximal limb bones like the humerus require additional strength. Differences in maturity between proximal and distal bones is also the result of the location and function of each bone. With the metacarpus being in the distal limb, bone maturity is likely to occur earlier than a bone such as the humerus in the proximal limb that continues to grow after 2 years [3]. In a bull it would be expected that increases in metacarpal length and cross sectional area would be limited after one year of age as a result of puberty acquisition [3,35].

An important biological cue for the halt of longitudinal bone growth and increases in bone content is puberty attainment [16]. As an animal reaches puberty, the resulting increase in oestrogen promotes longitudinal bone growth (growth spurt). However, in the later stages of puberty attainment, longitudinal bone growth slows resulting in epiphyseal closure [17]. The timing of bone maturity is likely to be altered by the absence of a hormonal cue that ceases longitudinal bone growth. Steers do not attain puberty so do not have the oestrogen cue to halt longitudinal bone growth resulting in a greater long bone length than bulls [19,36]. This concept has been reflected in the current study where increases in metacarpus length were not limited after one year of age. A similar result was previously reported by Gibson et al. [30], where steers had a greater total bone (metacarpus and humerus) length than bulls at a given body weight at 11 months of age. At this age, bulls were beginning to reach puberty, so differences in bone density because of bone maturity in bulls were not yet observed. In the current study, increases in total and cortical bone density at 24 months of age indicates bone maturity in the absence of a hormonal cue [20].

5. Conclusions

To conclude, growth in the metacarpus is not limited to one year of age in steers compared to what has previously been reported in bulls. However, increases observed after one year of age are only small. The lack of a pubertal cue for bone maturation in steers may delay the onset of bone maturity. In addition, the magnitude of loading (microstrain) from cattle locomotion is insufficient to induce a localized increase in bone density. The lack of difference in bone morphology in the medial and lateral condyles of the distal metacarpus reflects the even loading distribution observed in the forelimb of cattle.

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