THE EFFECT OF MORPHOLOGY ON THE MUSCULOSKELETAL SYSTEM OF THE MODERN BROILER

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Abstract

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This study compares various morphometric features of two strains of broilers, selected and 'relaxed' (ie random-bred), raised under two feeding regimes, ad-libitum*-fed and restricted-fed. We consider the possible consequences of the different body shapes on the musculoskeletal system. The* ad-libitum*-fed selected birds reached heavier bodyweights at younger ages, had wider girths, and developed large amounts of breast muscle which probably displaced their centre of gravity cranially. At cull weight, they had shorter legs than birds in the other groups and greater thigh-muscle masses; therefore, greater forces would have to be exerted by shorter lever arms in order to move the body. The tarsometatarsi were broader, providing increased resistance to greater loads, but the bones had a lower calcium and phosphorus content, which would theoretically make them weaker. Many of these morphological changes are likely to have detrimental effects on the musculoskeletal system and therefore compromise the walking ability and welfare of the birds.*

Keywords: *animal welfare, gait, lameness, morphology, musculoskeletal, poultry*

Introduction

In the modern broiler, heavy selection pressure has been directed toward obtaining rapid growth rates to high bodyweights and producing birds with more breast muscle. This selection has resulted in a dramatic change in body conformation compared to non-selected birds (Lilburn 1994; Webster 1994). The disproportionate increase in breast muscle compared to thigh muscle has been described in turkeys also (Nestor *et al* 1985; Nestor *et al* 1987). The effects of altered body conformation and scaling on locomotion have been studied in depth in species as diverse as rats, rabbits, dogs, man and elephants (Maynard Smith 1968; Alexander 1975; Currey 1975; Schmidt-Nielsen 1975). It is recognised that increased bodyweight puts greater demands on the skeleton and that body conformation tends to change in an attempt to minimise stresses on the bones. A strong correlation has been demonstrated between liveweight, growth rate, and "leg weakness" or lameness in poultry (Vestergaard & Sanotra 1999; Kestin *et al* 2001). Modern broilers are also less active (Sainsbury 1999; Weeks *et al* 2000), and there is considerable debate as to whether their altered gait and lack of activity are a result of the changed conformation, or of pain. Although some studies have demonstrated increased activity following administration of analgesics (McGeown 1999), others have not demonstrated a significant effect (Hocking 1994).

The work presented in this paper was designed to compare the morphology of different groups of broilers during growth and at the same final bodyweight, and to consider the possible consequences of the different body shapes on the musculoskeletal system. Two strains of birds were used ('relaxed' [ie random-bred] and selected), raised on two feeding regimes (*ad-libitum* and restricted), and culled at a commercial cull bodyweight of 2.4 kg. The morphometric measures determined were bodyweight, girth, thigh muscle diameter, femur length, tibiotarsal length, tarsometatarsal length and tarsometatarsal width. Post-mortem measurements were made of breast and thigh muscle mass and leg bone mass, as the relationship between leg muscle and bone mass is of primary importance when considering the potential effects of morphology on locomotion. Assuming that the muscles work normally, an increase or decrease in muscle mass should result in an increase or decrease in bone mass (Wagner 1979, quoting Doyle *et al* 1970), as the forces produced by muscles acting on bone are among the primary determinants of bone mass and strength (Frost 1997). Bone geometry and ash content were also compared as indicators of bone strength, and the bones were inspected histologically for evidence of tibial dyschondroplasia or other pathologies.

The gait patterns of the birds were objectively measured at various stages during growth, and the results are presented in an associated paper (see Corr *et al*, pp 159–171, this issue).

Materials and methods

Birds and treatments

Four treatment groups were used (Figure 1):

1) Thirteen female Ross 308 strain 'selected' broilers, fed *ad libitum*, and culled at six weeks (Sel-Al).
2) Ten female Ross 'relaxed' strain broilers, fed *ad libitum*, and culled at 12 weeks (Rxd-Al).
3) Ten female Ross 308 strain 'selected' broilers, restricted-fed, and culled at 13 weeks (Sel-Rd).
4) Nine female Ross 'relaxed' strain broilers, restricted-fed, and culled at 23 weeks (Rxd-Rd).

'Relaxed' strain broilers are maintained by Ross as a random-bred population; predecessors of the modern broiler, they have had no selection pressure since 1972. The uneven group sizes at cull resulted from one restricted-fed relaxed strain bird being excluded from the final analysis (single male) and a higher-than-expected survival rate of the *ad-libitum*-fed selected birds.

The birds were reared in floor pens on wood shavings; although the stocking densities differed (4.75 relaxed birds per m^2 and 3.85 selected birds per m^2), they were sufficiently low to enable all the birds to move freely. The *ad-libitum*-fed groups were kept in separate pens in one room, and the restricted-fed birds kept in separate pens in a second room. The conditions in each room were kept similar: heat lamps produced spot temperatures decreasing from 30°C to 25°C degrees over the initial 14 days, with room temperature kept between 23°C and 25°C. Thereafter, average room temperature was maintained between 20.5°C and 23.5°C, and average relative humidity between 48.8% and 57.7%. Room lighting was provided by two 250W bulbs in each room, and the 'daylength' was reduced from 23 h on day 1 to 14 h by day 5, thereafter being maintained on a 14 h light:10 h dark regime.

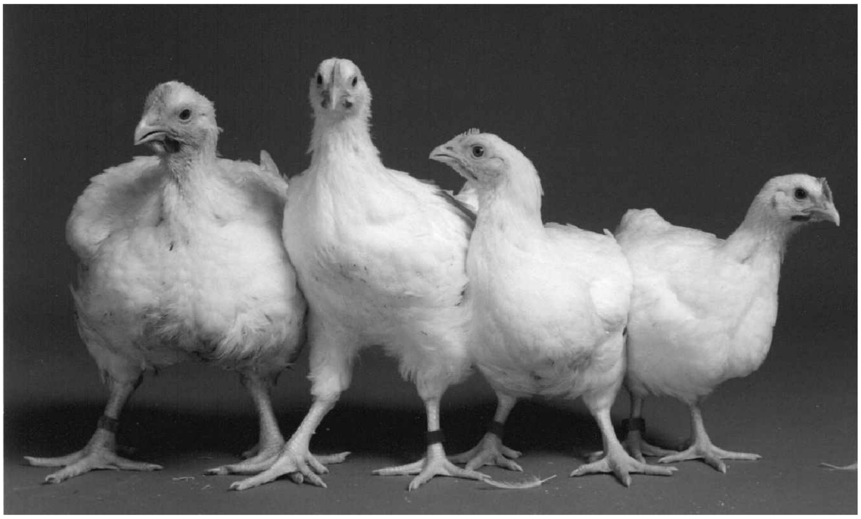

Figure 1 **Example of a bird from each treatment group at six weeks of age. Left to right: Sel-Al (*ad-libitum*-fed, Ross 308 selected broiler); Rxd-Al (*ad-libitum*-fed, relaxed broiler); Sel-Rd (restricted-fed, Ross 308 selected broiler); and Rxd-Rd (restricted-fed, relaxed broiler).**

Feeding regime

The birds were fed on the Roslin Broiler Starter diet (Roslin Nutrition, Midlothian) throughout life, with water available *ad libitum*. All chicks were fed *ad libitum* until day 11, after which the birds in the restricted-fed groups were fed using a level of restriction based upon the Ross Parent Stock Male (PSM) protocol (Ross Breeders 1995). It is recognised that broiler breeders raised on this level of restriction are chronically hungry, which has obvious welfare implications and which can be manifest in increased fearfulness and stereotypic pecking in females (Sainsbury 1999). Such behaviour was not manifest in the present birds, perhaps because of the low stocking density and periods of exercise. Pair-feeding was used, so that the same percentage restriction could be applied to both strains; the PSM ration was compared to the *ad libitum* intake of the selected birds, and the percentage restriction calculated. The *ad libitum* intake of the relaxed birds was measured, and the same percentage restriction was then applied to the relaxed restricted group. Any birds showing markedly lower bodyweight gains than others in the group were fed their ration individually. On reaching approximately 2.4 kg (at six weeks), the *ad-libitum*-fed selected birds were culled, and the restricted-fed selected birds continued on the PSM regime. The restricted-fed relaxed birds were then kept on 45% of the *ad-libitum*-fed relaxed birds' intake. When the *ad-libitum*-fed relaxed birds were culled, the restriction level for the remaining birds was estimated so as to maintain a similar weekly growth rate.

Morphometric measurements

The following measurements were made once per week, after feeding:

Bodyweight (kg): measured using a Sartorius balance (BP 34000, Sartorius AG, Germany, accurate to 0.1 g).

Girth (m): a piece of string was passed around the circumference of the thorax of the bird, tucked under the wings just behind the axillae, and its length measured (accurate to 0.1 mm).

Thigh muscle diameter (m): a piece of string was passed around the circumference of the top of the thigh, and its length measured (accurate to 0.1 mm).

Leg length (m): length of femur, tibiotarsus and tarsometatarsus were individually measured using calipers (RS Baty, RS Components, accurate to 0.1 mm) and then summed to give distance from greater trochanter of femur to large metatarsal pad.

At cull, tarsometatarsal width was measured at mid-shaft level, in both lateral (lat) and craniocaudal (CrCd) directions, using calipers (RS Baty, RS Components, accurate to 0.1 mm).

All measurements were taken by the same person to reduce variability. As no significant differences were found between the total leg length measurements of the right and left legs, the two values were averaged to produce a mean value for analysis. When the birds reached the target weight, a final set of morphometric measurements were made. The birds were then killed by cervical dislocation and subjected to post-mortem examination.

Post-mortem analysis

The breast and thigh muscles were dissected from the carcass and weighed, and the legs disarticulated at the hip joint and stored at –20°C for later analysis. Each bird was sexed prior to disposal of the carcass. At a subsequent stage, the leg bones were defrosted and stripped of soft tissue, and weighed. Each bone was then radiographed whole in two views (lateral and craniocaudal) and measurements made of tibial plateau angles, as described in Duff and Thorpe (1985a,b). Tibiotarsal torsions were calculated by 'capturing' a video image of the tibiotarsus on computer, viewed from the proximal to the distal joint along the length of the bone. Image analysis software (NIH Image, public domain) was then used to draw a line along the centre of rotation of each joint and measure the angle at which the two lines intersected (Figure 2). Rotation of the distal tibiotarsus medially with respect to the proximal tibiotarsus is described as 'internal' rotation; rotation of the distal tibiotarsus laterally is described as 'external' rotation. The tibiotarsi were then sectioned, and mid-shaft cortical sections (1 cm long) were sent for ashing to measure the mineral content of the bone. Proximal tibiotarsal epiphyseal sections were taken for subsequent histological examination to check for dyschondroplasia lesions (2 cm sections taken longitudinally and distally from the centre of the epiphysis). The ashing process was carried out using the technique described by Thorp and Waddington (1997). The histological processing consisted of fixing the tissue in 10% buffered neutral formalin, followed by decalcification in 10% Goodings and Stewart fluid. Paraffin sections were then taken at 4 μm and stained with haematoxylin and eosin.

Data analysis

Statistical analysis was performed on the data from the first six weeks, the period of most rapid growth, which represents the commercial life span of the modern broiler. The cull data (all groups at the same bodyweight) were also analysed in detail. As the groups were unbalanced, the group means and medians were generated using the residual maximum likelihood method (REML; Patterson & Thompson 1971). Bodyweight, girth and leg length were all transformed to logarithms for analysis: the medians are presented, as a more resistant representation of the average, along with the approximate standard error of the median (#SE median; Kendall & Stuart 1963). The first-order approximation of the SE of the median was calculated from median × SE of log median. The other parameters appeared to have a more normal distribution, and so the means (and SEs) are given. Statistically

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significant differences between the groups were calculated with Student's t-tests, using the maximum SE of the differences between groups to give a conservative estimate.

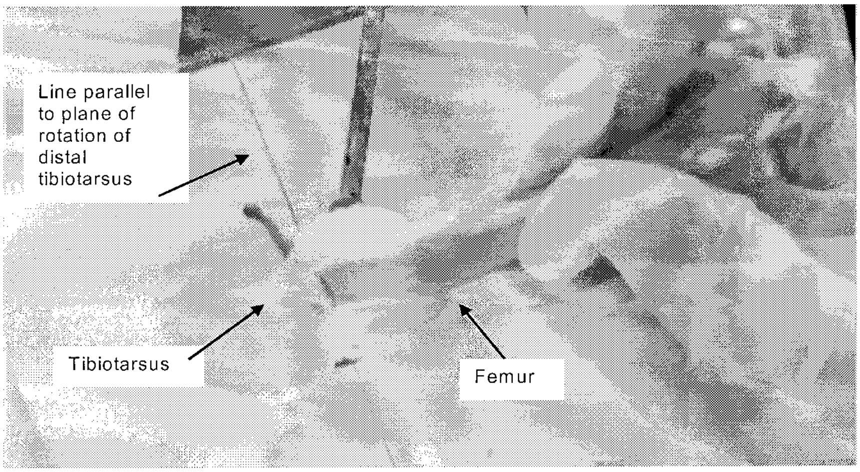

Figure 2 **Figure 2 illustrates the method used to determine degree of tibiotarsal rotation. A line was drawn on a piece of paper, and the distal epiphysis of the tibiotarsus lined up with this along a plane parallel to the estimated centre of rotation of the joint. The femur was then placed to approximate its normal articulation with the tibiotarsus, and the 'joint' flexed back and forth to establish the centre of rotation of the stifle joint. When the stifle was flexed approximately normally, the image was captured from above. Lines could then be drawn parallel to the estimated centre of rotation of each of the joints, and the angle between the two measured. In theory, the lines should be parallel and, if this is not the case, the angle will give an indication of the degree and direction of torsion of the tibiotarsal bone. This method was developed by the present author, who found the method used by Duff and Thorp (1985a,b) to be difficult to apply.**

Results

Table 1 presents the results of the weekly bodyweight, girth and leg length, and tarsometatarsal width measurements. The median bodyweights were significantly different between the groups at each stage of growth, but not at cull.

At most stages in the first six weeks of life, the median girths were significantly different between groups. At cull, there was no significant difference in median girth between the Sel-Al, Rxd-Al and Rxd-Rd birds, but the Sel-Rd birds had significantly larger median girths than the Rxd-Rd birds.

The median leg length of the Sel-Al birds was significantly greater than that of all other groups in the first six weeks of growth (except for the Sel-Rd birds at two weeks). Comparing the groups at cull weight, however, the Sel-Al birds had a significantly shorter median leg length than all other groups.

The results of the breast muscle mass, thigh muscle mass, bone mass and tarsometatarsal

Table 1 Weekly bodyweight, girth and leg length measurements.

	Group		Week 2	Week 3	Week 4	Week 5	Week 6	Cull
Body-weight (kg)	Sel-Al	Median	0.329†	0.705†	1.252†	1.755†	2.339†	2.339
		(# SE median)	(0.008)	(0.018)	(0.032)	(0.045)	(0.060)	(0.060)
	Rxd-Al	Median	0.163†	0.295	0.484†	0.691†	0.919†	2.372
		(# SE median)	(0.005)	$^{a,c***, b**}$ (0.009)	(0.001)	(0.020)	(0.027)	(0.069)
	Sel-Rd	Median	0.282†	0.464†	0.694†	0.902†	1.126†	2.345
		(# SE median)	(0.008)	(0.014)	(0.020)	(0.026)	(0.033)	(0.069)
	Rxd-Rd	Median	0.151†	0.263	0.358†	0.471†	0.634†	2.365
		(# SE median)	(0.005)	$^{a,c***, d**}$ (0.008)	(0.011)	(0.014)	(0.002)	(0.073)
Girth (m)	Sel-Al	Median	0.178	0.250†	0.315†	0.359†	0.427†	0.427
		(# SE median)	$^{b,d***, c*}$ (0.003)	(0.004)	(0.005)	(0.005)	(0.006)	(0.006)
	Rxd-Al	Median	0.151	0.184	0.227†	0.248†	0.297	0.431
		(# SE median)	$^{a,c***, d**}$ (0.003)	^{a,c***} (0.003)	(0.004)	(0.004)	^{a,d***} (0.005)	(0.007)
	Sel-Rd	Median	0.169	0.213†	0.256†	0.280†	0.310	0.449
		(# SE median)	$^{a*, b,d***}$ (0.003)	(0.004)	(0.004)	(0.005)	^{a,d***} (0.005)	^{d**} (0.008)
	Rxd-Rd	Median	0.141	0.176	0.206†	0.223†	0.243†	0.418
		(# SE median)	$^{a,c***, b**}$ (0.002)	^{a,c***} (0.003)	(0.004)	(0.004)	(0.004)	^{c**} (0.007)
Leg length (m)	Sel-Al	Median	0.104	0.172†	0.206†	0.234†	0.266†	0.266†
		(# SE median)	^{b,d***} (0.001)	(0.001)	(0.002)	(0.002)	(0.002)	(0.002)
	Rxd-Al	Median	0.093	0.143	0.173†	0.201	0.224	0.307
		(# SE median)	^{a,c***} (0.001)	$^{a,c***, d**}$ (0.001)	(0.001)	$^{a,d***, c**}$ (0.002)	$^{a,d***, c*}$ (0.002)	$^{a***, c**, d*}$ (0.003)
	Sel-Rd	Median	0.104	0.156†	0.186†	0.208	0.230	0.319
		(# SE median)	^{b,d***} (0.001)	(0.001)	(0.002)	$^{a,d***, b**}$ (0.002)	$^{a,d***, b*}$ (0.002)	$^{a***, b**}$ (0.003)
	Rxd-Rd	Median	0.094	0.137	0.159†	0.178†	0.202†	0.316
		(# SE median)	^{a,c***} (0.001)	$^{a,c***, b**}$ (0.001)	(0.001)	(0.002)	(0.002)	$^{a***, b*}$ (0.003)

Significance level: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$
a = significantly different from group Sel-Al
b = significantly different from group Rxd-Al
c = significantly different from group Sel-Rd
d = significantly different from group Rxd-Rd
† = significantly different from all other groups at $P < 0.001$

Maximum SE of difference of log medians for same level of factor

	Age of bird	Treatment group
Bodyweight	0.04251	0.02752
Girth	0.02481	0.02275
Leg length	0.01270	0.009741

***F*-statistics**: 3 and 38 degrees of freedom. All are statistically significant at $P < 0.001$ except for girth at cull. $*P < 0.05$.

	Week 2	Week 3	Week 4	Week 5	Week 6	Cull
Bodyweight	189.0	265.1	377.1	399.9	397.3	—
Girth	40.5	96.8	128.5	161.9	209.0	3.0*
Leg length	51.9	147.2	171.9	178.6	187.0	110.8

diameter measurements at cull are presented in Table 2. There was no significant difference in breast or thigh muscle mass (total and %) between the selected groups at cull. The selected birds had significantly greater breast and thigh muscle mass (total and %) than the relaxed birds. Within the relaxed groups, the restricted-fed birds had significantly greater thigh muscle mass (total and %) and, although their total breast muscle mass was not significantly greater, the restricted-fed birds had a significantly higher percentage of breast muscle mass than the *ad-libitum*-fed birds. The selected birds had a significantly higher mean ratio of breast to thigh muscle than the relaxed birds, but there was no significant difference in the mean ratio in birds of the same strain at cull.

All groups had significantly different total and percentage leg bone mass at cull. There were significant differences in lateral tarsometatarsal diameter between all groups at cull bodyweight. The median craniocaudal (CrCd) diameter was significantly greater in the Rxd-Rd birds than the Sel-Al and Rxd-Al birds at cull, but not significantly different to the Sel-Rd birds.

Table 3 illustrates the bone mineral values at cull. There were significant differences in percentage of ash between all the groups. The Rxd-Rd birds had significantly higher mean percentage calcium (% Ca) and percentage phosphorus (% P) levels than birds in the other groups. There was no significant difference in mean % Ca levels between the other groups, but the mean % P values were significantly lower in the Sel-Al birds than in either of the restricted-fed groups. There was no significant difference between the Ca:P ratio in any of the groups at cull.

The tibiotarsal torsion and tibial plateau angle measurements are shown in Table 4. Two of the selected birds had tibial plateau angles of greater than 25°. None of the tibiotarsi showed abnormal degrees of external rotation (ie > 20°); however, an increased number of internally rotated tibiotarsi occurred in the *ad-libitum*-fed selected birds. No evidence of tibial dyschondroplasia was found upon histological examination of the proximal tibiotarsal sections.

Discussion and conclusions

Morphometric measurements during growth

The fact that modern broilers have been selected to grow much heavier at a more rapid rate than their predecessors (Lilburn 1994) was confirmed in the present experiment. The *ad-libitum*-fed selected birds grew to 2.4 kg in approximately half of the time taken by the *ad-libitum*-fed relaxed birds. Approximately 19% of the bodyweight of the *ad-libitum*-fed selected birds at six weeks was made up of pectoral muscle, compared to the 12% estimated by Acer *et al* in 1993. The pectoral muscle is the main flight muscle, which accounts for around 15% of the bodyweight of the 'average' bird (Greenewalt 1962, quoted in Schmidt-Nielsen 1975), in agreement with the findings for the relaxed birds in this study. Selective breeding has therefore produced a bird with 4–5% more pectoral muscle; however, this muscle is often affected by different pathologies (Mitchell 1999), and these birds cannot fly. It is more usual for birds that lose the ability to fly to show a decrease in pectoral muscle (Raikow 1985). The fact that the restricted-fed relaxed birds had a higher percentage (although not total) breast muscle mass compared to the *ad-libitum*-fed birds of the same strain suggests that the pectoral muscles are highly conserved and are maintained at the expense of the rest of the body. The disproportionate increase in breast muscle compared to thigh muscle resulting from selection is also interesting, and has previously been described in broilers (Lilburn 1994) and turkeys (Nestor *et al* 1985; Nestor *et al* 1987).

Table 2 **Cull data: breast muscle mass, thigh muscle mass, bone mass and tarsometatarsal diameter.**

			Sel-Al	Rxd-Al	Sel-Rd	Rxd-Rd	Max SE of differences between means or log medians
Breast muscle mass	Total (kg)	Median (# SE median)	0.443 [b,d***] (0.012)	0.346 [a,c***] (0.011)	0.479 [b,d***] (0.015)	0.379 [a,c***] (0.012)	0.0462
	% of body-weight	Mean (SE)	19.02 [b,d***] (0.397)	14.14 [a,c***, d**] (0.453)	20.13 [b,d***] (0.453)	16.03 [a,c***, b**] (0.478)	0.6760
Thigh muscle mass	Total (kg)	Median (# SE median)	0.260 [b***, d*] (0.005)	0.226 [a,c***, d*] (0.005)	0.268 [b***, d*] (0.006)	0.244 [a,b,c*] (0.006)	0.0325
	% of body-weight	Mean (SE)	11.14 [b***, d**] (0.182)	9.25 [a,c***, d**] (0.207)	11.25 [b***, d**] (0.207)	10.27 [a,b,c**] (0.219)	0.3090
Leg bone mass	Total (kg)	Median (# SE median)	0.090 [b,c***, d**] (0.001)	0.075† (0.001)	0.105† (0.002)	0.083 [a**, b,c***] (0.001)	0.0261
	% of body-weight	Mean (SE)	3.847† (0.055)	3.165† (0.062)	4.541† (0.062)	3.504† (0.065)	0.0925
Breast:thigh muscle ratio		Mean (SE)	1.708 [a**, d*] (0.036)	1.530 [a**, c***] (0.041)	1.800 [b,d***] (0.041)	1.556 [a*, c***] (0.043)	0.0608
Tarsometatarsal diameter (lat) (m)		Median (# SE median)	0.0135 [b*, c***, d**] (0.0001)	0.0130 [a*, c,d***] (0.0001)	0.0147 [a, b***] (0.0002)	0.0142 [a**, b***] (0.0002)	0.0166
Tarsometatarsal diameter (CrCd) (m)		Median (# SE median)	0.0154 [d**] (0.0002)	0.0150 [c**, d***] (0.0002)	0.0159 [b**] (0.0002)	0.0162 [a**, b***] (0.0002)	0.0184

Significance level: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$
a = significantly different from group Sel-Al
b = significantly different from group Rxd-Al
c = significantly different from group Sel-Rd
d = significantly different from group Rxd-Rd
† = significantly different from all other groups at $P < 0.001$

***F*-statistics**: 3 and 38 degrees of freedom. All are statistically significant at $P < 0.001$.

Total breast muscle mass	23.03
% breast muscle mass	37.64
Total thigh muscle mass	11.99
% thigh muscle mass	20.86
Total leg bone mass	67.64
% leg bone mass	89.34
Breast:thigh muscle ratio	9.85
Tarsometatarsal diameter (lat)	23.88
Tarsometatarsal diameter (CrCd)	7.52

Table 3 Cull data: bone mineral values.

		Sel-Al	Rxd-Al	Sel-Rd	Rxd-Rd	Max SE of differences
% Ash	Mean (SE)	42.08 b*, c,d*** (1.431)	47.34 a,c*, d*** (1.632)	52.94 a***, b,d* (1.632)	59.36 a,b***, c* (1.720)	2.433
% Calcium (Ca)	Mean (SE)	20.34 d*** (0.673)	21.03 d** (0.767)	22.00 d* (0.767)	24.65 a***, b**, c* (0.809)	1.144
% Phosphorus (P)	Mean (SE)	7.44 c*, d*** (0.248)	8.23 d** (0.283)	8.36 a*, d** (0.283)	9.58 a***, b**, c** (0.298)	0.422
Ca:P ratio	Mean (SE)	2.746 (0.065)	2.557 (0.074)	2.617 (0.074)	2.579 (0.078)	0.1108

Significance level: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$
a = significantly different from group Sel-Al
b = significantly different from group Rxd-Al
c = significantly different from group Sel-Rd
d = significantly different from group Rxd-Rd

***F*-statistics**: 3 and 38 degrees of freedom.

Parameter	*F*-statistic	*P*-value
% Ash	21.95	$P < 0.001$
% Calcium	6.05	$P < 0.002$
% Phosphorus	10.12	$P < 0.001$
Calcium:phosphorus ratio	1.53	not significant

Table 4 Tibial plateau angle (TPA) and tibiotarsal torsion measurements.

	Leg	Sel-Al	Rxd-Al	Sel-Rd	Rxd-Rd
Mean TPA (degrees) (SD)	L	22.3 (4.29)	19.2 (3.08)	17.7 (3.93)	19.9 (3.5)
	R	23.2 (3.39)	19.7 (3.83)	17.4 (3.91)	20.2 (2.7)
No. birds with mean TPA > 25°		2	0	0	0
Tibiotarsal torsion (degrees) (SD)	L	6.9 (3.4)	3.9 (2.7)	4.8 (2.2)	3.3 (3.3)
	R	4.6 (2.6)	6.1 (3.4)	5.1 (2.6)	3.5 (2.2)
No. birds with external rotation > 20°		0	0	0	0
No. birds with internal rotation > 5°		6	1	2	1

It is difficult to estimate pure breast muscle mass *in vivo* as girth measurements also include the body cavity. Although the *ad-libitum*-fed selected birds had the greatest girths up to six weeks, there was no significant difference in girth between the *ad-libitum*-fed selected birds and either of the relaxed groups at cull, despite the significantly higher total and percentage breast muscle masses in the former birds. Girth measurements record the circumference of the chest, and if the breast muscle develops in a cranial direction rather than laterally, an increase in breast muscle without an accompanying increase in girth could result. The horizontal orientation of the avian vertebral column results in the centre of gravity of birds being located well forward of the hip (Gatesy & Biewener 1991), and work by Abourachid (1993) on giant turkeys has shown that selected pectoral hypertrophy displaces the centre of gravity cranially in comparison to smaller birds. It seems likely that this is also the case in the *ad-libitum*-fed selected broilers; the effect of this on gait is discussed in an associated paper (see Corr *et al*, p 159–171, this issue).

The rapid increase in bodyweight and girth in the *ad-libitum*-fed selected birds was accompanied by a rapid growth in leg length, so that these birds had the longest legs up to the age of six weeks. Comparing all the groups at the same cull bodyweight, however, the *ad-libitum*-fed selected birds had the shortest legs, and the restricted-fed selected birds the longest legs of all the groups, suggesting that the selected birds have a higher genetic potential for bone growth than their predecessors.

Comparisons of morphometric measurements at the same bodyweight

One of the primary determinants of bone mass and strength is the force produced by muscles acting on bone (Frost 1997). Assuming that the muscles work normally, a change in muscle mass is normally reflected in similar changes in bone mass (Wagner 1979, quoting Doyle *et al* 1970). This was found to be the case in the present experiment, despite studies which suggest that muscle function is poor in modern selected birds (Mitchell 1999). At cull, the selected strains had significantly greater thigh muscle mass and leg bone mass than the relaxed strain birds. There was no significant difference in the percentage of thigh muscle mass within the selected strains at cull; however, the restricted-fed birds had greater bone mass than the *ad-libitum*-fed birds. This is in agreement with the results of other studies, which have shown that slower growth allows the more slowly maturing skeletal system to 'catch up' with the muscular system (Frost 1997). As leg bone mass should increase up to skeletal maturity, it was surprising to find that it is greater in the *ad-libitum*-fed selected birds than in the restricted-fed relaxed group, as only the latter had reached full skeletal maturity (at around 134 days; Reiland *et al* 1978). This is further evidence that selective breeding is having an effect on increasing leg bone mass, which contrasts with the results of Emmerson *et al* (1991) that although selection for increased bodyweight produced increased muscle mass, changes in bone mass were negligible. The increase in leg bone mass that accompanies the increase in muscle mass in all of the groups should have a positive effect on walking ability, assuming that the muscles are physiologically normal; there is, however, evidence that muscle damage is common in broilers (Mitchell 1999).

Because the peak force that a muscle can generate is proportional to its cross-sectional area, the moment produced by a muscle is the product of its area and length, which in turn is the muscle volume (Van der Meulen *et al* 1993). In isometric (ie geometrically similar) subjects, volume is directly proportional to weight, so muscle moments would be proportional to muscle mass. The heavier bodyweight of the *ad-libitum*-fed selected birds will result in greater forces being required to overcome inertia, and this is made difficult by the shorter legs (moment arms). Thus, larger forces will need to be generated by the muscles during walking in these birds, in comparison to the longer-legged restricted-fed birds, for example, and these large forces will be acting on bones that are still immature. If the resultant strains exceed 'safe limits', this will lead to microdamage and pathological remodelling (Frost 1997).

Factors affecting bone strength

Bone strength depends on a number of factors, two of the most important being cross-sectional area and mineral content. In the present study, tarsometatarsal diameter was used as a measure of the cross-sectional area of the bone, although this may not be a true

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representation if the widths of the cortices vary between the groups. The main difference in diameter between the tarsometatarsi of the different groups was in the mediolateral direction, those of the selected birds being wider than those of the *ad-libitum*-fed relaxed birds. Within the strains, the slower-growing restricted-fed birds had wider tarsometatarsal diameters than those fed *ad-libitum*. This is because bone development lags behind the development of the rest of the body during periods of rapid growth, only catching up when muscle strength and bodyweight tend to plateau at maturity (Frost 1997). This may reflect an adaptation to weight-bearing, or an inherently limited rate at which the cross-sectional area can increase (Sumner & Andriacchi 1996). Because bone development lags behind increasing bodyweight, peak strains on bones can be greater during growth than in adulthood (Frost 1997). Slowing growth rate by restricting food intake would allow bones to develop in a way which should improve the strength of the skeleton and therefore decrease the damage caused by the peak microstrains.

Recent work in poultry comparing the quality of cortical bone (assessed histologically) with the ash content found that bone assessed as 'poor' had the lowest ash content (Thorp & Waddington 1997). Bone that was assessed as poor quality (from 35-day-old broilers) had an ash content of 47.7% (Thorp & Waddington 1997), which is 5.6% higher than that of the *ad-libitum*-fed selected birds in the present study. An increase in the mineral content of only a few per cent results in increased maximum and yield stress (and modulus of elasticity) and, therefore, the ability of bone to resist the demands placed upon it (Currey 1975; Currey 1988; Rose *et al* 1996). Although the Ca:P ratios of the birds in the present study did not vary between the groups, the ratios were higher than the 'normal' ratio of 2:1 quoted by Thorp and Waddington (1997), which they suggest may disrupt the structure of the hydroxyapatite crystal, weakening the bone. Thus, based on the percentage of ash, the *ad-libitum*-fed selected birds had the poorest quality bone of all the birds, despite carrying a similar bodyweight. They had the widest tarsometatarsi, however, and it is well known that an increased resistance to bending during growth is a result of changing geometric, rather than mineral, properties of the bone (Sumner & Andriacchi 1996).

Pathology

Post-mortem examination of the bones was undertaken to screen for sub-clinical pathology — in particular, the common problems of tibiotarsal torsion and tibial dyschondroplasia. Tibial plateau angles were also measured in order to assess tibial bowing, which is often associated with tibial dyschondroplasia (Lynch *et al* 1992). Although two birds showed greater tibial plateau angles than the maximum of 25° quoted as normal (Lynch *et al* 1992), no evidence of tibial dyschondroplasia was found upon histological examination of any of the proximal epiphyseal tibiotarsal sections. All of the *ad-libitum*-fed selected broilers had visually apparent valgus angulation of the intertarsal joint (as described by Duff & Thorp 1985a,b); however, the angles were not measured in the present experiment. Mild valgus angulation of the knee joint is also seen in humans, and enables the tibia to be kept vertical while the femur inclines towards the median from a slightly adducted hip; a marked valgus abnormality, however, leads to a pathological gait (Whittle 1991).

Some of the birds also had internal tibiotarsal rotation (particularly the *ad-libitum*-fed birds), which is in agreement with work by Duff and Thorp (1985 a,b) who found a high incidence of internal rotation in *ad-libitum*-fed broilers. Although Duff and Thorp suggested that this was pathological, a subsequent publication by Lynch *et al* (1992) quotes a normal range for tibiotarsal torsion as –5° to 20°, making allowance for a mild degree of internal torsion. None of the birds in the present study were clinically lame, and so all were retained in the study; results of subsequent gait analysis (Corr *et al*, see p 159–171, this issue) suggest that the effect of mild internal torsion on gait is, on its own, insignificant.

Animal welfare implications

This study quantifies various morphological characteristics of the modern broiler and compares them to those of its predecessor of 25 years ago. The rapid growth rate to high end-bodyweights that is demanded of these birds creates high loads on bones that are still immature. The potential through selective breeding to manipulate the rate at which soft tissues such as muscle develop is not matched in bone, the growth rate of which is inherently limited. The altered distribution of body mass, in particular muscle mass, also alters the forces acting on these bones. Thus, many of the selection traits desired in the modern commercial bird appear to markedly increase the stresses on the musculoskeletal system, and may therefore be detrimental to walking ability. An objective gait analysis study of these birds is presented in Corr *et al* (pp 159–171, this issue).

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