

## RESEARCH ARTICLE

# The gait dynamics of the modern broiler chicken: a cautionary tale of selective breeding

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### SUMMARY

**One of the most extraordinary results of selective breeding is the modern broiler chicken, whose phenotypic attributes reflect its genetic success. Unfortunately, leg health issues and poor walking ability are prevalent in the broiler population, with the exact aetiopathogenesis unknown. Here we present a biomechanical analysis of the gait dynamics of the modern broiler and its two pureline commercial broiler breeder lines (A and B) in order to clarify how changes in basic morphology are associated with the way these chickens walk. We collected force plate and kinematic data from 25 chickens (market age), over a range of walking speeds, to quantify the three-dimensional dynamics of the centre of mass (CoM) and determine how these birds modulate the force and mechanical work of locomotion. Common features of their gait include extremely slow walking speeds, a wide base of support and large lateral motions of the CoM, which primarily reflect changes to cope with their apparent instability and large body mass. These features allowed the chickens to keep their peak vertical forces low, but resulted in high mediolateral forces, which exceeded fore–aft forces. Gait differences directly related to morphological characteristics also exist. This was particularly evident in Pureline B birds, which have a more crouched limb posture. Mechanical costs of transport were still similar across all lines and were not exceptional when compared with more wild-type ground-running birds. Broiler chickens seem to have an awkward gait, but some aspects of their dynamics show rather surprising similarities to other avian bipeds.**

Key words: broiler chicken, gait, locomotion, leg weakness, morphology, selective breeding.

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### INTRODUCTION

Although Darwin detailed how organisms evolve through natural selection (Darwin, 1859), he built his case partly on the knowledge that humans have used an analogous principle in the domestication of plants and animals for thousands of years. This has allowed livestock breeders to fully exploit desired phenotypic traits, resulting in dramatic and rapid changes in appearance and behaviour from their wild ancestors. A prime example of these dramatic changes can be seen in the modern broiler (a type of chicken raised specifically for meat), which has extremely rapid growth rates [18 standard deviations from its original rate across ~50 years of breeding (Whitehead et al., 2003)], a significantly larger pectoral muscle mass and increased meat yield (Barton, 1994; Lilburn, 1994; Webster, 1995; Nicholson, 1998; Corr et al., 2003a; Havenstein et al., 2003a; Havenstein et al., 2003b). However, this seeming success in the production efficiency of the modern broiler has come with unwanted consequences. In particular, musculoskeletal abnormalities and poor walking ability (commonly referred to together as ‘leg weakness’) are the most prevalent causes of culling and late mortality in the modern broiler (Pattison, 1992; Knowles et al., 2008).

Typically, leg weakness is characterised using a subjective gait scoring method, which assesses the walking ability of birds based on an abstract ideal of a ‘normal’ gait. Normal birds are considered more agile than those with an ‘abnormal’ gait, and in the worst cases, extremely abnormal birds may be incapable of sustained

walking (Kestin et al., 1992). These gait scoring methods have been used extensively within the scientific community to understand the health and welfare implications in poultry (e.g. McGeown et al., 1999; Danbury et al., 2000; Weeks et al., 2000; Sandilands et al., 2011), but the actual relationship between this impaired walking ability and specific leg problems remains unclear (for a review, see Bradshaw et al., 2002). The difficulties are apparent; potential links of gait mechanics to pathology and walking ability remain merely inferential, the chance of detecting a subtle gait change correlated to pathology appears low and hence requires large sample sizes (Sandilands et al., 2011), and part of the difficulty in associating gait changes with certain pathologies is that chickens often have multiple pathologies. The way a chicken walks can therefore be a product of the underlying pathology and/or stresses, plus the bird’s attempt to compensate for it.

Our first aim is therefore to quantify the locomotor dynamics of the modern broiler as an exploratory analysis of how selection has actually altered the way these birds walk and perhaps contributed to lameness. Because few studies have actually detailed objective measures of the modern broiler’s gait (Reiter and Bessei, 1997; Corr et al., 1998; Corr et al., 2003b; Corr et al., 2007), here we establish the ‘normal’ gait characteristics of the modern broiler. We do this as an essential first step toward the longer-term goal of quantitatively characterising, identifying and understanding abnormal gaits in different lineages of wild and domestic poultry, including broilers. We also clarify possible misconceptions associated with what may

have partly evolved to be an awkward gait for effective locomotion *versus* the individual perception of a 'good' *versus* 'bad' gait or 'leg weakness' in broilers. This is important to examine, because future considerations for the welfare of the modern broiler are likely to be based heavily on visual aspects of their gait.

Ironically, broiler chickens, like other galliform birds, may be considered as specialist walkers [based on their dominant locomotor mode (Tickle et al., 2007; Nudds et al., 2011)]. Yet their exaggerated lateral motions (Corr et al., 2003b) suggest that they may share more in common with other waddling, more aquatic species such as penguins, geese or ducks (Griffin and Kram, 2000; Abourachid, 2001; Usherwood et al., 2008; Nudds et al., 2011). Such waddling birds are often described as 'awkward' or 'ungainly' walkers, yet the mechanics of waddling birds still conform with the classical pendulum model of walking bipeds, associated with the conservation of mechanical energy (Cavagna, 1975; Cavagna et al., 1976; Cavagna et al., 1977). As much as 70% of the external work required to lift and accelerate the centre of mass (CoM) can be recovered as a result of this energy saving mechanism (Cavagna et al., 1977; but see Donelan et al., 2002). The second aim of our study quantifies the three-dimensional dynamics of the CoM in order to determine how broiler chickens modulate the force and mechanical energy of locomotion. Altered behavioural patterns and reduced activity levels have been reported in these birds (Weeks et al., 1994; Estevez et al., 1997; Bizeray et al., 2001; Weeks et al., 2000), which are thought to be attributable to conformation-related gait alterations causing fatigue (Abourachid, 1993; Corr et al., 2003b). We can test whether broilers require excessive work (using the metric of the mechanical cost of transport), requiring more mechanical energy from the limb muscles.

Finally, we evaluate the effects of conformation on locomotor dynamics, by investigating two pureline commercial broiler breeder lines with high performance (in terms of meat production) characteristics. These lines are typically crossbred by commercial poultry production systems in order to produce the modern broiler with desired characteristics (Anthony, 1998; Yang and Jiang, 2005). Differences in the pelvic limb musculature of these study groups have already been shown quantitatively, suggesting that differences in the gait characteristics of these lineages may exist (Paxton et al., 2010). Additionally, when the two purelines are compared at the farm level, Pureline A birds generally yield greater breast muscle mass per unit body mass and have lower average gait scores (poorer walking ability), whereas Pureline B chickens tend to have a larger body mass (~30% difference in some cases) with generally higher gait scores (H.P., unpublished data). We aim to determine whether these three lineages have adopted different locomotor strategies as a result of their altered morphology.

In addition, studies have suggested an apparent instability in broiler chickens, which – in line with the waddling gait of penguins (Kurz et al., 2008) – has been considered, somewhat speculatively, as more susceptible to falls. Specifically, broiler chickens appear to have more excessive lateral motions than more ancestrally typical ground-running birds (Cavagna et al., 1977; Gatesy and

Biewener, 1991; Rubenson et al., 2004). We present the first study to investigate, albeit with an admittedly simple metric, the dynamic stability of the modern broiler. We do this by considering their gait variability and its potential role in locomotor stability (Winter, 1989; Holt et al., 1995; Dingwell and Cavanagh, 2001; Dingwell and Marin, 2006). By doing this, we aim to further highlight how morphological changes may have led to difficulties with locomotor stability in broiler chickens.

## MATERIALS AND METHODS

Male commercial line birds (~42 days old) were used in this study, including two pureline commercial broiler breeder lines, referred to as Pureline A and B, and a commercial broiler strain (Table 1). The main morphological characteristics for these groups (collected from multiple cadaveric specimens) are also detailed in Table 2. These included breast muscle mass ( $\pm 0.1$  g; pectoralis; i.e. pectoralis major, and supracoracoideus; i.e. pectoralis minor; combined), girth ( $\pm 0.1$  cm), hip width ( $\pm 0.1$  mm), keel length ( $\pm 0.1$  mm) and total leg length ( $\pm 0.1$  mm). Hip width was taken as the distance between the trochanteric crests of the femora (birds were similarly positioned in each case), girth was measured around the circumference of the thorax of the bird (tucked under the wings), and total leg length was taken as the sum of the individual pelvic limb bones (femur, tibiotarsus and tarsometatarsus), measured from the most proximal point to the most distal point on the medial or lateral side of the bone. The bird populations were all raised under the same management conditions to ensure that any differences found were not attributed to husbandry factors, which are well known to influence the growth and leg health of broilers (Sørensen et al., 1999; Su et al., 1999; Vestergaard and Sanotra, 1999; Kestin et al., 2001; Scott, 2002; Dawkins et al., 2004; Mench, 2004; Brickett et al., 2007; Buijs et al., 2009). Those birds that were visibly lame or incapable of sustained walking were excluded from this study.

Motion capture was used to study individual birds using eight Qualisys MCH 500 cameras (Gothenberg, Sweden) that were synchronised to a Kistler 9287B force plate (Kistler Instruments, Alton, UK). The trochanteric crest of the hip and the distal phalanx of the middle toe of each limb were marked with infrared-reflective motion capture markers, thereby simplifying each limb as a linear segment. The birds were encouraged to walk over the force plate (500 Hz) parallel to the view of the cameras (167 Hz), and the marker position and the ground reaction forces in the vertical, fore–aft and mediolateral directions were recorded. All the birds had known body masses ( $\pm 0.1$  kg), which were taken immediately after the trials for each individual were finished.

The kinematic and force plate data were then analysed using two computer programs, Qualisys Track Manager (QTM) and MATLAB (The MathWorks, Natick, MA, USA). QTM formed a three-dimensional image of the markers' coordinates and these data were then further processed with the force plate data using custom MATLAB software. All trials were processed, but those trials where there were large gap ranges between the coordinates or where the bird was distracted were removed before further analysis. The

Table 1. Mean subject data for chicken breeds used in this study

Bird group	No. of individuals	No. of steps	Mass (kg)	CoM height (m)	Mean velocity ( $\text{m s}^{-1}$ )	Velocity range ( $\text{m s}^{-1}$ )
Pureline A	8	118	2.8 $\pm$ 0.3 <sup>a</sup>	<b>0.21<math>\pm</math>0.008<sup>b</sup></b>	0.25 $\pm$ 0.07	0.10–0.43
Pureline B	8	90	2.7 $\pm$ 0.4 <sup>a</sup>	<b>0.20<math>\pm</math>0.008<sup>a</sup></b>	0.26 $\pm$ 0.08	0.10–0.45
Broiler	9	130	<b>3.5<math>\pm</math>0.3<sup>b</sup></b>	<b>0.22<math>\pm</math>0.007<sup>c</sup></b>	0.34 $\pm$ 0.17	0.11–1.10

Data are means  $\pm$  s.d. CoM, centre of mass. Means in a column (mass and CoM height only) with no common superscript differ significantly at the 0.05 level between bird groups, emphasised in bold.

Table 2. General morphological characteristics of the chicken breeds used in this study

Bird group	Girth ( $\times 10^{-2}$ )	Hip width ( $\times 10^{-2}$ )	Keel length ( $\times 10^{-2}$ )	Total leg length ( $\times 10^{-2}$ )	Breast muscle mass (% body mass)
Pureline A	25.3 $\pm$ 0.6 <sup>a</sup>	6.34 $\pm$ 0.16 <sup>a</sup>	9.38 $\pm$ 0.45 <sup>a</sup>	17.8 $\pm$ 0.59 <sup>a</sup>	<b>22.1<math>\pm</math>1.6<sup>c</sup></b> (N=128)
Pureline B	24.4 $\pm$ 1.2 <sup>a</sup>	<b>6.90<math>\pm</math>0.28<sup>b</sup></b>	8.92 $\pm$ 0.79 <sup>a</sup>	18.4 $\pm$ 0.97 <sup>a</sup>	<b>20.1<math>\pm</math>1.4<sup>a</sup></b> (N=202)
Broiler	24.7 $\pm$ 1.3 <sup>a</sup>	6.60 $\pm$ 0.17 <sup>a</sup>	8.27 $\pm$ 1.21 <sup>a</sup>	18.6 $\pm$ 0.58 <sup>a</sup>	<b>20.6<math>\pm</math>1.0<sup>b</sup></b> (N=18)
K-S test	0.852	0.493	0.000	0.489	0.000
Levene's test	0.141	0.106	0.003	0.715	0.000

Data originate from birds used in a previous muscle architecture study (Paxton et al., 2010), as well as from data collected on farms to provide a general overview of how morphology differs between the bird groups. The data therefore do not necessarily correspond directly to the subjects used in this study, but were all selected using the same criteria as set out here. To make valid comparisons across bird populations, the data (body measurements only) were normalised to negate the effect of body mass (length  $\propto$  body mass<sup>1/3</sup>). Values reported here are means  $\pm$  s.d. (N=10, unless otherwise stated). Means in a column with no common superscript differ significantly at the 0.05 level and are highlighted in bold. *P*-values for the Kolmogorov–Smirnov and Levene's test are also presented.

kinematic data were filtered (Winter et al., 1974) using a low-pass, zero-lag fourth-order Butterworth digital filter with a cut-off frequency of 10 Hz. The same filter type was used for the ground reaction force data, with a cut-off frequency of 75 Hz. The kinematic data (foot markers only) were used to identify foot-down and foot-off events and these identified steps were subsequently analysed. This also allowed us to investigate any possible asymmetries (i.e. left–right limb differences) that may exist in the broiler.

Ergonomic analysis was conducted in each step to quantify mechanical energy fluctuations and to calculate the mechanical work required to move the CoM. Because the chickens walked slowly, and did not necessarily start walking 'on cue', there may have been some baseline drift from the force plates (an unavoidable limitation of the sensors recording over longer periods of time). To check and correct for this possibility, we assumed that the birds supported their own body mass through consecutive strides and the vertical forces were corrected accordingly. In order to reduce the error in position over time, the initial velocity conditions were calculated following methods adapted from Daley et al. (Daley et al., 2007). A path-matching technique was used where the initial velocity calculated from the kinematic data was used as an initial guess, which was then corrected to provide a base match between the CoM position calculated using the kinematics over time and the CoM position calculated through integration of the force plate data. The initial velocity selected was the value that minimised the divergence (sum of the squared differences) between the two paths and these conditions were used to calculate CoM velocity and position by the double integration of the accelerations from the force plate data.

Observation of the broilers through the length of the trial showed that they rarely walked in a straight line. The fore–aft and mediolateral forces and the CoM velocity in these two directions could therefore be under-/over-estimated depending on the direction the bird was walking in relation to the plate. The forces were thus corrected based on the angle between the CoM velocity and the force plate coordinate system. Peak forces were recorded along with step width and step length, which were defined from the lateral position of the CoM and the fore–aft position of the CoM, respectively. CoM height was defined as the average CoM position across a step. The leg length (in metres) and the leg angle (in degrees) were calculated using the CoM position and the toe marker position data. Based on basic trigonometry, if  $dX$  refers to the horizontal distance between the CoM position and the toe marker and  $dZ$  refers to the vertical distance between the CoM position and the toe marker, leg length =  $\sqrt{(dZ^2 + dX^2)}$  and leg angle =  $180 - [\tan^{-1}(dZ/dX)]$ . The trackway width (measured separate to step width, in order to consider the outward splay of the lower leg) was also calculated, measured as the lateral separation between the markers on the feet during the

double support phase and expressed as a fraction of CoM height. The vertical and lateral displacement of the foot during swing was also considered – i.e. the peak displacement of the foot during swing relative to its position during stance – as a measure of limb circumduction and to investigate foot path variability.

The average horizontal velocity, duty factor (the fraction of the total stride cycle during which the foot is in contact with ground) (Biewener, 1983; Alexander, 1985; McMahon, 1985; Taylor, 1985) and the Froude number for each step were also recorded. The Froude number (*Fr*) was calculated as  $Fr = v^2 g^{-1} l^{-1}$ , where  $g = 9.81 \text{ m s}^{-2}$ ,  $l$  is mean hip height and  $v$  is mean velocity. The mechanical cost of transport (MCoT;  $\text{J kg}^{-1} \text{ m}^{-1}$ ) was also considered:  $\text{MCoT} = W m^{-1} L^{-1}$ , where  $W$  is absolute work performed (J),  $m$  is body mass (kg) and  $L$  is step length (m).

Only data that were considered steady state were used to draw results and conclusions in this study, as it was important to establish typical cyclical movements in these birds without halting or other perturbations. Steady state was defined based on the ground reaction force impulse and the change in CoM velocity over a step. A fore–aft impulse of 0–2 N s and a CoM velocity change of less than 35% during a step were used. The data were then sorted into eight speed categories for statistical analysis. A minimum of five data points per speed category per bird group was set in order to consider their contribution to the relationships observed as valid. Data were omitted where this condition could not be met. Whilst our statistical tests could manage a limited number of data points, because of the unsteady nature of these birds and our objective to establish normal gait characteristics, we wanted to ensure that the results were not influenced by potentially more spurious values. The computer package SPSS (IBM, Armonk, NY, USA) was used for statistical analysis to check for differences between the relationships of bird group, speed and the right or left foot with step width, step length, step frequency, leg length and angle, displacement of the foot, trackway width, peak forces, CoM energies, work performed and MCoT between bird groups. The data were analyzed using a linear mixed model, with speed, the foot used in each step (right/left) and bird group (Pureline A, Pureline B and the commercial broiler) as the fixed effects, the individual bird as the random effect and each factor previously mentioned (MCoT, step frequency, etc.) as the dependent variable. This procedure allowed the data to exhibit correlated and non-constant variability. It estimated the effects of speed, foot used and bird group on the dependent variables while adjusting for correlation due to repeated trials on each bird. *P*-values ( $\leq 0.05$  deemed significant) were taken into consideration when analyzing the data and drawing conclusions.

Additionally, as a measure of kinematic variability, the coefficient of variation (ratio of the standard deviation to the mean) for a number

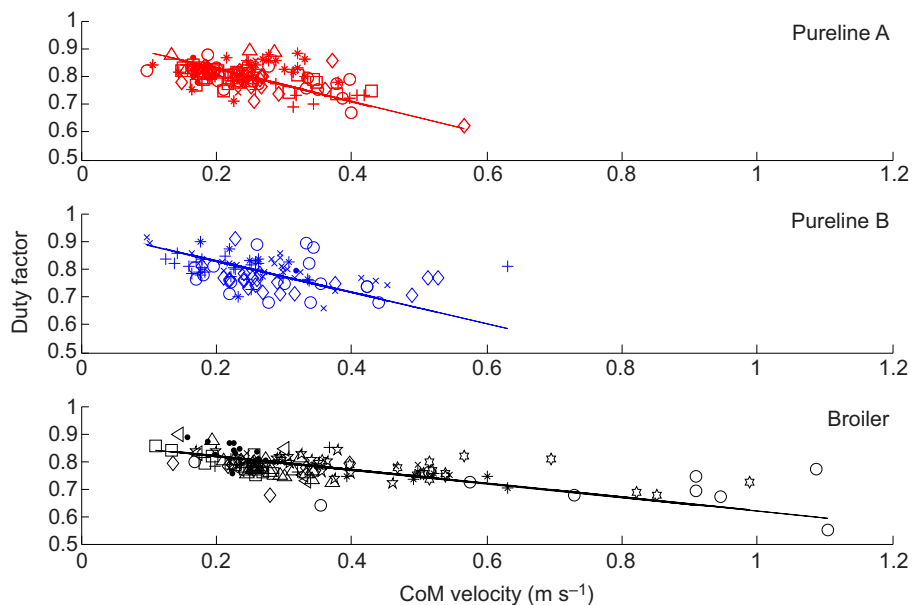


Fig. 1. Duty factor versus centre of mass (CoM) velocity for individual steps from walking chickens. Each symbol represents an individual bird, with the same symbol indicating multiple steps per bird used for this analysis. The regression lines represent a strong relationship ( $r^2 > 0.4$ ) between duty factor and CoM velocity for Pureline A and the broiler population, with a more moderate relationship ( $r^2$  between 0.2 and 0.4) for Pureline B chickens. The slopes of all three lines are statistically different from 0 ( $P < 0.001$ ).

of variables was used in order to have a comparable measure of dispersion among the three groups. To test for differences in morphology, a one-way ANOVA was used to test the differences among group means for significance. To validate the use of this parametric test, assumptions of normal distribution and equal variances were tested using Kolmogorov–Smirnov and Levene’s tests, respectively (results displayed in Table 2). Where these assumptions were not met, an independent Kruskal–Wallis test was used. If significant differences were found ( $P \leq 0.05$ ), a Bonferroni *post hoc* test was used to determine which groups were significantly different from each other. Regression analyses were also used to determine the relationship between CoM velocity and duty factor (Fig. 1), as well as any significant slope differences between step variables (Fig. 2).

We report the locomotor attributes of the modern broiler at their ‘preferred’ walking speed (mean velocity =  $0.25 \pm 0.02 \text{ m s}^{-1}$ ) – i.e. the speed category used most commonly by the three groups (~40% of the data in each group) – as well as any significant relationships with speed. Although work performed is a scalar quantity, we consider the absolute values for work performed as separate components for each direction of motion in order to fully evaluate the mechanical work based on the magnitude and direction of each force vector.

All birds were examined post mortem to identify any pathological condition that may have affected the observed gait, in particular, femoral head necrosis, severe valgus deformities [greater than 45 deg is associated with lameness (Leterrier and Nys, 1992)], tibial dyschondroplasia or gross swelling of the joints.

## RESULTS

Gross abnormalities were not found during post-mortem examination. We therefore considered these birds to have normal limb function based on the absence of any gross pathology. It must be noted that satisfying the conditions of steady state led to differing amounts of data being excluded from this study. The largest number of steps was discounted from Pureline A (47%; 308 out of 661 ‘unsteady’ steps), with 33% (221 out of 661 ‘unsteady’ steps) and 20% (132 out of 661 ‘unsteady’ steps) being discounted from Pureline B and the broiler data sets, respectively. Collectively this accounted for 66% of the total number of steps (999) originally collected.

Very subtle morphological differences existed between the populations of our study birds (Table 2), with only significant differences in hip width ( $F_{2,27} = 16.5$ ,  $P < 0.001$ ) and breast muscle mass ( $P < 0.001$ ). Pureline B birds had wider hips than both the broiler and Pureline A populations. Breast muscle mass varied significantly between the three groups. Pureline A had an additional 2% body mass of breast muscle mass compared with Pureline B and the broiler population, but total leg length was not statistically different between groups. Across all chicken populations, girth was ~30% larger than leg length across all bird populations. CoM height also varied between groups ( $F_{2,319.4} = 85.3$ ,  $P < 0.001$ ; Table 1). Pureline B chickens had the smallest CoM height, which was ~5% smaller than Pureline A birds and ~10% smaller than the broiler population.

Initial analysis of the CoM velocity and duty factor (Fig. 1) shows that the general trend among all populations was for CoM velocity to increase with a decrease in duty factor, as expected. The broiler population, which had the largest body mass (Table 1), seemed able to achieve a much broader speed range than the pureline populations, with a few broiler individuals reaching speeds between 0.6 and  $1.1 \text{ m s}^{-1}$ . The largest fluctuations in CoM velocity can be seen in the lateral component (Table 3), with the highest fluctuations reported in Pureline A chickens. This component also differed depending on the foot used (larger for right steps;  $F_{1,311} = 6.49$ ,  $P = 0.011$ ), and was generally smaller (~16%) in Pureline A birds ( $F_{2,311} = 5.59$ ,  $P = 0.004$ ).

An increase in forward velocity was achieved by increasing step length and step frequency (Fig. 2), with a preference to increase step frequency at a rate slightly faster than that of step length (based on significant differences between the slope values of the two lines,  $P < 0.001$ ). Stance duration also decreased, whereas swing duration was kept almost constant (Fig. 3). Step width decreased with an increase in speed, with the magnitude of this effect varying significantly between bird groups. Step width decreased at a faster rate in Pureline B chickens and to a lesser degree in Pureline A chickens and the broiler population. Step width changes were more variable than changes in step length across all chicken populations. This is seen more clearly if we consider these values at the birds’ preferred walking speed (Table 4). Variability in step width is shown to be approximately two times higher (~30%) than the variability

Table 3. Trackway width, lateral velocity and foot displacement (lateral and vertical) at preferred walking speed in chickens

Bird group	Relative trackway width	Lateral velocity ( $\text{m s}^{-1}$ )		Lateral displacement (m)		Vertical displacement (m)
		Right	Left	Right	Left	
Pureline A	0.52±0.16	<b>0.13±0.05<sup>b</sup></b> (55%)	<b>0.09±0.05<sup>b</sup></b> (56%)	0.037±0.023 <sup>a</sup>	0.026±0.023 <sup>a</sup>	<b>0.082±0.032<sup>b</sup></b>
Pureline B	0.53±0.17	0.12±0.05 <sup>a</sup> (42%)	0.12±0.05 <sup>a</sup> (42%)	<b>0.055±0.024<sup>b</sup></b>	<b>0.039±0.033<sup>b</sup></b>	<b>0.056±0.018<sup>a</sup></b>
Broiler	0.48±0.10	0.12±0.03 <sup>a</sup> (33%)	0.14±0.04 <sup>a</sup> (29%)	0.039±0.020 <sup>a</sup>	0.020±0.029 <sup>a</sup>	<b>0.091±0.024<sup>c</sup></b>

Data are means ± s.d. Relative trackway width was calculated by dividing trackway width by mean hip height.

Means in a column with no common superscript differ significantly at the 0.05 level and are highlighted in bold. The coefficient of variation for lateral velocity is shown in parentheses.

in step length (~15%). Pureline B birds took longer steps than both the Pureline A and the broiler populations ( $F_{2,85,2}=7.58$ ,  $P=0.001$ ), and this corresponded with a significantly lower step frequency ( $F_{2,58,0}=5.89$ ,  $P=0.005$ ). Trackway width was not significantly different between groups ( $F_{2,140,0}=2.66$ ,  $P=0.073$ ), remaining ~51% of mean hip height across all bird populations (Table 3).

Analysis of the chickens' general limb motions across a step cycle (Fig. 4) shows that leg angle did not change by more than ~10 deg through the stance phase of locomotion and was relatively consistent across steps (given the small standard deviations), in contrast to the swing phase of locomotion, where leg angle was much more variable. Changes in overall leg length were small between stance and swing phases, with the more noticeable differences between these events seen in the broiler population. This relates to the pathway of the feet during swing (Table 3), with the broiler population lifting their feet roughly a third higher than Pureline B birds with each step. In all bird populations, circumduction of both limbs was evident ( $F_{2,303}=5.49$ ,  $P=0.005$ ), with a significantly larger lateral displacement of the right foot ( $F_{1,303}=1.97$ ,  $P<0.001$ ). This did not correlate with lateral velocity. The largest lateral displacement of both limbs was seen in Pureline B birds, which also had a significantly larger sweep angle ( $F_{2,318}=11.49$ ,  $P<0.001$ ; Table 4). Thus Pureline B birds took longer steps while drawing their feet further away from the body but at a lower elevation than broilers did.

The resulting ground reaction forces (Fig. 5) show that our study birds all tended to support forces equal to or slightly more than their body weight during a step, with peak vertical forces (Table 4) not exceeding 1.4 times body weight. These peak vertical forces were significantly larger in the broiler population (~15%) compared with the Pureline A population ( $F_{2,67,9}=6.31$ ,  $P=0.003$ ). Mediolateral forces generally exceeded fore–aft forces, with both representing 10–15% of the peak vertical force. The subsequent direction of the mediolateral force corresponded to which foot was placed on the ground, with a general trend for birds to roll laterally over their supporting leg with each step. These forces were also larger in the right limb in all bird populations ( $F_{1,296,0}=73.2$ ,  $P<0.001$ ), which was more evident in the Pureline B and broiler populations, where the mediolateral forces were generally two times larger in the right limb (Table 4). Overall, the broiler population experienced significantly larger (~30%) mediolateral forces than the pureline groups ( $F_{2,84,3}=10.3$ ,  $P<0.001$ ).

The limb motions used by the birds led to a minimal change in CoM displacement (Fig. 5), which was generally less than 5% of hip height, corresponding to very small changes in gravitational potential energy. Fluctuations in kinetic energy were negligible and changes in CoM energies across all bird populations were small (fluctuating around zero) but extremely variable, with standard deviations much larger than value means (Table 4).

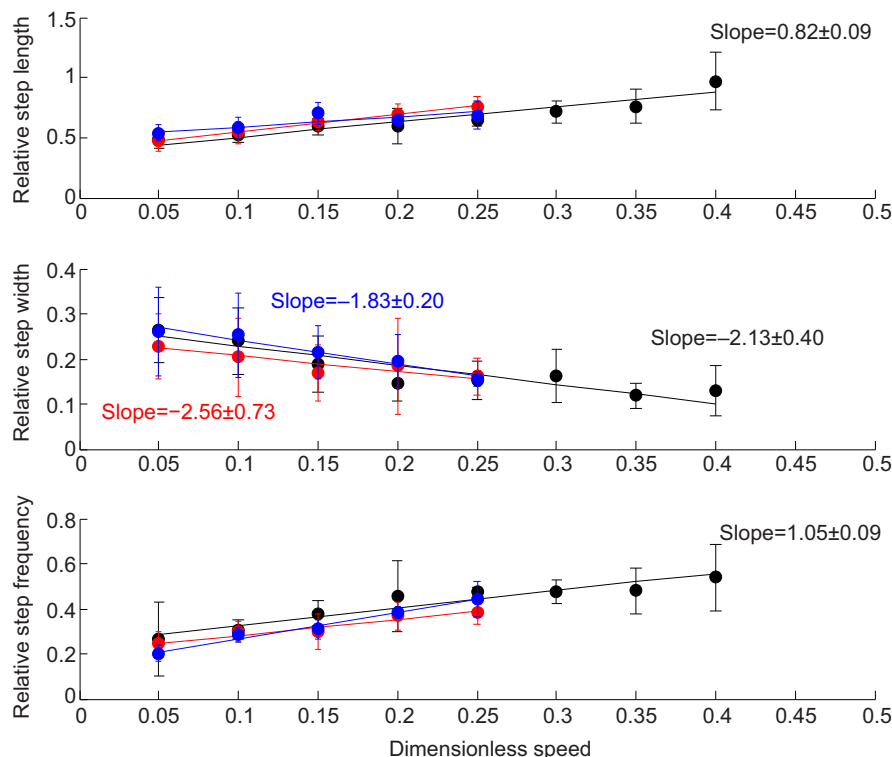


Fig. 2. Step variables change with speed in walking chickens. Data are means ± s.d. The different coloured data points refer to Pureline A (red), Pureline B (blue) and the broiler population (black). Relative values were calculated by dividing step length and step width by mean hip height. Relative step frequency was calculated using the following equation,  $f=(hg^{-1})^{0.5}$ , where  $g=9.81 \text{ m s}^{-2}$  and  $h$  is mean hip height (Alexander, 1977; Alexander and Jayes, 1983). The slope values were tested for significant differences between bird populations, i.e. the coefficient for the interaction between the dependent variable and the bird group is 0. Mean slope values are displayed if no significant differences exist.

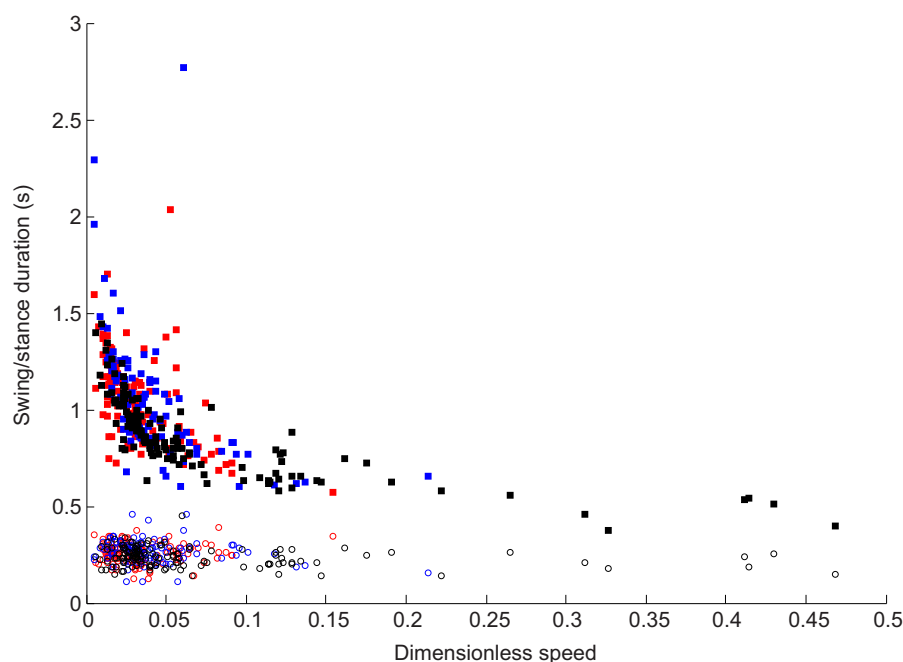


Fig. 3. Stance (squares) and swing phase (circles) durations in walking chickens across their speed range. The different coloured data points refer to Pureline A (red), Pureline B (blue) and the broiler population (black). Individuals are not distinguished, thus data points may represent multiple steps from one bird.

The subsequent work performed in the vertical and mediolateral directions was significantly smaller in Pureline A ( $F_{2,48.4}=9.32$ ,  $P<0.001$  and  $F_{2,194.0}=14.2$ ,  $P<0.001$ , respectively). Across all birds, the work performed in the mediolateral direction was of similar magnitude to the work performed in the fore–aft direction. Despite the subtle differences in locomotor dynamics observed between lines, the MCoT (work performed per kilogram body mass over a step) was not significantly different between groups ( $F_{2,68.5}=1.43$ ,  $P=0.247$ ; Fig. 6). Remarkably, when compared with other ground-running birds (ostrich and guineafowl) for which adequate data exist, the MCoT appears to follow simple body-size scaling patterns (i.e. larger species toward the bottom of the plot) rather than showing a sharp divergence between specialised running birds and the more sedate, artificially selected domestic chickens.

## DISCUSSION

Leg weakness (encompassing lameness and poor walking ability) is a topical issue concerning the health and welfare of the modern broiler chicken. Unfortunately, there are many difficulties associated with establishing the cause of leg weakness in poultry and very little is understood about their gait. Our study therefore had three major purposes: (1) to determine how selection has actually altered the way that production-line chickens walk; (2) to determine whether any changes in locomotor dynamics require excessive work, requiring more mechanical energy from the limb muscles; and (3) to establish whether a change in morphology in these chickens leads to different locomotor mechanisms. Hence, our study helps to illuminate how morphological changes may have contributed to lameness or other difficulties with locomotion in the broiler chicken.

Table 4. Dynamic gait variables for the study chickens at their preferred walking speed

	Pureline A	Pureline B	Broiler
Step variables			
Number of steps	46	39	56
Relative step length	0.54±0.09	<b>0.58±0.09*</b>	0.53±0.01
Relative step width	0.20±0.09	0.25±0.09	0.24±0.07
Relative step frequency	0.30±0.04	<b>0.28±0.03*</b>	0.31±0.04
Sweep angle (deg)	36.8±7.4	<b>40.0±8.0*</b>	34.8±5.3
Peak forces (BW)			
Vertical	1.18±0.12	1.27±0.30	1.38±0.10 <sup>a</sup>
Fore–aft	0.10±0.04	0.11±0.04	0.12±0.03
Mediolateral (right foot)	0.12±0.09	0.18±0.06	<b>0.24±0.04*</b>
Mediolateral (left foot)	0.11±0.06	0.09±0.04	<b>0.11±0.04*</b>
CoM energies			
ΔGravitational potential energy (J)	0.06±0.16	0.04±0.45	0.01±0.29
ΔKinetic energy (J)	−0.02±0.14	−0.04±0.16	0.05±0.09
ΔTotal energy (J)	0.04±0.14	−0.02±0.43	0.05±0.23
Work performed (absolute values)			
Vertical (J)	<b>0.60±0.20*</b>	0.83±0.64	0.94±0.30
Fore–aft (J)	0.20±0.08	0.21±0.05	0.22±0.06
Mediolateral (J)	0.19±0.14	0.20±0.11	<b>0.26±0.11*</b>

Data are means ± s.d. \*Significant differences at the 0.05 level between bird groups. Only significant asymmetries are reported; superscript 'a' indicates a significant difference from Pureline A birds. BW, body weight; CoM, centre of mass.

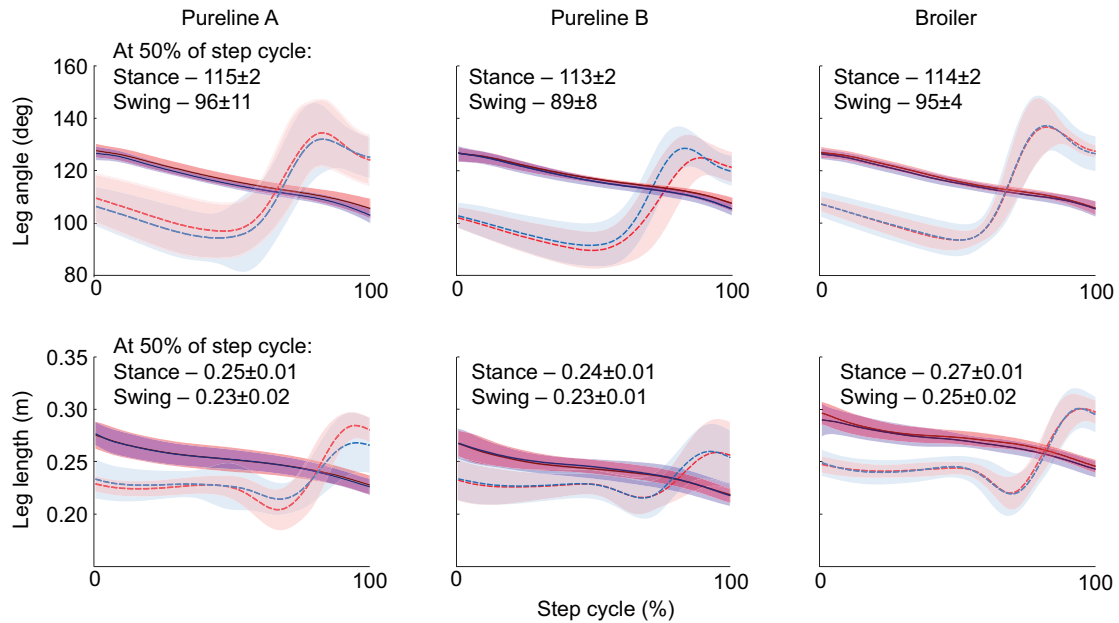


Fig. 4. Leg length and angle at preferred walking speed in chickens. Data are means  $\pm$  s.d. (shaded areas). Stance (solid lines) and swing (dashed lines) phase are shown for the right (red) and left foot (blue).

It is well known that distinct selection pressures are applied on a line-by-line basis, so we would expect morphological differences to exist amongst our three study groups. Consequently, we found subtle differences including a large pectoral muscle mass, accounting for  $\sim 20\%$  of total body mass ( $\sim 2\%$  larger in Pureline A chickens compared with Pureline B and the broiler population), and differences in hip width between the study populations (larger in Pureline B). This disproportionate increase in pectoral muscle mass to body mass is well documented (e.g. Havenstein et al., 1994a; Havenstein et al., 1994b; Lilburn, 1994), but under natural conditions is usually only seen in other Galliformes that require this large muscle to power a rapid take-off; e.g. grouse or partridges (Hartman,

1961; Tobalske and Dial, 2000). Broiler chickens are essentially flightless at any stage of ontogeny (authors' personal observations), and previous literature has suggested that the influence of this alone may put greater demands on the pelvic limb muscles, affecting the birds' walking ability (Abourachid, 1993; Corr et al., 2003b). The logic underlying this presumed relationship between pectoral mass and pelvic limb mechanics is that a more cranially positioned CoM requires more limb muscle effort for support. This is not uncommon among other bipeds, where the potential displacement of the CoM (greatly influenced by body size and shape) has been found to have a strong influence on aspects of locomotion [e.g. postural stability in humans (Fregly et al., 1968; Corbeil et al., 2001)], such as a

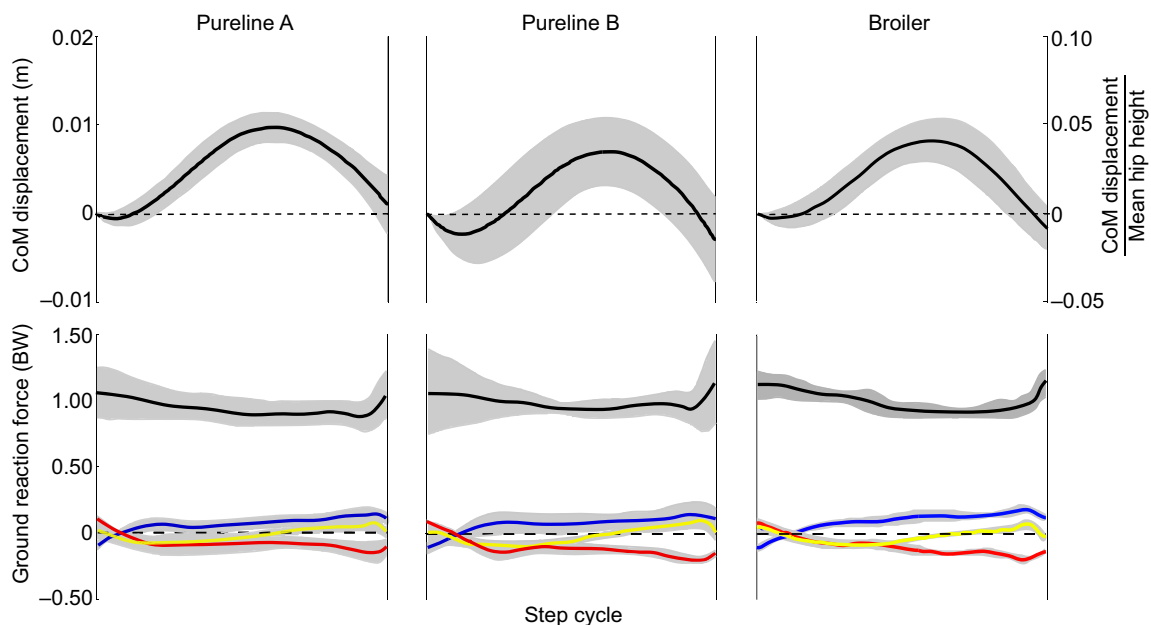


Fig. 5. The ground reaction forces and CoM displacements at the preferred walking speed of three chicken populations. Data represented are means  $\pm$  s.d. (shaded areas). Vertical forces (black), fore-aft forces (yellow) and mediolateral forces (red, right foot; blue, left foot) are shown.

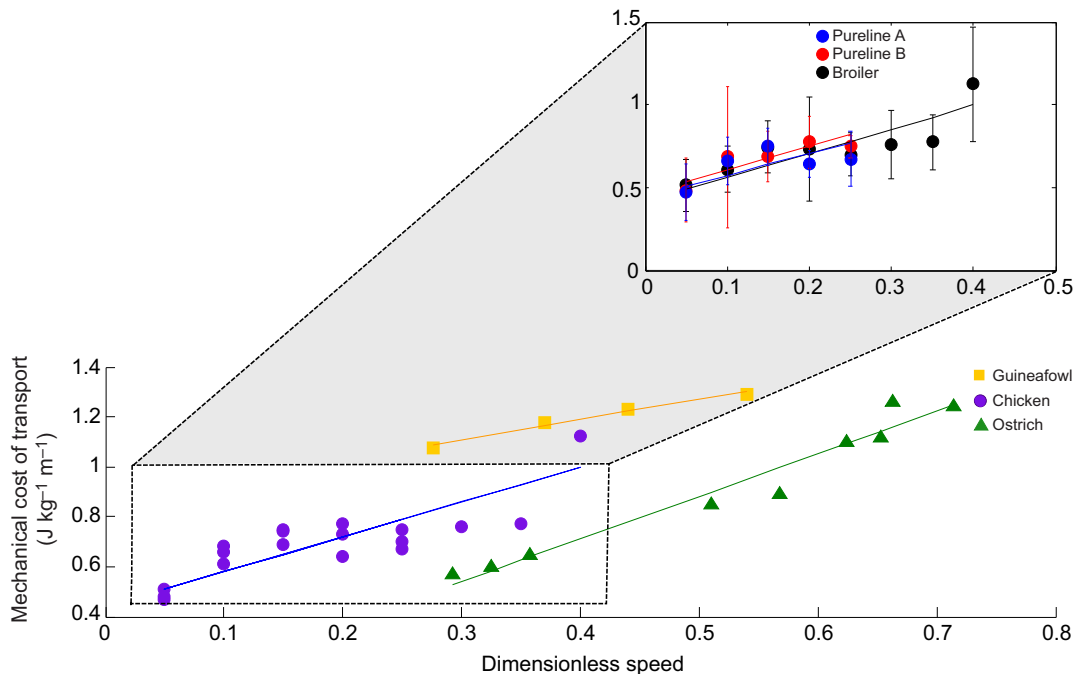


Fig. 6. The mechanical cost of transport of domestic chickens at their preferred walking speed. Data for the commercial line birds are means  $\pm$  s.d. All other data are means only. Note that data for the three chicken populations are shown together in purple at the bottom left for comparison to the guineafowl and ostrich data, and separately in the inset at the top right to illustrate differences among them.

wider pelvis (Pureline B birds), in combination with the large pectoral muscle mass (Hutchinson, 2004). Yet it remains unclear how other morphological changes may affect gait.

Initial evaluation of the gait of our three study populations of chickens reveals common features with other avian bipeds [guineafowl (Gatesy, 1999); quail (Reilly, 2000); other avian taxa (Gatesy and Biewener, 1991; Abourachid, 2000; Abourachid, 2001; Rubenson et al., 2004; Nudds et al., 2011)], including typical associations seen with increased speed, such as a preference to increase step frequency at a slightly faster rate than step length, a decrease in step width and a decrease in stance duration. This also coincides with a relatively constant swing phase duration. However, our study birds were still walking at substantially slower speeds than other ground-running birds and even slower than waddling birds, such as ducks (Usherwood et al., 2008) and penguins (Griffin and Kram, 2000), which also have relatively short legs and exhibit a comparatively narrower range of speeds than ground-running birds. The average duty factor of the commercial lines studied ( $0.79 \pm 0.05$ ) is still representative of other slow-walking animals including humans (Alexander, 1989; Reilly, 2000; Aerts et al., 2000; Zani et al., 2005).

Typically in human gait studies, individuals who walk more slowly than healthy controls are deemed to have some form of gait disability, but slowing down can simply reflect a 'safer' and more 'tentative' strategy for moving around (Winter, 1989; Powers et al., 1999; Dingwell and Cavanagh, 2001). This assessment of disability is a common subjective view of locomotion in human obesity studies, because obese humans have a similar problem of carrying extra body mass (Messier, 1994; Messier et al., 1996; Browning and Kram, 2009; Spyropoulos et al., 1991). Recent studies have shown that slower walking velocities serve to increase dynamic stability (Dingwell and Marin, 2006; England and Granata, 2007) and consequently domestic chickens may benefit from reduced falling risks at the cost of increased variability in their locomotor movements. However, it has been shown that individuals can still

display decreased stability despite this compensatory mechanism (Kang and Dingwell, 2008). Approximately 65% of the total data were excluded from this study (did not meet criteria for steady state) because birds were walking at even slower speeds than reported here, and halting significantly between steps. These halting movements were often sporadic in nature, with no association with step number or trial number, and therefore the reasons for this random unsteadiness were difficult to ascertain. It could be related to physical constraints, such as decreased strength (DeVita and Hortobagyi, 2000) or flexibility (Kerrigan et al., 2001), or even exercise fatigue, which is known to affect gait in humans with evidence of poorer dynamic stability (Wojtys et al., 1996; Yoshino et al., 2004; Granata and Gottipati, 2008). From personal observations, the chickens often became breathless with the mild exertion of walking, and thus needed frequent rest between trials. The percentage to live weight of hearts and lungs of broilers is much smaller as a result of selection (Havenstein et al., 1994a; Havenstein et al., 1994b; Havenstein et al., 2003b; Schmidt et al., 2009), and so the influences of their cardiovascular system and perhaps a reduced 'cardiovascular fitness' on their locomotor ability are important to consider in future studies.

Irrespective of this, a few individuals of the broiler population were able to achieve a much broader speed range, which is perhaps surprising, considering that a larger body mass is typically associated with poorer walking ability (Kestin et al., 1999; Kestin et al., 2001; Bokkers et al., 2007; Naas et al., 2009). The question then remains as to whether this broad speed range is indicative of a 'good' walking bird and/or whether it simply reflects differences in the gait characteristics of these commercial lines. Firstly, the variation in the lateral velocity of the CoM was substantially smaller in the broiler population compared with the pureline birds. If we use this reduced variation as an indicator of improved lateral balance in walking broilers (Winter, 1989; Holt et al., 1995), this supports our initial suggestion that the broiler is perhaps a 'better' walking bird.



The differences in gait parameters seen (Table 4) were generally quite subtle, with the main changes seen in Pureline B birds, which have a more crouched limb posture (lower CoM height for same total leg length). Their longer step length, lower step frequency and larger sweep angle are typical of this postural change (Gatesy and Biewener, 1991). This is also associated with significantly greater circumduction and less vertical displacement of the foot during swing. Two plausible explanations for this crouched limb posture may be their wider pelvis and a more cranially positioned CoM, although more detailed biomechanical analyses are needed to test this speculation. However, difficulty in walking was perhaps more evident in Pureline A birds (48% of data not meeting requirements for steady state), which carry more breast muscle mass compared with the other populations (Table 2). Pureline A birds are 'front heavy', with the breast muscle mass concentrated at the cranial end of the keel. We therefore suggest that not just the breast muscle mass, but also the way it is distributed along the length of the keel, potentially has a major effect on the way that domestic chickens walk. To test this speculation, future studies could test whether alterations in CoM caused by such changes in morphology cause alterations in joint moments or tissue forces.

Across all bird populations, we found that our study chickens generally took shorter steps than other ground-running birds, related to their much slower velocities, and had an extremely wide trackway width, substantially (~18%) larger than hip width. As a result, these birds held their feet in a position more lateral to the hip, which allows them to increase their lateral base of support and also provides a larger potential for mediolateral motions of the CoM (Donelan et al., 2001). This lateral motion was seen across all commercial lines and is a common feature of waddling birds, usually attributed to their short legs and wide base of support (Pinshow et al., 1977; Griffin and Kram, 2000; Abourachid, 2001; Usherwood et al., 2008; Nudds et al., 2011). Our study's commercial line birds moved their CoM ~23% of hip height with each step and subsequently rolled their body laterally over the planted foot whilst the contralateral limb was in swing phase. Adjusting step width and step length are also key to redirecting the CoM to remain within the base of support and prevent falling (Winter, 1991), and, similar to humans, the chickens studied have a more variable step width than step length. These chickens may rely on more precise foot placement to control their lateral stability (Kuo, 1999; Bauby and Kuo, 2000) in contrast to penguins, which have been shown to have a more consistent step width and rely more on modulation of their trunk instead (Kurz et al., 2008). Further perturbation studies are needed to test whether this variance is associated with precise placement of the foot and is not simply the result of a lack of control or instability, which is commonly observed in these broiler populations. If waddling clearly provides some benefits for penguins (Griffin and Kram, 2000; Kurz et al., 2008), what does waddling mean for the modern broiler and its generation lines?

The observed lateral motions resulted in high mediolateral forces, which generally exceeded fore–aft forces across all bird populations and were also substantially larger in the right limb. The reason for this asymmetry is not clear, but may be linked to limb dominance and a subsequent preference to use the right limb for balance control, because our study birds also showed greater lateral displacement of the right foot. Similar to elderly individuals with imbalance, domestic chickens may swing the contralateral limb more laterally to counterbalance the evident lateral roll over the supporting leg (Chou et al., 2003). This would explain why the subsequent mediolateral forces experienced by the left limb were substantially reduced. The mediolateral forces were

significantly larger in the broiler population, which is likely attributable to their evidently greater limb motions, with the broiler population lifting their limbs significantly higher during swing and consequently exhibiting the largest changes in leg length. A gradual decline in leg length and leg angle is still evident through the stance phase of all three bird groups, which probably is associated with slight flexion–extension of the knee (Jacobson and Hollyday, 1982; Johnston and Bekoff, 1992) and toes (Reilly, 2000), supported by our personal observations during these experiments. The angle of the limb was highly variable during the swing phase, which likely corresponds to the high variation in the vertical and lateral displacement of the foot during swing before being placed on the ground to establish a new base of support for gait progression. The significantly greater vertical forces reported in the broilers compared with Pureline A birds are presumably the direct result of this group of birds tending to lift their feet much higher off the ground with each step. Pureline B birds still experienced similar peak forces, despite their more crouched limb posture, which would usually be considered as a strategy to reduce the peak vertical forces experienced by the limb, in a manner similar to bent-knee running in humans (McMahon et al., 1987). This group may have a more plodding gait, involving greater impacts of the feet with the ground early in stance phase.

If the chicken populations studied were indeed walking steadily over ground, the kinetic energy and potential energy changes would be the same at the beginning and the end of each step and would fluctuate around zero (Alexander and Jayes, 1978; Griffin et al., 2004). The changes in CoM energies did indeed fluctuate around zero, but were extremely variable, highlighting the apparent instability of walking in purelines and broilers. It is therefore difficult to determine whether these birds perform similar quantities of positive and negative work, and thus how much their muscles may be actively contributing to each step. The broiler population appeared to have significantly different kinetic energy changes to the Pureline B population, but we hesitate to make inferences from these data. In all three commercial lines, the fluctuations in kinetic energy were small and the CoM displacement across a step was also minimal, reflecting small changes in gravitational potential energy. Passive pendular mechanics are well used among other cursorial birds and other terrestrial animals (Cavagna et al., 1977; Heglund et al., 1982; Blickhan and Full, 1992; Muir et al., 1996; Griffin and Kram, 2000; Ahn et al., 2004; Rubenson et al., 2004; Biewener, 2006; Biknevicius and Reilly, 2006), but this is usually achieved at intermediate walking speeds in birds (Cavagna et al., 1977; Rubenson et al., 2004). The capacity for these commercial line birds to therefore recover mechanical energy through pendular mechanics is likely to be low as a direct result of their slow walking speeds. This has also been reported in other slow-walking animals [geckos (Farley and Ko, 1997); alligators (Willey et al., 2004); tortoises (Zani et al., 2005); elephants (Ren and Hutchinson, 2008)].

The subtle gait differences among this study's three groups led to varying amounts of work performed on the CoM in different directions. For example, the largest amount of mediolateral work was performed by the broiler population, whereas the shorter steps and lower peak vertical forces of the Pureline A birds allowed this group to perform less work in the vertical direction. Despite the subtle differences in gait reported here, these commercial line birds not only have similar mechanical costs of transport, but when compared with the ostrich and guineafowl, appear to perform no greater mechanical work. The mechanical cost of transport of these commercial lines is substantially lower than that of guineafowl at the same walking speed, and our results are consistent with the

widely accepted evidence that the cost of transport decreases with increasing body size (Langman et al., 1995). The large lateral motions of our study chickens result in similar amounts of work performed in the lateral and fore-aft directions, but it is possible that the relatively small limb movements we report here compensate for the mechanical work of moving the body CoM in the lateral direction. Constraining step length also has the additional advantage of reducing mechanical work, because step length increases mechanical work to a greater extent than step width (Donelan et al., 2001; Donelan et al., 2002). The observed waddling movements therefore do not, as sometimes thought, require excessive work. However, slight caution should be taken when interpreting these values. It must be noted that the MCoT was calculated using the combined limbs method, which is known to underestimate the external mechanical work performed in walking (Donelan et al., 2002). As a result, these values are likely to be an underestimation of the true magnitude in broilers, guinea fowl and ostrich, especially when the mechanical work performed by each individual pelvic limb is unknown.

Unfortunately, a low MCoT does not necessarily correlate with low metabolic costs. Contradictory patterns exist in the literature, with mechanical energy recovery associated with low and high metabolic costs. These metabolic costs can be associated with a number of factors, including step-to-step transitions or step width (Donelan et al., 2002), the cost of muscular force generation (Kram and Taylor, 1990; Kram et al., 1997; Hoyt et al., 2000; Griffin et al., 2003), the swing phase of locomotion (Marsh et al., 2004) or even slow walking speeds (Langman et al., 1995). Indeed, the absence or poor use of pendulum-like energy exchange that we report here, as well as the active, lateral limb movement of their limbs that we suggest chickens use for stability, may also exact a metabolic cost (Donelan et al., 2001; Shipman et al., 2002). Hence, the relationship between the mechanical work and the metabolic cost of locomotion is difficult to assess and has not been measured in the modern broiler chicken. Testing this issue is particularly difficult because the commercial chicken lines used in this study are unable to walk steadily and consistently long enough to obtain reliable direct measurements of metabolic cost; hence either validated indirect measurements on other birds or else novel ways of measuring metabolic cost directly are needed to determine how costly walking is for these chickens.

Our study has shown how subtle changes in the morphological characteristics of the broiler chicken and its generation lines can lead to changes in locomotor dynamics. We have highlighted the potential mechanical benefits of slow walking speeds, a wide base of support and large lateral, essentially 'waddling' motions for the broiler, as well as showing that the seemingly awkward gait of the broiler may not be as 'inefficient' as previously thought. Actually, the gait of the modern broiler shows rather surprising similarities to other avian bipeds. However, the influence of broilers' unusual three-dimensional movements on the occurrence of skeletal pathologies is unknown. These large lateral motions, which appear to be essential for the forward progression of the broiler, could play a role in the development of skeletal pathologies; a speculation that deserves testing in the future.

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#### AUTHOR CONTRIBUTIONS

All authors contributed equally to this work. H.P. collected the experimental data, and H.P. and M.A.D. were involved in the main analysis. H.P. wrote the paper and all authors discussed the results and implications and commented on the manuscript.

#### COMPETING INTERESTS

No competing interests declared.

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