Title:

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

Heather Paxton*, Monica A. Daley*, Sandra A. Corr*†, John R. Hutchinson*

Structure and Motion Laboratory*
Department of Comparative Biomedical Sciences
The Royal Veterinary College
University of London
Hatfield, Hertfordshire, UK

Division of Surgery†
School of Veterinary Medicine and Science
University of Nottingham
Sutton Bonington, Leicestershire, UK

Contact information:
Heather Paxton; hpaxton@rvc.ac.uk
Phone +44 (0) 1707 666 456

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 3D 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 to 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

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, 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; Sandiland et al., 2011), but the actual relationship between this impaired walking ability and specific leg problems remains unclear (see review; 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 (Sandiland 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. Since 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 characterizing, 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 laid 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., 2010). 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, 2008; Nudds et al., 2010). 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, 1977). As much as 70% of the external work required to lift and accelerate the centre of mass can be recovered due to this energy saving mechanism (Cavagna et al., 1977; but see Donelan et al., 2002). The second aim of our study quantifies the 3D dynamics of the centre of mass (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., 2000; 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 cross-bred 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. Paxton, 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.

Methods:

Male commercial line birds (approximately 42 days old) were used in this study including two pureline commercial broiler breeder lines, referred to as pureline A and B respectively, and a commercial strain broiler (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 (± 0.1g; pectoralis; i.e. pectoralis major, and supracoracoideus; i.e. pectoralis minor; combined), girth (± 0.1cm), hip width (± 0.1mm), keel length (± 0.1mm) and total leg length (± 0.1mm). 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 the 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 (Sorenson 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 which 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) which were synchronised to a Kistler 9287B force plate (Kistler Instruments Ltd, 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 (500Hz) parallel to the view of the cameras (167Hz) 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 (± 0.1kg), which were taken immediately after the trials for each individual were finished.

The kinematic and force plate data were then analysed using two computer programmes, Qualisys Track Manager (QTM) and Matlab (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 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 10Hz. The same filter type was used for the ground reaction force data, with a cut-off frequency of 75Hz. 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. Since 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 which 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 dependent 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 track way 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 $g = 9.81 m s^{-2}$, l = mean hip height and v = mean velocity. The mechanical cost of transport (MCoT; $J kg^{-1} m^{-1}$) was also considered ($MCoT = W m^{-1} L^{-1}$), where W = absolute work done (J), m = body mass (kg) and L = 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, due to the unsteady nature of these birds and our objective to establish normal gait characteristics, we wanted to ensure the results were not influenced by potentially more spurious values. The computer package SPSS (Statistical Package for the Social Sciences, Chicago, Illinois) was used for the 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 done and the mechanical cost of transport (MCoT) between bird groups. The data were analyzed using a linear mixed model, with speed, the foot used in each step (right/ left) and the 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 the bird group on the dependent variables while adjusting for correlation due to repeated trials on each bird. P-values (≤ 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 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 analysis of variance (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 the Kolmogorov-Smirnov statistic and the Levene’s test (results displayed in Table 2). Where these assumptions were not met, an independent Kruskal-Wallis test was used. If significant differences were found (p-value ≤ 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. 3).

We report the locomotor attributes of the modern broiler at their 'preferred' walking speed (mean velocity = 0.25 ± 0.02 m s^{-1}) -- i.e. the speed category used most commonly by the three groups (approximately 40% of the data in each group), as well as any significant relationships with speed. Although work done is a scalar quantity, we consider the absolute values for work done 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 degrees is associated with lameness; Letterier 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 were discounted from pureline A (47%; 308 steps out of 661 'unsteady' steps), with 33% (221 steps out of 661 'unsteady' steps) and 20% (132 steps 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 to pureline B and the broiler population, but total leg length was not statistically different between groups. Across all chicken populations, girth was approximately 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 0.6-1.1 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 dependent 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 slightly faster rate than 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 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 approximately 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 more than approximately 10 degrees 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 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 to pureline A ($F_{2, 67.9} = 6.31$, $p = 0.003$). 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 pureline B and the broiler population, 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 centre of mass displacement (Fig. 5), which was generally less than 5% of hip height, corresponding to very small changes in gravitational potential energy (GPE). Fluctuations in kinetic energy (KE) 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).

The subsequent work done 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 done in the mediolateral direction was of similar magnitude to the work done in the fore-aft direction. Despite the subtle differences in locomotor dynamics observed between lines, the MCoT (work done per kg 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 to 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 specialized 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. Unfortunately, there are many difficulties associated with establishing the cause of leg weakness in poultry and very little 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.

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 approximately 20% of total body mass (~ 2% larger in pureline A chickens compared to 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, 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 (pers obs., all authors), 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 relation 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 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, 2001; Rubenson et al., 2004; Nudds et al., 2010) 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 to ground-running birds. The average duty factor of the commercial lines studied (0.79 ± 0.05) is still representative of other slow-walking animals/ 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, 2007; 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) due to birds walking at even slower speeds than reported here, and halting significantly between steps. These halting movements were often sporadic in nature, with no association to 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 (De Vita 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 are much smaller as a result of selection (Havenstein et al., 1994a,1994b; Havenstein et al., 2003; 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, 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 to 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 to 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 (approximately 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, 2008; Nudds et al., 2010). Our study’s commercial line birds moved their CoM approximately 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 if 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 (Jacobsen 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 broiler compared to pureline A 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 approximately zero, but were extremely variable, highlighting the apparent instability of walking in purelines and broilers. It is therefore difficult to determine whether these birds do similar quantities of positive and negative work, and so 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 KE were small and the CoM displacement across a step was also minimal, reflecting small changes in GPE. 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, Wiley et al., 2004; tortoise, Zani et al., 2005; elephants, Ren and Hutchison, 2008).

The subtle gait differences among this study’s three groups led to varying amounts of work done on the CoM in different directions. For example, the largest amount of mediolateral work was done by the broiler population, whereas the shorter steps and lower peak vertical forces of the pureline A birds allowed this group to do less work in the vertical direction. Despite the subtle differences in gait we report, these commercial line birds not only have similar mechanical costs of transport, but when compared to the ostrich and guineafowl, appear to do 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 done in the lateral and fore-aft direction, 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, 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 done in walking (Donelan et al., 2002). As a result, these values are likely to be an underestimation of the true magnitude, in broilers, guineafowl and ostrich, especially when the mechanical work performed by each individual pelvic limb is unknown.

Unfortunately, a low mechanical cost of transport 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 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.

Acknowledgements

We thank Cobb-Vantress Inc., especially Roy Mutimer and Kate Barger, for their support on this project which was part of a CASE Industrial Partnership PhD studentship to H.P., funded by the Biotechnology and Biological Sciences Research Council (BBSRC) of the United Kingdom. Additional support from BBSRC grant number BB/I02204X/1 to J.R.H. and M.A.D. is acknowledged. Other members of the Structure & Motion Lab are thanked for their assistance during experiments and data analysis, including but not limited to Sharon Warner and Rebecca Fisher. We also thank undergraduate student Will Parker for assistance in experiments and dissections. Two anonymous reviewers gave helpful constructive criticisms that improved this manuscript.

References:

Abourachid, A. (2001). Kinematic parameters of terrestrial locomotion in cursorial (ratites) swimming (ducks) and striding (quail and guinea fowl). *Comp. Biochem. Physiol. A: Mol. Integr. Physiol.* **131**, 113-119.

Abourachid, A. (2000). Bipedal locomotion in birds: the importance of functional parameters in terrestrial adaptation in Anatidae. *Can. J. Zoo.* **78**, 1994-1998.

Abourachid, A. (1993). Mechanics of standing in birds: functional explanation of lameness problems in giant turkeys. *Br. Poult. Sci.* **34,** 887-898.

Aerts, P., Van Damme, R., Van Elsacker, L. (2000). Spatio-temporal gait characteristics of the hind-limb cycles during voluntary bipedal and quadrupedal walking in bonobos (Pan paniscus). *Am. J. Phys. Anthropol.* **111**, 503-517.

Ahn, A.N., Furrow, E., Biewener, A.A. (2004). Walking and running in the red-legged running frog, Kassina maculate. *J. Exp. Biol.* **207**, 399-410.

Alexander, R.M. (1989). Optimisation and gaits in the locomotion of vertebrates. *Physiol. Rev.* **69**, 1199-1227.

Alexander, R.M. (1985). The maximum forces exerted by animals. *J. Exp. Biol.* **115,** 231-238.

Alexander, R.M., Jayes, A.S. (1978). Vertical movements in walking and running. *J. Zool.* **185**, 27-40.

Anthony ***NB*** *(*1998). A review of genetic practices in poultry: efforts to improve meat quality. *J. Muscle Food.* **9**, 25-33.

Arthur, J.A., Alburs, *G.A.A.* (2003). Industrial perspective on problems and issues associated with poultry breeding. In: *Poultry Genetics, Breeding and Biotechnology*. Wallingford, *UK:* CABI Publishing Co.

Barton, N.F. (1994). Breeding meat type poultry for the future targets for selection, limits to performance and market requirements for chicken. In: *Proc 9th Eur Poult Conf, Glasgow, UK*, 33-38.

Bauby, C.E., Kuo, A.D. (2000). Active control of lateral balance in human walking. *J. Biomech.* **33**, 1433-1440.

Bennett, R.M., Christiansen, K., Clifton-Hadley, R.S. (1999). Direct costs of endemic diseases of farm animals in Great Britain. *Vet Rec.* **145**, 376-377.

Bessei, W. (2006). Welfare of broilers: a review. *W. Poult. Sci. J.* **62**, 455-466.

Biewener, A.A. (2006). Patterns of mechanical energy change in tetrapod gait: pendula, springs and work. *J. Exp. Zool.* **305**, 899-911.

.

Biewener, A.A. (1983). Allometry of quadrupedal locomotion: The scaling of duty factor, bone curvature and limb orientation to body size. *J. Exp. Biol.* **105**, 147-171.

Biknevicius, A.R., Reilly, S.M. (2006). Correlation of symmetrical gaits and whole body mechanics: debunking myths in locomotor biodynamics. *J. Exp. Zool.* **305**, 923-934.

Bizeray, D., Leterrier, C., Constantin, P. (2000). Typology of activity bouts in the broiler chicken: A new approach for simplifying observational methods. *Br. Poult. Sci.* **42**, S11-12.

Blickhan, R., Full, R.J. (1992) Mechanical work in terrestrial locomotion. In: *Biomechanics: A Practical Approach,* Oxford University Press.

Bokkers, E., Zimmerman, P.H., Bas Rodenburg, T., Koene, P. (2007). Walking behaviour of heavy and light broilers in an operant runway test with varying durations of feed deprivation and feed access. *Appl. Anim. Behav. Sci.* **108**, 129-142.

Bradshaw, R.H., Kirkden, R.D., Broom, D.M. (2002). A review of the aetiology and pathology of leg weakness in broilers in relation to their welfare. *Avian Poult. Biol. Rev.* **13**, 45-103.

Brickett, K.E., Dahiya, J.P., Classen, H.L., Gomis, S. (2007). Influence of dietary nutrient density, feed form, and lighting on growth and meat yield of broiler chickens. *Poult. Sci.* **86**, 2172-2181.

Browning, R.C., Kram, R. (2007). Pound for pound: Working out how obesity influences the energetic of walking. *J. Appl. Physiol.* **106**, 1755-1756.

Buijs, S., Keeling, L., Rettenbacher, S., Van Pouke, E., Tuyttens, F.A.M. (2009). Stocking density effects on broiler welfare: identifying sensitive ranges for different indicators. *Poult. Sci.* **88**, 1536-1543.

Cavagna, G.A. (1975). Force platforms as ergometers. *J. Appl. Physiol.* **39**, 174-179.

Cavagna, G.A., Heglund, N.C., Taylor, C.R. (1977). Mechanical work in terrestrial locomotion: Two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243-R261.

Cavagna, G.A., Thys, H., Zamboni, A. (1976) The sources of external work in level walking and running. *J. Physiol.* **262**, 639-657.

Chou, L.S., Kaufman, K.R., Hahn, M.E., Brey, R.H. (2003). Mediolateral motion of the center of mass during obstacle crossing distinguishes elderly individuals with imbalance. *Gait Post.* **18**, 125-133.

Corbeil, P., Simoneau, M., Rancourt, D., Tremblay, A., Teasdale, N. (2001). Increased risk for falling associated with obesity: mathematical modeling of postural control. *IEEE Trans. Neural. Syst. Rehabil. Eng.* **9**, 126-136.

Corr, S.A., McCorquodale, C., McDonald, J., Gentle, M., McGovern, R. (2007). A force plate study of avian gait. *J. Biomech.* **40**, 2037-2043.

Corr, S.A., Gentle, M.J., McCorquodale, C.C., Bennett, D. (2003a). The effect of morphology on the musculoskeletal system of the modern broiler. *Anim. Welfare* **12**, 145-157.

Corr, S.A., Gentle, M.J., McCorquodale, C.C., Bennett, D. (2003b). The effect of morphology on walking ability in the modern broiler: a gait analysis study. *Anim. Welfare* **12**, 159-171.

Corr, S.A., McCorquodale, C.C., Gentle, M.J. (1998). Gait analysis of poultry. *Res. Vet. Sci.* **65**, 233-238.

Daley, M.A., Felix, G., Biewener, A.A. (2007) Running stability is enhanced by a proximo-distal gradient in joint neuromechanical control. *J. Exp. Biol.* **210**, 383-394.

Danbury, T.C., Weeks, C.A., Chambers, J.P., Waterman-Pearson, A.E., Kestin, S.C. (2000). Self-selection of the analgesic drug carprofen by lame broiler chickens. *Vet. Rec.* **146**, 307-311.

Darwin, C. (1859). On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. London: John Murray.

Dawkins, M.S., Donnelly, C.A., Jones, T.A. (2004). Chicken welfare is influenced more by housing conditions than by stocking density. *Nature* **427**, 342-344.

De Vita, P., Hortobagyi, T. (2000). Age causes a redistribution of joint torques and power during gait. *J. Appl. Physiol.* **88**, 1804-1811.

Dingwell, J.B., Cavanagh, P.R. (2001). Increased variability of continuous over-ground walking in neuropathic patients is only indirectly related to sensory loss. *Gait Post.* **14**, 1–10.

Dingwell, J.B., Marin, L.C. (2006). Kinematic variability and local dynamic stability of upper body motions when walking at different speeds. *J. Biomech.* **39**, 444-452.

Donelan, J.M., Kram, R., Kuo, A.D. (2002). Simultaneous positive and negative external mechanical work in human walking. *J. Biomech.* **35**,117-124.

Donelan, J.M., Kram, R., Kuo, A.D. (2001). Mechanical and metabolic determinants of the preferred step width in human walking. *Proc. Roy. Soc. Lond. B.* **268**, 1985-1992.

England, S.A., Granata, K.P. (2007). The influence of gait speed on local dynamic stability of walking. *Gait Post.* **25**, 172-178.

Estevez, I., Newberry, R.C., Arias de Reyna, L. (1997) Broiler chickens: A tolerant social system? *Etologia* **5**, 19-29.

Farley, C.T., Ko, T.C. (1997) Mechanics of locomotion in lizards. *J. Exp. Biol.* **200**, 2177-2188.

Fregly, A.R., Oberman, A., Graybiel, A., Mitchell, R.E. (1968) Thousand aviator study: nonvestibular contributions to postural equilibrium functions. *Aero. Med.* **39**, 33-37.

Gatesy, S.M. (1999). Guineafowl hind limb function I: cineradiographic analysis and speed effects. *J. Morphol.* **240**, 127-142.

Gatesy, S.M., Biewener, A.A. (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool.* **224**, 127-147.

Granata, K.P., Gottipati, P. (2008). Fatigue influences the dynamic stability of the torso. *Ergonomics* **51**, 1258-1271.

Griffin, T.M., Kram, R. (2000). Penguin waddling is not wasteful. *Nature* **408**, 929.

Griffin, T.M., Main, R.P., Farley, C.T. (2004). Biomechanics of quadrupedal walking: how do four-legged animals achieve inverted pendulum-like movements? *J. Exp. Biol.* **207**, 3545 -3558.

Griffin, T.M., Roberts, T.J., Kram, R. (2003). Metabolic cost of generating muscular force in human walking: insights from load-carrying and speed experiments. *J. Appl. Physiol.* **95**,172-183.

Hartman, F.A. (1961). *Locomotor mechanisms of birds*. Smithson. Misc. Collns. **143**, 1-91.

Havenstein, G.B., Ferket, P.R., Qureshi, M.A. (2003a). Growth, livability and feed conversion of 1957 versus 2001 broilers when fed representative 1957 and 2001 broiler diets. *Poult. Sci.* **82**, 1500-1508.

Havenstein, G.B., Ferket, P.R., Qureshi, M.A. (2003b). Carcass composition and yield of 1957 versus 2001 broilers when fed representative 1957 and 2001 broiler diets. *Poult. Sci.* **82**, 1509-1518.

Havenstein, G.B., Ferket, P.R., Scheideler, S.E., Larson, B.T. (1994a). Growth, livability, and feed conversion of 1957 vs. 1991 broilers when fed “typical” 1957 and 1991 broiler diets. *Poult. Sci.* **73**, 1785–1794.

Havenstein, G.B., Ferket, P.R., Scheideler, S.E., Rives, D.V. (1994b). Carcass composition and yield of 1991 vs. 1957 broilers when fed “typical” 1957 and 1991 broiler diets. *Poult. Sci.* **73**, 1795–1804.

Heglund, N.C., Fedak, M.A., Taylor, C.R., Cavagna, G.A. (1982). Energetics and mechanics of terrestrial locomotion. IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 57-66.

Holt, K.G., Jeng, S.F., Ratcliffe, R., Hamill, J. (1995). Energetic cost and stability during human walking at the preferred stride frequency. *J. Motor. Behav.* **27**, 164-178.

Hoyt, D.F., Wickler, S.J., Cogger, E.A. (2000). Time of contact and step length: the effect of limb length, running speed, load carrying and incline. *J .Exp. Biol.* **203**, 221-227.

Hutchinson, J.R. (2004). Biomechanical modelling and sensitivity analysis of bipedal running ability. I. Extant taxa. *J. Morphol.* **262**, 421-440.

Jacobsen, R.D., Hollyday, M. (1982). A behavioural and electromyographic study of walking in the chick. *J. Neurophys.* **48**, 238-256.

Johnston, R.M., Bekoff, A. (1992). Constrained and flexible features of rhythmical hindlimb movements in chicks: kinematic profiles of walking, swimming and airstepping. *J. Exp. Biol.* **171**, 43-66.

Kang, H.G., Dingwell, J.B. (2008). Effects of walking speed, strength and range of motion on gait stability in healthy older adults. *J. Biomech.* **41**, 2899-2905.

Kerrigan, D.C., Lee, L.W., Collins, J.J., Riley, P.O., Lipsitz, L.A. (2001). Reduced hip extension during walking: healthy elderly and fallers versus young adults. *Arch. Physic. Med. Rehab.* **82**, 26-30.

Kestin, S.C., Knowles, T.G., Tinch, A.E., Gregory, N.G. (1992). Prevalence of leg weakness in broiler chickens and its relationship with genotype. *Vet. Rec.* **131**, 190-194.

Kestin, S.C., Su, G., Sorensen, P. (1999). Different commercial broiler crosses have different susceptibilities to leg weakness. *Poult. Sci.* **78**, 1085-1090.

Kestin, S.C., Gordon, S., Su, G., Sorenson, P. (2001). Relationships in broiler chickens between lameness, liveweight, growth rate and age. *Vet. Rec.* **148**, 195-197.

Knowles, T.G., Kestin, S.C., Haslam, SM., Brown, S.N., Green, L.E., Butterworth, A., Pope, S.J., Pfeiffer, D., Nicol, C.J. (2008). Leg disorders in broiler chickens: Prevalence, risk factors and prevention. *PLoS ONE* **3**, e1545.

Kram, R., Taylor, C.R. (1990). Energetics of running: A new perspective. *Nature* **346**, 265-266.

Kram, R., Domingo, A., Ferris, D. (1997). Effect of reduced gravity on the preferred walk–run transition speed. *J. Exp. Biol.* **200**, 821–826.

Kuo, A. (1999). Stabilization of lateral motion in passive dynamic walking. *Int. J. Robot Res.* **18**, 917-930.

Kurz, M.J., Scott-Pandorf, M., Arellano, C., Olsen, D., Whitaker, G. (2008). The penguin waddling gait pattern has a more consistent step width than step length. *J. Theor. Biol.* **252**, 272-276.

Langman, V.A., Roberts, T.J., Black, J., Maloiy, G.M.O., Heglund, N.C., Weber, J.M., Kram, R., Taylor, C.R. (1995). Moving cheaply: energetics of walking in the African Elephant. *J. Exp. Biol.* **198**,629-632.

Letterier, C., Nys, Y. (1992). Composition, cortical structure and mechanical properties of chicken tibiotarsi: Effects of growth rate. *Br. Poult. Sci.* **33**, 925-939.

Lilburn, M.S. (1994). Skeletal growth of commercial poultry species. *Poult. Sci.* **73**, 897-903.

Marsh, R.L., Ellerby, D.J., Carr, J.A., Henry, H.T., Buchanan, C.I. (2004). Partitioning the energetics of walking and running: swinging the limbs is expensive. *Science* **303**, 80-83.

McGeown, D., Danbury, T.C., Waterman-Pearson, A.E., Kestin, S.C. (1999). Effects of carprofen on lameness in broiler chickens. *Vet. Rec.* **144**, 668-671.

McMahon, T.A. (1985). The role of compliance in mammalian running gaits. *J. Exp. Biol.* **115**, 263-282.

McMahon, T.A., Valiant, G., Frederick, E.C. (1987). Groucho running. *J. Appl. Physiol.* **62**, 2326-2337.

Mench, J.A. (2004). Lameness. In: *Measuring and Auditing Broiler Welfare*. CABI, Wallingford, UK.

Messier, S.P. (1994). Osteoarthritis of the knee and associated factors of age and obesity effects on gait. *Med. Sci. Sport Ex.* **26**, 1446-1452.

Messier, S.P., Ettinger, W.H., Doyle, T.E. (1996). Obesity: Effects on Gait in an Osteoarthritic Population. *J. Appl. Biomech.* **12**, 161-172.

Muir, G.D., Gosline, J.M., Steeves, J.D. (1996). Ontogeny of bipedal locomotion: walking and running in the chick. *J. Physiol.* **493**, 589-601.

Naas, I.A., Paz, I.C.L.A., Baracho, M.S., Menezes, A.G., Bueno, L.G.F., Almeida, I.C.L., Moura, D.J. (2009). Impact of lameness on broiler well-being. *J. Appl. Poult. Res.* **18**, 432-439.

Nicholson, D. (1998). Research, is it the broiler industry's partner into the new millennium? *W. Poult. Sci. J.* **54**, 271–278.

Nudds, R.L., Folkow, L.P., Lees, J.J., Tickle, P.G., Stokkan, K.A., Codd, J.R. (2010). Evidence for energy savings from aerial running in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). *Proc. Roy. Soc. B.* doi:10.1098/rspb.2010.2742.

Pattison, M. (1992). Impacts of bone problems on the poultry meat industry. In: *Bone Biology and Skeletal Disorders in Poultry*, Carfax Publishing Co., Abingdon.

Paxton, H., Anthony, N.B., Corr, S.A., Hutchinson, J.R. (2010). The effects of selective breeding on the architectural properties of the pelvic limb in broiler chickens: a comparative study across modern and ancestral populations. *J. Anat.* **217**, 153-166.

Pinshow, B., Fedak, M.A., Schmidt-Nielsen, K. (1977). Terrestrial locomotion in penguins: it costs more to waddle. *Science* **195**, 592–594.

Pontzer, H. (2007). Predicting the cost of locomotion in terrestrial animals: a test of the LiMb model in humans and quadrupeds. *J. Exp. Biol.* **210**, 484-494.

Pontzer, H. (2005). A new model predicting locomotor cost from limb length via force production . *J. Exp. Biol.* **208**, 1513-1524.

Powers, C.M., Heino, J.G., Rao, S., Perry, J. (1999). The influence of patellofemoral pain on lower limb loading during gait. *Clin. Biomech.* **14**, 722–72.

Reilly, S.M. (2000). Locomotion in the quail (coturnix japonica): the kinematics of walking and increasing speed. *J. Morph.* **243**, 173-185.

Reiter, K., Bessei, W. (1997). Gait analysis in laying hens and broilers with and without leg disorders. *Equine Vet. J.* **23**, 110-112.

Ren, L., Hutchinson, J.R. (2008). The three-dimensional locomotor dynamics of African (Loxodonta africana) and Asian (Elephas maximus) elephants reveal a smooth gait transition at moderate speed. *J. Roy. Soc. Interface* **5**, 195-211.

Rubenson, J., Heliams, D.B., Lloyd, D.G., Fournier, P.A. (2004). Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase. *Proc. R. Soc. Lond. B* **271**, 1091-1099.

Sandilands, V., Brocklehurst, S., Sparks, N., Baker, L., McGovern, R., Thorp, B., Pearson, D. (2011). Assessing leg health in chickens using a force plate and gait scoring: how many birds is enough? *Vet. Rec.* **168**, 77.

Schmidt, C.J., Persia, M.E., Feierstein, E., Kingham, B., Saylor, W.W. (2009). Comparison of a modern broiler line and a heritage line unselected since the 1950s. *Poult. Sci.* **88**, 2610-2619.

Scott, T.A. (2002). Evaluation of lighting programs, diet density, and short-term use of mash as compared to crumbled starter to reduce incidence of sudden death syndrome in broiler chicks to 35 days of age. *Can. J. Anim. Sci.* **82**, 375-383.

Shipman, D., Donelan, J.M., Kram, R., Kuo, A.D. (2002). Metabolic cost of lateral leg swing in human walking. In: *World Congress of Biomechanics*, Canada.

Sorenson, P., Su, G., Kestin, S.C. (1999). The effect of photoperiod: scotoperiod on leg weakness in broiler chickens. *Poult. Sci.* **78**, 336-342.

Spyropoulos, P., Pisciotta, J.C., Pavlou, K.N., Cairns, M.A., Simon, S.R. (1991). Biomechanical gait analysis in obese men. *Arch. Physic. Med. Rehab.* **72**, 1065–1070.

Su, G., Sorenson, P., Kestin, S.C. (1999). Meal feeding is more effective than early feed restriction at reducing the prevalence of leg weakness in broiler chickens. *Poult. Sci.* **78**, 949-955.

Taylor, C.R. (1985). Force development during sustained locomotion: A determinant of gait, speed and metabolic power. *J. Exp. Biol.* **115**, 253-262.

Tickle, P., Nudds, R., Codd, J. (2009). Uncinate Process Length in Birds Scales with Resting Metabolic Rate. PLoS ONE **4**, e5667.

Tickle, P.G., Ennos, A.R., Lennox, L.E., Perry, S.F., Codd, J.R. (2007). Functional significance of the uncinate processes in birds. *J. Exp. Biol.* **210**, 3955-3961.

Tobalske, B.W., Dial, K.P. (2000). Effects of body size on take-off flight performance in the Phasianidae (Aves). *J. Exp. Biol.* **203**, 3319-3332.

Usherwood, J.R., Szymanek, K.L., Daley, M.A. (2008). Compass gait mechanics account for top walking speeds in ducks and humans. *J. Exp. Biol.* **211**, 3744-3749.

Vestergaard, K.S., Sanotra, G.S. (1999). Relationships between leg disorders and changes in the behaviour of broiler chickens. *Vet. Rec.* **144**, 205-209.

Waldenstedt, L. (2006). Nutritional factors of importance for optimal leg health in broilers: A review. *Anim. Feed. Sci. Tech.* **126**, 291-307.

Webster, J. (1995). *Animal Welfare: A Cool Eye Towards Eden.* Cambridge, MA, Blackwell Science.

Weeks, C.A., Danbury, T.D., Davies, H.C., Hunt, P., Kestin, S.C. (2000). The behaviour of broiler chickens and its modification for lameness. *Appl. Anim. Behav. Sci.* **67**, 111-125.

Weeks, C.A., Nicol, C.J., Sherwin, C.M., Kestin, S.C. (1994). Comparison of the behaviour of broiler chickens in indoor and free-range environments. *Anim. Welfare* **3**, 179-192.

Whitehead, C.C., Fleming, R.H., Julian, R.J., Søresen, P. (2003). Skeletal problems associated with selection for increased production. In: *Poultry Genetics, Breeding and Biotechnology*, CABI Publishing, Wallingford, UK

Wiley, J.S., Biknevicius, A.R., Reilly, S.M., Earls, K.D. (2004) The tale of the tail: limb function and locomotor mechanics in *Alligator mississippiensis. J. Exp. Biol.* **207**,553-563.

Winter, D.A. (1989). Biomechanics of normal and pathological gait: implications for understanding human locomotor control. *J. Mot. Behav.* **21**, 337-55.

Winter, D.A., Sidwall, H.G., Hobson, D.A. (1974). Measurement and reduction of noise in kinematics of locomotion. *J. Biomech.* **7**, 157-159.

Wojtys, E.M., Wylie, B.B., Huston, L.J. (1996). The effects of muscle fatigue on neuromuscular function and anterior tibial translation in healthy knees. *Am. J. Sport Med.* **24**, 615-621.

Yang, N., Jiang, R.S. (2005). Recent advances in breeding for quality chickens. *W. Poult. Sci. J.* **61**, 373-381.

Yoshino, K., Motoshige, T., Araki, T., Matsuoka, K. (2004). Effect of prolonged free-walking fatigue on gait and physiological rhythm. *J. Biomech.* **37**, 1271-1280.

Zani, P.A., Gottschall, J.S., Kram, R. (2005). Giant Galapagos tortoises walk without inverted pendulum mechanical energy exchange. *J. Exp. Biol.* **208**, 1489-1494.

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

Data represented are mean ± s.d. 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 for the chicken breeds used in this study

Data originates 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 (lengths α body mass$^{1/3}$). Values reported here are mean ± s.d. (sample size = 10, unless otherwise stated within the table). Means in a column with no common superscript differ significantly at the 0.05 level and are highlighted in bold.

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

Data represented are mean ± s.d. Means in a column with no common superscript differ significantly at the 0.05 level. The coefficient of variation for lateral velocity is shown in brackets.

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

Data represented are mean ± standard deviation. * represents significant differences at the 0.05 level between bird groups. Only significant asymmetries are reported; (^{a}) refers to significant differences from pureline A birds.

Figure 1 – Duty factor against 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 ($p < 0.001$).

Figure 2 – Step variable changes with speed in walking chickens

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

Figure 3 – Stance and swing phase durations in walking chickens

The stance (□) and swing phase (○) durations for all commercial line chickens across their speed range. The different coloured data points refer to pureline A (red), pureline B (blue) and the broiler population (black) respectively. Individuals are not distinguished; thus data points may represent multiple steps from one bird.

Figure 4 – Leg length and angle at preferred walking speed in chickens

Data represented are means ± s.d. (shaded areas). Stance (solid line) and swing (dashed line) phase are both shown for the right (red) and left foot (blue).

Figure 5 – The ground reaction forces and CoM displacements at the preferred walking speed of three chicken populations.

Data represented are means ± s.d. (shaded areas). Vertical forces (black), fore-aft forces (yellow) and mediolateral forces (red- right foot and blue-left foot) are shown.

Figure 6 - The mechanical cost of transport of domestic chickens at their preferred walking speed

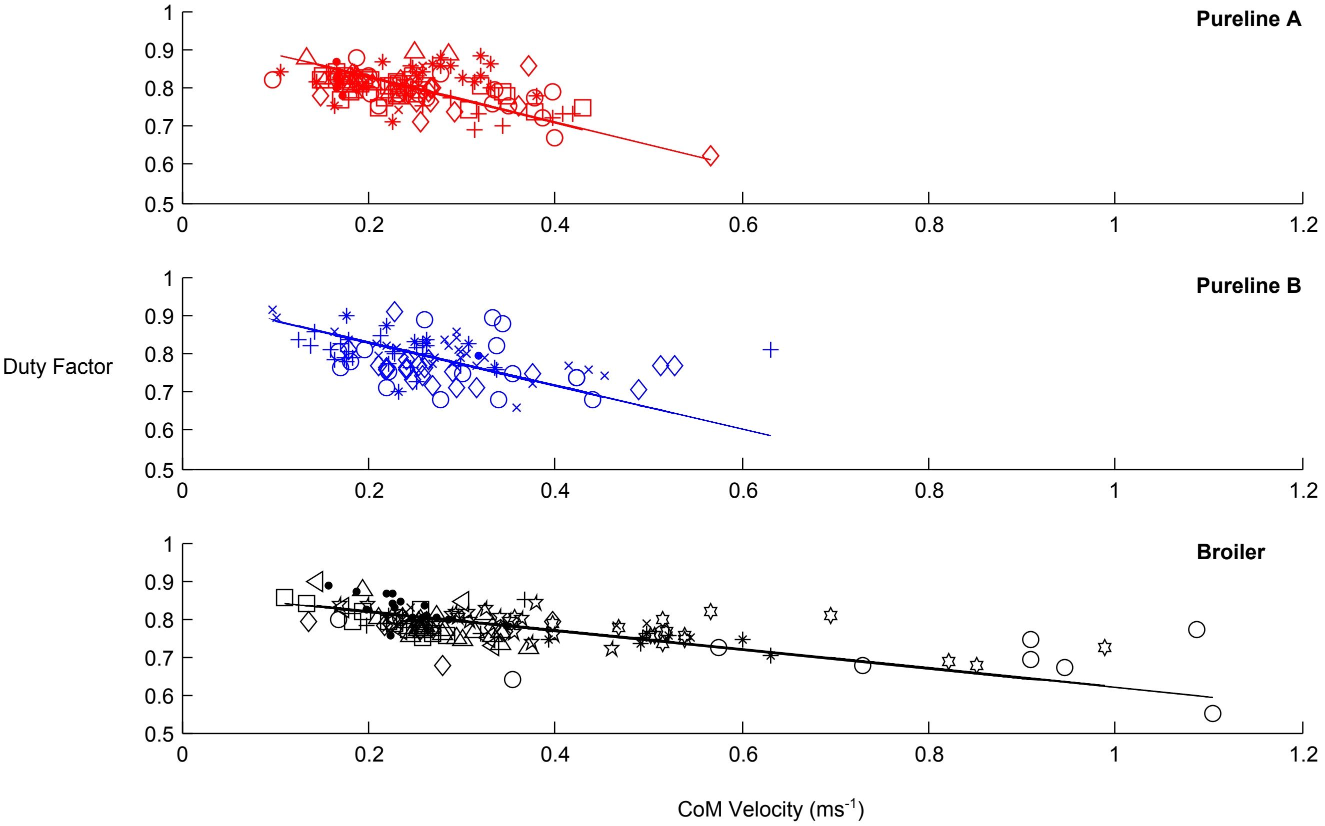
Data represented for the commercial line birds are means ± s.d. All other data are means only. Note that data for the three chicken populations are shown together in purple at the bottom left for comparison to the guineafowl and ostrich data, and separately in the inset at the top right to illustrate differences among them.

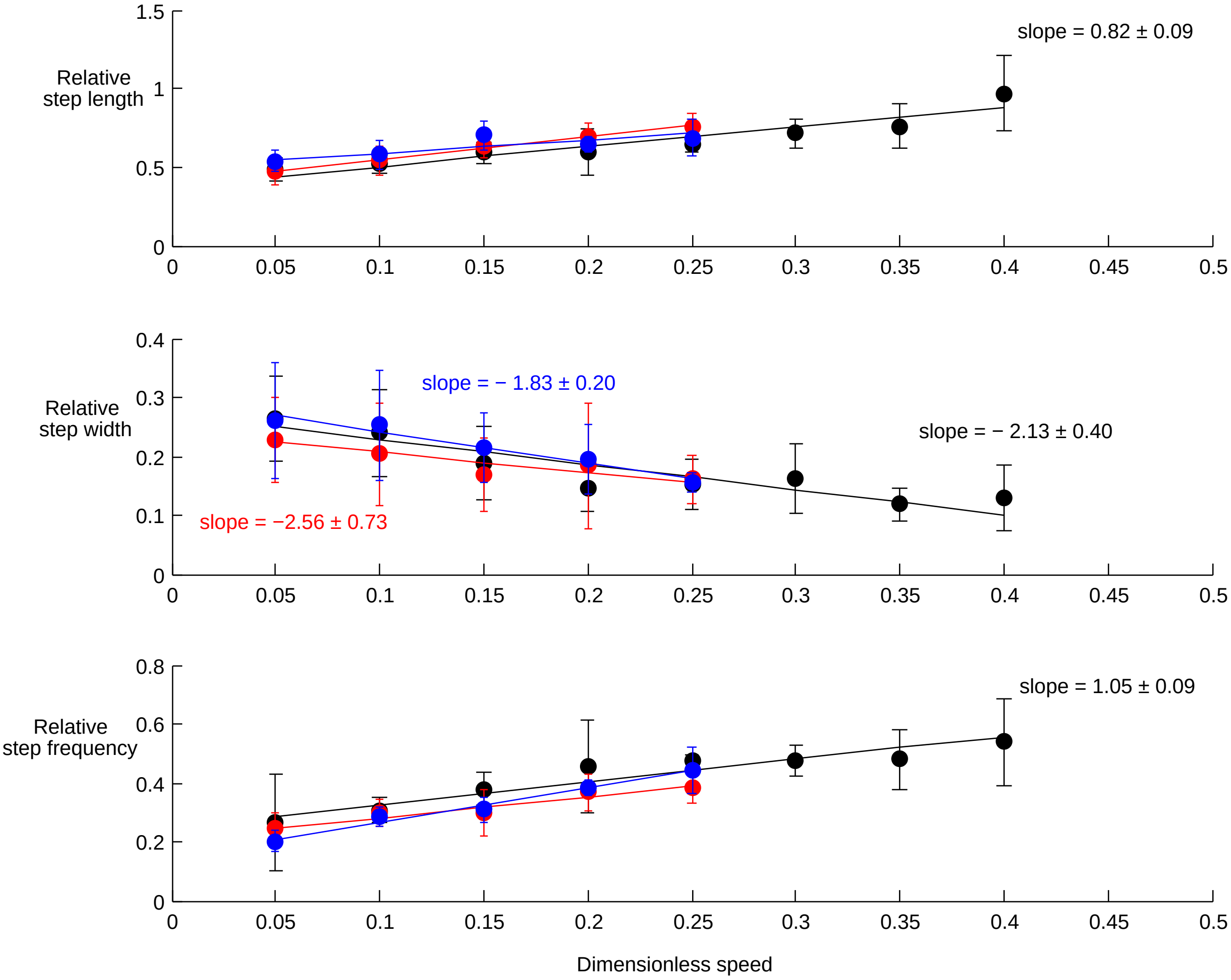
Bird Group	**No. of Individuals**	**No. of steps (n)**	**Mass (kg)**	**CoM Height (cm)**	**Mean Velocity (ms^{-1})**	**Velocity Range (ms^{-1})**
Pureline A	8	118	2.8 ± 0.3^{1}	**0.21 ± 0.008^{2}**	0.25 ± 0.07	0.10 - 0.43
Pureline B	8	90	2.7 ± 0.4^{1}	**0.20 ± 0.008^{1}**	0.26 ± 0.08	0.10 - 0.45
Broiler	9	130	**3.5 ± 0.3^{2}**	**0.22 ± 0.007^{3}**	0.34 ± 0.17	0.11 - 1.10

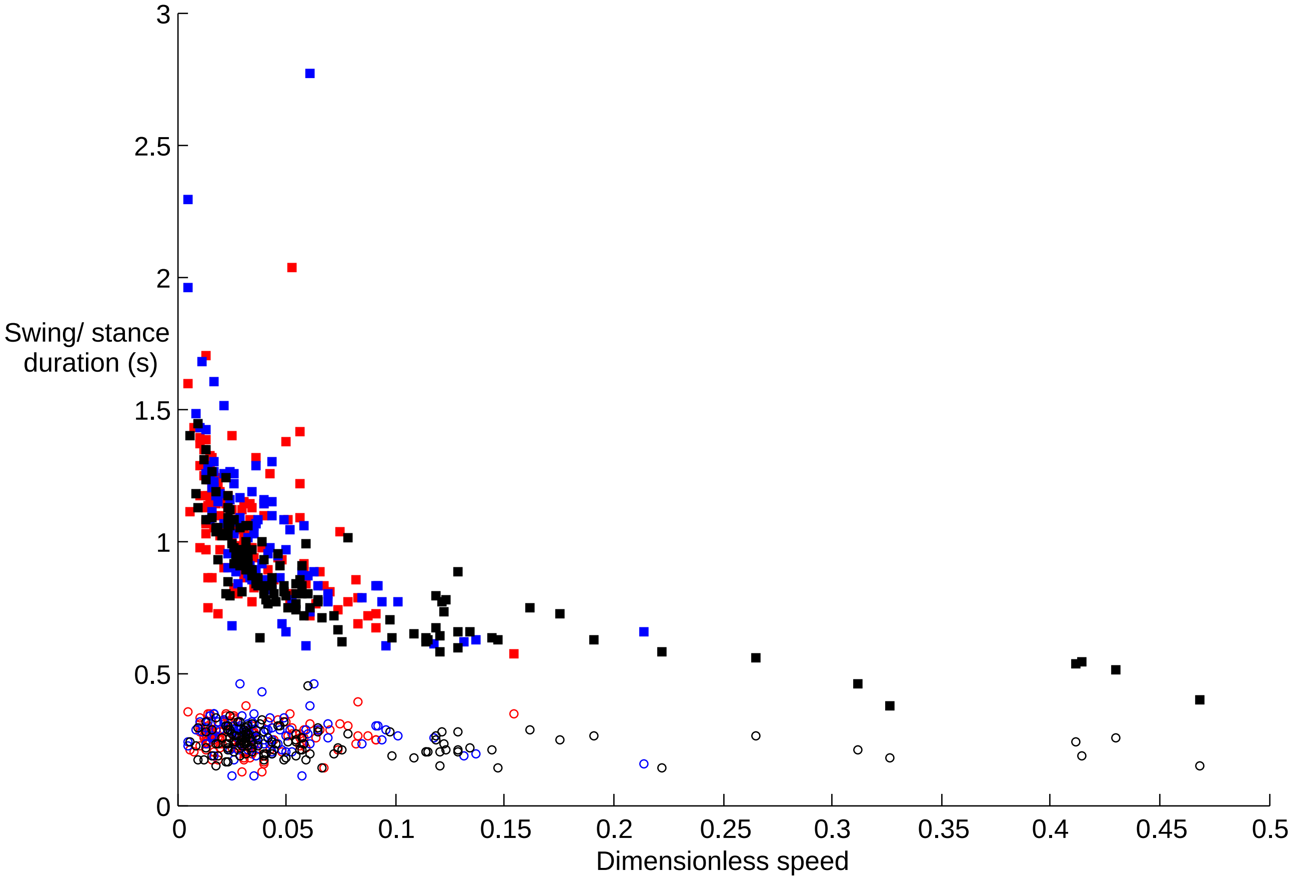
Bird Group	**Girth (x 10^{-2})**	**Hip Width (x 10^{-2})**	**Keel length (x 10^{-2})**	**Total Leg Length (x 10^{-2})**	**Breast Muscle Mass (% body mass)**
Pureline A	25.3 ± 0.6^{1}	6.34 ± 0.16^{1}	9.38 ± 0.45^{1}	17.8 ± 0.59^{1}	**22.1 ± 1.6^{3}** (n = 128)
Pureline B	24.4 ± 1.2^{1}	**6.90 ± 0.28^{2}**	8.92 ± 0.79^{1}	18.4 ± 0.97^{1}	**20.1 ± 1.4^{1}** (n = 202)
Broiler	24.7 ± 1.3^{1}	6.60 ± 0.17^{1}	8.27 ± 1.21^{1}	18.6 ± 0.58^{1}	**20.6 ± 1.0^{2}** (n = 18)
K-S test significance	0.852	0.493	0.000	0.489	0.000.
Levene's test significance	0.141	0.106	0.003	0.715	0.000

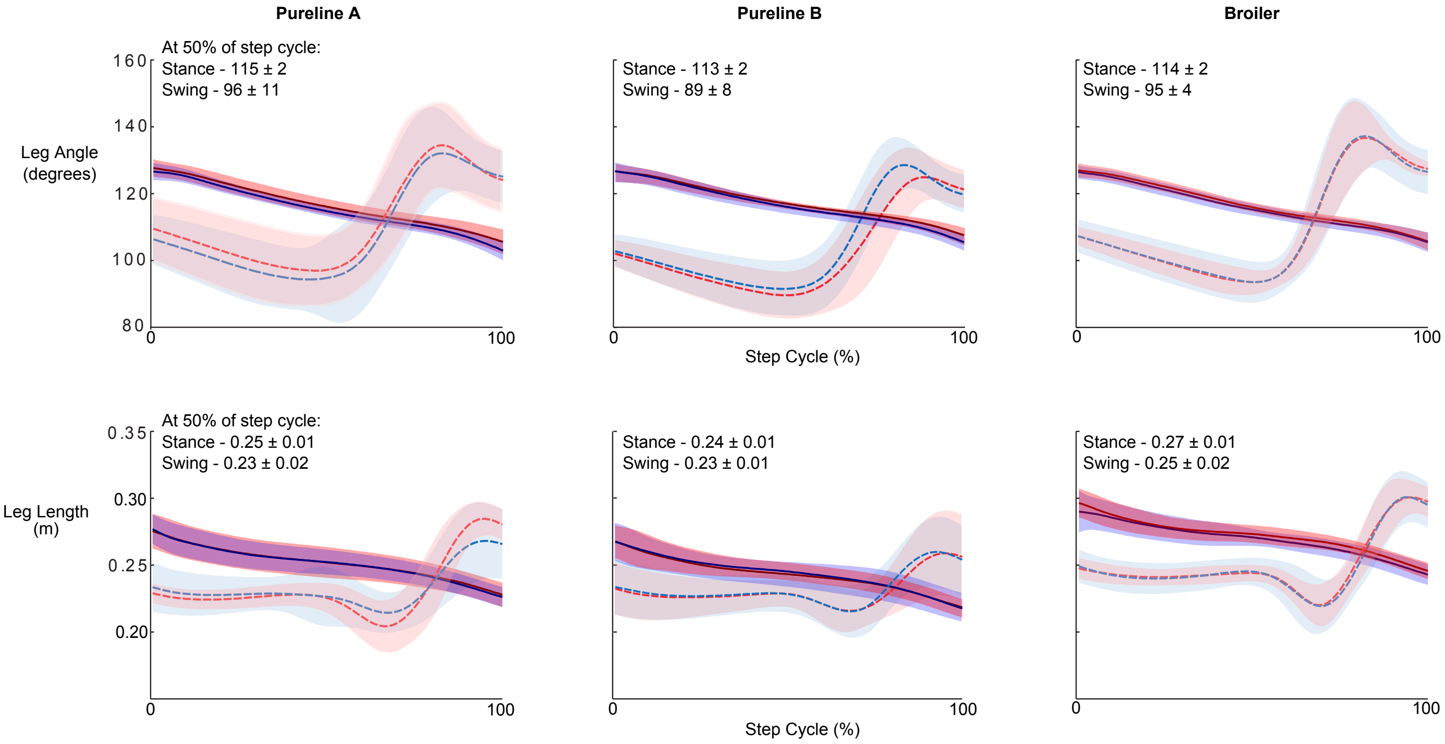
Bird Group	**Trackway width**	**Lateral velocity (ms^{-1})**		**Lateral displacement (m)**		**Vertical displacement (m)**
		Right	Left	Right	Left	
Pureline A	0.52 ± 0.16	**0.13 ± 0.05^{2}** (55%)	**0.09 ± 0.05^{2}** (56%)	0.037 ± 0.023^{1}	0.026 ± 0.023^{1}	**0.082 ± 0.032^{2}**
Pureline B	0.53 ± 0.17	0.12 ± 0.05^{1} (42%)	0.12 ± 0.05^{1} (42%)	**0.055 ± 0.024^{2}**	**0.039 ± 0.033^{2}**	**0.056 ± 0.018^{1}**
Broiler	0.48 ± 0.10	0.12 ± 0.03^{1} (33%)	0.14 ± 0.04^{1} (29%)	0.039 ± 0.020^{1}	0.020 ± 0.029^{1}	**0.091 ± 0.024^{3}**

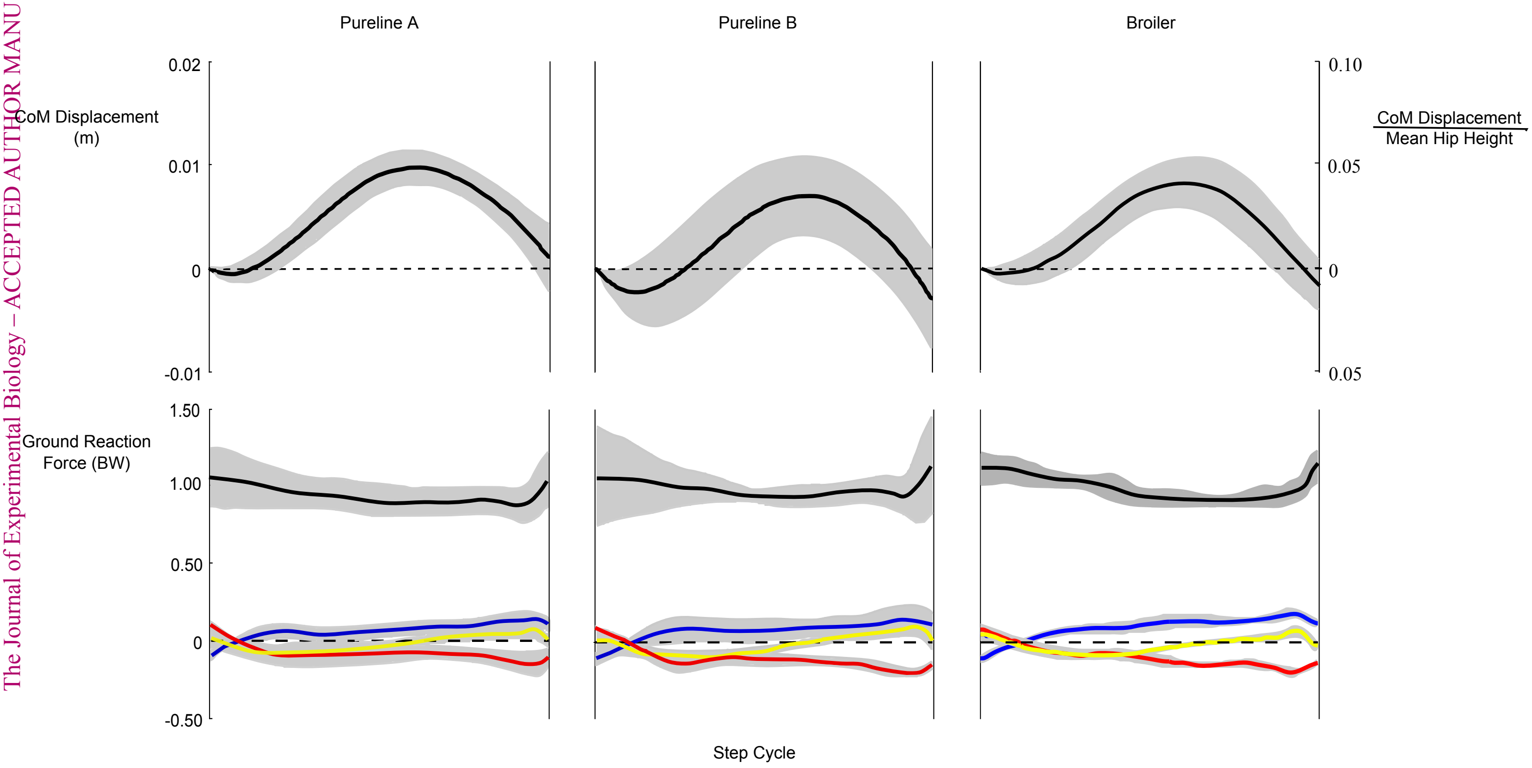
	Bird Population		
	Pureline A	**Pureline B**	**Broiler**
Step variables:			
Number of steps (n)	46	39	56
Relative step length	0.54 ± 0.09	**0.58 ± 0.09***	0.53 ± 0.01
Relative step width	0.20 ± 0.09	0.25 ± 0.09	0.24 ± 0.07
Relative step frequency	0.30 ± 0.04	**0.28 ± 0.03***	0.31 ± 0.04
Sweep angle (˚)	36.8 ± 7.4	**40.0 ± 8.0***	34.8 ± 5.3
Peak forces (BW) :			
Vertical forces	1.18 ± 0.12	1.27 ± 0.30	1.38 ± 0.10[a]
For-aft forces	0.10 ± 0.04	0.11 ± 0.04	0.12 ± 0.03
Mediolateral forces (Right foot)	0.12 ± 0.09	0.18 ± 0.06	**0.24 ± 0.04***
Mediolateral forces (Left foot)	0.11 ± 0.06	0.09 ± 0.04	**0.11 ± 0.04***
CoM Energies:			
Δ Gravitational 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
Δ Total energy (J)	0.04 ± 0.14	-0.02 ± 0.43	0.05 ± 0.23
Work Done (absolute values):			
Vertical direction (J)	**0.60 ± 0.20***	0.83 ± 0.64	0.94 ± 0.30
For-aft direction (J)	0.20 ± 0.08	0.21 ± 0.05	0.22 ± 0.06
Mediolateral direction (J)	0.19 ± 0.14	0.20 ± 0.11	**0.26 ± 0.11***

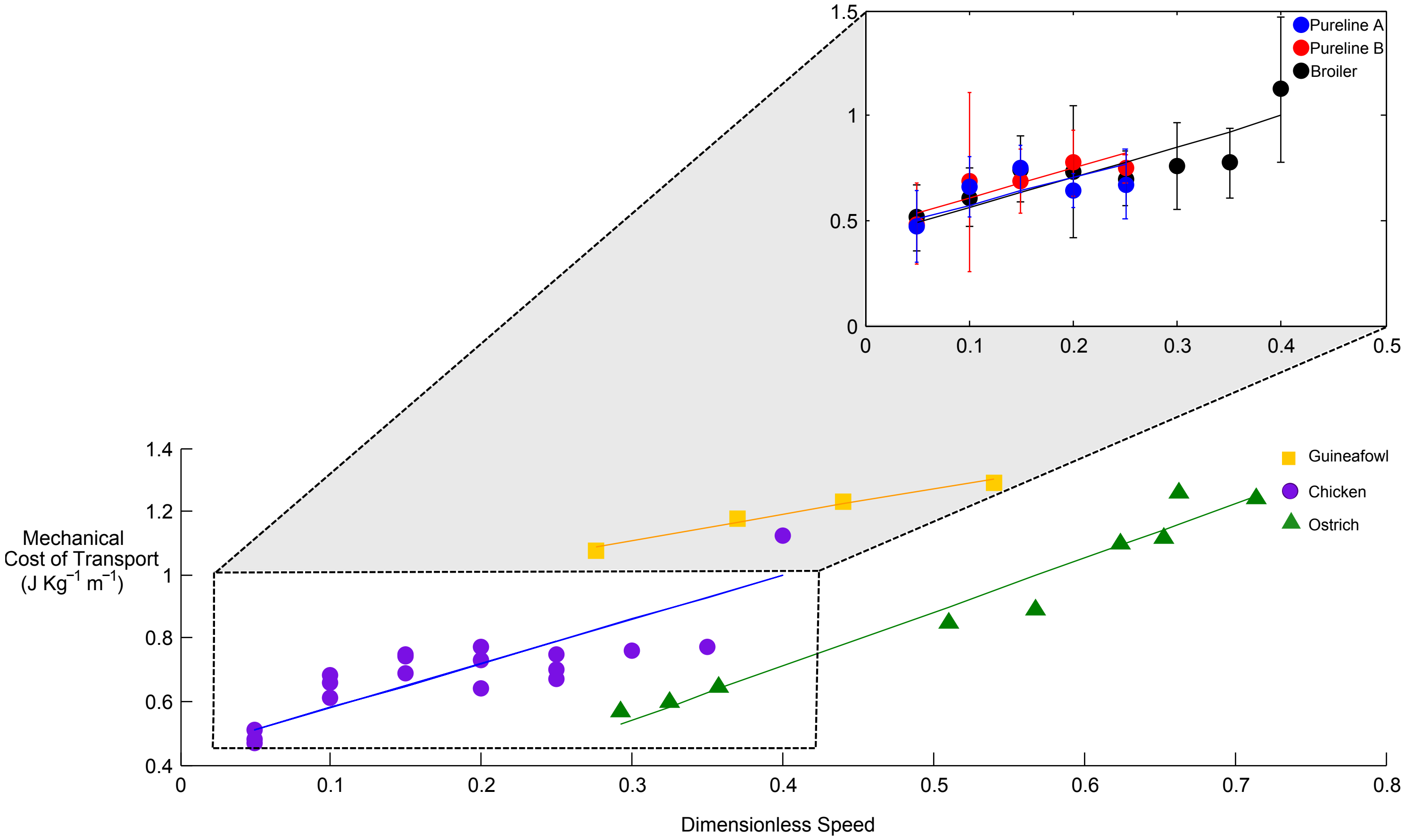

Pureline A
Pureline B
Broiler
Duty Factor
CoM Velocity (ms^{-1})
1
0.9
0.8
0.7
0.6
0.5
0
0.2
0.4
0.6
0.8
1
1.2


Relative step length
1.5
1
0.5
0
slope = 0.82 ± 0.09
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
Relative step width
0.4
0.3
0.2
0.1
0
slope = − 1.83 ± 0.20
slope = − 2.13 ± 0.40
slope = −2.56 ± 0.73
Relative step frequency
0.8
0.6
0.4
0.2
0
slope = 1.05 ± 0.09
Dimensionless speed


Swing/ stance duration (s)
0
0.5
1
1.5
2
2.5
3
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
Dimensionless speed


Pureline A
Pureline B
Broiler
Leg Angle (degrees)
160
140
120
100
80
0
100
At 50% of step cycle:
Stance - 115 ± 2
Swing - 96 ± 11
Stance - 113 ± 2
Swing - 89 ± 8
Stance - 114 ± 2
Swing - 95 ± 4
Step Cycle (%)
Leg Length (m)
0.35
0.30
0.25
0.20
At 50% of step cycle:
Stance - 0.25 ± 0.01
Swing - 0.23 ± 0.02
Stance - 0.24 ± 0.01
Swing - 0.23 ± 0.01
Stance - 0.27 ± 0.01
Swing - 0.25 ± 0.02
Step Cycle (%)


Pureline A
Pureline B
Broiler
CoM Displacement (m)
0.02
0.01
0
-0.01
0.10
0.05
0
0.05
CoM Displacement / Mean Hip Height
Ground Reaction Force (BW)
1.50
1.00
0.50
0
-0.50
Step Cycle


1.5
1
0.5
0
0
0.1
0.2
0.3
0.4
0.5
Pureline A
Pureline B
Broiler
Mechanical Cost of Transport (J Kg^{-1} m^{-1})
1.4
1.2
1
0.8
0.6
0.4
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Dimensionless Speed
Guineafowl
Chicken
Ostrich