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RESEARCH ARTICLE

Waddle and shuffle: gait alterations associated with domestication in turkeys

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ABSTRACT

Domestication has altered turkey morphology by artificially selecting for increased muscle mass and breast meat. Artificial selection has resulted in birds that weigh up to 3 times more than their wild counterparts, with relatively little change in the length of their bones and limbs. Considering these structural changes, it seems probable that domestic turkey locomotor kinematics and kinetics would also be altered. To examine the locomotor dynamics of wild and domestic turkeys, we had both strains walk down a runway with a force plate at the center to measure their ground reaction forces and gait parameters. The location of their center of mass was also quantified using a force plate and bi-planar x-ray and found to be further anterior in the domestic strain. The domestic turkeys locomoted across a lower range of speeds (0.25–1.64 ms^{-1}) than the wild turkeys (0.26–3.26 ms^{-1}) and increased their stride frequency at a higher rate. They also displayed large lateral oscillations, i.e. waddling, during walking that translated into relatively high medio-lateral ground reaction forces and lateral kinetic energy (3.5 times higher than that of wild turkeys). The results indicate that domestic turkey locomotion is not simply a slowed down version of wild turkey locomotion. The changes in gait observed are similar to the shuffling gait present in some human populations, such as Parkinson's patients, which serves to increase stability. The domestic turkey's increased body mass and more anterior center of mass position may require these kinematic and kinetic gait differences.

KEY WORDS: Kinetic energy, Ground reaction force, Domestication, Waddle, Center of mass

INTRODUCTION

Artificial selection of domestic animals has led to alterations in morphology through the desire to enhance certain physical traits. The poultry industry has selected for traits that have decreased the time to market and increased meat production (Yost et al., 2002). The turkey, *Meleagris gallopavo* Linnaeus 1758, in particular has undergone large changes in muscle morphology and mass, with some broad-breasted white (domestic) strains reaching over 3 times the body mass of wild turkeys (Stover et al., 2018). Selection for breast meat has also resulted in pectoral hypertrophy in the domestic strains (Stover et al., 2018; Velleman et al., 2003), leading to an altered distribution of body mass (Abourachid, 1993; Stover et al., 2018). All of this extra body mass is supported by hindlimb bones that are only slightly longer than those of wild turkeys (Stover et al., 2018). Structurally, domestic turkeys are not scaled-up wild turkeys, with selection leading to altered skeletal dimensions and proportionally greater pectoral muscle mass.

Given the morphological differences between broad-breasted white and wild turkey strains, we expect that the locomotion of domestic turkeys should be affected by the structural changes resulting from artificial selection. Surprisingly, when Abourachid (1991) investigated the gaits of male traditional and domestic turkeys, no significant differences were detected in duty factory (stance phase percentage of cycle duration) or stride length. However, large lateral oscillations (side-to-side motions) of more than 15 deg in the broad-breasted strain were noted in the posterior view. Some chicken and duck varieties, which have undergone a similar selective regime, experience locomotor consequences of increased body mass including increased stride width, slow walking speeds, increased double support and large lateral motions accompanied by high medio-lateral ground reaction forces (GRFs) (Caplen et al., 2012; Corr et al., 2007; Duggan et al., 2016; Paxton et al., 2013). Selecting birds with a healthy gait is an integral part of the poultry breeding practice, and yet the kinetic characteristics of domestic turkey locomotion have yet to be described. Establishing a baseline gait description is important for being able to identify walking abnormalities associated with musculoskeletal disorders that continue to be a major animal welfare concern (Hocking, 2014; Julian, 1998, 2005).

Wild and domestic turkeys provide an opportunity to discern the relationships between evolved morphological alterations and adjustments in locomotor kinematics and mechanics. Besides domestication, there are other instances of body structure changes inducing locomotor variations within and among species. Obesity in humans is associated with altered features of gait dynamics, including increased double support phase, lateral swaying and higher GRFs (Browning and Kram, 2007). Carrying a heavy load can similarly elicit differences in gait, and the anatomical positioning of the load influences GRFs (Birrell et al., 2007). We can also gain insight by looking at gait differences across a wide size range of bipedal species. One comparative study on bipedal locomotor kinematics included three organisms with a large body mass disparity but similar limb lengths (emu, rhea and human) and found that they had remarkably similar stride frequencies (Gatesy and Biewener, 1991). Identifying gait similarities and variations can reveal links between body structure and motion.

The goal of this study was to identify whether wild and domestic turkeys display similar gait kinematics and kinetics, despite the significant morphological transformations of domestication. The increase in body mass, relatively short hindlimb bones and altered distribution of muscle mass in today's domestic turkeys may make maintaining equivalent gait dynamics difficult.

MATERIALS AND METHODS

Animals

Eastern wild and broad-breasted white (Hybrid Converter 2013) turkey poults, *Meleagris gallopavo*, were obtained 3 days post-hatch

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Received 12 March 2018; Accepted 19 June 2018

Journal of Experimental Biology (2018) 221, jeb180687. doi:10.1242/jeb.180687

List of symbols and abbreviations

CoM	center of mass
$\boldsymbol{g}$	acceleration due to gravity
GRF	ground reaction force
h	hip height
KE	kinetic energy
KE_{FA}	kinetic energy in the fore–aft direction
KE_{ML}	kinetic energy in the medio-lateral direction
PE	gravitational potential energy
v	velocity

from licensed breeders and housed in the Animal Care Facilities at Brown University. All turkeys were maintained on an *ad libitum* water and 28% protein commercial poultry diet for the first 8 weeks and then transitioned to regular poultry feed. The two strains were raised together in a common open pen environment where they could move freely. Domestic females were procured at 18 weeks of age from a local farm and had been raised on pasture until brought into the Animal Care Facility. A second group of laboratory-raised wild females were used for collecting multiple footfalls in the autumn of 2014. Wild female (n=5 and 4), wild male (n=5), domestic female (n=5) and domestic male turkeys (n=6) were used in this study. All animal use was approved by the Brown University Animal Care and Use Committee, IACUC no. 1602000189, and complied with state and federal legislation and regulation.

Force data acquisition

A 6.25 m track-way covered with treadmill tread for traction was constructed with a space for a force platform at the halfway point. Three different force plate arrangements were used. A single force plate (Kistler 9281B, Kistler USA, Amherst, NY, USA) was masked off to a contact region of 30 cm, about the step length of a wild turkey, to capture single footfalls. The same force plate with no mask or two force plates (AMTI MC3A-100 and MC3A-6-250, Advanced Mechanical Technology, Inc., Watertown, MA, USA) in sequence were used to acquire consecutive footfalls and periods of double support. The width of the track-way was restricted to 0.61 m to keep the turkeys moving along a straight path. Unrestrained turkeys were encouraged to walk across the force platform and GRFs were recorded in the vertical, fore–aft and medio-lateral directions. Single and multiple steps were collected from each turkey moving at different speeds, starting with slow walking and progressing up to aerial phase running if the bird was capable and willing. Data were A/D converted at 4 kHz (USB-6259 DAQ, National Instruments, Austin, TX, USA) and recorded onto a PC running Igor Pro 6.0 (Wavemetrics, Lake Oswego, OR, USA).

Movements in the lateral and anterior views were captured using two high-speed digital video cameras (Photron Fastcam 1024 PCI or Photron Fastcam SA4, San Diego, CA, USA). Video was collected at 250 Hz and analyzed using DLTdv5 (Hedrick, 2008) in Matlab (MathWorks, Inc., Natick, MA, USA). Velocity was obtained by tracking a marker placed 10 cm above the greater trochanter of each turkey.

Data analysis

Forces were analyzed in Igor Pro 6.0. The minimum and maximum forces in each direction were recorded from each trial and the difference between them was used as the force range produced by an individual turkey. Forces in the vertical, fore–aft and medio-lateral directions were divided by the body mass of each turkey to normalize the data.

Stance duration was recorded as the amount of time an individual foot was in contact with the ground, obtained from both video and force plate data. Stride period was obtained by recording the timing of foot touchdown to the subsequent touchdown of the same foot, with the inverse to calculate stride frequency. Stride width was measured as the distance between the midpoints of each foot above the third digit during mid-stance when both feet were in contact with the ground and normalized to the hip height of each bird. Duty factor was calculated as the fraction of the stride period when the foot was in contact with the ground, or stance duration divided by stride period. Each group of turkeys differed in morphology, so Froude number and relative velocity were calculated to normalize the velocity range, incorporating each individual's hip height. The Froude number (Fr) was calculated by using the hip height of the standing individual and the velocity during each trial using the equation:

$$Fr = \frac{v^2}{\boldsymbol{g}h}, \quad (1)$$

where v is the velocity, $\boldsymbol{g}$ is the acceleration due to gravity and h is the hip height. The relative velocity was calculated by taking the square root of the Froude number.

Energy magnitude and phase calculations

Consecutive footfalls on either the single or dual force plate set-up were collected to calculate the changes in potential and kinetic energy during walking (absolute velocity range of 0.24 to 1.07 m s^{-1}) for each group of turkeys over two or three steps. The absolute velocity range chosen for analysis was a conservative estimate below the gait transition speed of 1.18–1.57 m s^{-1} as reported by Gatesy and Biewener (1991), and verified from our Froude number calculations in the female wild and domestic turkeys. These data were collected from four male domestic turkeys (4–6 strides analyzed per individual, absolute velocity mean 0.40±0.08 m s^{-1}), five female domestic turkeys (1–7 strides analyzed per individual, absolute velocity mean 0.52±0.23 m s^{-1}), four female wild turkeys (3–5 strides analyzed per individual, absolute velocity mean 0.72±0.15 m s^{-1}) and three male wild turkeys (4–6 strides analyzed per individual, absolute velocity mean 0.70±0.11 m s^{-1}). Walking velocities for each trial were obtained from video and used as the initial velocity for energy analysis; trials were only used if the bird was walking at a relatively constant speed, with a forward velocity change of less than 35%. For the trials using two force plates, the forces were summed. We applied the usual force plate ergometry approach to calculate the center of mass velocities from the forces in each direction and the body mass of each turkey (Donelan et al., 2002). The directional velocities were then integrated to calculate displacements of the center of mass. The instantaneous magnitudes of potential and kinetic energies were calculated across the stride cycle using the methods from Donelan et al. (2002). The fluctuations in energy magnitudes were calculated by taking the difference between the minimum and maximum energies within a single stride cycle. The phase, or difference in timing between energy peaks, was calculated with the equation:

$$\text{Phase} = \frac{|\text{KE}_{\text{peak time}} - \text{PE}_{\text{peak time}}|}{(\text{stride cycle duration}/2)} \times 360, \quad (2)$$

where $\text{KE}_{\text{peak time}}$ is the time of maximum kinetic energy in either the fore–aft or medio-lateral direction, and $\text{PE}_{\text{peak time}}$ is the time of maximum potential energy. According to the calculation in Eqn 2, a phase of 0 deg would indicate KE and PE were completely in phase (i.e. simultaneous peaks), with no energy exchange, and

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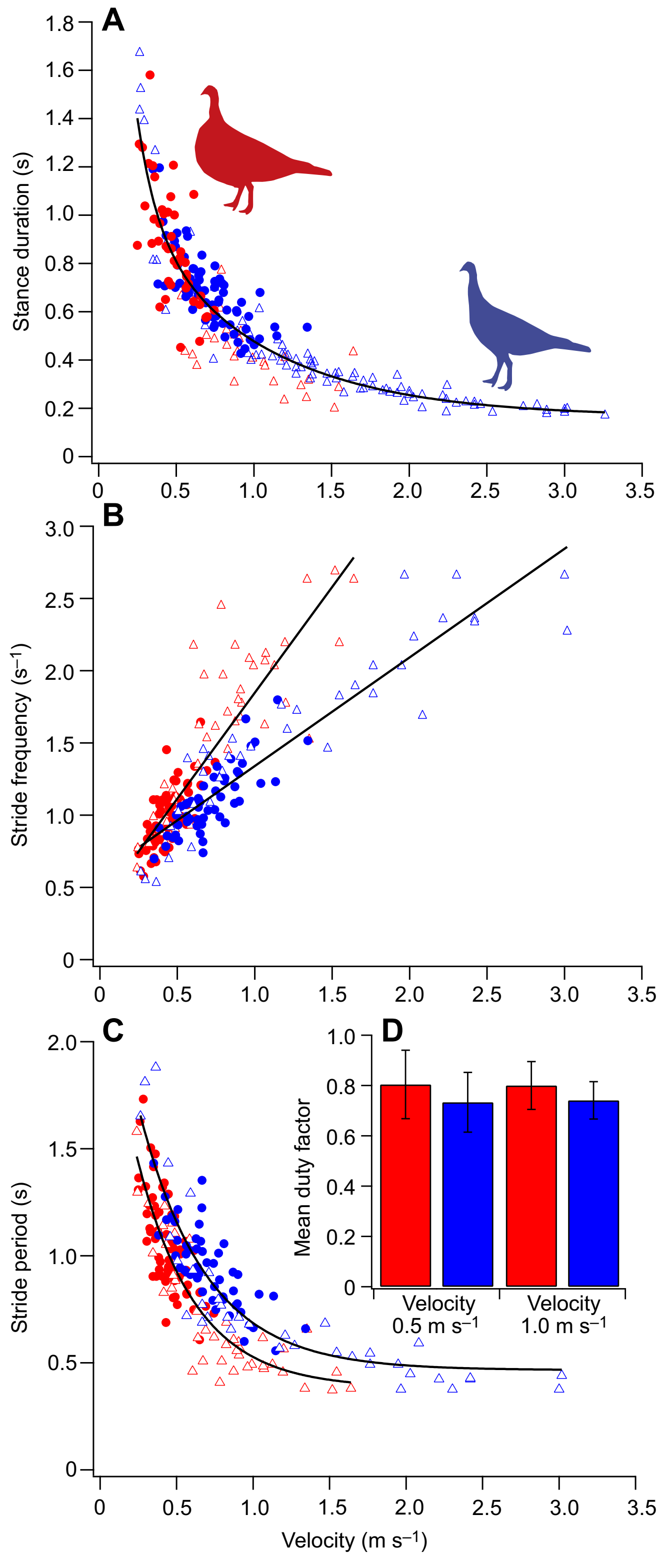

Fig. 1. Stance duration, stride frequency and stride period versus velocity for all birds. (A) Stance durations are similar for all turkeys (red, domestic turkeys; blue, wild turkeys; open triangles, females; filled circles, males). (B) Stride frequency increased at a higher rate in domestic turkeys than in wild turkeys. (C) Domestic turkeys had shorter stride periods than wild turkeys for any given speed. (D) The domestic turkey's foot is in contact with the ground for a relatively greater fraction of the stride period, as indicated by the mean duty factor. Duty factor was averaged from 0.4 to 0.6 $m\ s^{-1}$ (average velocity 0.5 $m\ s^{-1}$) and from 0.9 to 1.1 $m\ s^{-1}$ (average velocity 1.0 $m\ s^{-1}$), with error bars indicating standard deviation for that range (red bars, domestic, n=9; blue bars, wild, n=7).

180 deg would indicate KE was completely out of phase with PE, affording the maximum possible energy exchange (Cavagna et al., 1977) (see below for out-of-phase examples). The KE in the vertical direction was calculated but was not included in the analyses because of the extremely low magnitude and inability to differentiate phasing.

Center of mass position

Three female turkeys from each strain were used to determine the position of the center of mass (CoM). Biplanar fluoroscopy was used to capture the position of the body while the turkeys stood on a force plate (Kistler 9281B, Kistler Instruments AG, Winterthur, Switzerland). Force plate signals were A/D converted at 4 kHz (NI-6259 DAQ) and recorded with a PC running Igor Pro 6.0 (Wavemetrics). The location of the center of pressure in force plate coordinate space was calculated using the relative force components and moments acting on the force plate.

The origin of the coordinate system of the force plate was located in x-ray coordinate space by hanging a plumb line studded with metal beads directly over the force plate origin and recording x-ray images of the plumb line. The center of pressure on the force plate was used to determine the location of the CoM in the standing turkey in relation to the force plate origin. Each turkey was CT scanned to create 3D bone models of the pelvis and femora. The videos were undistorted and calibrated, and the markers on the plumb line were digitized using XMALab (Knörlein et al., 2016). Then, Scientific Rotoscoping (Gatesy et al., 2010) in Autodesk Maya (2013, Autodesk Inc., San Rafael, CA, USA) was used to determine the position and orientation of the pelvis in the standing birds. Center of pressure coordinates from the force plate were input to pinpoint the CoM position in 3D coordinate space. The distance from the CoM to the center point between the acetabula on the pelvis was measured in the cranial/caudal plane. This distance was normalized by pelvis length.

Statistics

The SMATR package in R was used to perform standard major axis (SMA) regressions for the GRFs normalized to body mass and stride frequency versus velocity at which the turkey was moving (http://www.bio.mq.edu.au/ecology/SMATR; Warton et al., 2006). Turkeys were separated by strain and sex for this analysis. SMATR uses a likelihood ratio test comparing it with a chi-squared distribution to test for common slopes and shifts in elevation using the Wald statistic. If no common slope is found between the groups, then a *post hoc* pairwise comparison was performed. A nested ANOVA was used to compare the energy magnitudes, energy phase shift, duty factor, stride width and CoM positions by strain, with individual as a nested effect within strain, using JMP Pro 12.0 (64 bit, SAS Institute, Cary, NC, USA).

RESULTS

The wild female turkeys locomoted over the widest range of velocities, followed by domestic females, wild males and finally domestic males (Fig. 1, Table 1). Only the females of each strain reached a Froude number over 0.5; however, the wild males did achieve a maximum relative velocity over 0.6, indicating they may be within the gait transition zone from walking to running (Alexander, 1977). Stance duration, or foot contact time, decreased across velocity

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Table 1. Average body mass (M_b), average hip height and normalized kinematic parameters for each turkey group

				Velocity (m s^{-1})		Froude number		Relative velocity	
Strain/sex	*n*	M_b (kg)	Hip height (m)	Min.	Max.	Min.	Max.	Min.	Max.
Wild female	5	3.9±0.4	0.32	0.26	3.26	0.02	3.19	0.14	1.79
Wild male	5	9.3±3.8	0.41	0.35	1.34	0.03	0.45	0.17	0.67
Domestic female	5	10.2±1.5	0.39	0.53	1.64	0.07	0.78	0.27	0.88
Domestic male	6	16.2±1.5	0.42	0.25	0.74	0.02	0.13	0.12	0.36

very quickly at first and then much more slowly (Fig. 1). All groups of turkeys fell on the same general trend line for stance duration. Domestic turkeys tended to have a lower stride period for any given speed and a higher stride frequency (F=101.391, P=0.001, n=11 domestic turkeys, 109 strides, and n=12 wild, 89 strides). Duty factor at a given speed was higher in domestic turkeys overall (F=6.1449, P=0.018), but did not decrease as expected with speed in either strain, indicating that both wild and domestic turkeys may transition from walking to grounded running. Domestic turkeys had a significantly greater stride width (41±3% of hip height) during walking than the wild turkeys (17±2%) (F=44.1165, P<0.001).

GRFs

The large domestic turkeys had relatively high vertical GRFs because of their large body mass. For comparison, all forces were normalized to body mass (Fig. 2A,B). The relationships between normalized GRFs and velocity were compared among the four turkey groups. The large male turkeys maintained very low normalized peak vertical forces across their low range of absolute velocity, keeping the vertical forces very close to 1.0 body mass (M_b) (Fig. 3A). The resultant vector magnitudes showed the same pattern as the normalized vertical force but were shifted to marginally greater magnitudes; for example, the wild females' resultant vector magnitudes were on average 0.041±0.045 M_b greater than the normalized vertical forces. It should be noted that for the few trials where the normalized vertical force was slightly less than 1.0 M_b, the resultant vector magnitudes confirmed that the turkeys were supporting their body mass during the peak of the GRF. The low vertical forces at slower speeds are associated with a long double support period in both strains of turkeys, as seen by the high duty factors (Fig. 1D). The slopes of the normalized peak vertical force versus absolute speed among the four groups were not significantly different from each other; however, there were shifts in elevation and shifts along common slopes (i.e. same slopes over a different range in velocities) (Table 2).

Fore–aft GRFs increased significantly with absolute speed (Fig. 3B, Table 2). The slopes for the male and female domestic turkeys were significantly higher than those for both the male and female wild turkeys. The wild female turkeys had the lowest slope but as they covered the largest range of speeds, they still reached some of the highest fore–aft forces.

Medio-lateral GRFs also increased with absolute speed for all turkey groups (Fig. 3C). The domestic male turkey slope was the highest and was significantly different from that of all the other groups (Table 2). The difference in large male domestic turkey medio-lateral force magnitude was easily distinguishable from that of the small female wild turkeys at any given speed (Fig. 2B). This also

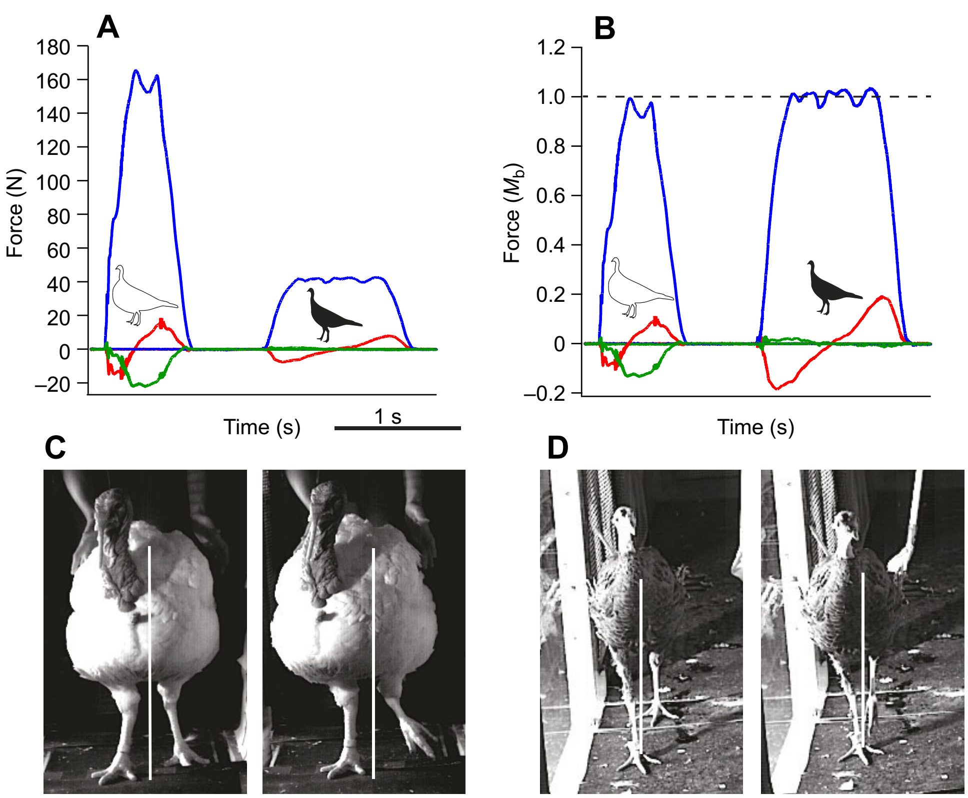

Fig. 2. Comparison of lateral oscillations with ground reaction forces and images from walking trials between a domestic male turkey and a wild female turkey, the two extremes of body size. (A) Ground reaction forces (GRFs) for a domestic male (16.95 kg, white) walking at 0.52 m s^{-1} and a wild female (4.2 kg, black) walking at 0.46 m s^{-1}. The vertical (blue), fore–aft (red) and medio-lateral (green) force examples show the difference in magnitude between the two strains. At very slow speeds, the small female wild turkeys often did not display a double-peaked vertical GRF. (B) The same GRFs from A, normalized to each bird's body mass. (C) An image sequence showing the double-support and single-support phases of a domestic turkey walking, with a line positioned in between the turkey's ankles to show the lateral displacement during mid-stance. (D) An image sequence of a wild turkey showing the much smaller lateral oscillation during the single-support phase of walking.

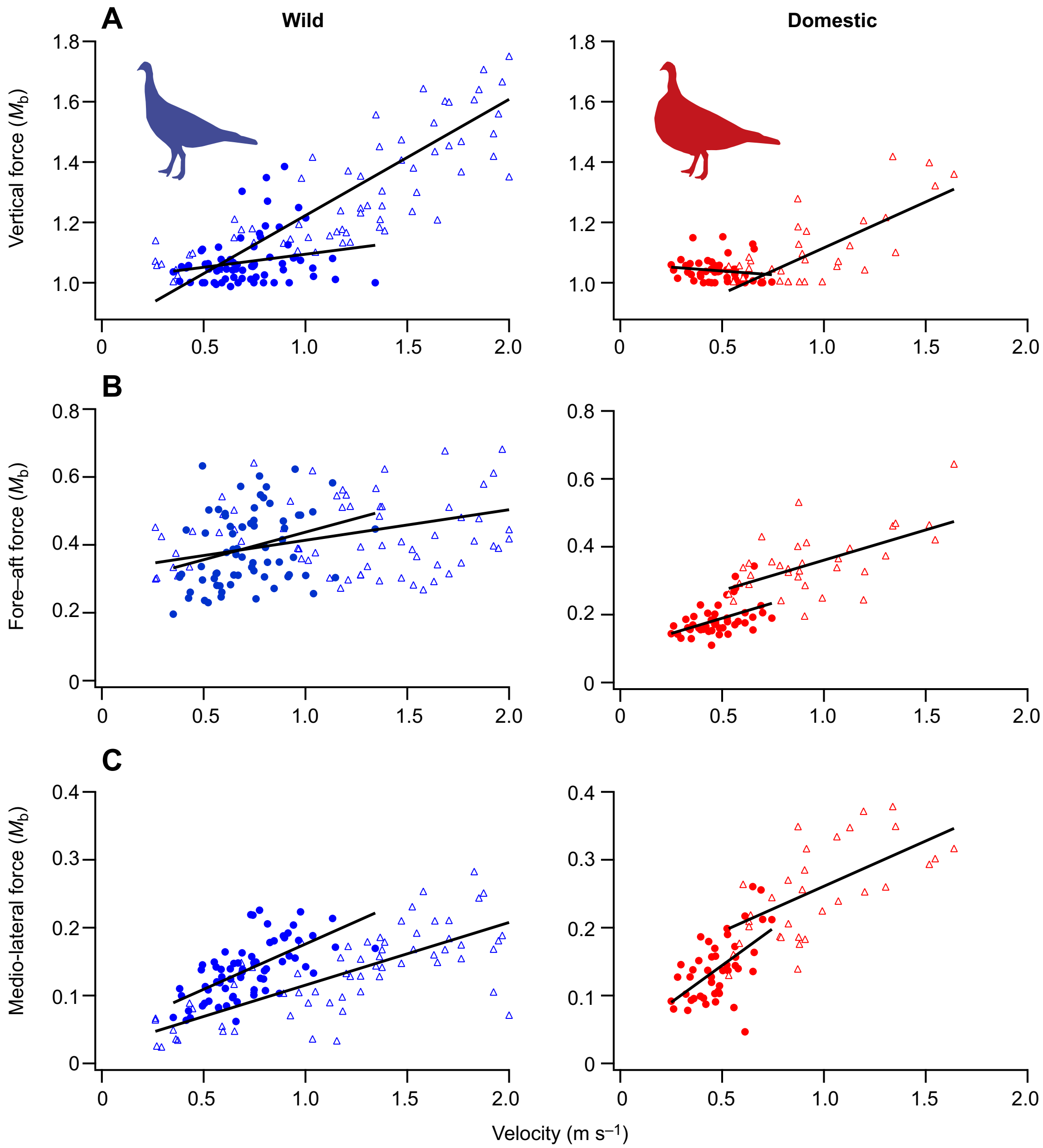

Fig. 3. Peak GRFs for turkey strains and sexes across velocity, normalized to body mass (M_b). Velocity for wild females was truncated at 2 m s^{-1} to facilitate comparisons. Filled blue circles, wild male (*n*=5 individuals, 69 total steps); open blue triangles, wild female (*n*=5, 88); filled red circles, domestic male (*n*=6, 45); open red triangles, domestic female (*n*=5, 33). (A) Vertical GRFs increased significantly with running velocity for females of both strains but the slope was not significantly different from zero for males of either strain. (B) Fore–aft GRFs increased with velocity for both strains and sexes. (C) Medio-lateral GRFs also increased with velocity, with domestic male medio-lateral forces increasing at the highest rate.

translated into large visible lateral oscillations of the body during walking in the male domestic turkey, versus no distinguishable medio-lateral movement in the female wild turkeys (Fig. 2C,D). The turkey groups with intermediate body masses, female domestic and male wild turkeys, had intermediate medio-lateral force slopes and the female wild turkeys had the lowest slope. Overall, the medio-lateral forces increased at a higher rate with absolute velocity as the turkeys increased in body mass.

Pendular energy exchange

Gravitational PE of the CoM and kinetic energy in the fore–aft (KE_{FA}) and medio-lateral (KE_{ML}) direction were calculated across two or three steps on the force plate and normalized to M_b (Fig. 4). The KE fluctuation magnitudes were significantly different between strains in both the fore–aft and medio-lateral direction (Fig. 5A). The domestic turkeys had greater fluctuations in KE_{ML}, 3.5 times that of the wild birds, easily discernible in the raw data (Fig. 4), while the wild turkeys had KE_{FA} magnitudes 1.7 times that of the domestic turkeys. The KE_{ML} of the domestic turkeys remained high compared with that of the wild turkeys across all velocities, even at speeds approaching potential gait transitions. PE fluctuations were not significantly different between the two strains. In the domestic turkey, fluctuations in KE_{ML}, KE_{FA} and PE were similar in magnitude (Fig. 5A).

Exchange between KE and PE requires that they fluctuate out of phase. Both KE_{ML} and KE_{FA} phase shifts were not significantly different between strains (Table 3), with averages falling midway between in phase and out of phase for both strains (Fig. 5B).

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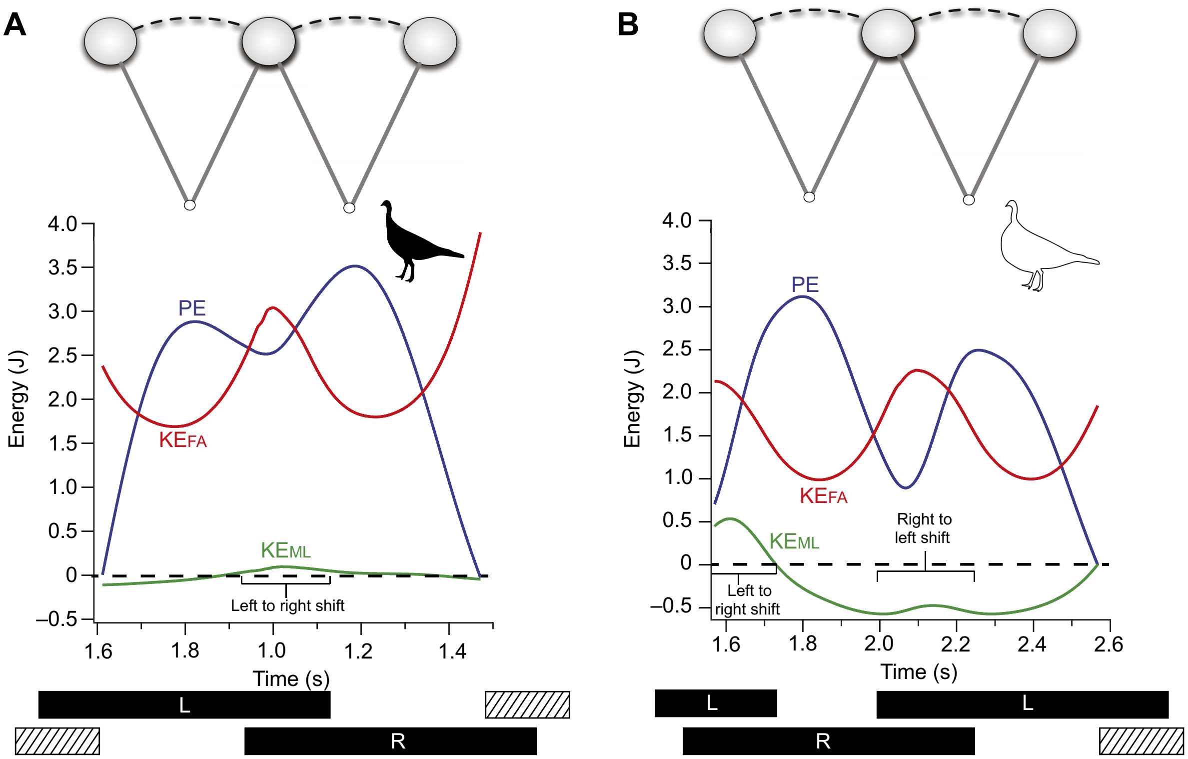

Fig. 4. Examples of the calculated fluctuations in energy of the center of mass (CoM) for each strain. (A) Instantaneous changes in potential energy (PE, blue lines), fore–aft kinetic energy (KE_{FA}, red lines) and medio-lateral kinetic energy (KE_{ML}, green lines) during two walking steps from a wild male turkey (absolute velocity 0.774 m s^{-1}, relative velocity 0.38); note the relatively low KE_{ML} magnitude. PE peaks during mid-stance, as denoted by the fore–aft pendulum model above, while KE_{FA} and KE_{ML} both peak as the bird transitions from the left to the right foot. (B) The energy fluctuations from a domestic female turkey (absolute velocity 0.432 m s^{-1}, relative velocity 0.22). Note the much larger KE_{ML} fluctuating about zero as the turkey shifts its weight from one foot to the next.

CoM position

The CoM in the domestic turkeys was positioned 26% farther anterior from the acetabulum than in the wild turkeys, when expressed as a fraction of pelvis length (Fig. 6). The absolute distance of the CoM from the acetabulum was 10.9±1.6 cm in the domestic turkeys and 7.0±1.0 cm in the wild turkeys.

DISCUSSION

The domestic turkeys in this study move differently from the wild turkeys in a few immediately observable ways. First, they locomote across a lower range of speeds, keeping their vertical GRFs relatively low (Figs 1A and 3A). Second, male and female domestic turkeys have large lateral oscillations during walking, evident in their large fluctuations in medio-lateral GRF and energies (Figs 2, 3C and 5). Finally, domestic birds also walk with a higher stride frequency, meaning that they are taking shorter, faster steps to maintain the same speed as a wild turkey, while also taking wider steps. Hence, domestic turkey locomotion has its own set of kinematic and kinetic gait characteristics and is not simply a slowed-down version of wild turkey locomotion.

Waddling gait

Walking with large lateral oscillations is often identified in the literature as waddling, a behavior that has been noted in penguins, geese and ducks (Abourachid, 2001; Kurz et al., 2008; Pinshow et al., 1977). The larger lateral oscillations we detected in the domestic turkey (Fig. 2C) confirm previous results (Abourachid, 1991), and are consistent with a waddling gait. Our GRF measurements indicate that this motion corresponds to higher medio-lateral forces in the domestic turkey as well (Fig. 3C).

These higher medio-lateral forces are consistent with results from other species with increased body mass, such as broiler chickens and obese humans, who also employ lateral oscillations and can exhibit high medio-lateral GRFs (Browning and Kram, 2007; Caplen et al., 2012; Paxton et al., 2013). Increased body mass is just one of the morphological changes that correlate with waddling; others include wide stance width and altered CoM position. Domestic turkeys have increased body mass, only slightly longer limbs, wider stride width during walking (current study) and muscle mass distribution differences compared with wild turkeys (Stover et al., 2018), as well as a more anterior CoM position (Fig. 6). Any or all of these structural modifications could contribute to the waddle.

It remains to be determined how waddling affects the metabolic and mechanical cost of locomotion in domestic turkeys. Waddling was once thought to be energetically wasteful (Pinshow et al., 1977), but there is evidence that waddling can save mechanical energy during walking, as is the case in penguins (Griffin and Kram, 2000). In penguins, the lateral KE from waddling allows them to recover more mechanical energy from each stride by increasing the total KE that can be converted to PE. In addition, penguins' lateral movements also make the total KE more out of phase with PE. Likewise, the domestic turkey has much higher medio-lateral energy fluctuations than the wild turkey, somewhat out of phase with PE, making mechanical energy savings possible for them as well.

Waddling is liable to have health repercussions for domestic turkeys. Current gait scoring methods to evaluate poultry locomotor problems use the descriptor 'wobble' to depict medio-lateral movement, deeming it an abnormality (Garner et al., 2002). Our study demonstrates that increased medio-lateral forces are associated with the wobble, which may contribute to loads that the

Table 2. The standard major axis regression results for vertical, fore–aft (FA) and medio-lateral (ML) forces versus velocity

	Total trials	R^2	Slope	*P*	Lower CI	Upper CI	Intercept	Lower CI	Upper CI	*P*-value for slope comparisons between groups: Domestic males	Domestic females	Wild males	Wild females
Vertical force													
Domestic males	45	0.002	−0.3324	0.327	−0.4485	−0.2464	1.1984	1.1477	1.2491	–	E, S	E, S	E, S
Domestic females	33	0.482	0.4377	<0.0001*	0.3373	0.5682	0.6848	0.5694	0.8003	E, S	–	E	E, S
Wild males	69	0.037	0.4482	0.112	0.3536	0.568	0.7491	0.6676	0.8305	E, S	E	–	S
Wild females	88	0.835	0.4214	<0.0001*	0.3863	0.4597	0.7827	0.7205	0.8449	E, S	E, S	S	–
FA force													
Domestic males	45	0.221	0.3849	0.001*	0.2943	0.5034	0.00189	−0.049979	0.05376	1	0.255	0.038*	0.001*
Domestic females	33	0.336	0.3074	<0.0001*	0.2291	0.4126	0.059394	−0.032696	0.151485	0.255	1	0.003*	0.001*
Wild males	69	0.087	0.5504	0.014*	0.4369	0.6934	−0.002911	−0.099897	0.094075	0.038*	0.003*	1	0.001*
Wild females	88	0.26	0.1763	<0.0001*	0.1468	0.2118	0.192793	0.136276	0.24931	0.001*	0.001*	0.001*	1
ML force													
Domestic males	45	0.316	0.3874	<0.0001*	0.3012	0.4982	−0.04521	−0.094	0.00358	1	0.041*	0.001*	0.001*
Domestic females	33	0.279	0.2524	0.002*	0.1858	0.3428	0.01464	−0.06425	0.09354	0.041*	1	0.287	0.001*
Wild males	69	0.409	0.2084	<0.0001*	0.173	0.2511	−0.01129	−0.0405	0.01792	0.001*	0.287	1	0.001*
Wild females	88	0.597	0.1195	<0.0001*	0.1043	0.1368	−0.01827	−0.04601	0.00947	0.001*	0.001*	0.001*	1

*Significant difference between slopes. E indicates a change in elevation of a common slope, S indicates a shift along a common slope. CI, confidence interval.

joints experience during walking (Figs 2B and 3C). In humans, there are many musculoskeletal disorders associated with obesity due to increased external knee adduction moments and increased joint loading (Wearing et al., 2006). It is possible that increased medio-lateral GRFs and lateral oscillations could put more stress on the joints of the domestic turkey, possibly contributing to some of the knee and hip issues often associated with domestication, such as angular bone deformity, straddle legs and rotated tibia, as well as exacerbating tibial dyschondroplasia and osteochondrosis (Julian, 1998; Riddell, 1980; Siller, 1970). Gait scoring is a subjective visual scoring method, which, while fairly repeatable between observers (Garner et al., 2002; Kestin et al., 1992), as a selection method in turkeys (Neeteson et al., 2016) has not eliminated the waddling movement.

Domestic turkeys and shuffling gait

Many of the kinematic and kinetic differences between wild and domestic birds are characteristic of the ‘shuffling gait’ of some human populations. Short quick steps, higher step frequency, shuffling feet and a stooped stance without arm swing illustrate a shuffling, or festinant, gait (Knutsson, 1972; Murray, 1967). The most common human example of a shuffling gait is found in Parkinson’s disease patients. During walking, the trunk is flexed forward, stooping, and the movement of the feet is described as shuffling, with long stance durations and decreased walking speed (Morris et al., 2001; Murray et al., 1978). This is similar to the slow-walking domestic turkeys with relatively long stance durations and high stride frequency (Fig. 1). Additionally, Smith–Magenis syndrome cases have been reported to be associated with a festinant gait (Elsea and Girirajan, 2008). Turkeys also share certain gait features with other human disorders. Prader–Willi syndrome is a chromosomal disorder with clinical features including muscular hypotonia and severe obesity. Prader–Willi gait is characterized by slow short stride lengths in the anterior direction that limit the velocity of progression, long stance phases seemingly to avoid overloading a single limb, as well as medio-lateral hip movements (Cimolin et al., 2010; Vismara et al., 2007). Medio-lateral movements are also seen in patients with ataxia, obese juveniles and those displaying a Trendelenberg gait due to muscle weakness (McGraw et al., 2000; Mitoma et al., 2000; Trendelenberg, 1998). The gaits characteristics of the human disorders described above have largely been attributed to an effort to maintain stability and balance.

We hypothesize that domestic turkeys, like humans, may assume a shuffling gait in order to increase their stability during locomotion. The shorter, faster steps necessary for the domestic turkeys to move at any given velocity may help explain the speed limit we observed (Fig. 1). Biomechanical and/or neurological limits could be responsible for the required increase in stability during walking. We have shown that the massive increase in pectoralis muscle mass has shifted the CoM position more anterior in the domestic turkey relative to that of the wild turkey (Fig. 6). This change in CoM position is reminiscent of the stooped stance associated with Parkinson’s disease, which requires bringing the CoM closer to the stance foot to increase balance and dynamic stability. Domestic turkeys with increased body mass are also similar to humans carrying a load, approximating a wild turkey with a heavy backpack, although front-pack may be a more appropriate descriptor of the heavy pectoralis muscle. Significant increases in medio-lateral forces have been reported in humans carrying loads, likely caused by a continual shift of the CoM further from the neutral position, contributing to decreased stability (Birrell et al., 2007). Ducks also shift their CoM via trunk translations during terrestrial locomotion, ostensibly to

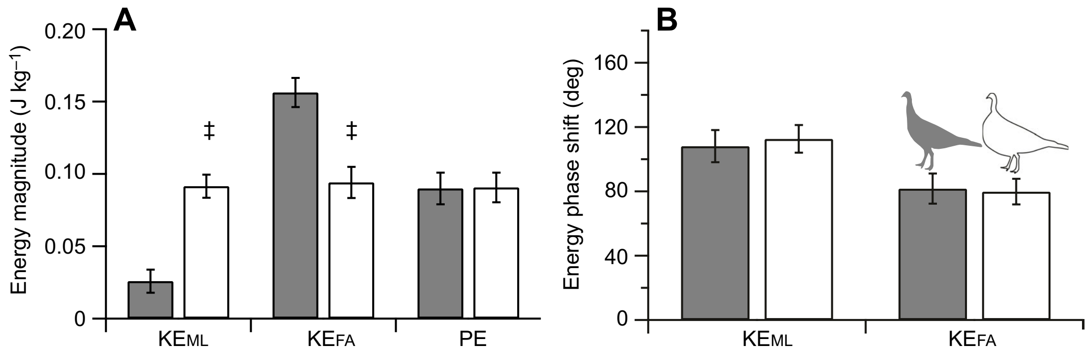

Fig. 5. The calculated fluctuations in KE and PE and the phase relationships of KE to PE for both turkey strains during walking. (A) The magnitude of the KE_{ML} fluctuation was significantly higher in the domestic turkey, by over 3.5 times ($^‡P$<0.0001). KE_{FA} was significantly higher in the wild turkeys ($^‡P$<0.0001), and the PE was not significantly different between strains (P=0.3536). (B) The KE_{ML} phase and the KE_{FA} phase were not significantly different between strains. In phase (0 deg phase shift) would describe spring mechanics, while completely out of phase (180 deg phase shift) would indicate that the bird is walking and exchanging energy via a pendular mechanism. For the range of velocities between 0.24 and 1.07 m s^{-1}, both turkey strains have energy phases mid-way between in phase and out of phase, indicating that there is some energy exchange possible.

increase stability (Provini et al., 2012). Finally, the extra girth present in the domestic turkey due to increased body mass and pectoralis mass could hinder the path of the turkey's legs during walking.

Alternatively, changes in gait may reflect challenges to stability that are cognitive or neurological in origin. Domestication has decreased animals' brain size (Clutton-Brock, 1999), thought to result from pedomorphosis in domestic animals, with certain sensory centers undergoing significant reductions (Ebinger, 1995). In addition, domestic turkeys continue to increase in both body mass and girth, even after bone growth slows, which could affect their sensory perception for resolving their own position and distances, therefore affecting motor control for balance (Carrier, 1996). It is also possible that the selection for increased body mass has resulted in decreased sensory or motor resolution; for example, the number of axons innervating a given amount of muscle tissue may be decreased, again compromising control (More et al., 2010). Any or all of these neural deficits could contribute to the domestic turkeys' issues with stability and balance.

Domestic turkeys may move slower than wild turkeys to maintain stability, but there are other potential explanations for the observed slow speeds and altered kinematics. The hindlimb muscles likely do not produce as much force per kilogram body mass, as their cross-sectional areas would only be expected to scale with body mass$^{0.67}$, not keeping up with the extra body mass support demands. In addition, domestic turkeys have been selected for desirable traits such as increased muscle mass and tenderness (Fletcher, 2002), probably influencing the muscle composition, which in turn could affect muscle function. Cardiovascular and respiratory changes associated with domestication may also impose limits on locomotor function. The heart and lung mass of chickens scale with negative allometry across ontogeny (Tickle et al., 2014), which continues to be a major animal welfare concern for poultry as it is presumed that they outgrow their cardiovascular capacity (Julian, 1993; Wideman, 2007). Finally, motivation should not be overlooked when considering the top speed of the turkeys. It is difficult to know that an animal is reaching a true performance limit; however, we feel that the combination of treats (dried meal worms and white bread) and exuberant chasing from behind gave the domestic turkeys incentive to move at close to their maximum speed.

Concluding remarks

The domestic turkey is a prime example of how an organism's morphology is closely linked to its locomotor mechanics in a delicate balance to maintain stability. Domestic turkeys are limited to a lower speed range than wild turkeys; however, when comparing their movements at the same speeds, domestic turkeys' gait is distinctive. Artificial selection for increased body mass in domestic turkeys has given rise to locomotor changes that are apparent in the GRF signature and fundamental mechanics, such as the motion of the center of mass. Domestic turkeys seem to have adopted a shuffling gait in order to maintain stability, despite or perhaps due to their suite of morphological alterations.

Selective practices have attempted to breed turkeys that minimally waddle, but this movement may be necessary to sustain a stable gait. Others have suggested improvements to gait scoring by focusing on characteristics of a balanced gait and even applying camera monitoring with image analysis of lateral oscillations, which we also support to improve gait heritability (Aydin, 2017; Duggan et al., 2016, 2017). The domestic turkeys displayed a consistent pattern of kinematic and kinetic gait parameter relationships with

Table 3. Summary of ANOVA results for average energy magnitudes and phase with respect to potential energy (PE)

Strain	Magnitude (J kg^{-1})	s.e.	F-ratio	P-value	Phase	s.e.	F-ratio	P-value
KE_{ML}								
Wild	0.026	0.007	41.5653	<0.0001*	108.2	10.06	0.1131	0.7377
Domestic	0.092	0.007			112.7	8.56		
KE_{FA}								
Wild	0.156	0.010	31.4499	<0.0001*	81.66	9.42	0.0225	0.8812
Domestic	0.094	0.011			79.81	8.02		
PE								
Wild	0.090	0.010	0.8759	0.3536				
Domestic	0.091	0.010						

KE_{ML}, kinetic energy in the medio-lateral direction; KE_{FA}, kinetic energy in the fore–aft direction. Asterisks indicate significance.

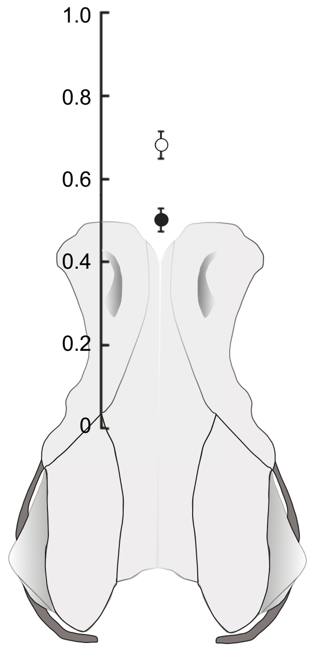

Fig. 6. The position of the CoM, relative to the acetabulum, for the two turkey strains. Data for wild (filled circle, n=3, 0.502±0.082) and domestic (open circle, n=3, 0.683±0.099) turkeys are shown normalized to total pelvis length. The domestic turkeys' CoM position is significantly more anterior than the wild turkeys' CoM (F=17.6845, P=0.0007).

speed. Deviations from these established relationships in turkeys may be a more repeatable assessment of potential gait abnormalities than gait score, as originally suggested in ducks (Duggan et al., 2017). Future studies should address the skeletal stresses experienced during walking across ontogeny to determine the effect that a shuffling gait has on the domestic turkeys' joints and development.

Acknowledgements
The authors would like to thank Erika Tavares, Allison Rubenstein, Elizabeth McGinn, Jackie Alois and Elizabeth Rao, as well as Drs Chris Arellano, Ariel Camp, Terry Dial and Nicolai Konow for their assistance during turkey walking data collection and/or video analysis.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: K.K.S., T.J.R.; Methodology: K.K.S., T.J.R.; Formal analysis: K.K.S., T.J.R.; Investigation: K.K.S., E.L.B., T.J.R.; Resources: E.L.B., T.J.R.; Data curation: K.K.S.; Writing - original draft: K.K.S.; Writing - review & editing: E.L.B., T.J.R.; Supervision: E.L.B.; Funding acquisition: K.K.S., E.L.B., T.J.R.

Funding
Funding support came from the National Institutes of Health (grant no. AR055295) and National Science Foundation (grant no. IOS-1354289) to T.J.R., the National Science Foundation (grant numbers 1661129, 1655756) to E.L.B., the Bushnell Graduate Research and Education Fund, and a Sigma Xi Grant-in-Aid of Research to K.K.S. Deposited in PMC for release after 12 months.

Data availability
The raw and calculated data, CT scans, bone models and bi-planar x-ray video supporting this article can be accessed via the X-ray Motion Analysis Research Portal at xmaportal.org, study ID BROWN21.

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