

## Compass gait mechanics account for top walking speeds in ducks and humans

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### SUMMARY

The constraints to maximum walking speed and the underlying cause of the walk–run transition remains controversial. However, the motions of the body and legs can be reduced to a few mechanical principles, which, if valid, impose simple physics-based limits to walking speed. Bipedal walking may be viewed as a vaulting gait, with the centre of mass (CoM) passing over a stiff stance leg (an ‘inverted pendulum’), while the swing leg swings forward (as a pendulum). At its simplest, this forms a ‘compass gait’ walker, which has a maximum walking speed constrained by simple mechanics: walk too fast, or with too high a step length, and gravity fails to keep the stance foot attached to the floor. But how useful is such an extremely reductionist model? In the present study, we report measurements on a range of duck breeds as example unspecialized, non-planar, crouch-limbed walkers and contrast these findings with previous measurements on humans, using the theoretical framework of compass gait walking. Ducks walked as inverted pendulums with near-passive swing legs up to relative velocities around 0.5, remarkably consistent with the theoretical model. By contrast, top walking speeds in humans cannot be achieved with passive swing legs: humans, while still constrained by compass gait mechanics, extend their envelope of walking speeds by using relatively high step frequencies. Therefore, the capacity to drive the swing leg forward by walking humans may be a specialization for walking, allowing near-passive vaulting of the CoM at walking speeds 4/3 that possible with a passive (duck-like) swing leg.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/211/23/3744/DC1>

Key words: walk, run, gait, transition, inverted pendulum.

### INTRODUCTION

Walking animals use immensely complex combinations of muscle and nerve actions to drive and control their limbs. However, the mechanical principles underlying walking may be simple and general. Walking – in humans at least – is a relatively stiff-limbed gait without aerial phases and is often described as acting as an ‘inverted pendulum’, with kinetic energy  $E_k$  at the beginning of each stance phase translating to gravitational potential energy  $E_p$  as the centre of mass (CoM) rises to its highest point near mid-stance, and returning as  $E_k$  as the body falls towards the end of stance. In its simplest form, walking as an inverted pendulum can be described by a ‘compass gait’ model (McGeer, 1990; Alexander, 1995; Goswami et al., 1997; Garcia et al., 1998) (see also Saunders et al., 1953; Kuo, 2007). This model is planar, has completely rigid limbs, exactly one point-foot in contact with the ground at any time and instantaneous transition between legs. The mechanically-imposed speed limits to walking with compass gait are now well understood (Usherwood, 2005; Srinivasan and Ruina, 2006): at high speeds, especially at high step lengths, the acceleration due to gravity is insufficient to provide the centripetal acceleration requirements of vaulting in an arc over a stiff stance limb. But how generally can such an extremely simple model be useful? Does compass gait mechanics actually restrict walking speeds in humans? And is compass gait mechanics informative for unspecialized bipedal walkers with the relatively crouched limbs and ‘blurred’ walk–run transition typical of many birds (Gatesy and Biewener, 1991; Hancock et al., 2007)? Birds are living bipedal dinosaurs and achieve walking and running gaits despite limb structures markedly different from the familiar mammalian bipeds – humans. Furthermore, some birds walk despite specialization for swimming, resulting in widely spaced hips and foot placements, and further deviation from the assumptions of the compass gait model. Ducks, therefore, present a

fascinating comparison with humans: is the mechanical approximation of a compass gait relevant to walking in such a non-specialized walker?

In the present study, we report forceplate-derived measurements of waddling, walking and running in three breeds of duck. We use the term ‘energy recovery’ ( $ER$ ) (Cavagna et al., 1977) to describe the maximum potential for changes in CoM  $E_k$  and  $E_p$  to be passive, consistent with the inverted pendulum model of walking. We use  $ER$  to distinguish between ‘walking’ (high  $ER$ ) and ‘running’ (low  $ER$ ) gaits. The importance of lateral motions – ‘waddling’ – to the potential passive qualities of walking is demonstrated by calculating  $ER$ s both including and excluding the  $E_k$  associated with lateral motions.

The three duck breeds, Aylesbury, Mallard and Indian Runner, are all derived from mallards *Anas platyrhynchos* (Linnaeus 1758) but have radically different forms (Fig. 1A). The Aylesbury is large, selected for the table. The Mallard used was close to wild-type, if overweight due to domestication. The Indian Runner or Penguin Duck has an upright form associated with highly reduced femora, and was bred for both egg-laying and a ‘peculiar’ shape and carriage (Ashton and Ashton, 2002). Although Aylesbury ducks were clearly not bred for walking efficiency, they demonstrate a reasonable proficiency at walking; historically, they were walked from Aylesbury to London for market, a distance of approximately 70 km (>40 miles). The morphology of all ducks shows some degree of compromise between walking and swimming capability (Biewener and Corning, 2001). They were selected for this study precisely because they cannot be considered specialist cursors. Are these compromised, semi-aquatic animals capable of, and constrained by, the mechanics of inverted pendulum-like walking? And how do they contrast with relatively stiff-limbed humans that are presumably more specialized for effective walking?

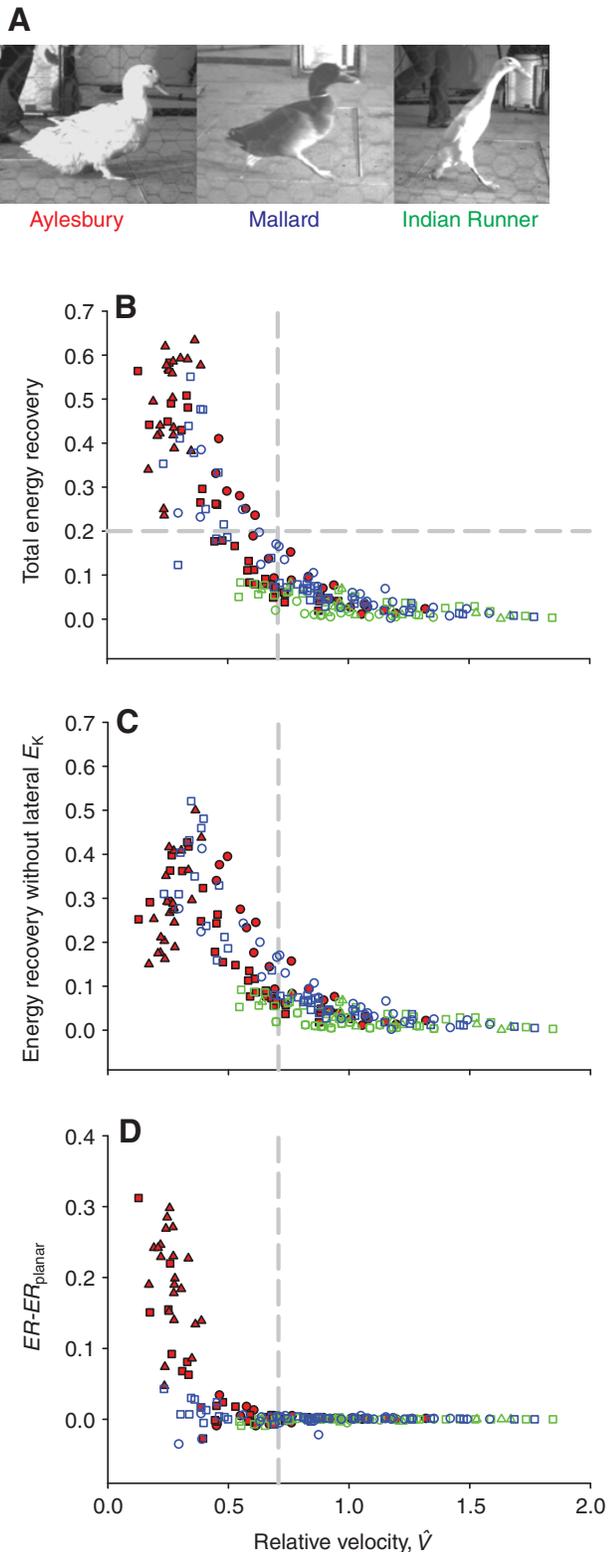


Fig. 1. Energy recoveries ( $ER$ s) for Aylesbury (red), Mallard (blue) and Indian Runner (green) ducks including (B) and excluding (C) the kinetic energy ( $E_k$ ) associated with lateral motions (the difference is displayed in D). An  $ER$  of 1 indicates that changes in potential and kinetic energies of the centre of mass throughout a step has the potential to be completely passive, consistent with inverted-pendulum mechanics. Different symbols indicate different individuals. Vertical broken lines indicate Froude number=0.5 for reference; the horizontal broken line (in B) shows the cut-off used to distinguish between walking and running for Fig. 3.

### The compass gait boundary

The range of possible relative velocities  $\hat{V}$  and step angles swept from the vertical (see Materials and methods) while walking with a compass gait is dependent on the extent to which the vaulting of the body over the stiff stance limb can be considered passive. If the only condition is that sufficient gravity acts in line with the leg to provide enough centripetal acceleration to avoid a toe-drag or take-off (Fig. 2A, blue line), then step angles approaching 90 deg. are theoretically possible. As higher instantaneous speeds are possible near mid-stance (gravity acts directly in line with the leg), mechanical energy has to be applied to both raise and accelerate the body throughout the first half of stance and has to be removed throughout the second half ( $ER=0$ ). By contrast, with completely passive vaulting mechanics ( $ER=1$ ) lower maximum step angles are achievable. This is because the body moves most quickly (highest  $E_k$ ) at the extremes of leg angle (lowest  $E_p$ ). At this point, not only does a smaller component of gravity act in line with the leg but the requirement for centripetal acceleration of the body about the foot is also highest (Usherwood, 2005). Achieving both passive body mechanics and ‘take-off’ avoidance results in a lower net horizontal velocity for a given leg angle than the constraints of take-off avoidance alone (Fig. 2A).

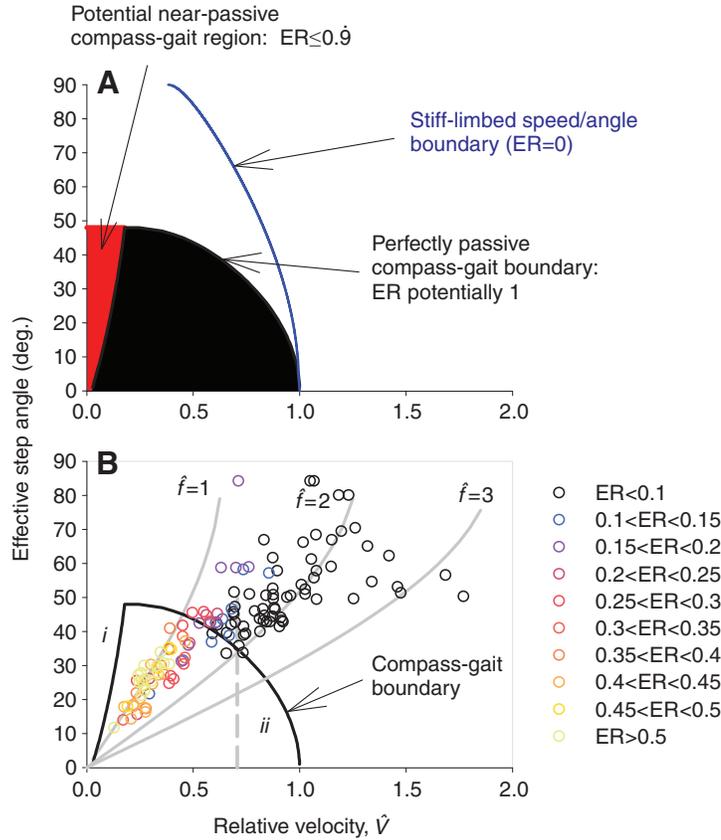
For perfectly passive vaulting of the body over the foot, there is also a low-speed/high step-angle boundary: very low speeds at high step angles (large step lengths) are impossible because there is insufficient  $E_k$  to allow the CoM to rise passively over mid-stance (boundary  $i$  in Fig. 2B and Fig. 3) – the body would simply rock upwards and fall back again without ever making it completely over the stance foot. This boundary is probably of more theoretical than applied interest as, with an infinitesimally small energy input to hold, control and release the body at the top of the vault, very slow walking is feasible with large step angles (Fig. 2A, the region in red) with very nearly passive body motions.

With each speed and step angle combination, a step frequency is explicit. This is indicated in a relative form  $\hat{f}$  (Fig. 2B and Fig. 3), which gives the step frequency as a multiple of that expected for a swing leg acting as an ideal passive pendulum with mass focused at the foot (see Materials and methods).

### MATERIALS AND METHODS

Three Aylesbury (77 steps, mass=3.61±0.68 kg, leg-length  $L_{leg}=0.163±0.015$  m, means±s.d. throughout), two near wild-type Mallard (70 steps, mass=1.81±1.6 kg;  $L_{leg}=0.165±0.01$  m) and three Indian Runner ducks (54 steps, mass=1.12±0.14 kg,  $L_{leg}=0.115±0.02$  m) were motivated to locomote along an array of 6 Kistler 9287B forceplates sampling at 500 Hz, following procedures approved by The Royal Veterinary College. A range of speeds was elicited for each subject by clapping and waving. Fore-aft, lateral and vertical forces, along with centres of pressure were inspected to identify sequences in which locomotion was steady and in line with the forceplates [mean change in horizontal velocity over a step was  $<0.01±0.10$  ms<sup>-1</sup> (±s.d.)]. Individual steps were analyzed from mid-stance to mid-stance, identified by the crossing of the fore-aft forces from decelerative to accelerative. The forward progression of the centre of pressure from mid-stance to mid-stance provided step length  $L_{step}$ , and, with the step period, the magnitude of horizontal velocity  $V$ , required both as an integration constant in determining changes in speed and kinetic energy and for calculating relative velocity  $\hat{V}$ , where:

$$\hat{V} = \frac{V}{\sqrt{gL_{leg}}} \quad (1)$$



Here,  $g$  is the magnitude of gravity ( $9.81 \text{ m s}^{-2}$ ) and  $L_{\text{leg}}$  the functional leg-length, taken as the height from the ground to the hip during quiet standing.  $\hat{V}$  is equivalent to the square root of the most commonly used form of Froude number  $Fr$  in terrestrial animal locomotion studies. Relative step frequency is presented in a non-dimensional form  $\hat{f}$ :

$$\hat{f} = f\pi \sqrt{\frac{L_{\text{leg}}}{g}}, \quad (2)$$

indicating the step frequency  $f$  as a proportion of the natural pendular frequency for a leg swinging about a stationary hip over small angles with the leg mass situated at the foot (an ‘ideal’ pendulum). Note that, as step (as opposed to stride) frequency is used, and the compass gait model assumes a duty factor of exactly 0.5, the period taken by a passively swinging limb to swing from foot off to foot on would be half that of a full pendulum cycle. This formulation intentionally errs on the side of familiarity and simplicity rather than realism: more detailed study of the passive nature of swing legs would have to consider jointed pendulums (see Mochon and McMahon, 1980), vaulting (or observed) hip motions and duty factors deviating from 0.5. One layer of realism that can be added without an undue increase in complexity is the deviation from the point-mass aspect of the ‘ideal’ pendulum. In order to consider ‘real’ pendulums with distributed masses, the effective pendulum length  $EPL$  is a useful concept: it gives the length an ideal pendulum would need to be in order to swing at the same frequency as the real pendulum.

$$EPL = \frac{I_{\text{leg}}}{m_{\text{leg}} L_{\text{legCom}}}, \quad (3)$$

where  $I_{\text{leg}}$  is the moment of inertia (second moment of mass) of the swing leg about its pivot (the hip),  $m_{\text{leg}}$  is the mass of

Fig. 2. Step angle as a function of speed from theoretical compass gait predictions (A), and from forceplate observations of Mallard and Aylesbury ducks, coded by energy recovery ( $ER$ ) (B). Perfectly passive ( $ER=1$ ), stiff-limbed compass gait walking constrains both lower (*i*) and upper (*ii*) speeds (black area in A); with a small energy input ( $ER \leq 0.9$ ), the low-speed constraint is lost (red area); without any passive potential-kinetic energy interchange ( $ER=0$ ) higher step angles and speeds are possible (blue line) until  $\hat{V}=1$ . Underlying grey curves (in B) indicate the contours associated with step frequencies normalized by the ideal pendular frequency of the swing leg with point mass at the foot. Ducks walk (with high  $ER$ s, yellows and reds) with near-passive step frequencies and transition to running (low  $ER$ s, blues and black) at higher speeds, with higher-than-passive step frequencies.

the swing leg, and  $L_{\text{legCoM}}$  is the distance between pivot and swing leg CoM. The passive swing frequency is relatively insensitive to mass distribution. A constant (rod-like) leg-mass distribution would result in  $EPL = \frac{2}{3}L_{\text{leg}}$ , and a passive step frequency of  $\sqrt{\frac{3}{2}}=1.22$  that of an ideal pendulum of the same length.

Fluctuations in  $E_p$  and  $E_k$  due to motions in each of the three axes were calculated from forceplate data following conventional methods pioneered by Cavagna (Cavagna, 1975): measured forces (on known body masses) give CoM accelerations; when integrated, these give velocities (from which  $E_k$  is determined), which, when integrated, give motions of the CoM (changes in height allowing calculation of changes in  $E_p$ ). Integration constants for determining velocities were based on the assumption that the gait was steady and symmetrical over a stride. The  $ER$  was calculated:

$$ER = \frac{\Delta^+ E_p + \Delta^+ E_k - \Delta^+ E_m}{\Delta^+ E_p + \Delta^+ E_k}, \quad (4)$$

where the prefix  $\Delta^+ E$  denotes the sum of the positive increments of energy change (in a symmetrical bipedal gait, this is equivalent to the amplitude) and  $E_m$  is the total external mechanical energy ( $E_k + E_p$ ) of the body. To identify the importance of lateral, or ‘waddling’, motions to the potential passive nature of the  $E_k - E_p - E_k$  interchanges,  $ER$  was also calculated excluding the  $E_k$  associated with lateral motions,  $ER_{\text{planar}}$ . It should be remembered that  $ER$  is a measure only of the mechanically passive nature of the CoM: it provides no measure of ‘internal’ work, leaves the potential for considerable simultaneous, counteracting muscular work (see Donelan et al., 2002) and does not inform whether the CoM is vaulting following a path expected from relatively stiff limbs (see Usherwood et al., 2007).

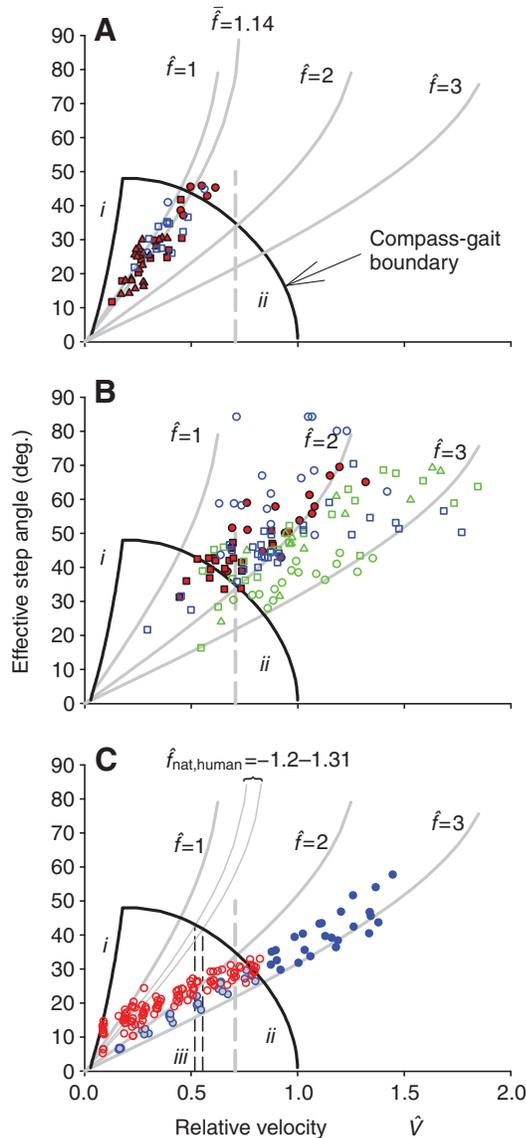


Fig. 3. Step angle as a function of speed for ‘walking’ ducks [A, determined as having energy recovery ( $ER$ ) $\geq 0.2$ ] or ‘running’ ducks (B,  $ER < 0.2$ ), and walking and running humans [C, walking in red ( $N=11$  subjects), running in blue ( $N=5$  subjects)], with running at below maximum possible walking speed with grey fills). Ducks are coloured according to breed, with symbols denoting subject, as for Fig. 1. Underlying black and grey lines indicate the compass gait boundary and step frequencies described for Fig. 2. The vertical grey broken line denotes  $\hat{V}=0.7$  ( $Fr=0.5$ ), usually identified as the walk–run transition speed for humans. Vertical broken black lines in C mark the range in maximum speeds predicted if humans walked both with passive swing limbs and while constrained by compass gait mechanics.  $\hat{f}_{nat, human}$  indicates the frequency consistent with a passive, pendular swing leg action for humans.

An effective step angle swept before and after the vertical,  $\Phi$  was determined from the forceplate-derived step lengths  $L_{stance}$  and the measured leg-length:

$$\Phi = \sin^{-1} \left( \frac{L_{stance}}{2L_{leg}} \right). \quad (5)$$

It should be noted that this may differ from any true kinematic angle, as it assumes a compass-like gait with a single foot on the ground at any time and symmetry about the vertical.

### Human data

Kinematic data from previous studies of humans walking (Bertram, 2005) or running (Gutmann et al., 2006) on treadmills were kindly provided by John Bertram. In these studies, the full range of speeds achievable during walking ( $N=11$  subjects) and running ( $N=5$  subjects) were measured. The highest walking speeds were moderately uncomfortable and slightly above the preferred walk–run transition speed. The low running speeds were certainly unnatural, extending well below the preferred run–walk transition speed.

## RESULTS AND DISCUSSION

### Waddling and walking

At low speeds,  $ER$  (Fig. 1B) for Aylesbury and Mallard ducks is as high as 75%, close to that recorded in cursorial birds (Cavagna et al., 1977; Heglund et al., 1982), humans (Cavagna et al., 1977) and penguins (Griffin and Kram, 2000). At the lowest speeds, this  $ER$  is only achieved by the Aylesbury ducks if lateral, or ‘waddling’,  $E_k$  is included (Fig. 1C,D):  $ER_{planar}$  indicates the  $ER$  without consideration of lateral motions and falls at the lowest speeds. This is not to suggest that waddling improves efficiency – side-to-side motions are presumably not the purpose of locomotion. A better view is that, at low speeds and, given widely splayed foot placement (presumably due to artificial selection for size or natural selection for swimming capability), lateral forces, displacements and movements are inevitable. However, these (inevitable but ‘pointless’) motions have the potential to be achieved largely passively, though perhaps not without metabolic implications (Donelan et al., 2001).

### Running

At  $\hat{V} > 0.7$  (or  $Fr > 0.5$ ),  $ER$  are universally low – above these speeds, no duck maintains passive, inverted pendulum-like energy interchanges. Low  $ER$ s may be interpreted as suggesting a ‘bouncing’ or ‘running’ gait; however, this terminology must be treated with caution. It appears most unlikely that ducks are specialized for elastic energy storage and recovery. They have relatively short legs and thick tendons, probably reflecting some of the compromises in form associated with evolutionary pressures for swimming performance. Therefore, low  $ER$ s should be taken as departure from inverted pendulum behaviour, perhaps as ‘pseudo-elastic’ bouncing (Srinivasan and Ruina, 2006; Ruina et al., 2005) but not necessarily involving extensive elastic storage and recoil. Nonetheless, a running gait, even without elastic energy storage, may be a gait choice that minimizes mechanical work and energetic costs at higher speeds under the fundamental constraints of legged bipedal locomotion in gravity (Srinivasan and Ruina, 2006).

Despite occasional slow trials, no steps of the Indian Runners displayed high  $ER$ s – ‘running’ gaits were maintained at low speeds (see also Fig. 3B). The fact that this is mechanically possible is clear from observations of humans: it is perfectly possible to ‘run’ at no net forward speed (Fig. 3C). Given the ability of all three duck breeds tested to achieve ‘running’ mechanics (albeit predominantly ‘grounded running’ without aerial phases) but the failure of Indian Runners to display inverted-pendulum walking mechanics (high  $ER$ ), perhaps a better, if distinctly awkward, classification of Indian Runners might be as ‘Indian Not-Walkers’. Both the Mallards and Indian Runners did achieve aerial phases (‘running’ distinguished by the traditional kinematic definition) at their highest speeds (Movies 2 and 3 in supplementary material). This differs from the findings of Abourachid (Abourachid, 2001), presumably because the birds in the previous study achieved  $\hat{V}$  only up to 0.7. Running with an aerial phase was not observed by any of the Aylesbury ducks (Movie 1 in supplementary material shows a typical gait).

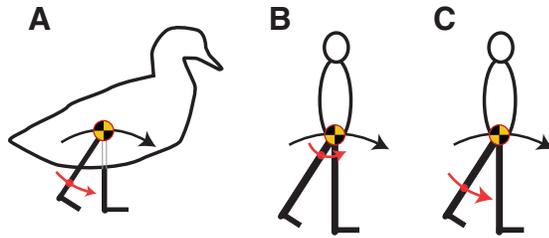


Fig. 4. CoM trajectories (black arrows) for compass gait walking and motions of the effective pendulum length (*EPL*) (red arrows) for the swing leg for (A) walking ducks assuming the swing leg is passive, and with *EPL* appropriate for mean observed walking frequencies; (B) a walking human with passive swing leg if the mass distribution were such that the step frequency was that observed at high speeds ( $\hat{f}=2$ ;  $EPL=L_{\text{leg}}/4$ ); (C) a walking human with *EPL* appropriate for reported mass distributions. Fast human walking cannot be achieved with a passive swing leg.

### The walk–run transition in ducks

While discontinuities in kinematics with increasing speed suggest gait transition in some birds (Hayes and Alexander, 1983; Gatesy and Biewener, 1991; Gatesy, 1999), the gait transition of ducks from a slow vaulting or ‘walking’ gait (using a mechanical definition) to a faster ‘running’ gait is blurred (Fig. 1B), typical of a number of bird species. In contrast to humans and most mammalian quadrupeds, there is no discontinuity in mechanics apparent with increasing speed. Although a discontinuity in stride parameters is reported in the relatively small and crouched painted quail between relative velocities of 0.6 and 0.8 (Gatesy and Biewener, 1991), such a transition is difficult to determine for ducks. However, when step angle and *ER* are considered together, especially when viewed with the boundary determined by compass gait mechanics (Fig. 2B), a distinction between walking and running gaits can be perceived. Walking (high *ER*) is achieved with near-passive swing or step frequencies; running, with low *ER* and beyond the boundary determined by compass gait mechanics, is achieved with above-passive step frequencies. Taking any observed *ER* value as the sole distinguishing boundary between walking and running – especially in cases where *ER* varies without discontinuities with speed – is certainly arbitrary; however, in order to highlight the relationship between speed, step frequency and *ER* displayed in Fig. 2B,  $ER \geq 0.2$  is used as an objective, quantitative condition for walking (Fig. 3A). For steps at  $ER \geq 0.2$ , the mean step frequency is  $1.14 \hat{f}$ . If the swing leg was passive, this would equate to an *EPL* of 0.78 (see Materials and methods) (Fig. 4A). Considering a real pendulum of even mass distribution results in a passive frequency of  $1.22 \hat{f}$ , swing leg mechanics in walking ducks can be considered near-passive. Therefore, ducks do not walk above a speed consistent with both compass gait and passive swing leg mechanics.

### The walk–run transition in humans

The fact that compass gait walking above  $\hat{V}=1$  is impossible has been understood for many years (e.g. Alexander, 1989): above this speed, gravity cannot keep the CoM connected to the stance foot (in contact with the ground) with a stance limb in compression. More recently, similar constraints have been identified but for finite stance angles (Usherwood, 2005; Srinivasan and Ruina, 2006). Combined with some constraint on step frequency, this suggested an account for the observed walk–run transition speed of humans at approximately  $\hat{V}=0.7$  ( $Fr=0.5$ ) (Usherwood, 2005). Since this, research on human swing-limb mechanics (Doke et al., 2005; Doke

and Kuo, 2007) highlights that fast human walking is not actually achieved with passive swing-limb mechanics (see also Mochon and McMahon, 1980). Indeed, if humans were constrained to walking with a passive (duck-like) swing leg,  $\hat{f}$  would be of the range from 1.2 [derived from Doke et al. (Doke et al., 2005)] to 1.3 [from Doke and Kuo (Doke and Kuo, 2007)] – close to that for a leg of even mass distribution of  $\hat{f}=1.22$  (see Fig. 4B,C). In order to achieve passive swing leg mechanics at observed step frequencies near top walking speeds ( $\hat{f} \approx 2$ ), *EPL* would have to be a quarter of the leg-length – most unlikely even with considerable leg flexion. If humans did walk with step frequencies determined by passive swing leg mechanics, and were constrained to walking with compass gait mechanics, they (like ducks) would be limited to maximum walking speeds of  $\hat{V}=0.5$  – only 3/4 the observed transition speed (Fig. 3C). Instead, humans increase the range of their walking speeds, while still complying with the constraints of compass gait CoM mechanics, by driving their swing-limbs at well above their natural pendular frequencies. High step frequencies (short step lengths or small step angles) have previously been identified as effective in reducing the energetic losses due to suddenly redirecting the CoM at the start of each step (Kuo, 2001; Kuo, 2002; Donelan et al., 2002); the increased potential walking speed with forced swing legs described here provides an alternative, though certainly not mutually exclusive, account for the relatively high step frequencies of walking humans.

### Limitations and future work

The compass gait model predictions of constraints to step angle and speed presented in the current study are limited to the extreme cases of perfect, near-perfect and absent *ER* (Fig. 2A), and are based on the assumption of completely stiff stance limbs and consequently a duty factor of exactly 0.5. While this is an appealing and extremely reductionist abstraction allowing simple and intuitive predictions, real bipeds walk with intermediate *ER* and somewhat compliant limbs. In many cases, even the distinction between walking and running using *ER* can be obscure or arbitrary. The extent to which additional layers of realism – for instance, a certain degree of limb compliance – can be added to the model before its generality and predictive nature is lost remains to be determined.

Further forceplate measurements of walking bipeds are required to investigate whether it is the ducks or the humans (or both) that stand out as unusual. Also, the 4-legged analogue to the passive compass gait, a 4-bar linkage model (Usherwood et al., 2007) will be further developed to investigate whether similar constraints apply to quadrupeds.

### Consequences and implications

The maximum speed of walking in both specialist (humans) and facultative (ducks) cursors appears constrained by compass gait mechanics. Humans increase their maximum walking speeds by driving their swing-limbs at above natural pendular frequencies. From the combination of the limitations imposed by compass gait mechanics and the cost of driving swing-limbs, predictions concerning maximum walking speeds can be made. Anything restricting the driving of the swing-limb – for instance massive boots or massive lower limb prosthetics – would be predicted to reduce maximum walking speed. Conversely, anything enhancing driving of the swing-limb, for instance spring-like torques about the hip or low-mass prosthetics, should permit higher walking speeds. Therefore, while the compass gait is an exceedingly reductionist model of bipedal walking, it is both effective in accounting for the walk–run transition speed in humans and ducks, and allows useful,

intuitive predictions with application to prosthetic and orthotic designs.

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