

Research



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Biomechanics

Mechanical evidence that flamingos can support their body on one leg with little active muscular force

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Flamingos (Phoenicopteridae) often stand and sleep on one leg for long periods, but it is unknown how much active muscle contractile force they use for the mechanical demands of standing on one leg: body weight support and maintaining balance. First, we demonstrated that flamingo cadavers could passively support body weight on one leg without *any* muscle activity while adopting a stable, unchanging, joint posture resembling that seen in live flamingos. By contrast, the cadaveric flamingo could not be stably held in a two-legged pose, suggesting a greater necessity for active muscle force to stabilize two-legged versus one-legged postures. Our results suggest that flamingos engage a passively engaged gravitational stay apparatus (proximally located) for weight support during one-legged standing. Second, we discovered that live flamingos standing on one leg have markedly reduced body sway during quiescent versus alert behaviours, with the point of force application directly under the distal joint, reducing the need for muscular joint torque. Taken together, our results highlight the possibility that flamingos stand for long durations on one leg without exacting high muscular forces and, thus, with little energetic expenditure.

1. Introduction

Why do flamingos stand on one leg? Flamingos are thought to stand on one leg to reduce muscle fatigue [1] or heat loss [1,2]. The muscle fatigue hypothesis assumes that standing for long periods requires sufficiently high levels of active contractile force that would fatigue muscle, necessitating alternating stance from one leg to the other. Conversely, the heat loss hypothesis assumes that the energetic cost of activating muscles for the one-legged stance is smaller than any heat savings realized. While increased energy cost for generating muscle contractile forces [3] could negate any benefits from reducing muscle fatigue or heat loss, whether high levels of muscle activity are required for a flamingo to stand on one leg is unknown.

Here, we examined whether it is *possible* for flamingos to stand on one leg with minimal active muscle forces. We investigated two aspects of postural stability that can exact high muscle forces: *body weight support* and *maintaining balance*. To our knowledge, this is the first functional investigation of one-legged standing in flamingos to explore both musculoskeletal anatomy and behaviour.

Using cadaveric manipulation, we tested whether a passive stabilizing mechanism, or stay apparatus [4,5], in the proximal joints could allow flamingos to maintain a one-legged postural configuration without active muscle force. Although flamingos often sleep standing on one leg, there has been no direct evidence that they can passively support body weight. The horizontally oriented femur [6,7] requires large knee and hip joint moments to support body weight and creates a poor effective mechanical advantage [8] for proximal muscles (figure 1a–c; see the electronic supplementary material).

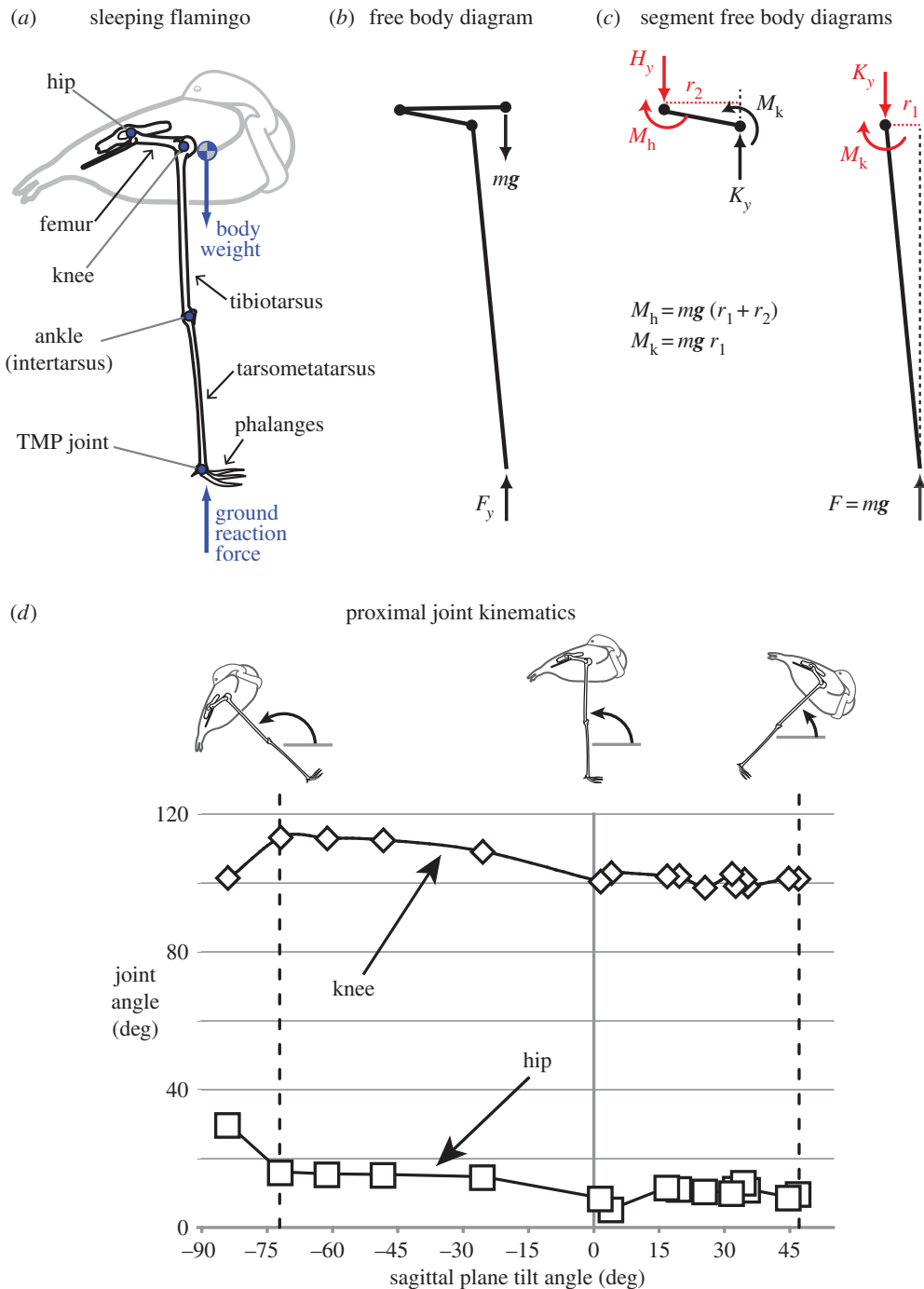


Figure 1. Passively engaged gravitational stay in flamingo proximal limb. (a) Limb posture of a sleeping flamingo. TMP, tarsometatarsophalangeal. (b) In quiet standing, the vertical reaction force at the foot (F_y) equals the body weight (mg) with negligible horizontal forces. (c) Free body diagrams of limb segments represented as massless rigid links (tibiotarsus and tarsometatarsus assumed as one segment). Horizontal femur gives poor effective mechanical advantage to muscles [8], requiring large knee (M_k) and hip (M_h) joint moments. Knee (K_y) and hip (H_y) reaction forces equal mg . (d) Hip (squares) and knee (diamonds) joint angles plotted against the anteroposterior tilt of the cadaver in the one-legged stance. Dashed lines indicate where joints became unstable.

We also measured balance behaviours in live flamingos standing on one leg. We characterized the location of force application under the foot and postural sway dynamics across quiescent and active conditions. These data provide important behavioural descriptions necessary to generate further hypotheses regarding the active and passive mechanisms used in the one-legged stance by flamingos.

2. Material and methods

(a) Cadaver experiments

Two fresh-frozen adult Caribbean flamingo cadavers (*Phoenicopterus ruber*) were obtained from Birmingham Zoo (Birmingham,

AL, USA). We performed kinematics analyses and dissections on fully thawed specimens. Two adjustable bone clamps attached to a vertical strut held the cadaver by one leg at the distal tibiotarsus, emulating a one-legged stance. We tilted the body forwards and backwards in the sagittal plane while tracking limb segment markers to calculate knee and hip joint angles (30 Hz, Dartfish).

(b) Live bird experiments

Over eight sessions, we collected ground reaction components and reference video on eight juvenile Chilean flamingos (*Phoenicopterus chilensis*) at Zoo Atlanta (Atlanta, GA, USA; mass: 0.25–1.40 kg, leg length: 0.17–0.40 m) as they stood on a force plate (200 Hz, AMTI HE6X6). Trials included visibly active (eyes open) and quiescent

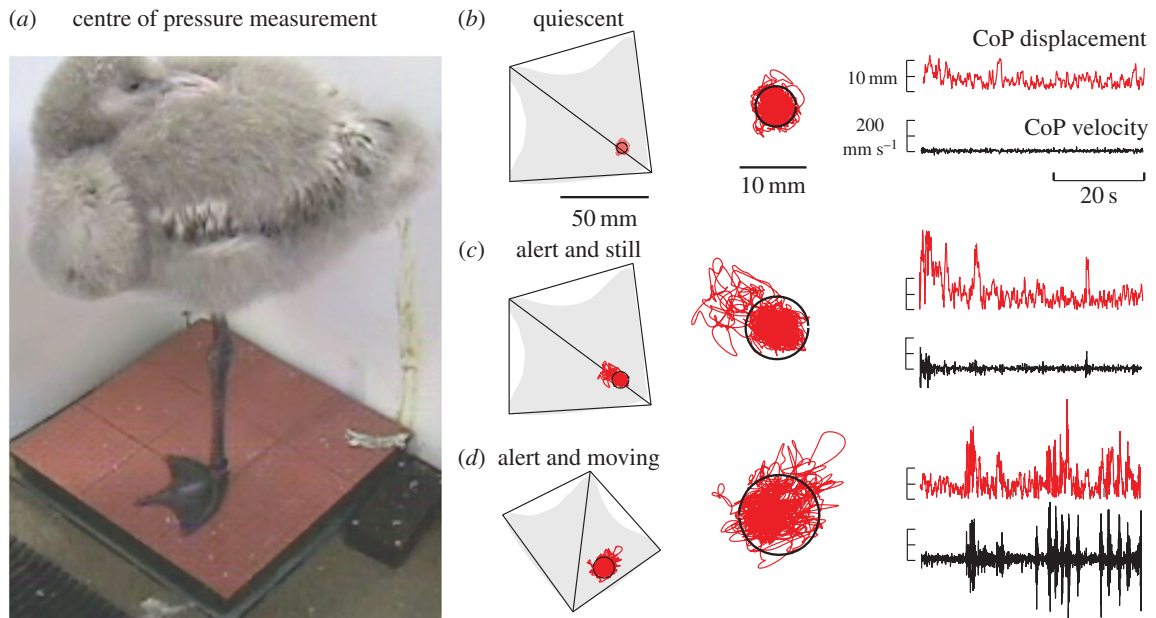


Figure 2. Representative flamingo exhibiting decreased postural sway with decreased activity. (a) Force plate for measuring centre of pressure (CoP) displacement and velocity underneath the foot. (b) When quiescent (eyes closed), CoP stayed beneath the tarsometatarsophalangeal (TMP) joint within a 95% confidence radius (black circle) of 3.0 mm over 3 min. Peak and root mean square (RMS) CoP velocities were 31 mm s^{-1} and 6 mm s^{-1} , respectively. (c) When alert and still (eyes open), the CoP displacement radius increased to 4.7 mm. Peak CoP velocity (133 mm s^{-1}) was fourfold greater and the RMS velocity (11 mm s^{-1}) nearly doubled. (d) When alert (eyes open) and moving (grooming and shaking), the CoP displacement radius doubled (6.0 mm). Peak CoP velocity (362 mm s^{-1}) was more than 11-fold greater and the RMS CoP velocity (48 mm s^{-1}) increased more than sevenfold.

(eyes closed) birds standing on one and two legs. We digitized toe positions from video and computed the centre of pressure (CoP) location on the force plate surface (Matlab, Mathworks). For each trial, we calculated the 95% confidence radius of CoP excursion from a mean location and peak CoP velocity. We characterized CoP dynamics as a bounded random walk by plotting mean squared displacement Δx^2 versus time interval Δt over 0–10 s intervals. Here, $\Delta x^2 = 2D\Delta t$ describes a random walk with diffusion constant D [9]. For each trial, we fit Δx^2 versus Δt to an equation $\Delta x^2 = A(1 - e^{-a\Delta t})$, depicting the Δx^2 upper bound and exponential time constant a (goodness of fit: $r^2 = 0.97 \pm 0.03$).

3. Results and discussion

We observed that flamingo functional anatomy can passively generate proximal joint moments for bodyweight support on one leg. In a one-legged pose, the force of bodyweight engaged the cadaver's proximal joints into a fixed joint configuration visually resembling live flamingos standing on one leg. The joints largely remained fixed as the tibiotarsus was tilted forwards and backwards through 119° in the sagittal plane (hip: $13.9 \pm 5.7^\circ$, knee: $104.5 \pm 5.4^\circ$; figure 1*d*; see electronic supplementary material, movie S1). Upon physical manipulation, the knee joint resisted extension, but not flexion, suggesting a unidirectional stay apparatus in the proximal limb. Little joint movement (less than 10°) occurred when we applied a downward force (approx. $5\text{--}10^3 \text{ N}$) on the body anterior to the knee, consistent with the effect of gravity on the centre of mass. A downward force applied posteriorly near the tail, however, caused the body to pitch backwards (see electronic supplementary material, movie S1).

We found that a stable joint configuration could only be achieved when placing the cadaver such that the foot was directly beneath the body, as adopted in one-legged standing. For example, joint configuration remained fixed when the tibiotarsus was adducted 20° from vertical in the frontal

plane. When aligned vertically, approximating a two-legged stance, the joints rapidly became unstable and could no longer support the body weight (electronic supplementary material, movie S1). This suggests that the unidirectional stay apparatus is engaged only within a small range of frontal plane angles compared with a 119° range in the sagittal plane.

We identified three biomechanical conditions for a unidirectional, passively engaged gravitational stay in one-legged standing flamingos. First, having the body centre of mass located anterior to the knee joint generates passive gravitational knee extensor and hip flexor moments (electronic supplementary material, movie S1). Second, anatomical range of motion limits in the knee and hip oppose these gravitational moments to constrain joint configuration. Third, the foot must be placed medially to the hip joint in the frontal plane to engage and maintain this joint configuration (electronic supplementary material, movie S1). If any conditions are not met, the system reverts to a three-link, open kinematic chain with free joint movement. Previously identified bony and cartilaginous morphological structures at the hip [10] and knee [11,12] may play an important role in the kinematic constraints of this stay apparatus (electronic supplementary material, figures S3 and S4). Regardless of the specific joint articulations, however, the functional anatomical interactions create biomechanical conditions for passive body weight support in the proximal limb during the one-legged stance.

What are the characteristics of one-legged balance in living flamingos, and could they be achieved through active versus passive mechanisms? In quiescent birds (eyes closed), CoP movements were remarkably small and located directly under the tarsometatarsophalangeal (TMP) joint (figure 2*a*). The body was in a resting posture, similar to what we observed in the upright cadaveric specimen. The point of force application directly under the joint requires little to no net joint torque about the TMP joint. In a notable 20 min continuous trial, a flamingo stood on one leg, initially awake (eyes open)

and then became quiescent, possibly falling asleep (eyes closed; electronic supplementary material, movie S2). During this quiescent state, the CoP location was maintained in a small radius under the TMP joint (figure 2*b*). By contrast, when awake (eyes open) in the resting posture, and demonstrably active (grooming, shaking and vocalizing), there were large, rapid CoP movements (figure 2*c,d*). When quiescent, the CoP stayed within a 95% confidence radius = 3.2 ± 0.5 mm (5–10% foot length); this increased to 5.1 ± 0.4 mm when active ($p < 0.01$). The larger and persistent CoP deviations away from its location beneath the TMP joint were only seen in awake and active conditions and require larger net torque about the TMP joint. Peak CoP velocity doubled when awake (79 ± 1 mm s⁻¹) versus quiescent (40 ± 19 mm s⁻¹, $p < 0.01$), and increased sevenfold in active conditions (296 ± 15 mm s⁻¹, $p < 0.01$, figure 2*d*). CoP diffusion dynamics, characterized by the mean squared distance over the same time constant in both activity levels ($p > 0.7$), was lower when quiescent (1.7 ± 0.7 mm²) versus active (4.5 ± 0.6 mm²; $p < 0.05$). Our results show that the balance behaviour of a quiescent flamingo standing on one leg is consistent with that of a vertical, balanced inverted pendulum, which is achievable with little muscle activity. This observation is consistent with the idea that flamingos could maintain balance with little to no muscle activity when asleep, although from behavioural data we cannot rule out the possibility that high tonic levels of muscle coactivity are used to maintain balance. The CoP motion in active conditions could be due either to active balance corrections during movement, or to passive stabilization mechanisms. Direct measurement of muscle activity during one-legged standing, perhaps in a more tractable bird species, is needed to fully resolve these issues.

Our results suggest that muscle activity could be lower in a one-legged than in a two-legged standing posture due to the engagement of a unidirectional, passive, gravitational stay apparatus, and the tightly localized point of force application under the TMP joint during quiescent one-legged standing. Although passive digital locks have been found in distal segments of perching birds [13] and hanging bats [14],

this is the first demonstration, to our knowledge, of a passive, gravity-driven body weight support mechanism in the proximal joints of a bird. Further, as we did not observe large postural sway when standing on one leg, there may also be passive mechanisms for balance, which may be particularly important during sleep. In horses, muscle forces in sleep-standing are reduced by approximately 98% via passive mechanisms [4,5,15]. As flamingos primarily use their legs for prolonged standing [16] and not locomotion, it seems likely that one-legged standing should be energetically efficient. Other ancillary benefits for the one-legged stance, such as reduced heat loss [2,17–19], may not be as important for non-aquatic and tropical birds that also stand on one leg [1]. We therefore propose the hypothesis that rather than to reduce muscle fatigue or heat loss, flamingos stand on one leg to reduce muscular energy expenditure. While we lack direct evidence, reduced energy expenditure could more generally explain how many birds with varied morphologies and ecological niches can benefit from this uniquely avian behaviour.

Ethics. Zoo Atlanta and Georgia Institute of Technology IACUCs approved all procedures using live animals (A06037).

Data accessibility. Supporting data and materials from this work have been archived in the Dryad repository and can be accessed at: <http://dx.doi.org/10.5061/dryad.917km> [20].

Authors' contributions. Y.-H.C. and L.H.T. contributed equally to conception, design and data collection. Y.-H.C. analysed kinematics data and L.H.T. analysed centre of pressure data. Y.-H.C. and L.H.T. equally co-wrote the manuscript, approved of the final version and agree to be accountable for its content.

Competing interests. We have no competing interests.

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