Supplementary Materials for

Predictive simulations of running gait reveal a critical dynamic role for the tail in bipedal dinosaur locomotion

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Published 22 September 2021, Sci. Adv. 7, eabi7348 (2021)
DOI: 10.1126/sciadv.abi7348

The PDF file includes:

- Supplementary Text
- Figs. S1 to S6
- Table S1
- Legends for movies S1 to S4
- Legends for data S1 and S2
- References

Other Supplementary Material for this manuscript includes the following:

- Movies S1 to S4
- Data S1 and S2
Supplementary Text

Here a detailed outline of the simulation and analysis approaches used is given. For convenience, all pronumerals used in equations S1–11 are described in Table S1.

Tinamou running simulations

The optimal control problem (OCP) of generating a steady gait cycle was set up using direct collocation methods (66) in much the same fashion as for the human simulations of (14). The gait cycle is assumed to be perfectly cyclic and symmetrical with respect to the left and right limbs, and as such the common approach of simulating half a gait cycle was employed (25, 81).

The OCP was posed thus: find the time-varying states $x(t)$ and controls $u(t)$, and simulation duration $t_{\text{final}}$, that minimized the objective function

$$J = \frac{1}{d} \int_{t_0}^{t_{\text{final}}} \left( \sum_{m=1}^{M} w_1 a_m^2 + \sum_{j=1}^{L} w_2 T_j^2 + \sum_{n=1}^{N} w_3 \bar{q}_n^2 + \sum_{m=1}^{M} \frac{d a_m^2}{d t} + \sum_{m=1}^{M} \frac{d F_m}{d t} \right) dt,$$

subject to bounds on the states and controls

$$x_{\text{min}} \leq x(t) \leq x_{\text{max}},$$
$$u_{\text{min}} \leq u(t) \leq u_{\text{max}},$$

system dynamic equations

$$f(x(t), \dot{x}(t), u(t)) = 0,$$

and path constraints on system behavior

$$\Phi(x(t), \dot{x}(t), u(t), t) = 0,$$
$$\Psi(x(t), \dot{x}(t), u(t), t) \leq 0.$$

The objective function aimed to minimize four terms:

1. The sum of squared muscle activations ($a_m$) across all $M$ muscles (= 72 in the current model, 36 per leg), integrated across the simulation. The relevance of this 'effort' term likely varies depending on the speed of locomotion, with a higher weighting (implying greater pertinence of economy) probably occurring in walking compared to running. However, for consistency in the current study the respective weighting term was set to a constant low value in all simulations ($w_1 = 0.01$).

2. The sum of squared passive joint moments ($T_i$) across all $L$ DOFs in the legs (=12 in the current model), integrated across the simulation. In life, soft tissues (e.g., ligaments) will contribute to resisting extreme joint angles by providing passive restorative moments. In the absence of empirical data, passive moments were programmatically implemented as a double-exponential function of joint angle (82, 83); a single function was applied to each limb DOF by scaling to the respective bounds such that restorative moments started to be encountered when a given joint moved to within ~15° of its upper or lower bound. A modest weighting term ($w_2 = 1$) was used to discourage over-reliance of the model on passive moments in generating propulsive forces.

3. The sum of squared coordinate accelerations ($\bar{q}_n$) across all $N$ DOFs in the pelvis and legs (= 18 in the current model), integrated across the simulation. This encourages the use of
smoother model kinematics and keeps the OCP better conditioned than if such a term was not included; a nominal weighting of $w_3 = 1$ was used.

4. The sum of squared time derivatives of muscle activations ($da/dt$) and tendon forces ($dF_T/dt$) across all $M$ muscles, integrated across the simulation. The inclusion of this term, with a very low weight ($w_4 = 0.001$), was to improve numerical conditioning of the OCP, avoiding situations for which these slack controls are not uniquely defined by optimality conditions (14).

The bounds on the leg DOF generalized coordinates were set based on the range of motion observed for each joint, determined by bone-on-bone collision in the musculoskeletal model (19). The bounds on pelvic (trunk) pitch were set as $[10^\circ, 45^\circ]$, so as to keep the head and eyes facing up and forward as observed in prior experimental studies (19, 61). Bound on the generalized velocities and accelerations of all DOFs were set wide enough to allow for rapid movements, as would occur at faster speeds of locomotion. All other state and control bounds were set as per previous human simulations (14). A variety of equality ($\Phi$) and inequality ($\Psi$) path constraints were imposed to guide system behaviour, including: implicit muscle excitation–activation and activation–contraction dynamics; implicit skeletal dynamics; zero residuals at the ground–pelvis joint (i.e., dynamic consistency); minimal separation of the feet of 2 cm (approximately one foot width) so that they did not touch or interpenetrate during gait; and net moment balance between muscle–tendon unit (MTU) forces, passive moments, external joint moments and light joint damping ($\zeta = 0.0002 \text{ N} \cdot \text{m} / \text{rad}$, applied to improve simulation smoothness and biological realism) at each limb DOF. The simulation was also constrained so that skeletal states (except forward translation of the pelvis) and muscle states were cyclic and symmetrical at the end with respect to the start; for example, states of the left hindlimb at the end of the simulation (half gait cycle) were identical to those of the right hindlimb at the start. Lastly, a constraint was imposed such that the average forward speed of the model matched some specified target speed, allowing us to explicitly control the speed of locomotion (9, 14, 25).

The above OCP, which is of infinite dimensionality, was transcribed to a nonlinear program of finite dimension via direct collocation in CasADi 3.4.5 (84), accessed via custom MATLAB scripts (v 9.5, MathWorks, Natick, MA, USA; see Supplementary Data 1). It was discretized across 50 evenly spaced mesh intervals and state continuity was enforced at each transitional mesh point. A ‘cold start’ initial guess was used, comprising a static, bilaterally symmetrical standing posture (derived as an approximation of the midstance pose in walking (19)) that translated forward over the simulation duration. To improve numerical conditioning, optimization variables were scaled as per previous human simulations (14), although one difference was that the scaling factor used for $da/dt$ was increased in the current study (set to 400), because of the rapid movements used in the faster speed simulations. The interior-point solver IPOPT 3.12.3 (85) was then used to solve the nonlinear program, run on a standard 2.4 GHz laptop processor (i7-4700HQ, Intel, Mountain View, CA, USA).

Coelophysis running simulations

The overall approach to OCP formulation and solving as used for the tinamou was applied to Coelophysis, using the simplified model of muscle force production (with the best combination of MTU stiffness and strength). Five additional modifications were made to the OCP to account for differences specific to the Coelophysis model. Firstly, since the simple muscle model developed above was used here, path constraints for activation–contraction dynamics were not included. Secondly, additional cyclicity and symmetry path constraints were necessitated for the DOFs controlling the neck, back and tail joints; for lateroflexion DOFs, symmetry was imposed by requiring that the states at the end of the simulation (half gait cycle) were of the same magnitude but opposite sign compared to the beginning of the simulation. Thirdly, in addition to passive joint moments defined in the same fashion for the other DOFs, the neck, back and tail
joints were actuated by torque motors, whose excitation–activation dynamics was described by a simple first-order differential equation \((14)\); the proximal tail joint was also actuated by the caudofemoralis longus (CFL) muscle, which ran from near the tail base to the fourth trochanter of the femur. Fourthly, whereas the hip, knee and ankle DOFs were actuated solely by MTUs, the MTP joint also had a torque motor appended to it, acting as a ‘reserve’ on account of only two MTUs crossing the joint (due to uncertainty in distal limb muscle reconstruction \((17, 76)\)).

The final principal modification to the OCP was the formulation of the objective function, which contained three further terms:

\[
J = \frac{1}{d} \int_{t_0}^{t_{\text{final}}} \left( w_1 \sum_{m=1}^{M} a_m^2 + w_{2,\text{axial}} \sum_{a=1}^{A} a_a^2 + w_{2,\text{MTP}} \sum_{\beta=1}^{B} a_\beta^2 + w_3 \sum_{i=1}^{L} \dot{T}_i^2 + w_4 \sum_{n=1}^{N} \dot{\beta}_n^2 + w_5 \sum_{m=1}^{M} \frac{d a_m^2}{d t_m} + w_6 v_{\text{head}}^2 + w_7 \left( x_{\text{left}}^2 + x_{\text{right}}^2 \right) \right) dt . \quad (S7)
\]

We additionally sought to minimize:

1. The sum of squared torque motor activations \((a_a, a_\beta)\) across all axial \((A = 7)\) and MTP \((B = 2)\) motors, integrated across the simulation. This term was weighted differentially \((w_{2,\text{axial}} = 0.01, w_{2,\text{MTP}} = 0.2)\) to discourage over-reliance on the MTP torque motors.

2. The mediolateral speed of the head \((v_{\text{head}})\), computed from a virtual point located midway between the orbits. In preliminary simulations prior to the inclusion of this term, the head oscillated strongly from side to side, which was considered unlikely as retinal and vestibular stability would be desirable during locomotion \((86, 87)\), especially for a predatory species such as \textit{Coelophysis}. Thus, inclusion of this term kept the head close to the midline.

3. The mediolateral distance of the feet from the midline \((x_{\text{left}}\text{ and } x_{\text{right}})\). Fossil footprints of Triassic non-avian theropods \((88)\) demonstrate that the feet were positioned close to the midline at fast speeds, sometimes even crossing over \((31)\); the inclusion of this term encouraged the narrow step width phenomenon to be replicated in the simulation. In preliminary simulations prior to the inclusion of this term, the model used markedly wider mediolateral foot placements, but an otherwise highly similar pattern of axial kinematics (including phasing of the tail with respect to hindlimb protraction–retraction). No such term was included in the tinamou simulations, on the grounds that a decrease in step width with increasing speed has not been demonstrated in this species; indeed, their ‘relative stability index’ is much lower than that for other birds known to modulate step width in accordance with speed \((-0.18)\) \((31)\). In order to achieve a narrow step width but simultaneously avoid limb collision in the \textit{Coelophysis} simulation, a number of interpenetration path constraints were concomitantly imposed, using the position of virtual points located on the digits, metatarsus and distal tibia.

As with the tinamou, a ‘cold start’ initial guess was used when solving the OCP, consisting of a bilaterally symmetrical standing posture translating forward over time. The bounds on joint angles were set as the ranges of motion used in the derivation of MTU polynomials above, with
all other bounds set as per the tinamou simulation. Maximum speed locomotion was derived in the same iterative fashion as used for the tinamou.

In the ‘synchronized tail’ simulation, an additional term was introduced into the objective function of equation S7, which encouraged left hip extension and proximal tail lateroflexion to oscillate with respect to one another in a fashion opposite to that observed in the nominal simulation:

$$J = \frac{1}{d} \int_{t_0}^{t_{\text{final}}} \left( \sum_{m=1}^{M} w_1 a_m^2 + \sum_{\alpha=1}^{A} w_2,_{\text{axial}} a_\alpha^2 + w_2,_{\text{MTP}} \sum_{\beta=1}^{b} a_\beta^2 + \sum_{l=1}^{I} w_3 T_l^2 + \sum_{n=1}^{N} w_4 q_n^2 + \sum_{m=1}^{M} w_5 \frac{da_m}{dt}^2 + w_6 v_{\text{head}}^2 + w_7 (x_{\text{left hip}}^2 + x_{\text{proximal tail lateroflexion}}^2) + w_8 q_{\text{left hip extension}} q_{\text{proximal tail lateroflexion}} \right) \, dt \, , (S8)$$

where $w_8 = 10$. According to the sign conventions of the joints in the model (see Supplementary Data 2), the relative phasing of tail lateroflexion and hip flexion–extension will be opposite to that in the nominal simulation to a greater extent when the product of left hip extension and proximal tail lateroflexion is more negative (see also Fig. 3C).

Angular momentum calculations
For a given Coelophysis test simulation, we sought to examine each body segment’s angular momentum about the instantaneous location of the whole-body COM, expressed in terms of the global coordinate system (see Fig. S3B): $X$ is about the craniocaudal/roll axis (coronal plane), $Y$ is about the vertical/yaw axis (horizontal plane) and $Z$ is about the mediolateral/pitch axis (sagittal plane).

Taking the simulation output of model kinematics through time, we used the BodyKinematics analysis tool in OpenSim (59) to express segment positions and orientations, and linear and angular velocities, in the global coordinate system. For each segment, its angular momentum about the whole-body COM at each instant in time is given as (89):

$$H_G = H_G + r \times \mathbf{L} \, , \text{ or } \frac{1}{dt} \left( \sum_{m=1}^{M} w_1 a_m^2 + \sum_{\alpha=1}^{A} w_2,_{\text{axial}} a_\alpha^2 + \sum_{\beta=1}^{b} w_2,_{\text{MTP}} a_\beta^2 + \sum_{l=1}^{I} w_3 T_l^2 + \sum_{n=1}^{N} w_4 q_n^2 + \sum_{m=1}^{M} w_5 \frac{da_m}{dt}^2 + w_6 v_{\text{head}}^2 + w_7 \left( x_{\text{left hip extension}}^2 + x_{\text{proximal tail lateroflexion}}^2 \right) + w_8 q_{\text{left hip extension}} q_{\text{proximal tail lateroflexion}} \right) \, dt \, , (S9)$$

where $H_G$ is the segment’s angular momentum about its own COM, $r$ is the position vector describing the location of the segment’s COM relative to the whole-body COM, $\mathbf{L} = \eta \mathbf{v}$ is the linear momentum of the segment (of mass $\eta$, with the velocity vector $\mathbf{v}$ expressed relative to the whole-body COM), $\mathbf{I}$ is the segment’s inertia tensor and $\mathbf{\omega}$ is the segment’s angular velocity. Each of these terms is expressed in the global coordinate system; however, the inertia tensor is by default defined in terms of the local coordinate system of the segment, and in any case its components in the global coordinate system will change over time. Thus, it needed to be recalculated according to the instantaneous orientation of the segment’s local coordinate system with respect to the global coordinate system. Letting $T_{\text{LIG}}$ denote the transform expressing the
orientation of the segment’s local coordinate system with respect to the global coordinate system at a given instant in time, the inertia tensor as expressed in the global coordinate system was computed using the similarity transformation (90):

$$I_G = T_{LG}^T I_L T_{LG}.$$  \hspace{1cm} (S11)

The total angular momentum of the system at each instant in time was then obtained by summing the contributions from each segment with respect to the three global axes.

In addition to computing segmental contributions to whole-body angular momentum, patterns of temporal association between segments, and the extent of segmental angular momentum cancellation, were explored using principal components analysis, as per previous studies (37, 91). Since axial segments could exhibit two oscillations of movement per stride (Fig. 3C), imposed symmetry constraints on the gait cycle means that they may potentially cancel out their own momentum in the second half of the stride. As such, PCA was applied to both the first half and the whole stride cycle.
Fig. S1. (caption on following page)
Fig. S1. Tinamou muscle excitation patterns in the 2.62 m/s running simulation. These are compared to previously published exemplar experimental data (electromyographic recordings) for those muscles that have been investigated; simulated excitations are in reds and oranges, empirical recordings are in blue. Muscles are collated together into ‘functional groups’ based on their primary action to aid interpretation (see legend for color codes). Gray region denotes stance phase, taken as when vertical force exceeds 2% of body weight. Data were digitized from the raw traces reported in the original studies and scaled according to swing and stance phase durations. Sources of data are as follows: IC, guineafowl running at 1.0 m/s (92); ILPR, guineafowl running at 1.0 m/s (92); ILPOa + p, guineafowl running at 2.5 m/s (93); AMB, guineafowl running at 1.0 m/s (92); FMTI, guineafowl running at 1.0 m/s (92); excitations for other heads of the femorotibiales are shown here for completeness; ILFB, guineafowl running at 1.0 m/s (92); FCLP, guineafowl running at 1.5 m/s (94); FCLA, guineafowl running at 1.5 m/s (94); FCM, guineafowl running at 1.0 m/s (92); IFE, guineafowl running at 1.0 m/s (92); ITCr, guineafowl running at 1.0 m/s (92); ITM, guineafowl running at 1.0 m/s (92); ITCaa + p, guineafowl running at 1.0 m/s (92); ISF, juvenile chickens walking at variable speed (95); CFP, guineafowl running at 1.0 m/s (92) (the caudal head was studied but is expected to show a similar excitation pattern to the pelvic head); PIFML, guineafowl running at 1.0 m/s (92); GL, guineafowl running at 1.3 m/s (96); GI, guineafowl running at 1.5 m/s (94); GM, guineafowl running at 2 m/s (97); FL, guineafowl running at 1.5 m/s (98); TCF, guineafowl running at 1.5 m/s (98); TCt, guineafowl running at 1.5 m/s (98); FPP2, guineafowl running at 1.5 m/s (98); FPP3, guineafowl running at 1.5 m/s (98); FP4, guineafowl running at 1.3 m/s (96). Note that for the ISF, raw signal traces were not reported, instead represented as average ranges ± one standard deviation (95). See (19) for key to muscle abbreviations.
Fig. S2. (caption on following page)
**Fig. S2. Simplified model of muscle force production.** (A) Graphical illustration of the relationship between the component of muscle force due to passive stretch ($P$) and normalized muscle–tendon unit length ($l_{MTU}^*$) for different muscle–tendon unit stiffnesses ($k_{MTU}$). (B) The minimum strength ($F_{max}$, in multiples of body weight, BW) that each muscle–tendon unit in a tinamou model with simple muscles required in order for the model to match the 3.4 m/s maximum speed achieved using a model with Hill-type muscles, shown for a range of muscle–tendon unit stiffnesses. Note that having almost any stiffness was ‘better’ than not having any at all ($k_{MTU} = 0$): it markedly reduced the degree to which muscle strength had to be scaled as a multiple of BW. A value of $k_{MTU} = 2$ required muscle strength to be scaled the least, which is arguably the most desirable. (C) Comparison of ground reaction forces and kinematics between a Hill-type model and a simple model of muscle force production for the tinamou, in 3.4 m/s running simulations; these collectively demonstrate much similarity between the two models’ results (see also Movie S2); ‘tY’ ad ‘tZ’ refer to translations in the vertical and mediolateral direction, respectively. In the plot for ground reaction force (shown for the right leg), the solid and dashed arrows indicate the end of the stride for the Hill and simple model simulations, respectively. In the plots for kinematics, curves are normalized to the same stride duration. Note that some of the apparent offset between a given pair of kinematic curves is explained by how stance phase commencement was detected (and thus temporal alignment of the purple and green curves is performed); see the temporal trace of $F_Y$ for an equivalent offset, where there is a prolonged period of low ground reaction force in the simple model simulation before the commencement of the stance phase proper.
Fig. S3. Coelophysis musculoskeletal model. (A–B) The model shown in lateral (A) and oblique craniolateral (B) views. Illustrated are joint axes, the center-of-mass location of each segment (green spheres) as well as the body as a whole (green and black sphere), and the extent of zero-density air spaces (blue). Also indicated in B are the orientations of the global axes, and their respective body rotations. (C) The location of the tail joints in the alternate tail model investigated. (D) A single contact sphere was applied to the digits (terminal) segment of each leg, used to model foot–ground interaction in the simulations, with location and radius as shown. (E–F) The paths of the 33 muscle–tendon unit actuators in the right hindlimb, shown in lateral (E) and cranial (F) views.
Fig. S4. Additional results of the *Coelophysis* maximal speed running simulation. (A) Recovered temporal patterns of right leg ground reaction forces compared to predictions of a scaling-based statistical model derived from locomotor data of 12 extant bird species (28). (B) Correspondence of stance duration, duty factor and stride length for the simulations vs. scaling-based predictions (28). (C) Activation patterns for key hip extensor (CFL, caudofemoralis longus; ADD2, adductor femoris 2) and deep dorsal thigh (IFE, iliofemoralis externus; ITCa, iliotrochantericus caudalis, anterior head) muscles; gray region denotes the stance phase, defined as when vertical force exceeds 1 N (a different threshold was used here compared to the tinamou because of the absolutely larger size of the model). Note in particular the second burst in activity during swing phase for both the IFE and ITCa (arrows), demonstrating a dual function for these particular muscles. (D) Illustration of variation in the craniocaudal position of the whole-body center-of-mass (COM, green and black sphere) explored in sensitivity analysis. (E) Comparison of key kinematic parameters for the two COM position variants and the alternate tail model (cf. Fig. S4C). (F) Detailed comparison of kinematics between each model variation and those obtained using the nominal model, reported as root mean square deviation for each coordinate, except forward translation. (G) Ground reaction force profiles for the right foot for each model in the sensitivity analyses.
Fig. S5. First principal component describing segmental contributions to angular momentum in the nominal and ‘synchronized tail’ Coelophysis simulations. This is an extension of the results presented in Fig. 4, and here is shown for each of the global axes (X = roll, Y = yaw, Z = pitch), considering both the full stride cycle and only half a stride cycle; ‘Prox.’ = proximal, ‘Dist.’ = distal, ‘met.’ = metatarsus. Also reported is the percentage of variance explained by the first principal component for each axis and simulation. Note that different body segments make different contributions to (or cancellations of) angular momentum about a given axis depending on whether a half or full stride is considered. For example, in the nominal simulation, the neck and tail’s relevance to pitch angular momentum is most evident in a half cycle (because both dorsiflex twice every stride), whereas the relevance of the limbs is most evident in a full cycle (because the limbs protract–retract only once per stride).
**Fig. S6. Angular momentum results for ‘no tail’ Coelophysis simulation.** (A) First principal component describing segmental contributions to angular momentum, shown for each of the global axes (X = roll, Y = yaw, Z = pitch), considering both the full stride cycle and only half a stride cycle; ‘met.’ = metatarsus. Also reported is the percentage of variance explained by the first principal component for each axis. (B) Time histories of yaw and pitch angular momentum ($H_Y$ and $H_Z$, respectively).
Table S1. Description of variables included in equations S1–11.

| Variable | Description |
|----------|-------------|
| $A$      | number of axial degrees of freedom |
| $a_{\alpha}, a_{\beta}$ | torque motor activation ($\alpha =$ axial, $\beta =$ metatarsophalangeal) |
| $a_m$    | muscle activation |
| $B$      | number of metatarsophalangeal degrees of freedom |
| $d$      | forward distance travelled by pelvis |
| $f$      | functional describing system dynamics, expressed in implicit form |
| $F_T$    | normalized MTU force |
| $H_G, H_O$ | angular momentum ($G =$ about segment center of mass, $O =$ about whole-body center of mass) |
| $I$      | segment inertia tensor |
| $J$      | total value of objective function |
| $L, l$   | refers to coordinates influenced by passive joint moments |
| $L$      | linear momentum |
| $M, m$   | refers to muscles |
| $N, n$   | refers to coordinates (model degrees of freedom) |
| $q$      | generalized coordinate |
| $\dot{q}$ | generalized acceleration |
| $r$      | position of segment center of mass relative to whole-body center of mass |
| $T$      | passive joint moments |
| $t$      | time |
| $t_0$    | start of simulation |
| $t_{\text{final}}$ | end of simulation |
| $T_{A|B}$ | transform expressing orientation of coordinate system A with respect to coordinate system B |
| $u$      | controls in skeletal dynamics (generalized accelerations) and muscle dynamics (time derivatives of activations and tendon forces) |
| $u_{\text{min}}, u_{\text{max}}$ | lower and upper bounds on controls |
| $v_{\text{head}}$ | mediolateral speed of the head |
| $v$      | segment velocity |
| $w$      | weighting (penalty) term for a given component in the objective function |
| $x_{\text{left}}, x_{\text{right}}$ | mediolateral distances of the left and right feet from the midline |
| $x$      | states describing skeletal dynamics (generalized coordinates and velocities) and muscle dynamics (activations and tendon forces) |
| $x_{\text{min}}, x_{\text{max}}$ | lower and upper bounds on state variables |
| $\dot{x}$ | times derivative of the states |
| $\zeta$  | damping coefficient |
| $\eta$   | segment mass |
| $\Phi$   | functional describing equality path constraints |
| $\Psi$   | functional describing inequality path constraints |
| $\omega$ | angular velocity |
Legends for Supplementary Movies

**Movie S1.** Animation of the walking (0.39 m/s) and running (2.62 m/s) tinamou simulations, showing kinematics, ground reaction forces and muscle activation patterns, played at 0.2× (walking) or 0.1× (running) real speed. Also shown is the location of the instantaneous whole-body center of mass.

**Movie S2.** Animation comparing simulation results using a Hill model of muscle force production (green) vs. using the simplified muscle model (purple), showing kinematics and muscle activation patterns, played at 0.05× real speed. For ease of comparison, the simulation for the simple model is temporally scaled to match the duration of the Hill model.

**Movie S3.** Animation of the maximal speed running (6.65 m/s) *Coelophysis* simulation, showing kinematics, ground reaction forces and muscle activation patterns, played at 0.05× real speed. Also shown is the location of the instantaneous whole-body center of mass.

**Movie S4.** Animation comparing simulation results for the nominal (green) vs. ‘synchronized tail’ (blue) *Coelophysis* simulations, running at 5.7 m/s and played at 0.1× real speed.

Legends for Supplementary Data

**Supplementary Data 1:** MATLAB and C++ code used to set up and execute the tinamou and *Coelophysis* running simulations, and then retrieve and analyze results. The main script is located in the ‘OCP’ folder. Note that the free software CasADi ([https://web.casadi.org/](https://web.casadi.org/)) must be installed prior to use. See the included README file for further information.

**Supplementary Data 2:** Musculoskeletal model files for the original and modified *Coelophysis* model used in this study, viewable in the free software OpenSim ([https://simtk.org/projects/opensim](https://simtk.org/projects/opensim)).
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