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Source: *Philosophical Transactions: Biological Sciences*, Vol. 358, No. 1437, Modelling in Biomechanics, (Sep. 29, 2003), pp. 1525-1533

Published by: The Royal Society

Stable URL: <http://www.jstor.org/stable/3558287>

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Bipedalism in lizards: whole-body modelling reveals a possible spandrel

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This paper illustrates how simple mechanical models based on morphological, ethological, ecological and phylogenetic data can add to discussions in evolutionary biology. Bipedal locomotion has evolved on numerous occasions in lizards. Traits that appear repeatedly in independent evolutionary lines are often considered adaptive, but the exact advantages of bipedal locomotion in lizards remain debated. Earlier claims that bipedalism would increase maximal running speed or would be energetically advantageous have been questioned. Here, we use 'whole body' mechanical modelling to provide an alternative solution to the riddle. The starting point is the intermittent running style combined with the need for a high manoeuvrability characterizing many small lizard species. Manoeuvrability benefits from a caudal shift of the centre of mass of the body (body-COM), because forces to change the heading and to align the body to this new heading do not conflict with each other. The caudally situated body-COM, however, might result in a lift of the front part of the body when accelerating (intermittent style), thus resulting in bipedal running bouts. Based on a momentum–impulse approach the effect of acceleration is quantified for a mechanical model, a virtual lizard (three segments) based on the morphometrics of *Acanthodactylus erythrurus* (a small lacertid lizard). Biologically relevant input (dimensions, inertial properties, step cycle information, etc.) results in an important lift of the front part of the body and observable distances passively covered bipedally as a consequence of the acceleration. In this way, no functional explanation of the phenomenon of lizard bipedalism is required and bipedalism can probably be considered non-adaptive in many cases. This does not exclude, however, some species that may have turned this consequence to their benefit. For instance, instantaneous manipulation of the position of the centre of the body-COM allows stable, persisting bipedal running. Once this was achieved, the bipedal spandrel could be exploited further.

Keywords: lizards; bipedalism; adaptation; modelling

1. INTRODUCTION

In biology, a comparative approach is commonly used to solve evolutionary questions. In this paper we want to show how simple theoretical mechanical models can contribute to discussions in this discipline. The present model builds on morphological, ethological, ecological and phylogenetic data. These are essential to appreciate the aim, the concept and the boundaries of the working space of the model. Therefore, this information will be provided, step-by-step, framing the model and evaluating the output.

Within extant vertebrates, bipedal striding gaits are habitual in only birds and humans. Many lizards are known to run bipedally too (more than 50 species as compiled from Snyder (1949, 1952, 1962), Christian *et al.* (1994), Irschick & Jayne (1999) and our own observations), but the degree varies from a few occasional bipedal strides (e.g. some lacertids) to superb bipedal performance (e.g. *Basiliscus* or *Chlamydosaurus*). These species belong to 11 out of the 24 (sub-) families of legged lacertilians and are scattered over the phylogenetic tree.

As bipedalism is probably not an ancestral trait for lacertilians, parallel evolution must have occurred.

In the 1950s and early 1960s, Snyder (1949, 1952, 1954, 1962) argued that bipedal locomotion allowed lizards to run faster because of the much larger strides they can take. A number of morphological adaptations were listed, but the author conscientiously stated that 'skeletal and muscular adaptations of bipedal lizards, while on the whole distinct in trend, differ only to a small degree of magnitude from those of quadrupeds' (Snyder 1954, p. 31). More importantly, this author further stated that some of the proposed adaptations might be related to speed rather than to bipedality as such. This accords pretty well with the later experimental findings by Irschick & Jayne (1998, 1999). They found no arguments for a speed advantage of bipedal above quadrupedal performance for several species. Snyder (1949, 1952, 1954, 1962) also suggested that bipedal running is energetically more economical as no internal work needs to be done to move the front limbs. However, it is known that similar-sized bipeds and quadrupeds with an overall comparable body-build have very similar locomotor costs (see for instance Taylor & Rowntree 1973; Fedak & Seeherman 1979; Roberts *et al.* 1998).

Thus, a selective advantage of bipedal running is not directly evident and it can be questioned whether bipedal

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One contribution of 20 to a Theme Issue 'Modelling in biomechanics'.

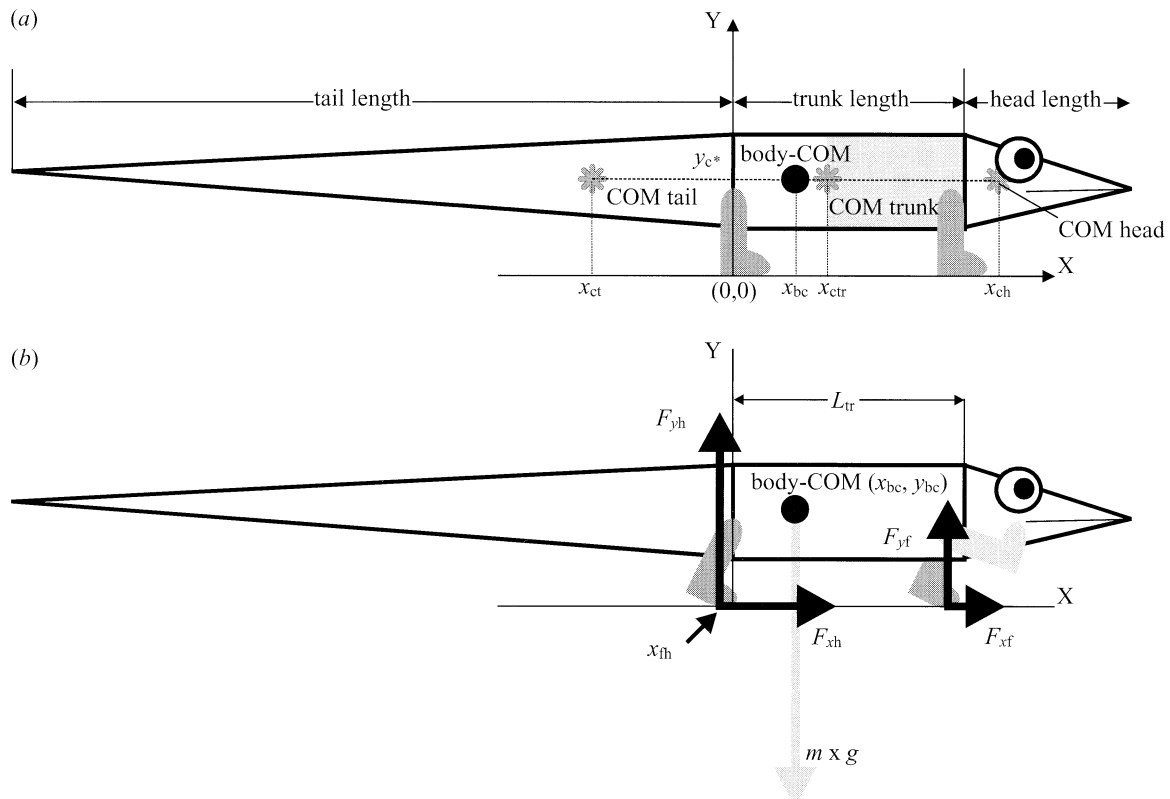


Figure 1. (a) The geometry of the model (see text). (b) External forces acting on a quadrupedally running model (see text).

performance, when present, is truly adaptive in all these lizard species. If not, it might well be just a mechanical consequence of executing another ecological function. Irschick & Jayne (1999) already proposed that bipedality in lizards could be inherent to the high hip torques occurring during fast running. In this paper, we want to explore this ‘consequence’ hypothesis further. Therefore, whole-body mechanics is applied on a simple model based on the morphometrics of a typical lacertid lizard, *Acanthodactylus erythrurus*. First, however, both the initial geometry and inertial properties of the model and the ecological and ethological basis for the theoretical analysis must be explained.

2. METHODS

(a) The model: initial geometry and inertial properties

The model is an assemblage of a cylinder and two cones (figure 1a). The lengths and masses of these elements equal those of the head and neck, the trunk and the tail. Leg masses are incorporated in the trunk segment.

The posture depicted in figure 1a represents the body configuration at the start of the simulations. The used frame of reference (figure 1a,b) has its origin at the level of the trunk–tail boundary and on the substrate (further called the pelvis bound frame of reference). For this posture, vertical starting positions of the COM of the three body segments are identical (y_c^* in figure 1a). The conical geometry and the assumed homogeneous mass distribution of the head and tail determine the horizontal positions of the COM of the cones (i.e. 0.206 times the cone height, measured from the base). The horizontal position of the COM of the cylindrical trunk segment (x_{ctr} in figure 1a) depends

Table 1. Morphometrics of an *Acanthodactylus erythrurus* specimen used as input for the model. Values in brackets refer to positions of the COM of the head, tail and trunk according the simple cone and cylinder geometries.

<i>Acanthodactylus erythrurus</i>	
total length (m)	0.194
head length (m)	0.026
trunk length (m)	0.041
tail length (m)	0.127
total mass (kg)	0.012
fractional tail mass	0.21
fractional head mass	0.19
x_{ct} (m)	-0.023 (-0.026)
x_{ctr} (m)	0.016 (0.018)
x_{ch} (m)	0.049 (0.046)
x_{bc} (m)	0.014
y_{bc} (m)	0.009

upon the user-defined position x_{bc} (figure 1a) of the body-COM (input variable for the simulations) at the onset of the simulations. Logically, its value must be chosen in such a way that the resulting x_{ctr} is situated within the trunk segment (see Appendix A, § Aa). As the parts of the trunk in front and behind x_{ctr} of the cylindrical segment are by definition equal in mass, a non-homogeneous mass distribution applies to the trunk (i.e. densities of the rostral and caudal cylindrical trunk part may differ; see figure 1a). Table 1 compares the x -coordinates of the starting configuration (figure 1a) from the model with those obtained from a male *A. erythrurus* specimen, sectioned in 2.5 mm slices. Obviously, the model represents the actual species pretty well.

During the simulations, segments are allowed to rotate with respect to each other in the sagittal plane. This affects the position of the COM of the segments (x_c^* , y_c^*) and of the body-COM (x_{bc} , y_{bc}) in the pelvis bound frame of reference (see Appendix A, § Aa)

The moment of inertia of each body segment about a transversal axis through its COM is defined by the geometry of the elements (see Appendix A, § Ab).

(b) *The eco-ethological perspective and its functional correlates*

According to Pough (1980), 80% of all lizard species have a body mass below 0.02 kg. This implies that most lizards are small compared with the structure of the habitat they are living in. Shrubs, ripples, branches, stones, crevices, etc., may all represent obstacles forcing a lizard from its linear path when moving from A to B. Moreover, most of these species are very fast for their size (Van Damme & Van Hooydonck 2001). Relative speeds as high as 40 snout-vent lengths per second are not exceptional. All together, this results in a highly manoeuvrable (i.e. turning), swift and intermittent (i.e. many accelerations) style of locomotion for the majority of lizard species and there is no doubt that anybody who has ever tried to catch lizards will appreciate this statement. With its mass of *ca.* 0.012 kg and a top speed of 3.1 m s^{-1} (Bauwens *et al.* 1995), *A. erythrurus*, the model species, can be considered representative of a small agile lizard.

Following Jindrich & Full (1999), making a turn can be split in two components: changes of the heading (i.e. the orientation of the velocity vector of the COM) and rotations about the body-COM to align the body with the new heading. Changing the orientation of the velocity vector implies centripetal GRFs acting on the body. These forces originate from pushing forces of the legs extending *externally* to the curved path. In the trotting gait, typically used by lizards, this force will alternate step-by-step between the fore and the hind limb. To align the body with the heading, a moment about the body-COM must be generated by GRFs acting on the legs too. When the body-COM of the animal is far in front in the trunk, this moment will mainly derive from pushing forces of the hind limb, *internal* to the curved path. The contralateral forelimb, contacting the ground simultaneously when trotting, is of nearly no use because of the much shorter moment arm. With the body-COM at the rear end of the trunk, the reverse is true; the required moment is mainly generated by pushing of the *external* forelimb. Only in the latter case the forces needed to rotate do not conflict with the required centripetal forces!

The position of the body-COM, however, also influences the rotational inertia. Figure 2 presents the moment of inertia for the model as a function of the position of the body-COM along the trunk. (Note that, owing to the rotational symmetry of the model in the starting posture, the moment of inertia about a vertical axis through the body-COM is identical to this for a transversal axis.) From this graph, it is obvious that the inertial resistance against rotation is smallest with the body-COM positioned far in the back of the trunk. This adds nicely to the above conclusion about manoeuvrability. It is further remarkable that the optimal position of the body-COM of the model to minimize rotational inertia (i.e. *ca.* 13 mm in front of the acetabulum of the pelvis) coincides very well with the measured position of the body-COM in the model species *A. erythrurus* (*ca.* 14 mm in front of the pelvis; see table 1). This further supports the reliability of the model.

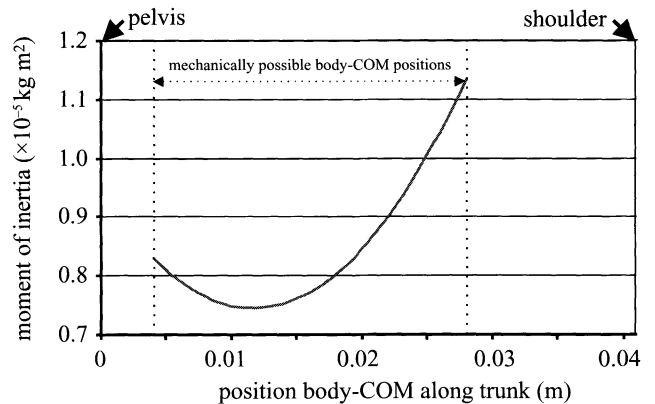


Figure 2. Moment of inertia of the model as a function of the position of the body-COM along the trunk (see text).

Intermittent lizard locomotion is further characterized by many velocity changes (accelerations). Figure 1b shows the external forces acting on the quadrupedally trotting model at a certain instant during an acceleration phase (transversal forces are not considered). From the equations of motion (see Appendix A, § Ac) the vertical forces acting on the fore limb F_{yf} can be deduced as

$$F_{yf} = [m_{\text{tot}}/L_{\text{tr}}][(a_y - g)(x_{bc} - x_{\text{th}}) - a_x y_{bc}], \quad (2.1)$$

where g is -9.81 m s^{-2} ; m_{tot} is body mass; L_{tr} is trunk length; a_x is the instantaneous fore-aft acceleration of body-COM; a_y is the instantaneous up-down acceleration of body-COM; and x_{th} is the position of the point of application of the GRF on the hind limb in the moving XY-frame; see figure 1b.

Important conclusions can be drawn from this equation. The higher the running acceleration (i.e. a_x), the less vertical force is taken by the fore limbs. Therefore, given a fixed coefficient of friction between palmar and ground surfaces, a higher a_x implies less propulsion that can be generated by the fore limbs. As many lizards have a highly intermittent style of running, this might explain the obvious hind-limb dominance characterizing many species.

The above equation yields $F_{yf} = 0$, when

$$a_x = (a_y - g)(x_{bc} - x_{\text{th}})/y_{bc}, \quad (2.2)$$

or when multiplied by body mass:

$$F_x = F_y(x_{bc} - x_{\text{th}})/y_{bc}, \quad (2.3)$$

with F_x and F_y the total horizontal and vertical GRF, respectively. When this particular condition applies, there is no longer a force transfer between the fore limbs and the ground. If a_x (or F_x) increases further beyond this boundary, negative GRFs (i.e. pulling forces) at the fore limbs are needed to maintain the quadrupedal gait. As such pulling forces are obviously not present during fast running, lifting of the front part of the body must occur. When the acceleration in the running direction ceases again (smaller F_x s), gravity will (potentially; see § 4 below) bring the front part of the body back to the ground.

From these equations it is obvious that lifting of the front part of the body will occur at a lower acceleration (or horizontal force) when the ratio x_{bc}/y_{bc} becomes smaller. In other words, the higher and/or the more caudal the body-COM is located, the more the lizard tends to acquire a bipedal posture when accelerating. However, we argued that a caudal shift of the body-COM might enhance the manoeuvrability of a lizard. It must

therefore be examined whether a morphology suitable for better turning and manoeuvring in lizards leads intrinsically to lifting of the front part of the body when running intermittently.

To explore whether bipedal running postures are potentially just the consequence of GRF when the body accelerates, the next two questions need to be answered: (i) do lizards accelerate fast enough to elicit bipedal running postures and (ii) can this also result in longer, clearly observable stretches of bipedal running, because obviously the lizard must become quadrupedal again due to gravitation when the body acceleration ceases?

(c) *The model: synthetic GRF profiles*

To answer these questions, relevant body accelerations as a result of synthetic GRF profiles will be simulated. A trotting gait is assumed (diagonal limb pairs move in synchrony) and DFs (Alexander 1977*a,b*) are smaller than or equal to 0.5. Lateral forces are not considered and both vertical and fore-aft forces are modelled according to the momentum-impulse theorem. The equations and the rationale are described in Appendix A, § Ad.

Figure 3*a* shows the resulting force profiles for the first 18 steps of the model (hence also of *A. erythrurus*; see table 1) accelerating from standstill to *ca.* 3 m s⁻¹ in 15 steps (7.5 strides). The braking impulse grows to its maximum in five steps. At 3 m s⁻¹, the stride frequency of *Acanthodactylus* is *ca.* 20 Hz and DF equals *ca.* 0.4 in this species (B. Van Hooydonck, unpublished data). As Irschick & Jayne (1998) showed that stride duration and DF are fairly constant for accelerating lizards from the second stride on, stride frequency and DF are kept constant in this (figure 3) and any further simulation.

From the fore-aft forces, accelerations of the body-COM can be calculated (force/body mass). Integration results in forward speed, double integration in forward displacement. Speed and displacement as a result of the force profile shown in figure 3*a* are presented in figure 3*b*. The displacement profile is very similar to what is measured for accelerating lizards (Irschick & Jayne 1998; Huey & Hertz 1984; P. Aerts, unpublished data; figure 3*b*). The inset (figure 3*c*) shows how the simulated stride length increases during the acceleration phase. This corresponds to what is described by Irschick & Jayne (1998) for similar sized lizards, fastly accelerating to similar speeds (*ca.* 3 m s⁻¹).

(d) *The model: angular displacements*

As soon as F_x has exceeded the boundary set by equation (2.3), the GRFs act solely at the level of the hind limb-substrate interface. The moment of these forces about a transversal axis though the body-COM must equal at any instant the rate of change of the total angular momentum of the body (Zatsiorsky 2002). For a multi-segmented body the total angular momentum is given by the sum of the local and remote terms of the constituting elements (see Appendix A, § Ae). In the present simulations, tail and head are kept parallel to the ground surface (see figure 4), which means that the local terms of the angular momentum of these two segments are zero. (This bipedal behaviour is observed in many lizards, but note that active tail lifting during bipedal running bouts can occur (e.g. *Uma scoparia*; in Irschick & Jayne 1999.) Thus, for any appropriately small time increment (in this case, 1 ms), the change of the angular velocity of the trunk segment can be calculated from the total moment of the external forces and the change of the remote terms of the angular momenta of the three segments. From the angular trunk velocity, the angular displacement can be obtained. Before each

new iteration, the new position of the body-COM (x_{bc} , y_{bc}) is calculated.

It is important to notice that the position of the point of application of the GRF (x_{th} in figure 1*b*) changes with respect to the pelvis throughout the stance phase of the leg. At touch-down the force applies in front, at lift-off behind the girdle. In the model these touch-down and lift-off positions are symmetrical with respect to the acetabulum (pelvis-femur joint). Between these extremes, the position changes linearly with time. The distance between touch-down and lift-off position in the pelvis bound frame of reference (see figure 1) equals the step length, which is entirely determined by the running speed, the cycle frequency and the DF.

Simulations, starting with an initial acceleration followed by a steady locomotion bout, will proceed for 2 s, unless the position of the body-COM moves over the acetabulum. At that instant, the model would topple backwards just as a result of the GRFs acting on the body.

3. RESULTS: CAN OBSERVABLE BIPEDAL STRETCHES BE INDUCED BY INITIAL ACCELERATION?

As mentioned before, it must first be explored whether lizards accelerate fast enough to elicit bipedal running postures and whether this can also result in long, clearly observable, bipedal stretches. In § 2c we argued that the force profiles presented in figure 3*a* are representative for an explosive start. Figure 4 shows the effect of these GRFs on the body posture. At the beginning of the running bout, the body-COM is located 14 mm in front of the acetabulum of the pelvis (as argued in § 2b and figure 4) and 9 mm above the substrate (as deduced from video recordings of running *Acanthodactylus*).

It appears that a fast start can elicit bipedal running. In step two, the boundary acceleration is clearly exceeded and the fore limbs lose contact with the ground. Maximal trunk rotation (56° or 0.973 rad) is reached just prior (15 ms) to the end of the acceleration phase. At the end of the acceleration phase (after 375 ms), the body is still lifted 47° (0.821 rad). Only about one step later, the model proceeds on all fours again. In total, the lizard covers a noticeable distance of 0.78 m bipedally, solely as the result of its initial fast start.

Figure 5 illustrates what happens when the model attempts to accelerate somewhat faster (i.e. reaching the same speed in 14 steps instead of 15) or somewhat slower (in 16 steps instead of 15) to reach the same maximal speed as in the former simulation. All other input variables (inertial properties, stride frequency, DF,...) are kept identical. When accelerating faster, peak propulsive forces (during the second step; see figure 5) are *ca.* 7% higher; when using 16 steps to accelerate, they are 6% lower. Despite these relatively small differences in the according force profiles, the effects are large. When accelerating in 14 steps, the model topples backwards after about five steps because the body-COM moved beyond the acetabulum. Using 16 accelerating steps, the trunk movements consist of series of short lifts, diminishing in amplitude. The maximal amplitude equals 0.15 rad (*ca.* 9°) over a period which lasts only a few steps. After seven steps, nearly no lifting remains and after 13 steps the model proceeds in a regular trot, although the acceleration phase is

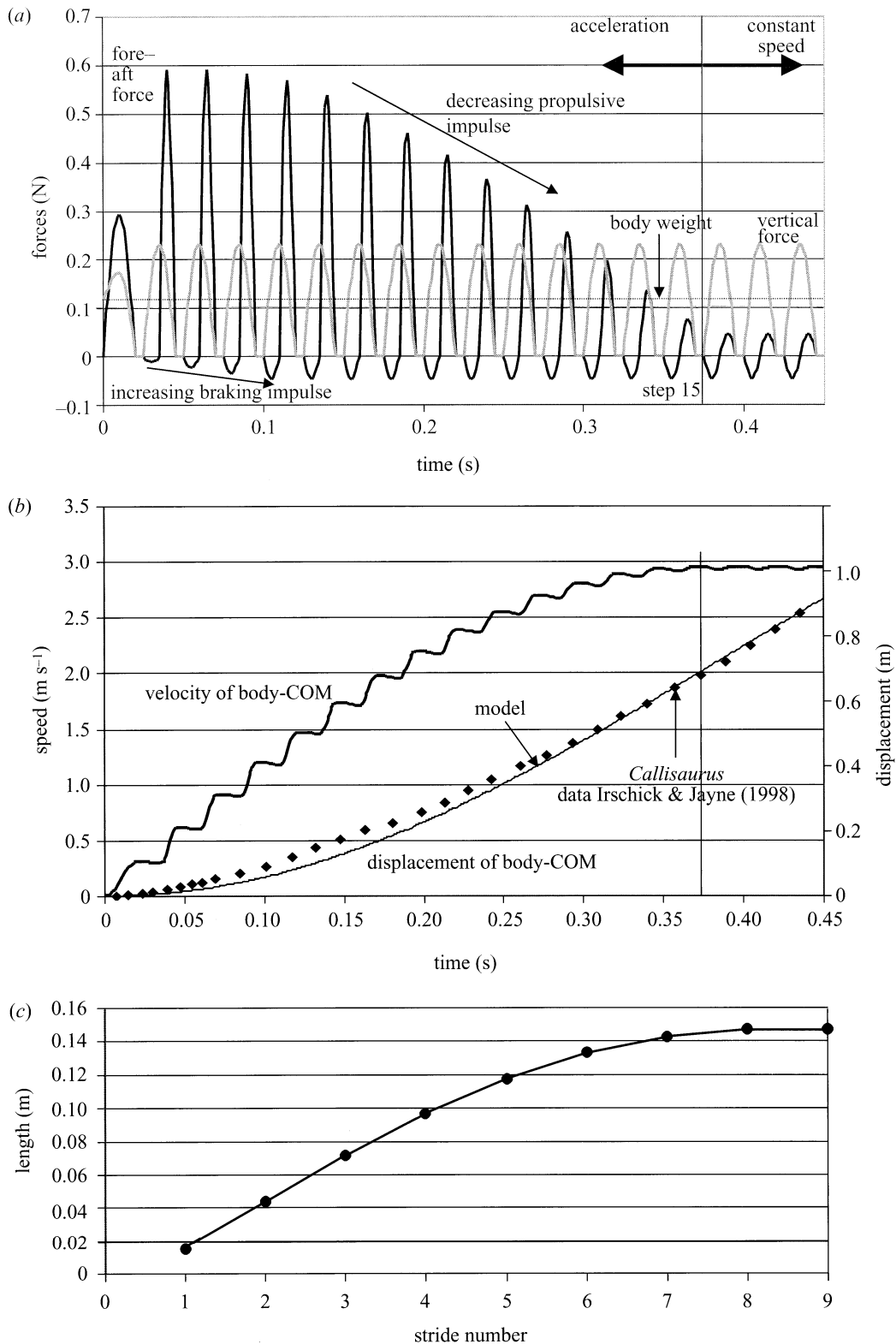


Figure 3. Simulated GRF profiles (a) and the resulting displacement and velocity (b) and stride lengths (c) (see text).

still going on. This pattern agrees perfectly well with high-speed video observations of many rapidly accelerating lizard species (for instance when they run forward on a moving belt): every now and then the fore limbs skip part of the gait cycle (our own observations).

Surprising, however, is the large effect of initial posture on lifting. Equation (2.3) showed that the higher the position of the body-COM, the more readily lifting will occur.

The third curve in figure 5 accords to a simulation entirely identical to '16-steps' acceleration (identical force profile). The only difference is that the body-COM at the start is situated 10% higher, compared with the former simulation. In reality such a difference may accord to a somewhat less sprawling initial posture or a slight extension of the transversal legs of a lizard. In this case, the body topples backwards again instead of lifting by the feeble

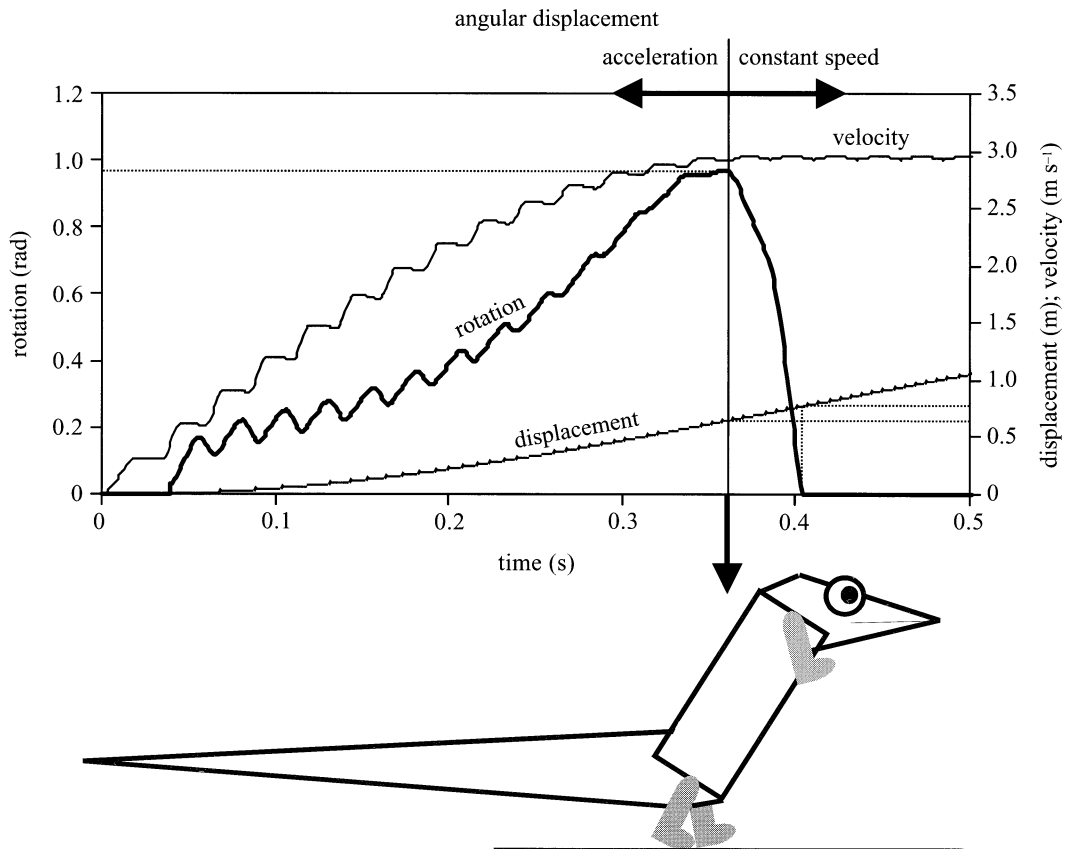


Figure 4. Rotation of the body as a result of the force profile presented in figure 3*a*. Cartoon represents the body configuration at maximal lift (see text).

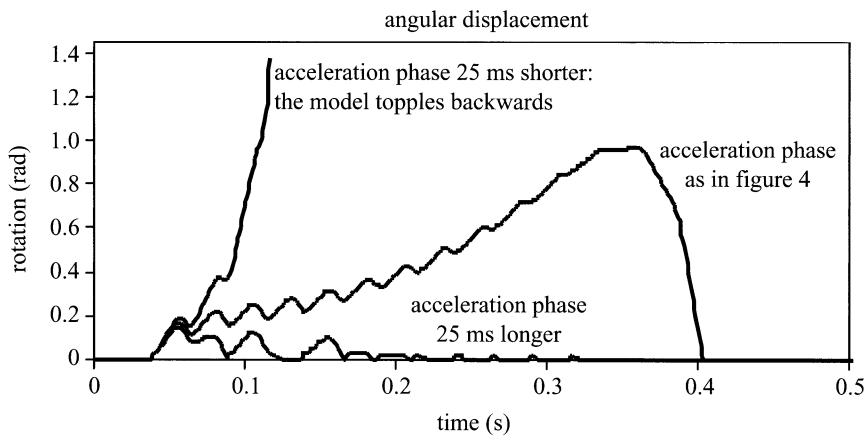


Figure 5. Postural changes for a simulation largely identical to that of figure 4 (i.e. acceleration in 14 and 16 steps, respectively; see text).

0.15 rad. Note that equation (2.3) also shows that the horizontal position of the body-COM will affect the rotation of the body. In the starting position, as represented in figure 1*a*, such a shift is only possible when the morphology (body proportions and inertia) of the model changes. The effects of morphological changes are beyond the scope of this paper, which focuses on the consequences of acceleration as such. Morphological effects will be discussed elsewhere (P. Aerts, unpublished data).

4. CONCLUSIONS

From these results, it appears that small-sized lizards are sensible to engage passively in bipedal running bouts, purely as a consequence of the fast accelerations inherent to their intermittent locomotion style. Adaptations for better manoeuvrability may affect this consequence positively. Although the model showed that bipedal behaviour may go on until acceleration has ceased, the bipedal

stretches as a result of the initial acceleration seem to be limited to *ca.* 1 m. However, some species (like *Basiliscus*, *Chlamydosaurus*, but also *U. scoparia* (D. Irschick, personal communication)) are known to excel in bipedal running, beating the performance of the model by many lengths. This, however, does not necessarily question the model or the theory behind it. The model proves that in biologically relevant circumstances, the physical phenomenon of losing ground contact with the fore limbs does occur. Compared with the model, however, real lizards are much more 'flexible' (morphologically and behaviourally) and aspects such as adjusting the posture of the limbs during acceleration are not included in the model. In this way, extension of the fore limbs may mask low-amplitude body lifting predicted by the model (as, for instance, in figure 5: 16 steps acceleration). However, 'flexibility' may also be used to extend the bipedal stretch, initiated by the acceleration. Active tail lifting during the acceleration phase, for instance, will affect the trunk rotation positively (through the increased local and remote angular momentum of the tail) so that less explosive accelerations may also lead to considerable trunk rotations. Keeping the tail fixed with respect to the body when the trunk 'falls' back at the end of the acceleration phase (remember that the tail is kept horizontal throughout the present simulations) will extend the bipedal stretch for the same reason. The model will even proceed in a bipedal running bout when, right at the instant the trunk starts lowering again, the body-COM is brought above the acetabulum. Also, changes in the spatial and temporal characteristics of the foot fall patterns (i.e. flexibility in behaviour) may result in similar effects (through inherently altered GRF patterns). This implies that species exposed to the acceleration effect illustrated by the model may have 'exploited the consequence' during evolution. When performing bipedally, for instance, larger steps can be taken without the danger of a hindering interaction between hind and fore limbs. This might lead to a better performance and once the bipedal habit is acquired, morphological adaptations such as the longer hind legs, can evolve to increase bipedal performance even further. Seen in this way, bipedalism in lizards must be considered a 'spandrel' (cf. the metaphor proposed by Gould & Lewontin 1979). The spandrels of the Basilica of San Marco in Venice are not built to support the magnificent mosaics. They are just an inherent consequence of the construction of the supporting arches. Only afterwards could they serve the exhibiting function they seemed to be built for. Similarly, bipedalism in lizards probably is a consequence, possibly serving the superb running performance it seems to be evolved for in some species.

APPENDIX A

(a) Calculation of the initial position of the centre of mass of the trunk (x_{ctr}); calculation of the position of the body-COM (x_{bc} , y_{bc}) after trunk rotation

These data can be obtained from the equations giving the position of the total COM of a multi-segmented body:

$$x_{bc} = \left(\sum_{i=1}^n x_{ci} m_i \right) / m_{tot}$$

$$y_{bc} = \left(\sum_{i=1}^n y_{ci} m_i \right) / m_{tot}$$

where n is the number of segments, x_{ci} , y_{ci} are the position of the COM of segment i ; m_i is the mass of segment i ; and m_{tot} is the total mass.

(b) Moment of inertia (I) of head and tail cones and cylindrical trunk about their centre of mass

$$I_{h,t} = 0.0576 L_{h,t}^2 m_{h,t} \quad (\text{head and tail}),$$

$$I_{tr} = m_{tr} (2x_{ctr}^2 + L_{tr}^2 - 2x_{ctr} L_{tr}) \quad (\text{trunk}),$$

where $I_{h,t, tr}$ is the moment of inertia of head, tail and trunk; $L_{h,t, tr}$ is length of head, tail and trunk; $m_{h,t, tr}$ is mass of head, tail and trunk; and x_{ctr} is the initial position of the trunk COM in the pelvis bound frame of reference.

(c) Equations of motion of the accelerating model

To maintain a quadrupedal gait the next set of equations of motion must apply (only fore-aft forces and vertical forces are considered):

$$F_{xh} + F_{xf} = m_{tot} a_x$$

$$F_{yh} + F_{yf} + m_{tot} g = ma_y$$

$$(F_{xh} + F_{xf}) y_{bc} + F_{yf} (L_{tr} - (x_{bc} - x_{fh})) - F_{yh} (x_{bc} - x_{fh}) = 0,$$

where g is -9.81 m s^{-2} ; m_{tot} is body mass; $a_{x,y}$ is the instantaneous fore-aft, up-down acceleration of body-COM; x_{bc} , y_{bc} are position body-COM; x_{fh} is the position of the point of application of the GRF on the hind limb in the moving XY-frame; $F_{xh,xf}$ is the horizontal force at the level of the fore and hind limb; $F_{yh,yf}$ are the vertical forces at the level of the fore and hind limb; and L_{tr} is the length of the trunk (see figure 1b).

(d) Synthetic ground reaction force profile

The calculation of the GRFs acting on the model depend upon the momentum-impulse equation:

$$\int_{t_1}^{t_2} \left(\sum F_{x,y} \right) dt = m_{tot} V_{2x,y} - m_{tot} V_{1x,y} = dp,$$

where $\Sigma F_{x,y}$ is resultant force in x or y direction; m_{tot} is mass; $V_{1,2}$ is velocity of the body at time t_1 and t_2 , respectively; and dp is change in momentum.

(i) Vertical forces

When vertical body oscillations are assumed constant during running, vertical GRFs (F_y) should equal body weight when averaged over (half) a stride ($dp = 0$). In lizards, vertical GRFs consist of a single, broad active peak (Christian 1994; Farley & Ko 1997) and can therefore be modelled in agreement with this boundary constraint as

$$F_{y(t)} = - \frac{\pi m_{tot} g}{4DF} \sin\left(\frac{\pi Fr}{DF} t\right),$$

where $F_{y(t)}$ is instantaneous vertical GRF; m_{tot} is mass; DF is duty-factor; Fr is stride frequency; g is -9.81 m s^{-2} ; and t is time varying between touch-down and lift-off of a limb

(see also Alexander, 1977a,b). For a quadrupedal trot, this force is shared by the diagonal limbs.

When starting from standstill, however, dp for the first step does not equal zero (a step being defined as the displacement of the body-COM when a foot contacts the ground). Assuming that the vertical velocity of the body-COM at the end of this first step is equal to that of a step in series, it follows that

$$dp_{1st} = m_{tot} \int_0^{CT} \frac{F_{y(t)} - m_{tot}g}{m_{tot}} dt = m_{tot}g \left(\frac{1}{Fr} - \frac{CT}{2} \right),$$

where dp_{1st} is the change in momentum during first step; and CT is the duration of first step.

To obtain a broad, single-peaked vertical force profile for the first step, starting at body weight and reducing to zero at the end of this first step, this equation can be reformulated as follows:

$$dp_{1st} = \int_0^{CT/2} \left(-m_{tot}g + \text{amp} \sin\left(\frac{\pi}{CT}t\right) \right) dt \\ + \int_{CT/2}^{CT} \left((-m_{tot}g + \text{amp}) \sin\left(\frac{\pi}{CT}t\right) \right) dt \\ - \int_0^{CT} (-m_{tot}g) dt.$$

From these equations, 'amp' can be calculated, which is the vertical force amplitude on top of body weight. Once known for a specific set of input values for m_{tot} , Fr and DF (CT is obtained from the latter two), the actual vertical force profile for the first step is given by the equations integrated in the first two elements of the above sum (for the mentioned intervals, respectively).

(ii) Fore-aft forces

During running at a constant speed, the impulse of the horizontal GRFs over (half) a stride should be zero ($dp = 0$). The typical profile (deceleration followed by an acceleration; e.g. Farley & Ko 1997) can therefore be represented by

$$F_{x(t)} = \frac{\pi m_{tot}g}{4rDF} \sin\left(\frac{2\pi Fr}{DF}t\right),$$

where $F_{x(t)}$ is the instantaneous horizontal GRF; and r is the ratio of the vertical to the horizontal peak forces. According to figs 2b and 3b in Farley & Ko (1997) (trotting *Coleonyx* and *Eumeces*), ' $r \approx 5$ '.

When accelerating from standing still to the maximal running speed (V_{max}), velocity (hence momentum) will increase step-by-step during the accelerating phase. Judging the displacement profiles of starting lizards (see for instance Irschick & Jayne (1998) and our own measurements), this step-by-step velocity increase can be modelled by means of a sine function,

$$V_{stn} = V_{max} \sin(\pi stnr/2SV),$$

where V_{stn} is the velocity at the end of step 'n'; SV is the total number of steps needed to reach maximal speed; and stnr is the step number ($0 < stnr < SV$). From this, the step-by-step change in momentum can be calculated.

From human sprint starts it is known that the initial braking impulse gradually grows to its maximum during

the first steps of the acceleration phase (M. Lafortune, NIKE Inc., personal communication). This braking impulse can be calculated as

$$I_{br} = \frac{m_{tot}g\pi}{4stnr \times r/SB \times DF}, \text{ if } stnr > SB; \text{ then } SB = stnr,$$

where I_{br} is the braking impulse during the first half of each step; and SB is the number of steps to reach maximal braking.

From the momentum-impulse theorem and a more general formulation for $F_{x(t)}$ (see above) it follows that

$$dp = I_{br} + I_{prop} = I_{br} + \int_{CT/2}^{CT} \left(-\text{amp} \sin\left(\frac{2\pi Fr}{DF}t\right) \right) dt,$$

where I_{prop} is the propulsive impulse during the second half of the each step; CT is the time the foot contacts the ground; and amp is the peak of the propulsive force. From this equation, 'amp' can be calculated, whereafter fore-aft force profiles can be deduced per step for a specific set of input values for m_{tot} , DF, Fr, SV and SB. The very first step is special in that no braking impulse is present and propulsion is delivered over the total time the limbs are extended. Taken together with the fact that vertical forces start from body weight instead of being zero at the beginning of the step (see above), the first step must be considered as a kind of leap.

(e) Angular displacement of the trunk

The moment of the GRF about the body-COM equals the rate of change of the sum of the local and remote terms of the angular momentum of the multi-segmented body. As head and tail are kept parallel to the ground surface it follows that

$$M_b dt = d(I_{tr}\dot{\alpha}) + d(m_{tr}r_{tr}^2\dot{\omega}_{tr}) + d(m_h r_h^2 \dot{\omega}_h) + d(m_t r_t^2 \dot{\omega}_t),$$

where M_b is the moment of GRF about the body-COM; I_{tr} is the moment of inertia of the trunk about its COM (local term); $m_{tr,h,t}$ is the mass of trunk, head and tail; $r_{tr,h,t}$ is the distance between COM of, respectively, trunk, head and tail and the body-COM; $\dot{\alpha}$ is the angular velocity of the trunk about its COM; and $\dot{\omega}_{tr,h,t}$ is the angular velocity of the COM of trunk, head and tail about the body-COM. From this equation, $\dot{\alpha}$ can be calculated and angular displacements of the trunk can be deduced.

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GLOSSARY

- body-COM: centre of mass of the body
 COM: centre of mass
 DF: duty factor
 GRF: ground reaction force