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## Criteria for dynamic similarity in bouncing gaits

Sharon R. Bullimore<sup>a,\*</sup>, J. Maxwell Donelan<sup>b</sup>

<sup>a</sup>Human Performance Lab, Faculty of Kinesiology, University of Calgary, 2500 University Drive NW, Calgary, AB, Canada T2N 1N4

<sup>b</sup>SFU Locomotion Laboratory, Simon Fraser University, Vancouver, BC, Canada V5A 1S6

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### Abstract

Animals of different sizes tend to move in a dynamically similar manner when travelling at speeds corresponding to equal values of a dimensionless parameter (DP) called the Froude number. Consequently, the Froude number has been widely used for defining equivalent speeds and predicting speeds of locomotion by extinct species and on other planets. However, experiments using simulated reduced gravity have demonstrated that equality of the Froude number does not guarantee dynamic similarity. This has cast doubt upon the usefulness of the Froude number in locomotion research. Here we use dimensional analysis of the planar spring–mass model, combined with Buckingham's Pi-Theorem, to demonstrate that four DPs must be equal for dynamic similarity in bouncing gaits such as trotting, hopping and bipedal running. This can be reduced to three DPs by applying the constraint of maintaining a constant average speed of locomotion. Sensitivity analysis indicates that all of these DPs are important for predicting dynamic similarity. We show that the reason humans do not run in a dynamically similar manner at equal Froude number in different levels of simulated reduced gravity is that dimensionless leg stiffness decreases as gravity increases. The reason that the Froude number can predict dynamic similarity in Earth gravity is that dimensionless leg stiffness and dimensionless vertical landing speed are both independent of size. In conclusion, although equal Froude number is not sufficient for dynamic similarity, it is a necessary condition. Therefore, to detect fundamental differences in locomotion, animals of different sizes should be compared at equal Froude number, so that they can be as close to dynamic similarity as possible. More generally, the concept of dynamic similarity provides a powerful framework within which similarities and differences in locomotion can be interpreted.

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**Keywords:** Locomotion; Froude number; Running; Dimensional analysis; Dimensionless

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### 1. Introduction

The 'dynamic similarity hypothesis' (Alexander, 1976; Alexander and Jayes, 1983) is one of the most general theories of terrestrial locomotion. It proposes that animals of different sizes use the same patterns of locomotion when travelling at speeds corresponding to equal values of the 'Froude number' ( $u^2/gl_{leg}$ , where  $u$  is forward speed,  $g$  is gravitational acceleration and  $l_{leg}$  is leg length). So, while a horse and a small dog are expected to move in a very different manner when travelling at the same

absolute speed, the dynamic similarity hypothesis predicts that, when travelling at the same Froude number, they will use, for example, the same sequence and relative timing of footfalls, the same ground reaction force relative to body weight, the same stride length relative to leg length and the same duty factor (stance time divided by stride time).

Empirical evidence indicates that the dynamic similarity hypothesis provides good predictions of basic locomotor parameters across a wide range of species of different sizes, particularly within groups of animals that are anatomically similar (Alexander, 1976; Alexander and Jayes, 1983; Blickhan and Full, 1993; Bullimore and Burn, 2006a; Farley et al., 1993). It has proven to be a powerful tool in locomotion research and has been widely used for comparing humans, animals and robots of different sizes, for separating the effects of size from the influence of other

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\*Corresponding author. Meakins-Christie Labs, 3626 rue St-Urbain, Montreal, QC, Canada H2X 2P2. Tel.: +1 514 398 3864x00128; fax: +1 514 398 7483.

E-mail addresses: [sharonbullimore@yahoo.com](mailto:sharonbullimore@yahoo.com) (S.R. Bullimore), [mdonelan@sfu.ca](mailto:mdonelan@sfu.ca) (J.M. Donelan).

factors and for predicting speeds of locomotion in extinct species and on other planets (reviewed by Vaughan and O'Malley, 2005).

However, Donelan and Kram (1997, 2000) demonstrated that equality of the Froude number does not guarantee dynamic similarity in either walking or running. They studied humans moving at equal Froude numbers, but at different combinations of speed and simulated reduced gravity, and found large deviations from dynamic similarity. Because the same subjects were used in each gravity condition, these deviations could not be explained by anatomical differences. This raises a number of important questions: Should the Froude number be used to define equivalent speeds for animals of different sizes? Is it valid to make predictions by assuming that locomotion will be dynamically similar at equal Froude number? Why does the Froude number predict dynamic similarity in Earth gravity, but not in simulated reduced gravity? Alexander (1989) argued that the Strouhal number, in addition to the Froude number, must be equal for dynamic similarity in running, but are these two criteria sufficient to guarantee dynamic similarity? Here we identify the criteria that must be met to ensure that bouncing gaits, such as trotting, hopping and bipedal running, will be dynamically similar. This provides a theoretical basis for predicting when the dynamic similarity hypothesis is likely to be correct, and therefore allows us to address the above questions.

The concept of dynamic similarity is much more general than the dynamic similarity hypothesis of Alexander and Jayes, and is widely used in engineering and physics. It is an extension of the more familiar concept of geometric similarity. Two geometrically similar objects are the same shape—i.e. one could be made identical to the other by multiplying all linear dimensions by a constant scale factor. For example, two equilateral triangles of any size are geometrically similar, while an equilateral and an isosceles triangle are not. Completely dynamically similar systems are geometrically similar and are also similar in terms of force and time. Therefore, if two systems are moving in a completely dynamically similar manner, the motion of one can be made identical to the motion of the other by multiplying all lengths by one scale factor, all forces by a another scale factor and all time periods by a third scale factor (Duncan, 1953).

It is often convenient to define dynamic similarity in terms of dimensionless parameters (DPs), rather than scale factors. A DP is a combination of parameters in which the units of measurement cancel out. Examples relevant to animal locomotion include stride length divided by leg length ('relative stride length') and the Froude number. A direct consequence of the scale factor definition of dynamic similarity given above is that completely dynamically similar systems have equal values of any DP that can be formed from mechanical parameters (the reasoning behind this is given in Appendix A). However, like complete geometric similarity, complete dynamic similarity is a theoretical idealisation. For practical purposes, dynamic

similarity is usually defined in terms of equality of a small number of DPs that describe the aspects of the system that are of interest. The DPs that have been used to assess whether locomotion is dynamically similar include: duty factor, relative stride length, relative peak force (the ratio of peak vertical ground reaction force to body weight), dimensionless leg stiffness and the phase relationships of the limbs (Alexander and Jayes, 1983; Blickhan and Full, 1993; Donelan and Kram, 2000; Farley et al., 1993). Although these represent only a small subset of the DPs that could be used, they provide a good description of the overall dynamics of locomotion and incorporate lengths, forces and times, the three types of measurement that comprise the definition of dynamic similarity.

Criteria for dynamic similarity can be obtained using the method of 'dimensional analysis' (Isaacson and Isaacson, 1975). This is the approach that we employ here and is described in detail in the next section. Before we could use dimensional analysis, we first needed to identify the parameters that are important in governing the dynamics of locomotion. This is problematic for a complex system, such as a moving animal, because an infinite number of parameters could potentially be used to describe the system. We solved this problem by utilising a mathematical model—a simplified representation of locomotion with only a few parameters. In general, if a model provides good predictions of the aspects of a system that are of interest, then dimensional analysis of its parameters can be used to obtain criteria for dynamic similarity.

The model that we used was the planar spring–mass model (Blickhan, 1989a; McMahon and Cheng, 1990). This model consists of a point mass bouncing on a massless, linear spring (Fig. 1). The mass represents the position of the centre of mass of the animal and the spring represents the combined effect of all limbs in contact with the ground at one time. This 'spring–mass system' alternates between ground contact phases, during which it rotates forwards about a single point of contact, and aerial phases, during which it moves ballistically. Because the model has only seven parameters and provides good predictions of basic locomotor dynamics (Blickhan, 1989a; Bullimore and Burn, 2007; Farley et al., 1993; He et al., 1991), it is suitable for defining criteria for dynamic similarity.

Blickhan (1989b) and Blickhan and Full (1993) used a dimensionless formulation of the parameters of the spring–mass model to define criteria for dynamic similarity and to compare different gaits and animals of different sizes. However, they did not formally determine the number of criteria required to predict dynamic similarity and their results have not been applied to resolving the issue of why the Froude number is able to predict dynamic similarity only under some circumstances. Here we build upon their work by: (i) using Buckingham's Pi-Theorem to demonstrate that equality of four DPs is required to ensure dynamic similarity in the spring–mass model; (ii) showing that this can be reduced to three DPs by applying the constraint of maintaining a constant average speed of

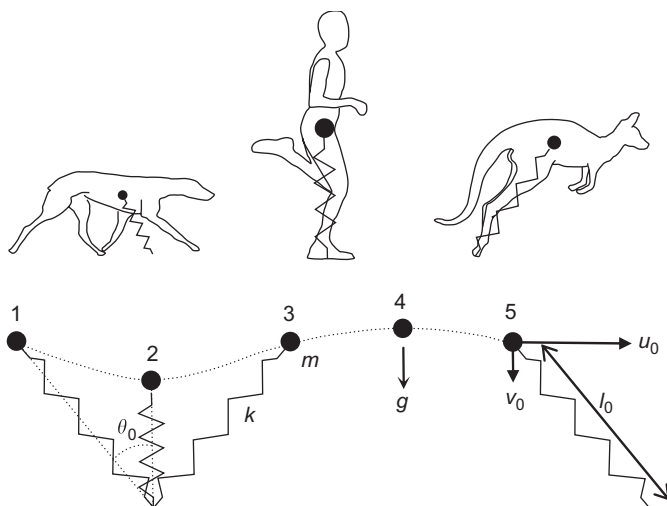


Fig. 1. Top: planar spring–mass model representing trotting, bipedal running and hopping. The point mass corresponds to the centre of mass of the animal and the massless, linearly elastic spring extends between the centre of mass and the centre of pressure and represents the action of all limbs that are in contact with the ground at one time. Bottom: spring–mass system modelling one complete step of locomotion.  $m$  is mass and  $k$  is spring stiffness. The system lands at an angle,  $\theta_0$ , to the vertical, with the spring at its natural length,  $l_0$  (1 and 5). The horizontal speed of the mass at landing is  $u_0$  and the vertical speed is  $v_0$ . The system rotates forwards throughout the stance phase, compressing until midstance (2) and then extending to return to its initial length at takeoff (3). During the aerial phase (4), the mass moves ballistically and its vertical acceleration is equal to gravitational acceleration, with magnitude  $g$ . The system lands with the same initial conditions at the start of the next step (5).

locomotion; (iii) using sensitivity analysis to assess the relative importance of each of the DPs for predicting dynamic similarity across a physiologically relevant parameter space, and (iv) demonstrating why humans do not move in a dynamically similar manner when running at equal Froude number in different levels of simulated reduced gravity, using the data of Donelan and Kram (2000). The paper is divided into three sections. The first section describes dimensional analysis of the planar spring–mass model and the use of Buckingham’s Pi-Theorem to determine the minimum number of criteria required to predict dynamic similarity. The second section presents the methods and results of the sensitivity analysis. The third section presents the reanalysis of the simulated reduced gravity data of Donelan and Kram (2000).

## 2. Dimensional analysis

The method of dimensional analysis, and the principles behind it, are explained in detail by Isaacson and Isaacson (1975) and, with reference to applications in biology, by McMahon and Bonner (1983). Dimensional analysis can be used to obtain criteria for dynamic similarity by the following process: (i) identify appropriate parameters to use in the analysis; (ii) use Buckingham’s Pi-Theorem to determine how many DPs should be formed from these parameters; (iii) derive an appropriate set of DPs. If two

Table 1

Dimensions of the parameters of the planar spring–mass model in terms of the reference dimensions: force ( $F$ ), length ( $L$ ) and time ( $T$ )<sup>a</sup>

Parameter	Dimensions
Mass ( $m$ )	$FL^{-1}T^2$
Spring stiffness ( $k$ )	$FL^{-1}$
Spring natural length ( $l_0$ )	$L$
Acceleration due to gravity ( $g$ )	$LT^{-2}$
Vertical landing speed ( $v_0$ )	$LT^{-1}$
Horizontal landing speed ( $u_0$ )	$LT^{-1}$
Landing angle ( $\theta_0$ )	Dimensionless

<sup>a</sup>Alternatively mass, length and time could have been used as reference dimensions. This would not have altered our conclusions. We chose to use force, length and time for consistency with Alexander and Jayes (1983).

systems have equal values of these DPs, then they will be dynamically similar (assuming a good choice of parameters was made in step (i)). The reason that these DPs constitute criteria for dynamic similarity is explained in Appendix B.

The planar spring–mass model has seven parameters (Fig. 1): mass ( $m$ ), spring stiffness ( $k$ ), spring natural length ( $l_0$ ), the magnitude of the acceleration due to gravity ( $g$ ), vertical landing speed ( $v_0$ ), horizontal landing speed ( $u_0$ ) and the landing angle of the spring relative to the vertical ( $\theta_0$ ). Buckingham’s Pi-Theorem tells us that a system with  $n$  parameters, that can be defined using  $r$  reference dimensions, can be described using  $n-r$  DPs. A ‘reference dimension’ is a physical quantity that can be used to define other physical quantities. For example, velocity can be defined in terms of the reference dimensions length and time. All the parameters of the spring–mass model can be defined in terms of three reference dimensions: force, length and time (Table 1). Because we have seven parameters, and three reference dimensions, Buckingham’s Pi-Theorem tells us that we need to form four DPs. These DPs must be independent, meaning that none of them can be formed by combining the others.

There are various ways in which the model parameters could be combined into four DPs. We use the DPs of McMahon and Cheng (1990), but an alternative formulation was used by Blickhan (1989a, b) and Blickhan and Full (1993). The DPs we use are: dimensionless spring stiffness ( $K$ ), dimensionless horizontal landing speed ( $U_0$ ), dimensionless vertical landing speed ( $V_0$ ) and the angle of the spring at landing ( $\theta_0$ ). These DPs are defined in Table 2. Although  $U_0$  and  $V_0$  are also Froude numbers, for the sake of clarity and consistency we reserved the term ‘Froude number’ for the Froude number used by Alexander and Jayes (1983). This Froude number is approximately equal to  $U_0$  squared, but uses average forward speed, instead of horizontal landing speed, which is slightly higher than average speed.

From Table 1 it can be seen that these DPs are dimensionless, i.e. the units of measurement cancel out. It can also be seen that they are independent because each of them contains at least one-dimensional parameter that is



Table 2  
Dimensionless parameters that were used as criteria for dynamic similarity in the planar spring–mass model

Name	Symbol	Equation <sup>a</sup>
Dimensionless spring stiffness	$K$	$kl_0/mg$
Dimensionless horizontal landing speed	$U_0$	$u_0/\sqrt{gl_0}$
Dimensionless vertical landing speed	$V_0$	$v_0/\sqrt{gl_0}$
Landing angle	$\theta_0$	$\theta_0$

<sup>a</sup>Dimensional parameters:  $k$  = spring stiffness,  $l_0$  = spring natural length,  $m$  = mass,  $g$  = acceleration due to gravity,  $v_0$  = vertical landing speed, and  $u_0$  = horizontal landing speed.

not present in any of the others. One advantage of this choice of DPs is that it separates the properties of the system ( $K$ ) from the initial conditions with which it is loaded ( $U_0$ ,  $V_0$ ,  $\theta_0$ ). Spring–mass models with equal values of these DPs will be completely dynamically similar. Animals that are performing gaits that can be modelled by the spring–mass model, and that have equal values of these DPs, will approach dynamic similarity in all aspects of locomotion that are well-predicted by this model.

In order to model locomotion at a constant average speed, a spring–mass model has to bounce symmetrically, with landing and takeoff angles of equal magnitude. If it does not do this, then it cannot generate equal braking and propulsive impulses and so cannot maintain constant speed. To achieve this symmetry in a model simulation, the values of three of the DPs are selected, and then the value of the fourth DP is varied until a symmetrical bounce is obtained (Blickhan, 1989a; McMahon and Cheng, 1990). Applying this constraint therefore means that one of the DPs is no longer independent of the others, and allows us to reduce the number of DPs required for predicting dynamic similarity in constant speed locomotion to three. Any three of the four DPs can be used (although, in practice, allowing  $V_0$  to vary does not work well because the  $\theta_0$  required for a given combination of  $K$  and  $U_0$  is insensitive to the value of  $V_0$ ). In the next section, we prescribe  $K$ ,  $U_0$  and  $V_0$  and vary  $\theta_0$  to obtain a symmetrical bounce. We chose to do this because it has been found that animals tend to keep  $K$  and  $V_0$  constant and to vary  $\theta_0$  as they change speed (Farley et al., 1993; He et al., 1991).

### 3. Sensitivity analysis

In the previous section, we identified four DPs that must be equal for bouncing gaits to be dynamically similar. It is also essential to know the relative importance of these DPs as criteria for dynamic similarity. For example, if one DP is 10 times less influential than the others under physiological conditions, then it would be reasonable to ignore it in most situations. Alternatively, if one DP is twice as influential as the others, smaller differences in this DP would be sufficient to cause detectable differences in locomotion. We address this issue by using sensitivity analysis to

determine the extent to which differences in  $K$ ,  $U_0$  and  $V_0$  (the ‘input DPs’) affect the values of duty factor, relative stride length and relative peak force (the ‘output DPs’) predicted by the planar spring–mass model. We chose these output DPs because they are often used to assess whether locomotion is dynamically similar.

#### 3.1. Methods

Thirty different values of each input DP were used, giving 27,000 combinations of input DPs. Each input DP was increased from its initial value in 29 increments of 5%. We conducted the analysis over a parameter space corresponding approximately to the ranges of the input DPs that have been reported in the literature. Values of  $K$  between 7.1 and 27.2 have been reported by Blickhan and Full (1993), while a  $K$  of approximately 45 was used by humans running in simulated reduced gravity (calculated from He et al., 1991). The walk–trot transition typically occurs at a Froude number of about 0.6 (Alexander and Jayes, 1983), corresponding to a  $U_0$  of 0.77, and the walk–run transition in humans in normal and simulated reduced gravity occurs at a Froude number of approximately 0.5 (Kram et al., 1997), corresponding to a  $U_0$  of 0.71. A human running 100 m in 10 s has a  $U_0$  of about 3.16. Blickhan (1989b) reported values for  $\beta$ , the angle of the velocity vector to the horizontal at landing, of  $6.66 \pm 0.7^\circ$  (SE) for runners and  $15.97 \pm 1.7^\circ$  for hoppers. We varied  $K$  between 10 and 41.2,  $U_0$  between 0.7 and 2.88 and  $V_0$  between 0.1 and 0.412 (giving  $\beta$  between  $2.0^\circ$  and  $30.5^\circ$ ). Because the highest value of each input DP was always equal to the initial value multiplied by  $(1.05)^{29}$ , we had to use ranges of  $K$  and  $U_0$  that were slightly smaller than the ranges reported in the literature in order to avoid using highly nonphysiological values of  $\beta$ .

For each combination of input DPs, a spring–mass model solution was obtained by integrating the dimensionless equations of motion (McMahon and Cheng, 1990) between the times of landing and takeoff (defined as when the spring returned to its natural length) using a Runge–Kutta algorithm (‘ode45’, Matlab version 6.5, The MathWorks, Inc., MA, USA). A value for  $\theta_0$  that gave a symmetrical bounce was obtained using an optimisation algorithm based on a golden section search and parabolic interpolation (‘fminbnd’, Matlab) to search for solutions between 0 and 1.2 rad that corresponded to a minimum in the difference between the magnitudes of the landing and takeoff angles. The maximum step size for the integrations was set to 0.01 s. Reducing the step size further had no effect on the first six decimal places of the calculated output DPs in several test simulations. Values of  $\theta_0$  that gave a symmetrical bounce were found for all 27,000 combinations of input DPs. The required angles varied between 0.18 and 0.86 rad and gave takeoff angles that were always within  $10^{-5}$  rad of landing angle.

Dimensionless aerial time ( $T_A$ ) was calculated as  $2V_0$  and dimensionless distance travelled during the aerial phase

( $L_A$ ) was calculated as  $2V_0U_0$  (Appendix C). The output DPs were calculated as:

$$\begin{aligned} \text{duty factor} &= T_C/2(T_C + T_A), \\ \text{relative stride length} &= 2(L_A + L_C), \\ \text{relative peak force} &= K\Delta L, \end{aligned}$$

where  $T_C$ ,  $L_C$  and  $\Delta L$  are the dimensionless contact time, horizontal distance travelled during ground contact and peak spring compression, respectively.

The sensitivity of output DP  $A$  to input DP  $X$  at the values of the input DPs  $X_i$ ,  $Y_j$ ,  $Z_k$  was calculated as follows:

$$\text{sensitivity of } A \text{ to } X = \left| \frac{A(X_{i+1}, Y_j, Z_k) - A(X_i, Y_j, Z_k)}{0.05 \cdot A(X_i, Y_j, Z_k)} \right|,$$

i.e. sensitivity was the absolute value of the ratio of the proportional change in the output DP to the proportional change in the input DP. The proportional change in input DP was always 0.05 because the input DPs were increased in 5% increments. A sensitivity of 1.0 indicates that a 5% change in the input DP caused a 5% change in the output DP.

### 3.2. Results

Over the parameter space used, duty factor varied between 0.14 and 0.43, relative stride length varied between 1.09 and 7.79 and relative peak force varied between 1.92 and 5.82. All sensitivity values were less than 1.0 (Fig. 2), indicating that the proportional change in the output DP was always less than the proportional change in the input DP. Sensitivity varied substantially across the parameter space, with the sensitivity of relative stride length to  $V_0$  having the greatest range (0.11–0.77).

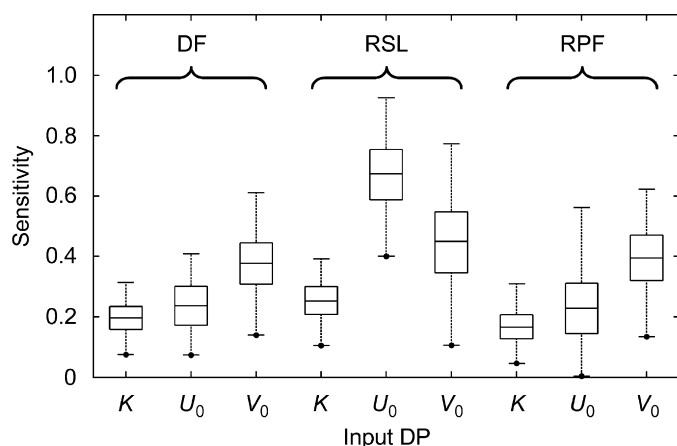


Fig. 2. Sensitivity of duty factor (DF), relative stride length (RSL) and relative peak force (RPF) to changes in the three 'input' DPs ( $K$ ,  $U_0$  and  $V_0$ ). Each boxplot describes the distribution of sensitivity values over a physiologically relevant parameter space. Boxes indicate interquartile range, the central bar indicates median, and the whiskers indicate range. All sensitivity values were less than 1.0 indicating that the output DP always changed proportionally less than the input DP.

Table 3

Sensitivity of relative stride length to  $K$ ,  $U_0$  and  $V_0$  at combinations of input DPs representative of running, trotting and hopping

	Sensitivity to		
	$K$	$U_0$	$V_0$
Human running at 3 m/s in $1g^a$ ( $K = 14.8$ , $U_0 = 0.98$ , $V_0 = 0.23$ )	0.29	0.68	0.35
Human running at 3 m/s in $0.2g^a$ ( $K = 39.2$ , $U_0 = 2.15$ , $V_0 = 0.25$ )	0.16	0.76	0.65
Human running at 8.1 m/s in $1g^b$ ( $K = 27.9$ , $U_0 = 2.49$ , $V_0 = 0.25$ )	0.16	0.73	0.65
Dog trotting at 2.8 m/s in $1g^c$ ( $K = 12.8$ , $U_0 = 1.26$ , $V_0 = 0.15$ )	0.32	0.53	0.30
Kangaroo hopping at 3.8 m/s in $1g^{c,d}$ ( $K = 10.0$ , $U_0 = 1.60$ , $V_0 = 0.39$ )	0.20	0.72	0.54

$g$  = Earth gravity.

Input DPs based on:

<sup>a</sup>He et al. (1991).

<sup>b</sup>Morin et al. (2006).

<sup>c</sup>Farley et al. (1993).

<sup>d</sup>Blickhan (1989b).

Comparison of the sensitivity of the output DPs to each of the input DPs was used to assess the relative importance of each of the input DPs as criteria for dynamic similarity—i.e. if the output DPs were less sensitive to one of the input DPs than to the others, that input DP was considered less important as a criterion for dynamic similarity. The relative importance of the input DPs varied substantially across the parameter space. Examples of the sensitivity of relative stride length to each of the three input DPs are shown in Table 3 for points in the parameter space representative of different modes of locomotion. This shows that, for a human running at 3 m/s in normal gravity, relative stride length is twice as sensitive to  $U_0$  as to  $K$  or  $V_0$ . Running at a simulated reduced gravity level of 20% of normal gravity or sprinting at 8.1 m/s takes the runner to a point in the parameter space where relative stride length is approximately four times as sensitive to  $U_0$  and  $V_0$  as to  $K$ . In these latter situations,  $K$  could vary four times as much as the other DPs before a measurable difference in relative stride length would be observed.

In general, the output DPs were less sensitive to  $K$  than to  $U_0$  or  $V_0$ , indicating that equality of  $K$  was usually the least important of the three criteria. Duty factor was least sensitive to  $K$  over 74% of the parameter space, relative stride length was least sensitive to  $K$  over 80% of the parameter space and relative peak force was least sensitive to  $K$  over 69% of the parameter space. On average, duty factor and relative peak force were most sensitive to  $V_0$  and relative stride length was most sensitive to  $U_0$ . Over more than 99.8% of the parameter space, however, sensitivity to each of the input DPs was within the same order of magnitude (i.e. the ratios of the sensitivities were between

0.1 and 10), indicating that none of the input DPs can be neglected as criteria for dynamic similarity.

Relative stride length was typically the most sensitive of the output DPs. It was the most sensitive to  $K$  over 71% of the parameter space, the most sensitive to  $U_0$  over 100% of the parameter space and the most sensitive to  $V_0$  over 73% of the parameter space.

#### 4. Simulated reduced gravity data

Our aim in this section was to determine why humans do not move in a dynamically similar manner when travelling at equal Froude number under different levels of simulated reduced gravity. The spring–mass model is a good model of running in simulated reduced gravity as well as in normal gravity (Bullimore and Burn, 2007), so the dynamic similarity criteria derived above also apply here. According to these criteria, deviations from dynamic similarity must be due to differences in one or more of  $K$ ,  $U_0$  or  $V_0$ . Here we are considering comparisons made at equal Froude number (and therefore equal  $U_0$ ), so  $K$  and/or  $V_0$  must be different.

To determine how  $K$  and  $V_0$  varied with gravity level, we reanalysed the data collected by Donelan and Kram (2000). They used 10 human subjects who ran on a force-measuring treadmill while reduced gravity was simulated by applying a constant upward force to the torso via a modified rock-climbing harness. Here, we use a subset of their data in which the subjects ran at four different Froude numbers and four different simulated gravity levels, to give a total of 160 trials. We calculated mean values of  $K$  and  $V_0$  for each trial and used regression analysis to determine the relationships of  $K$  and  $V_0$  to gravity level at each Froude number. We considered  $p \leq 0.05$  to be statistically significant.

$K$  decreased significantly as gravity increased so that, at 1.0g (where  $g$  indicates Earth gravity),  $K$  was about 50% of the value at 0.25g (Fig. 3). Unfortunately, it was not

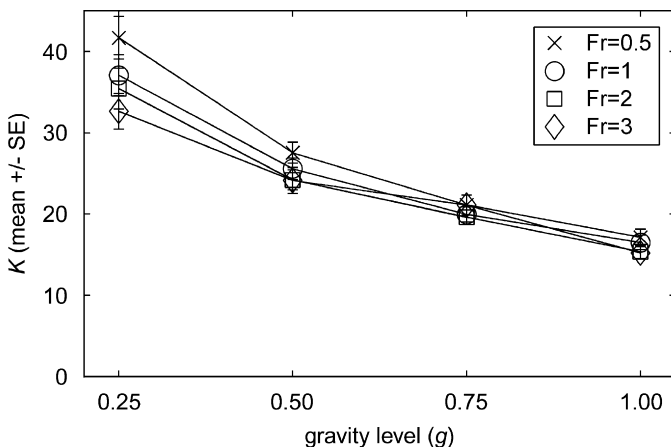


Fig. 3. Relationship of dimensionless spring stiffness ( $K$ ) to gravity level (multiples of Earth gravity,  $g$ ) for humans running in simulated reduced gravity at four different Froude numbers ( $Fr$ ).

possible to draw a definite conclusion as to whether  $V_0$  changed with gravity level. The data obtained from the force treadmill were noisier than the data typically obtained using force plates embedded in the ground and this made it difficult to detect the precise moment of ground contact. Because vertical velocity is changing rapidly at the time of ground contact, this had a large influence on the calculated landing velocity. We found that different methods of detecting ground contact led to different conclusions. When ground contact was detected by taking the time of the last minimum occurring in the force trace before peak force,  $V_0$  did not change significantly with gravity level. When ground contact was detected by linear extrapolation of the lower part of the force trace to zero force,  $V_0$  increased significantly with gravity level, except at a Froude number of 0.5 where the increase was not significant ( $p = 0.09$ ). Therefore, we conclude that the deviations from dynamic similarity at equal Froude number in simulated reduced gravity are due to changes in  $K$  with gravity level, and that further work would be needed to determine whether they are also due to changes in  $V_0$ .

#### 5. Discussion

##### 5.1. Criteria for dynamic similarity in bouncing gaits

We have shown that four DPs must be equal to ensure dynamic similarity in trotting, hopping and bipedal running and that this can be reduced to three DPs by applying the constraint of maintaining a constant average speed of locomotion. Several choices of these three DPs are possible and these need not necessarily include a Froude number. However, if the chosen DPs are independent, equality of those DPs will result in equality of the Froude number. Therefore, equal Froude number is a necessary, but not sufficient, condition for dynamic similarity in bouncing gaits.

The analysis presented here applies only to bouncing gaits, so our conclusions cannot be applied directly to walking. However, limb compression also has a significant influence on the mechanics of walking (Alexander, 1992; Lee and Farley, 1998) so a dimensional analysis of the parameters that govern walking dynamics would have to include a parameter which describes limb compression and would therefore yield at least one DP in addition to the Froude number. Furthermore, minimising metabolic cost in walking depends upon the active swinging of the legs, suggesting that a dimensionless hip stiffness may also be required (Doke et al., 2005). Therefore, the Froude number will also not be sufficient to predict dynamic similarity in walking. Geyer et al. (2006) presented a bipedal spring–mass model which is equivalent to the current model when it is used to represent running, but is also able to model walking. They described the model using three independent DPs: (in our notation)  $K$ , angle of attack ( $\pi/2 - \theta_0$ ) and dimensionless system energy. Before this model could be

used to define criteria for dynamic similarity in walking it would be necessary to establish that: (a) there is a unique solution to the model for any given set of values of the three DPs, at least within the physiological range; (b) the model is able to provide good predictions of experimentally measured walking dynamics. If these conditions were satisfied then these three DPs could be used as criteria for dynamic similarity in both walking and running.

The fact that the Froude number is successful in predicting dynamic similarity in animals of different sizes moving in Earth gravity implies that both  $K$  and  $V_0$  are independent of body mass. This is supported by the following analysis of the results of Farley et al. (1993) who used the spring–mass model to describe quadrupeds of a wide range of different sizes trotting at approximately equal Froude number. They found that  $k$  was proportional to  $m^{0.67}$  (where  $m$  is body mass) and  $l_0$  was proportional to  $m^{0.34}$ . Although they did not calculate it, this equates to  $K$  proportional to  $m^{0.01}$  ( $kl_0/mg \propto m^{0.67}m^{0.34}/m^1m^0 = m^{0.01}$ ). Stance time was proportional to  $m^{0.19}$  and duty factor was independent of size, so aerial time would also have been proportional to  $m^{0.19}$ . Approximating  $v_0$  as proportional to aerial time, which is exact only if the aerial phase is symmetrical (Appendix C), yields  $V_0$  proportional to  $m^{0.02}$  ( $v_0/\sqrt{gl_0} \propto m^{0.19}/(m^0m^{0.34})^{0.5} = m^{0.02}$ ). Therefore, both  $K$  and  $V_0$  were almost independent of size, explaining the utility of the Froude number at Earth gravity. Blickhan and Full (1993) also found  $K$  to be independent of size when they estimated it for various species of animals using scaling relationships from the literature. Conversely, we have shown that the reason that the Froude number does not predict dynamic similarity in simulated reduced gravity is that  $K$  is not independent of gravity level (Fig. 3). For (dimensionless)  $K$  to be independent of gravity level, the properties of the leg would have to be adjusted such that (dimensional)  $k$  in the model decreased in proportion to gravity—i.e.  $k$  would have to be a quarter of its normal value at  $0.25g$ . Although  $k$  did decrease with gravity, it did not change sufficiently to maintain dynamic similarity.

An important remaining question is why locomotion has evolved to be dynamically similar in animals travelling at equal Froude number; i.e. why  $K$  and  $V_0$  are independent of size. This is particularly significant because size-independence of  $K$  is not expected in geometrically similar animals with the same musculoskeletal tissue properties (Bullimore and Burn, 2004). One possible reason is that, because the Froude number is a ratio of inertial to gravitational forces, it provides an index of the mechanical environment in which the animal is moving. It seems likely that the optimal locomotor pattern for a given mechanical environment is independent of animal size. Therefore, dynamic similarity may be indicative of mechanical optimisation, as proposed by Alexander and Jayes (1983) and Alexander (1989).

An alternative approach to deriving criteria for dynamic similarity is to use ratios of forces that are known to have a significant influence on the system (Isaacson and Isaacson,

1975). The Froude number can be viewed as the ratio of inertial to gravitational force and  $K$  is the ratio of maximum spring force to body weight. Alexander (1989) used this approach to argue that both the Froude number and another dimensionless number, the Strouhal number, must be equal for dynamic similarity in running. The difficulty with this approach, however, is that it does not tell us how many DPs are required and does not help us to obtain DPs, such as  $\theta_0$ , that are not ratios of forces. In fact, spring–mass models with equal Froude and Strouhal numbers (or equal  $U_0$  and  $K$ ) can still move in manner that is far from dynamically similar if they have different values of  $V_0$  and  $\theta_0$  (Fig. 4). It should be noted, however, that Alexander (1989) did not state that equal Froude and Strouhal number are sufficient for dynamic similarity, only that they are necessary.

The dimensional analysis described here used all the parameters of the planar spring–mass model. Therefore, spring–mass models with equal values of  $K$ ,  $U_0$ ,  $V_0$  and  $\theta_0$  will be completely dynamically similar—i.e. they will have equal values of any other DP that could be used to describe them. However, the parameters of the spring–mass model constitute only a small fraction of the parameters that could be used to describe a moving animal. Therefore, these four DPs are criteria for dynamic similarity only in aspects of locomotion that are well predicted by the spring–mass model. Aspects of locomotion that are not well-predicted (such as horizontal forces, Bullimore and Burn, 2006b, 2007), or are not predicted at all (such as joint angles and tendon strains) could deviate substantially from

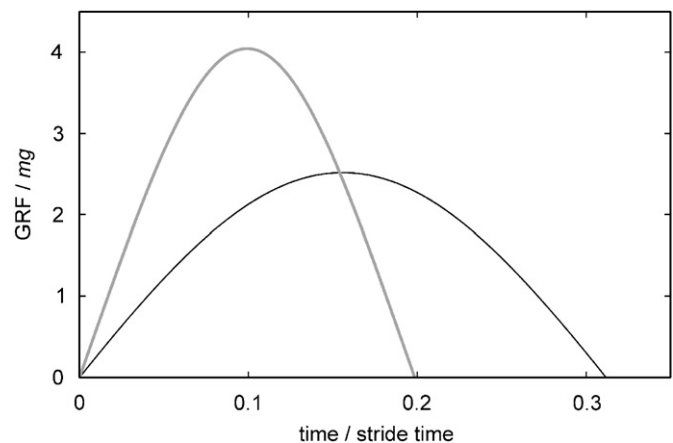


Fig. 4. Equality of two DPs is not sufficient to guarantee dynamic similarity. Ground reaction force (GRF) traces predicted by two spring–mass simulations with equal values of  $K$  and  $U_0$ . Simulation 1 (black line):  $K = 20$ ,  $U_0 = 2.8$ ,  $V_0 = 0.1$ . Simulation 2 (grey line):  $K = 20$ ,  $U_0 = 2.8$ ,  $V_0 = 0.3$ . For the spring–mass model, Strouhal number can be defined as  $\sqrt{k/m}(l_0/u_0)$  and Froude number as  $u_0^2/gl_0$ . Therefore, the two simulations also have equal Strouhal and Froude numbers because Strouhal number is  $\sqrt{K}/U_0$  and Froude number is  $U_0^2$ . GRF is shown relative to body weight ( $mg$ ) and time is shown relative to stride time so that the differences in relative peak force and duty factor are apparent. Relative stride length was 2.96 in simulation 1 and 5.52 in simulation 2. The differences in duty factor, relative stride length and relative peak force indicate that the two simulations are not dynamically similar.



dynamic similarity. In fact, some parameters must deviate from dynamic similarity in order to allow  $K$  to be equal in animals of different sizes (Bullimore and Burn, 2004). Therefore,  $K$ ,  $U_0$ ,  $V_0$  and  $\theta_0$  can be seen as criteria for 'partial dynamic similarity' in bouncing gaits.

### 5.2. Sensitivity analysis

The sensitivity analysis showed that the relative importance of  $K$ ,  $U_0$  and  $V_0$  as criteria for dynamic similarity varied greatly across the parameter space. This is important to take into account in experimental studies. Deviations from dynamic similarity will depend upon both the magnitudes of differences in  $K$ ,  $U_0$  and  $V_0$  and the sensitivity to these differences. This could mean, for example, that two animals appear dynamically similar at one Froude number, but not at another. In general, locomotion was least sensitive to  $K$  (sensitivity was always  $<0.4$ ), indicating that proportionally larger differences in  $K$  could occur without observable deviations from dynamically similar locomotion.

Relative stride length was typically the most sensitive of the output DPs. This may explain why Alexander and Jayes (1983) found greater differences in relative stride length than in duty factor when comparing quadrupeds of different sizes. This indicates that relative stride length is a useful DP to measure in order to determine whether deviations from dynamic similarity occur.

Over the parameter space that was used, sensitivity of duty factor, relative stride length and relative peak force to  $K$ ,  $U_0$  and  $V_0$  was always less than 1—i.e. the model outputs always changed proportionally less than the model inputs. This low sensitivity may be advantageous in that it would make locomotion more predictable and easier to control. For example, a sudden change in ground surface properties (which could be viewed as a change in  $K$ ) would cause only relatively small alterations in locomotor dynamics.

Sensitivity analysis was used here to assess the relative importance of the DPs as criteria for dynamic similarity, but it could also provide useful insight for answering other questions about locomotion. In general, any study into the effects of a perturbation on locomotion should be conducted at speeds of locomotion where sensitivity is high, so that the effects of the perturbation are maximised. The variation in sensitivity over the parameter space raises several interesting questions, such as: Do animals preferentially use low sensitivity regions of the parameter space when travelling over rough ground? Do gait transitions occur in regions of high sensitivity? Do animals use different control strategies in regions of high sensitivity? Is manoeuvrability greater in regions of high sensitivity?

### 5.3. Role of the concept of dynamic similarity in locomotion research

Empirically, it seems that the approach of comparing dimensionless locomotor parameters in animals moving at

equal Froude number is often successful in removing the effects of size, because  $K$  and  $V_0$  tend to be size-independent. From a theoretical viewpoint, however, there is no guarantee that locomotion will always be dynamically similar at equal Froude number. Therefore, caution needs to be exercised when using the concept of dynamic similarity to account for the effects of size on locomotion or to predict locomotor dynamics in extinct species. When this approach is used to account for size differences in experimental studies, *post hoc* analysis can be used to determine whether it has been successful. For example, in a study comparing adults and children, adults of a wide range of different sizes should be included. If dimensionless locomotor parameters are independent of size at equal Froude number in the adult subjects, this indicates that the approach has been successful in removing size effects and that remaining differences between adults and children can be attributed to other aspects of the maturation process.

If, as discussed above, dynamically similar locomotion arises because the optimal mechanical solution is size-independent, then dynamic similarity would not be expected when comparing animals in environments for which they are not adapted, such as simulated reduced gravity. Deviations from dynamically similar locomotion would also be expected to become greater as differences in anatomy, selection pressures and lifestyle increase. For example, a hopping kangaroo protracts its limbs during the aerial phase, while a running biped protracts each limb during the stance phase of the contralateral limb. Therefore, it is unlikely that these two animals would have the same optimal duty factor at the same Froude number. Similarly an animal whose legs had a high moment of inertia would be expected to have a lower optimal stride frequency than an animal with slender legs.

Dynamically similar locomotion also becomes less likely as size differences increase, because the dynamic similarity criteria become progressively less likely to be met. For example, larger mammals have more upright limbs and proportionally larger muscle moment arms (Biewener, 1989, 1990) and this plays an important role in maintaining the size-independence of  $K$  (Bullimore and Burn, 2004). However, there must be a limit to the size range over which this can occur. For example, to maintain the scaling measured by Biewener (1989), a 6000 kg *Tyrannosaurus* would have to have muscle moment arms that were 2.7 times longer than its ground reaction force moment arms, which seems unlikely. Therefore, it is probable that very large extinct species had lower values of  $K$  than extant species. If they ran in a manner that could be modelled by the spring–mass model, speeds predicted from stride length by assuming dynamic similarity with extant mammals are likely to be substantially overestimated (Fig. 5).

The concept of dynamic similarity can play another role in locomotion research, which does not rely upon whether or not locomotion is dynamically similar at equal Froude number. It provides a theoretical framework within which similarities and differences in locomotion can be

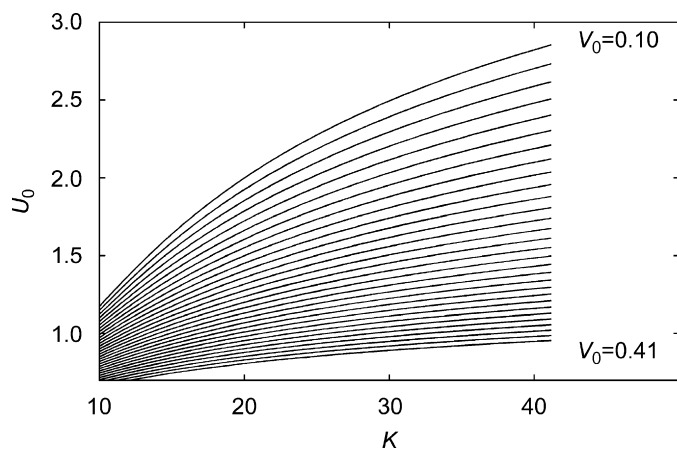


Fig. 5. Many different combinations of  $K$ ,  $U_0$  and  $V_0$  can give the same relative stride length in the spring–mass model. Each line shows combinations of  $K$  and  $U_0$  that give a relative stride length of 2.5 for a given value of  $V_0$ .  $V_0$  increases from 0.10 to 0.41 in the direction of decreasing  $U_0$ . If  $K$  were lower than required for dynamic similarity, speed (i.e.  $U_0$ ) predicted from relative stride length would be overestimated. Note that, although relative stride length was constant, duty factor and relative peak force were not the same in the different simulations, so locomotion would not appear dynamically similar. This emphasises the importance of measuring more than one DP to assess whether locomotion is dynamically similar.

interpreted. Once criteria for dynamic similarity within a certain gait have been identified, deviations from dynamically similar locomotion can be understood in terms of which of these criteria are not being met (e.g. see Blickhan, 1989b). For example, in a study of how locomotor dynamics change during growth, animals of different ages, and therefore sizes, could be compared at equal Froude number so that dynamically similar locomotion is possible. Locomotion could be characterised using dimensionless locomotor parameters such as relative stride length and duty factor. If these parameters are found to change systematically during growth,  $K$  and  $V_0$  could be calculated to determine whether these changes are due to differences in one or both of these DPs. The sensitivity of locomotion to  $K$  and  $V_0$  under the relevant conditions would also need to be taken into account. Changes in  $K$  could be explained in terms of changes in anatomy and muscle and tendon properties during growth, as well as the direct effects of size. Changes in  $V_0$  reflect differences in the dimensionless aerial times selected by the animals (Appendix C). This type of approach facilitates a mechanistic, rather than descriptive, interpretation of the influence of factors such as size, growth, gravity level and anatomy on locomotion.

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### Appendix A. Why does dynamic similarity imply equal DPs?

By definition, two systems that are completely dynamically similar can be made mechanically identical by taking one of the systems and multiplying all linear dimensions by a length scale factor ( $c_L$ ), all internal and external forces by a force scale factor ( $c_F$ ) and all time periods by a time scale factor ( $c_T$ ). Length, force and time can be considered as reference dimensions, so all other mechanical parameters can be defined in terms of them. Therefore, the scale factors for other mechanical parameters can be determined from  $c_L$ ,  $c_F$  and  $c_T$ . For example, by Newton's second law, mass is force divided by acceleration, so its scale factor must be  $c_F c_T^{-2} c_L^{-1}$ . Dynamic similarity, reference dimensions and the use of scale factors are discussed in Isaacson and Isaacson (1975).

A DP is a set of parameters combined in such a way that the units of measurement cancel out. Two dynamically similar systems will have equal values of any DP formed from mechanical parameters because the scale factors will also cancel out. This can be demonstrated using a simple example. If an animal with leg length  $L_{leg}$  is moving with a stride length  $L_{stride}$  its relative stride length is  $L_{stride}/L_{leg}$ . If a second animal has leg length,  $c_L L_{leg}$  and is moving in a manner that is dynamically similar to the first animal, its stride length must be  $c_L L_{stride}$  so that its relative stride length is  $c_L L_{stride}/c_L L_{leg}$ , which is equal to the relative stride length of the first animal. A similar argument could be applied to any other DP. Therefore, completely dynamically similar systems have equal values of all DPs formed from mechanical parameters.

### Appendix B. Why can dimensional analysis be used to define criteria for dynamic similarity?

We have stated that, if spring–mass models have equal values of  $K$ ,  $U_0$ ,  $V_0$  and  $\theta_0$ , then they will be completely dynamically similar—i.e. they will have equal values of any other DP that could be used to describe them. Here we demonstrate why.

The spring–mass model has seven parameters:  $k$ ,  $m$ ,  $l_0$ ,  $g$ ,  $u_0$ ,  $v_0$ ,  $\theta_0$ . Here we consider an arbitrary eighth dimensional parameter,  $p_{out}$ , that describes the behaviour of the system in some way. This could be stride length, stance time, peak vertical GRF etc. We know that some function,  $f$ , relates this parameter to the other parameters, but we do not know what it is (because the equations of motion for the model cannot be solved analytically). This can be expressed as:

$$p_{out} = f(k, m, l_0, g, u_0, v_0, \theta_0).$$

Buckingham's Pi-Theorem tells us that the above equation can be reduced to a relationship among  $8-3=5$  independent DPs (Isaacson and Isaacson, 1975). One option is to use  $K$ ,  $U_0$ ,  $V_0$ ,  $\theta_0$  and a fifth DP,  $\Pi_{out}$ , which contains  $p_{out}$  and some combination of the other dimensional parameters.

For example, if  $p_{out}$  is stance time ( $t_c$ ),  $\Pi_{out}$  could be  $t_c\sqrt{g/l_0}$ . The relationship between these five DPs can then be expressed as:

$$\Pi_{out} = \varphi(K, U_0, V_0, \theta_0).$$

Again, we do not know what the function  $\varphi$  is, but we can see that, if two systems have equal values of  $K$ ,  $U_0$ ,  $V_0$  and  $\theta_0$ , then they must have equal values of  $\Pi_{out}$ . Because  $p_{out}$  was an arbitrary parameter, this applies to any DP that could be formed by combining a parameter with some of the seven model parameters (e.g. relative stride length, relative peak force). It also applies to any other DPs that can be created by combining such DPs. For example, if two systems have equal values of the DPs  $t_c\sqrt{g/l_0}$  and  $t_s\sqrt{g/l_0}$ , where  $t_s$  is stride time, they must have equal values of  $t_c/t_s$ , i.e. duty factor.

### Appendix C. Modelling the aerial phase

If  $x$  is the vertical displacement of the centre of mass relative to its position at the start of the aerial phase, and is positive in the upward direction, then the motion of the centre of mass in the vertical direction during the aerial phase can be described as follows:

$$\ddot{x} = -g,$$

$$\dot{x} = -gt + v_T,$$

where  $t$  is time and  $v_T$  is the vertical speed of the centre of mass at the start of the aerial phase. At the end of the aerial phase, when  $t$  is equal to aerial time ( $t_a$ ):

$$\dot{x} = -v_0 = -gt_a + v_T \Rightarrow t_a = \frac{v_T + v_0}{g}.$$

If the aerial phase is symmetrical, as in our spring–mass model simulations, then  $v_T = v_0$ , so that  $t_a = 2v_0/g$  and is therefore proportional to  $v_0$ .

Dimensionless aerial time ( $T_A$ ) can be defined as  $t_a\sqrt{g/l_0}$ . Substituting for  $t_a$  gives:

$$T_A = \frac{2v_0}{g} \sqrt{\frac{g}{l_0}} = \frac{2v_0}{\sqrt{gl_0}} = 2V_0.$$

Dimensionless distance travelled during the aerial phase ( $L_A$ ) can be defined as  $l_a/l_0$  where  $l_a$  is the dimensional distance travelled and is equal to  $t_a u_0$ . This gives:

$$L_A = \frac{t_a u_0}{l_0} = \frac{2v_0 u_0}{gl_0} = 2V_0 U_0.$$

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