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Physical Insights Into Dynamic Similarity in Animal Locomotion. II. Observation of Continuous Similarity States

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1. Introduction

In previous studies, the physical theory of dynamic similarity in animals was deduced from the concept of mechanical similarity in analytical mechanics (Kokshenev, 2010, 2011). Unlike a mechanistic approach to the problem of dynamic similarity in biomechanics of locomotion treating the animate systems as freely falling in the gravitational field and resisting drag forces (Bejan & Marden, 2006), the model-independent physical theory, unifying running, swimming, and flying animals, can be outlined as follows.

Broadly speaking, animals of different body size L_b are dissimilar in their forward propagation speeds V and stride or stroke frequencies T^{-1} . However, when traveling or cruising for long distances at the proper body's resonant frequency $T_{res}^{-1} \sim \sqrt{\mu_{slow}/L_b}$, the animals are generally exploit the stationary dynamic regime characteristic of the constant uniform body pressure generated by slow locomotory muscles. The relevant muscular field $\mu_{slow} \propto L_b^{-1}$, scaling with body length by the same way as reaction elastic-force field, was observed indirectly (Kokshenev, 2011, Table 1) through the wingbeat frequency in hovering birds T_{res}^{-1} , first by Hill (1950) and then by Ellington (1991). The first direct observation of the body's *slow muscular field* scaling with body mass as $\mu_{slow} \propto M^{-1/3}$ in flying, running, and swimming animals has been established through the body force output by Alexander (1985) and Marden & Allen (2002). When an animal maintains the resonant cyclic conditions (in frequency and phase; Kokshenev, 2010) with increasing speed, the mechanical efficiency of the properly recruited fast locomotory muscles is higher than that of acting slow muscles, at least in adult species (e.g., Alexander, 1989). Moreover, the mechanically universal (i.e., frequency-, speed-, and force-independent) muscle stiffness $K_{fast} \propto M^{2/3}$ results in the body's *fast muscular field* $\mu_{fast} \sim g$, where g is the gravitational field, whose uniformity determines the dynamic similarity between animals across body mass through the basic scaling rules $V_{fast} \propto M^{1/6}$ and $T_{fast}^{-1} \propto M^{-1/6}$.

The *dynamic similarity patterns*, unifying different-sized animals at a certain dynamically similar slow or fast regime, are unambiguously determined by the reliable observation of just one of the basic scaling rules shown respectively in Tables 1 and 2 in Kokshenev (2011). Alternatively, the equivalent *theoretical observation* of just one *uniform* (across body mass) dimensionless determinant, such as the Strouhal number ($St_{slow} \sim St_{fast} \propto M^0$), the Froude

number ($Fr_{fast} \propto M^0$), the force-output number ($\mu_{fast}/g \propto M^0$), the limb duty factor ($\beta_{slow} \sim \beta_{fast} \propto M^0$), or the angle ($\Theta_{slow} \sim \Theta_{fast} \propto M^0$) sweeping by legs, wings, or tails during a stride or a stroke, implies the establishing of the discrete (isolated) dynamically similar states in animals moving in certain fast or slow gait.

In the previous chapter, the pattern of *efficient runners in quadrupeds*, unifying trotting and galloping quadrupeds (from a mice to a horse), was theoretically observed by both the basic scaling rules at well experimentally distinguished "equivalent" speeds (Heglund et al., 1974), "preferred" trotting and galloping speeds (Heglund & Taylor, 1988; Perry et al., 1988), as well as trot-to-gallop transient speeds (Heglund et al., 1974, Heglund & Taylor, 1988). When extended by bipeds and described by a whole spectrum of scaling rules, the latter pattern of similarity called by *efficient trotters and hoppers* was been studied in the domain of "physiologically equivalent" speeds (Farley et al., 1993), unifying near the trot-to-gallop transition running quadrupeds (from a rat to a horse) and hopping bipeds (tammar wallaby and red kangaroo).¹ It has been also demonstrated that the direct experimental observation of both two basic scaling rules is equivalent to the theoretical observation of the uniformity of the underlaid muscular field, i.e., $\mu_{fast} \sim V_{fast} T_{fast}^{-1} \propto M^0$. Other patterns of the established transient (walk-to-run) state and optimum-speed state, called by *efficient walkers in bipeds* and *efficient runners in mammals*, were theoretically observed through the scaling rules for, respectively, frequency and speed measured in bipeds, including humans (Gatesy & Biewener, 1991) and other terrestrial mammals (from the smallest bipedal rodent to the largest quadrupedal elephant, Garland, 1983). Likewise, the dynamic similarity in *efficient flyers and swimmers* associated with the fast dynamic regime of locomotion was established for dolphins, birds, and bats cruising with a high power efficiency (Taylor et al., 2003).

In the previous chapter, Alexander's hypothesis on the dynamic similarity between running different-sized animals, equalling Froude numbers (Alexander, 1976; Alexander & Jayes, 1983; Alexander, 1989), has been studied in the context of *discrete-state* dynamic similarity. These dynamically similar states of animate systems, moving in either the stationary-speed slow-muscle regime or the non-stationary fast-muscle regime, have been specified by optimal-speed, transient-mode, and transient-gait states, resulted in the mentioned above dynamic similarity patterns. Besides the central hypothesis on discrete-state dynamic similarity, the possible existence of gait-dependent characteristic similarity functions (of the *Froude variable* Fr) unifying animals across body mass, speed, and taxa at a certain gait, was also proposed by Alexander & Jayes (1983). From the theoretical point of view, the discrete-state similarity determined by equal Froude constants has been therefore suggested to be generalized to the *continuous-state dynamic similarity*, determined by the *dynamic similarity functions* provided by continuous data on the limb duty factors $\beta(Fr)$ and the Strouhal numbers $St(Fr)$ obtained by Alexander & Jayes (1983).

In this study, the theory of continuous dynamic similarity is developed and tested by the continuous dynamic similarity states revealed in walking and running mammals on the basis of systematic experimental data on the limb duty factor and relative stride length available for quadrupedal (Alexander & Jayes, 1983; Hutchinson et al., 2006) and bipedal (Gatesy & Biewener, 1991) animals. The developed concept of dynamic similarity hopefully provides

¹ Earlier, the continues dynamically similar states were established by Alexander & Jayes (1983) in trotting and galloping cursorial quadrupeds through the Froude numbers lying in the domain $2 \leq Fr \leq 3$. The corresponding local-state trot-gallop transition was estimated at $Fr_{trot-gall} = 2.5$ (Alexander & Jayes, 1983; Alexander, 2003).

further generalizations of the patterns of dynamic similarity revealed in animals across speed and taxa.

2. Materials and methods

2.1 Systematic experimental data

The available experimental data on gait-dependent characteristics of walking and running terrestrial animals based on the study of dimensionless numbers of dynamic similarity, are conventionally separated in two groups, represented by the discrete-state constant and continuous-state variable Froude parameters.

2.1.1 Discrete similarity data

The study by Farley et al. (1993) of the dynamic similarity in trotting quadrupeds (from a rat to a horse through a dog and a goat) extended by hopping bipeds (tammar wallaby and red kangaroo) has been performed near the trot-to-gallop transient states, whose dynamic similarity was revealed by closely spaced Froude numbers $Fr_{trans}^{(exp)} (= V_{trans}^2 / gL_b$, where L_b is hip height), limb duty factors $\beta_{trans}^{(exp)} (= \Delta T / T$, with ΔT is the ground contact time of one foot, and T is the stride period), and peak force output $F_{trans}^{(exp)}$, represented here as

$$Fr_{trans}^{(exp)} = 2.25 \pm 0.13, St_{trans}^{(pred)} = 0.40, \beta_{trans}^{(exp)} = 0.41 \pm 0.2, \text{ with } \mu_{trans}^{(max)} / g = 3.10. \quad (1)$$

The statistically averaged data for the mean Froude number and the limb duty factor were reported by Farley et al. (1993, p. 74). The relative force output is estimated here on the basis of $F_{trans}^{(exp)}$ discussed in Eq. (17) in Kokshenev (2011) and the failing Strouhal number is predicted below (Fig. 1).

More recently, the discrete-state dynamic similarity was established in 21 trotting horses by Bullimore & Burn (2006) at three constant Froude numbers $Fr_{trot}^{(exp)} (= 0.5, 0.75, \text{ and } 1)$. In their Table 4, the authors have shown that besides the stabilization across body mass of two determinants $Fr_{trot}^{(exp)} \propto M^0$ and $St_{trot}^{(exp)} \propto M^0$, the similar dynamic states are also indicated by the invariable duty factor $\beta_{trot}^{(exp)} \propto M^0$. The omitted scaling factors in statistically observed scaling relations are schematically reproduced here as

$$\begin{pmatrix} Fr_{trot}^{(exp)} \\ St_{trot}^{(exp)} \\ \beta_{trot}^{(exp)} \end{pmatrix} = \begin{pmatrix} 0.50 & 0.75 & 1.00 \\ 0.70 & 0.67 & 0.60 \\ 0.47 & 0.44 & 0.39 \end{pmatrix} \cdot M^0. \quad (2)$$

2.1.2 Continuous similarity data

Treating the estimated Froude numbers as a dynamic variable, changing with speed in walking and running terrestrial animals, the data on the measured gait-dependent mechanical characteristics were obtained by a number of researches. The available systematic data on continuous dynamic similarity in quadrupeds (from a small rodent to a rhinoceros, Alexander & Jayes, 1983), modern elephants (Hutchinson et al., 2006), land-dwelling birds (from a bobwhite to an ostrich) and two humans (Gatesy & Biewener, 1991) are provided in Table 1 in terms of the duty-factor similarity function $\beta_{gait}^{(exp)}$ and the Strouhal similarity function $St_{gait}^{(exp)}$ scaled by Froude variable Fr .

Animals	$a(Fr)^b$	$a_{walk}^{(exp)}$	$b_{walk}^{(exp)}$	$\pm\Delta b_{walk}^{(exp)}$	$a_{run}^{(exp)}$	$b_{run}^{(exp)}$	$\pm\Delta b_{run}^{(exp)}$
Quadrupeds curs.	$\beta_{gait}^{(exp)}$	0.52	−0.16	0.07	0.53	−0.28	0.03
Quadrupeds curs.	$St_{gait}^{(exp)-1}$	2.4	0.34	0.10	1.9	0.40	0.03
Bipeds	$a(Fr)^b$	$a_{walk}^{(exp)}$	$b_{walk}^{(exp)}$	$r_{walk}^{(exp)2}$	$a_{run}^{(exp)}$	$b_{run}^{(exp)}$	$r_{run}^{(exp)2}$
Birds	$\beta_{gait}^{(exp)}$	0.60	−0.09	0.69	0.56	−0.20	0.69
Humans	$\beta_{gait}^{(exp)}$	0.58	−0.08	0.93	0.40	−0.29	0.90
Bipeds	$\beta_{gait}^{(exp)}$	0.59	−0.09	—	0.47	−0.25	—
Birds	$St_{gait}^{(exp)-1}$	2.34	0.16	0.72	2.42	0.31	0.72
Humans	$St_{gait}^{(exp)-1}$	2.48	0.28	0.80	2.48	0.38	0.76
Bipeds	$St_{gait}^{(exp)-1}$	2.41	0.22	—	2.45	0.35	—
Elephants	$a+b\log(Fr)$	$a_{African}^{(exp)}$	$b_{African}^{(exp)}$	$r_{African}^{(exp)2}$	$a_{Asian}^{(exp)}$	$b_{Asian}^{(exp)}$	$r_{Asian}^{(exp)2}$
Elephants	$\beta_{eleph}^{(exp)}$	0.53	−0.16	0.89	0.51	−0.16	0.84
Elephants	$a(Fr)^b$	$a_{African}^{(exp)}$	$b_{African}^{(exp)}$	$r_{African}^{(exp)2}$	$a_{Asian}^{(exp)}$	$b_{Asian}^{(exp)}$	$r_{Asian}^{(exp)2}$
Elephants	St_{eleph}^{-1}	2.0	0.18	0.84	2.1	0.17	0.86

Table 1. The equations of linear least squares regression for the limb duty factor (β) and relative stride length ($= St^{-1}$, see, e.g., Table 2 below) obtained from walking and running animals. The data on African and Asian elephants are by Hutchinson et al. (2006, Table 3). The data on cursorial quadrupeds (a dog, a sheep, a camel, and a rhinoceros) are by Alexander & Jayes (1983, Table II). For quadrupeds, the limb duty factor data are the arithmetic means of forelimb and hindlimb data. The dynamic similarity functions for birds and humans are obtained here by the standard least squares regression of the continuous-state data reproduced from Figs. 5 and 7 in Gatesy & Biewener (1991). The scaling equations for bipeds are approximated by the geometric mean of those for birds and humans.²

2.2 Theory of continuous similarity

2.2.1 Statement of the problem

When Alexander’s central hypothesis exemplified in Eq. (2) is applied to the efficiently trotting dogs, a question arises whether the dogs observed at the same three constant Froude numbers will show the same Strouhal numbers and limb duty factors as in the horses? In other words, whether the equivalent dynamic similarity states chosen at certain fixed numbers Fr determine the same dynamic similarity states in horses indicated by the same equalized magnitudes of St and β ? Moreover, if a chosen small trotting horse and an estimated big trotting dog show the same Froude number, does it mean that other corresponding determinants and indicators of the dynamic similarity should be equal in magnitudes? All these questions are concern with the concept of continuous-state dynamic similarity justified by the universal gait-dependent dynamic similarity functions hypothesized by Alexander & Jayes (1983).

² For example, for the two similarity functions $y_1 = a_1x^{b_1}$ and $y_2 = a_2x^{b_2}$ the geometric mean function results in $y = \sqrt{y_1y_2}$, with the corresponding scaling factor $a = \sqrt{a_1a_2}$ and exponent $b = (b_1 + b_2)/2$.

Strictly speaking, the theory developed in the previous chapter tells us that the observation across body mass of a certain dynamically universal state through equal determinants is a sufficient, but not necessary condition for realization of the same or dynamically similar state in different-sized animals. Indeed, it has been demonstrated that the continues-state similarity pattern of *efficient runners in quadrupeds* can be equally observed through the close spaced discrete similar states indicated by non-equal Froude numbers in the domain¹ $2 \leq Fr \leq 3$. Since the spectrum of scaling rules of the dynamic similarity theory establishes the universality for solely scaling exponents, leaving aside the problem of scaling factors, the scaling equations empirically established for speed and frequency in dogs and horses may broadly differ in scaling factors, eventually providing different magnitudes in the set of determinants of discrete-state similarity (Fr, St, β) discussed above. Hence, this qualitative analysis suggests the dynamically equivalent states established in different-sized animals can be observed not by solely equal, but also different, generally closely spaced dimensionless numbers unified by the domains of continuous equivalent states distinguished via continues similarity patterns. The developed below theory is discussed in terms of the continuously similar states revealed via the extended set of determinants and indicators of similarity, such as the set (Fr, St, μ, β) exemplified by the transient mode-state *continuous similarity pattern* shown in Eq. (1).

2.2.2 Continuous similarity states

In this study, the discrete states of similarity unified by the generic regime of *fast* locomotion, are going to be generalized to continuous dynamic states described in Table 2.

Fast gait characteristics	Frequency	Length	Speed	Force	Mass
$T_{opt}^{-1}, T_{res}^{-1} \sim \sqrt{K/M}$	T^{-1}	$\mu^{\frac{1}{2}} \cdot L_b^{-\frac{1}{2}}$	$\mu \cdot V^{-1}$	$(\rho_b \mu^2 A)^{\frac{1}{2}} \cdot F^{-\frac{1}{2}}$	$\rho_b^{\frac{1}{6}} \mu^{\frac{1}{2}} \cdot M^{-\frac{1}{6}}$
$L_{gait}^{(max)} = L$	$\mu \cdot T^2$	L	$\mu^{-1} \cdot V^2$	$(\rho_b \mu A)^{-1} \cdot F$	$\rho_b^{-\frac{1}{3}} \cdot M^{\frac{1}{3}}$
$V_{gait}^{(max)} = LT^{-1}$	$\mu \cdot T$	$\mu^{\frac{1}{2}} \cdot L^{\frac{1}{2}}$	V	$(\rho_b A)^{-\frac{1}{2}} \cdot F^{\frac{1}{2}}$	$\rho_b^{-\frac{1}{6}} \mu^{\frac{1}{2}} \cdot M^{\frac{1}{6}}$
$K_{gait}^{(max)} = \Delta F / \Delta L_b$	T^0	L^0	V^0	F^0	$\rho_b^{-\frac{1}{3}} \mu \cdot M^{\frac{2}{3}}$
$\mu_{gait}^{(max)} / g = \Delta F / gM$	T^0	L^0	V^0	F^0	M^0
$St_{gait} = L_b / L$	T^0	$L_b L^{-1}$	V^0	F^0	M^0
$Fr_{gait} = V^2 / gL_b$	T^0	L^0	V^0	F^0	M^0

Table 2. The determinants suggested for dynamically similar states in animals moving in fast similar gaits. The data are reproduced from Table 2 in Kokshenev (2011). Here L is the dynamic (stride or stroke) length and L_b is the static (leg or wing) length in animals; A is the body’s cross-sectional area; ρ_b is the body density; $K_{run}^{(max)}$ is the maximum amplitude of body stiffness. Other notations are described in the text. The abbreviation for the fast muscular field $\mu = \mu_{run}^{(max)}$ is adopted.

Before further advancement of the discrete-state similarity theory, it is noteworthy that when a theoretical concept is applied to the real animate systems, several precautions should be taken. The relevant perfect and imperfect qualification in the application of dynamic similarity to real animals was discussed by Alexander (1989). From the theoretical point of view, deviations from the "perfect" uniformity in the dimensionless determinants and the indicators of discrete dynamically similar states may be exemplified by weak body-mass dependence of the swept

angle $\Theta_{run}^{(exp)} (= 0.60M^{-0.03})$ and the *relative body length change* $\varepsilon_{run}^{(exp)} (= 0.17M^{-0.04})$, revealed by the leg-spring model in quadrupeds and bipeds (Farley et al., 1993). The plausible reasons of deviations from the universality in dimensionless determinants of the similarity are (i) uncompensated external ground reaction forces and internal body reaction forces, resulting in deviation in body's rigidity, (ii) deviations from the condition of maximal locomotor efficiency and (iii) from the isometrically approximated scaling rules for muscle and bone masses with body mass. The latter effects are caused by small but finite mass allometric exponents (Prange et al., 1979) discussed in the problem of the primary locomotor functions of long skeletal bones (Kokshenev et al. 2003; Kokshenev, 2003, 2007) and striated and cardiac muscles (Kokshenev, 2008, 2009).

Following the original version of the dynamic similarity theory (Kokshenev, 2011), the similarity between equivalent discrete states established by the dimensionless determinants is also indicated by the uniform dimensionless scaling parameters, e.g., β , ε , or Θ , generally omitted in the scaling rules (e.g., Table 2). In the version of continuous-state dynamic similarity driven by continuous Froude variable, all other dimensionless parameters are also state-dependent continuous functions, e.g., $St(Fr)$, $\beta(Fr)$, or $\Theta(Fr)$. Following the concept of the unique similarity criterion (Kokshenev, 2011), each of these functions ambiguously determines the dynamic similarity between animals moving in certain gait. Hence, extending scaling relations from the discrete states to continuous states, the omitted in Table 2 dimensionless parameters should be restored.

Using the basic definitive equations for resonant frequency and optimum speed (Table 2), one obtains the basic gait-dependent relations of the continuous dynamic similarity, namely

$$T_{res}^{-1} \sim \sqrt{\frac{\mu_{gait}}{\varepsilon_b}} L_b^{-\frac{1}{2}}, V_{gait} \sim \sqrt{\frac{\mu_{gait}}{\varepsilon_b}} L_{gait} L_b^{-\frac{1}{2}}, \text{ with } \varepsilon_b = \frac{\Delta L_b}{L_b}, \quad (3)$$

where L_{gait} is the dynamic length. In turn, two corresponding dimensionless numbers

$$Fr_{gait} \sim \varepsilon_b^{-1} \frac{\mu_{gait}}{g} \left(\frac{L_{gait}}{L_b} \right)^2, St_{gait} = \left(\frac{L_{gait}}{L_b} \right)^{-1}, \text{ with } \varepsilon_b \sim \frac{L_{gait}}{L_b}, \quad (4)$$

follow from Table 2, along with the relative static length change ε_b approximated here by the basic relation $\Delta L_b \sim L$, common in linear scaling theory.

When the determinant Fr is chosen as an independent dynamic variable of continuous similarity, Eq. (4) yields *muscle-field similarity function*

$$\mu_{gait}(Fr) \sim gFrSt_{gait}(Fr), \quad (5)$$

where the omitted numerical factor is not universal and therefore insignificant in scaling theory. Bearing in mind the experimental data (Table 1), the *Strouhal similarity function* $St_{gait}^{(exp)}(Fr)$ and the *duty-factor similarity function* $\beta_{gait}^{(exp)}(Fr)$ can be presented as

$$St_{gait}^{(exp)}(Fr) \sim (Fr)^{-b_1} \text{ and } \beta_{gait}^{(exp)}(Fr) \sim (Fr)^{b_2}, \quad (6)$$

where the exponents b_1 and b_2 (observed experimentally in Table 1) are generally constrained by the basic definitive equations. One can therefore infer that the dynamic similarity between animate systems is controlled by the scaling exponents of the gait-dependent similarity

functions, determining continuous similarity. Using the experimental data for the exponents, one obtains a scaling prediction for the muscle-field determinant

$$\mu_{gait}^{(pred)}(Fr) \sim gFr^{b_3}, \text{ with } b_3 = 1 - b_1, \quad (7)$$

straightforwardly following from Eqs. (5) and (6).

3. Results and discussion

The continuous dynamic similarity theory is applied below to the data from running quadrupeds and bipeds (Table 1) on the basis of determinants (Table 2) already specified by the optimum-speed, crossover-gait (walk-to-run), and transient-run (trot-to-gallop) discrete states. The analysis is provided in terms of the continuous-state similarity determinants (Fr, St, β, μ) exemplified in Eq. (1) and in part in Eq. (2).

3.1 Quadrupeds including elephants

As mentioned,¹ the continuous dynamic similarity was first observed by Alexander & Jayes (1983) within the domain $2 \leq Fr \leq 3$ of transient trot-to-gallop dynamically similar states in running cursorial quadrupeds (Table 1). Following the authors, quadrupeds move in dynamically similar way, changing their fashion of locomotion at equal Froude numbers. The trot-to-gallop dynamic transitions were determined by the phase difference between the fore feet, indicating a transition between symmetrical (trot or pace) and asymmetrical (gallop or canter) modes of the run gait (Alexander & Jayes, 1983, Fig. 1). Although all transitions between mode patterns of locomotion are indicated by quantities at which one or more change discontinuously (Alexander & Jayes, 1983; Alexander, 1989, 2003), the *symmetry-mode transitions* are considered here as continuous, at least within the scope of relative stride length and limb duty factor functions, for which no abrupt changes were indicated. The continuous *trot-to-gallop transition*, associated in the cursorial quadrupeds (Table 1) with constant¹ $Fr_{trot-gall} = 2.5$, was re-discovered in quadrupeds (from a rat to a horse) by Farley et al. (1993) as shown in Eq. (1) and re-analyzed in Eq. (17) in Kokshenev (2011) by a number of scaling rules equally validating for discrete and continuous similar states (Table 2).

In contrast to run-mode transitions, a walk-to-run crossover in quadrupeds is associated with *discontinues* transient-gait states. In quadrupeds, excluding elephants, a gradual increasing of speed provokes abrupt changes in both the relative stride length and limb duty factors.

These changes revealed in the domain $0.61 \leq \beta_{walk-run}^{(exp)} \leq 0.67$ indicate the universal (mass independent) discontinues transition from a walk to a run determined by the dynamic similarity variable $Fr_{walk}^{(exp)} = Fr_{run}^{(exp)} = 0.40$ (Alexander & Jayes, 1983, Figs. 3 and 4). In Fig. 1, the scaling data on continuous dynamic similarity in quadrupeds by Alexander & Jayes (1983) are reproduced and the discontinues walk-to-run transition at $Fr_{walk-run}^{(exp)} = 0.40$ is shown by *unstable-state* points 1 and 2 (shown by closed stars), whereas the continuous trot-to-gallop transition is shown by the *continuous-state* points 4 and 5 (shown by open stars).

In the case of cursorial quadrupeds, the duty-factor similarity function (Fig. 1) established for trotting and galloping quadrupeds by Alexander & Jayes (1983) is remarkably consistent with the trot-to-gallop continuous transition states statistically described by Farley et al. (1993) and shown in Eq. (1). These transient-mode states, likely first revealed by Heglund et al. (1974), suggest a stabilization of the characteristic Strouhal number (Table 3) unifying quadrupeds and bipeds within the domain $2 \leq Fr \leq 3$ associated with the continuous similarity pattern of

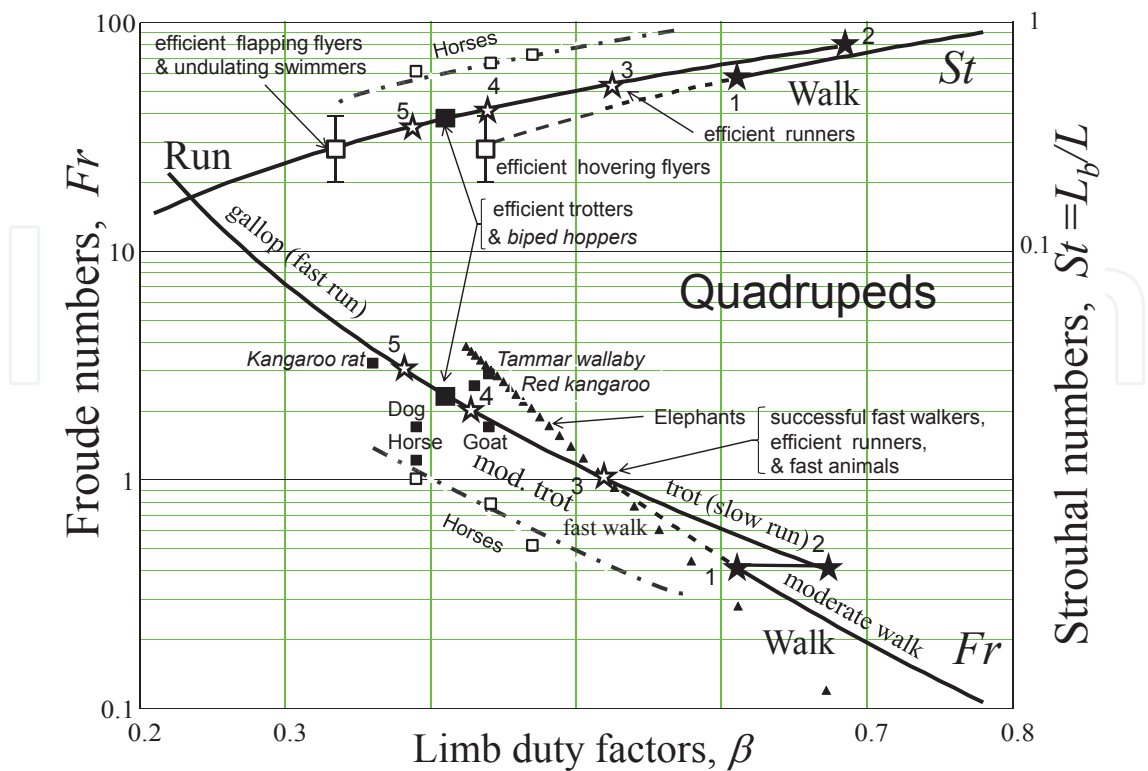


Fig. 1. The comparative analysis of the run-mode and walk-mode dynamic similarity functions in quadrupeds. The *solid lines* are regression data by Alexander & Jayes (1983) described in Table 1. The *dashed lines* are continuously extrapolated data. The *dashed-dotted lines* are the smoothed discrete-state data from trotting horses (shown by *open squares*) by Bullimore & Burn (2006) shown in Eq. (2). The *closed squares* represent those data by Farley et al. (1993, Table 1) for trotting quadrupeds and hopping bipeds (distinguished by *italic style*), which are limited by the experimental error shown in Eq. (1). The *open squares* tentatively represent the data on Strouhal numbers in cruising birds and fish by Taylor et al. (2003). The *closed triangles* are the averaged data from Asian and African elephants (Table 1) by Hutchinson et al. (2006). The open and closed *stars* indicate, respectively, continuous (stable) and discontinues (unstable) dynamic states. For more complete description of these and other characteristic points, see Table 3.

efficient trotters and hoppers (Table 3), evidently including the transient and optimal continuous states established at preferred trotting and preferred galloping speeds (Heglund & Taylor, 1988; Perry et al., 1988).

In the special case of trotting horses, the discrete-state data by Bullimore & Burn (2006), discussed in Eq. (2) and shown Fig. 1 by the open squares, are extended here by the data from a horse by Farley et al. (1993), as shown in Fig. 1 by the closed square. Although the smoothed data on trotting horses (shown by dashed point line in Fig. 1) coincide neither with the duty-factor function $\beta_{run}^{(exp)}$ nor the Strouhal function $St_{run}^{(exp)}$, which were suggested to be universal (Alexander & Jayes, 1983), the dynamic continuous similarity between trotting quadrupeds (excluding non-trotting elephants) and trotting horses can theoretically be established. Indeed, the corresponding smoothed lines in Fig. 1 are drawn by the same

Point	Mode states and patterns in animals	Fr	$St_{gait}^{(exp)}$	$\beta_{gait}^{(exp)}$	$\mu_{gait}^{(pred)} / g$
1	unstable walk in quadrupeds	0.40	0.57	0.61	0.55
2	unstable run in quadrupeds	0.40	0.76	0.67	1.10
3	efficient runners in quadrupeds	1.00	0.53	0.52	1.91
4	trans. moderate run in quadrupeds	2.00	0.40	0.43	2.90
5	transient fast run in quadrupeds	3.00	0.34	0.38	3.69
4→5	efficient trotters and hoppers ^(*)	2.25	0.40	0.41	3.10
3	successful fast walkers (elephants)	1.00	0.49	0.52	1.00
1	efficient walkers in bipeds (birds)	0.52	0.48	0.64	1.00
1	unstable fast walk in humans	0.40	0.52	0.62	0.85
1	unstable fast walk in bipeds	0.45	0.50	0.63	0.93
2	unstable slow run in humans	0.60	0.49	0.46	1.00
2	unstable slow run in bipeds	0.55	0.50	0.56	1.00
3	efficient runners in bipeds	1.00	0.41	0.47	1.47
4	efficient fast runners in bipeds	1.61	0.35	0.43	2.00
5	successful hoppers in bipeds	4.66	0.24	0.33	4.00

Table 3. The characteristic points, determining continuous and discontinues dynamically similar states in different-sized and different-taxa animals, are analyzed on the basis of the walk similarity and run similarity functions from cursorial quadrupeds (Figs. 1-5). The predictions for relative force output $\mu_{gait}^{(pred)} / g$ are from in Table 4. ^(*)The transient-state pattern introduced via Eq. (1).

$\mu_{gait}^{(pred)} / g = a(Fr)^b$	$a_{walk}^{(pred)}$	$b_{walk}^{(pred)}$	$a_{run}^{(pred)}$	$b_{run}^{(pred)}$	Discussed in
Quadrupeds cursorial	1.00	0.72	1.91	0.60	Fig. 2
Birds	1.73	0.84	1.57	0.69	Fig. 5
Humans	1.57	0.72	1.37	0.62	Fig. 5
Bipeds	1.65	0.78	1.47	0.65	Fig. 5
Elephants modern	1.00	0.82	1.00	0.83	Fig. 2
Elephants extinct	—	—	0.29	0.30	Fig. 2

Table 4. The predicted relative force-output similarity function determined in Eq. (7) and described in the text. The equations for bipeds are approximated by geometric mean of the data for birds and humans.² The data on the body mobility for extinct elephants are obtained with the help of Eqs. (13) and (14) in Kokshenev & Christiansen (2011).

scaling equations unifying trotting quadrupeds, namely

$$\beta_{trot}^{(exp)}(Fr) = 0.4\beta_{run}^{(exp)}(Fr) \text{ and } St_{trot}^{(exp)}(Fr) = 1.6St_{run}^{(exp)}(Fr),$$

(8)

which differ in insignificant scaling parameters discussed in Eq. (6). As mentioned in the Introduction, the revealed continuous dynamic similarity states is expected to provide further generalizations about movements of animals of different size and taxa. The continuous similarity patterns of *efficient flapping flyers* and *efficient hovering flyers* established within the domain $0.2 \leq St \leq 0.4$ for fast and slow flight modes by Taylor et al. (2003, Table 2) in cruising birds are schematically shown in Fig. 1, using, respectively, the run-mode $St_{run}^{(exp)}$ and walk-mode $St_{walk}^{(exp)}$ universal Strouhal functions from running and

walking quadrupeds by Alexander & Jayes (1983). As the result, the theoretically observed muscle duty factor $\beta_{flap}^{(pred)} \approx 1/3$ predicting in turn the muscle timing $\Delta T_{flap}^{(pred)} \approx T_{flap}/3$ (see Eq. (9) in Kokshenev, 2011), indicates that the wing muscle, driving the flap mode in a flight, is activated during one third time of the cycle period T_{flap} . This finding can be explained by the three-step cycling of the flight-motor individual muscles in birds, as clearly revealed by workloop technics (see e.g., Fig. 3B in Dickinson et al., 2000).

Coming back to terrestrial animals, the dynamic similarity predicted by inverted-pendulum model for the *walk-to-run crossover* was expected to be determined by $Fr_{walk-run}^{(mod)} = 1$ (e.g., Hildebrand, 1980; Cartmill et al., 2002). Also, the universal discrete state indicated by the model-independent duty factor $\beta_{walk-run}^{(pred)} = 0.5$ (e.g., Alexander & Maloiy, 1989; Alexander, 1992; Usherwood, 2005) could be generally expected, besides the muscular transient field $\mu_{walk-run}^{(pred)} = g$ (Kokshenev, 2011). However, such a continuous-state transition has been observed neither in bipeds, including humans, nor in quadrupeds, excluding elephants. As indicated by the walk-instability and run-instability points 1 and 2 in Fig. 1, the fast walk mode is avoided by cursorial quadrupeds. But if the fast walk mode would conventionally be activated by the continuous extrapolation of the universal walk-mode similarity function, the desirable continuous *walk-to-run transition* might be theoretically observable, as shown by the dashed line in Fig. 1. Surprisingly, the hypothetical continuous transition was remarkably *in vivo* established by Hutchinson et al. (2006) in modern African and Asiatic elephants, through the dynamic similarity determinant $Fr_{walk-run}^{(exp)} \approx 1$ and the limb duty factor $\beta_{walk-run}^{(exp)} \approx 0.5$, indicating dynamic similarity in elephants during the fast-walk-to-moderate-run continuous-state transition. In contrast with other quadrupeds, elephants, having the hindlimb more compliant than the forelimb (Kokshenev & Christiansen, 2010, Fig. 5) are able to avoid abrupt changes in the mean-limb duty factor during the fast-walk-to-run dynamic crossover. Moreover, elephants, being good walkers, most likely can achieve gradually the highest instability point in the fast-walk trajectory of body's center of mass, indicated in the theory of similarity by the transient muscular field $\mu_{walk-run}^{(pred)} = g$. Hence, the transient similarity state, shown by point 3 in Fig. 1, unifying a gait-crossover transient continuous state in the elephants and a mode-transient continuous state in other quadrupeds, suggests two different patterns of similarity: *successful walkers* and *efficient runners*. The last pattern in quadrupeds is in addition indicated by the universal muscular field evaluated as $\mu_{run}^{(exp)} \approx 2g$ (for details, see Table 3) characteristic of more extent pattern of efficient fast animals, including fast running mammals, reptiles, insects; flapping birds, bats, and insects; swimming fish and crayfish, as reported by Bejan & Marden (2006, Fig. 2C). When searching for continuous dynamic similarity states through the muscle-force field on the basis of Eq. (7), one obtains the scaling exponent $b_{run}^{(pred)} = 0.60$ using $b_{run}^{(exp)} = 0.40$ from Table 1, in the case of running cursorial quadrupeds. The corresponding scaling factor $a_{run}^{(pred)} = 1.91$ follows from the pattern *efficient trotters and hoppers* (Table 3) reliably established by Taylor et al. (1993) and employed as a reference point in Eq. (7). The resulted universal similarity function $\mu_{run}^{(pred)}(Fr)$ shown in Fig. 2 in turn predicts the data $\mu_{run}^{(pred)} = 1.91g$ failing for *efficient runners in quadrupeds* (Table 3).

In the case of *fast walking* (virtual) quadrupeds, the relative-force continuous similarity function $\mu_{walk}^{(pred)}(Fr)/g$ is obtained by a continuous extrapolation of the moderate-walk mode

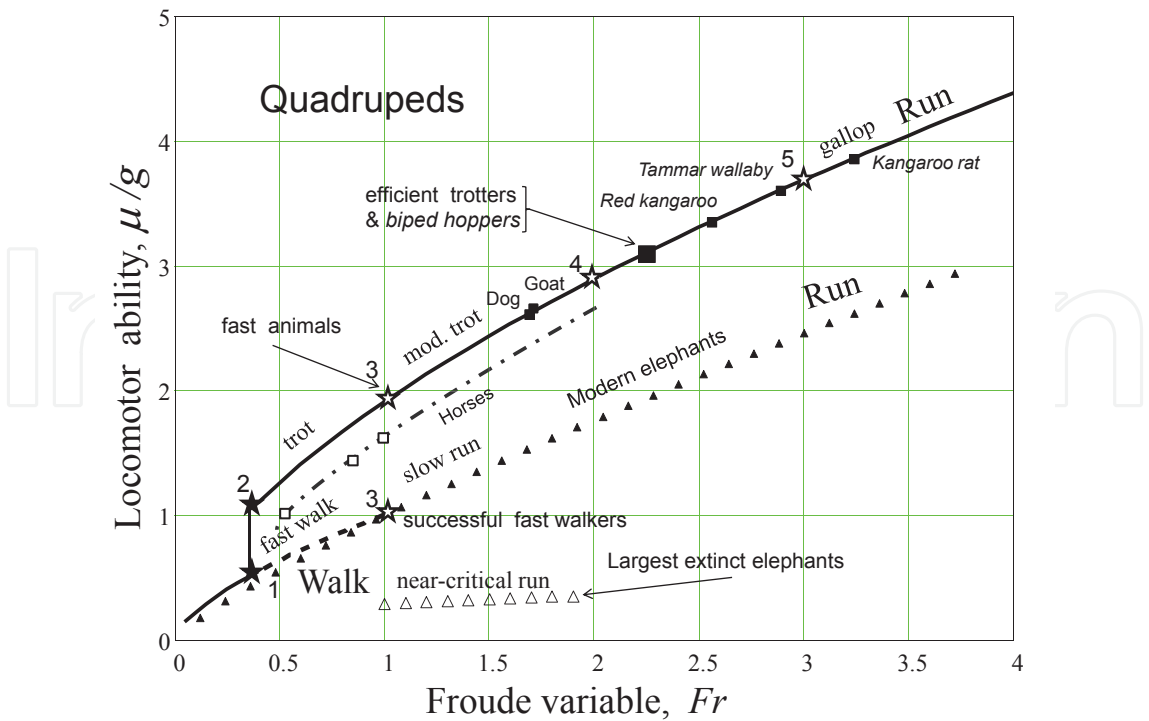


Fig. 2. Locomotor ability similarity function predicted for quadrupeds by the relative force-output. The *solid lines* are estimates for walking and running quadrupeds obtained via Eq. (7) with the help of the corresponding experimental data on the Strouhal similarity function (Tables 1 and 4). The *dashed line* extrapolates the data on slow-walk to fast-walk modes. The *dashed-dotted line* adjusted with *open squares* is a sketched estimate for trotting horses, also discussed in Fig. 1. The characteristic points and the pattern points are those shown in Fig. 1 and described in Table 3. The comparative data for bipeds are indicated by *italic style*. The *closed triangles* and *open triangles* are respectively the predicted data on the body ability in modern elephants and the body mobility in extinct elephants (Table 4).

to the fast-walk mode, where a transient state for the walk-to-run determinant $\mu_{walk-run}^{(pred)} = g$ predicted in Fig. 1 at $Fr_{walk-run}^{(mod)} = 1$ is employed as a reference point (Table 4). Likewise, in the case of slow running modern elephants, the relative-force similarity function is obtained on the basis of the data $St_{eleph}^{(exp)}(Fr)$ by Hutchinson et al. (2006) shown in Table 1, with the help of the same transient state in the walk-to-run continuous transition, also employed as the reference point determining the dynamic similarity at $Fr_{walk-run}^{(mod)} = 1$. One can therefore observe (Fig. 2) the dynamic similarity between poorly running (no trotting) modern elephants (shown by the closed triangles) and other hypothetical quadrupeds using the inverse gradient in the fore-hind limb locomotion function, common to both extant and extinct elephants (Kokshenev & Christiansen, 2010, Fig. 5). The data on low level *mobility* of largest extinct elephants (Kokshenev & Christiansen, 2011, Figs. 4 and 5), shown by open triangles in Fig. 2, are obtained by evaluation of the torsional and bending limb bone elastic forces, acting in running giants (Table 4).

3.2 Bipeds including humans

In humans, a discontinues walk-to-run crossover is generally observed at Froude numbers $Fr_{walk-run}^{(exp)} \approx 0.5$ (Thorstensson & Roberthson, 1987, Kram et al., 1997; Alexander, 1989;

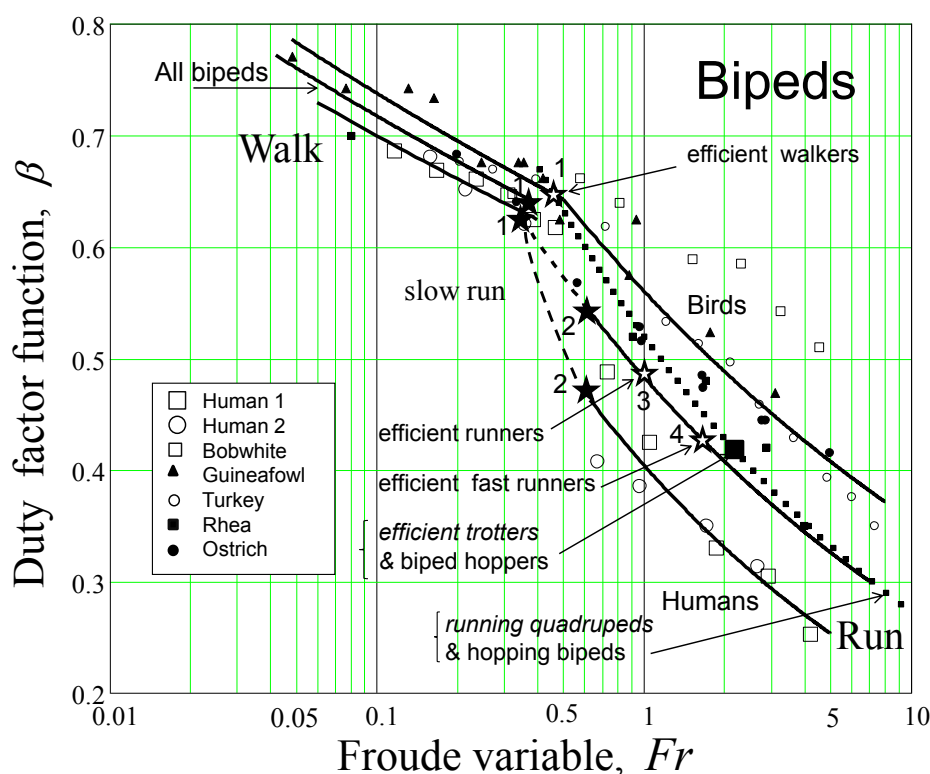


Fig. 3. The limb duty-factor similarity functions in bipeds. The *points* are the data by Gatesy & Biewener (1991) explained in the inset. The *solid lines* are statistical data from walking and running humans, birds, and bipeds as group (Table 1). The *dotted line* represents the continuous-state data from running cursorial quadrupeds (Fig. 1), excluding those for a slow run; other discrete-state data for quadrupeds are shown in *italic style*. The *dashed lines* indicate regions of the unstable slow run. The open and closed *stars* indicate, respectively, stable and unstable transient dynamic states. These and other patterns of similarity are described in the text and Table 3.

Ahlborn & Blake, 2002) and stabilization of the run mode is likely determined by the vertical component of muscular field $\mu_{walk-run}^{(pred)} = g$ (Ahlborn & Blake, 2002). Unlike elephants and other quadrupeds (Fig. 1), humans and birds expose similar behavior in a number of dynamic characteristics with changes in speed and gait (Gatesy & Biewener, 1991). Although a general consistency between patterns of gaits in humans and birds has been generally established, no clear characterization of the walk-to-run crossover was revealed (Gatesy & Biewener, 1991). The standard least squares analysis of the experimental data on limb duty factor and relative stride length (Gatesy & Biewener, 1991, Figs. 5 and 7) provided here (Table 1) is expected to shed light on the problem of the walk-to-run crossover in bipeds.

In Fig. 3, evident dynamic similarity between the walk modes in humans and birds is observed through the duty-factor similarity functions. Within the domains of continuous states (the solid lines in Fig. 3) treated within context of scaling relations shown in Eq. (6), the dynamic similarity between running humans and running birds can approximately be established on the basis of corresponding experimental data on duty-factor similarity functions (Table 3). As for the walk-to-run discontinues crossover in *bipeds*, the instability of walk modes generally occurs at Froude numbers $Fr_{biped}^{(exp)} = 0.45 \pm 0.05$ (the closed stars and

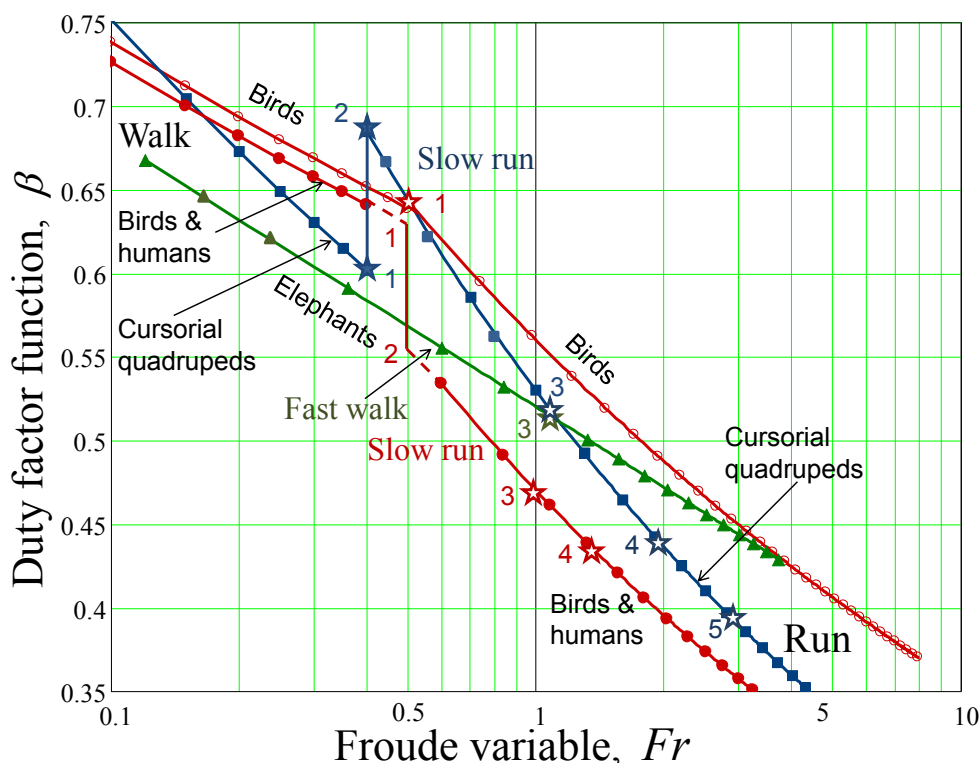


Fig. 4. The comparative analysis of the walk-to-run crossover in bipeds and quadrupeds. The *pointed lines* are the experimental data on duty-factor similarity functions (Table 1). Other notations are the same as in Figs. 1 and 3.

point 1 in Fig. 3), whereas the run modes show features of stabilization at $Fr_{biped}^{(exp)} = 0.55 \pm 0.05$ (the closed stars and point 2 in Fig. 3). However, when the *birds* are presented by the smoothed experimental data, they exhibit a common point of dynamic-state stabilization determined by a kink in the duty-factor similarity function revealed at $Fr_{bird}^{(exp)} = 0.52$ (the open star at point 1 in Fig. 3). Although elephants do not show such a kink at the walk-to-run continuous crossover (Fig. 1), the birds as group likely also may continuously pass the absolute instability point in the walk-mode trajectory (Kokshenev, 2011), as generally was expected by Ahlborn & Blake (2002) from the elastic-type-pendulum model considered at the conditions $Fr_{walk-run}^{(mod)} = 0.5$ and $\mu_{walk-run}^{(pred)} = g$. Since the experimental scaling data on stride frequency in fast walking and slow running birds ($1/T_{trans}^{(exp)} \propto M^{-0.178}$, Gatesy & Biewener, 1991) obey the scaling criterion of dynamic similarity (Table 2), a new similarity pattern *efficient walkers* may be suggested for birds continuously passing the universal walk-to-run crossover (Table 3).

Specifying the muscle-field similarity functions $\mu_{run}^{(pred)}(Fr)$ through Eq. (7), the continuous similarity transient state determined by $\mu_{run}^{(pred)} = g$ is adopted as a reference point, observed in starting to run humans, birds, and bipeds at $Fr_{run}^{(exp)} = 0.60, 0.52$, and 0.55 , respectively (Table 3). In order to obtain the slow-muscle-field similarity function $\mu_{walk}^{(pred)}(Fr)$ for birds, one uses a kink point equaling both the run and walk similarity functions. In the case of bipeds, the obtained run mode similarity function was interpolated to the corresponding walk mode

(the dashed line in Fig. 3), providing scaling parameter in the desirable function $\mu_{walk}^{(pred)}(Fr)$. Then, the relevant data for humans have been obtained as the data adjusting these from birds and bipeds by the geometric mean (Table 4).

The discussed above features of duty-factor similarity functions obtained from walking and running bipeds, including humans, and quadrupeds, including elephants, are reproduced in Fig. 4. One also may infer that bipeds and quadrupeds, showing overall (qualitative) dynamic similarity in a walk and a run gaits, are also generally similar when showing the activation of a slow-run mode within the transient domain, approximated by $0.4 \leq Fr \leq 1.1$. The exception is not running in a classical sense elephants (Hutchinson et al., 2006), continuously exploiting a fast-walk mode during the walk-to-run crossover.

In Fig. 5, the *efficient fast runners in bipeds* (Table 3) expose transient universal dynamic states close to those in the efficient fast runners in quadrupeds (point 4 in Fig. 5), thereby indicating the universal continuous slow-run-to-fast-run dynamic transition in terrestrial animals. These two patterns are therefore represent the fast running mammals, which belong to the generalized similarity pattern of efficient fast animals (Figs. 1 and 2). Likewise, another dynamic pattern of the continuous fast-walk-to-slow-run dynamic transition is presented by efficient walkers in birds shown by the transient-state point 1 in the inset in Fig. 5.

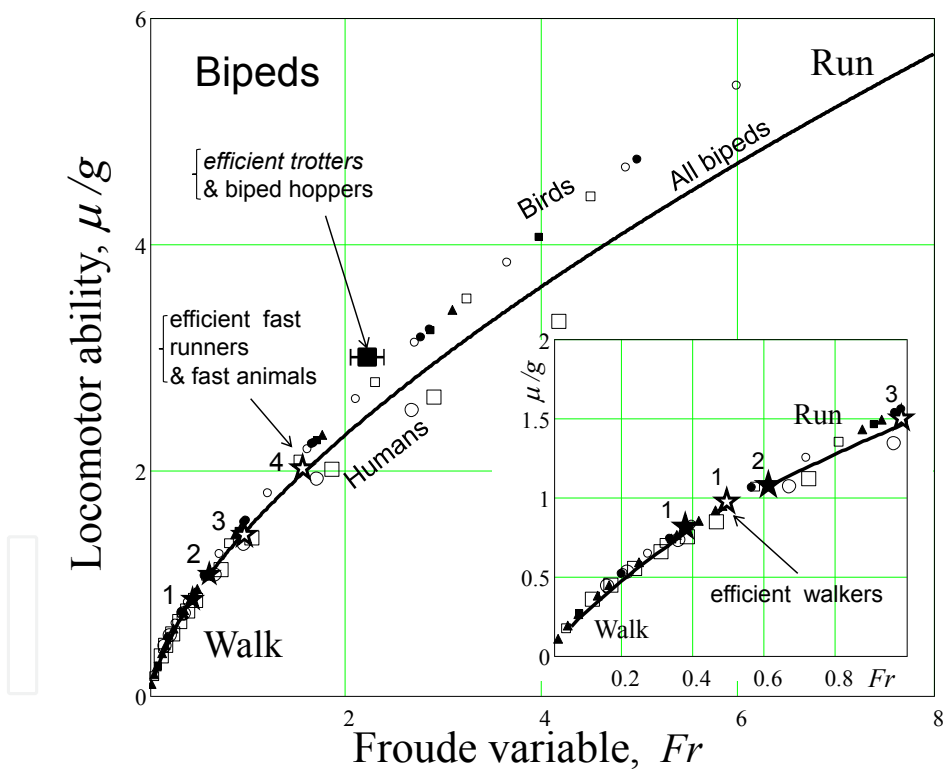


Fig. 5. The observation of the relative force-output similarity function in bipeds. The *solid lines* are the data on continuous dynamic similarity states from walking and running bipeds drawn by the corresponding scaling equations (Table 4). The *experimental points*, corresponding to those in Fig. 3, are drawn through the scaling equations for a run and a walk gaits in birds and humans (Table 4). The *characteristic points* are described in Table 3. The *inset* reproduces the enlarge data near the walk-to-run crossover approximated by continuous similarity states.

One may infer from the provided tentative analysis of continuous similarity states (Table 3) that animals patterned through the one similarity function can be observed slightly different through another one similarity function. Such deviations can be understood by the absence of the reliably established continuous similarity functions, as shown in Fig. 4. Further experimental studies of the domains of equivalent continuous similarity states in animals, moving in dynamically equivalent gaits, statistically searching for the similarity functions controlled by fixed scaling exponents, are needed.

4. Conclusion

Strictly speaking, different-sized animals are not geometrically similar. Moreover, different-taxa animals moving in a certain (slow or fast) gait cannot be patterned by the concept of dynamic similarity until the dynamic conditions unifying running, flying, and swimming are clearly established. In the case of terrestrial animals, when the experimental data from bipeds and quadrupeds, moving in two well distinguished (walk and run) gaits, are compared as two groups of biomechanical systems, no complete dynamic similarity neither inside of each group nor between the two groups can be established. Indeed, inside the bipeds as group, humans contrast to birds, since they are likely unable to explore the slow-run mode continuously near the walk-to-run crossover (Fig. 3). Likewise, cursorial mammals contrast to elephants, compared inside the group of geometrically similar quadrupeds (Fig. 1). When the dynamic similarity is considered between bipeds and quadrupeds, the crossover from a walk gait to a run gait does not occur at the dynamic conditions common to all terrestrial animals (Fig. 4). Less experimental data are available on locomotor mode patterns from flying animals and much less is known about swimming animals. One of the goals of the provided research is to clarify conditions of observation of the dynamic similarity in animals in light of the basic concepts proposed in theoretical biomechanics.

As demonstrated in the first part of this study (Kokshenev, 2011), the dynamic similarity in animals arises from the mechanical similarity existing between frictionlessly moving closed inanimate systems. When mapped onto efficiently moving weakly open dynamically similar biomechanical systems, the animals are conventionally represented (i) as dimensionless center of mass points, possessing a certain body mass M , (ii) propagating with speeds of amplitudes $V_{gait}^{(max)}$ optimized by the variational principle of minimum muscle-field action and (iii) accomplishing rotations at the resonant rate T_{gait}^{-1} . Within the framework of dynamic similarity concept, the geometric similarity between different-sized animals is introduced through the body static length L_b , related (isometrically) to body mass as $L_b \propto M^{1/3}$, that in turn introduces the geometric similarity between linear dimensions of all body's appendages (leg, wing, or tail). The dynamic similarity between animals is thus not due to nonexistent geometric similarity between body's shapes, but is determined by the dynamic-parameter similarity between the compared body's center of mass trajectories (Kokshenev, 2011). When attributed to the similarity temporal uniformity is already established by the resonant conditions, unifying moving animals across mass and taxa, the unique requirement, determining the observable similarity criterion, emerges as a condition of the linearity between the dynamic and static lengths, i.e., $L \sim L_b$, where L plays the role of the primary "geometric" parameter of dynamic trajectories. The accomplished uniformity in the spatial space of dynamic variables is therefore observed through the universal Strouhal numbers $S_{gait} = L_b/L$. Moreover, the scaling rules controlling the dynamic parameters of

similarly moving animals are eventually scaled by the body static length, as explicitly shown in Eq. (16) in Kokshenev (2011).

In this chapter, the discrete-state theoretical approach to the dynamic similarity in animals is generalized to the continuous similarity concept on the basis of continuous Froude variable, playing the role of scaling (similarity) parameter. In the discrete-state similarity theory, treating the body mass as scaling parameter, the scaling rules for fundamental observables and some part of dimensionless universal parameters are the determinants of discrete similarity. Another part of dimensionless universal parameters, playing the role of the indicators of discrete-state similarity, is commonly omitted in basic scaling relations of the theory, besides other insignificant scaling factors. In the continuous-state similarity theory, scaling relations should be substituted by more detail dynamically equivalent scaling equations, because all dimensionless indicators, being functions of continuous states through the Froude variable, now turn into the functions of determinants of continuous similarity. Given that the only one determinant is necessary for the observation of dynamically similar states in animals, each observable function of the only one continuous universal variable can determine the dynamic similarity behavior. It has been therefore shown that the surmise by Alexander & Jayes (1983) on the existence of the gait-similarity functions, determining the dynamic similarity in animals at a certain gait, is generally corroborated by the dynamic similarity theory.

The dynamic similarity patterns established in the previous chapter for running, flying, and swimming animals considered in certain localized dynamic states, are re-analyzed here through the experimental data on continuous dynamic similarity functions established for walking and running bipeds and quadrupeds. The three well distinguished domains of continuous dynamic states in terrestrial animals are now suggested to be explored in animals across taxa. These are the domains of optimum-speed (preferred-run, -flight, or -swim) continuous states, the crossover-gait domain of (walk-to-run, hover-to-flap) transient states, and transient-run domain of (moderate-run-to-fast-run, trot-to-gallop etc.) transient states. The analysis of available experimental data in terms of the four-parameter set of determinants of dynamic similarity (Table 3) resulted in further generalizations in patterns of continuous similarity. One evidently generalized pattern suggests to unify efficient trotters in horses and other trotters in cursorial quadrupeds (Fig. 1). Less evident patterns of dynamic similarity are (i) the efficient trotters unified with bipedal hoppers (Figs. 1, 2, 3, and 5) and (ii) the efficient runners in bipeds unified with those in quadrupeds (Fig. 2) and with all other fast flying and swimming animals (Figs. 1, 2, and 5). Another one tentative pattern is proposed for the efficient flapping flyers in birds and the efficient undulating swimmers unified with efficient gallopers in quadrupeds (Fig. 1).

As a predictive preliminary theoretical result, the dynamic similarity function for locomotor ability in animals (associated with the related body force output) is suggested for quadrupeds, including elephants and bipeds, including humans. The locomotor ability in large quadrupeds is twice as many as that in giant quadrupeds, presented by African and Asian elephants (Fig. 2). In turn, the locomotor ability of the 3-5-ton efficient modern adult elephants is expected to be three-five times as many as the corresponding body mobility for 10-20-ton low-level efficient extinct elephants, running at critical conditions, when compared at close spaced Froude variables (Fig. 2). Likewise, the birds, humans, cursorial and saltatorial mammals show surprisingly close in magnitude muscle-field similarity (Fig. 5), which is twice as many as poorly running modern elephants (Fig. 2).

The discontinuous changes revealed in continuous similarity functions from quadrupeds and bipeds (Figs. 1, 3, and 4) can also be expected in the corresponding relative force-output

similarity functions (Figs. 2 and 5). One may figure out that gait-dependent similarity functions in animals are generally piecewise functions, whose continuous-state domains are separated by discontinues transient dynamically similar states attributed to the gait-crossover transient states (Fig. 4). The suggested universal features revealed by continuous similarity approach challenge further experimental and theoretical studies of dynamic similarity in walking, running, hopping, flying, and swimming animals.

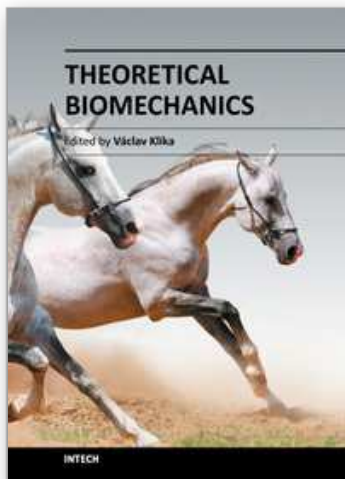
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During last couple of years there has been an increasing recognition that problems arising in biology or related to medicine really need a multidisciplinary approach. For this reason some special branches of both applied theoretical physics and mathematics have recently emerged such as biomechanics, mechanobiology, mathematical biology, biothermodynamics. This first section of the book, General notes on biomechanics and mechanobiology, comprises from theoretical contributions to Biomechanics often providing hypothesis or rationale for a given phenomenon that experiment or clinical study cannot provide. It deals with mechanical properties of living cells and tissues, mechanobiology of fracture healing or evolution of locomotor trends in extinct terrestrial giants. The second section, Biomechanical modelling, is devoted to the rapidly growing field of biomechanical models and modelling approaches to improve our understanding about processes in human body. The last section called Locomotion and joint biomechanics is a collection of works on description and analysis of human locomotion, joint stability and acting forces.

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