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The biological limits to running speed are imposed from the ground up

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[1]*Department of Applied Physiology and Wellness, Southern Methodist University, Locomotor Performance Laboratory, Dallas, Texas;* [2]*Kinesiology Department, Locomotion Laboratory, Rice University, Houston, Texas; and* [3]*Biomechanics Laboratory, College of Health Sciences, University of Wyoming, Laramie, Wyoming*

Weyand PG, Sandell RF, Prime DN, Bundle MW. The biological limits to running speed are imposed from the ground up. *J Appl Physiol* 108: 950–961, 2010. First published January 21, 2010; doi:10.1152/japplphysiol.00947.2009.—Running speed is limited by a mechanical interaction between the stance and swing phases of the stride. Here, we tested whether stance phase limitations are imposed by ground force maximums or foot-ground contact time minimums. We selected one-legged hopping and backward running as experimental contrasts to forward running and had seven athletic subjects complete progressive discontinuous treadmill tests to failure to determine their top speeds in each of the three gaits. Vertical ground reaction forces [in body weights (W_b)] and periods of ground force application (T_c; s) were measured using a custom, high-speed force treadmill. At top speed, we found that both the stance-averaged (F_{avg}) and peak (F_{peak}) vertical forces applied to the treadmill surface during one-legged hopping exceeded those applied during forward running by more than one-half of the body's weight (F_{avg} = 2.71 ± 0.15 vs. 2.08 ± 0.07 W_b; F_{peak} = 4.20 ± 0.24 vs. 3.62 ± 0.24 W_b; means ± SE) and that hopping periods of force application were significantly longer (T_c = 0.160 ± 0.006 vs. 0.108 ± 0.004 s). Next, we found that the periods of ground force application at top backward and forward running speeds were nearly identical, agreeing to within an average of 0.006 s (T_c = 0.116 ± 0.004 vs. 0.110 ± 0.005 s). We conclude that the stance phase limit to running speed is imposed not by the maximum forces that the limbs can apply to the ground but rather by the minimum time needed to apply the large, mass-specific forces necessary.

THE PROSPECT OF HUMANS RUNNING at speeds in excess of 50–65 km/h seems science fictional, but why? Racing horses, dogs, and even hopping kangaroos can readily travel at these speeds. Moreover, these animals do so with biological tissues and limb mechanics that are similar to those of human runners. Their muscles, tendons, and bones are made of the same materials and work in much the same way as those of humans (5, 14, 24, 32, 36). Their high-speed gaits, whether galloping, hopping, or bipedal running, involve using the limbs in a spring-like manner to allow the body to "bounce" along the ground much like a rubber ball (9, 11). These fundamental tissue and gait similarities beg a basic question: What factors prevent humans from running at much faster speeds than they actually do? The explanation undoubtedly involves both the stride mechanics selected in bouncing gaits and the functional limits of the biological tissues used to execute them. However, how these factors combine to impose the speed limits of terrestrial animals is not well understood.

Our previous work identified the interaction between the stance and swing phases of the stride that determines the mechanical limit to running speed (44). This limit follows from the mechanics used by individual runners to modulate their speeds: increases from intermediate to top speed are achieved by applying greater ground support forces, using shorter periods of foot-ground force application, repositioning the swing limbs more rapidly, and thereby taking less time in the air between steps. The limit to speed is reached when foot-ground contact times and effective vertical impulses (i.e., the product of foot-ground contact time and the vertical force exceeding the body's weight) decrease to the minimums that provide just enough aerial time to reposition the swing limb for the next step. Because the swing period consists of two aerial periods separated by the contact period of the opposite limb (Fig. 1*A*), human runners typically require aerial times of 0.12 s or more to attain the minimum swing time of ≈0.350 s generally observed at top speed.

One consequence of the manner in which gait mechanics limit running speed is a mechanical interdependence between the stance and swing phases of the stride (43, 44). Specifically, the vertical forces and impulses required to attain any speed are largely dependent on how rapidly the limbs can be repositioned (43). Relatively longer swing times lengthen the aerial times necessary for limb repositioning, thereby increasing the ground support forces and impulses required to elevate the body. Conversely, relatively shorter swing times have the opposite effect. We recently noted (43) that minimum swing times 20% shorter than typical values substantially reduce the vertical forces and impulses required to attain the same sprint running speeds.

Previous observations suggest the active muscles likely operate at their functional limits during the stance, but not the swing, phase of the stride (27, 31, 33, 35, 44). Although faster individuals have predominantly fast-twitch muscle fibers that contract and generate force more rapidly (15), these individuals do not swing their limbs more rapidly at their much faster top running speeds. For example, runners with top speeds varying by 1.8-fold (6.2–11.1 m/s) differ negligibly in their minimum swing times (44). This result is consistent with the possibility that much of the mechanical energy to reposition the limbs is provided by passive mechanisms of energy transfer rather than via active muscular power. In contrast, stance-phase mechanics differ between faster and slower runners in a manner consistent with established differences in muscle fiber composition and contractile properties (14, 15). At top speed, faster runners apply appreciably greater mass-specific ground forces and do so during shorter periods of foot-ground contact (44).

We undertook this study to identify the stance phase mechanics of human running that limit speed. The relative force
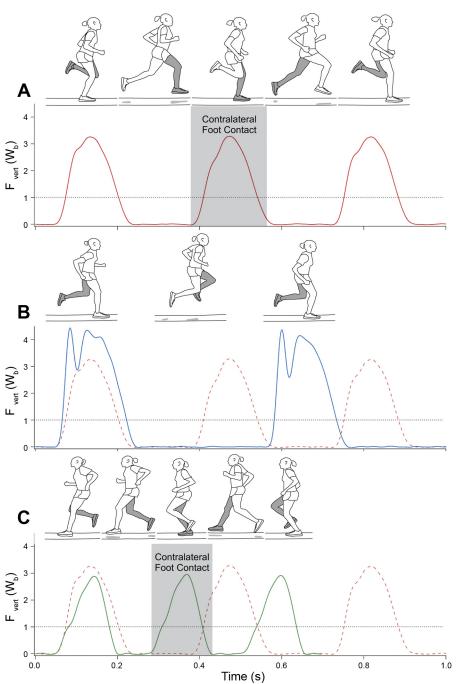

Fig. 1. Vertical ground reaction forces and contact and aerial periods of the step cycle vs. time for forward running (*A*), one-legged hopping (*B*), and backward running (*C*) for a representative subject at the same speed for all three gaits (5.0 m/s). The ground reaction forces for forward running from *A* are reproduced in *B* and *C* (dashed curves) to allow comparisons of the ground reaction forces and contact and aerial phase durations of these gaits with forward running. Note that the durations of the contact, aerial, and swing phases are appreciably shorter at top forward running speed.

and rate requirements for increasing running speed, and the force and rate properties of the extensor muscles of the human limb (1, 3, 21, 22, 25, 38), led us to hypothesize that a limit is imposed, not by the maximum forces the limbs can apply to the ground, but rather by how rapidly they can do so. We selected two gaits for comparison to forward running to test these possibilities: one-legged hopping and backward running. These gaits are similar to forward running in requiring the application of sufficiently large ground support forces during the stance phase to elevate the body for the next step and in involving only the relatively small horizontal forces necessary to maintain a constant speed. However, each comparison gait differs from forward running during the stance phase in an exper-

imentally desirable way. The first comparison gait, one-legged hopping, was selected to alter the amount of force applied to the ground, whereas the second, backward running, was selected to alter the rates of ground force application. In the first case, in keeping with the expected absence of a limitation on maximal ground force, we predicted that the ground support forces applied at top speed would be greater for one-legged hopping than for forward running. In the second case, in keeping with the expected rate limitation, we predicted that the periods of foot-ground contact during which force is applied would fall to the same minimum values at the different top speeds attained during backward and forward running.

METHODS

Theoretical Framework

For theoretical and conceptual purposes, we developed a quantitative framework that expresses speed in terms of the force and time variables we wished to test as potential limits. We recognized that we could accomplish this in a manner applicable to all three gaits by expressing the lengths of the step taken in terms of the ground forces applied and the frequencies of these steps in terms of the durations of foot-ground force application. Hence, our first step was simply to express speed as the product of the length and frequency of the steps taken:

$$\text{Speed} = L_{\text{step}} \cdot \text{Freq}_{\text{step}} \tag{1}$$

where L_{step} is the horizontal distance traveled during a step, here defined as the time between consecutive footfalls and therefore consisting of the stance and the subsequent aerial phases, and $\text{Freq}_{\text{step}}$ is the number of steps taken per unit time. Under conditions in which speed is constant and the center of mass has the same height at the first and last instants of the foot-ground contact period, the average vertical force applied during the contact period, when expressed in relation to the body's weight (F_{avg}/W_b), equals the ratio of the total step time (T_{step}) to contact time (T_c) and the ratio of the step length (L_{step}) to contact length (L_c):

$$F_{\text{avg}}/W_b = T_{\text{step}}/T_c = L_{\text{step}}/L_c \tag{2}$$

By rearranging the terms in *Eq. 2* to isolate L_{step}, the distance traveled between consecutive footfalls can be expressed as the product of the average vertical force applied to the surface in relation to the body's weight and the forward distance through which the body travels [contact length (L_c)], respectively, during the time of foot-ground contact:

$$L_{\text{step}} = (F_{\text{avg}}/W_b) \cdot L_c \tag{3}$$

Next, we expanded the $\text{Freq}_{\text{step}}$ term in *Eq. 1* to express step frequencies in terms of the durations of foot-ground contact. We did so by expressing step times as the sum of the contact (T_c) and aerial (T_{aer}) portions of each step:

$$T_{\text{step}} = T_c + T_{\text{aer}} \tag{4}$$

and step frequencies as the inverse of the period required to complete each step:

$$\text{Freq}_{\text{step}} = 1/(T_c + T_{\text{aer}}) \tag{5}$$

We then rearranged *Eq. 1* by substituting *Eq. 3* for L_{step} and *Eq. 5* for $\text{Freq}_{\text{step}}$ to obtain:

$$\text{Speed} = [(F_{\text{avg}}/W_b) \cdot L_c] \cdot [1/(T_c + T_{\text{aer}})] \tag{6}$$

Equation 6 allows the influence of each of these stride variables on forward speed to be evaluated quantitatively. However, for experimental purposes, all of the variables above were measured directly; none were calculated from the equations provided. Therefore, the validity of the assumptions used to derive our conceptual framework had no effect on the hypothesis testing process.

Experimental Design

To test our first hypothesis on maximum ground forces, we chose one-legged hopping as an experimental tool because this gait, in contrast to forward running, requires that the same limb, rather than alternating limbs, be used for consecutive footfalls. Logic and our preliminary data both suggested that this requirement would elevate ground force requirements (i.e., F_{avg}/W_b) at common speeds above those observed during forward running. Thus, we expected that both F_{avg}/W_b and T_{aer} would be substantially greater for one-legged hopping than forward running. In accordance with our first hypothesis that

maximum ground force does not limit human running speed, we predicted that for each subject F_{avg}/W_b would be greater for one-legged hopping than forward running at the respective top speeds in these two gaits.

Stance limb function dictates that an upper limit on the ground forces applied in bouncing gaits would ultimately be imposed by the force limits of the extensor muscles acting across the ankle, knee, and hip to counteract the ground reaction force. Because the logical origin of our maximum ground force hypothesis is the upper biological limit on the forces produced by the limb extensor muscles, we assessed both muscle and ground forces for our first hypothesis test. This was necessary because the leverage of the stance limb could conceivably differ between forward running and one-legged hopping. A specific concern was that subjects might use straighter limbs to more closely align the ground reaction force vector to their joint axes of rotation during one-legged hopping vs. forward running. If so, the ground reaction forces measured would not be directly representative of the counteracting limb extensor muscle forces. Accordingly, for this first hypothesis test, we used an inverse solution similar to that of Biewener et al. (4, 6) to estimate the stance limb extensor muscle forces produced at the hip, knee, and ankle joints during one-legged hopping and forward running. The technique relies on a balance of torques approach to determine the relationship between the net extensor muscle forces (F_m) needed to counteract the torque produced by the ground reaction force (F_g) acting at a distance R from each joint, in accordance with:

$$\text{EMA} = r/R = F_g/F_m \tag{7}$$

where r is the weighted mean moment arm of the extensor muscle group active at each joint and R is the perpendicular distance between the ground reaction force vector and the joint axis of rotation. The magnitude and direction of R is determined by the vertical and horizontal ground reaction forces and the location of the center of foot-ground pressure (4). Accordingly, this technique allowed us to estimate the muscle forces required per unit force applied to the ground in these two gaits.

To test our second hypothesis on maximal rates of ground force application, we chose backward running as an experimental tool because we knew from prior experience at slower speeds (47) that runners shorten both the contact and aerial portion of the stride at common speeds during backward vs. forward running (Fig. 1). Consequently, similar ground forces (F_{avg}/W_b) are applied with shorter contact lengths (L_c) when running backward vs. forward. Because forward speed during the contact phase is equal to L_c/T_c and L_c was expected to be relatively shorter when traveling backward, we anticipated that our subjects would have shorter periods of foot-ground contact (T_c) during backward vs. forward running at common speeds. In accordance with our second hypothesis that running speed is limited by the minimum periods during which the limbs can apply the ground force required, we predicted that for each subject T_c would fall to the same minimum values at the respective top backward and forward running speeds.

Recognizing that *Eqs. 1–7* apply equally to male and female runners and hoppers, we recruited both male and female subjects, thereby allowing our two hypotheses to be tested over a relatively broad range of top speeds, ground support forces, and foot-ground contact times.

Finally, we conducted our experiments on a treadmill rather than an overground runway with an in-ground force plate because of the advantages the treadmill offered for our experimental objectives. In contrast to a runway, the treadmill allows trial data to be collected for numerous consecutive footfalls, at the precise speeds of interest, and at the constant speeds dictated by the treadmill rather than the more variable speeds selected by the subject. We were well assured from previous studies that our treadmill data will generalize to overground conditions because neither the mechanics of ground force application

(18) being tested nor the sprint running performances (7, 19) of athletic subjects vary appreciably under the two conditions.

Subjects and Participation

We undertook our first and second hypothesis tests sequentially, with our first hypothesis test requiring the F_{avg}/W_b values to be obtained during top-speed forward running and one-legged hopping, and the evaluation of our second hypothesis requiring a comparison of the minimum T_c values obtained during top-speed forward and backward running. A total of 10 subjects, 5 men and 5 women, volunteered and provided written, informed consent in accordance with the requirements of the local Institutional Review Board. Nine of the 10 subjects had competitive athletic experience, and 9 were regularly active at the time of the study. Six subjects were competitive track athletes: two were competitive horizontal jumpers, two were combination sprint/jump specialists, one was a 400-m runner, and one was a 400-m hurdler. Three of the remaining subjects were regularly active at the time of the study, with one each participating in rugby, basketball, and step aerobics. The fourth subject was not active outside of her treadmill sessions at the time of the study.

Hypothesis test I: one-legged hopping vs. forward running. A total of seven subjects, four men [mass 69.0 ± 2.0 kg; leg length (L_o) 0.93 ± 0.02 m; means ± SE] and three women (mass 63.3 ± 1.2 kg; L_o, 0.90 ± 0.05 m) volunteered and participated in the first series of experimental tests. Subjects were habituated to treadmill running during one practice session and to one-legged hopping during either one or two habituation sessions before any top speed trials took place. The hopping habituation process was generally shorter for those subjects who were competitive jumpers ($n = 3$ in this portion of the study), all of whom had extensive experience with plyometric and bounding drills. Six of the seven subjects tested chose to hop on their right leg, whereas one subject preferred using her left.

Hypothesis test II: backward vs. forward running. A total of seven subjects, three men (mass 67.2 ± 0.3 kg; L_o 0.97 ± 0.01 m) and four women (mass 61.9 ± 1.5 kg; L_o 0.97 ± 0.04 m) volunteered and participated in our second series of experimental tests. Four of these subjects continued their participation after completing the initial experiments, whereas three of the earlier subjects were no longer available for testing. Therefore, the three newly recruited subjects also completed the backward and forward running protocols without completing the one-legged hopping protocol. All seven subjects were habituated to forward running with one practice session and backward running with two or more sessions. All subjects completed a minimum of three total backward running treadmill sessions.

Measurements

Top speed (m/s). All testing was conducted on a custom high-speed force treadmill (AMTI, Watertown, MA) with the subjects strapped into a safety harness that would suspend them above the treadmill in the event of a fall. Top speeds in all three gaits were determined via a progressive, discontinuous test to failure as follows. After a brief warm-up, the tests for each gait began at a trial speed between 2.0 and 3.0 m/s. The speed for successive trials was typically increased by 0.5–1.0 m/s at slower speeds and 0.2 m/s at faster speeds. All tests continued through a trial speed at which the subject was unable to complete the prescribed number of steps without drifting backward on the treadmill. Two to three attempts were typically made at the failure speed before the test was terminated. In every case, the top speed successfully attained was within 0.2 m/s of the failure speed. For each running and hopping trial, the treadmill belt was set at the desired trial speed while the subject stood on the treadmill platform straddling the moving belt. Once the belt had reached the desired speed, subjects transferred their weight onto the moving belt using the handrails adjacent to the treadmill and fixed at waist height. Subjects were allowed to take as many handrail-assisted steps as they chose prior to release. Trials were considered successful if a minimum of eight running or four hopping steps were completed without backward drift after full release of the handrails. Non-top-speed trials generally lasted 10–20 s. Subjects were encouraged to take as much rest as necessary for full recovery between trials. They generally chose to take <1 min between trials at slow and intermediate speeds and from 1 to 10 min between the fastest ones.

To minimize the risks of injury and muscle soreness, sessions were discontinued if the subjects reported muscle strain, discomfort, or tightness before top speed was reached. Subjects were allowed a minimum of 3 days to recover between top-speed running trials.

Treadmill force data. All force data were collected from our custom high-speed force treadmill using AMTI NetForce software after signal amplification and digitization (DigiAmp, AMTI). Data for each trial was collected for 10 s at 1,000 Hz and post-processed using analysis software that applied a Butterworth filter with a low-pass cut-off frequency of 30 Hz (Igor Pro:IFDL, Wavemetrics). The values at each speed represent means determined from a series of consecutive steps. For the slow- to intermediate-speed trials, mean values were determined from 8 to 16 consecutive steps for one-legged hopping and from 12 to 16 consecutive steps for both running gaits. For the trials at or near top speed, mean values were determined from a minimum of four and eight consecutive steps for one-legged hopping and both running gaits, respectively. Representative waveforms from the three gaits appear in Fig. 1.

Stance-averaged forces (F_{avg}). The average vertical ground reaction force applied during the contact period was determined from the time during which the vertical force signal exceeded a threshold of 40 N. Forces expressed as multiples of the body's weight (W_b) were determined by dividing the force recorded during each trial by the weight of the subject recorded on a platform scale immediately before treadmill testing (F_{avg}/F_{Wb}; see Fig. 1). Center of mass displacements during the stance phase were determined in accordance with Cavagna (10).

Peak forces (F_{peak}). Peak forces were the highest vertical ground reaction force values recorded over a 0.005-s interval during the last 80% of the foot-ground contact period. This practice discounted the early impact force peaks that can, in some instances (see Fig. 1*B*), exceed the limb force peaks that typically occur in the middle third of the contact period (28). Peak vertical force values were also expressed as multiples of the body's weight (F_{peak}/F_{Wb}).

Effective mechanical advantage (r/R). The relationship between the muscle moment arms and the ground reaction force moments acting across the ankle, knee, and hip joints were determined for one-legged hopping and forward running on a subset of three subjects in accordance with *Eq. 7* across a broad range of speeds [forward run: 2.5–10.5 m/s; one-legged hop: 2.5–7.0 m/s]. The mean moment arms of the extensor muscle groups (r_m; hip = 5.7 cm, knee = 5.5 cm, ankle = 3.7 cm) were the cadaver measurements reported by Biewener et al. (6). The measures of ground reaction force were calculated from the vector sum of the horizontal and vertical components of the ground reaction force measured from a minimum of four (mean = 9.4 ± 0.35) consecutive foot-ground contacts of the right limb. R was calculated as the distance between the two-dimensional coordinate location of each joint (Ariel Dynamics, Trabuco Canyon, CA), obtained from high-speed video (250 Hz; Redlake MASD, San Diego, CA) and the ground reaction force vector. This vector originates at the point of force application, or center of pressure (CoP), which was calculated from:

$$CoP = \frac{M_x - (F_y \cdot h)}{F_z} \qquad (8)$$

where M_x is the measured lateral component of the moment experienced by the force treadmill, F_y and F_z are, respectively, the horizontal and vertical components of the ground reaction force, and h is the distance below the belt surface of the M_x axis (4.5 cm for the force treadmill). Joint axes of rotation were identified by palpation and marked with reflective tape to acquire position data from the video record. A two-dimensional position matrix was used for calibration

purposes before each session. For this portion of the analysis, the force data was smoothed with a sixth-order zero-lag Butterworth low-pass digital filter with a 20-Hz cutoff (Igor Pro 5.0) and kinematically synchronized with the video data. The stance-averaged values of R were obtained from the middle portion of the stance phase, using an a priori minimum of one-half of the contact period. This treatment minimizes the influence of large and rapid fluctuations of the CoP at the beginning and end of stance caused by an undefined value of *Eq. 8* when force is not being applied to the treadmill. Means were determined for each subject at each joint as well as the entire limb across the speed ranges above for both gaits. Limb and joint values were taken from the right limb during both running and hopping since this was the limb that each of these subjects preferred for the hopping gait.

Contact times. The time of foot-ground contact (T_c; s) was determined from the continuous periods during which the vertical treadmill reaction force exceeded 40 N.

Contact lengths. Contact lengths (L_c; m) were determined by multiplying the time of foot-ground contact by the speed of the trial.

Aerial times. Aerial times (T_{aer}; s) were determined from the time elapsing between the end of one period of foot-ground contact and the beginning of the subsequent period.

Effective impulse. The effective impulse (Imp_{Eff}; $W_b \cdot s$), calculated as the product of the vertical force applied in excess of the body's weight $[(F_{avg}/W_b) - 1]$ and the period of foot-ground contact during which this force is applied $\{[(F_{avg}/W_b) - 1] \cdot T_c\}$.

Step times. Step time (T_{step}; s) was determined from the time taken to complete consecutive foot-ground contact and aerial periods (i.e., $T_c + T_{aer}$).

Step frequency. Step frequency ($Freq_{step}$; s^{-1}), the number of steps taken per second, was determined from the inverse of step time ($1/T_{step}$).

Step length. Step length (L_{step}; m), or the distance the belt traveled between consecutive periods of foot-ground contact, was determined by dividing the treadmill speed by step frequency.

Leg length. Leg lengths (L_o; m) were measured from the axis of rotation of the hip joint of the right leg to the ground at the outside of the right heel during erect standing. Hip joint axes of rotation were determined from palpation as the subject slowly swung the limb in the sagittal plane.

Statistics

We evaluated the between-gait comparisons (one-legged hopping vs. forward running and backward vs. forward running) for top speeds as well as F_{avg}, F_{peak}, r/R, L_c, L_{step}, T_c, T_{aer}, $Freq_{step}$ and estimated net extensor muscle forces at top speed using Student's paired *t*-tests in accordance with the expectations and hypothesis explicitly stated in the experimental design. All tests of significance were conducted with a critical alpha level of $P < 0.05$. All values reported are means ± SE.

RESULTS

Gait Mechanics as a Function of Speed

Regardless of whether subjects ran forward, hopped on one leg, or ran backward, they attained faster speeds by applying greater mass-specific forces (F_{avg}) to the running surface during shorter periods of foot-ground contact (T_c) as treadmill speed increased (Fig. 2). When considered from the slowest to fastest speeds attained in each gait, the mean relative decreases in T_c were greater than the relative increases in F_{avg} in all three cases (Figs. 2–4).
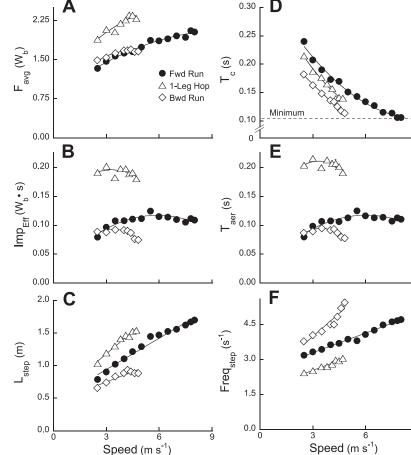

Fig. 2. Gait mechanics as a function of speed for a representative subject in all three gaits: stance average vertical force (*A*), effective impulses (*B*), step lengths (*C*), foot-ground contact times (*D*), aerial times (*E*), and step frequencies (*F*), each illustrated as a function of treadmill speed. In each gait, foot-ground contact times (T_c) decreased by a factor of roughly two or more, whereas the average vertical force (F_{avg}) applied during the contact period increased moderately. The effective vertical impulses (Imp_{Eff}) and the aerial times (T_{aer}) were considerably greater for one-legged hopping than for either forward or backward running. Error bars are obscured by most of the symbols.
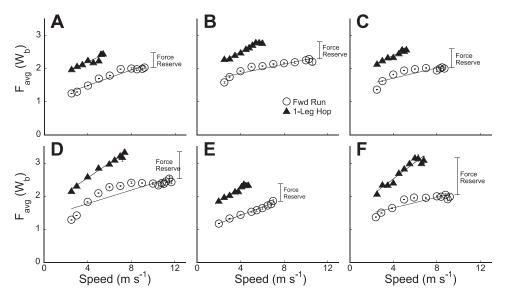
Fig. 3. The average vertical force applied during the foot-ground contact period as a function of speed for six individual subjects during forward running and one-legged hopping. Data are presented through the top speed of each subject in both gaits. For each subject, the average vertical force applied at the top running speed was appreciably less than that applied at the top one-legged hopping speed (i.e., the force reserve). These same data for *subject 1* appear in Fig. 2.

In our first gait comparison, we found that the ground forces (F_{avg}) required at common speeds during one-legged hopping were substantially greater than those required during forward running for all subjects (Figs. 1, 2*A*, and 3). Additionally, the increases in stance-average force with increases in speed during one-legged hopping were nearly double those for forward running (average slopes and intercepts for forward running: $F_{avg} = 1.26 + 0.098 \cdot$speed; one-legged hopping: $F_{avg} = 1.62 + 0.19 \cdot$speed; $n = 7$). These between-gait differences in the ground forces applied were due largely to the greater aerial times required by one-legged hopping. At common speeds, one-legged hopping aerial times were typically about twice as long as those observed during forward running (Figs. 1*B* and 2*B*).

In our second gait comparison, foot-ground contact times (T_c) were shorter, during backward vs. forward running at the same speeds (Figs. 2*A* and 4), because subjects used shorter contact lengths (L_c) while running backward (*Eq. 6*).

The net vertical displacements of the center of mass during the stance phase were slightly less than zero at top speed in each gait (forward run: -0.004 ± 0.008 m; one-legged hop:

-0.040 ± 0.012 m; backward run: -0.014 ± 0.004 m). Across all three gaits, the measured values of F_{avg} used in our analysis agreed with the values obtained from the ratios of T_{step}/T_c and L_{step}/L_c (*Eq. 3*) to within $<2\%$ (Table 1).

Gait Mechanics at Top Speed

Top speeds (m/s). Top speeds and mean values for all of the mechanical variables in *Eq. 6* are presented in Table 1 for the two experimental gaits with their corresponding forward running comparisons. For reliability purposes, four and six subjects, respectively, completed second one-legged hopping and backward running top speed treadmill tests on different days. For one-legged hopping, all duplicate top speed trials agreed to within 0.2 m/s or less with two subjects each being faster and slower, respectively, on their second trial. For backward running, all tests agreed to within 0.1 m/s with four subjects attaining identical top speeds on both trial days and the remaining two running 0.1 m/s faster on the day of the second trial.
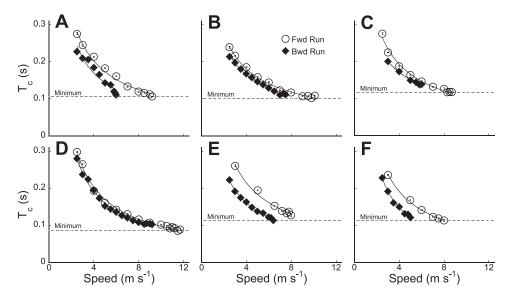

Fig. 4. Foot-ground contact times as a function of speed during forward and backward running for six individual subjects. Data are presented through the top speed of each subject in the respective gaits. Foot-ground contact times decreased by a factor of two or more for all subjects and reached similar individual minimums (dashed lines) in the two gaits. These same data for *subject 1* appear in Fig. 2.

Table 1. *Top-speed gait mechanics*

Gait	F_{avg}, W_b	L_c, m	L_{step}, m	T_c, s	T_{aer}, s	$Freq_{step}$, s^{-1}	Top Speed, m/s
Forward run (I)	2.08 ± 0.07	0.98 ± 0.04	2.05 ± 0.14	0.108 ± 0.004	0.119 ± 0.004	4.51 ± 0.08	9.20 ± 0.59
1-leg hop	2.71 ± 0.15*	0.89 ± 0.05	2.51 ± 0.26	0.160 ± 0.006*	0.274 ± 0.019*	2.36 ± 0.13*	5.75 ± 0.39*
Forward run (II)	2.10 ± 0.07	0.99 ± 0.03	2.06 ± 0.11	0.110 ± 0.005	0.121 ± 0.003	4.42 ± 0.19	9.10 ± 0.52
Backward run	1.75 ± 0.05*	0.74 ± 0.05*	1.29 ± 0.14*	0.116 ± 0.004	0.091 ± 0.007*	5.05 ± 0.19*	6.42 ± 0.57*

Values are means ± SE. Values were obtained from a minimum of four hopping and eight running steps for each subject. *Significantly different than forward running ($P < 0.05$).

Forces (F_{avg}, F_{peak}). Both the stance-averaged and peak vertical forces applied to the treadmill surface at the respective top speeds (Fig. 5) in our first gait comparison were, on average, more than 0.5 W_b greater during one-legged hopping than forward running (2.71 ± 0.15 vs. 2.08 ± 0.07 W_b and 4.20 ± 0.24 vs. 3.62 ± 0.24 W_b, respectively). Stance-averaged and peak vertical forces were also lower during backward than forward running (1.75 ± 0.05 vs. 2.10 ± 0.07 W_b, and 3.05 ± 0.11 vs. 3.60 ± 0.24 W_b, respectively; Figs. 5 and 6). Between-gait differences in the total ground reaction force, the vector sum of F_z and F_y, were nearly identical to the above differences in the vertical forces only (presented as F_{avg}) because the relative contributions of the horizontal forces were similarly small across all three gaits, accounting for only 2–3% of the F_z and F_y sum.

Limb effective mechanical advantage (EMA; r/R). The ratio of muscle moment arms (r) to the ground reaction force moments at the ankle, knee, and hip joint axes of rotation (R) during the stance phase appear in Table 2. The mechanical advantage of the extensor muscles acting across both the hip and ankle joints were significantly greater during forward running than one-legged hopping, while values at the knee were similar in the two gaits. The average net extensor muscle forces required for the entire limb were 70.3% greater for one-legged hopping than for forward running at top speed. The magnitude of this between-gait difference resulted from both the greater ground reaction forces required and the poorer
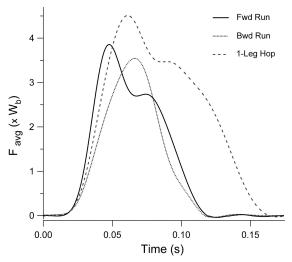
mechanical advantage of the limb during one-legged hopping vs. forward running (Table 2; Fig. 7).

Contact lengths (L_c; m). The forward distance the body traveled during the period of foot-ground contact was not significantly different during top-speed one-legged hopping and forward running (0.89 ± 0.05 vs. 0.98 ± 0.04 m, respectively). In contrast, top-speed backward running contact lengths were significantly shorter than those used during forward running (0.74 ± 0.05 vs. 0.99 ± 0.03 m, respectively).

Step lengths (L_{step}; m). The belt distance traveled between consecutive footfalls, or the length of the steps taken, was longer during one-legged hopping than forward running (2.51 ± 0.26 vs. 2.05 ± 0.14 m, respectively), but this difference was not significant. Step lengths were significantly shorter at top speed during backward vs. forward running (1.29 ± 0.14 vs. 2.06 ± 0.11 m, respectively).
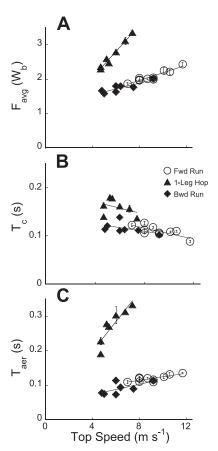
Fig. 5. Vertical ground reaction forces in units of the body's weight (W_b) vs. time for a single footfall from *subject 1* at top speed in each of the three gaits. Foot-ground contact times are longer, and both peak and stance-average forces are greater for one-legged hopping than for either forward or backward running. (Note that top forward running speed and contact time for *subject 1* were 8.0 m/s and 0.106 s, respectively.)

Fig. 6. The average vertical force applied (*A*), the durations of the foot-ground contact (*B*), and aerial periods (*C*) for different subjects at top speed in each of the three gaits. Within each gait, faster subjects applied greater mass-specific forces, had shorter contact times, and longer aerial times at top speed.

Table 2. *The effective mechanical advantage and net extensor muscle force during forward running and one-legged hopping*

Limb Joint	Effective Mechanical Advantage (r/R)		Extensor Muscle Force (xW_b)	
	Forward run	1-leg hop	Forward run	1-leg hop
Hip	2.42 ± 0.83	1.58 ± 0.51*	1.33 ± 0.14	2.95 ± 0.46*
Knee	0.67 ± 0.17	0.63 ± 0.20	4.18 ± 0.20	6.20 ± 0.58*
Ankle	0.56 ± 0.18	0.39 ± 0.07*	5.50 ± 0.52	9.66 ± 0.84*
Limb Average	1.22 ± 0.32	0.87 ± 0.21*	3.67 ± 0.25	6.25 ± 0.52*

Values are means ± SE. Ratio of measured ground reaction force moments to the anatomical muscle moments, or effective mechanical advantage (4, 6), and the estimated net extensor muscle forces during forward run (speed range: 2.5–10.5 m/s; $n = 23$ trials, stances analyzed = 209) and 1-leg hop (2.5–7.5 m/s; $n = 18$ trials, stances analyzed = 170). *Significantly different than forward running ($P < 0.05$).

Contact times (T_c; s). Although foot-ground contact times were generally similar when subjects hopped on one leg and ran at the same speeds (Fig. 5), at the respective top speeds one-legged hopping contact times were considerably longer than those measured during forward running (0.160 ± 0.006 vs. 0.108 ± 0.004 s, respectively; Figs. 2*A* and 5). In contrast, foot-ground contact times were shorter at the same backward and forward running speeds but virtually the same at the respective top speeds attained in the two gaits (0.116 ± 0.004 vs. 0.110 ± 0.005 s, respectively; Figs. 4 and 5).

Aerial times (T_{aer}; s). Aerial times were 2.3 times longer during one-legged hopping vs. forward running at top speed (0.274 ± 0.019 vs. 0.119 ± 0.004 s, respectively) and significantly shorter at backward vs. forward top speeds (0.109 ± 0.007 vs. 0.121 ± 0.003 s, respectively; Fig. 6).

Impulse$_{eff}$ ($W_b \cdot s$). The effective impulses were also 2.3 times greater at one-legged hopping vs. forward running top speeds (0.270 ± 0.02 vs. 0.115 ± 0.004 $W_b \cdot s$, respectively) and moderately less for backward vs. forward top-speed running (0.086 ± 0.006 vs. 0.119 ± 0.004 $W_b \cdot s$, respectively; Fig. 2*B*).

Step frequencies ($Freq_{step}$; s^{-1}). Steps were roughly half as frequent at one-legged hopping vs. forward running top speeds (2.36 ± 0.13 vs. 4.51 ± 0.08 Hz, respectively) and slightly more frequent during top speed backward vs. forward running (5.05 ± 0.19 vs. 4.42 ± 0.19 Hz, respectively).

DISCUSSION

We set out to determine whether the stance phase limit to running speed might be imposed by either of two functional limits on limb mechanics: the maximum force the limbs can apply to the running surface or the minimum period of time needed for force application. The one-legged hopping and backward running tests we employed as experimental contrasts to forward running provided complimentary and consistent results. Compared with forward running at top speed, we first found that our subjects were able to apply ground forces that were greater on average by more than one-half of their own body weight (0.63 ± 0.11 W_b) while hopping on one leg vs. running forward on two. Second, we found that the periods of foot-ground force application at top backward and forward running speeds agreed with one another to within an average of 6 ± 4 ms out of a total 110 ± 5 ms. These comparisons to forward running under top-speed conditions demonstrated first

that, when periods of ground force application were relatively longer, subjects were able to apply greater ground forces and second that, when the ground forces required were similar or slightly reduced, subjects were not able to apply force any more rapidly. Accordingly, we conclude that a limit to sprint running speed is imposed not by the maximum forces that can be applied to the ground but rather by the maximum rates at which the limbs can apply the forces required.

Hypothesis Test 1: One-legged Hopping vs. Forward Running

We selected one-legged hopping as an experimental gait to test the prevailing view that maximum limb extensor forces likely limit all-out running speeds on straight and moderately curved paths (13, 20, 39, 40). At common speeds, the need during one-legged hopping to reposition the same leg for consecutive periods of ground force application (Fig. 1*B*) did elevate the aerial times and vertical forces required to attain them compared with forward running (Figs. 1*B* and 2). This outcome was expected from the dependence of stance-limb vertical forces and impulses on the duration of the swing and
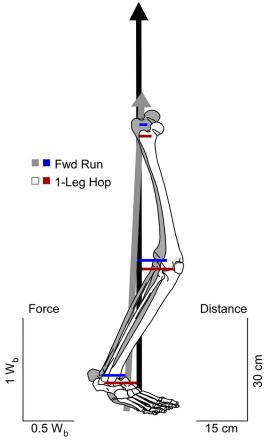

Fig. 7. Ground reaction moment arms during one-legged hopping (red bars and white limb) and forward running (blue bars and gray limb) were measured as the perpendicular distance (illustrated as horizontal) between the joint axis of rotation and the ground reaction force vector (black and gray arrows one-legged hopping and forward running, respectively). The product of the ground reaction force and the ratio of the ground reaction moment to the extensor muscle moment (4, 6) provides an estimate of the required net extensor muscle force. Using the measured mid-stance ground reaction forces shown here, and the ratios reported in Table 2, the limb-averaged muscle force estimates were significantly greater for hopping vs. forward running.

aerial phases (43). However, the outcome of primary relevance here was whether the ground forces applied at top speed would be greater during one-legged hopping than forward running. This was the case (Figs. 3, 5, and 6*A*): the average and peak vertical forces applied to the treadmill were 30.3 and 16.0% greater, respectively, for one-legged hopping vs. forward running. Although individual variability was present in the force difference observed between the two gaits (i.e., the force reserve; Fig. 3), every subject applied greater average and peak forces while hopping on one leg than while running forward on two. Moreover, the between-gait differences in ground forces substantially under-represented the differences in limb extensor muscle forces. When the poorer mechanical advantage of the limb and the greater ground reaction force required during one-legged hopping vs. forward running were both taken into account (Table 2), the average and peak forces generated by the extensor muscles at top speed were 82 and 63% greater, respectively, in the hopping gait. Clearly, the forces applied to the ground during top-speed forward running are substantially less than the maximums the limbs are capable of applying to the running surface.

Biological Limits on Muscular Force Production

Why would runners apply forces during all-out sprinting efforts that are substantially less than maximal, particularly if doing so would limit the very performances they are attempting to maximize? Our gait mechanics data, in conjunction with the established time course of force production by human skeletal muscle, suggest that periods of foot-ground force application at top forward running speeds may be too brief to allow the limb extensor muscles to develop maximum force. The profile of the ground reaction force (Fig. 5), the posture of the limb during high-speed running (6), and in vivo muscle force data (33) indicate that the forces generated by the extensor muscles peak roughly halfway through the contact period. Although these muscles are clearly activated well before the limb contacts the ground (31, 33), there is no appreciable development of muscular force until contact occurs (33). Accordingly, a reasonable approximation of the time to peak muscle tension is one-half of the measured periods of foot-ground contact. For the athletic subjects tested here, this half-period was 55 ± 3 ms at their top forward running speeds.

Several pieces of experimental evidence suggest that the periods of foot-ground force application during sprint running may be too short to allow the forces produced by the limb muscles to reach their contractile maximums (21, 22, 25). The time course of the development and transmission of muscular force in vivo in response to a single electrical impulse, or twitch, in human knee and ankle extensors is 81 and 120 ms, respectively, in young adult men (21). Thus the periods required for the limb muscles to generate and transmit peak isometric twitch forces in vivo are roughly two times longer than the time available during top speed running (Fig. 5). Moreover, if we eliminate the electromechanical delay by assuming that the knee and ankle extensor muscles develop force at their maximal tetanic contraction rates (dP$_{50}$: 21) throughout the 55-ms first half of the foot-ground contact period, these muscle groups would reach only 46 and 22%, respectively, of the in vivo isometric force maximums reported under full stimulation conditions (21). Although the quantitative influence of the different contractile conditions present in vivo during isometric vs. bouncing gait contractions is not known, the comparisons offered are consistent with a temporal constraint on the ground forces that can be applied during high-speed running.

Thus maximizing speed in bouncing gaits involves a trade-off between the magnitude of the ground forces applied and the step frequencies that can be attained as foot-ground contact periods become shorter at progressively faster speeds. Here, for example, the stance-average vertical forces applied to the surface were 30.2% lower, whereas step frequencies were nearly two times greater during forward running than one-legged hopping at top speed. Quantitatively, the much greater running step frequencies resulted from the relative brevity of both the aerial and contact phases of the step cycle. Mechanically, the brevity of the aerial phase resulted from the lesser vertical impulses brought about by the relatively lower forces and shorter contact times. Thus, these comparisons indicate that the ground force-step frequency combination that maximizes forward speed is set largely by the minimum time needed in the air in between steps.

Hypothesis Test II: Backward vs. Forward Running

Our second primary finding, that the periods of force application during top speed backward and forward running did not differ, is most easily interpreted if the ground force requirements of these gaits were equivalent. However, both the average and the peak forces observed in these two gaits at top speed were lower during backward vs. forward running (Table 1). The different patterns of ground force application in the two gaits (Fig. 5) result in part from a different orientation of the limb during backward running (47) that requires the extensor muscles to generate 1.14 times more force per unit ground force applied than during forward running. If we adjust for this factor, the average and peak forces required of the limb extensor muscles at the respective top speeds in these gaits were not different and agreed to within 5.3 ± 0.06 and 3.4 ± 0.06%, respectively. Thus the minimum times of force application observed at the different respective top speeds in these two gaits were nearly identical when the net forces required of the extensor muscles during the contact period were the same.

A logical question raised by our finding that the brief durations of ground force application limit the maximum ground forces that can be applied, is why runners do not choose to take the greater contact lengths and times that would allow them to apply greater ground forces. A considerable body of evidence indicates that the large ground and muscle forces required to support the body's weight constrain the excursions of the stance limb to a relatively narrow range of positions directly underneath the body (4, 6, 12, 27, 30). When limb excursion angles and contact lengths are increased beyond those selected naturally, performance suffers because both the limb's mechanical advantage and the natural spring-like rebound of the body in the latter portion of the contact period are compromised (17, 30).

Gait Mechanics and Sprinting Performance

Our findings here also offer insight into which gait mechanics can and cannot be modified to bring about changes in sprinting performance. Two features of bouncing gaits have

emerged as being mechanically constrained at similar levels across individuals: contact lengths and minimum swing times. In a previous investigation, we reported that there was little to no difference in the time that fast and slow runners take to reposition their limbs at top speed (44). Although sprint athletes have muscle fibers with faster contractile kinetics (15), faster muscle fibers do not appear to confer appreciable reductions in either aerial or swing periods at top speed. Nonetheless, the minimum time for completing the swing process (343 ± 6 ms) and the accompanying aerial times required for doing so largely determine the ground support forces and impulses utilized to attain any given speed (Fig. 2); they also directly affect the top speeds attained (*Eq. 6*). As can be seen for the three gaits illustrated in Fig. 6, the greater the aerial time requirement of the gait, the greater the slope of the force-speed relationship and the greater the force required to attain a given top speed.

The third constraint that has emerged here is largely biological and more variable: the lower limit to the periods of foot-ground contact during which the necessary ground forces can be applied. This limit clearly varies between individuals and likely does so in accordance with the individual differences in the contractile speeds of the fibers of the limb muscles. Here, within each of the three gaits examined (Fig. 6), and also previously (44), we found that faster subjects were able to apply greater mass-specific ground forces during shorter periods of foot-ground contact. These capabilities would be expected to be conferred by limbs with faster muscle fibers and greater rates of force development (8, 41).

These results identify two interventions, one physiological and one anatomical, that would improve sprint running performance given the stance phase limitation imposed by the minimum periods of ground force application. First, muscle fibers with more rapid contractile kinetics (34) may allow greater ground forces to be applied during the progressively shorter periods of foot-ground contact that sprinting at faster speeds requires. How fast might these faster muscle fibers allow humans to run? The quantitative relationships introduced in the METHODS can be used to formulate theoretical estimates of the top speeds that would be possible if faster muscle fibers were to permit the limbs to apply one-legged hopping ground force maximums while running. If, for simplicity, we assume no change in contact lengths or the minimum aerial times needed to reposition the swing limbs at top speed, the average and greatest individual top speed hopping forces (F_{avg}) of 2.71 and 3.35 W_b would allow top running speeds of 14.0 and 19.3 m/s and of 50 and 69 km/h, respectively. Second, limbs lengthened through evolution or perhaps prosthetically could substantially increase the top running speed attained at the minimum period of foot-ground force application. For example, a relatively small increase in leg length of 10 cm would increase contact lengths by 9 cm and the top speeds of the

subjects tested here from 9.1 to 9.8 m/s. The calculations and theoretical values that would result from these two interventions while holding the other variables in *Eq. 6* constant appear in the APPENDIX.

The mechanisms by which training interventions might increase running speeds most effectively have not been fully evaluated in the context of the gait mechanics considered here, but such efforts would likely offer additional insight into the relationship between the functional limits of musculoskeletal tissues and gait mechanics. Given the negligible extent to which muscle fiber speeds are enhanced via sprint training (22) and what appears to be a fairly rigid lower biological limit on minimum swing times (42, 44), the most effective training strategies may be those that enhance limb extensor muscle force production without increasing the body's mass or compromising rates of muscular force production.

The Biology of Speed: Limits, Trade-offs, and Adaptations from the Ground Up

Finally, while our data indicate that muscle fibers with relatively slow contractile kinetics impose a biological limit to sprint running speeds, slower fibers also economize the forces produced during standing and walking (3, 27, 41) and confer greater tendon and bone safety margins during rapid weight-bearing movements (4, 41). These functional trade-offs may explain why the fastest animal sprinters have adapted for running speed with little apparent alteration in muscle fiber speeds. The muscles of cheetahs and greyhounds function at rates that differ little from those of other running animals (16, 46). Rather, these animals have adapted for speed by developing gait mechanics that prolong their periods of ground force application. These quadrupeds gallop with pronounced backbone bending that increases their foot-ground contact times and lengths (2, 23) to values (39) that approach those of humans even though their limbs are only half as long (29). Relatively greater contact lengths and times allow faster running speeds to be attained before foot-ground contact times fall to the minimums that muscle fiber speeds permit.

Because humans have limbs of moderate length and cannot gallop, they lack similar options for prolonging periods of foot-ground force application to attain faster sprinting speeds at existing contact time minimums. Consequently, human running speeds in excess of 50 km/h are likely to be limited to the realms of science fiction and, not inconceivably, gene doping.

APPENDIX

Our results and the quantitative relationships provided in the METHODS permit a theoretical assessment of the top running speeds attained by limbs capable of applying greater forces to the ground or those that have been artificially lengthened. The estimates that appear

Table 3. *Theoretical top running speeds achieved via increased force application and leg length*

Measured/Theoretical	F_{avg}, W_b	L_c, m	L_{step}, m	T_c, s	T_{aer}, s	$Freq_{step}$, s^{-1}	Top Speed, m/s
Forward run (II) (measured)	2.10 ± 0.07	0.99 ± 0.03	2.06 ± 0.11	0.110 ± 0.005	0.121 ± 0.003	4.42 ± 0.19	9.10 ± 0.52
Δ F_{avg}* (theoretical)	2.71	**0.99**	2.68	0.071	**0.121**	5.22	14.0
Δ L_o* (theoretical)	**2.10**	1.08	2.27	**0.110**	**0.121**	4.32	9.80

*The theoretical ΔF_{avg} and ΔL_o (+0.10 m) top speeds were estimated in accordance with the algebraic procedure described in the APPENDIX and by assuming that the L_c and T_{aer} values measured during top speed forward running would not be altered by either condition. Bold entries identify the values not changed from those measured during top speed forward running.

in the DISCUSSION and Table 3 were determined by substituting *Eq. 4* into *Eq. 2* to give

$$F_{avg}/W_b = \frac{T_c + T_{aer}}{T_c} \qquad (A1)$$

which was solved with respect to T_c to yield:

$$T_c = \frac{T_{aer}}{\left(\dfrac{F_{avg}}{W_b} - 1\right)} \qquad (A2)$$

and then substituted into *Eq. 6*

$$Speed = \left(\frac{F_{avg}}{W_b} \cdot L_c\right) \cdot \left[\frac{T_{aer}}{\left(\dfrac{F_{avg}}{W_b} - 1\right)} + T_{aer}\right]^{-1} \qquad (A3)$$

to determine the theoretical top running speeds that would result from these two interventions with L_c and T_{aer} fixed at the values measured during top-speed forward running.

As noted in the DISCUSSION, the method above predicts running speeds of 14.0 and 19.3 m/s with F_{avg} values of 2.71 and 3.35 W_b, respectively. If, in slight contrast to the above, T_{sw} is fixed at the typical biological limit of 0.350 s, rather than T_{aer} being fixed at 0.121 s (and thereby allowing T_{sw} to fall to values lower than 0.350 s), slower theoretical top speeds of 12.5 and 16.1 m/s result.

All of the projected speeds are based on simplifying assumptions that ignore the incomplete understanding of the factors that determine and limit muscular force production in bouncing gaits.

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